

QUANTITATIVE METHODS IN SPATIAL CONSERVATION PLANNING

INTEGRATING CLIMATE CHANGE AND UNCERTAINTIES

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TESE APRESENTADA PARA OBTENÇÃO DO GRAU DE DOUTOR EM BIOLOGIA

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Aos meus pais e avós...
To my parents and grandparents...

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ABSTRACT

Spatial Conservation Planning is a scientific-driven procedure to identify cost effective networks of areas capable of representing biodiversity through time. This conceptually simple task accommodates sufficient complexity to justify the existence of an active research line with more than 20 years already. But cost-efficiency and representation of biodiversity is only part of the whole challenge of Spatial Conservation Planning. The recognition that Nature operates dynamically has stimulated researchers to embrace the additional challenges of developing methods to make conventional (static) conservation approaches more dynamic and therefore increase the chances that biodiversity are preserved in the longer term.

In this thesis, I present a set of tools to assist spatial conservation decision-making and address issues such as uncertainty and spatial dynamics of species ranges. These two topics are particularly relevant in the context of ongoing climate changes. I start by investigating two connectivity paradigms for the identification of conservation areas. In the first, a distance-based approach is applied for the identification of areas representing a set of species. In the second, I present a conceptual framework based on the analysis of environmental similarity between protected areas. The framework seeks to identify effective spatial linkages between protected areas while ensuring that these linkages are as efficient as possible. Then, I introduce a methodology to refine the matching of species distributions and protected area data in *gap analysis*. Forth, I present a comprehensive assessment for the expected impacts of climate change among European conservation areas. Finally, I address a framework for cost-efficient identification of the best areas that, in each time period, assist species' range adjustments induced by severe climate changes.

There exists a wealth of theoretical insight and algorithmic power available to ecologists. This thesis took advantage of it and (I hope) it offers useful guidance for genuine biodiversity protection.

Keywords:

Biodiversity, Climate change, Connectivity, Conservation planning, Efficiency, Graph theory, Mixed-integer programming, Protected areas, Species distribution models, Uncertainty.

RESUMO

O Planeamento Espacial para a Conservação é uma estratégia de base científica para a identificação das melhores áreas que assegurem a persistência da biodiversidade. Esta tarefa conceptualmente simples incorpora complexidade suficiente para motivar uma linha de investigação, activa nos últimos 20 anos. No entanto, eficiência e representatividade são apenas parte do domínio de actuação do Planeamento Espacial para a Conservação. Com o reconhecimento que a Natureza opera de forma dinâmica, tornou-se necessário responder a novos desafios: Como tornar as abordagens convencionais (estáticas) em conservação mais dinâmicas? E desta forma aumentar a probabilidade da biodiversidade persistir no futuro.

Nesta tese apresento um conjunto de ferramentas, no âmbito das tomadas de decisão de carácter espacial em conservação, para responder aos problemas de incerteza e dinâmica espacial das espécies. Tópicos particularmente relevantes num contexto actual de alterações climáticas. Começo por intervir sobre dois conceitos de conectividade na identificação de áreas para conservação. No primeiro, aplico regras de distância na identificação de áreas que assegurem a representação de um conjunto de espécies. No segundo, apresento um enquadramento teórico usando o conceito de semelhança ambiental entre áreas protegidas. Nesta abordagem procura-se identificar ligações funcionais entre áreas protegidas minimizando custos. Seguidamente, introduzo uma metodologia para apurar o cruzamento de informação de espécies e áreas protegidas em *gap analysis*. Em quarto lugar, apresento uma análise extensa sobre os impactos esperados das alterações climáticas sobre as áreas de conservação na Europa. Finalmente, introduzo uma abordagem para a identificação, a custo reduzido, das melhores áreas que, em cada período, facilitem o ajuste espacial das espécies induzido pelas alterações climáticas.

Existe um manancial teórico e um poder algorítmico extensos ao serviço dos ecologistas. Esta tese tirou partido da sua existência e espero que contribua para uma genuína protecção da biodiversidade.

Palavras-chave:

Alterações Climáticas, Áreas protegidas, Biodiversidade, Conectividade, Eficiência, Incerteza, Modelos de distribuição de espécies, Planeamento de Conservação, Programação mista, Teoria de grafos.

O planeta experimenta uma onda de extinções sem precedentes na história evolutiva mais recente. Dada a multiplicidade de serviços que a biodiversidade proporciona, é provável que destas perdas advenham consequências negativas ao bem-estar humano. São exemplos, a redução de bens alimentares, a perda de qualidade de recursos hídricos, a segurança energética e um aumento da vulnerabilidade a desastres naturais. Neste contexto, agências governamentais e não-governamentais imbuíram-se do propósito de gerir e proteger habitats de forma a preservar o seu valor ecológico e assegurar a sua persistência. A constituição de áreas protegidas revela-se como uma opção prioritária para atingir tais objectivos.

Existem, no entanto, fortes condicionantes socio-económicas à selecção destas áreas. Por um lado, a maioria das acções conservacionistas não é economicamente sustentável e dependem de apoios escassos (maioritariamente governamentais) disponibilizados. Por outro, a protecção de habitats impede que um conjunto de actividades e usos de solo com maior suporte sócio-económico tirem proveito de todo o seu potencial produtivo. Consequentemente, a constituição de áreas protegidas tende a ser definida por critérios políticos, relegando-as para locais onde o seu impacto sobre a economia é menor, não tendo em consideração critérios ecológicos. Em muitas situações, a protecção destas áreas não gera benefícios ecológicos e fomenta uma falsa noção de protecção da biodiversidade.

Face a estes constrangimentos, a conservação deve colher o máximo benefício com os escassos recursos económicos disponíveis, devendo, portanto, seguir um padrão de eficiência máxima. Problemas de optimização deste tipo, onde determinantes financeiras e ecológicas são analisadas conjuntamente, são tipicamente complexos de solucionar. Os últimos 30 anos, foram marcados pelo crescimento exponencial de propostas metodológicas de suporte à identificação de áreas prioritárias para a conservação assegurando a representação e persistência da biodiversidade.

Contudo, paralelamente a estes avanços metodológicos, os paradigmas da sociedade moderna culminaram no aumento da intensidade e da variedade das ameaças à biodiversidade e, consequentemente, ao aumento da complexidade dos sistemas social e ecológico onde radica a ciência da conservação. O incremento da população humana fomentou maior pressão sobre os habitats naturais e a sua consequente degradação, perda e fragmentação. Da mesma forma, o aumento do consumo energético traduziu-se na alteração da química da atmosfera e, consequentemente, do clima no planeta. As alterações climáticas intensificaram-se motivando uma plethora de respostas biológicas. Face a esta visão dinâmica da biosfera, os instrumentos convencionais de conservação mostram-se ineficazes. As projecções de deslocamento das áreas de distribuição das espécies sob cenários de alterações climáticas colocam um desafio às estratégias actuais de planeamento para a conservação. É necessário expandir os conceitos de protecção para além das áreas actualmente protegidas, nomeadamente com a protecção formal de novas áreas e a implementação de novas acções de conservação em áreas não protegidas, com importância na mobilidade das espécies.

Para que estas decisões sejam eficazes e robustas é necessária que sejam assistidas por modelos predictivos que informem sobre os padrões de distribuição da biodiversidade mais prováveis no futuro e que expressem de forma explícita a incerteza subjacente aos processos predictivos. A tese aqui apresentada intervém neste âmbito.

O reconhecimento de que a fragmentação de habitats naturais é uma das principais ameaças à biodiversidade motivou o desenvolvimento de modelos para selecção de áreas protegidas compactas e suficientemente próximas. Um dos modelos que mais avançou a este respeito permite definir áreas protegidas como regiões contíguas, cuja forma e extensão são fortemente determinadas pela localização de locais cujas características ecológicas ou de outra natureza os tornam de selecção obrigatória. Por exemplo, o afastamento destas áreas mandatórias implica o investimento em “áreas ligação” de baixo valor ecológico, o alongamento de áreas protegidas e o recorte da paisagem com estruturas lineares. Assim, no **capítulo II** é apresentado um modelo de programação mista que integra explicitamente o posicionamento e o valor ecológico de áreas mandatórias na selecção (a menor custo) de áreas protegidas. O modelo integra uma noção de vizinhança em torno das áreas mandatórias onde é dada

preferência de selecção de novas áreas. O modelo é ilustrado para dois estudos de média dimensão gerando soluções óptimas em tempo razoável.

No **capítulo III** é introduzido um modelo para identificação de “áreas de ligação” de habitats naturais. Contrariamente à sugestão anterior, as “áreas de ligação” não são definidas para complemento do valor ecológico das áreas protegidas mas para facilitação do movimento de espécies. O modelo foi desenvolvido de forma a operar em situações de lacuna de informação sobre as áreas de distribuição e padrões de dispersão das espécies, pelo que recorre a dados ambientais que, às escalas analisadas, melhor se ajustam à distribuição das espécies. O modelo rege-se numa óptica de eficiência (i.e., assegura a ligação de habitats a custo mínimo) e foi desenvolvido com base num problema de grafos (árvore mínima de Steiner) que melhor se acomoda na identificação de redes de ligação para múltiplas parcelas de habitat. O modelo assegura a ligação de diferentes tipos de habitats e integra informação sobre a localização de barreiras específicas para cada tipo de habitat. A capacidade operativa do modelo foi ilustrada para ligação das áreas protegidas na Península Ibérica utilizando a caracterização climática da região. Foi efectuada uma análise comparativa desta abordagem com uma abordagem equivalente sem informação ambiental. Conclui-se que para o mesmo nível de investimento obtêm-se soluções mais funcionais quando se integra a caracterização ambiental.

As abordagens quantitativas da análise do desempenho das áreas protegidas na representação de espécies (*gap analysis*) passam por cruzar os dados de distribuição das espécies (normalmente referenciados em unidades discretas de planeamento) com a distribuição das áreas protegidas (normalmente polígonos). De forma a aproximar a natureza de ambos os tipos de dados os polígonos de distribuição de áreas protegidas são convertidos em área protegida em cada unidade de planeamento. Esta conversão é feita usando uma regra arbitrária onde cada unidade de planeamento é classificada como protegida (ou não protegida) se a área protegida nela integrada é superior (ou inferior) a um valor de referência. No **capítulo IV** é feita uma justificação probabilística para implementar *gap analysis* usando os dados base de distribuição de áreas protegidas (i.e., superfície protegida em cada unidade de planeamento). Foram efectuadas comparações com abordagens típicas, usando diferentes valores de referência, e verificou-se que a convergência das abordagens varia de espécie para espécie e com o tempo (dado o dinamismo na distribuição de espécies). Esta última evidência sugere que a metodologia aqui introduzida apresenta maior consistência em aplicações onde se comparam análises de desempenho das áreas protegidas em diferentes períodos (i.e., nomeadamente para analisar o impacto de alterações climáticas). A abordagem de base probabilística foi ilustrada para analisar o desempenho das áreas protegidas ibéricas na representação de um pequeno conjunto de espécies vegetais não arbóreas num tempo presente e num cenário futuro marcado por alterações climáticas e consequente redistribuição de espécies.

No **capítulo V** são avaliados os desempenhos de dois esquemas de conservação de habitats na Europa (áreas protegidas definidas por cada país e a Rede Natura 2000 definida à escala da União Europeia) sob diferentes cenários de alterações climáticas. Pela primeira vez, um estudo deste cariz e desta dimensão integra um conjunto de premissas e avanços metodológicos que conferem maior robustez perante incertezas de diferente tipo. Assim, foi analisada a evolução da adequabilidade apenas nos locais onde as espécies foram observadas no presente; foram aplicados ensembles de múltiplos modelos de distribuição de espécies usando dados climáticos futuros gerados por três modelos de circulação global sob quatro cenários sócio-políticos desenvolvidos pelo Painel Intergovernamental para as Alterações Climáticas e foi usada a metodologia descrita no **capítulo IV**. O estudo sugere que mais de metade das espécies analisadas serão potencialmente afectadas negativamente nos dois sistemas conservação de habitats na Europa, com diferenças de susceptibilidade que variam com o grupo taxonómico, com a região e com o nível de alteração esperado. Ainda assim, as áreas protegidas detêm o potencial de cobrir melhor o espaço climático das espécies analisadas do que as áreas não protegidas, enquanto que o desempenho da Rede Natura na representação futura do espaço climático das espécies não se distinguirá das áreas não listadas sob as directivas europeias de conservação. São discutidas opções de conservação à escala Europeia capazes de integrar os efeitos ecológicos das alterações climáticas numa região altamente povoada.

Uma vez apreendida a variação do nível de representação das espécies em áreas protegidas por efeito de alterações climáticas é necessário identificar as áreas que se revestem de maior potencial para

assegurar uma boa representação das espécies com o decurso do tempo. No **capítulo VI** é apresentado um modelo de fluxos que visa efectivar essa selecção com base num índice de persistência futura das espécies que integra informação sobre níveis de adequabilidade climática local e capacidade dispersiva das espécies. O modelo visa seleccionar as áreas que maximizam o sucesso de persistência do conjunto das espécies em análise usando um investimento fixo. Contrariamente aos standards de conservação convencionais o modelo integra a possibilidade de reconduzir o investimento feito numa área em determinado período para uma outra área, num outro período. No final, é gerado um programa temporal de investimento e quantificado o nível esperado de persistência de cada espécie. Pode-se assim avaliar se o investimento disponível para aquisição de áreas limita a persistência esperada das espécies ou se existem condicionantes ecológicas (ex., capacidades dispersivas inferiores às taxas de alteração climática) que inviabilizam a adaptação natural das espécies. É discutido o potencial desta abordagem na avaliação do sucesso de diferentes opções de conservação (ex., facilitação dos movimentos naturais de adaptação versus colonização assistida). Fez-se uma ilustração das potencialidades do modelo usando a distribuição presente e futura (i.e., sob cenários de alterações climáticas) de um pequeno grupo de espécies na Península Ibérica.

Tendo em conta os níveis de complexidade que caracterizam a ciência de conservação, esta tese apenas se debruça numa leitura (possível) simplificada. Esta tese incorpora um conjunto de aspectos conceptuais inovadores no âmbito das opções de conservação; apresenta leituras matemáticas dos conceitos introduzidos e; sugere aproximações algorítmicas para resolver os problemas em análise. Ainda que os trabalhos apresentados tenham uma elevada base teórica, há um potencial prático que poderá ser explorado, podendo assistir um conjunto de medidas concretas para a protecção da biodiversidade. O sucesso das medidas de conservação resulta da aplicação da melhor ciência aos problemas existentes. Espero que esta tese dê um contributo válido para esse propósito.

PREFACE

“The rates, scales, kinds, and combinations of [global] changes occurring now are fundamentally different from those at any other time in history; we are changing Earth more rapidly than we are understanding it.”

Vitousek et al., 1997

This thesis is designed to give possible answers to a few challenges characterizing Spatial Conservation Planning. Its main objectives are:

- 1) to deliver a possible approach to reserve design, when proximity between areas is demanded and mandatory areas occur.
- 2) to develop a conceptual formulation to identify linkage-regions establishing connectivity between natural habitats of each of several types, accounting for type-specific barriers.
- 3) to present a probability-based approach to handle species positional uncertainty within grid cells when aligning information with protected area data.
- 4) to evaluate how climate change is expected to impact the performance of European conservation areas in representing species climatic space.
- 5) to propose an optimization procedure to identify the areas enabling species range adjustments under climate change. The method should integrate uncertain local suitability predictions and the potential to acquire and release priority areas through time, and be able to compare the impacts of greenhouse gas emissions scenarios (mitigation) with different levels of conservation funding (adaptation) for species persistence.

In order to achieve these objectives the thesis was structured in seven chapters.

Chapter I introduces Spatial Conservation Planning and contextualizes challenges stemmed from data uncertainty and climate change impacts.

Chapter II and **III** report two possible approximations to optimize protected area connectivity (spatial assessments, Figure I). The selection of self-sustaining protected areas should enable species to move between them. Therefore accounting for distance between protected areas should stand as an important aspect of reserve selection. Furthermore, protected area selection should attend to the existence of areas with attributes that make them irreplaceable. **Chapter II** integrates these two issues (**objective 1**). It presents a mixed integer programming formulation to guide the selection (with the minimum cost) of a set of areas covering targets of species' representation. The model uses the geographical position of mandatory areas to define a spatial window where species-complementary areas are selected to achieve representation targets. Optimal solutions for two small applications are presented and discussed. **Chapter III** addresses the **objective 2** and presents a conceptual view on connectivity where areas with no formal protection are useful. It builds on an iconic graph theory problem to construct a network of linkages for different types of habitats, using type-resembling areas and bypassing type-specific movement barriers. A climatic characterization of Iberian Peninsula and of Iberian protected areas was used for illustrative purposes.

Chapter IV introduces a method and a probabilistic explanation for the matching of species with protected area data in *gap analysis*. The method covers several species' distribution data types and overcomes the use of an arbitrary-chosen threshold value to align both specie and protected area data. Addressing **objective 3**, the study shows that the extent of species representations in protected areas is sensible to the choice of the matching procedure both on a static (snapshot-based) and on a dynamic (climate change born) scenario. Modeled data for a set of plant species occurring in Iberian Peninsula protected areas was applied to test the method.

Chapters V and VI address two complementary approaches for spatio-temporal assessments in conservation planning (Figure I). Responding to **objective 4**, **Chapter V** carries out a comprehensive *gap analysis* to evaluate the expected shifts of suitable climates of a broad set of species under different scenarios of climate change within European conservation areas. The taxonomic and geographic breadth of the analyses integrates different types of uncertainty that are integrated within a consistent evaluative framework. The framework uses: a) ensemble forecasting techniques applied to several greenhouse emission scenarios and different time-periods; b) the species-protected areas matching procedure presented in **Chapter IV**, and; c) cautious handling of climatic suitability predictions. **Chapter VI** addresses **objective 5**. It presents a network flow approach running under a probabilistic framework to generate a set of spatio-temporal “corridors” assisting species’ range adjustments through time. It integrates a scheduling procedure where a flexible area acquisition/ release planning is presented. Combining ensemble predictions of local climatic suitability with an optimization protocol for spatial prioritization, the framework allows to compare the expected gains from reduction of greenhouse gases with the ones expected with by increasing conservation funding.

My final chapter (**Chapter VII**) serves to synthesize and interpret this research, and to propose possible avenues to improve the studies herein presented.

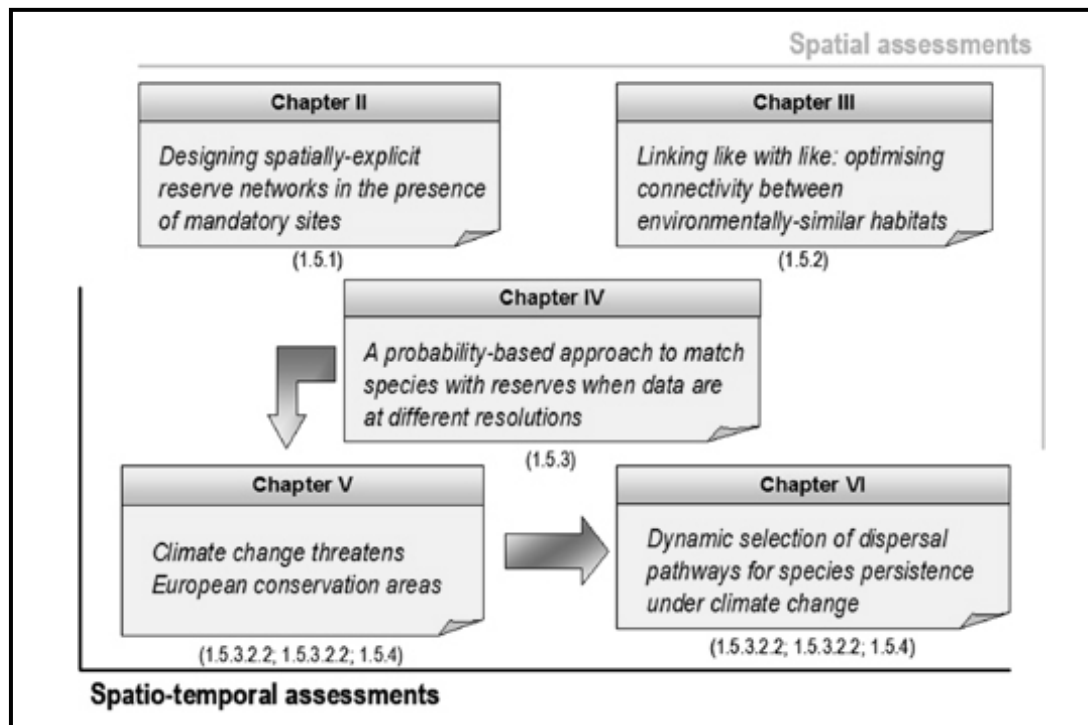


Figure I - Schematic overview of the thesis contents. In parenthesis the thesis sections respecting the challenges that motivated the studies. Arrows link close-related studies.

FORWARD

The present dissertation includes scientific writings published or submitted in co-authorship. The articles are the outputs of collaborative works, reflected in the lists of co-authors.

As a doctoral candidate presenting the current dissertation and leading author of all but one of the articles (Chapter VI), I was responsible for the specific scientific design and scheduling, statistical analyses, programming and writing. The thesis' advisors were deeply involved on the dissertation conceptual design and on the stages of work development, being also co-authors of the articles.

- **Chapter II** was published under the title “Designing spatially-explicit reserve networks in the presence of mandatory sites” (Alagador & Cerdeira. 2007, *Biological Conservation*, 137: 254-262, doi:10.1016/j.biocon.2007.02.008).
- **Chapter III** was submitted to an international peer-review journal under the title “Linking like with like: optimising connectivity between environmentally-similar habitats”.
- **Chapter IV** was published under the title “A probability-based approach for matching species with reserves when data is at different resolutions” (Alagador et al. 2011, *Biological Conservation*, 144: 811-820, doi:10.1016/j.biocon.2010.11.011)
- **Chapter V** was published under the title “Climate change threatens European conservation areas” (Araújo, Alagador et al. 2011, *Ecology Letters*, 14: 484-492, doi: 10.1111/j.1461-0248.2011.01610.x).
- **Chapter VI** was published under the title “Dynamic selection of dispersal pathways for species persistence under climate change” (Alagador et al. 2011, *Proceedings of the Global Conference on Global Warming 2011*). The work will be upgraded and soon submitted to a high profile journal.

Whereas the dissertation is a personal synthesis based on the mentioned articles where I benefited directly from the co-authors participation, I also gained indirectly from informal discussion on a collaborative basis.

During my PhD project, apart from the articles here presented I also collaborated in one more article, in a submission phase: Oliveira et al. Conserving the Brazilian semiarid (Caatinga) biome under climate change.

I have also participated in the workshop *Dynamic Conservation Planning*, held in North Queensland, Australia, 9-13rd November 2009, from where an article resulted: “Making decisions to conserve biodiversity under climate change”, leaded by Luke Shoo and submitted for publication in a high-profile scientific journal.

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“If I have seen further it is only by standing on the shoulders of giants”

Isaac Newton

Completing a PhD is truly a marathon event, and I would not have been able to complete this journey without the aid and support of countless people over the past four years. I must first express my gratitude towards my two supervisors: **Miguel Bastos Araújo**, for his leadership and scientific guidance, helping me to build the fundamentals of this work. His perspicacity, attention to detail and high scientific standards inspire my work, serving as a reference which I would like to reach one day. Along the hikes that he organized I was introduced to the Natural History of some Portuguese and Spanish spots like Barrancos, Serra da Arrábida, Sepulveda and mountains at North of Madrid; **Jorge Orestes Cerdeira**, for his guidance and magic teachings over these years. His extensive knowledge has given me a solid foundation to build my work on, while his keen eye for detail and unwavering dedication to a “clean” scientific process has improved the quality of my research. His support, hard work, and scholarship have set an example I hope to match some day. On a personal level, I am grateful for the friendship, encouragement and dedication that he has shown in the effort to further my education. He has gone beyond the call of duty to help me become a better thinker.

I feel glad and privileged for having been able to work together with the partners of this project. For their advice and help on the perception matters I would like to nominate **Mar Cabeza** (her insights on how conceptual issues and the real-world conservation biology may be linked helped me seeing that life is not only ideas - Chapters III, IV and V), **Maria Triviño** (her dedication and sensible touch on writings were of great aid – Chapter IV), **David Nogués-Bravo** (his smart insights and assertiveness contributed to empower one of the papers – Chapter VI), **Maria João Martins** (her great insight and experience on statistics gave me the fuel to design and execute most of the statistical analyses – Chapter V), **Raul Brás** (whose programming skills put my life easier – Chapter IV) and **Wilfred Thuiller** (his scientific excellence was accommodated within one of the papers – Chapter VI – while modeled species distribution data he made available concur to the realization of this work – Chapters V, VI and VII).

Thanks to the academic staff of the former **Department of Mathematics**, Instituto Superior de Agronomia (Lisbon, Portugal), by having prepared a Master programme where I got most of my mathematical and statistical skills, which I consider valorous to my career.

I would like to thank also to the colleagues on the **Biodiversity and Global Change Lab**, Museo Nacional de Ciencias Naturales (Madrid, Spain) that, from 2007 to 2011, provided me a stimulating, enduring and highly supportive surrounding, turning my time away from home more fun and interesting.

I extend my gratitude to the team working on the **Rui Nabeiro Biodiversity Chair**, Universidade de Évora (Évora, Portugal), by welcoming my stays with a pleasant and profitable environment that I am looking forward to experience again in the future.

By the kind invitations and the opportunities to collaborate with sounding people in this extensive research field of Biodiversity and Conservation I address my acknowledgements to the mentors of two workshops I participated. To **Bob Pressey** and **Steve Williams**, James Cook University (Queensland, Australia) who organized the workshop “*Dynamic Conservation Planning*” and **João Honrado**, Centro de Investigação de Biodiversidade e Recursos Genéticos (Oporto, Portugal) who leaded the workshop on “*Optimal monitoring of habitats and biodiversity across scales*”.

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“Se vi mais longe foi porque estive nos ombros de gigantes”

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**QUANTITATIVE METHODS IN SPATIAL CONSERVATION PLANNING
INTEGRATING CLIMATE CHANGE AND UNCERTAINTIES**

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CHAPTER I

General introduction

"The greatest challenge today, not just in cell biology and ecology but in all of science, is the accurate and complete description of complex systems. Scientists have broken down many kinds of systems. They think they know most of the elements and forces. The next task is to reassemble them, at least in mathematical models that capture the key properties of the entire ensembles."

E.O. Wilson, 1998

1.1 ECOLOGICAL CRISIS

Sociology, Anthropology, Economics and History were founded as sciences in an era where doctrines such as the human superiority over Nature, the unlimited economic growth, industrialization, urbanization and technologic developments were firmly embedded as panaceas for Humanity. These beliefs continue implicitly embedded in modern-society institutions, feeding current development models.

Until recently, societies conceived human being as inhabiting in the vacuum, orphan of Nature, without responsibilities for coming generations. By the sheer force of the naturally endowed intelligence, power of communication, capacity for institutional organization and relative freedom from instinctive behaviour, humans refashion the environment to one that is most suitable for their mode of existence, but distancing it from their roots. These problems, the ideologies they produce, the extent to which they contribute to biotic evolution or abort it, and the damage they inflict on the planet as a whole lie at the very heart of the modern ecological crisis (White Jr. 1967) that contains the danger of tearing down the Biosphere.

The proximate causes of biodiversity loss are relatively well understood, with habitat destruction, biotic homogenization, resource extraction, pollution and climate change (Sala *et al.* 2000; James *et al.* 2001), impacting biodiversity at different levels: habitats have suffered reductions of original cover (Millennium Ecosystem Assessment 2005; Butchart *et al.* 2010), species extinction rates exceed normal background rates by two to three orders of magnitude (Pimm *et al.* 1995; Barnosky *et al.* 2011), individual populations of many species have undergone significant abundance declines (Chapin III *et al.* 2000) and population genetic variability have been eroded by anthropogenic activities (Noss 1990). Consequently, decreased provisions of ecosystem services generate less socio-economic benefits (Millennium Ecosystem Assessment 2005; TEEB 2008).

1.2 FIRST STEPS INTO A CONSERVATION SCIENCE AND POLICY

Instigated by the direct consequences of biodiversity crisis on human welfare, a novel societal paradigm started emerging in the 1970s. More related with the ecologic values and the current-time needs a new ecologic paradigm has matured up to the point where the human relation with Nature is re-evaluated (Davidson-Hunt & Berkes 2002). Such a change brought a far-reaching transformation of our prevailing mentality of domination into one of complementarity, in which we see our role in the natural world as creative, supportive, and deeply appreciative of the needs of nonhuman life. Increments in conservation science and practice have been documented since then, and a global concern on the state of biodiversity culminated in important international laws and treaties. For example, the Convention on Biological Diversity agreed “to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional, and national level as a contribution to poverty alleviation and to the benefit of all life on Earth” (UNEP 1992).

Moreover, several schemes for biodiversity conservation were developed. If threats are severe or if species are very susceptible, intensive measures might be required in order to achieve at least the species' short-term maintenance. In the case of small populations it might be adequate to extract them from the natural habitat and try to enhance their viability off-site. Botanical gardens, zoos, gene banks, and captive breeding programs practice this ex-situ conservation. If the viability of species still is tolerably good, either by moderate threatening or by species experiencing low sensitivity to threats, it is preferable to conserve them on the site or “in situ”. Likewise, “in situ” conservation is the unique option to conserve the complexity of communities and ecosystems, thus safeguarding multiple species and their resources into the future. Protected areas are the main tools for “in situ” conservation.

1.3 SPATIAL-BASED CONSERVATION

Protected areas are among the most efficient and effective ways of conserving biodiversity and are generally considered the cornerstone of any effective strategy for conserving biodiversity. Worldwide, there are more than 100,000 protected areas covering nearly 14 million square kilometres in virtually every country of the world (IUCN & UNEP-WCMC 2007). They may well be one of the most stunning

conservation successes of the last century. The surface area of protected areas has doubled since 1975 covering nearly 10% of Earth's terrestrial surface. This is likely to continue as, for instance, the 11th "Aichi target" of the revised Convention on Biological Diversity (UNEP 2010) calls for 17 per cent protection of the world's terrestrial and inland ecosystems and 10 percent of coastal and marine areas by 2020. A celebration of global conservation success may be however premature (Butchart *et al.* 2010; Pereira *et al.* 2010).

Given the potentially numerous competing management goals for a given area, some of them with higher socio-economic appeal, protected areas are highly biased towards economically unproductive regions (Gaston *et al.* 2008; Joppa & Pfaff 2009; McDonald & Boucher 2011). Establishing protected areas imply several financial costs for the acquisition of land (Ando *et al.* 1998; Carwardine *et al.* 2008), for compensating land owners for foregone opportunities (Carwardine *et al.* 2008; Adams *et al.* 2010) and for conservation management (Grantham *et al.* 2008). Because protected areas have been commonly established for reasons other than protection of biodiversity, most of them are probably ineffective for conserving biodiversity (Rodrigues *et al.* 2004), resulting in a false (optimistic) perspective of biodiversity protection (Joppa & Pfaff 2011).

1.4 SYSTEMATIC CONSERVATION PLANNING

The field of Systematic Conservation Planning was developed as a response to the above mentioned opportunistic approaches in conservation, to ensure adequate representation and persistence of biodiversity. It applies a structured approach to prioritize and manage habitats deemed important for the persistence of natural values.

The last two decades have seen the development of increasingly sophisticated planning schemes accounting for biodiversity evaluation (benefits: rarity and phylogenetic diversity, e.g., Vane-Wright *et al.* 1991, Faith 1992; ecosystem services, e.g., Goulder & Kennedy 1997; gene diversity, e.g., Diniz Filho & Telles 2006; species traits, Loyola *et al.* 2008), economical considerations (costs: e.g., Wilson *et al.* 2006; Carwardine *et al.* 2008; Arponen *et al.* 2010) and socio-political constraints (pressures: e.g., Halpern & Warner 2003; Pinto *et al.* 2007; Araújo *et al.* 2008), within the frame of conservation science. In order to manage the complexities associated with such a multivariate decision-making, the spatial domain of Systematic Conservation Planning (Spatial Conservation Planning) makes use of a quantitative, transparent and replicable process of decision-assistance to identify with a minimum cost the best-valued areas to conserve or to maximize the biological benefit of the areas to protect given a fixed (normally scarce) budget. Spatial Conservation Planning involves a structured step-wise framework, consisting of: (1) selection of the relevant biological elements to protect (this refer not only to species and habitats but also to ecological processes and ecosystem services); (2) setting quantitative conservation targets (typically linked with representation and persistence); (3) evaluation of the performance of existing protected areas to fulfil conservation targets; (4) identification of preliminary arrangements of areas that complement current protected areas in meeting conservation targets; (5) development of an implementation strategy for achieving results (Margules & Pressey 2000; Pressey & Bottrill 2008); (6) elaboration of mechanisms for maintaining optimal conditions within individual protected areas.

Whilst Spatial Conservation Planning principles could be implemented as a series of manual processes, contemporary computer systems provide the opportunity to develop decision support tools that produce significantly faster, more efficient, real-time design solutions based upon quantitative scientific analyses of large spatial databases. Those systems employed in a spatial context are often termed spatial decision support systems, and often use mathematical algorithms to solve complex problems. They have the potential to provide conservation planners with baseline arrangements of sites that satisfy a number of conservation targets.

Even though these quantitative tools help retrieving the "better" solutions in Spatial Conservation Planning, there are knowledge-gaps and challenging questions still to be addressed. Resolving these issues contributes to approximate the "better" answers into the "best" solutions. Next, I present a few challenging topics that stimulated this thesis.

1.5 SOME CHALLENGES

1.5.1 Spatial requirements in protected area selection

Under the Spatial Conservation Planning paradigm, protected areas should be defined following a number of principles: comprehensiveness, representativeness, irreplaceability, flexibility, adequacy and efficiency (Box 1.1).

Whilst the principles of Spatial Conservation Planning are fairly well established, the methods for implementing these principles in the protected areas prioritization are many and varied.

Box 1.1 – Established properties for protected areas in Systematic Conservation Planning.

Comprehensiveness: A comprehensive reserve system is one that contains examples of many biodiversity features, where biodiversity features may include species, habitats, or ecological processes.

Representativeness: This concept is closely related to the idea of comprehensiveness, if we define each biodiversity feature at a finer scale (i.e., populations of a species, subtypes of an habitat), then comprehensively sampling the finer biodiversity elements is equivalent to represent the coarser features.

Irreplaceability: The irreplaceability of an area reflects how important its inclusion in the reserve system is if all conservation objectives are to be met. A completely irreplaceable area is essential to meeting conservation objectives, whereas an area with very low irreplaceability may be substituted by others. Irreplaceability can help determine which areas are priorities for conservation, but other constraints and considerations may mean that areas with lower irreplaceability are more suitable for conservation. For example, the vulnerability, the condition and/or cost of an area might influence its priority for protection.

Flexibility: a flexible conservation system is one that enables us to achieve our objectives efficiently in a number of ways. It might be important to take advantage of opportunities that arise for conservation, such as an area with high conservation value becoming available to acquire.

Adequacy: Representing comprehensively biodiversity within protected areas is not a guarantee to ensure its persistence and continued evolution of features contained within them. This aspect of conservation planning is not well developed. The idea of adequacy is commonly addressed in the form of target percentage of original extent or a target population size for each feature; by explicitly accounting for the protection of ecological and evolution processes, and considering spatial attributes in protected area design.

Efficiency: In the face of a large set of competing interests implementing a reserve system will be easier if involving the least possible cost to achieve the established conservation objectives. Optimizing efficiency brings complexity (i.e., solving difficulties) to protected area selection. It is also a sound platform from which to expand a protected area system.

One of the primary considerations in Systematic Conservation Planning is to identify the set of areas that meet conservation targets for the minimum cost. If the goal is for example to cover each feature at least once in the protected area network, there is obviously no point in including an area that adds only features that are already covered in the network. Consequently, areas should be selected that have disjoint feature pools and thus complement each other. This complementarity principle is vital to match comprehensiveness with efficiency.

Originally, the protected area selection problem was stated under two simple conservation conceptions. Under the first version, known as the set coverage problem, the objective is to minimize a cost function (such as the number or cost of selected areas) subject to the constraint that all species are covered (Margules *et al.* 1988; Possingham *et al.* 1993). Under the second version, called the maximal coverage problem, the objective is to maximize coverage subject to the constraint that the cost not exceeds a specified amount (ReVelle *et al.* 2002). Although easy stated, these problems are mathematically complex and their solving is dependent on data structure and size. Effective heuristic and optimization approaches for solving these problems have been developed (Arthur *et al.* 1997; Rodrigues & Gaston 2002). The simplicity of such formulations only takes into account the comprehensiveness and representativeness principles. Adequate (persistence-driven) protected area systems depend on many other criteria, including spatial configuration (Margules & Pressey 2000; Williams *et al.* 2004; Margules & Sarkar 2007).

Conventional rules of thumb for (adequate) protected area selection were proposed by Diamond (1975) and Wilson & Willis (1975), around the principles from equilibrium theories of Island Biogeography and Metapopulation Ecology. These rules incorporate a set of spatial criteria in which protected area size, form

and location take part. A particular interest has surrounded distance-based rules, also known as connectivity: “If small protected areas are necessary, they should be arranged spatially to maximize dispersal rates among them and, consequently, rescue effects”. The preferred ways of achieving this end are to position protected areas as closely as possible, by protecting smaller, natural area stepping stones between them, or by protecting linking corridors. Several optimization models for protected areas selection accounting for spatial configuration have been proposed (Williams *et al.* 2005a). Some use connectivity as an obligatory property to achieve (e.g., Cerdeira *et al.* 2005; Onal & Briers 2006), others assume connectivity an objective to be optimized (e.g., Briers 2002; Nalle *et al.* 2002; Onal & Briers 2002). The existence of areas whose importance makes them mandatory to be selected may impose problematic effects to the final spatial configurations, as they are the key element guiding the selection process. Until now, no model has been explicitly developed to account for such mandatory areas. **Chapter II** introduces such a contribution where distance-driven optimization is guided by the position of mandatory areas.

1.5.2 Environmental gradients and connectivity

Although biodiversity is a heterogeneous concept accounting for the multi-faceted, continuous variability of life, from genes to ecosystems, Spatial Conservation Planning makes use of only those biodiversity features that can be mapped (Brooks *et al.* 2004a). As mapping and measuring ecological processes are still in their infancy (Cowling *et al.* 1999; Brooks *et al.* 2004c), information on genetic and population diversity is still grossly insufficient for conservation purposes and species occupancy pattern data are still fragmentary and biased (Soberon & Peterson 2005), most spatial conservation efforts have necessarily targeted those biodiversity surrogates for which reliable data can be obtained. Surrogacy data usually fall in two broad categories: i) better known taxa, and ii) abiotic surrogates able to describe species occupancy patterns. Whilst the former makes use of either species distribution data (*autecology approach*) or synecological variables (*community-based approach*) as targets, abiotic surrogacy has relied on environmental variation as a well-known surrogate of biodiversity variation (the *environment-based approach*) (see, Faith & Walker 1996a; Ferrier 2002).

The long-latent disagreement over the superiority of either species or environment information, for both planning and for measuring the success of conservation efforts, has recently figured in debate (Araújo *et al.* 2004b; Brooks *et al.* 2004a; Brooks *et al.* 2004b; Cowling *et al.* 2004; Faith *et al.* 2004; Higgins & Ruokolainen 2004; Molnar *et al.* 2004; Pressey 2004), although its origin can be traced back to the approaches that preceded Spatial Conservation Planning framework (e.g., Dasmann 1972).

Those that favour the environment-based approach assert: that the main impediment to the use of species data is lack of reliability (Pressey 2004); that conservation planning must represent such other biodiversity attributes as land types, habitats or ecological processes (McKenzie *et al.* 1989; but see, Goldstein 1999) and; that ecosystems within species-poor areas may be crucial regarding the goods and services needed for nature functioning (Kareiva & Marvier 2003). In addition, other authors suggest that the use of broad-scale biodiversity attributes reflects the whole functional context surrounding biodiversity patterns (Ferrier & Guisan 2006).

On the other hand, defenders of the species-based approach claim that species are the relevant conservation unit and broad-scale biodiversity attributes are abstract and subjectively constructed, not necessarily reflecting species diversity (Araújo *et al.* 2001). A recent study showed that a complementary environmental approach proposed by Faith and Walker (1996a) to select areas for conservation to cover environmental diversity variation (environmental diversity) was not able to recover more species than expected by chance in some of the studied living groups at European extent (Araújo *et al.* 2003; debated with Faith 2003), probably due to the existence of a geographic pattern different from a purely environmental one. This inconsistency may be due, first, to the fact that many different groups are analyzed jointly even though each one reacts to variations in environmental diversity in a different way; thus the selected environmental descriptors are too general to fit each species requirements (see Faith 2003). Second, as Araújo *et al.* (2001) point out, many contingent factors, such as historical events and population-related processes, can modify the spatial distribution of biodiversity.

On the grounds that environmental diversity may act as an effective surrogate for patterns of biodiversity at lower organisational levels, several protected area selection approaches have been suggested. They have been discussed or conducted in terms of a variety of higher level organisational units (Bonn & Gaston 2005), like environmental gradients (e.g., Faith & Walker 1996a; Carvalho *et al.* 2011), environmental units (e.g., Woinarski *et al.* 1988; Pressey & Logan 1998; Lombard *et al.* 2003; Kati *et al.* 2004), land types (e.g., Wessels *et al.* 1999; Pressey & Taffs 2001; Beier & Brost 2010), geomorphological heterogeneity (e.g., Nichols *et al.* 1998; Pressey *et al.* 2003), ecological heterogeneity (e.g., Kati *et al.* 2010) and ecosystems (e.g., Noss 1996). Defenders of environmental representation within protected areas have also argued for the stability and evolutionary role of environmental structures as means to safeguard biodiversity from climate change impacts (Anderson & Ferree 2010; Beier & Brost 2010; Game *et al.* 2011).

However, the sole use of environmental surrogates for the identification of connectivity linkages between already established natural habitats has not been particularly assessed in the literature. The most common species-specific connectivity approaches start by identifying the relevant species to act for, along with the relevant environmental factors limiting species movements. These factors are then combined into a single resistance value, meant to inform the degree of suitability of an area to assist species movements. The 'effective distance', or cost of a path between habitat patches for a species, is the Euclidian distance weighted by the cumulative resistance values of all cells traversed (Adriaensen *et al.* 2003; Beier *et al.* 2008; Sawyer *et al.* 2011). The least cost paths are the combination of cells that minimizes effective distance between two patches and is used to inform optimal placement of a linkage.

This approach seems not to be the most efficient way to define connectivity when there are multiple natural habitat patches to be linked and does not respond to situations where direct species occurrence data is deficient. It is therefore essential: 1) to identify the mechanisms that regulate the patterns of species diversity at a given scale, 2) to integrate them into a multi-species connectivity conservation framework, and, 3) to develop a procedure that optimizes linkages between the areas seen to present similar species pools. **Chapter III** presents and discusses a proposal integrating these issues.

1.5.3 Spatial prediction problems in ecology

1.5.3.1 Distributional data

Conservation biology has often been called a crisis discipline (Pullin 1992; Wilson 1994). Its focus on rapidly altering ecosystems, biological extinctions, and the ultimate loss of biodiversity defines a discipline that lacks the luxury of time (Chapin III *et al.* 2000). Therefore, the biological and environmental data employed in conservation planning are that which are readily available and typically incomplete. This affects the accuracy of outcomes and introduces uncertainty and subjectivity into the planning process (Gaston & Rodrigues 2003).

The most basic non-manipulated data type are point locality data. It refers to a location where a species has been recorded. However, because detailed surveys over the entire possible range of most species are almost never available due to lack of resources, no region has totally complete point locality data, (Haila & Margules 1996; Hortal & Lobo 2006). In addition, even when extensive surveying is applied some species that are present may remain undetected. Both these processes result in omission errors (false-negatives). In order to reduce them, point data are frequently extrapolated to grid cells, where species are recorded as present (Hopkinson *et al.* 2000) while absence is presumed for grid cells containing no point records. As scaling up species occurrence data in this manner is an uninformed extrapolation, the use of larger grid cells results in higher rates of commission errors (false-positives), by which species are assumed present when it is not true. Both types of errors impact negatively and differently conservation planning assessments (see section 1.5.3.2). In uninformed approaches an adequate grid cell size permits to balance the effect of both types of errors (Rondinini *et al.* 2006).

The relationship between species locality data and environmental variables can be used to predict the distribution of a species at broader scales. Predictive distribution models have the ability to use incomplete information (e.g. spatially incomplete point locality data) to generate spatially comprehensive predictions of species distributions. Predictive distribution models may be applied either assuming a mechanistic or a

correlative relationship with the species distribution patterns (Soberon & Peterson 2005). Mechanistic models usually require detailed understanding of the physiological responses of species to environmental factors they are therefore difficult to develop for all but the most well understood species (e.g., Keith *et al.* 2008; Kearney & Porter 2009). Contrarily, since spatially explicit occurrence records are available for a large number of species, the vast majority of species' distribution models are correlative.

Several alternative correlative modelling algorithms (e.g. geometric, statistical and machine learning) have been developed (Thuiller 2003; Elith & Leathwick 2009), differing in the form of their output. Continuous predictions of species' distributions are the most common output form, but different studies attribute them distinct conceptualizations (i.e., a probability value; a favourability measure, e.g., Albert & Thuiller, 2008, or a suitability index, Araújo & Williams, 2000). Binary predictions (presence/ absence) are not the most common data form directly resulting from the species distribution models, but they are the operative support for most studies. Therefore, continuous information is often converted to presence/ absence data after a threshold value has been applied. For predictions above the threshold value the area is seen as highly suitable for the species to occur. Absences are taken for the predictions below the threshold value. The selection of the appropriate threshold value has been a rich analytic field, in which several methodologies have been proposed (Fleishman *et al.* 2001; Liu *et al.* 2005), to optimize the accuracy of predictions.

Aside from the above mentioned complications characterizing species distribution modelling frameworks, there are still other sources of uncertainty and, in some cases, arbitrariness. Distribution models built from environmental and geographically biased distributional data will misrepresent the distribution of species as well as their environmental responses (see, Hirzel *et al.* 2002; Hortal *et al.* 2007). If these biases are consistent across species (as they usually are), it is also quite likely that modelling errors will aggregate in space (Hortal & Lobo 2006). Predictive accuracy depends also on the sample size available (e.g., Wisz *et al.* 2008; Jiménez-Valverde *et al.* 2009), that may attenuate model robustness and stability (Elith *et al.* 2002; Loiselle *et al.* 2003; Heikkinen *et al.* 2006).

While effort is usually dedicated to developing the 'best' model for a species, in reality the final model is only one of many possible models. A number of studies have demonstrated that different modelling approaches have the potential to yield substantially different predictions (e.g., Loiselle *et al.* 2003; Segurado & Araújo 2004; Thuiller 2004; Elith *et al.* 2006). In view of these differences among models, selection of an appropriate algorithm is both difficult and crucial. To address these problems, some authors have suggested that predictions should be made on the basis of predictions of ensembles of different models (e.g., Thuiller 2004; Araújo *et al.* 2005c; Araújo & New 2007; Dormann 2007; Marmion *et al.* 2009), so that the final prediction emphasizes agreement of predictions, and quantification of inter-model variability. Ensemble forecasting avoids the requirement to select a single, best model from among many approximately equivalent models (Dormann 2007). It also avoids potential errors due to over-fitting and can capture different components of the true basis for species' presences, parts of which may be represented in different models (Araújo & New 2007; Algar *et al.* 2009). Unless the candidate set of models are carefully constructed and evaluated, some lack of congruence may be more due to model error (i.e. specification of an unrealistic model) than uncertainty about the correct model. A good ensemble architecture may also avoid all models being wrong in the same way (e.g., because the species is not in equilibrium), a fact that does not guarantee that ensembles are satisfactorily accurate (Buisson *et al.* 2010).

Other sources of uncertainty derive from deficiencies regarding knowledge of the processes to be modelled (i.e., epistemic uncertainty *sensu* (Elith *et al.* 2002; Regan *et al.* 2002)). For example, realized species distributions are shaped not only by environmental conditions, but also by a number of other key mechanisms which are commonly unavailable or unused. These include species dispersal capacity (Fielding & Bell 1997), biotic interactions (Heikkinen *et al.* 2007; Schweiger *et al.* 2008), biogeographical constraints and historical events (Colwell & Rangel 2009; Soberón & Nakamura 2009; Lobo *et al.* 2010) and landscape complexity (Chust *et al.* 2003; Ricotta & Anand 2006; Soberón 2010), most of which are unknown and difficult to consider in the modelling procedure.

Other dimensions of model uncertainty include the form the response function is allowed to take (linear, quadratic, smoothed and so on) (Elith *et al.* 2006), how to deal with spatial autocorrelation and

overdispersion (Heikkinen *et al.* 2006) and what threshold to be used to convert continuous outputs to presence/ absence data (Jiménez-Valverde & Lobo 2007; Lobo *et al.* 2010; Liu *et al.* 2011).

1.5.3.2 Uncertainties in reserve design

The need to treat uncertainty has been established in the context of population-viability decision analyses (e.g., Maguire 1986). Identifying and incorporating error information into the decision-making process are requisites for a modern conservation science. Nevertheless, uncertainty analysis is by large missing from most regional scale Spatial Conservation Planning, which needs to address high-dimensional optimization problems that are difficult to solve even without the extra complications introduced by uncertainty analyses.

As the fundamental input data, species' distributions carry imprecision that may lead to unsuccessful or sub-optimal conservation achievements (e.g., protected area representativeness, efficiency and adequacy). In some cases, uncertainty may be resolved or decreased, for example, by gathering supplementary data, improving knowledge on species ecology or, when applied, by refining predictions. However, this is not always feasible and decision making tools in Spatial Conservation Planning should account for the pervasive uncertainties within species distribution data. Specifically, analysis of uncertainty should encompass:

- 1) the balancing of commission and omission errors;
- 2) which data type to use;
- 3) resolution effects.

1.5.3.2.1 Commission/omission errors

In conservation terms, the cost of a false-positive error is that associated with selecting an area to be conserved because a species was predicted to be present in the area, but in fact was not. In such cases, the level of protection afforded by conservation areas is overestimated (Loiselle *et al.* 2003) and the uncertainty associated with the adequacy of selected areas is increased (Wilson *et al.* 2005). Contrarily, the cost of a false-negative error is that associated with excluding an area from the reserve network on the basis that the species was predicted to be absent from the area, when it was actually present. Omission errors determine inefficient conservation areas (Flather *et al.* 1997). A critical issue for conservation planning is whether errors arising from accepting false positives are more severe than errors arising from ignorance of the local heterogeneity of species distributions within coarser-resolution grid cells (Rondinini *et al.* 2006). There are no established rules to find the appropriate trade-off between such opposing sources of error and the decision as to whether to use downscaled or original coarse-resolution data must depend on the goals of the analyses and on a case by case assessment of risk (Araújo *et al.* 2005b; Ray & Burgman 2006). For example, in an effort to balance the errors of commission and omission that may occur when assigning a species distribution, Underwood *et al.* (2010) developed a hybrid approach where point locality occurrences are extrapolated using species dispersal capabilities and within such spatial windows species is only predicted to occur within predicted suitable areas.

The importance of uncertainty depends on the context of a decision and increases with larger landscapes and time horizons (Halpern *et al.* 2006) and with the number of analysed species (Burgman *et al.* 2005). For example, Flather *et al.* (1997) tested the effect of error accumulation through the process of overlaying species distribution maps into richness patterns and, consequently, on the patterns of selected priority areas. They concluded that even if species-specific distribution models present acceptable error rates, the composite richness may not be precise enough to guarantee the representation of species or optimal efficiency in the prioritized areas.

1.5.3.2.2 Data types

Previous studies showed that spatial prioritization of conservation areas is sensitive to the type of species distribution data (e.g., Turpie 1995; Freitag & Van Jaarsveld 1998; Polasky *et al.* 2000; Gaston & Rodrigues 2003; Wilson *et al.* 2005; Carvalho *et al.* 2010). Common spatial conservation applications use deterministic presence-absence data (either from sampling or from modelled data), where uncertainty is frequently framed by sensitivity analysis or resampling methodologies (e.g., Montecarlo simulations). However, under natural circumstances species' distributions are affected by a set of non-deterministic events, making probability the most natural data type to express distributional incertitude (Colyvan 2008). This uncertainty arises from two processes: accuracy, or the degree of veracity of the information (that translates into the probability of species occurrence), or; precision, as the degree of reproducibility (which is described by statistical functions Conroy *et al.* 2011). A proper algebra to combine such distributions can then be used to quantify and provide a series of distributions for the objective function (e.g., number of species represented with some confidence degree).

The first attempts to incorporate probabilistic data into Spatial Conservation Planning go back to Margules & Nicholls (1987) and Margules & Stein (1989) who, however, converted probabilistic data into binary data using thresholds. Recently, approaches have been suggested to deal directly with probabilistic data. The probabilistic version of the set covering problem (see section 1.5.1) was presented by Faith & Walker (1996b), using probabilities of persistence as species representation targets, and by Sarkar *et al.* (2004), who interpreted probabilities as expectancies to simplify problem solving. The probabilistic version of the maximal coverage problem (see section 1.5.1) was first formulated (under a biological context) by Cocks & Baird (1989). Two methods have been presented to deal with this problem. One approach addresses the ultimate objective of maximal coverage most directly (Polasky *et al.* 2000), but because the objective function involves sums of probabilities, each of which is a nonlinear function of the decision variables, linearized versions were developed (Arthur *et al.* 2002; ReVelle *et al.* 2002; Billionnet 2011). A second approach, which has been applied more often in the conservation literature, was named the threshold approach. The goal in the threshold approach is to maximize the number of species covered, where a species counts as covered only if the probability of coverage reaches a specified threshold (Margules & Stein 1989; Haight *et al.* 2000). Sarkar *et al.* (2004) compared the performance of distinct algorithms to solve all probabilistic versions of area selection problem.

Moilanen *et al.* (2006a; 2006b) applied the principles of info-gap theory to obtain robust spatial solutions for species representation. The philosophical principle behind info-gap resides on the evaluation of how much uncertainty can be allowed before a decision changes (Ben-Haim 2001). Info-gap decision theory provides a means of propagating the impact of uncertainty through the decision making process. In Spatial Conservation Planning info-gap robust solutions contain the areas where the species are represented with higher certainty. Of two areas with equal expected values (i.e., accuracy), the one with lower variance (i.e., higher precision) is preferred.

Conservation success is more than achieved species representation in a given time. It implies species persistence. Persistence brings a temporal dimension to the static approaches and therefore is embedded with added uncertainties. Uncertainty about persistence is primarily caused by anthropogenic factors, often called threat and vulnerability, which may cause the value of biodiversity in an area to be lost or degraded, but natural factors (e.g., species interactions, natural invasions or succession) may also lead to local extinctions. Williams & Araújo (2000) proposed a framework to optimize species persistence using probabilities of species occurrence, and Araújo & Williams (2000) suggested distinct forms to reach species persistence measures from probability of occurrence data and tested the sensitivity of priority area selection to these variants.

1.5.3.2.3 Within-grid cell species' positional uncertainty (resolution effects)

Choosing a grain (i.e. grid cell size) is partly a technical issue. For instance, grain size is related to the characteristics of the species data (e.g. geographical accuracy, sample size, field survey constraints, or autocorrelation structure (Guisan & Hofer 2003; Guisan *et al.* 2007), to the computer power (i.e. too many grid cells may require too demanding computer resources) and to the grid cell size of available environmental data used for modelling (Graham *et al.* 2004). Grain size is also a crucial ecological as well

as management issue (Latimer *et al.* 2006). Changing the grain size can influence the perception of a phenomenon, such as patterns of presence or abundance (Graham & Hijmans 2006), errors associated with measured predictor variables (McInerney & Purves 2011) or affect the relevance of the output for Spatial Conservation Planning (Araújo *et al.* 2005b). Typically, there is a concern that the scale of most data is too coarse to conduct conservation assessments (e.g., Hopkinson *et al.* 2000; Rouget 2003; Araújo *et al.* 2005b). Although coarse resolution assessments are important in determining areas to prioritize for protected area acquisition, especially where data are not available at finer resolutions (Fjeldså *et al.* 1999; Brooks *et al.* 2001), fine-resolution analyses (i.e., downscaling) must also be undertaken to ensure all species of conservation concern are adequately protected on actual reserves (Araújo *et al.* 2005b).

One of the issues surrounding the positional uncertainty of biological data within grid cells refers to how it impacts protected area representativeness assessments (i.e., *gap analysis*, Hopkinson *et al.* 2000; Araújo 2004). Traditionally, broad scale assessments use grid cell species' occurrence data (either from atlases records or by converting continuous outputs from predictive modelling) to be crossed with reserve data. Because of the uncertain position of species inside grids cells, uncertainty arises when to know if a species is within the grid cell's protected fraction or not. To overcome this lack of information, protected area polygon data are converted into grid cell based data, where the extent of protected areas within the grid cells is recorded. A threshold (cut-off) value is selected and grid cells with protected area above the threshold are considered totally protected and species occurrences within that grid cells are assumed under protection. This approach is highly arbitrary and the degree of species representation in protected areas is very sensible to the selected thresholds (Araújo 2004).

The explicit application of continuous data from species distribution modelling has not been tried under gap analysis. Their cautious use can be advantageous, as such information can be useful in performing assessments under uncertainty (see section 1.5.3.2.2). These data are frequently read as the probability of a species to occur in a given grid cell or, equivalently, as grid cell's suitability for the species to occur (but see, Tyre *et al.* 2003, for a criticism on the relation of probability of occurrence with habitat suitability). Taken in its homogeneous form, grid cell's suitability reads as the average adequacy for the species occurrence, across the grid cell's surface-area. But if assuming grid cells as heterogeneous entities, within which several mosaic of environments exist, grid cell's suitability may inform about the area containing suitable conditions for the species occurrence (Figure 1.1). These different treatments of species occurrences within grid cell's where the species is predicted to occur challenges protected area representativeness assessments (Hopkinson 2000).

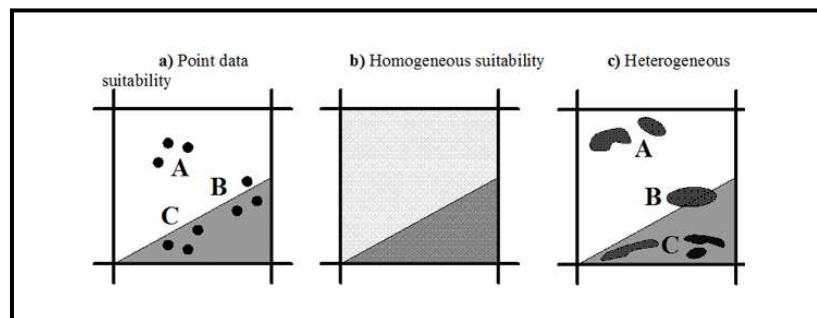


Figure 1.1 - The effect of species' position uncertainty when matching species data with protected area data within a grid cell. In **a**) three possible cases express in what extent commonly unavailable point data (black dots) match protected areas (dark gray) in a grid cell: A) no representation, B) partial representation, C) full representation. In **b**), knowledge-gaps in local species distribution are translated into a homogeneous suitability value (light gray). Crossing this value with protected area coverage results in an averaged species representation in the grid cell's protected area. In **c**), a suitability value translated into spots of suitable areas with grid cell. Depending on their position, the species is expected to be represented differently within protected areas: A) no representation, B) partial representation, C) full representation.

Species' distributions have been postulated to exhibit some degree of self-similarity across scales (Harte *et al.* 1999). As such, several studies have tested distinct modelling strategies to fine-grain species occurrence data (e.g., Collingham *et al.* 2000; Barbosa *et al.* 2003; Araújo *et al.* 2005b; Niamir *et al.* 2011). Typically, these approaches use correlative procedures to perform the analysis, after selecting a

set of environmental variables. Yet, dominant processes influencing species distributions at a broader scale are different from the conditioners of species distributions at finer scale. In order to respond to this limitation McPherson *et al.* (2006), proposed a more proximate approach, where intra-cell environmental heterogeneity is used to derive finer species distributions.

Chapter IV delivers a possible probabilistic understanding to the problem of crossing uncertain species occupancy patterns within grid cells with protected area data. This approach circumvents the use of arbitrary rules to match species with protected area data, a common procedure in broad scale gap analysis.

1.5.3.2.4 Other sources of uncertainty

Spatial Conservation Planning handles complex problems, relying on several factors that can influence the final decision. Apart from species distribution data, the effect of diverse conceptual variations has been tested.

Some studies examine how correlated spatial dynamics of species may cause synchronous fluctuations in metapopulation occupancy, resulting in the loss of populations living in a small group of cells (Moilanen & Cabeza 2005). Moilanen and Wintle (2007) devised a quantitative method introducing aggregation into the priority areas that, implemented in an optimization model, enables an optimal aggregation level to be accomplished without the need of arbitrary parameterizations. Also, O'Hanley *et al.* (2007b), Cabeza (2003) and Cabeza and Moilanen (2003) examined how population dynamics within unprotected habitats may interfere with the occupancy patterns within protected areas. Pressey *et al.* (2004) and Visconti *et al.* (2010) formulated conceptual models where the state of unprotected areas is taking into account for species retention. Additionally, Pressey *et al.* (2004) tested the sensitivity of 52 conservation measures to the scheduling of conservation actions across all the landscape.

Warman *et al.* (2004), Justus *et al.* (2008) and Vimal *et al.* (2011) scrutinized the influence of species' representation targets on the selection of conservation areas. Rondinni & Chiozza (2010) extended this analysis to test how different natures of representation targets affect final solutions. Arponen *et al.* (2005) presented a novel conceptualization for conservation achievements, proposing benefit functions to value species representation in a conservation network.

Socioeconomic factors influencing site availability and future land use might also be treated as forms of uncertainty in Spatial Conservation Planning. The lack of reliable data on the costs of conservation actions is one reason for cost data be frequently omitted during the prioritization process (Balmford *et al.* 2000; Odling-Smee 2005; Ferraro & Pattanayak 2006; Kremen *et al.* 2008). Planning with inaccurate cost data may not deliver the gains in conservation planning efficiency that studies predict (Ferraro & Pattanayak 2006; Perhans *et al.* 2008; Arponen *et al.* 2010). Carwardine *et al.* (2010) provide a practical approach to obtain conservation planning assessments when information on costs is uncertain. Balmford *et al.* (2003) performed a global analysis on conservation costs. They use socioeconomic development predictors to derive confidence intervals of costs devoted to conservation projects worldwide. Naidoo & Ricketts (2006) reviewed the integration of cost information in conservation, how they can be estimated or modelled in a spatially explicit manner, empirical examples of how plans differ when costs are formally considered and how cost information may fit dynamic conservation planning frameworks. Wilson *et al.* (2006) developed a dynamic approach to schedule conservation financial resources among global biodiversity hotspots and tested the variation of solutions when conservation budgets vary.

Aside from the cumulative effects of uncertainty in spatially-explicit contexts, several studies have analysed the influence of distinct factors framing conservation planning when dynamic (time-base decisions) approaches are conceived. Sequential decisions and issues associated with loss and availability of habitat over time as opposed to immediately implementing an entire reserve network have been proposed (e.g., Costello & Polasky 2004; Meir *et al.* 2004; Pressey *et al.* 2004; Drechsler 2005; Turner & Wilcove 2006). Strange *et al.* (2006), Mascia and Pailler (2011) and Fuller *et al.* (2010) look at the option to sell protected land on which biodiversity value has decreased. Rodrigues *et al.* (2000), Araújo *et al.* (2004a) and Rayfield *et al.* (2008) address temporal issues associated with variability in population locations due to changing conditions.

In spite of all these papers and more that warn about the consequences of uncertainties, it is still not standard practice to evaluate methods or plans under uncertainty, nor do commonly used methods address the bulk of these uncertainties in their algorithms and objective functions.

1.5.4 Climate change

Earth is experiencing a rapid global disruption to its climate, one of considerable physical complexity (Lemke *et al.* 2007). Such changes alter the fundamental abiotic environment in which species and communities exist. An increasing number of empirical studies document the ecological effects (e.g., changes in phenology, physiology, morphology, species interactions and distributions) of recent climate change (e.g., Parmesan *et al.* 1999; Hughes 2000; Warren *et al.* 2001; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006; Pimm 2009; Lavergne *et al.* 2010; Geyer *et al.* 2011), and several recent species extinctions have been linked to climate change (Pounds 1999; McLaughlin *et al.* 2002; Thomas *et al.* 2004; Pimm 2009; Barnosky *et al.* 2011).

The rate of global climate change increased through the 20th century, and should emissions of greenhouse gases continue at or above current rates, climate change in the 21st century will very likely exceed that observed over the 20th century (Lemke *et al.* 2007). Though we cannot be certain that, due to the differing combination of causal factors (Graham & Grimm 1990), future changes will be directly comparable to the recent past changes we can expect that the future changes in climate are likely to have a substantial impact on species' distributions and persistence. The ability of species (and ecosystems) to respond positively to climate change will depend on species-specific characteristics (e.g., potential for rapid adaptation, phenotypic plasticity, or dispersal capability; Parmesan 2006), current and future anthropogenic threats (e.g., habitat fragmentation), the extent to which future climate regimes present conditions beyond those previously experienced, and the natural resilience of biological systems to these changes (Thuiller 2007; Araújo *et al.* 2011).

Given the velocity of climate change (Loarie *et al.* 2009), in-place genotypic adaptation and phenotypic plasticity are likely to play a relatively minor role (Etterson & Shaw 2001; Gienapp *et al.* 2008; but see Bradshaw & Holzapfel, 2006). Changes in species distribution patterns are likely to be the relevant mechanism for species to adapt to climate change (Huntley 2007).

Spatial Conservation Planning needs to act anticipatively to these impacts. Predictive modelling provides the most comprehensive and flexible approach to generating probabilistic projections of species range changes under future climate scenarios (see section 1.5.3.1). The operative value of these "bioclimatic models" resides in the assumption that species distributions are directly dependant on local climate (Walter 1979). At its simplest it involves linking species current distributions with combinations of current climate data, then projecting spatial shifts of these "climate envelopes" using climate change scenario data. This correlative approach has come under criticism (Kearney *et al.* 2010). Aside from the shortcomings that species distribution models enclose for predicting within the same time period (see section 1.5.3.1), cross-time "bioclimatic modelling" is likely to exacerbate them (e.g., Thuiller 2004) and present additional flaws (Sinclair *et al.* 2010; Austin & Van Niel 2011), namely: 1) the impossibility to validate future predictions because there are no data against which predictions of future ranges can be tested (Araújo *et al.* 2005a, but see, Martinez-Meyer *et al.* 2004; Nogués-Bravo 2009; Araújo & Guisan 2006); 2) given that the relationship between a species' occurrence and environmental variables is typically non-linear, projecting likely distributions into novel climate space is problematic (Walker & Steffen 1997; Williams *et al.* 2007; Ackerly *et al.* 2010); 3) climate change is expected to induce non-stationarity of such variables, forcing a different way of dealing with them in models and associated predictions (Conroy *et al.* 2011); 4) models do not incorporate inter and intra-species interactions under different climate change scenarios (Davis *et al.* 1998, but see Araújo & Luoto, 2008); 5) these models assume that a species is in equilibrium with its environment, and therefore, do not consider possible adaptations or tolerance to climate change. They fail to include ecological and evolutionary processes that could allow species to persist in a heterogeneous landscape (Sykes *et al.* 1996; Dawson *et al.* 2011); 6) in their basic implementation, bioclimatic models ignore dispersal restrictions (Higgins *et al.* 2003; Dullinger *et al.* 2004; Neilson *et al.* 2005; Pearson 2006; Midgley *et al.* 2007; Keith *et al.* 2008); 7) there are uncertainties relating to the climate scenario models that influence the outputs of envelope models (Beaumont *et al.* 2008; Moss *et al.*

2010) and the variability in climate change projections among General Circulation Models; 8) there are also uncertainties relating to so-called 'unknown unknowns' where key processes are not yet recognized, understood or incorporated into model structure, or as parameters (Sutherland & Woodroof 2009). Yet such processes may play critical roles in ecosystem dynamics.

Even if a diversity of bioclimatic modelling constructions results in important uncertainties regarding the magnitude and spatial pattern of modelled range changes (Elith *et al.* 2010), evidence shows that models can recover the tendency of range change (i.e., increase or decrease) with reasonable accuracy and these have been reported for a extensive number of species worldwide (Thomas *et al.* 2004; Thuiller 2007). Their implication for conservation planning is considerable (e.g., Araújo *et al.* 2004a), since most established conservation-planning frameworks are based on climatic and biogeographic stability.

1.5.4.1 Spatial Conservation Planning and climate change

Protected areas are the cornerstone of conservation actions. Typically, protected areas are part of a static conservation concept developed to ensure biodiversity patterns and species persistence within a given area. This static approach is problematic given currently predicted long-term environmental changes due to a diverse array of climate-change-induced stresses (Huntley 2007; Araújo 2009). The anticipated changes in species distributions expected under climatic change, coupled with some species inability to genetically adapt to new climatic conditions or migrate to suitable climatic zones, could hinder the ability of protected areas to maintain some habitats and species populations in the future (Peters & Darling 1985; Halpin 1997; Hannah *et al.* 2005; Lovejoy 2006; Hannah *et al.* 2007; Hannah 2008). If climatic alterations take place as predicted, static protected areas may not assure habitat persistence and ecosystem functioning and may not, in the long run, support all the species they were designed to protect.

Anticipative conservation strategies that incorporate uncertainty associated with climate change impacts will be necessary to minimize biodiversity loss (Root & Schneider 2006; Coenen *et al.* 2008). Key components of these "climate change integrated conservation strategies" (Hannah *et al.* 2002) include the use of predictive models of species responses to climate change (Pearson & Dawson 2003), evaluation of projected impacts of climate change over current conservation areas (Araújo *et al.* 2004a) and a flexible rather than static approach to spatial prioritization (Lawler *et al.* 2010), for alternative future climate scenarios (Brooke 2008).

Several recent approaches have been made to assess the risks posed by climate change to theoretical and/or real-world protected areas (Table 1.1). However they have not been explicitly developed to robustly handle different sources of uncertainty altogether. Therefore, at least at regional, continental or global scales some doubt still exist about the extent of the projected impacts, and if protected area performance differ substantially from the unprotected regions (as protected areas are geographically biased, see section 1.3).

Chapter V delivers such an analysis to test in what extent the species occurring within European conservation areas will be affected by a changing climate in the recent future.

Once the existing protected areas do not provide enough area and suitable (climatic) conditions for species survival and reproduction through time, three effective strategies providing adaptive capacity to the biological systems will be imperative. First, increasing the size of protected areas increases the chances they will contain some areas suitable for species whose distributions must shift with a changing climate. This also increases the likelihood of them supporting undisturbed areas (e.g., climate refugia). Second, new protected areas need to be set aside relatively close to existing ones to facilitate inter-reserve movement to better accommodate distributional shifts of species and to enhance micro-evolutionary potential through increased population size and diversity (Hannah *et al.* 2007). Third, suitable inter-reserve connectivity will, in many cases, be facilitated by off-reserve conservation (Heller & Zavaleta 2009). Indeed, because the majority of land in almost all regions worldwide is not in formal protected areas and never will be, how it is managed can have major negative or positive impacts on biodiversity.

A crucial challenge for these approaches is determining where to expand current protected areas, to set aside new protected areas and to site corridors. A few studies have suggested different perspectives to look to this issue (Table 1.2). For the majority of them failure to explicitly acknowledge and treat

uncertainty may lead to sub-optimal decisions regarding species persistence and conservation resources allocation. A multi-species modelling tool accommodating such demands in a cost-efficient manner is therefore needed.

Chapter VI goes in this line. It presents a framework integrating species' modelling tools and network flows to obtain a set of dispersal pathways facilitating species' range shifts triggered by climate change.

Table 1.1 – Main goals, methods and achievements of a small and representative sample of peer-reviewed evaluations of climate change impacts over protected areas.

Reference	Spatial scale	Conservation áreas	taxa	Time-frame	Predictive methodology	Sensitivity analysis	General message
(Halpin 1997)	Global	UNESCO biosphere reserves	Ecoclimatic classes	Determined by emission scenarios	Empirical evaluation of recent past changes	•Greenhouse gas emission scenarios	•Frequency of ecoclimate impacts on reserve areas were generally higher than the global averages
(Rutherford <i>et al.</i> 1999)	South Africa	National designated protected areas	Plants	Mid 21st century	Mechanistic	•None	•About a third of the species are expected to disappear from protected areas
(Scott <i>et al.</i> 2002)	Canada	National designated protected areas	Biomes	2070-2099	Mechanistic	•Greenhouse gas emission scenarios •GCM •Model	•High biome turnover •Increased representation of southern biomes and decreasing of northern biomes
(Burns <i>et al.</i> 2003)	USA	National designated protected areas	Mammals	Determined by emission scenarios	Correlative (using ecosystem predictors)	•None	•High species turnover •Several species negative impacted
(Dockerty <i>et al.</i> 2003)	Great Britain	National designated protected areas	Plants	2020, 2050, 2080	Correlative	•Time periods •Greenhouse gas emission scenarios •GCM	•Spatial variability of expected species trends •High sensitivity of time of early effects across climate scenarios
(Araújo <i>et al.</i> 2004a)	Europe	Theoretical protected areas	Plants	2050	Correlative	•Area selection methods	•Conventional approaches to area prioritization lead to species subrepresentation. More dedicated indices allows higher species representation in the future
(Velarde <i>et al.</i> 2005)	Africa	National designated protected areas	Holdrige Life Zones	2065,2099	Correlative	•Time periods •GCM	•Extent coverage of the life zones within protected areas will lead to significant economic losses
(McClean <i>et al.</i> 2006)	Sub-Saharan Africa	Theoretical protected areas	Plants	2025, 2055, 2085	Correlative	•Time periods •Area selection models •"one for all" and "all for one" regional scope	•The valuation of grid cells enables to obtain sets of priority grid cells less expose to change
(Hannah <i>et al.</i> 2007)	Cape Floristic Region + México + Western Europe	National designated protected areas	Proteaceas + Birds and mammals + Plants	2050	Correlative	•None	•Current protected areas are able to cover the majority of the analysed species in the three regions
(Olson & Lindsay 2009)	USA	National designated protected areas	Breeding birds	2070-2099	Correlative	•Greenhouse gas emission scenarios	•Future priority areas, adequately representing all the species differ from the current protected areas
(Rayfield <i>et al.</i> 2008)	Canada	Theoretical forested areas	American marten	200yr simulation	Spatial explicit stochastic simulation	•Static versus dynamic area selection	•Dynamic protected areas retain more high quality habitat through time
(Hole <i>et al.</i> 2009)	Africa	Important Bird Areas	Africa breeding birds	2025, 2055, 2085	Correlative	•Time periods •Greenhouse gas emission scenarios •GCM •Modelling algorithm	•High species turnover (variable across regions) •Significant species representation
(Kharouba & Kerr 2010)	Canada	National designated protected areas	Butterflies	1900-1930, 1960-1990	Correlative	•Time periods	•Impacts on protected areas are expected to be similar to the unprotected areas
(D'Amen <i>et al.</i> 2011)	Italy	National designated protected áreas and Natura 2000	Amphibians	2040-2070	Correlative	•Greenhouse gas emission scenarios •Ensemble of modelling algorithms •Species dispersal abilities	•Negative impacts for many species •Differential spatial impacts •Need of complementary areas to guarantee future representation
(Hole <i>et al.</i> 2011)	Africa	Important Bird Areas	Africa breeding birds	2025, 2055, 2085	Correlative	•Time periods •Greenhouse gas emission scenarios •GCM •Modelling algorithm	•The extent of climate change impacts over protected areas is linked to a management scheme
(Wiens <i>et al.</i> 2011)	California (USA)	National designated protected areas	Climatic patterns	2038-2069	None	•None	•Disappearing and novel climates are positively biased towards protected areas
(Kujala <i>et al.</i> in press)	Finland	National designated protected areas	Birds	2050	Correlative	•Greenhouse gas emission scenarios •Modelling algorithm	•inverse relation between species cover in protected areas and trends in population status

Table 1.2 – Exemplificative peer-reviewed studies delineating a set of rules to identify the best areas supporting species' range adjustments under climate change.

Reference	Ecological scope	Species distribution data	Dispersal abilities	Model philosophy
(Williams <i>et al.</i> 2005b)	Multispecies	Predicted presence-absences	Dispersal rates	Anticipative complementary-based algorithms
(del Barrio <i>et al.</i> 2006)	Species-by-species	Predicted presence-absences	Spatially explicit simulation using climate and land cover resistance surface	Species-by-species modelling of species suitable habitats through time (mechanistic)
(Strange <i>et al.</i> 2006)	Multispecies	Dynamic predictions using local threats (e.g., climate change impacts)	None	Dynamic (adaptive) optimization model accommodating local threats
(Hannah <i>et al.</i> 2007)	Multispecies	Predicted presence-absences	Subsumed in species distribution data	Anticipative complementary-based algorithms using step-by-step or all-together strategies
(O'Hanley <i>et al.</i> 2007a)	Multispecies	Predicted presence-absences	None	Optimization robust to local ecological devaluation
(Fuller <i>et al.</i> 2008)	Multispecies	Predicted presence-absences	Subsumed in species distribution data	Anticipative optimization model
(Phillips <i>et al.</i> 2008)	Multispecies	Predicted presence-absences or suitability surfaces	Dispersal rates	Anticipative optimization model (network flows)
(Vos <i>et al.</i> 2008)	Species-by-species	Predicted presence-absences	Spatially explicit simulation using climate and land cover resistance surface	Species-by-species modelling of species suitable habitats through time (mechanistic)
(Rose & Burton 2009)	Species-by-species	Predicted presence-absences	Subsumed in species distribution data	Identification of climatic refugia
(Spring <i>et al.</i> 2010)	Habitat-based	None	Using habitat connectivity	Scheduling heuristic to optimize habitat connectivity
(Carroll <i>et al.</i> 2010)	Multispecies	Predicted presence-absences	Species specific kernel using habitat associations	Anticipative heuristic to identify regions with suitable conditions and in close proximity
(Beier & Brost 2010)	Land facets	None	Using spatial surrogates for connectivity	Control of land facet proximity using connectivity surrogates
(Graham <i>et al.</i> 2010)	Multispecies	Predicted suitability surfaces	Viterbi algorithm	Optimization model to design possible past species climate-adaptation pathways
(Game <i>et al.</i> 2011)	Multispecies + geophysical units + refugia	Present-time presence-absence	Environmental connectivity	Anticipative heuristic promoting environmental connectivity and climatic stability

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CHAPTER II

Designing spatially-explicit ecological reserve networks in the presence of mandatory sites

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*"Conservation is a state of harmony
between Men and land."*

Aldo Leopold, 1949

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DESIGNING SPATIALLY-EXPLICIT ECOLOGICAL RESERVE NETWORKS IN THE PRESENCE OF MANDATORY SITES

ABSTRACT

In the selection of reserve networks there are special sites whose ecologic, strategic or morphologic values dictate their inclusion. The existence of regional rare or confined-distribution species is one among other reasons that often determines the existence of such mandatory sites. Moreover, quite often these mandatory sites are located far apart. Although several methods have been proposed to accommodate structural connectivity in reserve selection, they were not devised to deal specifically with such mandatory sites. Those that encourage aggregation of sites by means of criteria incorporated in the objective function do not seem suitable to acquire consistent connectivity levels in the presence of mandatory sites. Methods that enforce “full connectivity” tend to produce long and narrow solutions, which results in efficiency deficits and biological unsuitability, as they force the selection of more sites of less quality to ensure connectivity. Hence specific methods to select ecological reserves when mandatory sites exist are needed. Here we discuss and propose a 0–1 linear programming model to deal with this issue. The model was applied in two data sets of forest breeding birds and butterflies. Its solutions and computational performances are discussed.

INTRODUCTION

In a world of a changing climate and increased human-directed impacts on ecosystems it urges to implement effective measures to protect biodiversity. Reserves should provide representative samples of biodiversity and combine additional biological considerations (Araújo *et al.*, 2002) with socio-economic ones (Williams *et al.*, 2003). Thus, limited resources should be used efficiently, harbouring the maximum diversity, or any other valued conservation feature, with minimum cost or area (Pressey *et al.*, 1993; Margules and Pressey, 2000; Rodrigues *et al.*, 2000). There are multiple methodological issues to consider in the selection and establishment of reserve networks. One issue of concern is the spatial arrangement of protected sites (Diamond, 1975; Margules *et al.*, 1982; Pressey *et al.*, 1997; Margules and Pressey, 2000) which should exhibit high levels of connectivity (Collinge, 1996; Tischendorf & Fahrig, 2000; Calabrese and Fagan, 2004).

Fragmentation as the opposite of connectivity, has impact on biodiversity, increasing isolation of habitats, endangering species and modifying population dynamics (Zidema *et al.*, 1996; Miller & Calle, 2000; Moilanen & Hanski, 2001; Malcolm & ReVelle, 2002). It may cause negative effects on species richness (Mace *et al.*, 1998) by reducing the probability of successful dispersal and establishment of populations (Brokaw, 1998), by limiting the capacity of a patch of habitat to sustain resident populations and, or by enhancing vulnerability of small fragmented populations to stochastic events (Kapos *et al.*, 2000) (but see, Araújo *et al.*, 2004 for a discussion on possible benefits of scattered areas on climate change). Connectivity has been understood as functional or structural according to whether ecological functions or only inter-site configurations are considered (Tischendorf & Fahrig, 2000; Calabrese and Fagan, 2004).

Functional connectivity explicitly accounts for species' specific responses to habitat, where structure and quality of both the matrix and the reserve network influence the conservation value of selection units (e.g., Cabeza and Moilanen, 2001; Moilanen & Cabeza, 2002; Cabeza, 2003; Westphal & Possingham, 2003; Cabeza *et al.*, 2004; Moilanen, 2005; Williams *et al.*, 2005; Moilanen & Wintle, 2006; Van Teeffelen *et al.*, 2006). It can be interpreted as an indicator of the dispersive aptitudes of populations for the establishment of genetic, demographic and energetic fluxes along the landscape, which are relevant for their persistence (Hanski, 1999; Macdonald & Johnson, 2001). Reserve selection methods implementing this type of connectivity should be established coupled with multi-representation targets to interface with the spatial population dynamics (Pressey *et al.*, 2003; Malcolm & ReVelle, 2005).

Structural connectivity is a spatial feature which only regards to the patterns of distribution of sites independently of any species' specific dispersal ability (Opdam *et al.*, 2003). The persistence of biological

units and ecosystem processes can benefit from structural connectivity (Lande, 1988; Frank & Wissel, 1998; Hanski & Ovaskainen, 2000). In particular, aggregation and compactness are likely to reduce edge effects (enhanced disturbance or predation, invasive species, changes in abiotic conditions, see, Gaston *et al.*, 2002).

Several methods have been proposed to accommodate structural connectivity in reserve selection. Some of these formulations include cost minimization options together with constraints forcing the existence of buffer zones surrounding certain selected sites (Williams & ReVelle, 1998; Clemens *et al.*, 1999); the maximization of the number of adjacent pairs of sites (Nalle *et al.*, 2002); enforcement of proximity between pair-sites, with the requirement that the sites representing a species will not be farther apart than a stated distance (Williams, 2006); minimization of the distances between pairs of sites to be included in the network (Nicholls & Margules, 1993; Briers, 2002; Önal and Briers, 2002), the summed distance between all pairs of sites (Briers, 2002; Nalle *et al.*, 2002), the maximum distance between sites (Önal & Briers, 2002), the boundary length, a measure of compactness, of a reserve network (Fischer and Church, 2003, 2005; Önal & Briers, 2003), or a combination of boundary length and total area (Possingham *et al.*, 2000; McDonnell *et al.*, 2002). All these models treat connectivity as a quantified target incorporated somehow in the objective function. Stricter proposals by Williams (2002), Cerdeira *et al.* (2005), Cerdeira & Pinto (2005), Önal & Briers (2005, 2006), Fuller *et al.* (2006) seek to identify “fully connected” reserves (i.e., consisting of a unique connected cluster) of minimum size, satisfying the species representations requirements.

Functional and structural responses may differ (With & King, 1997; Pimm & Lawton, 1998) as functional solutions may not be structurally connected, and vice versa. Yet, there are situations where the use of reserve selection methods based on structural connectivity may lead to networks that are functionally well connected. For example, when one wants to protect a large set of species belonging to the same functional group (i.e., with similar habitat response mechanisms), general assumptions can be made to circumvent the lack of information on effective ecological aptitudes of individual species, providing the habitats where they are more likely to disperse. Accordingly, when functional connectivity is intended but no practical approach is available, structural connectivity may be used, supplying robust solutions in terms of biological value.

The objective of this study is to develop a model for selecting reserve networks, which incorporates structural connectivity meant to operate in situations where special sites considered as mandatory sites exist. Mandatory sites are commonly present in the management of ecological reserves. This follows, among other reasons, from being highly irreplaceable for the protection of species (*cf.* Pressey *et al.*, 1994), being occupied by source populations, being refuge areas where species can survive extreme environmental conditions, or being central or peripheral in respect to the species' spatial distribution (Gaston *et al.*, 2002). Although, the inclusion of mandatory sites seems the least of the problems, as the selection process has no option to drop them out, the spatial configuration of the resulting reserves will be strongly conditioned by their presence. The existence of mandatory sites, particularly when distant from each other, may deteriorate the performance of existent approaches which account for structural connectivity to identify spatially-coherent reserve networks. Indeed, the “fully connected” models (Williams, 2002; Cerdeira *et al.*, 2005; Cerdeira & Pinto, 2005; Önal & Briers, 2005, 2006; Fuller *et al.*, 2006) will outcome long and narrow spatial structures. As a result one loses efficiency (Pressey *et al.*, 1994) and biological value by forcing the selection of more sites of less quality (Williams, 1998; Woodroffe & Ginsberg, 1998). Methods that search for efficient connected solutions by means of criteria incorporated in the objective function also do not seem suitable to acquire consistent connectivity levels in the presence of mandatory sites. For example, if mandatory sites would be quite apart, the minimum diameter reserve model of Önal & Briers (2002) would probably select the remaining sites somewhere on the convex hull defined by the mandatory sites. If minimization of the summed distances between all pairs of selected sites (e.g., Briers, 2002; Nalle *et al.*, 2002) was applied, the most probable solutions would configure clusters of selected sites equidistant from the mandatory sites, leaving them isolated and vulnerable. Models that seek boundary-length minimization (e.g., Fischer & Church, 2003, 2005; Önal & Briers, 2003) do not take special attention to the mandatory sites, and clusters of the remaining selected sites would probably be formed somewhere in the focal space.

It thus seems to be important to develop specific methods that explicitly account for the existence and location of these mandatory sites to induce spatial coherence and enhance the efficiency on the resulting reserve networks.

Our proposal is based on the idea that, for spatially-coherence, it may be realistic to let mandatory sites act like independent “attractive centres” allowing aggregation of different clusters around them. Ideally, it would be desirable to find efficient networks where fragmentation is confined to a number of clusters limited by the number of mandatory sites. This may reverse edges effects, encouraging the buffering and shielding of mandatory sites, which by their special character may be considered vulnerable.

We present and discuss a 0–1 linear model that goes in this direction. An application with two data sets is performed and reports on computational experiments to access the aptitude of the model are given.

MATERIALS AND METHODS

Data

To access the ability of the model we worked with two datasets. One data set (data from Standley *et al.*, 1996) represents the distribution (i.e., presence/absence records) of 118 species of forest breeding birds in the Berkshire's County, UK, on a grid map consisting of 391 (2 x 2 km) eligible parcels. The other set (data from Sawford, 1987) represents the distribution of 45 species of butterflies within 496 (2 x 2 km cells) eligible sites from Hertfordshire's County, UK.

We ranked the species according to their increasing number of occurrences in the landscape to determine a set of rare species (top 25%). This resulted in 30 rare species of forest breeding birds and 12 rare species of butterflies. The most frequent of the rare forest breeding birds occurs in 36 sites (9.2% of study area), and the most frequent rare butterfly species is presented in 14 sites (2.82% of study area). We assigned single representation targets (i.e., protection of at least one population) for the common (non-rare) species, and larger representation targets for the rare species as described below.

Mandatory sites result from a number of different reasons. However, in our computational experiments only those sites that become irreplaceable for species to be represented according to their targets are mandatory.

A first approach to deal with mandatory sites

We aim to develop a method to select sites satisfying species representation targets, and which accounts for connectivity around the mandatory sites. Ensuring species representation targets by means of integer linear programming can be straightly settled with

$$\sum_{i \in V_s} x_i \geq t_s, \text{ for every species } s \quad (1)$$

$$x_i \in \{0,1\}, \text{ for every site } i \in V \quad (2)$$

where V is the set of all candidate sites, $V_s \subset V$ is the set of sites where species s is represented, $t_s \geq 1$ is the specific target representation required for species s , and the 0-1 variable x_i indicates whether site i is selected ($x_i = 1$), or not ($x_i = 0$). To guarantee that the solutions include all the mandatory sites the equations

$$x_i = 1, \text{ for every mandatory site } i \quad (3)$$

are added.

If maximum efficiency disregarding the spatial aspects was intended, the objective function would be $\min \sum_{i \in V} x_i$ and the optimal solutions would have the minimum number of sites. When $t_s = 1$ this is the well known set covering problem (Cocks & Baird, 1989). A reasonable approach to enhance some level of connectivity when dealing with mandatory sites is to consider each one as an “attractive centre” for the remaining sites that will be selected to represent species. A simple procedure in this direction consists in minimizing the sum of distances from the selected sites to their nearest mandatory site. The resulting model is (1)–(3) with the objective function

$$\min \sum_{i \in V} D_i x_i \quad (4)$$

where D_i is the distance from site i to its nearest mandatory site.

This model certainly encourages the selection of sites around the mandatory sites. However, no other spatial relationship between sites is taken into account. For example, despite being considerably different as far as aggregation is concerned, the objective function (4) retrieves the same value for the two configurations in Fig. 1.

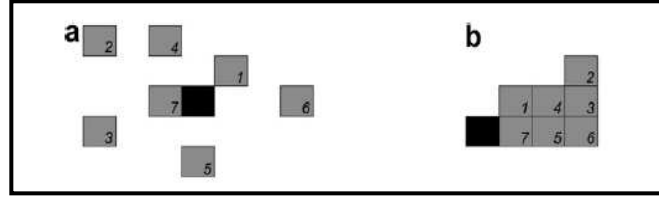


Fig. 1 – A fragmented (a); and an aggregated/connected (b) hypothetical configuration of a reserve system, each consisting of one mandatory site (dark square) and 7 other sites numbered 1–7 (gray squares). Both present the same value under the objective function (4).

The proposed mandatory-based model

If clustering of sites is important, as it happens when one intends to avoid edge effects, we would like the model to be able to distinguish the more aggregated configuration in Fig. 1b from the one in Fig. 1a. Therefore, we devised a way to give the model enough flexibility to differentiate between these patterns, turning those which are less fragmented more appealing. This was achieved with an objective function which associates to each site i the distance to the nearest selected site somewhere “in between” i and its nearest mandatory site. (The meaning of “in between” a site and its nearest mandatory site will be discussed later.)

To illustrate this idea consider the configurations in Fig. 2. The objective function (4) weights the set of sites in Fig. 2a as the sum of their distances to their nearest mandatory sites. Our suggestion is to assign to this set a weight equal to the sum of the distances corresponding to the arcs in Fig. 2b. The arc originating from site i links i to its nearest selected site “in between” i and its nearest mandatory site (Fig. 2b).

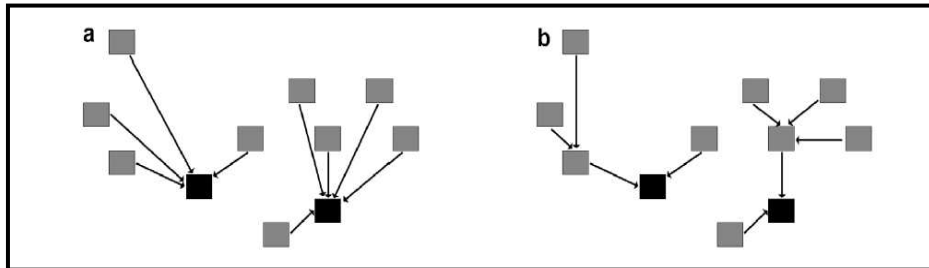


Fig. 2 – Illustration of different spatial layouts of the objective function (4) (a) and (9) with d_i as in (10) (b). The first one is related to the minimization of the summed distance to mandatory sites (distance-to-mandatory metric), the second one with the minimization of the summed distance to the nearest neighbor site (mandatory-based metric). Dark squares represent mandatory sites, gray squares represent selected sites, edges' length refers to distances.

Let H be the set of all mandatory sites. For each site $i \in V \setminus H$, let $h(i)$ be its nearest mandatory site (if there are more. Several possibilities for $V(i)$ can be envisaged. In our computational experiments we defined $V(i)$

to be the set of sites different from i in the rectangle having i and $h(i)$ as opposite vertices. (Another possibility could be $V(i) = \{j: \max\{d(i,j), d(j, h(i))\} < D\} \cup \{h(i)\}$, where $d(u,v)$ is the distance between sites u and v .)

We aim to introduce in the model (1)–(3) new variables that, for each chosen site i , identify the selected site j in $V(i)$ which is closest to i .

For this purpose we consider the variables y_i^j satisfying the constraints

$$\sum_{j \in V(i)} y_i^j = x_i, \text{ for every site } i \in VH \quad (5)$$

$$y_i^j \leq x_j, \text{ for every site } i \in VH \text{ and } j \in V(i) \quad (6)$$

$$y_i^j \in \{0,1\}, \text{ for every site } i \in VH \text{ and } j \in V(i) \quad (7)$$

In the presence of (7), each Eq. (5) ensures that, when site i is selected (i.e., $x_i = 1$) there will be exactly one site $j \in V(i)$ for which y_i^j will be equal to 1 and, in case i is not selected (i.e., $x_i = 0$), for every j in $V(i)$, y_i^j will be equal to 0.

Inequalities (6) restrict sites j in $V(i)$ for which y_i^j can take value equal to 1, to those sites that have been selected (i.e., $x_j = 1$).

When $x_i = 1$, to guarantee that the unique site j in $V(i)$ for which $y_i^j = 1$ will be the one closest to i , define

$$d_i = \sum_{j \in V(i)} d(i, j) y_i^j, \text{ for every site } i \in VH \quad (8)$$

and let

$$\min \sum_{i \in VH} d_i \quad (9)$$

be the objective function.

Indeed, if in any solution $y_i^j = 1$ and $x_k = 1$, for some $k \in V(i)$ such that $d(i, k) < d(i, j)$, then setting $y_i^k = 1$ and $y_i^j = 0$ would decrease d_i and consequently the value of the objective function.

With this model, contrarily to the previous one, the choice of a site depends on the spatial distribution of other selected sites and not only on the location of its nearest mandatory site. When a site i is chosen it will play, in some sense, the role of a mandatory site making the sites which are close to i more attractive for selection. Although in general this is a desirable feature to promote the aggregation of the chosen sites, if the distance D_i from i to $h(i)$, is large this can contribute to the formation of clusters far from every mandatory site.

In addition, the model does not explicitly enhance the search for highly efficient solutions. As an example, consider four consecutive sites on a vertical or horizontal line of a grid, and suppose that one of the extreme sites of that segment is a mandatory site. From these four sites only the two extreme ones in the line segment contributed to the objective value (9) with three units of distance. The remaining sites inflate the cost and are not considered in the model's objective.

These drawbacks can be overcome by taking as the objective function a convex combination of the objective functions of the two previous models (4) and (9) linked with (8). Such function will account, not only for the distance between a site and other selected sites, but also for the distance between that site and its nearest mandatory site. This amounts to replace the definition (8) of d_i by

$$d_i = \sum_{j \in V(i)} (\alpha d(i, j) y_i^j + \beta D_i) y_i^j, \text{ for every site } i \in VH \quad (10)$$

with $\alpha, \beta \geq 0, \alpha + \beta = 1$.

The 0–1 linear formulation for the resulting model is therefore (9), (1), (2), (3), (5), (6), (10) and, interestingly, instead of (7) stating that every variable y_i^j must be 0 or 1, it can be proved that only the non-negative constraints

$$y_i^j \geq 0 \text{ for every site } i \in \mathcal{V}H \text{ and } j \in \mathcal{V}(i) \quad (11)$$

should be added. Indeed, take any solution x, y of the above model with $y_i^{j_1}, y_i^{j_2}, \dots, y_i^{j_k} > 0$ summing 1. If j_s is a site, among $j_1, j_2, \dots, j_k$, for which the minimum value of $d(i, j_1), d(i, j_2), \dots, d(i, j_k)$ is attained, then the value of (9) will not increase and no constraint will be violated by letting $y_i^{j_s} = 1$ and $y_i^{j_l} = 0$, for every other $l = 1, 2, \dots, k$ different from s . This simplification speeds up the computational procedure.

This model permits to balance clustering and proximity around the mandatory sites. Clustering is enhanced by increasing the values of the parameter α . The weights assigned to β regulates levels of scattering of sites within the neighbourhood of mandatory sites.

Computational tests were performed on a computer with an Intel Pentium IV, 3.20 GHz processor and 504 MB RAM. CPLEX 9.0 was used to solve the integer programming problems.

RESULTS

We carried out several computational experiments with the forest breeding birds and the butterfly data sets with different representation targets for the rare species. Here we report results obtained requiring at least three sites for each rare species or, in case the species occurs in less than three sites, all the sites where the species is represented.

To provide a benchmark for efficiency, the solutions from the new developed mandatory-based (MB) model are compared with those of maximum efficiency (ME), in which species' representation requirements and inclusion of all mandatory sites are accomplished within the minimum number of sites. Fig. 3 shows the ME and the MB solutions obtained for each data set, and Table 1 describes some of their properties. Besides giving the number of sites, some measures are displayed to evaluate their spatial configurations. The boundary/area ratio was used as a measure of compactness. To assess the proximity of the selected sites from their nearest mandatory sites, the sum and the average of the distances from each site and its nearest mandatory site were computed. To analyse the performance with respect to the metric developed within the MB model, the value of (8) (the sum of distances of the edges that link each selected site to its nearest neighbour) is given. This metric can somehow rate the structural connectivity of the outcomes. Since this value depends on the number of selected sites, we also present the result of dividing the metric by the number of selected sites. We refer to these two values as the MB metric and the average MB metric, respectively.

The representation targets used for rare species have determined the existence of 10 and 11 mandatory sites, which are obligatory for the achievement of bird and butterfly species' representation, respectively.

ME solutions, shown in Fig. 3, consist of 23 and 20 sites scattered over the study area, and fail to guarantee a reasonable level of protection by buffering effects of close-by selected sites. The MB model was developed to promote buffering around mandatory sites. For breeding birds protection 30 sites were selected (Fig. 3) which is an increase on reserve size when compared with the ME solution. However (see Table 1), this additional number of sites decreases the boundary/area ratio index of compactness (1.60 vs. 1.91), better countering edge effects. The overall distance of sites to mandatory sites is 85.90 km (less 46% that the minimum set representation solution). When averaged by the number of sites selected this

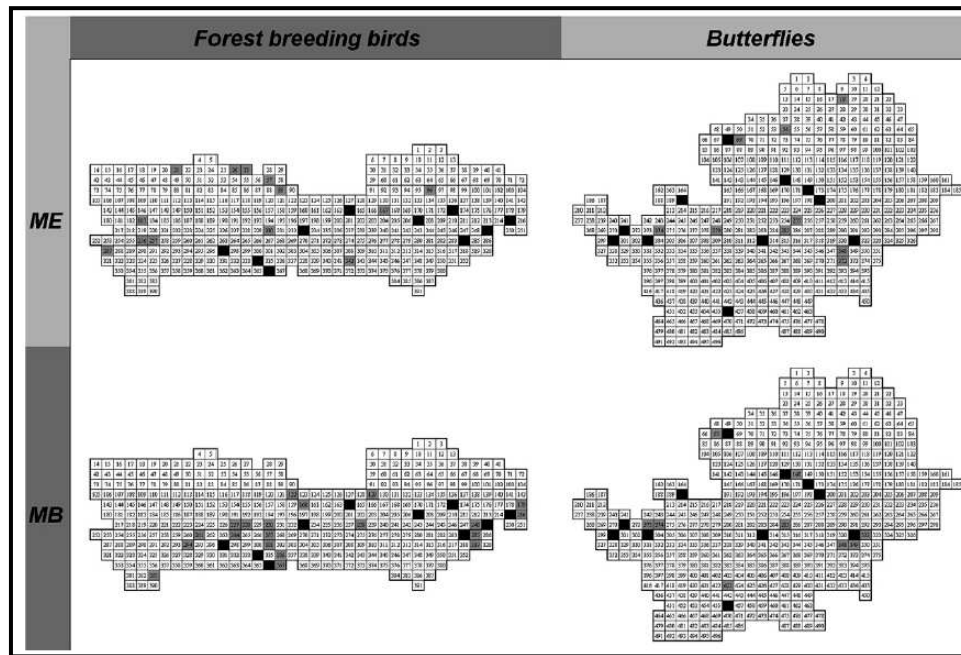


Fig. 3 – Selected grid cells under two tested models (MS: minimum set; MB: mandatory-based) applied over the forest breeding birds' and butterflies' data sets. Black cells indicate mandatory sites and gray cells other selected sites.

reduction passes to 65%. Curiously, for butterfly species' the MB model has delivered a solution with 20 sites to protect, equalling the ME solution (Fig. 3). The values of the spatial descriptors for the ME and MB solutions compare similarly as for the forest breeding birds (Table 1), which again indicates a better spatial coherence of the later. The differences between these values are mainly due to the rearrangement of three distant isolated sites (18, 54 and 279) of the ME solution (Fig. 3). The boundary/area ratio decreases from 1.90 of the ME solution to 1.65 of the MB solution. The sum of distances to mandatory sites is 59.48 km and 24.13 km for the ME and the MB solutions, respectively. The averages show the same proportion, since both solutions have the same number of sites.

With respect to the MB metric, the MB and the ME solutions applied over the breeding birds data set score 109.21 km and 172.74 km, respectively. This indicates that an improvement on proximity between sites was accomplished. One third of the sites of the MB solution are selected in a small region defined by the rectangle with cells 226 and 367 as opposite vertices (Fig. 3). This means that several sites were chosen close together, thus contributing to reduce the value of (8). An accumulation of selections also occurs in the right-hand side near the three mandatory sites 215, 249, 284. All mandatory sites, but 173 and 209, seem to be somehow reasonable protected by nearby sites. The averaged MB metric gives mean distance per site of 5.46 km (less 59% than ME solution), showing a better individual-site performance with respect to structural connectivity. Similarly, the ME and MB butterflies networks presents values for MB metric of 61.48 km and 28.13 km, respectively, and average MB metric values of 6.83 km/site and 3.12 km/site (Table 1).

ME models produced for both data sets have run very quickly, spending 0.02 s and 0.03 s. While the MB solution for the butterfly species' network was achieved within 0.08 s, the breeding birds' MB solution required 0.84 s, which is about 40 times more than the computational time needed to get the ME solution (Table 1). This is still, however, quite acceptable when applied to such a medium-sized data set.

DISCUSSION

Here we show that when explicitly accounting for the existence of mandatory sites, the proposed MB model can be a suitable tool to produce reserve networks designed to face edge effects and nearby matrix deregulations, among other stressors. This may bring a greater expectation of conservation success when planning for reserve selection.

Table 1 – Morphometric and spatial descriptors of the solutions produced by the two tested models (ME model and MB model) applied on forest breeding birds' and butterflies' data sets.

	Forest breeding birds		Butterflies	
	Solution ME	Solution MB	Solution ME	Solution MB
No. sites	23	30	20	20
No. mandatory	10		11	
Mandatory	104;173;207;215;233;249;294;334;365		68;100;147;172;271;300;313;321;450	
Boundary área (km ²)	1.91	1.60	1.90	1.65
DM (km)	159.44	85.90	59.48	24.13
Averaged DM (km/site)	12.26	4.30	6.61	2.68
MB (km)	172.74	109.21	61.48	28.13
Averaged MB (km/site)	13.29	5.46	6.83	3.12
CPU time (s)	0.02	0.84	0.03	0.08

No. sites: number of selected sites; No. mandatory: number of mandatory sites; mandatory sites: enumeration of the mandatory sites; boundary/area length: ratio between the outside perimeter of the reserve network and its area; DM: summed distance to mandatory sites (see Fig. 2a); averaged DM: averaged distance to mandatory sites, DM/No.sites; MB: mandatory-based metric: distance from each selected site to its closest neighbour (see Fig. 2b); averaged MB: averaged mandatory-based metric, MB/No.sites; CPU time: computational time.

A strong point of the MB approach resides on the ability to accommodate three attributes comprised within reserve selection (efficiency, inter-site distance, and protection of important sites), in a simple linear mathematical description. This representation seems to allow effective computations for at least medium-sized data sets.

The MB model is especially relevant for species exhibiting a metapopulational structure, which seem to be the case of many butterfly species (Thomas & Hanski, 1997; Hill *et al.*, 2001) and forest birds (Hinsley *et al.*, 1995; Fahrig, 2002). Their persistence resides in balance between extinctions and colonizations, which turns species difficult to persist if their populations are fragmented. Moreover, the high ecological value of source areas (i.e., where immigration fluxes guarantee most of the species' survival, Hanski & Ovaskainen, 2000), make those special sites potential candidates to be considered as mandatory.

Despite its positive aspects, several concerns regarding the MB model should be pointed out.

First, it could be argued that since the model incorporates the distance from each site to its nearest predetermined mandatory site, a network with one or a few remote sites may be preferred to an alternative with several tightly packed sites far from the mandatory site. This problem may be circumvented by tuning the α and β parameters in (10). Increasing α one can accent the distance between sites. Increasing β significance is given to the proximity to the nearest mandatory site. To judge on the differences between solutions, sensitivity analysis can be performed. Varying levels of aggregation and proximity stakeholders intervene on the selection process, allowing the guidance to more conceivable solutions.

A second aspect concerns an issue that arises upstream on the conservation planning process which is the identification of the mandatory sites (Pressey *et al.*, 1993). While the assumption of the pre-designation of these areas may be conceivable (e.g., "gap analysis", and the extension of existent reserve networks, Scott *et al.*, 1993), locating "prioritized" areas, i.e., irreplaceable areas, may be itself a difficult task (Pressey *et al.*, 1994). Indeed, choices can be grounded on a variety of actors such as location relative to sites already "reserved", cost, condition, and the occurrence of special features like rare species, distinctive landscapes or recreational opportunities. Each choice alters the representation of features, their assemblage patterns and therefore, the potential contribution of all the "unreserved" sites. If mandatory status for site i is assigned, two separated approaches are conceived regarding the MB model "protocol": (1) explicitly acting as a mandatory site of the MB model, i.e., making $x_i = 1$ and adding i to the list H of mandatory sites; or (2) forcing i to present by means of $x_i = 1$ but not including i in H , and therefore not being designated to act as an attractive area for the selection of other neighbour sites. Both approaches are expected to retrieve different solutions, and their viability is somehow linked with the protection status we want to give to each specific mandatory site. Once again we emphasize the aptitude of the model to deal with this issue, by allowing some degree of freedom for choices and assumptions.

The third issue relates to the identification of sites that should serve as the nucleus of an optimal cluster, which may be a complex problem. According to Shafer (1999), priority sites may not necessarily serve as

nucleus of clusters. In our model these attractive nucleus are identified with the mandatory sites. In point 2 of the previous comment, we explain how the MB model can handle this situation. It may also be desirable that certain non-mandatory sites perform the role of “attractors”. This can be easily achieved by including these sites in H .

CONCLUSIONS

The optimal solution may not necessarily be the ultimate plan selected by the resource manager. However, it provides the baseline of what can be accomplished at different investment levels against which alternative selections meeting additional objectives can be compared.

The present model is particularly useful to be applied on fragmented landscapes for which information about species specific response to fragmentation is not available. It is not intended to be the final answer along the implementation step of conservation planning. For the establishment of reserves suitable for the long-term persistence of biodiversity many elements, including those resulting from deep knowledge of the region, should be considered. Many land managers are either unaware of the methods, or perhaps more often, unaware of how they can be used to get the most from their local expert knowledge. Nevertheless, we trust that the outcomes of the model can provide a valuable basis to assist stakeholders in conservation planning. Hence, people will appreciate that models are just a tool for getting the most out of the assumptions on a quantitative way. This kind of decision support management makes area selection easily accessible and widespread, improving the chances of preserving the most of biodiversity.

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CHAPTER III

Linking like with like: optimising connectivity between environmentally-similar habitats

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*“Everything is vague to a degree you
do not realize till you have tried to
make it precise. “*

Bertrand Russell, 1918

LINKING LIKE WITH LIKE: OPTIMISING CONNECTIVITY BETWEEN ENVIRONMENTALLY-SIMILAR HABITATS

ABSTRACT

Habitat fragmentation is one of the greatest threats to biodiversity. To minimise the effect of fragmentation on biodiversity, connectivity between otherwise isolated habitats should be promoted. However, the identification of linkages favouring connectivity is not trivial. Firstly, they compete with other land uses, so they need to be cost-efficient. Secondly, linkages for one species might be barriers for others, so they should effectively achieve conservation targets. Thirdly, detailed information on the auto-ecology of most of the species is lacking, so linkages need being defined based on surrogates. In order to address these challenges we develop a novel framework to optimally link environmentally similar habitats. The assumption is that species with similar ecological requirements occupy the same environments, so environmental similarity provides a rationale for the identification of the areas that need to be linked. The identification of cost-efficient linkages accounting for barriers can be viewed as a new variant of the minimum Steiner tree problem in graphs, and to this end a heuristic algorithm that is capable of handling large datasets is presented. To illustrate the framework we identified linkages between environmentally-similar protected areas in the Iberian Peninsula. The Natura 2000 network is used as a positive 'attractor' of links while the human footprint is used as 'repellent' of links. For comparison, two types of networks are identified: networks aiming at linking environmentally-similar protected areas, termed as functional networks; and networks aiming at linking protected areas without consideration of environmental similarity between areas, termed as structural networks. Although functional networks present greater area requirements than equivalent structural approaches, higher conservation gains are expected by avoiding environmental barriers for some habitat types.

INTRODUCTION

Habitat fragmentation ranks among the highest threats to global biodiversity (Butchart *et al.* 2010; IUCN 2010). To minimise such threat, the identification of linkages allowing species dispersal between areas of high conservation value has been proposed (Fahrig & Merriam 1994; Hanski 1999). The underlying idea is that by promoting species movement, connectivity facilitates the rescue of small populations from local extinction (due to demographic or environmental stochasticity) while promoting the recolonization of suitable habitats (Bull *et al.* 2007). These mechanisms contribute to an increase of occupied areas, which in turn enhance species persistence and conservation effectiveness. Although a multitude of methods in conservation planning have been suggested to capture connectivity (e.g., Cerdeira *et al.* 2005; Onal & Briers 2005; Williams *et al.* 2005; Alagador & Cerdeira 2007; Minor & Urban 2008; Cerdeira *et al.* 2010), none has been specifically developed to use readily-available environmental data.

Connectivity measures provide estimates of how easy or difficult it is for a species to move across the landscape (Taylor *et al.* 1993). Common assessments of connectivity have been performed using structural or functional approaches. Structural connectivity deals with landscape patterns and configurations (Beier & Noss 1998; Goodwin 2003; Kindlmann & Burel 2008), focusing on the topological relationships among habitats (e.g., habitat corridors, ecological networks, amount of natural habitat, distances between natural habitat areas). Functional connectivity focuses on a range of processes and mechanisms determining the movements of species, such as matrix permeability, local subpopulation dynamics, maximum dispersal distance (Goodwin 2003; Belisle 2005; Chetkiewicz *et al.* 2006; Boitani *et al.* 2007; Vogt *et al.* 2007; Kindlmann & Burel 2008).

The relation between structural and functional connectivity is not trivial. It is possible to have high functional connectivity in a physically fragmented landscape with low structural connectivity, as long as most parts of the landscape support the ecological processes of interest (Taylor *et al.* 2006). Conversely, a structural connection may contain barriers for biodiversity flows (i.e., species movement, gene flow). Such barriers may be physical (e.g., topographic elements), environmental (e.g., environmentally-

unsuitable areas), or biotic (e.g., occurrence of predators or competitors like invasive species) (Goodwin 2003). It is generally accepted that because functional connectivity deals more directly with the ecological processes affecting species population dynamics, a functional framework for connectivity is more likely to promote biodiversity resilience and persistence than a structural one. However, because functional approaches are typically species specific, there are several cases where they cannot be applied since the relevant biological traits, including dispersal abilities, are commonly unavailable for large numbers of species (Chetkiewicz & Boyce 2009). To address such difficulties we propose a framework that uses widely available environmental data as a surrogate of landscape capacity for biodiversity flows.

The framework consists of: a) identification of environmentally-similar habitats (expected to accommodate groups of species with related environmental requirements); b) identification of environmental barriers (i.e., regions with a very distinct “environment” from the environmentally-similar areas to be linked), and; c) selection of cost-efficient linkages between environmentally-similar habitats, free from environmental barriers (i.e., not including regions environmentally distinct from the habitats to be linked). We handle a) and b) using cluster analysis and we tackle c) using a heuristic that treats the problem as a variant of the minimum Steiner tree (MST), which is a difficult (NP-hard; Garey & Johnson 1979) and classical optimisation problem in graphs (Du & Hu 2008).

We illustrate the framework using climatic data as a surrogate for the delineation of regions with biogeographical significance, the Natura 2000 network as a positive ‘attractor’ for the establishment of links between protected areas, and the Human Footprint Index as a ‘negative’ attractor of such links. We compare the outcomes from this approach, termed here as functional because it introduces biological criteria into the rules for connecting protected areas, with the outcomes of links that do not include such biological criteria (i.e., environmental data) and, as such, are termed structural.

METHODS

The framework is illustrated using the Iberian protected areas network as the areas to be connected. The region includes 580,696 grid cells (cells herein) resampled at UTM 1 km x 1 km. We considered 681 protected areas encompassing a wide range of national and international conservation conventions, and covering 80,871 cells. We assumed Natura 2000 to act as a positive attractor for the use of unprotected cells and therefore we associate, to each unprotected cell s , a “cost” ($c(s)$) proportional to the cell’s fraction not covered by Natura 2000. Thus, $c(s)=0$ for cells s completely covered by Natura 2000 sites. The reason why Natura 2000 sites are seen as positive attractors is because these areas are already committed to conservation and therefore implementation of conservation actions, such as the establishment of linkages between protected areas, are expected to be easier than with non-classified sites. Each unprotected cell was also associated with an index of human impact (the Human Footprint Index, $hf(s)$; Sanderson et al 2002), which is treated as a negative attractor; in practice, above a given value of human footprint it is assumed that cells are highly resistant to species movements and they are excluded as candidates for the establishment of links. Four climatic variables (averaged over 1961-1990) were selected for the climatic characterization of the Iberian Peninsula: the monthly maximum temperature, the monthly minimum temperature, total annual precipitation and the standard deviation of the monthly minimum temperature (see section 1 on Supplementary Material for details).

Environmental classification of protected areas

We used Principal Components Analysis (PCA) to reduce the dimensionality and the correlative effects of the raw climatic data. We retained the two PCA components that explained the greatest proportion of the variation in the data. These axes were then used to classify the Iberian Peninsula into areas sharing similar climates (see details on section 2 of Supplementary Material). Specifically, we computed the arithmetic mean of the two PCA components across all the cells in each individual protected area (i.e., a centroid). These centroids were chosen as operational units for the cluster analysis. We developed a k-means algorithm (Fielding 2007) to organize protected areas into homogeneous climatic classes (i.e., minimizing the summed Euclidean distances of each class-member to its respective class-centroid). The algorithm is a simulated annealing approach (Aarts et al. 1997), which, at each iteration, randomly selects

a protected-area centroid and considers the possibility of its allocation in a different class. We used 10,000 iterations for each 50 uniformly selected initial classification-seeds, and saved the best solution. The number of climatic types ($k=4$) was selected a priori to limit the number of climatic clusters in the Iberian Peninsula (i.e., alpine, continental, Mediterranean, and oceanic), in line with the Koppen-Geiger climatic classification for the region (Peel et al. 2007).

Identification of barriers

We considered two types of barriers. Areas with high human footprint were deemed highly resistant to dispersal, representing barriers for the movement of species. We termed these areas landscape barriers. We set a threshold, H , and excluded as candidate areas for linkages between protected areas the cells, s , for which $hf(s) > H$. We used $H \in \{50, 60\}$, as discarding cells with $H < 50$ would retrieve an excessively fragmented landscape and integrating cells with $H > 60$ could result in highly disturbed areas to be part of linkages (Table S3.1 and Fig. S3.2 on Supplementary Material).

We delineated the environmental barriers as follows. The centroids for each climatic class in the final cluster solution were used as archetypes of the climate within its class, and the Euclidean distances from the climate conditions of each cell (in the matrix and in protected areas) to the centroid of each class were computed. This defines k values, $d_i(s)$, for each cell, expressing the dissimilarity of cell s to every climatic class i .

Since we aimed to link environmentally similar protected areas using cells that do not significantly differ from the mean climatic conditions of protected areas in each climatic type, we set a threshold value B_i assuming that cells with $d_i(s) > B_i$ are environmental (climatic) barriers, not adequate to connect protected areas of class- i . We defined B_i accordingly to two scenarios. In the first, B_i was defined as the largest dissimilarity $d_i(s)$, among the protected cells s in every protected area of class- i . In the second scenario, the barriers for class- i were established as the 25% of the cells s not belonging to protected areas of class- i , with the largest dissimilarities values $d_i(s)$, i.e., B_i was set as the third-quartile of $d_i(s)$ (Fig. S3.1 on Supplementary Materials).

Connectivity algorithm

Linking at minimum cost protected areas within class i with no environmental barriers for that class, is a new variant of the (node weighted) Minimum Steiner Tree (MST) problem in graphs, where protected areas act as terminal nodes. For this variant, we developed a heuristic based on the (node version of) the minimum spanning tree approach for the MST problem (see Du & Hu 2008). First, a permutation of the climatic classes is defined, and the first class of the permutation (say class i) is considered. Next, the minimum cost paths (*min* cost paths: Dijkstra 1959) between every pair of protected areas in class- i is computed accounting for cells' costs. These *min* cost paths are then used to weight the edges of a complete graph whose nodes represent protected areas of class- i , and the minimum spanning tree for this graph (Kruskal 1956; Prim 1957) is obtained. The respective min cost paths were saved. The algorithm advances to the next class in the permutation using the same previous procedures but redefining costs to zero on the currently selected cells. Once all protected area classes have been considered, a procedure to eliminate redundant cells was applied to turn minimal the current solution (i.e., removing any cell from the minimal solution disconnects two protected areas of the same class). We applied this procedure for every permutation of the k classes and we saved as the final solution the best among the $k!$ solutions obtained (see a schematic diagram of the heuristic in Fig. 1).

Since the algorithm traces connectivity taking into account a continuous surface of climatic dissimilarity to a reference classification of protected areas, we call their solutions functional. To operate under a structural framework of connectivity we used the same algorithm, but assuming that all protected areas belong to the same climatic class and thus ignoring climatic barriers.

Depending on the specific parameterization of climatic barriers (B_i) and the human footprint threshold (H), pairs of protected areas of the same class might not be linked in the final solution. This happens when all paths connecting two protected areas belonging to some class- i include some cell, s , with $d_i(s) > B_i$ or

$hf(s) > H$ (Fig. 2a). A connected component is a maximal subset of protected areas of the same class linked together. We used the number of connected components in the solution (which strictly depends on the

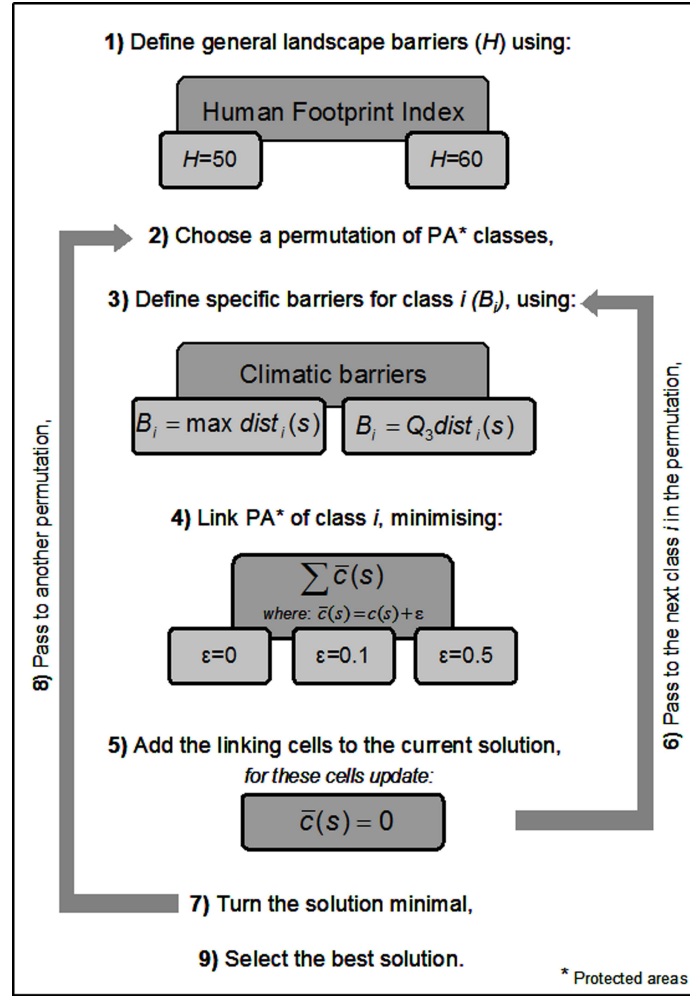


Fig. 1 Simplified overview of the procedures implemented in the connectivity algorithm.

values used for B_i and H) as an indicator of linkage effectiveness. A large number of connected components for a given class reflects a highly fragmented network and it is likely to indicate a reduced effectiveness for that class.

We also considered balancing the cost of the final solution with the number of selected cells. For every cell, s , we added a positive fixed term (ϵ) to the cost, $c(s)$, obtaining the modified cost $\bar{c}(s) = c(s) + \epsilon$. Larger ϵ values determine fewer cells in the solution (see Fig. 2b). We tested three different values ($\epsilon=0$; $\epsilon=0.1$ and $\epsilon=0.5$).

Comparing performances of structural and functional approaches

We ran the functional and structural connectivity models for each combination above described of H (a human footprint threshold that identifies landscape barriers for all species), B_i (threshold values defining barriers for species in each climatic type i) and ϵ (a penalty parameter for the number of cells or surface area in the solution). We compared solutions in terms of numbers of cells or surface area, cost, and effectiveness. To assess effectiveness on both approaches we proceeded as follows. For the structurally-built solution we reconstructed the protected areas climatic classification and for each climatic class- i we removed the barriers for that class. Then, we counted the number of connected components including

protected areas of class- i . This number indicates the extent to which class- i is “effectively” linked in the structural solution. It is therefore appropriate for comparison with the number of connected components in the corresponding functional solution.

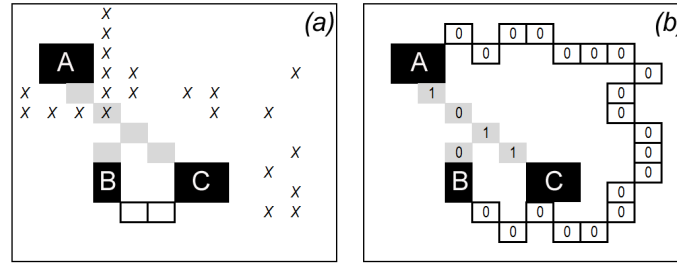


Fig. 2 The effect of (functional and structural) model parameterization, illustrated with an example where three protected areas (A, B and C) are to be connected. **a)** the effect of the human-footprint threshold (H) and climatic barriers (B_i). When H and B_i values do not isolate sets of protected areas grey cells are a likely solution to connect A, B and C. When H and B_i values determine a pattern where the exclusion of cells (crossed-cells) isolate sets of protected areas, a connection is only required to connect B and C (thick-bordered white cells), while A stays isolated. **b)** the effect of the epsilon value (ϵ). When $\epsilon < 0.2$ the “cheapest” connection is the one passing through the 20 thick-bordered white cells with $c(s)=0$ (solution cost = $20 \times \epsilon$). When $\epsilon > 0.2$ the cheapest connection is the one passing through the grey cells (solution cost = $3 \times (1 + \epsilon) + 2 \times \epsilon$).

RESULTS

Outputs from the functional and structural approaches obtained under different parameterizations ($\epsilon \times H \times B_i$) showed variability on the extent (Table 1) and patterning of the climate-based linkages between protected areas. While functional approaches retrieved solutions ranging from 5,328 km² to 6,666 km², structural approaches selected 4,873 km² to 6,373 km² for connectivity. This means that the functional approach produced solutions requiring 3.2% to 14.4% more area than analogous structural approaches, and also identified more area outside the Natura 2000 Network (i.e., linkages including 3.8% to 19.2% more area outside the Natura 2000 to be implemented). Models penalizing the number of cells and the total area in the solution ($\epsilon=0.5$) retrieved more distinct solutions between the approaches; a trend that is true for both $H=50$ and $H=60$ scenarios.

As expected, functional solutions performed better in avoiding climatic barriers than equivalent structural solutions. In fact, by identifying and bypassing climatic barriers, functional solutions included 6.0% to 35.2% less protected area components than structural approaches, a fact that is contingent on the spatial pattern of unsuitable areas provided by H and B_i . Differences in the number of components vary with the climatic classes, being linkages between protected areas in particular classes more challenged by barriers.

When barriers are the 25% more dissimilar cells outside protected areas of each type ($B_i > Q_3 d_i(s)$), greater differences between the functional and structural approaches were obtained for the alpine protected area network (Table 1). Functionally-based links between these protected areas retrieved few components (2 to 3) being 72.7% to 86.7% more effective guaranteeing connectivity than structurally-built links. Turning $H=50$ to $H=60$ greatly affected comparisons of both approaches for the continental protected areas, as effectiveness gains of the functional solutions varied approximately from 30% to 60%. This means that the general (landscape) barriers are the major determinant of fragmentation for these protected areas. Differences between approaches were less marked when connecting Mediterranean and oceanic protected areas, with gains in effectiveness of functional networks being approximately 15%. Using $H=50$ effectiveness gains in oceanic protected areas were narrower (3.0 to 5.9%).

Assuming climatic barriers in the form $B_i > \max d_i(s)$, the functional and structural modelling approximations retrieved a fully connected alpine protected area network and were equally effective for oceanic protected areas. This conformity of responses for both approaches suggests that, for these two climatic classes, there are no climatic barriers (the case of alpine protected areas), or they are so scarce that their overlap with the structural-based solutions is unlikely (the case of oceanic protected areas). In such cases, the

Table 1 Summary of solutions obtained with the functional (F) and structural (S) connectivity approaches. Solutions were obtained under different parameterizations of the human footprint threshold (H), the ϵ parameter, and climatic barriers $\max d_i(s)$ and $Q_3 d_i(s)$. Percentage-differences (Δ (%)) between the functional and the structural approach are presented for the total selected area, the selected area outside Natura 2000 Network, the total number of protected area components and for each climatic class (alpine, continental, Mediterranean and oceanic).

Number of protected area components																								
Total selected area (km²)						Selected area outside Natura (km²)			Alpine			Continental			Mediterranean			Oceanic			Total			
B_i	H	ϵ	F	S	Δ (%)	F	S	Δ (%)	F	S	Δ (%)	F	S	Δ (%)	F	S	Δ (%)	F	S	Δ (%)	F	S	Δ (%)	
$\max d_i$	50	0.0	6,361	6,140	3.6	2,083	1,988	4.8	1	1	0.0	19	25	-24.0	59	63	-6.3	31	31	0.0	110	120	-8.3	
		0.1	5,934	5,639	5.2	2,163	2,026	6.8	1	1	0.0	19	23	-17.3	59	62	-4.8	31	31	0.0	110	117	-6.0	
		0.5	5,331	4,901	8.8	2,473	2,244	10.2	1	1	0.0	19	25	-24.0	59	63	-6.3	31	31	0.0	110	120	-8.3	
	60	0.0	6,577	6,373	3.2	2,034	1,959	3.8	1	1	0.0	8	15	-46.7	43	45	-4.4	17	17	0.0	69	78	-11.5	
		0.1	5,890	5,622	4.7	2,138	2,010	6.4	1	1	0.0	8	14	-42.9	43	46	-6.5	17	17	0.0	69	78	-11.5	
		0.5	5,328	4,873	9.3	2,562	2,229	14.9	1	1	0.0	8	13	-38.5	43	45	-4.4	17	17	0.0	69	76	-9.2	
$Q3 d_i$	50	0.0	6,383	6,140	4.0	2,126	1,988	6.9	3	15	-80.0	20	31	-35.5	59	70	-15.7	32	34	-5.9	114	150	-24.0	
		0.1	5,985	5,640	6.1	2,193	2,026	8.2	3	14	-78.6	20	30	-33.3	59	69	-14.5	32	34	-5.9	114	147	-22.4	
		0.5	5,506	4,901	12.3	2,531	2,244	12.8	3	11	-72.7	20	27	-25.9	59	69	-14.5	32	33	-3.0	114	140	-18.6	
	60	0.0	6,666	6,362	4.8	2,143	1,956	9.6	2	15	-86.7	8	22	-63.6	43	51	-15.7	17	20	-15.0	70	108	-35.2	
		0.1	6,029	5,622	7.2	2,223	2,010	10.6	2	14	-85.7	8	20	-60.0	43	53	-18.9	17	20	-15.0	70	107	-34.6	
		0.5	5,576	4,875	14.4	2,657	2,229	19.2	2	11	-81.1	8	17	-52.9	43	54	-20.4	17	19	-10.5	70	101	-30.7	

numbers of components are determined by an isolation effect originated from the exclusion from analysis of cells with high H values (Fig. 2a). In contrast, for continental and Mediterranean protected areas the existence of climatic barriers resulted in discrepancies between the functional and structural approaches in terms of the resultant number of protected area components. For these climatic classes functional solutions accommodated 17.3% to 46.7% and 4.4% to 6.5% less components, respectively. This distinction was especially evident for $H=60$ (when there were less components than when $H=50$), indicating a more restrictive identification of linkages because less area is considered suitable to be selected.

Integrating efficiency and effectiveness of functional and structural solutions in a single analysis enables to assess the extent to which a fixed budget produces solutions performing differently in terms of effectiveness. Under the more restrictive scenario ($H=50$, $B_i > Q_3 d_i(s)$), the functional solution requiring less surface area targeted 5,506 km², encompassing 114 protected area components, while a similar sized structural solution (5,640 km²) integrated 147 protected area components (Fig. 3a). An equivalent loss of effectiveness for the structural solutions occurred when the selected area outside Natura 2000 was used as a measure of efficiency (Fig. 3b). In this case the least-costly functional solution targeting 2,126 km² differs equally from two structural solutions (with 2,026 km² and 2,244 km²) but accomplished 22.4% and 18.6% less protected area components, respectively.

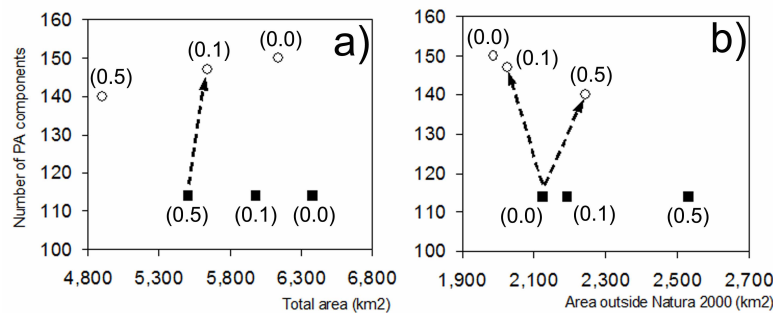


Fig. 3 Comparison of functional (filled squares) and structural (open circles) connectivity solutions in terms of efficiency (area selected) and effectiveness (number of protected area components), for the most conservative scenario under consideration ($H=50$, $B_i > Q_3 d_i(s)$). **a)** Assessing efficiency as total selected area, **b)** Assessing efficiency as the area of solution outside Natura 2000. By varying ϵ from 0, 0.1 and 0.5, more area outside Natura 2000 is to be selected. Arrows represent possible comparisons of similar cost solutions obtained with the functional and structural approaches.

Most of the linkages obtained under the different scenarios are concentrated in the east coast of the Iberian Peninsula (Fig. 4 and Fig. S4.2 on Supplementary Material), where higher densities of the smallest protected areas exist (see Table S2.3 on Supplementary Material). However, depending on the approach, localized and detailed differences occur, which can be raised from the nature of the targeted connectivity (functional versus structural) or from ϵ parameter effect. While long curvilinear linkages passing through regions with high Natura 2000 coverage appeared when $\epsilon=0.0$ (Fig. 2b; compare Fig. 4a versus 4b), with $\epsilon=0.5$ linkages become more linear and occupy less area, at the expense of higher costs. The differences between connectivity types are well illustrated by the fact that under the structural approach, climatic linkages connect protected areas close to each other, irrespective of their climatic characteristics. Under the functional approach linkages are established between climatically similar protected areas, which may require more area to be selected (compare Fig. 4a versus Fig. 4c).

DISCUSSION

This study presents a framework to assist the identification of linkages between natural habitats using environmental data. Familiar approaches typically model connectivity as a spatial property of landscape attributes (i.e., structural approaches) or as a species-specific requirement for dispersal (i.e., pure functional approaches). The proposed framework makes use of commonly available environmental data to

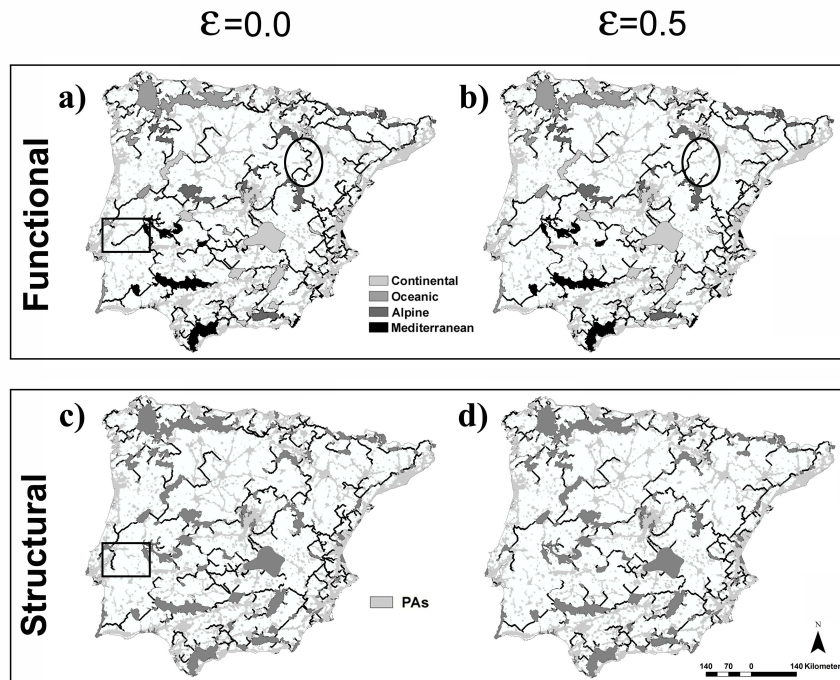


Fig. 4 Map of efficient linkages for Iberian Peninsula protected areas using a threshold on the human footprint index ($H=50$). **a)** and **b)** functional connectivity for four climatic classes of protected areas bypassing climatic barriers defined with $B > Q_3 d(s)$, using the area-penalty parameter $\varepsilon=0.0$ and $\varepsilon=0.5$, respectively; **c)** and **d)** structural connectivity approaches with $\varepsilon=0.0$ and $\varepsilon=0.5$, respectively. The ellipses mark regions where different ε values retrieved distinct solutions. The squares define regions where solution distinctiveness was attributed to the connectivity approaches (i.e., functional versus structural).

characterize similar biogeographical areas to be connected and it uses a heuristic approach to select cost-efficient linkages. In a way, this framework is a hybrid between a structural approach, as its main objective is cost minimisation, and a functional approach since it uses biologically-informed assumptions.

When data on individual species are lacking, environmental data could be seen as a valid alternative to derive patterns of biological distinctiveness and therefore help to define spatial regions with shared pools of co-occurring species. The assumption is that if different regions present different environmental characteristics, then they are more likely to be inhabited by different pools of species. Although this assumption is problematic for the selection of complementary sets of areas in reserve selection (see, Araújo *et al.* 2001; Araújo *et al.* 2004; Hortal *et al.* 2009), it is reasonable to consider that if a species occupying a given environment A is forced to move elsewhere, it should preferentially seek a similar environment A rather than a different environment B. In our example of the framework we used readily available high resolution climatic data but other variables could be used (e.g., vegetation types, topographic, geologic, biogeographic, phylogenetic and disturbance data). Once selected, there are different ways to aggregate and weight the relevant environmental variables. The approach to be used should reflect the differentiated relevance as predictors and the units of measurement of the different data types (Williams & Araújo 2002).

Most of the functional connectivity studies use the least-cost path (a graph-theoretic template) to determine the “best” linkages between a set of areas (Sawyer *et al.* 2011). However, because the least-cost path focuses on evaluations of dispersal costs between pairs of areas (Adriaensen *et al.* 2003), the outcomes may not be the most cost-efficient when multiple natural habitats are to be linked. Our framework addresses this difficulty by considering the minimum Steiner tree problem.

Expedite algorithms attain increasing importance in tackling real-world optimisation problems. With this in mind, we developed a heuristic algorithm to solve a node-weighted version of the minimum Steiner tree problem, when distinct sets of habitats exist and connectivity is required within each of them. The algorithm was developed in order to provide quick answers and multiple evaluations in reasonable time.

Using the Iberian dataset, solutions were obtained in $3,638 \pm 881$ sec (mean $\pm$ standard deviation), depending on the adopted parameterization (see Table S4.1 on Supplementary material). Our approach operates with a ϵ -parameter weighting the total cost with the total area requirements. Values $\epsilon=0$ result in long connectivity linkages passing through less costly (i.e., more attractive) regions. Higher ϵ values determine smaller linkages probably over more costly (i.e., less attractive) lands. Because cost and area do not often correlate, both variables have to take part in spatial conservation models (Carwardine *et al.* 2010). If the available budget is limited, higher weights should be given to optimise the cost-parcels in the objective function (i.e., lower epsilon values). Otherwise, tracing connectivity links across the matrix should impose fewer conflicts with landowners (i.e., less area requirements: higher epsilon values). By varying the ϵ -parameter from 0 to 0.5 we achieved a decrease of the area for functional connecting routes by $17.4\% \pm 1.4\%$ (mean $\pm$ standard deviation) depending on the analysed scenario, while increasing the total cost of the targeted areas by $20.9\% \pm 2.7\%$ and the mean cost of each connecting unit by $45.5\% \pm 4.8$. The algorithm is flexible enough to deal with the structural and functional connectivity approaches. Comparing such connectivity types within a consistent framework enables users to assess the costs obtained in effective conservation plans.

Functional approaches usually require more area than comparable structural ones but they are more ecologically meaningful. This results from two factors. First, functional approaches recognize and identify specific barriers, which are to be circumvented by the linkage arrangement. Second, while structural-based linkages are preferably designed linking the neighbouring (i.e., closer) areas (whatever their environmental class is), functional based-linkages are to be done between areas of the same environmental class, and therefore may require more area. These comparisons yield a consistent message: conservation targets can be accomplished for varying costs if the environmental heterogeneity of the matrix and cost data are formally considered in the planning process, like the one proposed in this study.

The lack of reliable data on the costs of conservation actions propelled us to use the Natura 2000 cover as an indicator of implementation costs in the Iberian Peninsula case-study. Regions classified as Natura 2000 are regulated by legislation limiting disturbing land-uses which facilitates the implementation of other complementary conservation measures. Therefore, we used the fraction of a cell outside Natura 2000 as a proxy for conservation costs. For a more comprehensive assessment, one would need supplementary data on cost, reflecting different components of the final conservation cost (Carwardine *et al.* 2010): land acquisition costs (e.g., unimproved land values, property sales, agricultural profitability), opportunity costs (i.e., costs of foregone uses), costs directly linked with conservation actions (e.g., restoration, management, etc.) and social values (e.g., history of land ownership, amenability to conservation, future expectations). Overlooking costly but biologically important areas or prioritizing areas of low biological value because they are cheap may result from highly inaccurate cost estimates (Naidoo *et al.* 2006). Therefore, improvements in the accuracy of cost data may imply efficiency gains.

The framework that we present is flexible and accounts for distinct conservation scenarios. In our study we used protected areas as targets for connectivity, assuming that each protected cell belongs to no more than one climatic type (i.e., climatic types do not overlap). Other ecological meaningful attributes can be targeted for connectivity and may even contain areas where classification overlaps. For example, our framework may be applied to connect vegetation patches classified by vegetation type. In this case, distinct vegetation types may occur within each vegetation patch. It can also be applied to connect populations of a species when several (metapopulation) species exist. Because different species may occupy the same area, populations of different species may overlap. If one wants to assure the persistence of local genetic identities, connectivity may focus on populations with similar gene pools when distinct gene pools exist. Conversely when facilitating evolutionary adaptation (e.g., to climate change) connectivity may be targeted to link populations with different gene pools. In these cases, overlap of genotypes may occur in a single area.

Distinct conservation objectives, dictated by different conservation agents, may be approached similarly and therefore modelling frameworks to be used should be flexible. In our analysis, we confine the environmental requirements for the connectivity linkages to the avoidance of environmental barriers. However, one could also minimise the total environmental dissimilarity for each habitat type in the same linkages. This would bring two different components to the objective function (cost of selection and level of

environmental dissimilarity). To solve this dual-criteria problem, one could fix one of the two components while optimizing the other, or sum parameter-weighted versions of both components. Both approaches allow us to vary the appropriate parameter over a range, in order to fill out a trade-off curve of total environmental dissimilarity required (or implied survival probability) vs. total cost.

Natural habitats may be so heavily fragmented that continuous swaths of land are not possible to be targeted for conservation. Furthermore, there are species whose ecological capabilities allow crossing some amount of inhospitable land. In these cases, defining connectivity links as stepping-stones may result an effective and less-conflicting conservation measure, as less area is required. Modelling spatial relationships with graphs (like we present herein) enables to delineate stepping-stones as a connectivity pattern. In order to be effective, the “functional distance” between targeted areas should match species dispersal abilities and species ecological requirements.

One can also increase the connectivity robustness if redundant linkages are defined for each habitat type/species (Pinto & Keitt 2009). Although the proposed approach was not developed to deal specifically with redundancy, it can produce a network of redundant connectivity routes if several solutions are saved and joint together. A possibility for maintaining the independence of redundant routes would be to remove from analysis previously selected cells.

Long connectivity linkages are likely to be ineffective and costly. Under such circumstances it may be wiser to avoid connecting distant habitat areas, as long as they are not critical for the remaining ones. As a possibility, *a priori* expert knowledge or a distance-threshold (e.g., maximum dispersal distance) may be used to define several sub-areas where habitats need to be connected (e.g., Fig. S4.3 on Supplementary Material). The here presented heuristic should be applied independently in each sub-area.

Finally, it is critical to realize that if the main interest of conservation is the persistence of species in fragmented landscapes, appraising any measure of connectivity is not sufficient. Connectivity is meant to reflect the capacity of species movement, but there is more in population persistence than movement. Questions concerning persistence can only be approached with models addressing population dynamics acting in a much finer scale than the one illustrated in this study. Here, we defined connectivity using coarse scale environmental surrogate data. In order to proceed, data should be validated and distance to on-the-ground management shortened with a final step: looking to the resulting maps, and examining them through a conservationist’s eye.

CONCLUSION

The identification of functional links between conservation areas remains hampered by lack of data about individual species’ dispersal requirements. Therefore, alternative approaches for the identification of such links using biologically meaningful surrogates are welcomed. We introduce a framework aiming to identify regions potentially supporting biological connectivity between protected areas when detailed species data are lacking. The framework uses environmental gradients to characterize habitats and identify those to be connected, while defining the regions more likely to assist dispersal between habitat areas. Combined with optimization procedures aimed at finding cost-efficient sets of links between patches, the approach offers an alternative methodology to define functional-like links between conservation areas that does not require detailed information on the auto-ecology of the species. Our framework is general and can accommodate distinct conservation targets and surrogates. It balances the total area selected with the cost of their selection, thus permitting to adjust different budgets and levels of conflicts with competing land-uses. The framework may be modified to integrate ecological requisites into the main objective (e.g., maximizing total environmental similarity between the selected linkages and the areas they connect) and to deliver redundant non-overlapping linkages more robust to deleterious stochastic effects. Robustness may also be integrated by the identification of shorter linkages, produces using a predefined distance threshold, or defining several sub-maps within each the framework runs independently from the others.

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Supplementary Material

LINKING LIKE WITH LIKE: OPTIMISING CONNECTIVITY BETWEEN ENVIRONMENTALLY-SIMILAR HABITATS

1. Data description

1.1. Protected Areas

PAs in the Iberian Peninsula (IP) include Spanish data provided by “Ministerio de Medio Ambiente y Medio Rural y Marino” and Portuguese data provided by “Ministério do Ambiente, do Ordenamento do Território e do Desenvolvimento Regional”. Both data sets were integrated in one map (Fig. S1.1) using ArcGIS 9.2. (ESRI, 2006) and it accounts for 681 protected areas, covering 80,871 cells (aprox.14% of the total area). These areas include a wide range of national conservation classes such as National Parks or Natural reserves as well as international conservation areas such as RAMSAR sites or the Man and the Biosphere areas. The European Natura 2000 Network was not incorporated because its conservation management measures are less strict and is usually based on low intensity agricultural practices (Ostermann, 1998). Natura data was used instead to define how attractive are areas to be used as links (see section 3.1 on this Supplementary Material)

1.2. The Natura 2000 Network

The Natura 2000 data was downloaded from the European Environment Agency site : <http://www.eea.europa.eu>.

1.3. The Human Footprint Index

The data for the Human Footprint Index map (Sanderson, 2002) was used as way to characterize the human impact on the landscape (or naturalness, if considered inversely) and to identify suitable areas for the establishment of connectivity linkages. The 1km² resolution data was downloaded from webpage of the Wildlife Conservation Society: <http://www.wcs.org/humanfootprint/>

1.4. Climatic data

The climatic data was provided by the Agencia Estatal de Meteorología de España and by the Instituto de Meteorología de Portugal for the time period 1961-1990 at 1km² resolution. Measurements were recorded by 2,173 rainfall and 51 thermometric stations in Spain and 89 rainfall and 51 thermometric stations in Portugal.

Four climatic variables were derived from the monthly data and averaged for the considered time period: maximum daily temperatures per month (*maximum temperature*: °C), minimum daily temperatures per month (*minimum temperature*: °C), total monthly precipitation (*accumulated precipitation*: mm) and the monthly standard deviation of the minimum daily temperature (°C). The selection of these variables was driven by their reduced level of pairwise correlation and because species' distributions are considered highly dependent on them (e.g. Whittaker, 2007; Hawkins, 2003).

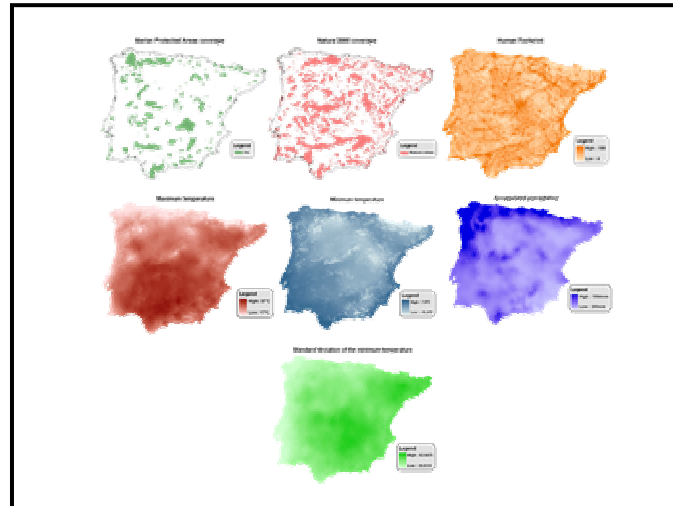


Fig. S1.1 Spatial distribution of the different data used in this study.

2. Climatic characterization of protected areas

A Principal Component Analysis (PCA) was carried out for obtaining a simplified but informative climatic characterization of climate in Iberian Peninsula. A PCA is recommended prior to clustering because it is suggested that the linear components retaining most variance are the most relevant for the clustering procedure. PCA also assisted in the removal of uninformative data retaining low variance as a result of spatially homogeneous patterns (Fielding, 2007).

We retained the first two principal components which explained approximately 57% (PC1) and 30% (PC2) of the total variance (Table S2.1). The first component was mainly determined by the *maximum temperature*, *accumulated precipitation* and the *standard deviation of the minimum monthly temperature* (Table S2.2) whereas the second component was mainly determined by the *minimum temperature*. The third component, not included in the subsequent cluster analysis, was dominated by the precipitation variable.

The spatial pattern of the most explicative principal component variable (PC1) differentiates a north-western Iberian region very humid, with few thermal oscillations (typical from the Eurosiberian region) and the majority of the Central and Southern Iberian area characterized by stronger Mediterranean influence (Fig. S2.1).

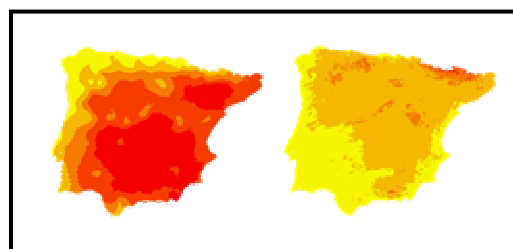


Fig. S2.1 Spatial pattern in Iberian Peninsula of the first (PC1) and second (PC2) principal components.

Table S2.1 Characterization of the first four principal components (eigenvalues and explained variance).

Factors	Eigenvalue		Variance (%)	
	Value	Cumulative	Value	Cumulative
1	2.307438	2.307438	57.68596	57.6860
2	1.190173	3.497611	29.75432	87.4403
3	0.349566	3.847177	8.73914	96.1794
4	0.152823	4.000000	3.82058	100.0000

Table S2.2 Characterization of the first four principal components (eigenvectors per variable).

Eigenvectors	Factor 1	Factor 2	Factor 3	Factor 4
Max tmp	0.578674	-0.305971	0.381001	-0.652960
Min tmp	-0.018986	-0.903150	0.036006	0.427391
Accum prec	-0.576365	0.023014	0.815590	-0.045682
Std min tmp	0.576696	0.300287	0.433999	0.623613

Table S2.3 Characterization of Iberian Peninsula PA sizes.

PA class	Mean area (km ²)	Standard deviation of area (km ²)
All PAs	97.043	610.787
Continental	87.883	501.469
Oceanic	132.326	1062.756
Alpine	123.936	387.563
Mediterranean	75.687	434.564

3. Characterization of the unprotected matrix

3.1 the Natura 2000 coverage to assess “attractive areas” for connectivity

We used free software from the Metapopulation Research Group at Helsinki University (*MRG GIS*) to obtain the percentage of Natura 2000 area within each grid cell. We acknowledged the implementation of MRG GIS to Evgeniy Meyke.

3.2 Climatic barriers

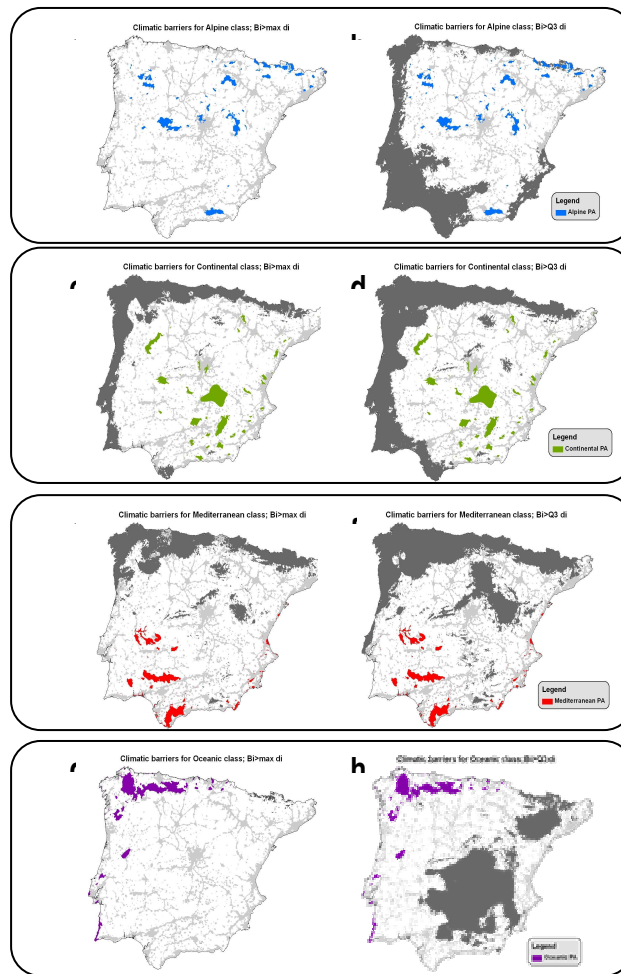


Fig. S3.1 Map of climatic barriers (grey areas) for each climatic class (continental, oceanic, alpine and Mediterranean) for the Iberian Peninsula protected areas using a variation of the node-weighted MST problem with $H=50$ **a**) and **b**) continental climate with $B_i > \max d(s)$, and $B_i > Q_3 d(s)$, **c**) and **d**) oceanic climate with $B_i > \max d(s)$, and $B_i > Q_3 d(s)$, **e**) and **f**) alpine climate with $B_i > \max d(s)$, and $B_i > Q_3 d(s)$, **g**) and **h**) Mediterranean climate with $B_i > \max d(s)$, and $B_i > Q_3 d(s)$.

3.3 The Human Footprint Index as general landscape characterizer

The scale of the human footprint index ranges from 0 to 100 (**Table S3.1**). We choose two threshold values to be used in the analyses ($H=50$ and $H=60$; **Fig. S3.2**) reflecting different levels of land commitment to species' dispersal. With $H=50$ we assumed natural areas close to cities unsuitable for species' dispersal, while with $H=60$, those areas were assumed to support species' dispersal

Table S3.1 Correspondence of human footprint values to different land uses.

Human footprint value	Type of area
91-100	Areas in city centres of big cities like Madrid or Barcelona
61-90	Suburban areas
50-60	Natural areas close to cities. Rural areas
19-49	Natural areas modified by humans activities
4-18	Isolated areas further away from cities such as mountains

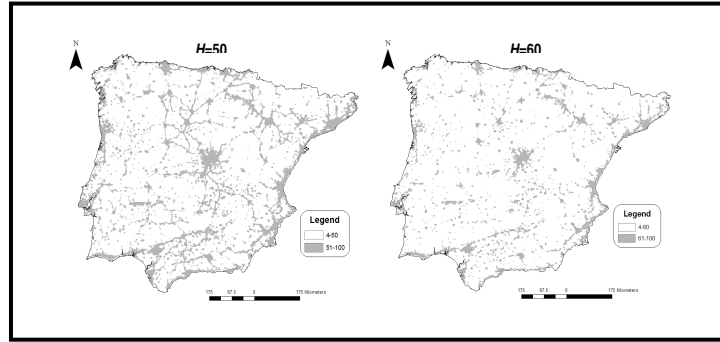


Fig. S3.2 Map of the Human Footprint Index in Iberian Peninsula highlighting regions excluded after the using $H=50$ and $H=60$ (used in article's main text).

4. Analytical data

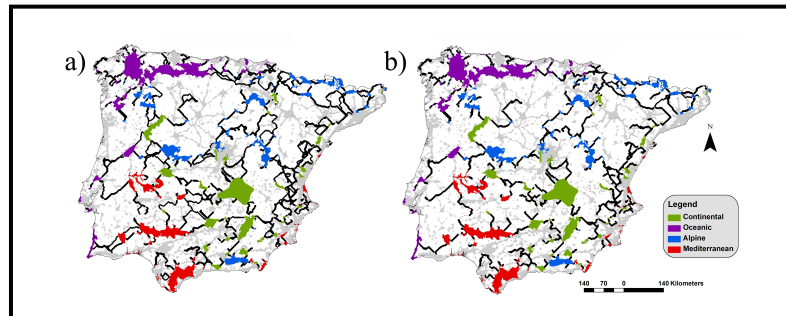


Fig. S4.1 Map of efficient functional linkages for four climatic classes of Iberian Peninsula protected areas (blue: alpine; green: continental; red: Mediterranean; purple: oceanic) using a variation of the node-weighted MST problem with $H=50$ and barriers as $B > \max d_i(s)$. **a)** not penalising total targeted area, $\epsilon=0.0$ (6,351km² of which 2,083km² outside Natura 2000 sites), **b)** penalising total targeted area, $\epsilon=0.5$ (5,331km² of which 2,473km² outside Natura2000 areas).

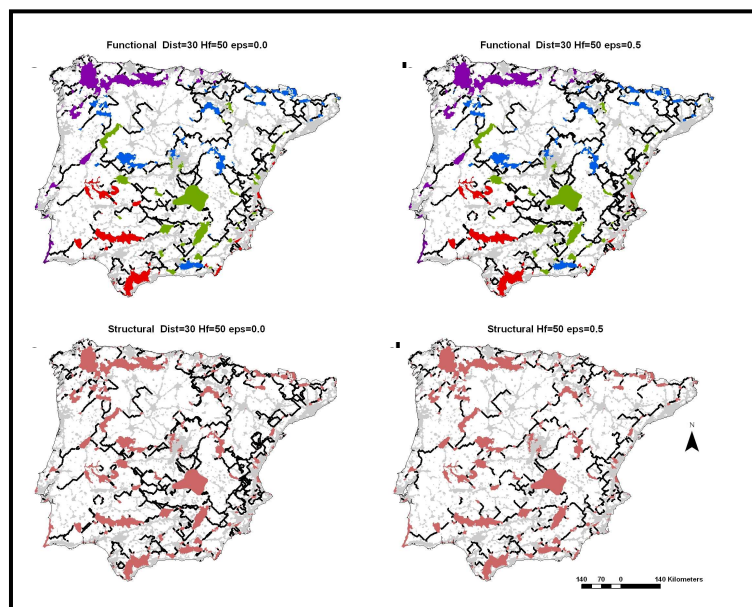


Fig. S4.2. Map of efficient linkages for Iberian Peninsula protected areas using a variation of the node-weighted MST problem with $H=50$ and a 30km distance between protected areas defining sets requiring connectivity. **a)** and **b)** functional approaches for four climatic classes of protected areas (blue: alpine; green: continental; red: Mediterranean; purple: oceanic) with barriers defined as $B > \max d_i(s)$, and $\epsilon=0.0$ (4,755km² of which 1,740km² outside Natura 2000 sites) and $\epsilon=0.5$ (3,793km² of which 1,967km² outside Natura 2000 sites), respectively; **c)** and **d)** structural connectivity approaches with $\epsilon=0.0$ (5,154km² of which 1,722km² outside Natura2000 areas) and $\epsilon=0.5$ (3,961km² of which 1,938km² outside Natura 2000 sites), respectively.

Table S4.1 Running times (sec.) to obtain functional approaches using several parameterizations threshold values for the Human Footprint Index (H); penalty-parameter for number of cells (ϵ) and climatic barriers (B)

H	ϵ	Running times	
		B	
		$max d_i$	$Q_3 d_i$
50	0.0	4,560	2,945
	0.1	3,840	2,689
	0.5	3,399	2,278
60	0.0	5,279	3,830
	0.1	4,534	3,321
	0.5	4,079	2,907

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CHAPTER IV

A probability-based approach to match species with reserves when data are at different resolutions

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“Uncertainty is a direct consequence of the complexity of nature. All the facets of a complex phenomenon are impossible to measure with absolute precision, because the act of measuring itself affects its perception.”

Heisenberg, 1958

A PROBABILITY-BASED APPROACH TO MATCH SPECIES WITH RESERVES WHEN DATA ARE AT DIFFERENT RESOLUTIONS

ABSTRACT

Gap analysis is a protocol for assessing the extent to which valued biodiversity attributes are represented within protected areas. Such analysis involves overlaying the distribution of biodiversity features (e.g. species) with protected areas, but the protocol entails arbitrary assumptions that affect the outcome of the assessments. In particular, since species' distributions are usually mapped at a coarser resolution than protected areas, rules have to be defined to match the two data layers. Typically, a grid cell is considered protected if a given proportion is covered by protected areas. Because the effectiveness of protected areas is dependent on the definition of such arbitrary proportions (i.e., thresholds), errors of commission and omission in the level of species' representation are bound to exist. We propose an alternative approach whereby the contribution of a cell for the representation of species is defined as the expected value of a hyper-geometric random variable. We compare the conventional approach based on fixed thresholds with this new probability-based approach for both static and dynamic conservation scenarios, using a virtual dataset and a 100-plant-species' dataset for Iberian Peninsula. Results support the view that traditional fixed thresholds yield inconsistent results. Because present different distributional patterns coinciding differently with reserves, species-specific and time-specific thresholds should be used. Our approach enables to easily obtain these more adequate threshold values, thus offering a promising method for gap analyses. Future studies should seek to evaluate the performance of this method empirically in different conservation planning contexts.

INTRODUCTION

Protected areas (hereafter termed reserves) are the cornerstone of *in situ* conservation strategies. Given their significance for biodiversity conservation, it is important to assess how well they meet their goals (Margules & Pressey 2000). Gap analysis is a procedure to assess reserve representativeness (Scott et al. 1991) that aim to ensure that a viable collection of biological attributes (e.g., species) is protected from disturbances. Information on species' representation within reserves is used to identify gaps that may be filled through the establishment of new areas for conservation.

The implementation of gap analysis is commonly supported by geographical information systems, which facilitate the overlay of maps of species' distributions with maps of reserves. At national to continental scales, species and reserve data are often recorded at different resolutions. Species data are available as occurrence records on regular grid cells, while reserves are typically represented by polygons (e.g., data from the World Database on Protected Areas). To match both types of data, arbitrary thresholds are used for deciding when reserves of varying size and position should be considered present or absent from a particular grid cell (Hopkinson et al. 2000). These thresholds vary from any coverage greater than zero to more conservative choices, where greater proportions of the grid cells need to be covered by reserves in order for the grid cell to be considered "protected". Although conceptually simple, the rules used for matching species' distributions and reserve coverage data affect the assessment of species' conservation status in reserves to a variable but usually not negligible extent.

Araújo (2004) was the first to warn against the impacts of thresholds on gap analysis assessments. He provided evidence that assessments measuring the degree of species' representations in reserves were contingent on the threshold used to assign reserves to grid cells and that little (biological) guidance existed for the selection of a reliable threshold. Araújo (2004) concluded that careful examination of the impacts of using different threshold values when mapping reserves should be performed. However, most subsequent gap analyses failed to provide justifications for the chosen thresholds, and in some cases, even omitted to report them (for some examples of threshold-based approaches used in gap analyses after 2004, see Table 1).

Although the sensitivity of gap analysis to varying thresholds has been demonstrated, the solutions to solve the problem remain elusive. Araújo (2004) suggested an approach to circumvent the arbitrariness of threshold choices based on an analysis of species' accumulation curves. He proposed that a threshold of 50% would be adequate for the particular studied system. However, the use of thresholds (single, "optimal", or a range of values) presents conceptual weaknesses. First, common threshold applications use a fixed value to map reserves, but different species may require different thresholds, and this cannot be assessed with species' accumulation curves that are, by definition, calculated from the complete species' pool used in the analysis. For example, if a restricted-range species is mostly distributed in small and isolated reserves, then conservative threshold choices (i.e., filtering out grid cells with low reserve coverage) may not adequately quantify this species' protection.

Second, because reserve size and density vary from region to region, reserve coverage in grid cells is likely to be biased to lower or higher values depending on the region. In the same way, adopting a fixed threshold on evaluations based on maps produced under different resolutions (i.e., grid cell extents) is likely to deliver different sets of protected grid cells, which would lead to ambiguity when comparing biodiversity representation within reserves.

Third, the use of thresholds impedes the use of all available information on reserve coverage. Thresholds convert the continuous information on grid-cell reserve coverage into binary classifications of fully protected or unprotected. Such conversions are prone to high rates of commission and omission errors that accumulate across the set of grid cells under analysis (Whittaker *et al.* 2005; Rondinini *et al.* 2006).

Furthermore, apart from these limitations, threshold values on reserve data are not amenable to use in less common analytical designs. There are cases where species' distribution data come from statistical modeling frameworks where species' probabilities of occurrence are obtained for each grid cell. In such situations, statistically-informed cut-off values are applied to define presence/ absence of species in each grid cell (Liu *et al.* 2005). Because this threshold-like procedure on species data is also flawed by significant error rates (e.g., Araújo *et al.* 2005), adopting a two-threshold approach in gap analysis may increase uncertainties.

Another issue that has been ignored is the effect of the choice of thresholds when species' distributions change with time, for example, as a response to climate change. As mentioned above, since threshold values impact species differently depending on how species' distributions and reserves relate, changes in species' distributions by means of dynamic threats (e.g., climate change) are likely to be inconsistently treated by threshold values. Therefore, the use of approaches capable of responding to the above-mentioned weaknesses is critical for achieving more robust solutions in gap analyses assessments.

Here, we propose a novel approach to circumvent the use of thresholds in gap analyses. Rather than using a threshold to convert reserves into either present or absent, the proportion of grid cells that is covered by areas with conservation status is taken into account. A probabilistic framework is then developed that estimates how likely species are represented in reserves within every grid cell. We use virtual and plant species' distributions data in the Iberian Peninsula to compare levels of species' representation in reserves obtained with our probability-based approach and different thresholds. We also seek to determine if comparisons of levels of species' representation in reserves with random areas differ when assessed with conventional threshold approaches versus the proposed methodology. By using species' distribution modeling outputs (i.e., probabilities of occurrence) for the present and the future, we discuss the robustness of various approaches when assessing reserve representativeness under climate change.

Table 1. Overview of gap analysis studies where cut-off threshold values were applied to reserve data. Only papers published after 2004 were reviewed because Araújo (2004) produced a similar review for the period prior to 2004: reference: bibliographic reference; region: geographical focus of the studies; resolution: grid cell extent; protected area type: type of protected areas (PAs); criteria for protected area grid assignment: criteria used to assign grid cells as protected or not; taxonomic data: taxonomic scope of the studies; grid-based data type: type of original data for taxonomic layers.

reference	region	resolution	protected areas type	criteria for protected areas grid-assignment	taxonomic data	grid-based data type
Araújo et al. 2007	Iberian Peninsula	50x50km cells	National PAs	2, 5, 10 and 20%-cover thresholds	amphibians, reptiles, birds, mammals and plants	presence from sampling records
Burgess et al. 2005	Sub-Saharan Africa	1x1° cells	National PAs and forest conservation areas	10, 25, 33 and 50%-cover thresholds	plants	presence/ absence from range maps
De Klerk et al. 2004	Sub Saharan Africa	1x1° cells	National PAs	10, 25 33 and 50%-cover thresholds	Afrotropical birds	presence from sampling records
Estrada et al. 2008	Andalusia (Spain)	10x10km cells	Natural Conservation areas Network of Andalusia	25%-cover	terrestrial mammals	favourability values (fuzzy classification)
Fjeldsa et al. 2004	Sub-Saharan Africa	1x1° cells	National PAs	5, 10, 25, 33 and 50%-cover thresholds	mammals	presence from sampling records
Freemark et al. 2006	British Columbia	640km2 hexagons	Provincial PAs	omitted	threatened birds	presence/ absence from range maps
Hannah et al. 2007	Mexico (MX), Cape Floristic Region, South Africa (CFR) and Europe (EU)	10x10km (MX);1.8km2 (CFR);50 km2 (EU)	National PAs	omitted	birds and mammals (MX); Proteacea plants (CFR), Plants (EU)	presence/ absence after a threshold value on probabilities
López-López et al. 2007	Castellón Province, Spain	1x1km cells	Important Bird Areas	omitted	golden eagle	probability values (3 classes)
Maiorano et al. 2006	Italy	2x2km cells	National PAs	10%-cover threshold	terrestrial vertebrates	presence/ absence after a threshold value on probabilities
Martínez et al. 2006	Spain	10x10km cells	Natura 2000	omitted	lichens	presence/ absence after a threshold value on probabilities
Papes and Gaubert 2007	Africa and Asia	5x5km cells	formal and proposed IUCN PAs	omitted	viverrid mammals	presence/ absence after a threshold value on probabilities
Rondinini et al. 2005	Africa	1km² cells	Existing system of PAs	omitted	amphibians and mammals	probability values (3 classes)
Sánchez-Fernández et al. 2008	Iberian Peninsula and Balearics	10'x10' cells	Natura 2000	25%-cover threshold	water beetles	presence from sampling records
Stoner et al. 2007	Tanzania	5x5km and 10x10km cells	national parks, game conservation areas, partially protected game-controlled areas	omitted	large herbivores	presence from sampling records
Thomaes et al. 2008	Belgium	5x5km cells	Natura 2000	0-10%; 10-50% and 51-100%-cover thresholds	saproxylic stag beetle	presence/ absence after a threshold value on probabilities
Traba et al. 2007	Spain	10x10km cells	Natural Protected Areas and Special Protected Areas under EU Birds Directive	20%-cover threshold	birds	presence from sampling records
Trisurat 2007	Thailand	200x200m cells	National PAs	omitted	vegetation types	presence/ absence from range maps

MATERIAL AND METHODS

Virtual data

We produced a small virtual dataset to illustrate how the threshold approach differs from a threshold-free approach in evaluating species' representation in reserves. Probabilities of occurrence (s_i) for three hypothetical species (sp_A , sp_B , sp_C) in each one of ten grid cells (i) ordered by non-increasing values of reserve coverage (r_i) are shown in Table 2. Range sizes for the hypothetical species and total area with reserves are obtained by summing s_i and r_i for all i , respectively. Species were simulated to represent a variety of patterns such that one species had a similar probability of occurrence across the protected grid cells (sp_A); one species had a biased distribution towards grid cells with higher protected coverage (sp_B); and one species had a biased distribution towards grid cells with lower protected coverage (sp_C).

Table 2. Data for an illustrative example. Probability of occurrence (s_{ij}) for three hypothetical species (sp_A , sp_B , sp_C) in each of ten cells (i) ordered by non-increasing values of the fraction of reserve coverage (r_i). Species' range sizes and total protected area ($range$) are obtained by summing s_i and r_i , respectively. Species were simulated to represent a variety of distributions: a species with a similar probability of occurrence values across the protected grid cells (sp_A); a species with a biased distribution towards grid cells with higher reserve fractions (sp_B); and a species with a biased distribution towards grid cells with smaller reserve fractions (sp_C).

i		1	2	3	4	5	6	7	8	9	10	range
r_i		0.99	0.77	0.60	0.47	0.36	0.28	0.22	0.17	0.14	0.00	4.0
s_{ij}	sp_A	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.00	1.0
	sp_B	0.25	0.25	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.0
	sp_C	0.00	0.00	0.00	0.00	0.25	0.10	0.20	0.10	0.25	0.10	1.0

The Iberian Peninsula dataset

We used 100 plant-species' distributions (Table S1, Supplementary material) from a larger pool of 1298 European plant species modeled for another study (Araújo et al. 2011). The species set was randomly selected following two conditions: 1) species should have at least 20 registered occurrences in the Iberian Peninsula (approximately one percent of the analyzed area); and 2) a wide variety of sizes of the European ranges, taken as the proportion of the total 50-degree grid cells in analysis where a species occurs, should be represented.

Probabilities of occurrence of each species in each 10-degree Iberian Peninsula grid cell were obtained from models investigating correlations of species' presences/absences at European level with climate predictors for a baseline period (i.e., averaging predictors for 1961-1991) and 2080 (i.e., averaging predictors for 2051-2080) (Araújo et al. 2011). Probabilities were filtered by downscaled recorded occurrences of species in the baseline period (i.e., atlas records). Where species were not recorded, probabilities were set to zero. With such approach, we reduced commission errors associated with projections of species' distributions in areas where they were not recorded, thereby adopting a conservative and precautionary approach for conservation assessments.

The Iberian Peninsula reserve data were also extracted from the analysis performed by Araújo et al. (submitted) in which the proportion of each grid cell area within reserves was computed (Fig. S1, Supplementary material). Grid cells were considered protected if the fraction of the protected area equaled or exceeded a threshold value R . A sequential set of 11 area-proportional threshold values were chosen, ranging from a small residual value above zero to 1 (0^+ , 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.80, 0.90 and 1), to define 11 grid-based binary maps of Iberian Peninsula reserves (Fig. S2, Supplementary material).

Measuring species' representation levels in reserves

Conservation assessments are typically performed in relation to previously defined targets (Rondinini & Chioza 2010). Targets are commonly specified as the total area (in square kilometers) or the proportion of the total area of a biodiversity feature's distribution that should be in a reserve. Because our analysis takes place with species with different range sizes here we consider the proportional target for species' representation in reserves (i.e. values in the interval [0,1]).

We propose to compute a species representation index in reserves (*SRI*) with the expression below, which is flexible enough to accommodate different transformations of data (by means of the intervenient f and g functions):

$$SRI = \frac{\sum_{i=1}^N f(r_i) \cdot g(s_i)}{\sum_{i=1}^N g(s_i)} \quad (1)$$

where N is the number of grid cells; s_i is probability of occurrence for the species in grid cell i and r_i is the fraction of grid cell i considered protected. The choice of f and g determines a particular approach for assessing species' representation in reserves. For the case when both species and reserve data are binary-transformed after using S and R as thresholds, respectively (i.e., a two-threshold approach), $f(r_i)=1$ when $r_i \geq R$ and 0 otherwise, and $g(s_i)=1$ when $s_i \geq S$ and 0 otherwise. Because it only generates binary layers of species and reserve data, this case is comparable to commonplace grid-based gap analyses, in which recorded data on species are used instead of modeled data. In this circumstance, $g(s_i)=1$ in places where a species occurs and $g(s_i)=0$ where it does not occur. When species' probabilities of occurrence are used instead (preferably corrected for commission errors) and only reserve data are binary-transformed (i.e., a one-threshold approach), $f(r_i)$ follows the two-threshold approach and g is the identity function (i.e., $g(s_i)=s_i$).

With the two-threshold approach the *SRI* is calculated as the proportion of grid cells where a species is assumed to occur that coincides with reserves. Under the one-threshold approach the *SRI* is obtained by taking the sum of species' probabilities of occurrence across the grid cells assumed to be protected divided by the sum of species' probabilities of occurrence across all analyzed grid cells.

When data allows, we advocate to measure species' representation in reserves simply taking f and g in Eq.

(1) as identity functions, i.e., $SRI = \sum_{i=1}^N r_i \cdot s_i / \sum_{i=1}^N s_i$. We term this proposal the continuous approach.

Below we give a probabilistic support for the interpretation of the continuous *SRI* as the sum, across all grid cells, of the expected relative area of the region that is simultaneously suitable for the species and under some protection status.

Consider a random experiment where: i) a grid cell i is split into M squares with equal area; ii) $M \cdot r_i$ squares are covered with reserves; and iii) $M \cdot s_i$ squares are extracted, without replacement, among the M squares to represent the territory occupied by the species. If X is a random variable representing the number of squares marked in step ii) among those squares selected in step iii), then this experiment can be viewed as follows. If a grid cell is divided in M squares, $M \cdot r_i$ of them protected and $M - M \cdot r_i$ not protected then X counts those squares from the $M \cdot s_i$ squares that are protected (see Fig. S3, Supplementary material). Accordingly, X follows a hypergeometric distribution with parameters M , $M \cdot r_i$ and $M \cdot s_i$ and an expected value equal to $M \cdot r_i \cdot s_i$. The random variable X/M represents the proportion of squares in grid cell i that are simultaneously protected and occupied by the species. Therefore, its expected value is $E(X/M) = r_i \cdot s_i$. We propose to use this value as a predictor of the fraction of the grid cell in the intersection of the territory covered by reserves and occupied by the species. This value represents the contribution of grid cell i to the representation of the species in the protected territory (i.e., components of the sum in the numerator of Eq. (1)). The variance of X/M can also be derived using $Var(X/M) = s_i \cdot r_i (1 - r_i) (1 - s_i) / (M - 1)$. For large values of M , $Var(X/M) \approx 0$, thus making

$E(X/M)=r_i s_i$ a precise measure for the proportion of the area in grid cell i that is simultaneously protected and occupied by the species.

There is a relation between threshold-based and continuous *SRI*. The *SRI* for the one-threshold approach is a stepwise (decreasing) function of thresholds R , ranging between 0 and 1. Therefore, the continuous *SRI* lays in some minimal interval $[a, b]$ bounded by two threshold-based *SRI* values. In general, determining the thresholds R corresponding to a and b , requires the knowledge of s_i . However, for species that are equally distributed across partially protected grid cells (e.g., sp_A Table 2), it is possible to analytically determine the thresholds R^* for which the two approaches converge, without knowing s_i . To show this, let us assume that the grid cells are ordered by non-increasing r_i values (i.e., $r_1 \geq r_2 \geq \dots \geq r_N$). In doing so, there is an integer $0 \leq K^* \leq N$ such that (with the convention $s_0=r_0=0$)

$$\sum_{i=0}^{K^*} s_i \leq \sum_{i=1}^N r_i \cdot s_i < \sum_{i=1}^{K^*+1} s_i ,$$

and therefore, $R^*=r_{K^*}$.

For species that are equally distributed, i.e., $s_i=s$, $\sum_{i=1}^{K^*} s_i = sK^*$ and $\sum_{i=1}^N r_i s_i = s \sum_{i=1}^N r_i$,

$$\text{and therefore } K^* = \left\lfloor \sum_{i=1}^N r_i \right\rfloor .$$

We use the virtual data set to illustrate the mechanics of the one-threshold and continuous approaches as well as how they generate the *SRI*. We also use the Iberian Peninsula example to illustrate differences obtained with both approaches using a large number of species with varying distributional patterns. Analyses were performed for the baseline (present) and 2080 periods.

Randomization tests

The degree to which reserve networks represent species better than expected by chance alone is often assessed under gap analyses frameworks (e.g., Araújo *et al.* 2007). Here we tested how the performance of the threshold-based and continuous approaches varied against a null model obtained by randomly selecting reserves. Randomizations included the selection of an equal number of random cells as the protected grid cells. For threshold-based approaches, this means randomly selecting a number of grid cells equal to the number of protected grid cells obtained with thresholds. For the continuous approach, because the full range of reserve coverage information is maintained in the analysis, an equivalent randomization test is produced by redistributing the s_i values within the N grid cells.

For the virtual-data example ($N=10$), we performed all possible permutations of s_i values (10! permutations), thus producing an exact rank of species' representation values (*SRI*) to compare the performances of reserves produced with the threshold-based and the continuous approaches. For each species in the Iberian case study, we conducted 9999 permutations for each one of the chosen thresholds and for the continuous approach.

For each species, the *SRI* values obtained using the real reserve networks (produced with different threshold values and with the continuous approach) were then compared with those obtained using the corresponding random set of reserves. We performed one-tail tests by counting the number of permuted outcomes in which the *SRI* was lower (or higher) than the real *SRI*. Specifically, we were interested in checking whether the real *SRI* was greater than the 95th percentile (or lower than the 5th percentile) of the *SRI* values obtained from a random selection of grid cells. Analyses were performed for the baseline period and 2080.

RESULTS

Measuring species' representation levels in reserves

Virtual data

For the three virtual species, representation levels within virtual reserves differed when a set of threshold values and the continuous approximation were applied (Table 3).

When $R=0.10$, all the grid cells with some fraction of reserve land were assumed to be completely protected, and therefore all the range of sp_A , sp_B and most of the range of sp_C were assumed to be within reserves. Otherwise, if $R=0.60$, then 33% of the sp_A distribution, 100% of the sp_B distribution and 0% of the sp_C distribution coincided with reserves. Therefore, a detailed analysis proved that the one-threshold approach is unstable, producing SRI values that are highly contingent on the particular threshold used. For example, species sp_C is completely distributed within grid cells with low protected fractions ($r \leq 0.36$). When one optimistically assumed a small threshold value, for example, $R=0.10$ or $R=0.20$, then a large fraction of the species distribution was predicted to be within a reserve, which did

Table 3. The percent of species' ranges within reserves (SRI) for the example in Table 1 in which several threshold values (R) and the continuous approach were applied.

	$SRI(\%)$						
	$R=0.90$	$R=0.75$	$R=0.60$	$R=0.45$	$R=0.30$	$R=0.20$	continuous
sp_A	11.0	22.0	33.0	44.0	55.0	77.0	44.0
sp_B	25.0	50.0	100	100	100	100	74.0
sp_C	0.0	0.0	0.0	0.0	25.0	55.0	21.4

not seem realistic given the small sizes of reserves. Conversely, when we assumed a strict threshold value, $R > 0.36$, then no sp_C distribution was predicted to coincide with reserves, although the species occurs in grid cells in some of the protected areas. The continuous approach weights the species' probabilities of occurrence in grid cell i with reserve coverage at i Eq. (1). In doing so, the SRI values were 44% for sp_A distribution, 74% for sp_B distribution and 21% for sp_C distribution. These values seem consistent with an intuitive perception of the species' distributions. We examined the sensitivity of species' representation levels in reserves to a more extensive set of R values (Fig. 1). Note that sensitivity differs from species to species depending on how the species are distributed across the protected grid cells. Because sp_A approximates an evenly distributed species, the analytical formula for R^* could be applied across partially protected grid cells. In our example, $K = 3.96 \approx 4.00$; this means that both approaches produced very similar SRI values ($SRI=44.0\%$) for sp_A when a threshold $R=r_A=0.47$ was considered (or any R in the interval $[0.36; 0.47]$). For sp_B , an approximated R^* was in the interval $[0.60; 0.77]$, while for sp_C was in the interval $[0.28; 0.36]$ (see Table 3).

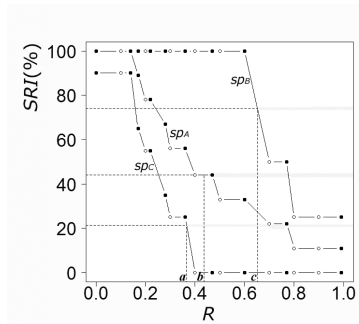


Figure 1. Representation levels within reserves (SRI) for the three species (sp_A , sp_B , sp_C) in the hypothetical example (Table 2) after using several threshold values (R : open dots for an *ad hoc* sequence of increasing values: 0+, 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.80, 0.90 and 1; black dots for values equal to the fraction of reserve coverage in grid cells: Table 2). Threshold values producing representation values equivalent to the continuous approach (R^*) are represented by a , b and c for sp_A , sp_B and sp_C , respectively.

The Iberian Peninsula dataset

The proportion of the Iberian Peninsula that was considered protected varied according to the different threshold values used to assign reserves to grid cells (Fig. S2, Supplementary material). For the most liberal scenario ($R=0+$) in which all partially-protected grid cells were assumed to be fully protected, 27.6% of the Iberian Peninsula was considered protected. When applying the more conservative threshold ($R=1$), where grid cells that were fully covered by reserves were actually considered to be protected, the percentage of the Iberian Peninsula area that was considered to be protected decreased to 0.4%. The real figure, obtained with polygonal reserve mapping, was 4.55%, which would correspond to the area covered when choosing a threshold value between 0.5 and 0.6.

Variations in threshold values also caused perceived levels of species representation in reserves to vary accordingly. For the baseline period, the averaged *SRI* taken across species varied from 39.5% to 0.6% for $R=0+$ and $R=1$, respectively (Fig. 2), with species exhibiting different sensitivities to threshold values depending on their occupancy patterns. For the more liberal $R=0+$, *Aconitum burnatii* (sp68), *Cystopteris montana* (sp7) and *Cardamine bellidifolia* (sp90) were predicted to have more than three quarters of their Iberian range within reserves (97.7%, 85.6% and 75.8%, respectively), while *Silene uniflora* (sp52), *Malcolmia triloba* (sp86) and *Camelina microcarpa* (sp94), the species with lower *SRI*s, were predicted to have 18.0%, 19.2% and 20.9%, respectively, of their Iberian range within reserves.

When gap analysis is undertaken using the more conservative threshold $R=1$, the three species that previously had the highest *SRI* were predicted to have no Iberian range within reserves, while species predicted to have a greater representation were *Equisetum sylvaticum* (sp3: 3.1%), *Selaginella selaginoides* (sp1: 2.6%) and *Corydalis cava* (sp79: 2.6%). In addition, 22 other species had no representation in reserves.

Across the sequence of the analyzed thresholds, there was no clear consistency in species' rankings with respect to their levels of representation within reserves (Fig. 2). *Aconitum burnatii* (sp68) appeared different from other species because it has a considerably higher *SRI* across all but the highest of the analyzed thresholds. This species has a restricted range in two regions on the NE and SE of the Iberian Peninsula (Fig. S4, Supplementary material) coinciding with protected areas. Moreover, grid cells where this species is expected to be better represented (i.e., having higher probability of occurrence) coincide with grid cells with a greater reserve coverage that were converted to "protected" grid cells using most of the threshold applications, except for the most conservative one ($R=1$) (Fig. S2, Supplementary material).

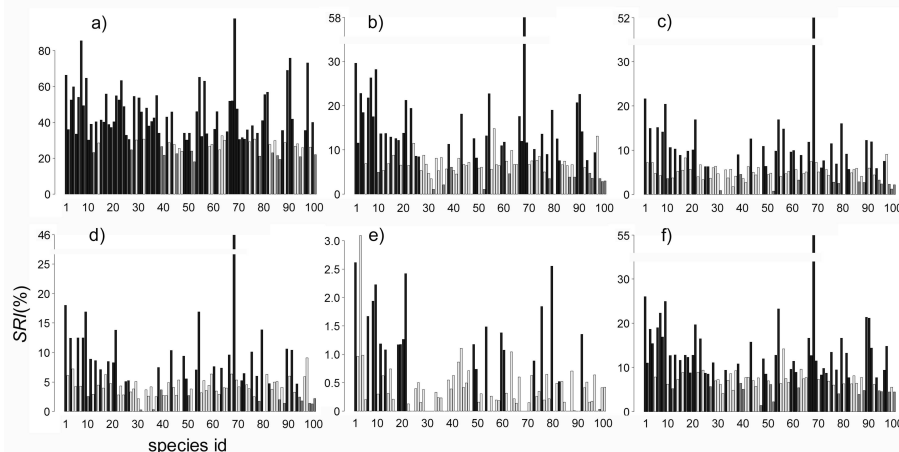


Figure 2. Species' representation levels (*SRI*) within Iberian Peninsula reserves for the baseline period. *SRI* values were obtained using the one-threshold approach applying five threshold values to reserve data, a) $R=0+$, b) $R=0.40$, c) $R=0.50$, d) $R=0.60$, e) $R=1$ and f) the continuous approach. Darker-grey bars indicate species with higher *SRI* values than 95% of a set of 1000 random areas, medium-grey bars indicate species with lower *SRI* values than 95% of random areas, lighter-grey bars indicate species whose *SRI* values are not significantly different from the random areas.

Within the range of threshold values, the majority of species' *SRI* curves followed very closely the accumulated frequency of reserve-coverage in Iberian Peninsula (Fig. S5, Supplementary material).

Because *SRI* co-vary with the occurrence of reserves across grid cells after application of a threshold, this pattern is likely to signal the species that have approximately equal probabilities of occurrence in the partially protected grid cells where they are predicted to occur (similar to *sp_A* in Fig. 1 and *Ceratophyllum demersum* in Fig. S4, Supplementary material), including both species with wide and restricted ranges (Table S1, Supplementary material). There were also species whose *SRI* departed from this trend, exhibiting *SRI* curves constantly over the reserve-coverage cumulative frequency curve (e.g., *Aconitum burnatii* in Fig. S4, Supplementary material) or constantly below the reserve-coverage cumulative frequency curve (e.g., *Fumaria gaillardotii* in Fig. S4, Supplementary material). Species that follow these patterns (similar to *sp_B* or *sp_C* in Fig. 1, respectively) are characterized by distributions biased towards higher and lower reserve coverage across grid cells, respectively. Species with restricted ranges are more sensitive to variations in threshold values. This translates into step patterns in the *SRI* curves. Flat sections originate when a range of threshold values does not change the protection status of the grid cells where the species have high probabilities to occur, while abrupt increases reflect substantial changes in the protection status of grid cells where species are very likely to occur.

The threshold values that resulted in *SRI* similar to those obtained with the continuous approach differed by species (Table S2a, Supplementary material). These R^* varied from 0.14 for *Sagina nodosa* (sp47) to 0.55 for *Silene behen* (sp56), with a mode in the 0.35 to 0.40 R^* class (Fig. S6, Supplementary material).

For 2080, there were no radical shifts in expected species' representations within the Iberian reserves when compared to the baseline period. With $R=0^+$, the three species with the highest *SRI* and the three species with the lowest were the same in 2080 and in the baseline period. Moreover, these species exhibited similar *SRI* for the both periods. With $R=1$, the three species with the highest *SRI* were *Silene boryi* (sp53: 3.2%), *Corydalis cava* (sp79: 3.1%) and *Ranunculus hederaceus* (sp75: 2.4%). As in the baseline period, 25 species were predicted to have no representation in reserves (Table S2b, Supplementary material). For intermediate threshold values (Fig. S5, Table S2b, Supplementary material), *SRI* varied in the same way as observed for the baseline period. Most species followed the cumulative reserve coverage curve, indicating that they are distributed equally among all the partially conserved grid cells. With the predicted shifts resulting from climate modifications in the Iberian Peninsula for 2080, portions of species' distributions in reserves are expected to change. Consequently, the relationship between *SRI* variation and threshold values is also expected to change. In fact, from the 100 plant species in the analysis, the sensitivities to threshold values for 27 species differed between the baseline period and 2080 (Fig. S5, Supplementary material). From these, 22 species had R^* that significantly differed between the baseline and 2080 (Fig. 3). *Silene behen* (sp56) had the most pronounced difference ($R^*=0.55$ in the baseline and $R^*=0.31$ in 2080). Overall, R^* values obtained for 2080 differed significantly from the R^* values for the baseline period (Wilcoxon signed-rank test: $W = 485$, $P\text{-value}<0.05$). For 2080, *Sagina nodosa* (sp47) had the lowest R^* ($R^*=0.14$), while *Corydalis cava* had the highest value (sp79: $R^*=0.49$) (Fig. S6, Table S2b, Supplementary material).

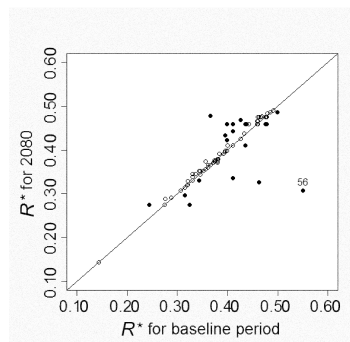


Figure 3. Threshold values that generate *SRI* values close to the *SRI* values obtained using the continuous approach (R^*) for the baseline period and 2080. Results are shown for 100 plant species in the Iberian Peninsula. The diagonal line represents similar values of R^* for both periods. Open circles identify species with similar values of R^* in both periods. Solid circles identify outlier species. A large difference between R^* in the baseline and 2080 periods is expected for *Silene behen* (sp56).

Randomization tests

Virtual data

We analyzed how different thresholds determine different appraisals of the performance of a virtual reserve when compared to random sets of areas with equivalent sizes. Species sp_A is characterized by a perfectly balanced distribution of probabilities across grid cells with different extents of reserve coverage. In this case, any redistribution of the s_i across the N grid cells resulted in an SRI smaller than or equal to the real value for both approaches (Table 4).

Table 4. Permutation assessments for the illustrative example presented in Table 2 and continued in Table 3. All possible redistributions of reserve coverage values (r_i) across species' probabilities of occurrence (s_i) are compared to the real (*real*) percent of species' range sizes within reserves (SRI) using several threshold values (R) and the continuous approach. The distribution of SRI values obtained from permutations is summarized by minimum (*min*) and maximum (*max*) SRI values and by the percentage of permutation events generating higher (*% higher*) and lower (*% lower*) SRI values than the real SRI .

		$R=0.90$	$R=0.75$	$R=0.60$	$R=0.45$	$R=0.30$	$R=0.20$	$R=0.10$	continuous
sp_A	<i>real SRI</i>	11.1	22.2	33.3	44.4	55.5	77.7	100	44.0
	<i>min-max</i>	0.0-11.1	11.1-22.2	22.2-33.3	33.3-44.4	44.4-55.5	66.6-77.7	88.8-100	33.4-44.4
	<i>% higher</i>	0.0*	0.0*	0.0*	0.0*	0.0*	0.0*	0.0*	0.0*
	<i>% lower</i>	10.0	20.0	30.0	40.0	50.0	70.0	90.0	90.0
sp_B	<i>real SRI</i>	25.0	50.0	100	100	100	100	100	74.0
	<i>min/max</i>	0.0-50.0	0.0-75.0	0.0-100	0.0-100	0.0-100	0.0-100	50.0-100	7.8-83.8
	<i>% higher</i>	10.0	4.4*	0.0*	0.0*	0.0*	0.0*	0.0*	2.2*
	<i>% lower</i>	70.0	77.8	99.2	96.7	91.7	70.8	30.0	97.5
sp_C	<i>real SRI</i>	0.0	0.0	0.0	0.0	25.0	55.0	90.0	21.4
	<i>min/max</i>	0.0-25.0	0.0-50.0	0.0-70.0	0.0-80.0	10.0-90.0	30.0-100	75.0-100	15.5-67.1
	<i>% higher</i>	60.0	86.7	96.7	99.5	92.9	76.7	40.0	98.4
	<i>% lower</i>	0.0*	0.0*	0.0*	0.0*	6.3	11.7	30.0	1.6*

* combinations of species and approaches for which reserves perform better (in *% higher*) or worse (in *% lower*) than 95% of the possible permutations.

Species sp_B has higher probabilities of occurrence in grid cells with larger reserve coverage and is absent from seven grid cells where $r_i < 0.60$. Therefore, for thresholds resulting in seven or fewer grid cells protected ($R > 0.17$), the minimum value for the SRI taken from permutations was $SRI=0$, which corresponded to the species representation in the grid cells where it is absent. Similarly, for threshold values that produced a reserve system composed of three or more grid cells ($R \leq 0.60$), the permutation retrieving the highest SRI ($SRI=100\%$) corresponded to the selection of grid cells $i=1, 2$ and 3 , which were the only grid cells where the species is expected to occur with $s_i > 0$. For this species, all thresholds except for $R=0.90$ produced reserve systems with higher representation than at least 95% of the selected random sets with equivalently sized grid cells. In the continuous approach species are also better represented in reserves than expected by chance. The minimum species representation level in reserves was obtained in permutations where the reserve coverage of grid cell $i=10$ ($r_i=0$) was assigned to the grid cells where the species has a greater probability of occurrence ($i=3$) and when the two other grid cells with a smaller reserve extent ($i=8$ and 9) were assigned to the other grid cells where the species occurs with a probability of 0.25 . In this case,

$$SRI = 0.17 \times 0.25 + 0.10 \times 0.25 + 0.00 \times 0.50 \times 100 = 7.8\%.$$

The higher permuted SRI value occurred when the grid cell with a larger reserve coverage ($i=1$) was assigned to the grid cell where the species occurs with a higher probability ($i=3$), while the two other grid cells with elevated reserve coverage ($i=2$ and 3) were assigned to $i=1$ and 2 . In this case,

$$SRI = 0.99 \times 0.50 + 0.77 \times 0.25 + 0.60 \times 0.25 \times 100 = 83.8\%.$$

In contrast to sp_B , the distribution of sp_C is biased towards grid cells with smaller reserve coverage.

When conservative to moderate threshold values ($R > 0.30$) were used sp_C appeared less represented in reserves than in random selected areas. The continuous approach produced the same result because the majority of the permutations redistributed grid cells with elevated r_i in the grid cells where the species occurs with some probability. That is by aligning grid cells 1 to 4 with non-zero species' probabilities, high values of reserve coverage weighted the species' local probability of occurrence, producing higher SRI than in the real distribution.

The Iberian Peninsula dataset

In the Iberian Peninsula dataset, randomization tests for the baseline and 2080 periods applied across the thresholds indicated better species representation in Iberian Peninsula reserves than in 95% of equivalent random choices of grid cells for most of the analyzed species (Fig. 2; Table S2a, Table S2b, Supplementary material). This was particularly true for the more optimistic threshold value ($R = 0^+$). In fact, like sp_A in the virtual data example (Table 2), most of the plant species in the analysis have approximately equitable distributions across partially-conserved grid cells (Fig. S5, Supplementary material), which make them better represented in reserves than expected by chance for most of the threshold values (P -value < 0.05). There was a general trend across species where increasing threshold values led to poorer performing reserves; however, some species presented contrasting patterns being less represented in reserves, even when using $R = 0^+$, than in most of the equivalent random sets (Fig. 2; Table S2a and Table S2b, Supplementary material). In contrast, one fifth of the species continued to be better represented in reserves, that were produced with the more stringent threshold value ($R = 1$), than expected by chance.

With the continuous approach, the Iberian reserves were expected to perform better than expected by chance for about half of the species and to perform worst for one tenth of the species. This result was similar for the baseline period and 2080, although for 29 species' levels of significance varied (i.e., P -values; see Table S2a, Table S2b, Supplementary material). Similarly for some species, reserve systems obtained using equivalent thresholds (R^*) performed differently from the continuous approach. Once again, differences came only from levels of significance.

DISCUSSION

Uncertainty in conservation planning arises from a variety of sources such as information gaps, natural system dynamics, several descriptive modeling architectures and contextual misunderstandings (Elith *et al.* 2002; Regan *et al.* 2009). Here we assess a particular source of uncertainty influencing the interpretation and adequate implementation of gap analysis in conservation planning: the decision as to whether grid cells should be considered fully conserved when reserves only partially cover the grid cells being analyzed. The common approach to circumvent such a problem is to choose an arbitrary and fixed threshold that converts the grid cell into being either protected or unprotected. However thresholds affect the perception of whether species are to be considered well represented or underrepresented in reserves (see Fig 2). In this study, we propose an approach to estimate species' representation in reserves that circumvents problems associated with the use of arbitrary thresholds to match species with reserves.

As discussed above, the definition of SRI given by Eq. (1) accommodates conventional threshold approaches, where just one or both of the species and reserve datasets are converted to a binary classification system (i.e., presence/ absence). However, the major benefit of the proposed SRI is its capacity to use the full breadth of information (i.e., continuous data) regarding species' distributions and reserve coverage (i.e., the continuous approach). By avoiding thresholds and calculating the proportion of the grid cell i where species' ranges coincide with reserves, $r_i.s_i$, we can also estimate the proportion of the grid cell where species' range is not confined into reserves, $(1-r_i).s_i$. Assuming that a species has a uniform probability of occurrence inside grid cell i , these proportions can be directly read as the probabilities of occurrence inside and outside reserves. Such inferences may then be used in the context of probability-based reserve selection algorithms (Polasky *et al.* 2000; Williams & Araújo 2002; Cabeza *et*

al. 2004). Importantly, the suggested approach presents low variance, and is thus a robust measure to be used in gap analysis.

Several target-based conservation programs are based upon population viability analysis (Cabeza & Moilanen 2001; Rondinini & Chioza 2010) in which demographic data (e.g., abundance) are used as a proxy of species persistence in reserves (Faith *et al.* 2003; Godet *et al.* 2007; Grouios & Manne 2009). To assess a species' representation level in reserves, given the abundances a_i of the species in each grid cell i , Eq. (1) can be used with s_i replaced by a_i . As for occurrence data, the continuous approach consists of taking f and g as the identity function with the following probabilistic interpretation: $a_i r_i$ is the expected value of the random variable representing the number of individuals (assumed to be randomly located in the grid cell) occurring in the reserve, which has a binomial distribution with parameters a_i and r_i .

Because reserves are often actively managed to minimize threats (Gaston *et al.* 2002), species are more likely to be present, to be abundant and to have higher rates of increase within reserves than in equivalent sized non-protected areas (Hopkinson *et al.* 2000; Caro *et al.* 2009). To incorporate in *SRI* such non-independence between the species conservation achievement and the degree of protection of the grid cells, we can use function f (with values ranging in $[0,1]$) in Eq. 1 to weight reserves against non-protected areas. This gives

$$SRI = \frac{\sum_{i=1}^N f(r_i) \cdot s_i}{\sum_{i=1}^N s_i} . \quad (2)$$

Values of $f(r_i) > r_i$ ($f(r_i) < r_i$) would contribute to increase (decrease) *SRI*, expressing that the species tends to favor (avoid) reserves over non-protected areas. This has the following probabilistic interpretation. Each parcel in the numerator can be interpreted as the product of the species probability of occurrence in grid cell i , s_i , by the conditional probability that the species is in the reserved area given that it occurs in the grid cell, $f(r_i)$. This product is precisely the probability that the species is represented in the grid cell's protected fraction. If reserves have no effect on the presence of species, the conditional probability $f(r_i)$ is simply the fraction of grid cell i under protection, i.e., $f(r_i) = r_i$. If the species tend to favor (avoid) reserves over non-protected areas, then the conditional probability $f(r_i)$ is greater (lower, resp.) than r_i . Interestingly, this interpretation also relates threshold-based approaches with the continuous application. If a specific threshold R generates a *SRI* higher than the one obtained by the continuous approach, then it is implicitly assumed that the species is attracted by reserve systems. If the choice of the threshold produces a lower *SRI* than the one from the continuous application, an undesirable effect of reserves on species is assumed. If the *SRI* obtained by the threshold and the continuous approaches converge (R^*), then a neutral effect of reserves is accepted.

Dynamic threats do probably intervene in the redistribution of species. Species are likely to change their distributions towards newly suitable regions, and therefore their representation levels in static reserves are likely to be altered (Heller & Zavaleta 2009). Assessments of trends in reserve representativeness are therefore adequate to anticipate such changes (Dockerty *et al.* 2003; Leroux *et al.* 2007; Hole *et al.* 2009; Kharouba & Kerr 2010; Kujala *et al.* submitted). However, this dynamic component of biodiversity does not fit the common use of fixed thresholds for matching species and reserves in different timeframes. Here, we have seen that R^* is likely to change as species change their distributions in time (Fig. 3; Table S2a, Table S2b, Supplementary material). Therefore, while it seems incorrect to maintain the same threshold value to assess a species occurrence in reserves over time, the definition of two arbitrary and uninformed threshold values would also probably make the analysis flawed.

For many species, the quantification of suitability gains and losses within reserves depends on the threshold selected. For example, *Cystopteris montana* (sp7) and *Ulmus glabra* (sp21) appear to be winners from the baseline period to 2080 when applying $R=0.40$, while when applying $R=0.50$, they appear to be losers (Fig. 4; Table S2c, Supplementary material). In contrast, *Malcolmia ramosissima* (sp87) is predicted to be a loser species when $R=0.40$ and a winner species when $R=0.50$. A species specific threshold like that implicitly defined by the continuous approach seems to be more adequate because it

uses (consistently) the full breath of distributional information for each species in order to derive species suitability trends in protected areas (Araújo *et al.* 2011).

The performance of quantitative conservation plans is constrained by the quality of input data (Cabeza & Moilanen 2001; Meir *et al.* 2004; Grand *et al.* 2007). Conventional threshold-based assessments of species' representations in reserves are prone to distributional errors (i.e., omission and commission errors, Rondinini *et al.* 2006) as grid cells are assumed totally protected or not protected at all. As more grid cells are analyzed in regional assessments, these errors are likely to accumulate, leading to flawed results on reserve representativeness. Some species will appear less represented in reserves than they actually are, while others will be erroneously assumed to be over-represented. Reserve selection algorithms based on these analyses are likely to produce costly, inefficient solutions (Wilson *et al.* 2009). The continuous approach presented here produces a fine-tuned quantitative assessment of species' representation within reserves when using grid-data and it thus deflates omission and commission errors.

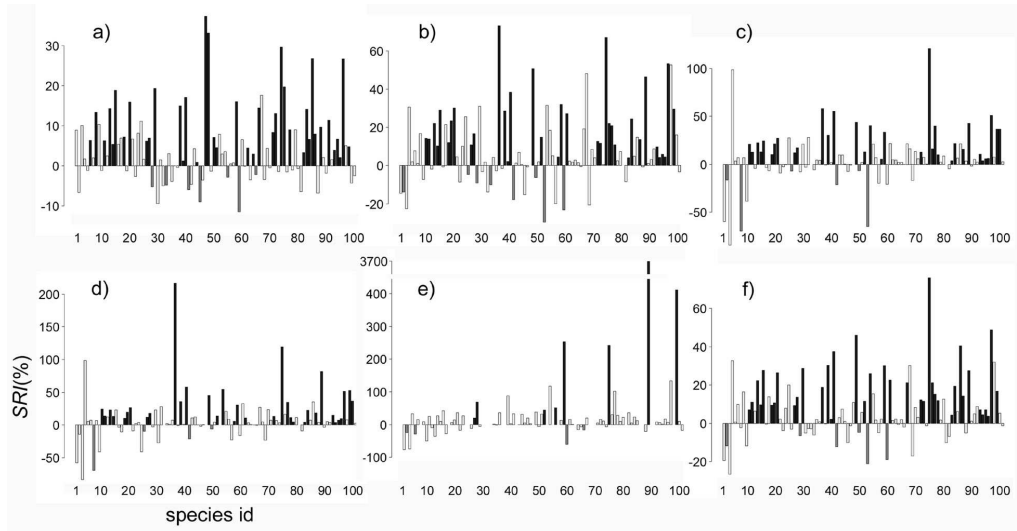


Figure 4. Analysis of the percentage variation in species' representation in reserves (*SRI%*) from the baseline period to 2080 using the one-threshold approach applying five threshold values to reserve data, a) $R=0^+$, b) $R=0.40$, c) $R=0.50$, d) $R=0.60$, e) $R=1$ and f) the continuous approach. Darker-grey bars indicate species with higher *SRI* values than 95% of a set of 1000 random areas, medium-grey bars indicate species with lower *SRI* values than 95% of random areas, lighter-grey bars indicate species whose *SRI* values are not significantly different from the random areas.

CONCLUSIONS

We demonstrated that conservation planning is sensitive to errors arising from arbitrary decisions used to match species' distributions and reserve coverage data that are originally mapped at different resolutions. These errors are seldom quantified leading to inefficiencies in the analysis of reserve performance. Here we present an approach that directly uses the full breadth of available data for species' distributions and reserve coverage, in order to match species with reserves in a more effective and rigorous manner. Our approach has several advantages: 1) it allows to use species' probabilities of occurrence (i.e., [0,1] rather than binary data) and reserve coverage (i.e., continuous approach); 2) it can work with species' abundance data instead of probabilities of occurrence; 3) it allows to specify, for each species, the (equivalent) threshold R^* for which threshold-based and continuous approaches coincide; 4) it handles situations when species are more (or less) likely to occur in reserves (i.e., attractiveness); 5) it provides an interpretation of the threshold-based outcomes in terms of the species' reserve attractiveness, by comparison with the continuous approach; and finally 6) it is easy to compute.

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SUPPLEMENTARY MATERIAL

A PROBABILITY-BASED APPROACH TO MATCH SPECIES WITH RESERVES WHEN DATA ARE AT DIFFERENT RESOLUTIONS

Table S1. Species distribution data for Iberian Peninsula for the baseline period and 2080. Observed presence/absence data are summarized by the grid cell range (number of grid cells where species has been observed) and relative grid cell range (proportion of Iberian Peninsula grid cells where species has been observed). Predicted data from bioclimatic models summarize the probability-based range (sum of all probability values for species in Iberian Peninsula) and relative probability-based range (probability-based range divided by number of grid cells in the Iberian Peninsula map).

id	Name	baseline period				2080	
		observed		predicted		predicted	
		cell range	relative cell range	probab range	relative probab range	probab range	relative probab range
1	<i>Selaginella selaginoides</i>	139	0.06	63.56	0.03	15.58	0.01
2	<i>Isoetes velata</i>	191	0.08	44.62	0.02	36.07	0.02
3	<i>Equisetum sylvaticum</i>	55	0.02	27.91	0.01	8.91	0.00
4	<i>Trichomanes speciosum</i>	50	0.02	7.34	0.00	3.36	0.00
5	<i>Asplenium onopteris</i>	759	0.33	384.17	0.17	394.54	0.17
6	<i>Asplenium septentrionale</i>	351	0.15	118.80	0.05	56.42	0.02
7	<i>Cystopteris montana</i>	27	0.01	9.53	0.00	4.13	0.00
8	<i>Polystichum aculeatum</i>	316	0.14	147.58	0.06	75.87	0.03
9	<i>Gymnocarpium dryopteris</i>	146	0.06	74.64	0.03	25.62	0.01
10	<i>Pinus halepensis</i>	739	0.32	322.40	0.14	359.88	0.16
11	<i>Juniperus communis</i>	803	0.35	429.03	0.19	246.20	0.11
12	<i>Juniperus thurifera</i>	335	0.15	165.16	0.07	24.91	0.01
13	<i>Taxus baccata</i>	685	0.30	290.48	0.13	145.65	0.06
14	<i>Salix atrocinerea</i>	1531	0.66	764.78	0.33	319.51	0.14
15	<i>Populus tremula</i>	407	0.18	247.42	0.11	107.40	0.05
16	<i>Juglans regia</i>	296	0.13	75.44	0.03	67.98	0.03
17	<i>Betula pendula</i>	117	0.05	83.58	0.04	43.37	0.02
18	<i>Corylus avellana</i>	933	0.40	527.07	0.23	361.64	0.16
19	<i>Quercus ilex</i>	486	0.21	221.95	0.10	270.40	0.12
20	<i>Quercus petraea</i>	459	0.20	298.79	0.13	164.89	0.07
21	<i>Ulmus glabra</i>	314	0.14	144.17	0.06	65.01	0.03
22	<i>Osyris quadripartita</i>	198	0.09	79.09	0.03	70.23	0.03
23	<i>Thesium alpinum</i>	96	0.04	26.87	0.01	14.76	0.01
24	<i>Polygonum alpinum</i>	83	0.04	13.70	0.01	5.79	0.00
25	<i>Fallopia convolvulus</i>	1211	0.52	643.67	0.28	516.84	0.22
26	<i>Rumex acetosella</i>	1531	0.66	1048.96	0.45	710.91	0.31
27	<i>Rumex tingitanus</i>	577	0.25	155.78	0.07	156.43	0.07
28	<i>Emex spinosa</i>	332	0.14	177.16	0.08	233.93	0.10
29	<i>Polycnemum majus</i>	185	0.08	47.71	0.02	29.87	0.01
30	<i>Atriplex laciniata</i>	91	0.04	9.63	0.00	12.78	0.01
31	<i>Atriplex littoralis</i>	95	0.04	16.87	0.01	19.41	0.01
32	<i>Salicornia procumbens</i>	78	0.03	16.96	0.01	13.15	0.01
33	<i>Salsola soda</i>	369	0.16	150.65	0.07	225.10	0.10
34	<i>Amaranthus graecizans</i>	418	0.18	164.07	0.07	218.82	0.09
35	<i>Amaranthus lividus</i>	369	0.16	92.93	0.04	146.99	0.06
36	<i>Aizoon hispanicum</i>	169	0.07	49.18	0.02	54.68	0.02
37	<i>Mesembryanthemum nodiflorum</i>	225	0.10	121.15	0.05	141.73	0.06
38	<i>Arenaria grandiflora</i>	667	0.29	280.14	0.12	93.52	0.04
39	<i>Arenaria leptoclados</i>	2092	0.91	1487.58	0.64	1389.12	0.60
40	<i>Arenaria obtusiflora</i>	446	0.19	236.05	0.10	73.60	0.03
41	<i>Minuartia mediterranea</i>	195	0.08	45.30	0.02	73.72	0.03
42	<i>Minuartia hamata</i>	386	0.17	143.62	0.06	51.03	0.02
43	<i>Minuartia verna</i>	267	0.12	94.11	0.04	82.18	0.04
44	<i>Stellaria media</i>	2306	1.00	1907.24	0.83	1333.66	0.58
45	<i>Cerastium perfoliatum</i>	294	0.13	76.32	0.03	16.96	0.01

46	<i>Cerastium diffusum</i>	649	0.28	375.68	0.16	149.28	0.06
47	<i>Sagina nodosa</i>	54	0.02	12.97	0.01	5.28	0.00
48	<i>Paronychia kapela</i>	449	0.19	141.89	0.06	83.71	0.04
49	<i>Spergula arvensis</i>	1286	0.56	713.53	0.31	529.40	0.23
50	<i>Spergularia maritima</i>	606	0.26	246.85	0.11	231.47	0.10
51	<i>Agrostemma githago</i>	1390	0.60	770.34	0.33	767.28	0.33
52	<i>Silene uniflora</i>	139	0.06	90.75	0.04	33.95	0.01
53	<i>Silene boryi</i>	215	0.09	46.06	0.02	19.50	0.01
54	<i>Silene pusilla</i>	32	0.01	9.30	0.00	7.92	0.00
55	<i>Silene inaperta</i>	838	0.36	278.13	0.12	249.40	0.11
56	<i>Silene behen</i>	33	0.01	5.91	0.00	13.52	0.01
57	<i>Silene nocturna</i>	1254	0.54	701.47	0.30	802.54	0.35
58	<i>Cucubalus baccifer</i>	724	0.31	288.26	0.12	193.57	0.08
59	<i>Saponaria glutinosa</i>	210	0.09	54.32	0.02	35.71	0.02
60	<i>Dianthus subacaulis</i>	344	0.15	81.27	0.04	31.80	0.01
61	<i>Dianthus serrulatus</i>	441	0.19	140.30	0.06	123.17	0.05
62	<i>Nymphaea alba</i>	547	0.24	144.56	0.06	104.00	0.05
63	<i>Nuphar lutea</i>	222	0.10	38.42	0.02	23.40	0.01
64	<i>Ceratophyllum demersum</i>	611	0.26	195.92	0.08	217.98	0.09
65	<i>Nigella damascena</i>	978	0.42	622.19	0.27	742.04	0.32
66	<i>Aconitum lycoctonum</i>	280	0.12	98.88	0.04	50.16	0.02
67	<i>Aconitum anthora</i>	99	0.04	17.05	0.01	12.70	0.01
68	<i>Aconitum burnatii</i>	24	0.01	3.43	0.00	1.40	0.00
69	<i>Clematis recta</i>	158	0.07	23.67	0.01	25.88	0.01
70	<i>Ranunculus muricatus</i>	1127	0.49	670.55	0.29	753.80	0.33
71	<i>Ranunculus parviflorus</i>	1076	0.47	544.38	0.24	477.95	0.21
72	<i>Ranunculus flammula</i>	923	0.40	504.70	0.22	251.37	0.11
73	<i>Ranunculus ophioglossifolius</i>	546	0.24	254.38	0.11	299.87	0.13
74	<i>Ranunculus lateriflorus</i>	158	0.07	37.72	0.02	22.59	0.01
75	<i>Ranunculus hederaceus</i>	628	0.27	186.21	0.08	56.95	0.02
76	<i>Ranunculus tripartitus</i>	355	0.15	98.82	0.04	123.67	0.05
77	<i>Papaver dubium</i>	1026	0.44	587.47	0.25	387.79	0.17
78	<i>Roemeria hybrida</i>	1371	0.59	830.12	0.36	619.03	0.27
79	<i>Corydalis cava</i>	195	0.08	51.33	0.02	49.35	0.02
80	<i>Fumaria gaillardotii</i>	40	0.02	12.38	0.01	26.32	0.01
81	<i>Fumaria sepium</i>	174	0.08	88.64	0.04	132.96	0.06
82	<i>Sisymbrium officinale</i>	1882	0.81	1484.29	0.64	1314.51	0.57
83	<i>Descurainia sophia</i>	1033	0.45	614.33	0.27	273.15	0.12
84	<i>Erysimum cheiri</i>	461	0.20	150.91	0.07	94.72	0.04
85	<i>Erysimum linifolium</i>	308	0.13	95.33	0.04	46.40	0.02
86	<i>Malcolmia triloba</i>	547	0.24	135.64	0.06	92.59	0.04
87	<i>Malcolmia ramosissima</i>	106	0.05	55.53	0.02	55.73	0.02
88	<i>Malcolmia africana</i>	467	0.20	175.13	0.08	114.29	0.05
89	<i>Cardamine resedifolia</i>	113	0.05	26.06	0.01	15.33	0.01
90	<i>Cardamine bellidifolia</i>	40	0.02	10.80	0.00	2.09	0.00
91	<i>Cardamine flexuosa</i>	539	0.23	289.61	0.13	121.44	0.05
92	<i>Clypeola jonthlaspi</i>	964	0.42	546.31	0.24	454.16	0.20
93	<i>Erophila verna</i>	1723	0.75	1354.24	0.59	1172.86	0.51
94	<i>Camelina microcarpa</i>	1183	0.51	574.61	0.25	331.13	0.14
95	<i>Hymenolobus procumbens</i>	775	0.34	332.39	0.14	323.13	0.14
96	<i>Iberis amara</i>	352	0.15	89.61	0.04	37.43	0.02
97	<i>Biscutella cichoriifolia</i>	37	0.02	7.19	0.00	10.10	0.00
98	<i>Diplotaxis erucoides</i>	915	0.40	431.33	0.19	457.40	0.20
99	<i>Brassica fruticulosa</i>	173	0.07	48.81	0.02	83.84	0.04
100	<i>Crambe hispanica</i>	305	0.13	70.58	0.03	105.22	0.05

Table A2a Species' representation indices (SRI) in the baseline period for 100 plant species in Iberian Peninsula using a sequence of 11 threshold criteria, R (in grid cell areal proportion), the continuous approach, and the equivalent threshold, R^* (threshold value in parenthesis). A null model was performed in order to evaluate if SRI are significantly different from SRI produced with random trials ($n=9999$). +++, ++, + for values higher than the 99.9th, 99th and 95th percentiles, ---, --, - for values lower than the 0.1th, 1st and 5th percentiles. Non-significant values are not marked by any sign.

id	R=0.00	R=0.10	R=0.20	R=0.30	R=0.40	R=0.50	R=0.60	R=0.70	R=0.80	R=0.90	R=1	continuous	R*
1	66.27+++	50.42+++	37.15+++	33.26+++	29.62+++	21.66+++	18.03+++	15.72+++	10.52+++	7.53+++	2.61+	26.02+++	24.84+++ (0.48)
2	36.01+	26.73+++	17.41+	13.57+	11.59+	7.19	6.10	4.68	3.57	2.40	0.96	11.06+	10.62 (0.43)
3	52.50+++	35.04++	28.38++	23.17++	22.78+++	15.00+	12.42+	9.92+	6.73	6.73+	3.09	18.65+++	18.44 (0.48)
4	59.84+++	33.95++	29.61+++	18.51+	18.51++	7.22	7.22	7.22	6.84	3.15	0.98	15.41+	15.34 (0.43)
5	33.48+++	18.99++	13.67+	9.54	6.92	4.79	4.21	3.09	1.95	1.41	0.20	7.90	7.8-- (0.36)
6	53.89+++	36.18+++	27.28+++	24.17+++	21.81+++	15.15+++	12.50+++	10.22+++	8.84+++	7.07+++	1.66++	19.00+++	18.72+++ (0.48)
7	85.56+++	62.78+++	45.65+++	28.75+	26.31++	4.30	4.30	4.30	2.12	2.12	0.00	22.32++	19.78 (0.46)
8	49.33+++	31.55+++	24.53+++	20.92+++	17.53+++	14.18+++	12.51+++	9.7+++	6.76+++	5.67+++	1.93+++	16.93+++	16.71+ (0.46)
9	64.60+++	47.84+++	35.56+++	31.80+++	28.20+++	20.41+++	16.91+++	14.68+++	10.44+++	8.00+++	2.23+	24.97+++	24.02+++ (0.48)
10	30.18+	15.19	10.99	7.72	4.94-	3.59-	2.56-	2.28	1.58	1.01	0.30	6.22	5.85-- (0.35)
11	39.00+++	24.64+++	18.84+++	15.73+++	13.71+++	10.63+++	8.87+++	7.37+++	5.30+++	4.00+++	1.18+++	12.75+++	12.54 (0.46)
12	23.19-	13.00	7.63-	6.41	5.38	3.77	2.90	1.97	1.32	0.96	0.62	5.21-	4.94-- (0.41)
13	40.26+++	25.45+++	19.46+++	16.43+++	13.73+++	10.29+++	8.65+++	6.87+++	4.95+++	3.82+++	1.08++	12.88+++	12.6 (0.46)
14	28.50	15.84	12.01	8.79	6.94	5.21	4.48	3.61	2.14	1.54	0.31	7.36	7.14-- (0.38)
15	41.35+++	24.42+++	17.64+++	14.74+++	12.92+++	8.89+++	7.10++	5.72+	3.95+	3.21+	0.74	11.66+++	11.48 (0.46)
16	40.16+++	19.87+	16.24+	12.02+	8.79	5.54	3.96	3.01	2.67	1.49	0.21	8.92	8.79-- (0.4)
17	55.72+++	29.77+++	21.73++	16.53++	12.63++	8.29	6.27	5.24	2.75	1.60	0.00	12.83+++	12.63 (0.4)
18	38.81+++	24.34+++	18.95+++	15.26+++	12.19+++	9.81+++	8.50+++	7.15+++	4.89+++	3.75+++	1.17+++	12.35+++	12.24 (0.4)
19	37.07+++	20.32++	14.58+	10.30	6.57	5.71	4.72	4.27	2.59	2.22	1.17+	8.80+	8.74-- (0.33)
20	40.33+++	24.95+++	18.94+++	15.56+++	13.80+++	10.13+++	8.31+++	7.06+++	4.61++	4.02+++	1.26++	12.77+++	12.74 (0.46)
21	54.74+++	36.98+++	30.04+++	24.79+++	21.23+++	16.95+++	13.83+++	11.23+++	7.27+++	5.89+++	2.42++	19.67+++	19.56+++ (0.47)
22	52.46+++	24.14++	15.75+	9.89	6.50	4.00	2.83	1.82	0.75	0.39	0.13	8.98	8.12-- (0.31)
23	63.30+++	41.01+++	31.43+++	23.53+++	19.41+++	6.70	4.33	4.33	2.42	2.42	0.00	16.52++	13.85 (0.48)
24	48.72++	21.35	18.73	13.41	11.52	3.34	2.79	0.00	0.00	0.00	0.00	9.43	8.77 (0.46)
25	32.83+++	18.71+++	14.23+++	11.44+++	8.65+++	6.32++	5.09++	3.91	2.90+	2.14+	0.39	8.72+++	8.69-- (0.4)
26	30.50+++	17.97+++	13.25+++	10.44+++	8.51+++	6.29+++	5.25+++	4.32+++	3.03++	2.36+++	0.50	8.55+++	8.51-- (0.4)
27	24.56-	12.77-	8.73-	6.96	5.39	3.67	3.34	2.77	2.09	1.46	0.15	5.70-	5.6-- (0.39)
28	54.42+++	29.61+++	19.86+++	12.73++	8.79	6.06	3.84	3.33	2.17	1.25	0.38	11.12++	10.92 (0.32)
29	30.18	13.26	10.61	8.49	6.80	6.42	5.09	3.71	1.45	1.45	0.00	7.02	6.8-- (0.37)
30	53.57+++	15.96	9.87	6.33	4.71	4.71	2.13	2.13	0.00	0.00	0.00	7.26	6.88-- (0.29)
31	45.80+++	18.88	11.51	4.59	3.47	0.91-	0.29-	0.29-	0.29	0.00	0.00	6.21	5.63-- (0.27)

32	30.64	15.58	7.91	3.46 ⁻	1.10 ⁻	0.00 ⁻	0.00 ⁻	0.00	0.00	0.00	0.00	4.15	3.77 ⁻ (0.24)
33	48.04 ⁺⁺⁺	23.98 ⁺⁺⁺	16.06 ⁺⁺	10.74	8.13	5.60	3.66	3.27	1.93	0.91	0.33	9.45 ⁺	9.12 ⁻ (0.35)
34	38.02 ⁺⁺⁺	17.98	12.98	8.34	5.30	3.73	2.61	2.11	1.05 ⁻	0.49 ⁻	0.24	7.14	7 ⁻ (0.33)
35	40.39 ⁺⁺⁺	19.51 ⁺	14.96 ⁺	11.21 ⁺	8.25	5.73	4.16	4.16	3.07	1.52	0.23	8.62	8.58 ⁻ (0.39)
36	42.44 ⁺⁺⁺	12.99	9.03	5.42	2.13 ⁻	1.82	0.34 ⁻	0.34 ⁻	0.12 ⁻	0.00	0.00	4.87	4.21 ⁻ (0.32)
37	54.97 ⁺⁺⁺	27.09 ⁺⁺⁺	16.89 ⁺⁺	9.68	5.74	4.18	2.50	1.82	0.00 ⁻	0.00 ⁻	0.00	9.30	9.19 ⁻ (0.31)
38	33.92 ⁺⁺⁺	21.30 ⁺⁺⁺	16.51 ⁺⁺⁺	13.56 ⁺⁺⁺	11.33 ⁺⁺⁺	9.00 ⁺⁺⁺	7.47 ⁺⁺⁺	6.37 ⁺⁺⁺	4.17 ⁺⁺⁺	2.98 ⁺⁺	0.55	10.88 ⁺⁺⁺	10.72 ⁻ (0.46)
39	26.46 ⁻	14.20 ⁻	10.38 ⁻	7.85 ⁻	6.09 ⁻	4.58 ⁻	3.67 ⁻	2.98 ⁻	2.07	1.49	0.39	6.48 ⁻	6.43 ⁻ (0.38)
40	21.65 ⁻	11.72 ⁻	7.08 ⁻	6.25 ⁻	5.39	3.61	2.71	2.23	1.82	1.51	0.63	5.09 ⁻	5.08 ⁻ (0.41)
41	42.98 ⁺⁺⁺	22.16 ⁺⁺	14.45	6.48	4.55	2.72	2.72	2.72	1.09	1.09	0.00	7.73	7.66 ⁻ (0.28)
42	28.59	16.06	11.97	9.70	8.17	6.31	4.87	4.18	3.09	1.84	0.86	7.83	7.82 ⁻ (0.41)
43	45.82 ⁺⁺⁺	31.05 ⁺⁺⁺	23.67 ⁺⁺⁺	20.46 ⁺⁺⁺	18.14 ⁺⁺⁺	12.6 ⁺⁺⁺	10.35 ⁺⁺⁺	8.67 ⁺⁺⁺	5.96 ⁺⁺⁺	4.48 ⁺⁺⁺	1.11	15.81 ⁺⁺⁺	15.22(0.48)
44	27.61	15.42	11.33	8.62	6.69	5.04	4.07	3.32	2.23	1.62	0.42	7.05	6.99 ⁻ (0.38)
45	22.41 ⁻	13.15	8.83	7.53	6.46	4.40	2.78	2.61	2.05	1.12	0.49	5.79	5.47 ⁻ (0.44)
46	25.49	15.27	12.22	9.14	7.17	6.13	5.37	4.28	2.61	2.09	0.71	7.70	7.34 ⁻ (0.38)
47	23.75	6.97	0.00 ⁻	0.00 ⁻	0.00 ⁻	0.00	0.00	0.00	0.00	0.00	0.00	1.45 ⁻	0 ⁻ (0.14)
48	33.95 ⁺⁺	22.32 ⁺⁺⁺	16.40 ⁺⁺⁺	14.21 ⁺⁺⁺	12.6 ⁺⁺⁺	10.90 ⁺⁺⁺	9.41 ⁺⁺⁺	8.18 ⁺⁺⁺	5.39 ⁺⁺⁺	4.04 ⁺⁺⁺	1.17 ⁺	11.97 ⁺⁺⁺	11.67(0.46)
49	30.04 ⁺⁺	17.58 ⁺⁺⁺	13.33 ⁺⁺	10.09 ⁺	8.18 ⁺⁺⁺	6.41 ⁺⁺⁺	5.53 ⁺⁺⁺	4.64 ⁺⁺⁺	3.12 ⁺⁺	2.31 ⁺⁺	0.74 ⁺⁺	8.54 ⁺⁺⁺	8.5 ⁻ (0.38)
50	33.98 ⁺⁺⁺	17.72 ⁺	12.37	8.64	5.93	4.50	2.69 ⁻	2.39	1.37	0.80 ⁻	0.16	6.99	6.84 ⁻ (0.34)
51	23.95 ⁻	13.36 ⁻	9.52 ⁻	7.65 ⁻	6.13	4.81	3.82	2.87	1.96	1.65	0.30	6.21 ⁻	6.17 ⁻ (0.4)
52	17.99 ⁻	6.92 ⁻	4.99 ⁻	2.66 ⁻	1.09 ⁻	0.76 ⁻	0.00 ⁻	0.00 ⁻	0.00 ⁻	0.00	0.00	2.23 ⁻	1.89 ⁻ (0.32)
53	45.93 ⁺⁺⁺	25.82 ⁺⁺⁺	20.88 ⁺⁺⁺	17.86 ⁺⁺⁺	13.22 ⁺⁺⁺	9.80 ⁺⁺	7.05 ⁺	5.92 ⁺	4.90 ⁺	3.24 ⁺	1.48 ⁺	12.83 ⁺⁺⁺	12.4(0.41)
54	65.12 ⁺⁺⁺	48.39 ⁺⁺⁺	36.81 ⁺⁺⁺	27.47 ⁺⁺⁺	22.75 ⁺⁺⁺	16.92 ⁺⁺	16.92 ⁺⁺	16.92 ⁺⁺⁺	8.53 ⁺	4.18	0.00	23.26 ⁺⁺⁺	22.75 ⁺ (0.37)
55	32.06 ⁺⁺⁺	15.08	10.41	7.22	5.65	4.06	3.15	2.44	1.91	1.14	0.26	6.39	6.28 ⁻ (0.35)
56	62.90 ⁺⁺⁺	28.92	26.35 ⁺	18.18	14.85	14.85 ⁺	5.23	5.23	0.00	0.00	0.00	14.23	8.18(0.55)
57	33.67 ⁺⁺⁺	18.04 ⁺⁺⁺	12.62 ⁺	9.26	6.67	4.73	3.56	2.94	2.20	1.45	0.19	7.54	7.54 ⁻ (0.36)
58	26.69	14.57	10.96	7.99	6.45	5.22	4.45	2.39	1.16 ⁻	1.12	0.18	6.64	6.5 ⁻ (0.4)
59	27.64	19.69	12.91	12.82 ⁺	10.97 ⁺	9.63 ⁺⁺	6.38	5.63 ⁺	4.55 ⁺	2.84	1.38 ⁺	9.65 ⁺	9.63 ⁻ (0.5)
60	36.20 ⁺⁺	22.76 ⁺⁺⁺	15.76 ⁺	14.8 ⁺⁺⁺	11.76 ⁺⁺⁺	9.95 ⁺⁺⁺	7.62 ⁺⁺	6.47 ⁺⁺⁺	5.23 ⁺⁺	3.54 ⁺	1.07 ⁺	11.44 ⁺⁺⁺	11.4(0.47)
61	45.91 ⁺⁺⁺	22.32 ⁺⁺⁺	14.65 ⁺	10.17	7.47	5.62	3.46	2.89	1.89	1.10	0.31	8.94 ⁺	8.93 ⁻ (0.32)
62	24.60	13.40	9.77	6.29 ⁻	4.62 ⁻	3.29 ⁻	2.93	2.35	1.09 ⁻	0.97	0.00	5.46 ⁻	5.45 ⁻ (0.35)
63	32.44	18.84	12.88	10.79	9.91	8.88 ⁺	7.39 ⁺	6.44 ⁺	5.24 ⁺	2.23	1.04	9.61	9.43(0.48)
64	30.03	17.85 ⁺	12.53	8.31	6.73	4.78	4.05	3.47	2.11	1.45	0.21	7.46	7.43 ⁻ (0.35)
65	34.79 ⁺⁺⁺	18.33 ⁺⁺	13.01 ⁺	9.41	6.69	5.08	3.99	3.35	2.20	1.30	0.13	7.75	7.66 ⁻ (0.35)
66	51.82 ⁺⁺⁺	35.37 ⁺⁺⁺	27.72 ⁺⁺⁺	22.51 ⁺⁺⁺	17.60 ⁺⁺⁺	11.87 ⁺⁺⁺	9.58 ⁺⁺⁺	8.46 ⁺⁺⁺	5.52 ⁺⁺	3.82 ⁺	0.60	16.68 ⁺⁺⁺	16.68 ⁺ (0.46)
67	51.98 ⁺⁺⁺	29.19 ⁺⁺⁺	20.85 ⁺⁺	17.42 ⁺⁺	11.98 ⁺	7.44	6.36	6.36	3.96	2.73	0.00	12.73 ⁺⁺	11.98(0.4)

68	97.73+++	76.62+++	76.54+++	76.48+++	58.41+++	52.40+++	45.79+++	45.79+++	44.13+++	31.94+++	0.00	54.85+++	52.4+++ (0.49)
69	47.51+++	26.62++	19.73++	16.31++	11.67+	7.24	5.36	3.88	1.66	1.66	0.00	11.55+	10.55 (0.46)
70	30.41++	16.73+	12.06	9.03	6.70	5.07	4.20	3.31	2.19	1.41	0.15	7.36	7.32~ (0.37)
71	31.41+++	18.15+++	13.40++	9.60	7.55	6.06+	5.22++	4.09+	2.72	1.95	0.62	8.33++	8.32~ (0.36)
72	30.55+	19.68+++	15.17+++	12.11+++	10.15+++	7.66+++	6.44+++	5.47+++	3.68+++	2.97++	0.88++	9.83+++	9.72~ (0.44)
73	35.70+++	20.83+++	14.44+	9.71	7.65	5.65	4.54	3.97	2.67	1.98	0.26	8.75+	8.55~ (0.37)
74	29.05	15.11	10.58	8.53	8.53	4.35	3.85	3.00	1.90	0.93	0.34	6.91	6.86~ (0.43)
75	38.05+++	24.40+++	19.25+++	15.82+++	13.64+++	11.53+++	10.13+++	8.79+++	5.69+++	5.13+++	1.84+++	13.51+++	13.41 (0.44)
76	30.63	14.95	10.45	6.77	5.02	2.81~	2.52	1.77	1.68	0.96	0.19	6.05	5.96~ (0.36)
77	33.95+++	21.03+++	14.49+++	11.13+++	9.05+++	6.89+++	5.98+++	4.77+++	2.67	2.05	0.65	9.46+++	9.45~ (0.37)
78	21.03~	9.94~	6.91~	4.88~	3.54~	2.53~	1.76~	1.39~	1.02~	0.69~	0.22	4.11~	4.07~ (0.34)
79	40.89+++	29.43+++	24.03+++	20.58+++	19.04+++	16.07+++	13.85+++	10.78+++	5.94+++	5.63+++	2.55++	16.67+++	16.07 (0.49)
80	55.48+++	17.30	14.80	7.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.32	3.81~ (0.32)
81	56.84+++	31.29+++	21.73+++	16.18+++	12.52++	9.16+	6.32	5.27	3.37	1.68	0.49	13.26+++	12.52 (0.38)
82	27.70	16.56+++	12.27+++	9.60+++	7.60+++	5.71+++	4.76+++	3.79+++	2.52+	1.90+	0.52++	7.75+++	7.72~ (0.4)
83	23.02~	13.00~	9.95	8.46	6.67	4.90	3.75	2.92	2.05	1.61	0.52	6.33	6.19~ (0.44)
84	29.81	17.86	13.99+	9.51	7.50	5.65	4.98	4.23	1.54	1.25	0.15	8.17	8.02~ (0.37)
85	21.37~	13.37	10.82	7.73	6.47	5.90	5.12	2.21	0.89	0.85	0.00	6.44	6.1~ (0.46)
86	19.24~	10.04~	5.94~	4.56~	3.88~	2.90~	2.01~	1.34~	0.62~	0.33~	0.00	3.95~	3.88~ (0.37)
87	35.50+	18.28	13.95	8.83	6.66	4.06	4.06	4.01	2.04	1.36	0.71	7.76	6.66~ (0.35)
88	28.58	11.72~	8.36~	6.26~	3.91~	2.76~	1.37~	1.32~	0.91~	0.46~	0.00	4.86~	4.49~ (0.37)
89	68.91+++	47.88+++	36.53+++	29.44+++	20.68+++	12.25+	10.60++	10.6++	8.70+++	5.39+	0.00	21.41+++	20.68+ (0.4)
90	75.78+++	56.85+++	43.83+++	26.82++	22.63+	6.01	6.01	6.01	4.19	2.56	0.00	21.19++	17.86 (0.46)
91	41.85+++	27.29+++	22.47+++	17.49+++	14.18+++	11.90+++	10.40+++	8.86+++	5.75+++	4.61+++	1.35+++	14.42+++	14.18 (0.4)
92	26.68	13.58~	9.84~	7.74	6.02	4.40	3.25	2.68	1.92	1.32	0.41	6.18	6.02~ (0.38)
93	28.00	16.25+	11.97+	9.64+++	7.67+++	5.91++	4.70++	3.80+	2.72++	2.10+++	0.51	7.73+++	7.71~ (0.4)
94	20.86~	10.87~	7.71~	6.09~	4.74~	3.29~	2.44~	1.89~	1.33~	1.03~	0.16	4.77~	4.76~ (0.4)
95	25.81	12.52~	7.69~	5.42~	3.62~	2.38~	1.81~	1.34~	0.60~	0.37~	0.17	4.58~	4.39~ (0.33)
96	35.43+++	20.03+	14.13	12.12+	9.43+	7.52+	5.91	4.52	2.98	2.65	0.63	9.42+	9.21~ (0.41)
97	73.1+++	31.54++	22.14+	18.00+	13.12	9.09	9.09	9.09	5.05	5.05	0.00	14.86+	13.12 (0.4)
98	26.08	11.69~	8.01~	5.69~	3.56~	2.36~	1.38~	1.26~	0.57~	0.43~	0.03~	4.49~	4.44~ (0.34)
99	39.88+++	14.42	10.42	4.57~	2.89~	1.27~	1.27~	1.25	1.25	0.84	0.41	5.58	5.19~ (0.29)
100	22.01~	10.70~	8.40~	4.59~	2.99~	2.22~	2.22~	2.2	1.75	1.30	0.42	4.49~	4.21~ (0.31)

Table A2b Species' representation indices (SRI) for 2080 for 100 plant species in Iberian Peninsula reserves using a sequence of 11 threshold criteria, R (in grid cell areal proportion), the continuous approach, and the equivalent threshold, R^* (threshold value in parenthesis). A null model was performed in order to evaluate if SRI are significantly different from SRI produced with random trials ($n=9999$). +++, ++, + for values higher than the 99.9th, 99th and 95th percentiles, ---, --, - for values lower than the 0.1th, 1st and 5th percentiles. Non-significant values are not marked by any sign.

id	R=0.00	R=0.10	R=0.20	R=0.30	R=0.40	R=0.50	R=0.60	R=0.70	R=0.80	R=0.90	R=1	continuous	R*
1	72.22+++	53.91+++	37.55+++	26.42+++	25.31+++	8.73	7.59	6.96	4.99	2.03	0.62	20.96+++	19.63(0.46)
2	33.63+	24.05+++	15.58+	11.58	9.98	6.01	5.23	4.01	3.18	2.17	0.72	9.76+	9.19--(0.43)
3	57.80++	36.86+	27.24+	17.74	17.64	2.32	2.00	1.66	1.27	1.27	0.81	13.68	9.33(0.48)
4	60.89+++	38.28+++	32.27+++	24.18++	24.18+++	14.34+	14.34+	14.34++	12.28++	7.53+	1.31	20.44+++	17.97(0.47)
5	33.11+++	18.75+++	13.69+	9.48	7.05	4.96	4.45	3.24	2.06	1.40	0.14	7.96	7.91---(0.36)
6	57.32+++	39.89+++	30.59+++	26.47+++	23.5+++	16.2+++	13.39+++	11.19+++	9.83+++	8.05+++	1.92++	20.85+++	20.35+++ (0.48)
7	87.27+++	65.41+++	49.31+++	27.5+	26.6+	1.31	1.31	1.31	0.48	0.48	0.00	21.81+	16.95(0.46)
8	55.96+++	38.94+++	28.71+++	24.95+++	20.46+++	15.13+++	13.32+++	11.01+++	8.21+++	6.17+++	2.11++	19.70+++	19.24++ (0.46)
9	71.29+++	51.91+++	35.83+++	28.42+++	26.17+++	12.55+	9.98+	9.30+	6.68+	3.75	1.11	22.00+++	19.14(0.48)
10	29.83	15.26	11.43	8.39	5.64	4.35	3.18	2.68	1.86	1.24	0.38	6.65	6.58---(0.35)
11	41.47+++	26.94+++	20.69+++	17.48+++	15.63+++	11.98+++	10.10+++	8.4+++	5.88+++	4.36+++	1.08++	14.16+++	14.03(0.47)
12	23.77	15.55	6.75-	6.26	5.29	3.61	3.25	2.88	2.34	1.37	0.40	5.54	5.32---(0.34)
13	46.01+++	31.04+++	23.73+++	20.15+++	16.77+++	12.6+++	10.62+++	8.77+++	6.5+++	5.05+++	1.37++	15.75+++	15.74+ (0.46)
14	30.03+	17.04+	12.99+	9.75+	7.66+	5.90+	5.07+	4.24+	2.53	1.72	0.34	8.06++	7.93---(0.38)
15	49.14+++	31.35+++	22.78+++	19.48+++	16.68+++	11.07+++	8.72+++	7.33+++	5.33++	4.09++	1.06	14.89+++	14.63(0.47)
16	42.32+++	20.32+	16.50+	12+	8.74	5.36	3.82	2.40	2.23	1.00	0.15	8.89	8.74--(0.4)
17	59.61+++	36.19+++	25.66+++	19.75+++	15.34+++	7.74	5.60	5.02	3.05	1.52	0.00	14.61+++	13.24(0.46)
18	41.60+++	26.59+++	20.59+++	16.57+++	13.67+++	10.83+++	9.35+++	7.88+++	5.37+++	4.13+++	1.24+++	13.52+++	13.39(0.42)
19	36.61+++	20.68+++	15.19+++	11.44+	8.12	6.93+	5.64+	5.11+	3.63+	3.10++	1.34++	9.74+++	9.47---(0.35)
20	46.77+++	30.88+++	23.72+++	20.33+++	17.94+++	12.91+++	10.51+++	8.95+++	6.19+++	5.09+++	1.72++	16.15+++	15.97(0.48)
21	58.42+++	40.89+++	31.06+++	25.74+++	22.22+++	15.42+++	12.55+++	10.66+++	7.24+++	5.14++	1.99+	20.09+++	18.87++ (0.48)
22	51.06+++	22.51+	15.48	9.16	5.94	3.90	2.88	2.00	0.97	0.54	0.16	8.64	7.29--(0.31)
23	68.49+++	48.22+++	33.08+++	24.12+++	21.36++	6.67	4.49	4.49	2.06	2.06	0.00	17.82++	17.5(0.46)
24	54.17+++	27.96+	22.23+	18.52+	14.48+	4.26	1.64	0.00	0.00	0.00	0.00	11.31	10.82(0.46)
25	33.39+++	18.76+++	13.92+++	10.98+++	8.25+++	5.87+	4.60	3.71	2.77	2.03	0.35	8.47+++	8.32---(0.4)
26	32.39+++	19.34+++	14.26+++	11.35+++	9.43+++	7.04+++	5.87+++	4.88+++	3.45+++	2.69+++	0.6+	9.34+++	9.29---(0.41)
27	26.27	14.16	9.84	7.91	6.29	4.30	3.94	3.31	2.54	1.81	0.25	6.48	6.47---(0.39)
28	51.59+++	27.42+++	18.55+++	11.59+	7.99	5.59	3.73	3.33	2.30	1.53	0.36	10.40++	10.09--(0.32)
29	36.04+	18.36	13.95	11.04	8.91	7.76	6.25	4.71	2.16	2.16	0.00	9.03	8.91--(0.37)
30	48.52+++	16.98	10.24	6.32	4.57	4.57	1.55	1.55	0.00	0.00	0.00	6.89	6.32--(0.29)
31	46.50+++	17.81	10.93	4.35	3.53	1.16	0.37-	0.37	0.37	0.00	0.00	6.05	5.11---(0.27)

32	29.13	14.50	8.29	3.86	0.95 ⁻	0.00 ⁻	0.00 ⁻	0.00	0.00	0.00	0.00	4.04	3.86 ⁻⁻⁻ (0.27)
33	45.74 ⁺⁺⁺	22.31 ⁺⁺⁺	14.83 ⁺	9.93	7.31	5.28	3.74	3.41	1.92	1.00	0.34	8.87 ⁺	8.61 ⁻⁻⁻ (0.34)
34	39.18 ⁺⁺⁺	18.17 ⁺	13.22	8.82	5.53	3.89	2.63	2.13	1.14 ⁻	0.47 ⁻	0.23	7.28	7.09 ⁻⁻⁻ (0.34)
35	38.82 ⁺⁺⁺	19.44 ⁺	14.88 ⁺	11.48 ⁺	8.03	5.96	4.45	4.45	3.29	1.81	0.31	8.69 ⁺	8.68 ⁻⁻⁻ (0.39)
36	42.45 ⁺⁺⁺	14.36	10.68	6.87	3.69	2.88	1.07 ⁻	1.07	0.66	0.06	0.00	5.80	5.76 ⁻⁻⁻ (0.32)
37	54.76 ⁺⁺⁺	26.94 ⁺⁺⁺	17.01 ⁺⁺	9.71	5.66	4.15	2.48	1.84	0.00 ⁻	0.00 ⁻	0.00	9.28	9.2 ⁻ (0.31)
38	39.01 ⁺⁺⁺	27.81 ⁺⁺⁺	20.37 ⁺⁺⁺	17.73 ⁺⁺⁺	14.58 ⁺⁺⁺	11.73 ⁺⁺⁺	10.12 ⁺⁺⁺	8.79 ⁺⁺⁺	6.46 ⁺⁺⁺	4.69 ⁺⁺⁺	1.03	14.17 ⁺⁺⁺	14.15(0.46)
39	26.78 ⁻	14.60 ⁻	10.60 ⁻	8.02 ⁻	6.22 ⁻	4.66 ⁻	3.72 ⁻	3.06	2.14	1.53	0.40	6.62 ⁻	6.57 ⁻⁻⁻ (0.38)
40	25.36	15.64	9.07	8.32	7.46	5.61	4.28	3.59	3.04	2.60	0.83	7.00	6.96 ⁻ (0.41)
41	40.43 ⁺⁺⁺	19.71	12.66	5.59	3.74 ⁻	2.14 ⁻	2.14	2.14	0.90	0.90	0.00	6.79	6.23 ⁻⁻⁻ (0.29)
42	27.27	17.22	11.17	9.46	8.27	6.93	5.38	4.84	3.66	2.47	0.86	8.05	7.77 ⁻ (0.41)
43	47.79 ⁺⁺⁺	32.68 ⁺⁺⁺	24.78 ⁺⁺⁺	21.37 ⁺⁺⁺	19.40 ⁺⁺⁺	13.82 ⁺⁺⁺	11.6 ⁺⁺⁺	10.11 ⁺⁺⁺	6.88 ⁺⁺⁺	5.21 ⁺⁺⁺	1.45 ⁺	16.99 ⁺⁺⁺	16.78 ⁺ (0.48)
44	27.87	15.57	11.40	8.64	6.73	5.04	4.08	3.38	2.30	1.66	0.44	7.12	7.1 ⁻⁻⁻ (0.38)
45	20.38 ⁻	12.68	7.26 ⁻	6.22	5.48	4.07	2.72	2.46	1.95	1.21	0.60	5.21	4.69 ⁻⁻⁻ (0.41)
46	24.58	14.72	11.86	8.91	7.13	6.08	5.40	4.61	2.95	2.24	0.73	7.60	7.55 ⁻⁻⁻ (0.37)
47	32.64	6.42	0.00 ⁻	0.00 ⁻	0.00 ⁻	0.00	0.00	0.00	0.00	0.00	0.00	1.61 ⁻	0 ⁻ (0.14)
48	45.22 ⁺⁺⁺	32.71 ⁺⁺⁺	23.17 ⁺⁺⁺	21.04 ⁺⁺⁺	19.01 ⁺⁺⁺	15.69 ⁺⁺⁺	13.68 ⁺⁺⁺	12.07 ⁺⁺⁺	8.43 ⁺⁺⁺	5.86 ⁺⁺⁺	1.62 ⁺	17.49 ⁺⁺⁺	17.48 ⁺⁺ (0.48)
49	29.64 ⁺	16.83 ⁺	12.87 ⁺	9.53	7.67 ⁺	5.98 ⁺	5.19 ⁺⁺	4.32 ⁺⁺	3.00 ⁺	2.22 ⁺	0.69 ⁺	8.14 ⁺⁺	7.99 ⁻⁻⁻ (0.38)
50	36.39 ⁺⁺⁺	19.28 ⁺⁺	13.17	8.73	6.04	4.58	2.80	2.49	1.31 ⁻	0.82 ⁻	0.21	7.39	7.35 ⁻⁻⁻ (0.33)
51	25.04 ⁻⁻⁻	14.43	10.46	8.58	7.04	5.44	4.34	3.34	2.41	2.04 ⁺	0.44	6.93	6.83 ⁻⁻⁻ (0.43)
52	19.40 ⁻	5.99 ⁻⁻⁻	3.33 ⁻⁻⁻	1.58 ⁻	0.77 ⁻	0.27 ⁻	0.00 ⁻	0.00 ⁻	0.00 ⁻	0.00	0.00	1.76 ⁻⁻⁻	1.58 ⁻⁻⁻ (0.27)
53	47.3 ⁺⁺⁺	29.09 ⁺⁺⁺	24.29 ⁺⁺⁺	20.37 ⁺⁺⁺	17.4 ⁺⁺⁺	13.78 ⁺⁺⁺	10.88 ⁺⁺⁺	9.18 ⁺⁺⁺	7.51 ⁺⁺⁺	6.15 ⁺⁺⁺	3.22 ⁺⁺⁺	16.16 ⁺⁺⁺	15.96(0.44)
54	67.42 ⁺⁺⁺	57.01 ⁺⁺⁺	39.29 ⁺⁺⁺	31.13 ⁺⁺⁺	26.96 ⁺⁺⁺	20.46 ⁺⁺	20.46 ⁺⁺⁺	20.46 ⁺⁺⁺	10.79 ⁺	5.10	0.00	26.84 ⁺⁺⁺	20.46(0.48)
55	31.16 ⁺⁺	14.87	10.23	7.30	5.94	4.34	3.43	2.59	2.05	1.37	0.40	6.50	6.45 ⁻⁻⁻ (0.35)
56	63.22 ⁺⁺⁺	29.16 ⁺	26.27 ⁺	16.23	11.88	11.88	4.04	4.04	0.00	0.00	0.00	13.54 ⁺	13.01(0.31)
57	33.93 ⁺⁺⁺	18.09 ⁺⁺⁺	12.74 ⁺	9.43	6.98	4.98	3.77	3.06	2.33	1.58	0.22	7.70 ⁺	7.66 ⁻⁻⁻ (0.37)
58	30.96 ⁺	17.86 ⁺	13.84 ⁺	10.93 ⁺	8.52 ⁺	6.96 ⁺⁺	5.81 ⁺⁺	3.75	2.29	2.05	0.64	8.64 ⁺⁺	8.52 ⁻ (0.4)
59	24.45	17.11	10.00	9.86	8.43	7.61	5.36	4.60	4.07	2.79	0.56	7.83	7.77 ⁻⁻⁻ (0.49)
60	38.55 ⁺⁺⁺	25.38 ⁺⁺⁺	18.33 ⁺⁺⁺	17.39 ⁺⁺⁺	14.95 ⁺⁺⁺	12.11 ⁺⁺⁺	10.11 ⁺⁺⁺	8.84 ⁺⁺⁺	7.01 ⁺⁺⁺	5.70 ⁺⁺⁺	1.24 ⁺	14.02 ⁺⁺⁺	13.91(0.48)
61	45.86 ⁺⁺⁺	21.78 ⁺⁺⁺	14.56 ⁺	10.30	7.65	5.90	3.83	3.25	2.20	1.32	0.32	9.07 ⁺	8.99 ⁻ (0.33)
62	25.71	13.71	9.75	6.41 ⁻	4.70 ⁻	3.44 ⁻	3.02	2.40	1.10 ⁻	0.96	0.00	5.58 ⁻	5.44 ⁻⁻⁻ (0.35)
63	31.30	18.44	12.68	11.07	10.20	9.06 ⁺	7.42 ⁺	6.56 ⁺	5.42 ⁺	2.10	0.88	9.56	9.06 ⁻ (0.48)
64	30.93 ⁺	18.31 ⁺	12.78	8.55	6.84	4.88	4.05	3.50	2.06	1.36	0.20	7.60	7.57 ⁻⁻⁻ (0.35)
65	34.03 ⁺⁺⁺	17.81 ⁺⁺	12.73 ⁺	9.29	6.66	5.07	3.98	3.24	2.12	1.26	0.11 ⁻	7.60	7.58 ⁻⁻⁻ (0.35)
66	59.33 ⁺⁺⁺	43.32 ⁺⁺⁺	32.73 ⁺⁺⁺	27.12 ⁺⁺⁺	20.97 ⁺⁺⁺	14.4 ⁺⁺⁺	12.14 ⁺⁺⁺	11.09 ⁺⁺⁺	7.34 ⁺⁺⁺	4.54 ⁺	0.72	20.23 ⁺⁺⁺	19.77 ⁺⁺⁺ (0.46)
67	61.14 ⁺⁺⁺	41.60 ⁺⁺⁺	28.26 ⁺⁺⁺	22.61 ⁺⁺⁺	17.75 ⁺⁺⁺	8.64	6.66	6.66	4.29	1.82	0.00	16.56 ⁺⁺⁺	16.07(0.46)

68	94.42+++	76.95+++	67.43+++	54.76+++	46.39+++	43.59+++	35.15+++	35.15+++	31.42+++	22.98+++	0.00	45.54+++	43.59+++ (0.49)
69	49.59+++	28.43+++	20.96++	16.90++	12.64+	8.22	6.61	4.79	1.89	1.89	0.00	12.50++	11.67 (0.46)
70	30.26++	17.16+	12.41	9.20	6.97	5.36	4.50	3.48	2.07	1.37	0.15-	7.58	7.53-- (0.37)
71	34.04+++	20.21+++	14.90+++	10.77+++	8.51+++	6.83+++	5.91+++	4.72+++	3.18+	2.32+	0.73+	9.35+++	9.3-- (0.36)
72	34.55+++	22.28+++	17.04+++	13.58+++	11.33+++	8.20+++	6.86+++	6.05+++	4.17+++	3.24+++	0.98+	10.95+++	10.58-- (0.46)
73	35.21+++	20.28+++	14.12+	9.54	7.70	5.65	4.69	3.97	2.57	1.97	0.24	8.64+	8.48-- (0.37)
74	37.67++	24.14++	16.98+	14.25+	14.25+++	9.59+	8.44+	7.23+	5.16+	3.47	1.18	12.16++	11.95 (0.44)
75	45.58+++	29.32+++	23.19+++	19.79+++	16.66+++	13.41+++	11.77+++	10.72+++	7.25+++	6.41+++	2.40+++	16.39+++	15.64 (0.46)
76	30.18	15.91	11.62	8.29	6.06	3.94	3.39	2.84	2.66	1.57	0.39	6.96	6.89-- (0.37)
77	37.00+++	23.29+++	16.28+++	12.37+++	10.03+++	7.59+++	6.66+++	5.51+++	3.19+	2.41+	0.83+	10.58+++	10.54-- (0.37)
78	20.83--	10.02--	6.98--	4.94--	3.64--	2.58--	1.85--	1.47--	1.06--	0.73--	0.24	4.18--	4.05-- (0.35)
79	44.59+++	33.16+++	25.54+++	22.71+++	20.45+++	17.45+++	15.41+++	12.78+++	7.90+++	6.94+++	3.12+++	18.77+++	17.45+ (0.49)
80	55.13+++	15.79	13.01	5.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.69	2.91-- (0.32)
81	53.16+++	29.36+++	19.94+++	14.64+++	11.48++	8.75+	5.74	5.07	3.38	2.08	0.66	12.35+++	12.17 (0.37)
82	28.62+	17.24+++	12.77+++	9.97+++	7.92+++	5.92+++	4.95+++	3.99+++	2.73+++	2.04+++	0.54+++	8.08+++	8.04-- (0.4)
83	26.28	15.32	11.67	10.10+	8.30+	5.96	4.58	3.58	2.48	2.04	0.64	7.55	7.53-- (0.46)
84	31.80+	18.78+	14.59+	10.26	7.86	6.01	5.32	4.71	1.84	1.22	0.17	8.67	8.38-- (0.37)
85	27.11	20.51+	15.39+	10.94	7.44	7.15	6.92+	5.02	1.63	0.67	0.00.	9.04	8.91-- (0.33)
86	20.77--	11.12--	6.65--	5.30--	4.41-	3.37-	2.38-	1.74--	0.94-	0.61-	0.00	4.51-	4.41-- (0.37)
87	33.08	16.61	13.24	8.45	6.62	4.20	4.20	3.30	1.80	1.18	0.56	7.37	6.62-- (0.35)
88	31.35	13.83	10.23	7.69	5.72	3.95	2.50-	2.07	1.51	1.16	0.11	6.20	6.18-- (0.38)
89	70.32+++	50.67+++	37.28+++	29.77+++	20.92+++	12.04+	10.25+	10.25++	7.70++	4.71+	0.00	21.67+++	20.92+ (0.4)
90	74.40+++	60.96+++	49.57+++	25.26+	23.35+	6.32	6.32	6.32	2.97	0.96	0.00	22.26++	16.94 (0.46)
91	46.64+++	30.56+++	24.56+++	19.15+++	15.42+++	12.19+++	10.79+++	9.37+++	6.30+++	4.86+++	1.46++	15.69+++	15.42 (0.4)
92	27.10	14.31	10.27	8.27	6.62	4.87	3.74	3.10	2.24	1.57	0.44	6.62	6.62-- (0.39)
93	29.09++	17.08+++	12.57+++	10.04+++	7.99+++	6.12+++	4.86+++	3.96+++	2.82+++	2.16+++	0.51+	8.07+++	8.04-- (0.4)
94	22.26--	11.72--	8.22--	6.46--	5.02--	3.49--	2.61--	2.08--	1.46-	1.14	0.18	5.10--	5.07-- (0.4)
95	26.34	12.95-	7.89--	5.52--	3.79--	2.53--	1.99-	1.45--	0.63--	0.38--	0.18	4.75--	4.6-- (0.33)
96	44.88+++	29.42+++	20.67+++	18.29+++	14.48+++	11.36+++	8.96++	7.37++	5.32++	4.55++	1.48+	14.02+++	13.85 (0.46)
97	76.79+++	45.96+++	32.49+++	25.04+++	20.05++	9.76	9.76	9.76+	4.88	4.88	0.00	19.61+++	17.48 (0.46)
98	27.33	12.91-	8.82--	6.55-	4.62-	3.22--	2.11--	1.79--	1.01-	0.81-	0.15	5.24--	5.11-- (0.35)
99	38.16+++	14.24	11.20	5.09-	3.36-	1.73-	1.73	1.45	1.45	0.96	0.45	5.87	5.49-- (0.29)
100	21.46-	10.70-	8.46-	4.22-	2.90-	2.28--	2.28-	2.04	1.51	1.18	0.35	4.43-	4.22-- (0.3)

Table A2c Percentage variation of species' representation indices (*SRI*) from the baseline period to 2080 for 100 plant species in Iberian Peninsula reserves using a sequence of 11 threshold criteria, *R* (in grid cell areal proportion), and the continuous approach. A null model was performed in order to evaluate if *SRI* are significantly different from *SRI* produced with random trials (n=9999). +++, ++, + for values higher than the 99.9th, 99th and 95th percentiles, ---, --, - for values lower than the 0.1th, 1st and 5th percentiles. Non-significant values are not marked by any sign. *undef* refers to undefined values (i.e., when *SRI* for the baseline period is 0.00).

id	R=0.00	R=0.10	R=0.20	R=0.30	R=0.40	R=0.50	R=0.60	R=0.70	R=0.80	R=0.90	R=1	continuous
1	8.97	6.91	1.07	-20.57	-14.54	-59.67	-57.88	-55.7	-52.58	-73.08	-76.16	-19.43
2	-6.61	-10.03	-10.52	-14.7	-13.87	-16.39	-14.29	-14.26	-10.72	-9.78	-24.73	-11.75
3	10.09	5.19	-4.00	-23.46	-22.58	-84.51	-83.92	-83.25	-81.15	-81.15	-73.82	-26.63
4	1.75	12.77	8.98	30.63	30.63	98.58	98.58	98.58	79.64	139.15	33.44	32.65
5	-1.12	-1.27	0.15	-0.59	1.95	3.48	5.71	4.99	5.89	-0.14	-28.33	0.70
6	6.35+	10.24+	12.16+	9.52	7.75	6.93	7.13	9.54	11.25	13.85	15.41	9.74
7	2.00	4.19	8.01	-4.36	1.13	-69.63	-69.63	-69.63	-77.17	-77.17	undef	-2.29
8	13.44+	23.42++	17.04	19.25	16.71	6.63	6.40	13.54	21.57	8.75	9.02	16.33
9	10.35	8.51	0.76	-10.61	-7.18	-38.49	-40.99	-36.59	-35.97	-53.19	-50.19	-11.88
10	-1.17	0.47	4.01	8.76+	14.27++	21.14+++	24.33+++	17.32++	17.61+	21.99+	24.81	7.00+
11	6.33++	9.33++	9.79++	11.18++	14.01++	12.72+	13.80+	14.06+	11.00	9.06	-9.05	11.00+++
12	2.52	19.60	-11.50	-2.25	-1.77	-4.24	12.04	46.00	77.09+	42.13	-35.18	6.42
13	14.28+++	21.97+++	21.97+++	22.68+++	22.14++	22.53+	22.77+	27.58++	31.34+	32.07+	27.19	22.36+++
14	5.38+++	7.60++	8.16++	10.85+++	10.4++	13.18++	12.99+	17.50++	18.03++	11.56	10.16	9.57+++
15	18.86+++	28.36+++	29.13+++	32.2+++	29.11++	24.56+	22.77	28.15+	34.73+	27.31	42.57	27.64+++
16	5.38	2.24	1.59	-0.11	-0.63	-3.26	-3.68	-20.21	-16.28	-33.02	-27.65	-0.35
17	6.98	21.55+	18.05	19.51	21.48	-6.62	-10.60	-4.31	10.82	-4.85	undef	13.85
18	7.18+++	9.25+++	8.64+++	8.63+++	12.15+++	10.41++	9.99+	10.22+	9.83+	10.07	6.14	9.52+++
19	-1.23	1.76	4.23	11.01	23.56++	21.29+	19.57+	19.8+	40.50++	39.64+	14.15	10.72+
20	15.96+++	23.80+++	25.22+++	30.68+++	30.07+++	27.37+	26.53+	26.68+	34.33+	26.46	36.58	26.48+++
21	6.72	10.56	3.39	3.84	4.66	-8.99	-9.27	-5.1	-0.34	-12.79	-17.7	2.15
22	-2.66	-6.76	-1.70	-7.40	-8.62	-2.52	1.86	9.73	29.50	38.34	27.41	-3.79
23	8.20	17.57	5.25	2.52	10.08	-0.44	3.68	3.68	-14.73	-14.73	undef	7.86
24	11.18	30.96	18.69	38.12	25.72	27.52	-41.20	undef	undef	undef	undef	19.95
25	1.68	0.27	-2.13	-4.07	-4.57	-7.04	-9.59	-5.09	-4.32	-4.89	-11.14	-2.92
26	6.21+++	7.62+++	7.58+++	8.74+++	10.84+++	11.89+++	11.85+++	13.12+++	13.7+++	13.63+++	19.80++	9.30+++
27	6.95+++	10.88+++	12.75+++	13.77+++	16.75+++	17.08++	17.76+++	19.66++	21.48++	24.40+	68.99+	13.68+++
28	-5.20	-7.38	-6.57	-8.96	-9.06	-7.73	-2.92	-0.01	5.63	22.54	-4.77	-6.47
29	19.39+	38.46++	31.40+	30.06	31.02	21.00	22.82	26.98	48.64	48.64	undef	28.70+
30	-9.43	6.42	3.78	-0.28	-3.04	-3.04	-27.20	-27.2	undef	undef	undef	-5.10

31	1.53	-5.67	-5.03	-5.11	1.74	27.81	27.71	27.71	27.71	undef	undef	-2.59
32	-4.93	-6.96	4.78	11.75	-13.83	undef	undef	undef	undef	undef	undef	-2.77
33	-4.78	-6.96	-7.66	-7.54	-9.98	-5.72	1.97	4.16	-0.39	9.26	1.53	-6.11
34	3.06	1.05	1.83	5.82	4.31	4.24	0.81	0.67	8.13	-4.06	-1.31	2.03
35	-3.90	-0.33	-0.52	2.36	-2.68	4.01	6.94	6.94	7.36	19.08	35.99	0.80
36	0.03	10.47+	18.22++	26.66++	73.18+++	57.92++	216.41+++	216.41++	450.30++	2778.03++	undef	18.87++
37	-0.38	-0.57	0.71	0.29	-1.41	-0.66	-0.82	1.57	undef	undef	undef	-0.24
38	14.98+	30.56++	23.39+	30.74+	28.63+	30.36+	35.53+	38.02	54.92+	57.16	87.95	30.31++
39	1.23++	2.87+++	2.15++	2.15+	2.12+	1.70	1.30	2.64+	3.42+	2.31	3.11	2.22+++
40	17.16+++	33.44+++	27.99+++	33.1+++	38.55+++	55.2+++	57.93+++	61.28+++	67.18++	71.74+	32.99	37.46+++
41	-5.94-	-11.04-	-12.38-	-13.69-	-17.81--	-21.41--	-21.41--	-21.41-	-17.56-	-17.56	undef	-12.2--
42	-4.63	7.23	-6.72	-2.47	1.21	9.71	10.59	15.61	18.43	34.02	-0.21	2.82
43	4.29	5.23	4.70	4.47	6.93	9.68	12.02	16.70	15.50	16.31	31.59	7.45
44	0.95+	0.95	0.58	0.25	0.58	0.10	0.24	1.92	3.02	2.76	4.95	0.96
45	-9.03-	-3.55	-17.75-	-17.33-	-15.19	-7.42	-2.00	-5.64	-5.03	8.25	20.53	-10.11
46	-3.57	-3.62	-2.92	-2.54	-0.62	-0.81	0.51	7.70	12.72	7.47	2.59	-1.30
47	37.44++	-7.84	undef	undef	undef	undef	undef	undef	undef	undef	undef	10.92
48	33.2+++	46.6+++	41.33+++	48.1++	50.86++	43.9+	45.41+	47.52+	56.41	44.91	37.9	46.04+++
49	-1.33	-4.23-	-3.48-	-5.54-	-6.20-	-6.75-	-6.20-	-6.92-	-3.91	-4.09	-5.72	-4.66-
50	7.08++	8.77++	6.49	1.07	2.01	1.83	4.09	4.24	-4.38	1.59	32.00	5.68
51	4.56+++	8.00+++	9.83+++	12.18+++	14.79+++	13.09+++	13.66+++	16.2+++	22.99+++	23.67+++	44.85++	11.52+++
52	7.84	-13.37	-33.21-	-40.64-	-29.73-	-64.80--	undef	undef	undef	undef	undef	-21.11-
53	2.99	12.67	16.30	14.05	31.62	40.55+	54.34+	55.11+	53.16	89.79	117.15	25.94+
54	3.53	17.82	6.74	13.34	18.53	20.91	20.91	20.91	26.52	22.01	undef	15.40
55	-2.81-	-1.37	-1.78	1.08	5.15	6.86	8.79	6.36	7.41	20.56+	51.44+	1.75
56	0.50	0.82	-0.27	-10.74	-19.97	-19.97	-22.69	-22.69	undef	undef	undef	-4.85
57	0.78	0.28	0.92	1.78	4.60+	5.27+	5.86+	4.22	5.79	9.30	12.95	2.20
58	16.02+++	22.53+++	26.25+++	36.74+++	32.03++	33.48++	30.58+	57.02+++	97.72+++	82.82++	252.93+	30.06+++
59	-11.54-	-13.13-	-22.56-	-23.06-	-23.13-	-21.04	-16.04	-18.21	-10.38	-1.67	-59.47-	-18.9-
60	6.50	11.53	16.35	17.54	27.16+	21.72	32.68	36.77	34.12	60.78	15.76	22.56+
61	-0.10	-2.42	-0.60	1.32	2.39	4.87	10.6+	12.53+	16.66+	19.59+	1.17	1.49
62	4.49+++	2.34	-0.30	1.85	1.84	4.47	2.93	2.31	0.96	-0.34	undef	2.15
63	-3.49	-2.12	-1.56	2.61	2.85	2.05	0.37	1.85	3.38	-5.85	-15.64	-0.56
64	2.98++	2.57	2.01	2.95	1.50	2.02	-0.05	0.85	-2.33	-6.49	-5.78	1.88
65	-2.17-	-2.81-	-2.09	-1.29	-0.48	-0.23	-0.21	-3.51	-3.87	-2.64	-15.95-	-1.94
66	14.51+	22.49+	18.05	20.48	19.16	21.35	26.75	31.15	33.15	18.88	19.80	21.27+

67	17.64	42.53+	35.51	29.84	48.16	16.14	4.66	4.66	8.37	-33.32	undef	30.07
68	-3.39	0.43	-11.90	-28.4	-20.59	-16.81	-23.24	-23.24	-28.79	-28.07	undef	-16.98
69	4.39	6.78	6.24	3.62	8.36	13.44	23.30	23.42	13.58	13.58	undef	8.20
70	-0.51	2.56	2.87	1.88	4.03	5.64	7.22	5.23	-5.79	-2.78	4.86	3.03
71	8.38+++	11.33+++	11.24+++	12.22+++	12.76+++	12.57+++	13.18++	15.57+++	16.78++	18.83++	16.55	12.22+++
72	13.09+++	13.19+++	12.32+++	12.13++	11.67+	7.07	6.43	10.57	13.15	9.30	10.82	11.46+++
73	-1.39	-2.63	-2.22	-1.71	0.67	0.08	3.33	-0.07	-3.53	-0.94	-6.58	-1.26
74	29.66+++	59.78+++	60.53+++	67.12+++	67.12++	120.62+++	119.05++	140.87+	172.13+	273.64+	241.74+	75.87+++
75	19.80+++	20.13+++	20.48+++	25.11+++	22.16++	16.26+	16.24	22.02+	27.38+	25.02	30.31	21.31+++
76	-1.46	6.40	11.23+	22.57++	20.91+	40.05++	34.56+	60.18++	58.99+	63.17+	102.68	15.15++
77	8.98+++	10.72+++	12.37+++	11.14++	10.79+	10.06+	11.30+	15.41++	19.51+	17.49+	27.83	11.82+++
78	-0.98	0.73	1.02	1.23	2.60	2.12	4.80+	5.88+	4.41	5.77	9.78	1.71
79	9.05	12.67	6.31	10.34	7.39	8.58	11.24	18.52	32.89	23.15	22.43	12.58
80	-0.63	-8.72	-12.09	-23.44~	undef	undef	undef	undef	undef	undef	undef	-10.08
81	-6.48	-6.17	-8.20	-9.52	-8.36	-4.52	-9.10	-3.79	0.12	23.87	35.97	-6.85
82	3.31+++	4.10+++	4.14+++	3.86+++	4.11+++	3.56++	4.05++	5.40+++	8.07+++	7.27+++	5.25	4.26+++
83	14.15+++	17.82+++	17.24+++	19.39+++	24.5+++	21.64+++	22.14++	22.56++	21.02+	27.17+	23.55	19.29+++
84	6.65++	5.15	4.28	7.86	4.91	6.41	6.91	11.18	19.61+	-2.61	12.14	6.15
85	26.84+	53.42++	42.19+	41.67+	14.89	21.31	35.19	127.21+	84.05	-21.25	undef	40.45+
86	7.95+++	10.86+++	11.84++	16.23+++	13.7++	15.93+	18.14+	29.63+++	50.67+++	88.03+++	undef	14.28+++
87	-6.81	-9.12	-5.08	-4.24	-0.62	3.45	3.45	-17.6	-11.85	-13.17	-20.69	-5.09
88	9.68+++	18.02+++	22.41+++	22.86+++	46.43+++	43+++	81.9+++	57.16+++	66.05+++	149.74+++	3700.29+++	27.50+++
89	2.05	5.82	2.07	1.12	1.20	-1.74	-3.33	-3.33	-11.46	-12.60	undef	1.21
90	-1.82	7.22	13.08	-5.80	3.20	5.12	5.12	5.12	-29.26	-62.68	undef	5.04
91	11.45+++	11.99++	9.28	9.47	8.70	2.39	3.70	5.80	9.51	5.30	7.80	8.83
92	1.55	5.4+++	4.34++	6.85++	9.84+++	10.51++	14.98+++	15.88+++	16.71+++	18.54+++	6.26	7.12+++
93	3.92+++	5.09+++	5.01+++	4.13+++	4.20+++	3.54++	3.41++	4.02++	3.85+	2.70	1.37	4.37+++
94	6.69+++	7.79+++	6.64++	6.08+	5.91+	5.88+	7.02+	9.95+	10.05+	9.92	16.65	7.00++
95	2.04+	3.39+	2.58	1.88	4.63+	6.17+	9.71++	8.63+	4.78	4.98	7.38	3.70+
96	26.69+++	46.85+++	46.33+++	50.96++	53.53++	51.2+	51.53+	63.05+	78.70+	71.57	133.11	48.81+++
97	5.05	45.74	46.72	39.15	52.78	7.43	7.43	7.43	-3.38	-3.38	undef	31.96
98	4.81++	10.37+++	10.16+++	14.96+++	29.67+++	36.69+++	52.98+++	42.59+++	76.79+++	86.49+++	410.98++	16.66+++
99	-4.32	-1.26	7.44	11.42	16.15	36.53+	36.53+	15.77	15.77	14.16	10.33	5.26
100	-2.49	-0.01	0.73	-8.08	-3.21	2.67	2.67	-7.09	-13.7	-9.10	-17.79	-1.23

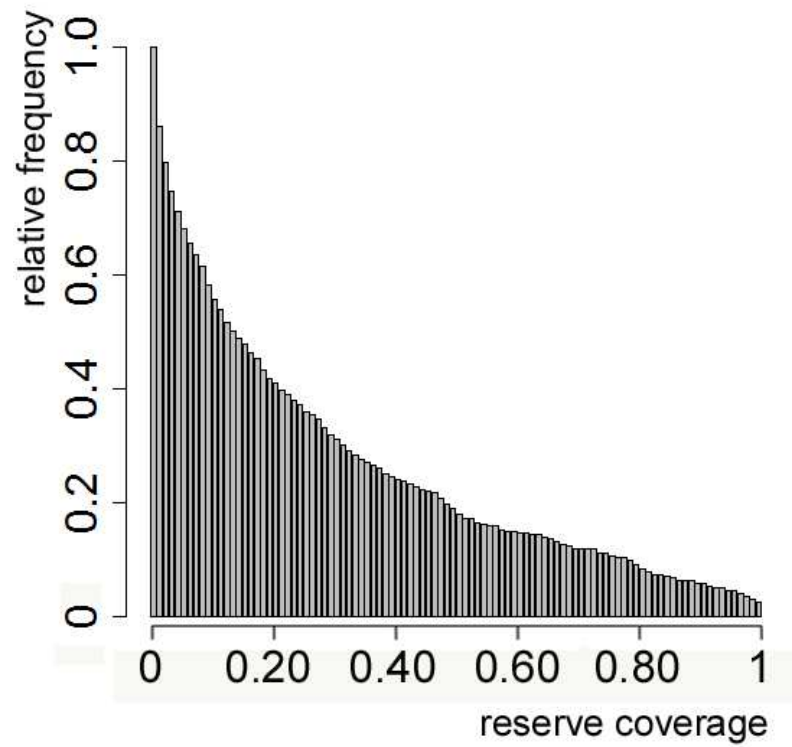


Fig. S1. Cumulative distribution of reserve coverage in Iberian Peninsula 10-degree cells, excluding grid cells with no reserve coverage. x-axis for 0.01-width interval classes for reserve coverage.

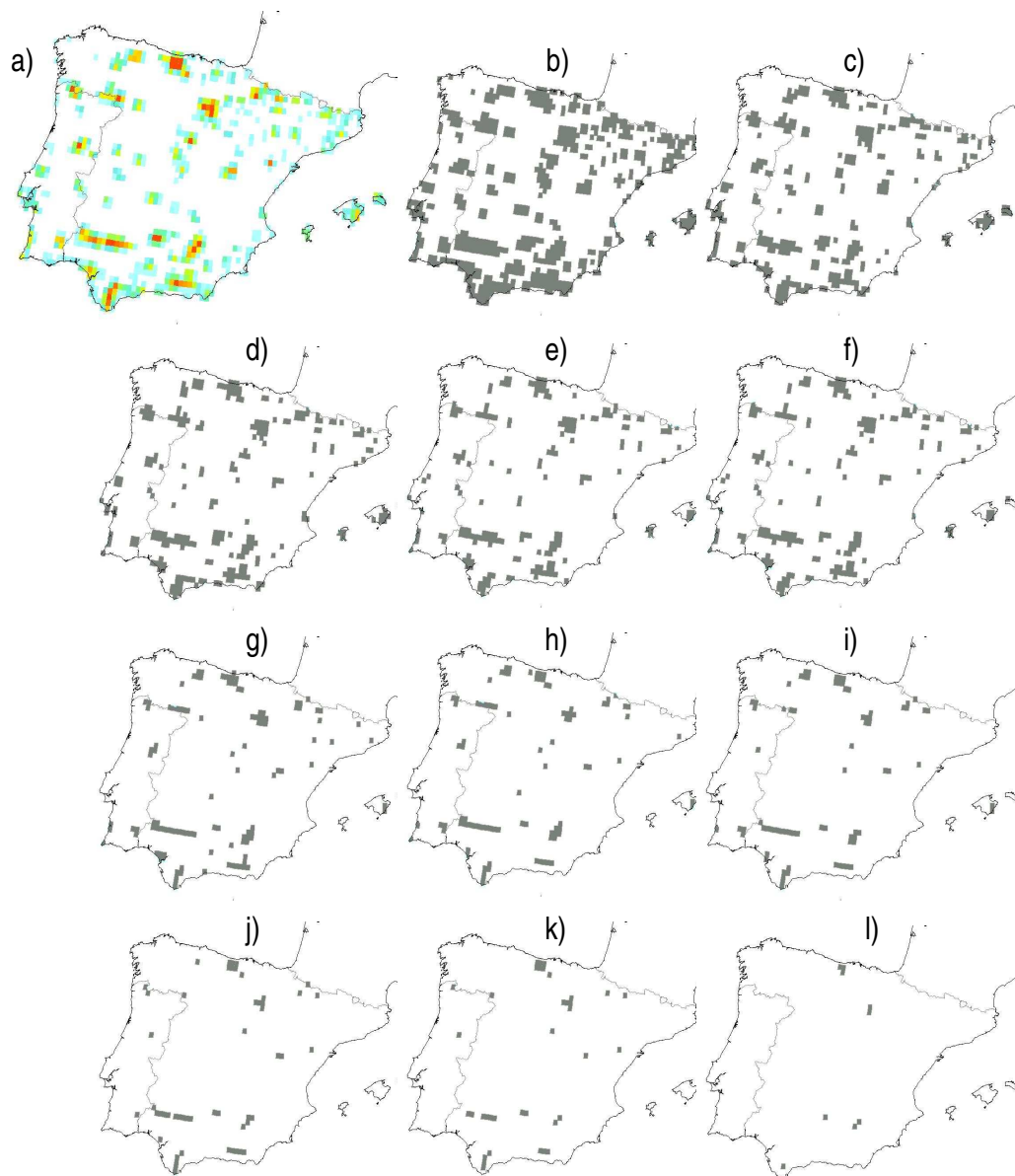


Fig. S2. Maps of Iberian Peninsula reserves (IUCN ivi). **a)** grid map of percent reserve coverage (reddish grid cells for high reserve coverage; blue grid cells for low reserve coverage; white grid cells for no reserve coverage) ; **b-l)** binary grid maps obtaining using $R=0^+$, $R=0.10$, $R=0.20$, $R=0.30$, $R=0.40$, $R=0.50$, $R=0.60$, $R=0.70$, $R=0.80$, $R=0.90$ and $R=1$, respectively, covering 27.6%, 15.4%, 11.3%, 8.6%, 6.6%, 5.0%, 4.0%, 3.3%, 2.3%, 1.6% and 0.4% of Iberian Peninsula grid cells (grey grid cells are assumed totally reserved; white grid cells are assumed non reserved).

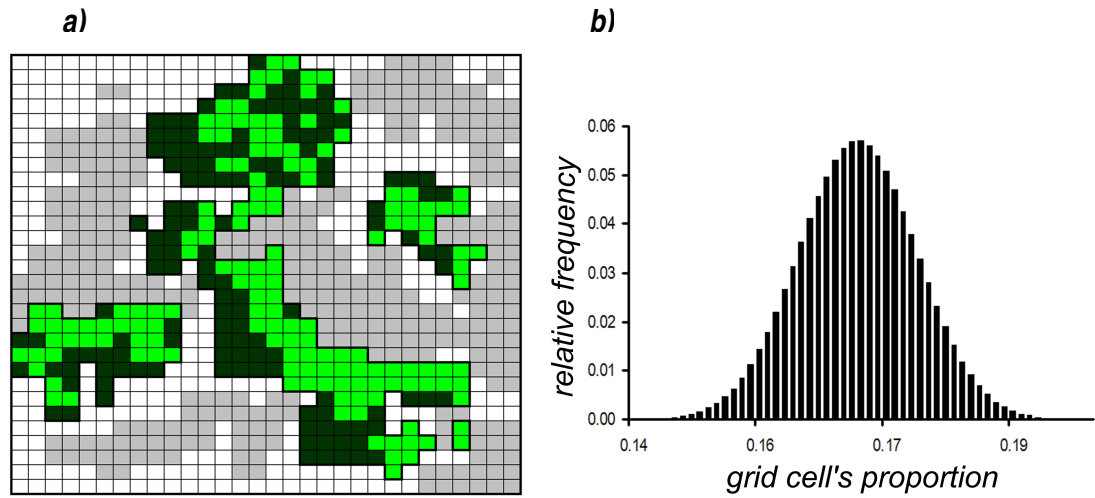


Fig. S3. The matching of species with reserves within a grid cell interpreted as a hypergeometric experiment. If X is a hypergeometric variable illustrating the match of a species ($s=0.53$) with reserves ($r=0.32$) in a partitioned grid cell ($M=900$) then **a)** is a random outcome from X , where in white squares species and reserves are absent, in grey squares species is present and reserves absent, in dark green squares reserves are present and species is absent, and in light green squares species and reserves are present (i.e. the match of species with reserves). **b)** a frequency curve for X/M , where the x-axis shows the proportion of the 900 squares where species and reserves match.

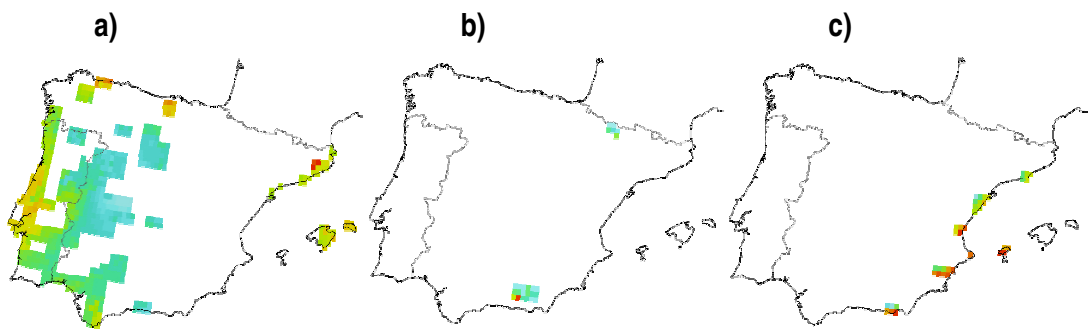


Fig. S4. Probabilities of occurrence for three species in the baseline period. **a)** a uniformly distributed species across Iberian Peninsula reserves where it occurs (id=64, *Ceratophyllum demersum*), **b)** a non-uniformly distributed species biased towards larger reserves (id=68, *Aconitum burnatii*), and **c)** a non-uniformly distributed species biased towards smaller reserves (id=80, *Fumaria gaillardotii*). Reds for high probabilities of occurrence, blues for low probabilities of occurrence.

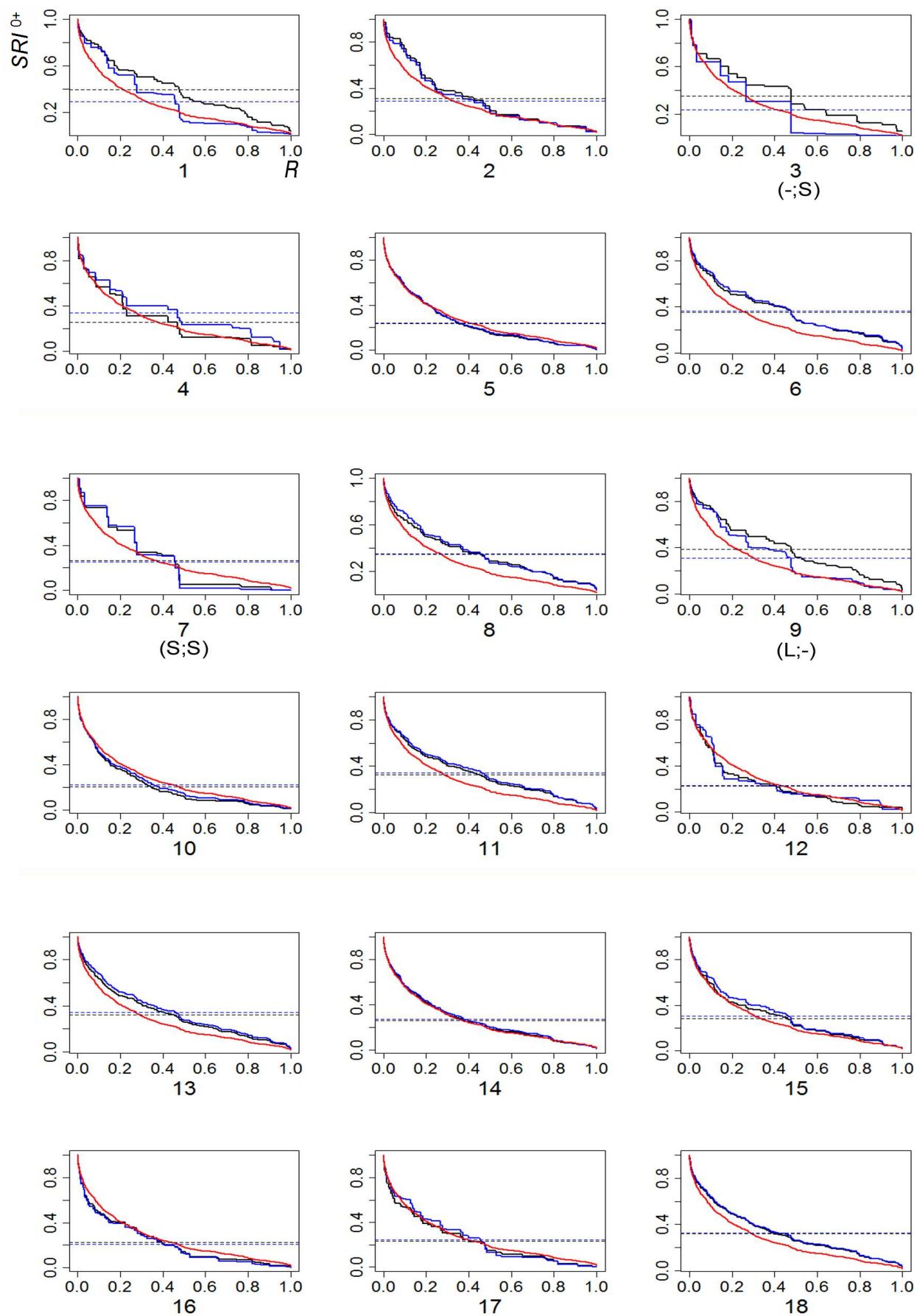


Fig. S5 (continue)

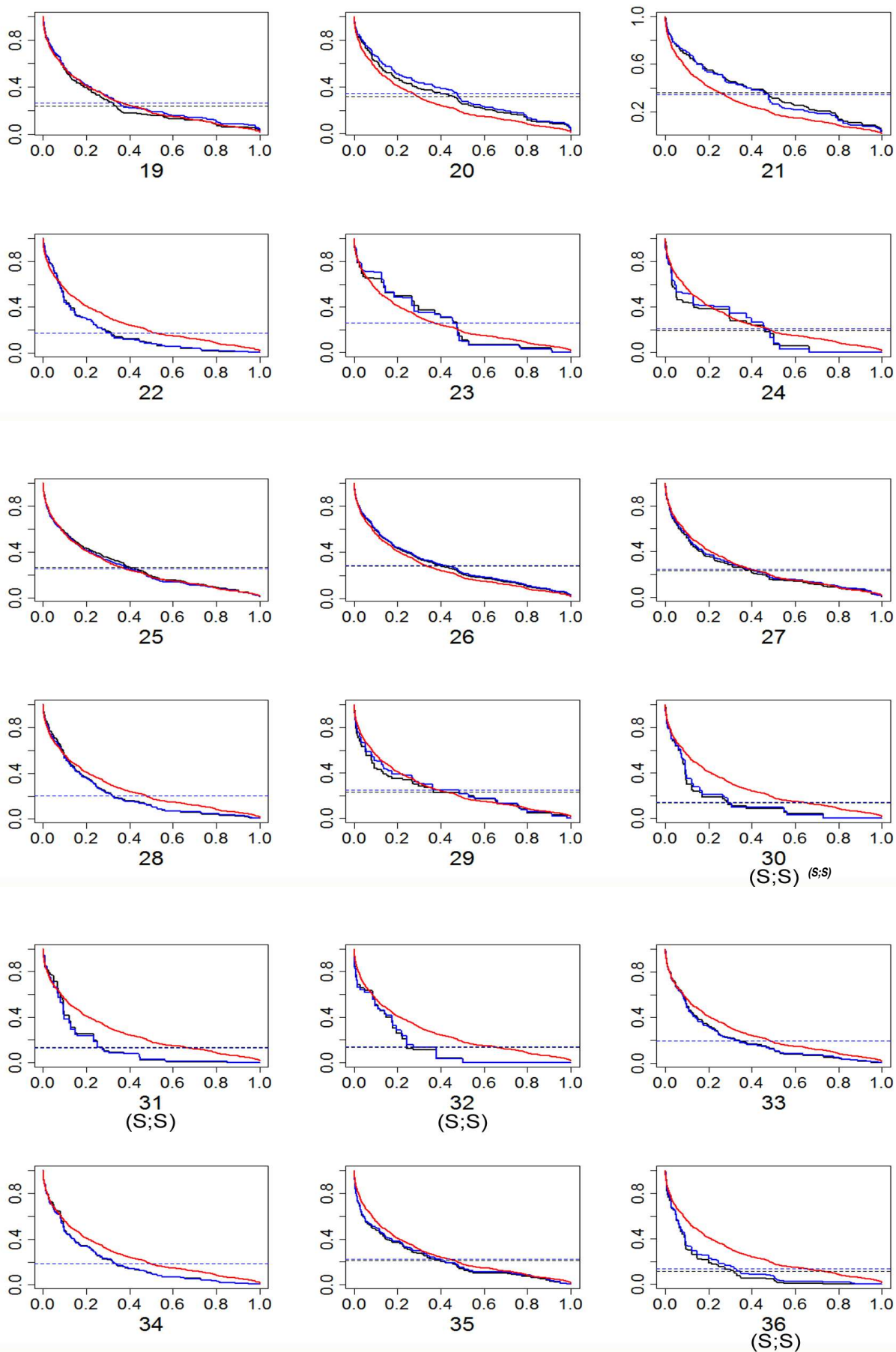


Fig. S5 (continue)

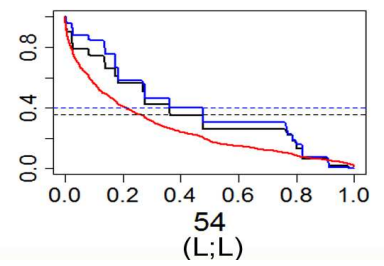
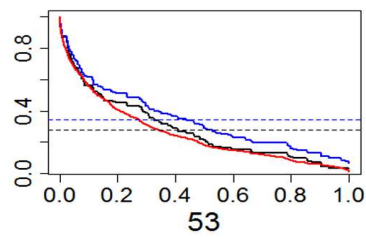
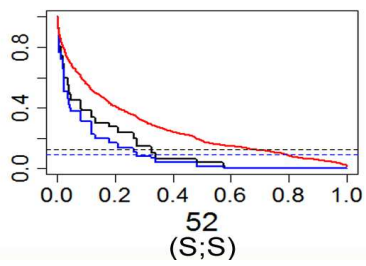
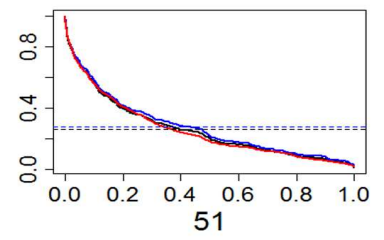
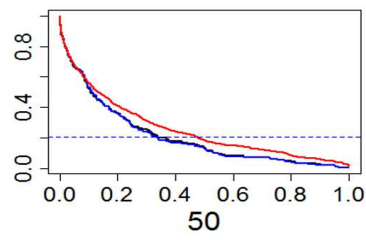
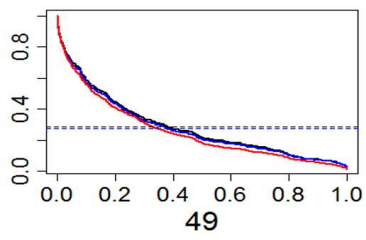
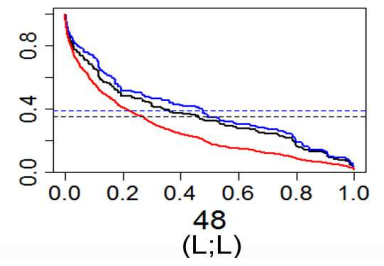
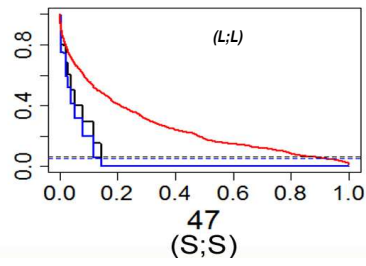
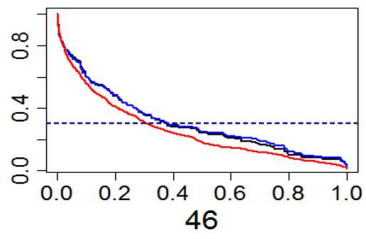
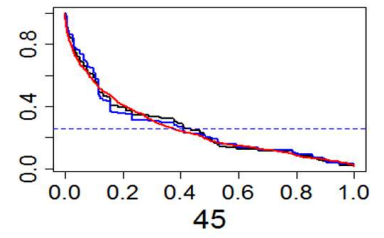
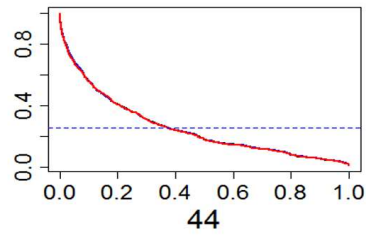
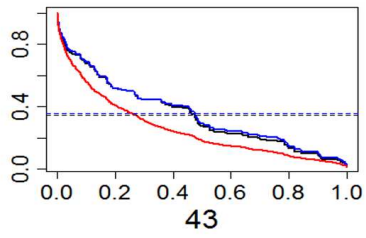
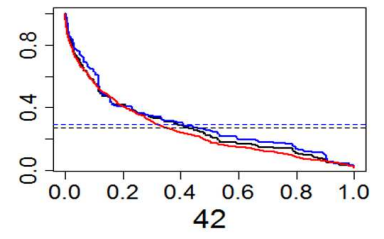
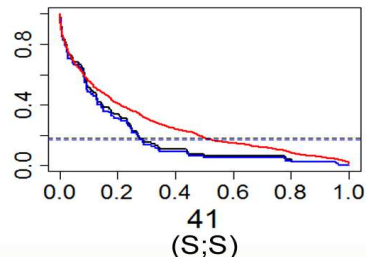
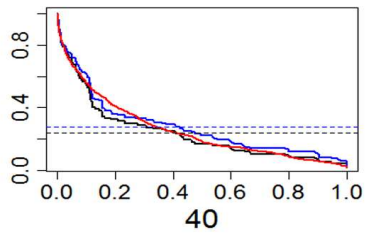
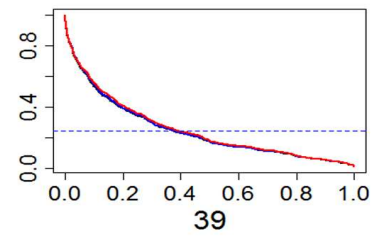
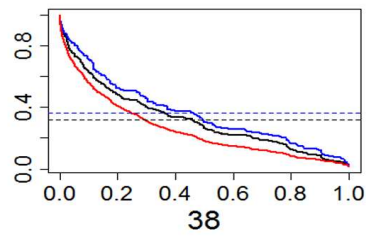
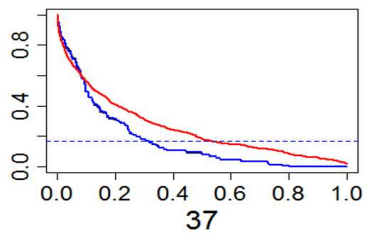


Fig. S5 (continue)

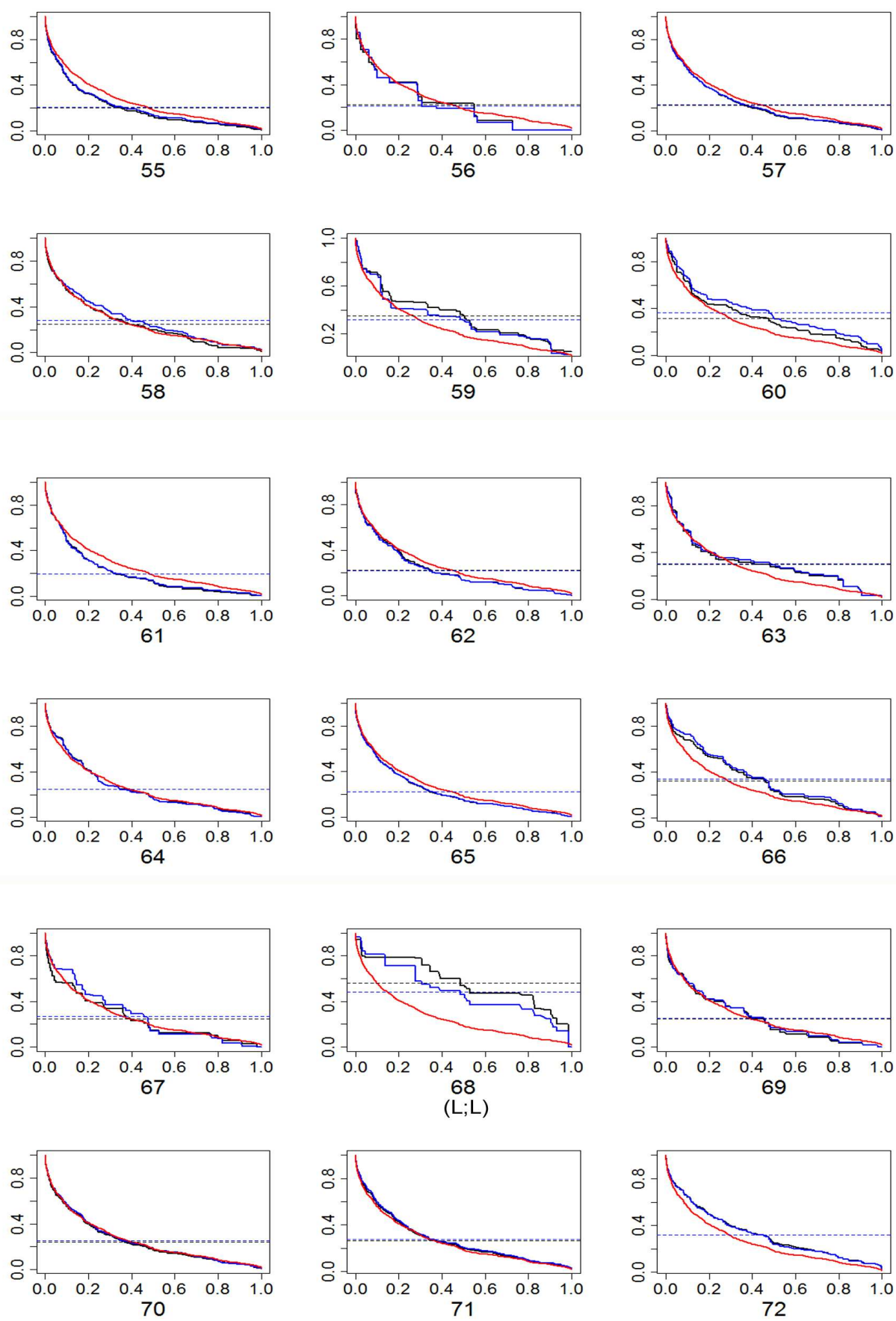


Fig. S5 (continue)

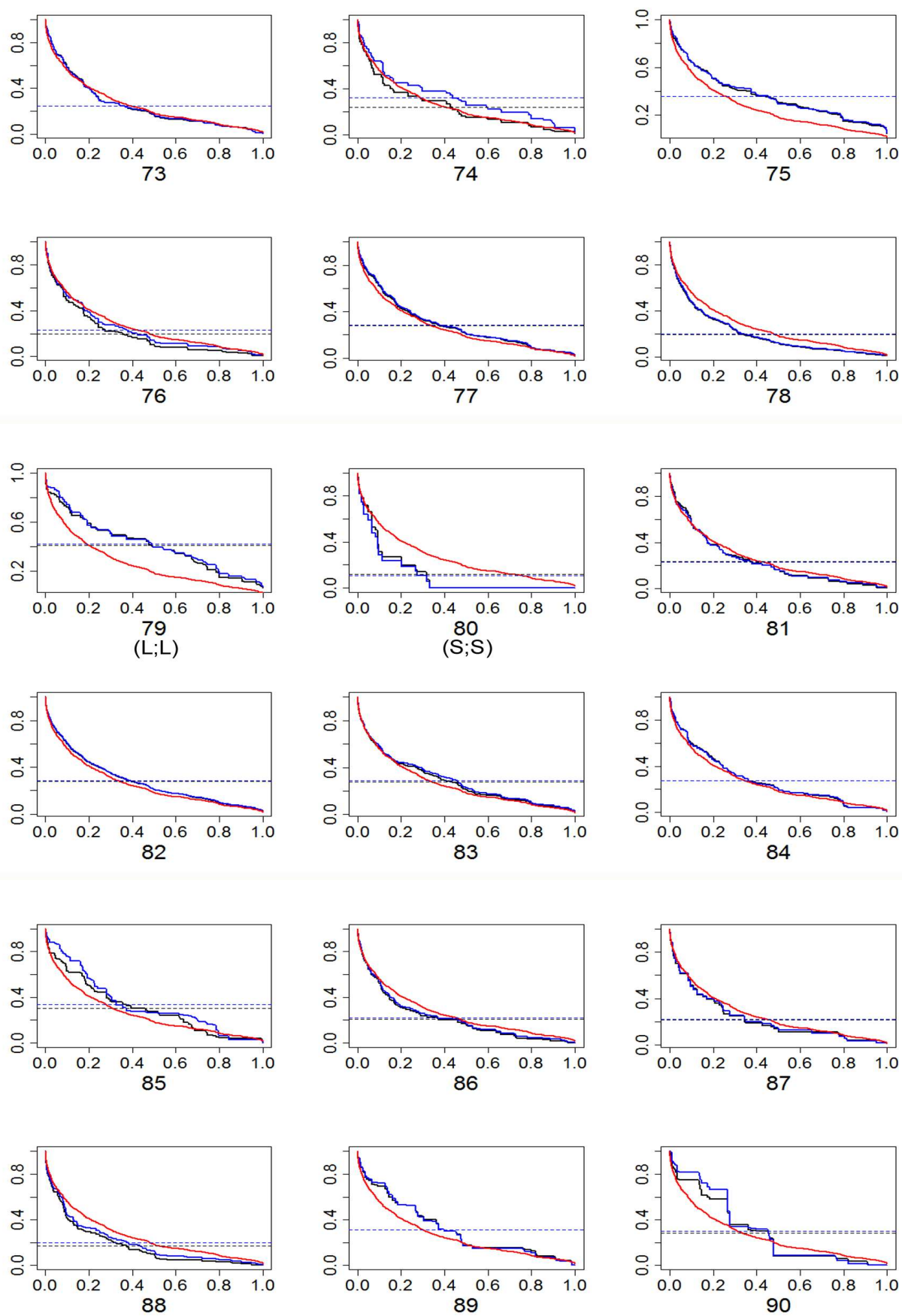


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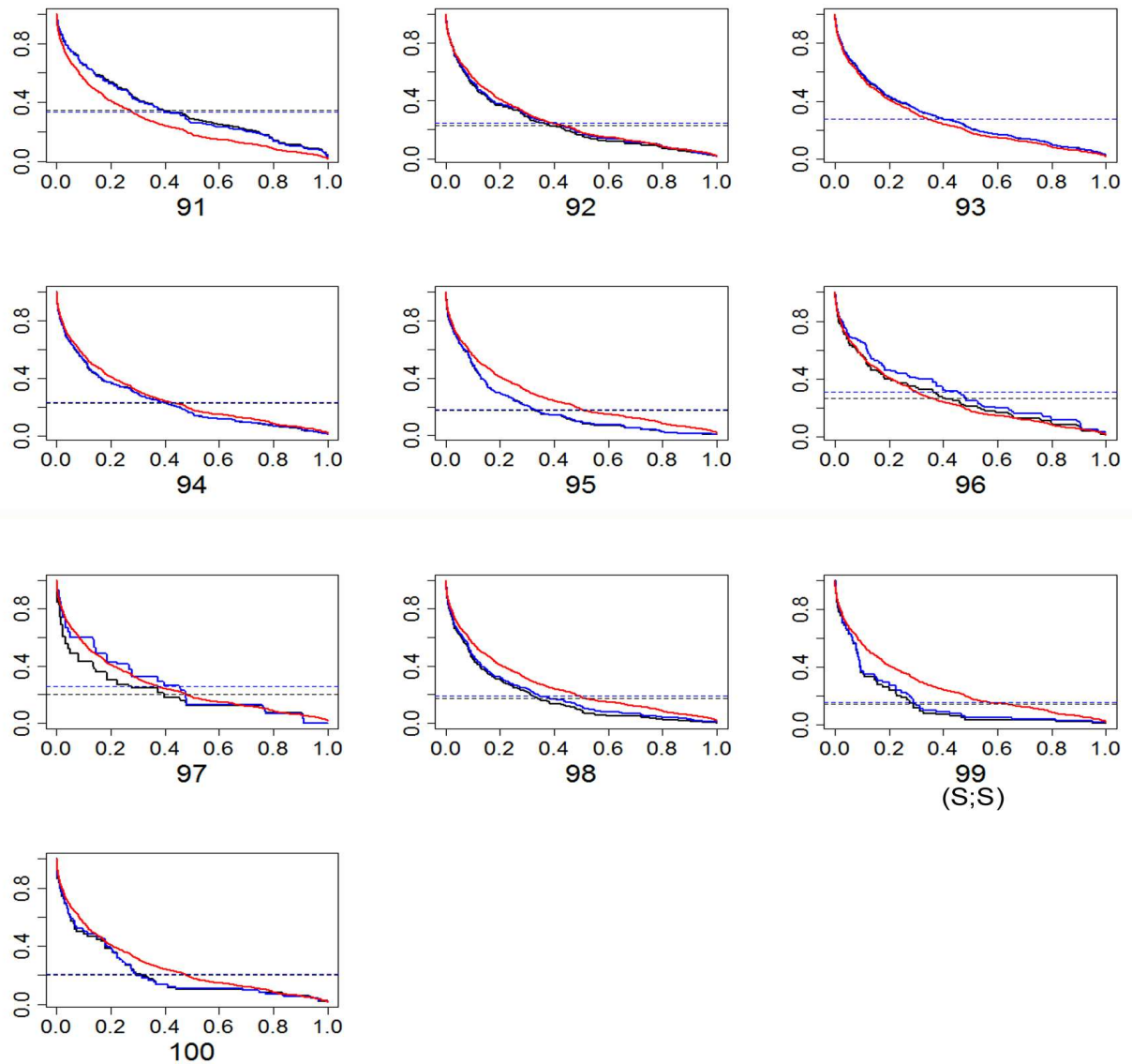


Fig. S5. Variation of scaled species' representation indices (SRP^+) along a gradient of possible threshold values (R) defining the Iberian Peninsula reserve system, for the 100 plant species in analysis. SRI values are scaled to SRI obtained with $R=0^+$ (SRI^{0+}). Horizontal lines mark SRI values obtained with the continuous approach. Black lines for baseline period, blue lines for 2080, red line for the cumulative curve of reserve coverage. Fourteen species (1, 3, 9, 52, 53, 54, 59, 67, 68, 74, 85, 90, 96, 97) show marked differences in the line patterns for the two periods. From these just five species (3, 9, 68, 74 and 90) continue to show R^* similar for the two periods. L and S refer to species markedly biased to "large or clustered" and "small and scattered" reserves, respectively. Species uniformly partitioned across different reserve sizes are not marked. L and S are showed in pairs with the first position referring to the baseline period and the second to 2080.

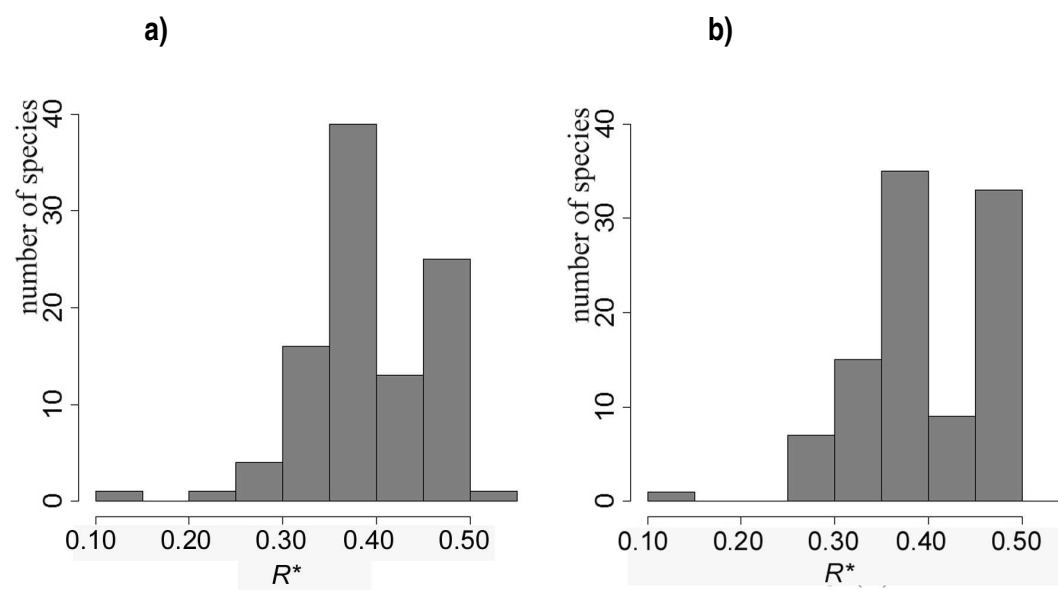


Fig. S6. Frequency classes for equivalent thresholds (R^*) for 100 plant species in Iberian Peninsula for **a) baseline period and; **b)** 2080.**

CHAPTER V

Climate change threatens European conservation areas

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David Nogués-Bravo, Wilfried Thuiller

"We shall best understand the probable course of natural selection by taking the case of a country undergoing some physical change, for instance, of climate."

Charles Darwin, 1859

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doi: 10.1111/j.1461-0248.2011.01610.x.

CLIMATE CHANGE THREATENS EUROPEAN CONSERVATION AREAS

ABSTRACT

Europe has the world's most extensive network of conservation areas. Conservation areas are selected without taking into account the effects of climate change. How effectively would such areas conserve biodiversity under climate change? We assess the effectiveness of protected areas and the Natura 2000 network in conserving a large proportion of European plant and terrestrial vertebrate species under climate change. We found that by 2080, $58 \pm 2.6\%$ of the species would lose suitable climate in protected areas, while losses affected $63 \pm 2.1\%$ of the species of European concern occurring in Natura 2000 areas. Protected areas are expected to retain climatic suitability for species better than unprotected areas ($p < 0.001$), but Natura 2000 areas retain climate suitability for species no better and sometimes less effectively than unprotected areas. The risk is high that ongoing efforts to conserve Europe's biodiversity are jeopardized by climate change. New policies are required to avert this risk.

INTRODUCTION

With more than 100,000 sites across fifty-four countries, Europe has more protected areas than any other region in the World. In addition to protected areas (e.g., national parks, natural parks, nature reserves, protected landscapes, etc.), which are designated by individual countries, the European Union (EU) established the Natura 2000 network to ensure the long-term survival of its most valuable biodiversity. The Natura 2000 network includes two sets of areas: Special Protection Areas (SPAs) are classified under the Birds Directive to help conserve important sites for rare and vulnerable birds; Special Areas of Conservation (SACs) are classified under the Habitats Directive to conserve rare and vulnerable non-bird animals, plants and habitats. In the 27 countries that constitute the EU, the Natura 2000 contributes 27,661 sites covering 117 million hectares (17% of the EU surface) (E.C. 2009). Even though a variety of conservation areas exist in Europe, a common assumption is that successful management is achieved by protecting the valued features from the processes that threaten them. Yet, it is becoming evident that in addition to providing sustainable management of habitats and ecosystems, effective conservation strategies need to mitigate impacts of climate change. While actions to mitigate climate change and its impacts are being debated worldwide, biologists are finding evidence that across a wide range of taxonomic and functional groups species already are responding to climate change by altering their phenology, and geographical distributions (Hickling *et al.* 2006; Lenoir *et al.* 2008). Forecasts project even greater changes for the 21st century (e.g., Pereira *et al.* 2010; Thuiller *et al.* 2011). Some species might persist only if they can colonize new areas when their former ranges become unsuitable, while others might persist in areas where they retain portions of their current ranges (Hannah *et al.* 2007). The conservation of such 'climate refugia' is of critical importance for biodiversity, but are existing European conservation areas up to the task?

Assessments of climate change impacts on biodiversity have often used bioclimatic envelope models (BEM). These models use associations between climate and species' occurrences to enable projections of future altered potential distributions of species under climate change scenarios. Implementations of these methods as well as their uncertainties have been extensively reviewed (e.g., Araújo & Guisan 2006; Heikkinen *et al.* 2006; Elith & Leathwick 2009). Although specific uses of BEM have been criticized (e.g., Botkin *et al.* 2007), models including a thorough treatment of algorithmic uncertainties followed by careful interpretation of results remain a useful tool for forecasting continental-wide impacts of climate change on large numbers of species (Araújo *et al.* 2005b; Green *et al.* 2008; Kearney *et al.* 2010; Dobrowski *et al.* 2011). Essentially, ensembles of BEMs have been shown to successfully project the direction of range changes for most species under climate change, being less effective in the estimating the magnitude of such changes (Araújo *et al.* 2005b).

We assessed impacts of climate change on ca. 75% of terrestrial vertebrates ($n=585$) of Europe and ca. 10% of the European flora ($n=1298$). Even though the proportion of plant species available for modelling is

smaller than for vertebrates, they provide a representative sample of the species' responses to climate change since most life forms among European plants are included (Thuiller *et al.* 2005). Uncertainty was handled within an ensemble forecasting framework (Araújo & New 2007), implemented with 7 bioclimatic modelling techniques x 3 general circulation models x 4 emission scenarios, and were projected into a baseline period and 3 periods in the future (see material and methods); 336 projections were obtained for each 1883 species, yielding a total of 632,688 projections. To avoid errors arising from estimating losses of species across modelled areas of distribution where species do not occur, changes in climatic suitability scores for species were assessed only for cells that overlap with species actual ranges. We also explored uncertainties arising from the emergence of non-analogues climates in the 21st century (Fitzpatrick & Hargrove 2009).

Studies have occasionally examined impacts of climate change on conservation areas (Hannah *et al.* 2007; Coetzee *et al.* 2009; Hole *et al.* 2009), but they did not compare impacts inside and outside conservation areas. Thus, it is difficult to assess the relative contribution of conservation areas for protecting regional biodiversity in these studies. To overcome this limitation, we compared projected shifts inside and outside conserved areas and tested whether current protection offers any buffer to climate change. Two sets of analyses are performed. Firstly, we assess the ability of nationally designated protected areas (hereafter termed protected areas, Fig. S1) to retain suitable climate conditions for all species considered. Species gaining suitable climate conditions are termed 'winners', whereas species losing suitable climate conditions are termed 'losers'. Secondly, we examine potential impacts of climate change on subsets of species of conservation concern. Specifically, we examine impacts on globally threatened species (vulnerable, endangered, critically endangered according to the World Conservation Union IUCN) in protected areas, and on species prioritized by the EU legislation (hereafter termed Bird & Habitat Directive species) and occurring in Natura 2000 sites (Fig. S1). The protected areas assessment is performed for 38 European countries (the Council of Europe member states excluding Turkey, Russia and the former Soviet republics), whereas the Natura 2000 analysis is performed for the European Union (EU) 26 Countries (excluding Cyprus).

MATERIALS AND METHODS

Species data

We modelled 1883 European species: 1,298 plants (Jalas & Suominen 1972-1996); 136 mammals (Mitchell-Jones *et al.* 1999); 343 breeding birds (Hagemeijer & Blair 1997); 42 amphibians (Gasc *et al.* 1997); and 64 reptiles (Gasc *et al.* 1997). Species with less than 20 records and mammals or birds with life cycles that are strictly aquatic or marine were not modelled. Plant species included all European pteridophytes, a sample of spermatophytes comprising representatives of all gymnosperm families (Coniferales, Taxales and Gnetales) and a fraction of angiosperm dicotyledons (Salicales, Myricales, Juglandales, Fagales, Urticales, Proteales, Santales, Aristolochiales, Balanophorales, Polygonales, Centrospermae, and Ranales), but no monocotyledons. The original grid is based on the Atlas Florae Europaeae (AFE), with cell boundaries following the 50 km lines of the Universal Transverse Mercator (UTM) grid, except near the border of the six-degree UTM zones and at coasts. The vertebrate atlases use slightly different grid-systems, including different rules to represent data on islands and coasts. Hence, vertebrate data were converted to the AFE grid system by identifying unique (though sometimes approximate) correspondence between cells in these grids (Williams *et al.* 2000). The European mapped area (2,434 grid cells) excludes most of the eastern European countries (except for the Baltic States) where recording effort was both less uniform and less intensive.

Climate data

A set of climate parameters were derived from data provided by the Climate Research Unit at the University of East Anglia (Mitchell *et al.* 2004). The data provides monthly values for 1901–2000 in a 10' grid resolution (ca. 16x16 km). Average monthly temperature and precipitation in grid cells covering the mapped area of Europe were used to calculate mean values of four different climate parameters for 1961–1991 (referred to as 'baseline data'). Variables included mean temperature of the coldest month (°C),

mean annual summed precipitation (mm), mean annual growing degree days ($> 5^{\circ}\text{C}$), and a moisture index calculated as the ratio of mean annual actual evapotranspiration over mean annual potential evapotranspiration. Choice of variables was made to reflect two primary properties of the climate (energy and water) that have known roles in imposing constraints upon species distributions as a result of widely shared physiological limitations (e.g., Whittaker *et al.* 2007). All data were developed at a spatial resolution of $10'$ across 11°W - 32°E longitude and 34°N - 72°N latitude and then projected to the AFE 50 km grid using bilinear interpolation.

Climate projections were derived for 1991-2020 (referred to as 2020), 2021-2050 (2050), and 2051-2080 (2080) from three climate models (CGCM2, CSIRO2, and HadCM3) (Mitchell *et al.* 2004). The modelled climate anomalies were scaled based on four scenarios proposed by the IPCC (Nakicenovic *et al.* 2000). The A1FI scenario describes a globalized world under rapid economic growth and global population that peaks in mid-century and declines thereafter. Concentrations of CO_2 increase from 380 ppm in 2000 to 800 ppm in 2080, and temperature rises by 3.6 K. The A2 scenario describes a heterogeneous world with regionally oriented economic development. Per capita economic growth and technological change are slower than in the other scenarios. Global concentrations of CO_2 increase from 380 ppm in 2000 to 700 ppm in 2080, and temperature rises by 2.8 K. The B1 scenario describes a convergent world with global population that peaks in mid-century and declines thereafter, as in A1, but with a rapid change towards the introduction of clean and resource-efficient technology. Concentrations of CO_2 increase from 380 ppm in 2000 to 520 ppm in 2080, and temperature rises by 1.8 K. The B2 scenario describes a world in which the emphasis is on local solutions to socioeconomic and environmental sustainability. It is a world with continuously increasing global population (at a rate lower than A2), intermediate levels of economic development, and less rapid and more diverse technological change than in B1 and A1 scenarios. Concentrations of CO_2 increase from 380 ppm in 2000 to 550 ppm in 2080, and temperature rises by 2.1 K.

Protected areas

Two conservation areas datasets were used (see Fig. S1): The World Database of Protected Areas (<http://www.wdpa.org>) and the NATURA 2000 GIS (European Commission, Directorate-General Environment, personal communication). WDPA-UNEP contains point and polygon data for protected areas, whereas the NATURA 2000 GIS database contains polygon data alone. Only protected areas of IUCN categories I-VI were considered. WDPA-UNEP data (point and polygon layers) were downloaded and then clipped to the geographical area of Europe. Points overlapping with polygons and points with no information on area coverage were removed. For each data point with surface area information, a polygon (circle) of corresponding surface area was created, centred at the point coordinates. All WDPA-UNEP and NATURA 2000 layers were converted to Lambert Equal Area Azimutal 10/52 projection to match the biodiversity data. The ATEAM-project geographical window (<http://www.pik-potsdam.de/ateam/>) was used to obtain the percentage of each $10'$ grid cell overlapping with conservation areas polygons (Fig. S1). Computations were performed separately for NATURA 2000 areas and WDPA areas, with custom made functions for GIS (available upon request to MC).

Bioclimatic modelling

An ensemble of BEM was generated for each 1883 species considered. The ensemble included projections with seven methods: Generalised Linear Models (GLM), Generalised Additive Models (GAM), Boosted Regression Trees (BRT), Classification Tree Analysis (CTA), Artificial Neural Networks (ANN), Flexible Discriminant Analysis (FDA), and Surface Range Envelope (SRE). Models were calibrated for the baseline (1961-1991) using 80% random sample of the initial data and evaluated against the remaining 20% data, using the Area Under the Curve (AUC) of the Receiver Operation Characteristic (ROC) and the True Skill Statistic (TSS) (Liu *et al.* 2010). Projections were performed 10 times, each time selecting a different 80% random sample while verifying model accuracy against the remaining 20%. Verification or internal evaluation does not allow assessing the predictive performance of the models—independent evaluation data would be required for this purpose—but it provides a measure of internal consistency of the models. Here, the evaluation statistics were used to consider the possibility of exclusion of species on

the basis of poor matching between predictions and observations. Here, species with AUC <0.7 or TSS values <0.3 would be removed from the analysis. However, it was found that no species needed to be removed in addition to the species removed for being mainly aquatic or having too small range sizes (Fig. S2). For the final assessment, models were calibrated using 100% of the species distribution data as it has been shown that random removal of presence records adds a non-trivial amount of uncertainty in future projections (Araújo *et al.* 2009). Given the ensemble of projections obtained with the seven BEM and the three climate models, we calculated a consensus for each period and scenario. The consensus was based on a weighted mean probability of occurrence per species and per grid cell, where weights are obtained from the TSS obtained on the evaluation data (Marmion *et al.* 2009). The range of uncertainties obtained with the seven modelling techniques was also calculated (Table S4). All models were run using default options of the BIOMOD package (Thuiller *et al.* 2009).

Assessing climate change impacts on species

Assessments of climate change impacts on biodiversity typically start with measurements of changes in the size and position of bioclimatic envelopes. This procedure can be problematic if impacts of climate change are assessed for protected areas, because envelopes represent potential distributions of species and it is changes in the actual distributions of species that matter for conservation planning. Using the full bioclimatic envelopes to assess the impacts of climate change on protected areas would amount to estimating species losses from areas where they might not occur, thus undermining the usefulness of the assessment. To overcome this problem we restricted calculations of changes in climatic suitability to grid cells where species occur at present time. To do so, we downscaled species atlas information (originally at 50 km grid cell size) to 10' grid cells (Araújo *et al.* 2005a): if a species occurs in a 50 km grid cell, it was assumed to occur in each of the respective 10' grid cells with suitable climate; otherwise, it was assumed absent. Our analysis measures the exposure of species distributions to climate changes but it does not account for species migrating into conservation areas. Essentially, this is analogous to making an assumption of no dispersal.

Assessing impacts of climate change on conservation areas

Matching species distributions with conservation areas

Although the European grid cells used in the assessment are of near-equal size (10' latitude and longitude), the area conserved in each one of them varies (Fig. S1). For example, in Belgium the average size of protected areas is 170 hectares (ha), whereas in Portugal it is 13,430 ha. In order to account for variation in conservation areas coverage when assessing species' conservation status in grid cells, we applied an index derived from a probabilistic estimation of the matching between species' climate suitability and the proportion of the grid cells that is conserved (Alagador *et al.* 2011). Starting with the assumption that modelled climate suitability for species is uniformly distributed within grid cells, the matching of climate suitability with conserved (S_n^{cons}) and non-conserved area ($S_n^{no.cons}$), in a given grid cell, can be expressed for every species as:

$$(1) \quad S_n^{cons} = S_n \times CA_n$$

$$(2) \quad S_n^{no.cons} = S_n \times (1 - CA_n)$$

Where S_n is the suitability score of grid cell- n for a given species and CA_n is the proportion of the grid cell n covered by conservation areas; both S_n and CA_n range from 0 to 1. Values for S_n^{cons} range from 0, for grid cells that are unsuitable for the species or for cells with no areas conserved, to 1, for cells with climate suitability equal one and for cell fully conserved. Values for $S_n^{no.cons}$ also range between 0, for grid cells where the climate is unsuitable for the species or where conservation areas fully covered by the grid cell, to 1, for grid cells where climate suitability equals one and there are no areas conserved. This method avoids the multiple problems of using arbitrary thresholds for deciding whether grid cells are protected or not (Araújo 2004; Alagador *et al.* 2011).

For each one of the T combinations of timelines (baseline, 2020, 2050 and 2080) and emission scenario (A1FI, A2, B1, B2), we quantified the expected climate suitability S for each species within conservation areas (S_T^{cons}) and outside conservation areas ($S_T^{no.cons}$) as:

$$(3) \quad S_T^{cons} = \sum_{n=1}^N S_n^{cons}$$

$$(4) \quad S_T^{no.cons} = \sum_{n=1}^N S_n^{no.cons}$$

where N is the number of grid cells in the analysis. For assessments focused on individual countries, N ranges from $N=1$, for Monaco and Liechtenstein, to $N=2874$, for Sweden. When the assessments are made for the whole of Europe the geographic window varies because $N=12409$ for European protected areas (i.e., countries associated with the council of Europe) and $N=17122$ for the NATURA 2000 (i.e., EU countries). Changes in S_T^{cons} and $S_T^{no.cons}$ were calculated for each species with reference to the baseline period ($T=baseline$). Species projected to have increased climate suitability in conservation areas in each future time slice ($T=future$) were termed winners ($S_{future}^{cons} / S_{baseline}^{cons} > 1$), while species projected to have decreased climate suitability were termed losers ($S_{future}^{cons} / S_{baseline}^{cons} < 1$). Numbers of winner and loser species were obtained for three geographic levels (European, country, and grid cell). Standardized assessments of the proportion of winner and loser species at the country and grid-cell levels were obtained by dividing the number of winner and loser species in a particular time slice in the future by the total number of species present in the baseline period, respectively.

A null model for estimating the relative effectiveness of protected areas under climate change

We generated a null model to evaluate how European conservation areas (CA) perform in comparison to a random set of areas of equivalent total surface R .

$$(5) \quad R = \sum_{n=1}^N CA_n$$

For protected areas $R= 2078.74$ and for NATURA 2000 $R=2192.41$. We developed a procedure to generate random sets of areas following the frequency distribution of conservation areas coverage in Europe, for protected areas and NATURA 2000. We undertook 1000 permutations of grid cells by randomly locating conservation area coverages across grid cells and keeping constant, for the first analysis, the coverage of protected areas and, for the second, NATURA 2000 sites. In each permutation, S_T^{cons} was assessed for each species, T combinations of timelines (baseline, 2020, 2050 and 2080), and emission scenario (A1FI, A2, B1, B2). A null expected distribution of the proportion of winners and losers for each T combination was produced. The modelled proportion of losers and winners in conservation areas was then compared against the frequency distribution values from random trials at 95, 99, and 99.9 percentiles.

Auxiliary analyses

Mcnemar chi-squared tests of marginal homogeneity were applied to analyse differences in the proportion of loser species in each climatic scenario and period considered (function *mcnemar.test* in R). We assessed the six possible scenario combinations (A1FI vs A2; A1FI vs B1; A1FI vs B2; A2 vs B1; A2 vs B2 and B1 vs B2) for all species in protected areas and for species of European concern in Natura 2000. Because the number of Red-Listed species is small, the number of dissimilar occurrences in the contingency table (winner/loser or loser/winner) is less than 20 for these data. For this case, we used Wilcoxon-signed ranked test for paired samples. Wilcoxon rank-sum tests were also used to compare

range sizes of cold-adapted Bird & Habitat Directive species with warm-adapted Bird & Habitat Directive species.

RESULTS

Most vertebrate and plant species ($58\% \pm 2.6$; Median $\pm$ SD) are projected to lose suitable climate conditions within existing protected areas by 2080 (Fig. 1, full set of results in Table S2). Birds and mammals are projected to have greater proportions of loser than winner species in all scenarios, whereas amphibians are projected to have more losers than winners under A1FI and A2 and more winners under B1 and B2 scenarios (Fig. 1). Increases in climate suitability for species are expected for most reptiles in protected areas under all emission scenarios ($67\% \pm 3.7$). This is unsurprising since ectothermic species

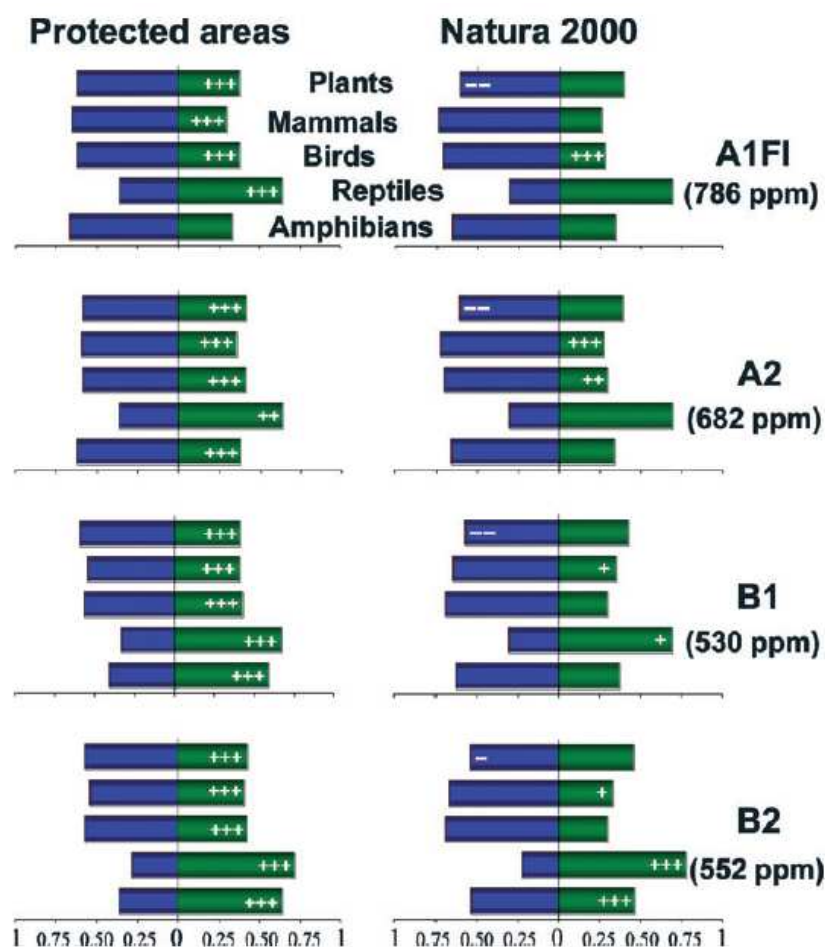


Fig. 1. Proportion of species projected to gain (winners; green) or lose (losers; blue) climatic suitability in European conservation areas under four emission scenarios by 2080 (ppm are 'part per million' concentrations of CO₂eq). Projections are provided for all modelled species in protected areas and for EU Bird & Habitat Directive species occurring in the Natura 2000. Conservation areas retaining more climatic suitability for species than expected in randomly selected unprotected areas are marked with +++ (P<0.001), ++ (P<0.01), + (P<0.05), whereas conservation areas retaining less climatic suitability for species than expected in randomly selected unprotected areas are marked with -- (P<0.01) and - (0.05).

are known to benefit from warming in temperate regions (Araújo *et al.* 2006), although local behaviour and population dynamics can alter, sometimes reverse, coarse projections from bioclimatic models (Sinervo *et al.* 2010). Amphibians are also ectotherms but they do not benefit from increases in aridity, which is the prediction for the southwest of Europe under the A1FI and A2 scenarios (Schroter *et al.* 2005). Projections also indicate that negative impacts of climate change are expected to be high among species of European conservation concern. Bird & Habitat Directive species ($n=323$) have higher proportions of plant and animal species losing climatic suitability in the Natura 2000 ($63\% \pm 2.1$, Table S2) than species in protected areas. In fact, the Natura 2000 is less effective in retaining suitable climate for plant species than sets of randomly selected unprotected areas of the same total area ($p < 0.001$ for A1FI, A2, B1; $p < 0.05$ for B2). For half of the remaining combinations of taxonomic groups and scenarios, the Natura 2000 provides no better buffer against climate change than areas outside the network, with the exception of birds ($p < 0.001$) (Fig. 1). In contrast, nationally-designated protected areas are projected to retain climatic suitability for species better than randomly selected unprotected areas with the same total area ($p < 0.001$). The one exception is amphibian species, under the A1FI scenario, where protected areas provide no better protection than randomly chosen unprotected areas. When threatened species are examined ($n=53$), protected areas retain climatic suitability no better than randomly selected unprotected areas for birds and reptiles (under the A1FI and A2 scenario), but they retain suitable ranges for the other taxa and climate scenarios well ($P < 0.05$ or 0.01 , see Table S1). Differences in changes of climate suitability between protected areas and Natura 2000 are partly related with topography. Most protected areas are in mountains (median altitude=367.40 meters) or rugged environments (median standard deviation, SD, of altitude=814.90). The Natura 2000 also prioritizes farmlands and these are located in lower (median altitude=324.69) and flatter lands (median SD of altitude=638.08). Indeed, altitude and SD of altitude for the Natura 2000 were measured for the fraction of land that does not overlap with protected areas. Differences in altitude (Wilcoxon $W=13.4e6$) and SD of altitude ($W=11.6e6$) between protected and Natura 2000 areas are significant ($P < 0.001$). Because proportional range losses arising from climate change are usually more pronounced in flatlands than in rugged terrains (Peterson 2003; Loarie *et al.* 2009), the Natura 2000 is more vulnerable to climate change.

Losses of climatic suitability generally increase with greenhouse-gas emissions for IUCN Red-Listed species occurring in protected areas ($r^2=0.82$, $p < 0.001$), and similar relationship is recorded for the full set of species in protected areas and Bird & Habitat Directive species in the Natura 2000 ($r^2=0.71$, $p < 0.001$). In the worst-case scenario, with CO₂ equivalent concentrations increasing from ca. 380ppm in 2000 to ca. 800ppm in 2080, and European temperatures rising by $3.6K \pm 0.6$ in 2080 (A1FI scenario), the proportion of loser species in protected areas exceeds 60% and is the greatest among all four emission scenarios (A1FI=62%, A2=58%, B1=57%, B2=55%; McNemar test $\chi^2 > 37.3$, $P < 0.001$, Table S2). A similar trend is projected for the Red-listed species in protected areas and the Bird & Habitat Directive species in Natura 2000 (Table S2).

A geographical analysis reveals that loser species are predominant over winners across most protected and Natura 2000 areas. Higher proportion of winner species is projected in conservation areas of northern Scandinavia and Britain and in mountains such as the Alps, the Pyrenees and the Carpathians (Fig. 2). A country-by-country analysis reveals that all but two countries (Finland and Sweden) have more loser than winner species in Natura 2000 sites (Fig. 2, Table S3). The number of countries with a higher ratio between winners and losers is greater for protected areas than for Natura 2000, but the general tendency is for increased numbers of winners in the colder edges of Europe (Fig. 2). As expected, differences in thermal tolerance play a major role in accounting for the excesses of winners over losers in these areas. Many warm-tolerant species exist in high latitudes and altitudes and these will gain climatic suitability with climate warming, but the overwhelming majority of alpine and sub-arctic species of European concern (i.e., 97.2%) are projected to lose suitability (Fig. 3). Indeed, because such cold-adapted species have smaller ranges (range sizes at quartiles 25%=35.5, 50%=135.5, 75%=260) than warm-adapted species (25%=366; 50%=1706; 75%=2214), they are exposed to the double jeopardy of being rare and more negatively affected by climate change (Fig. 3).

Uncertainties from extrapolating beyond the climatic values used for calibration of the models are restricted to southern Europe, particularly the Iberian Peninsula (Figure 4), thus not affecting the robustness of the results in most of Europe.

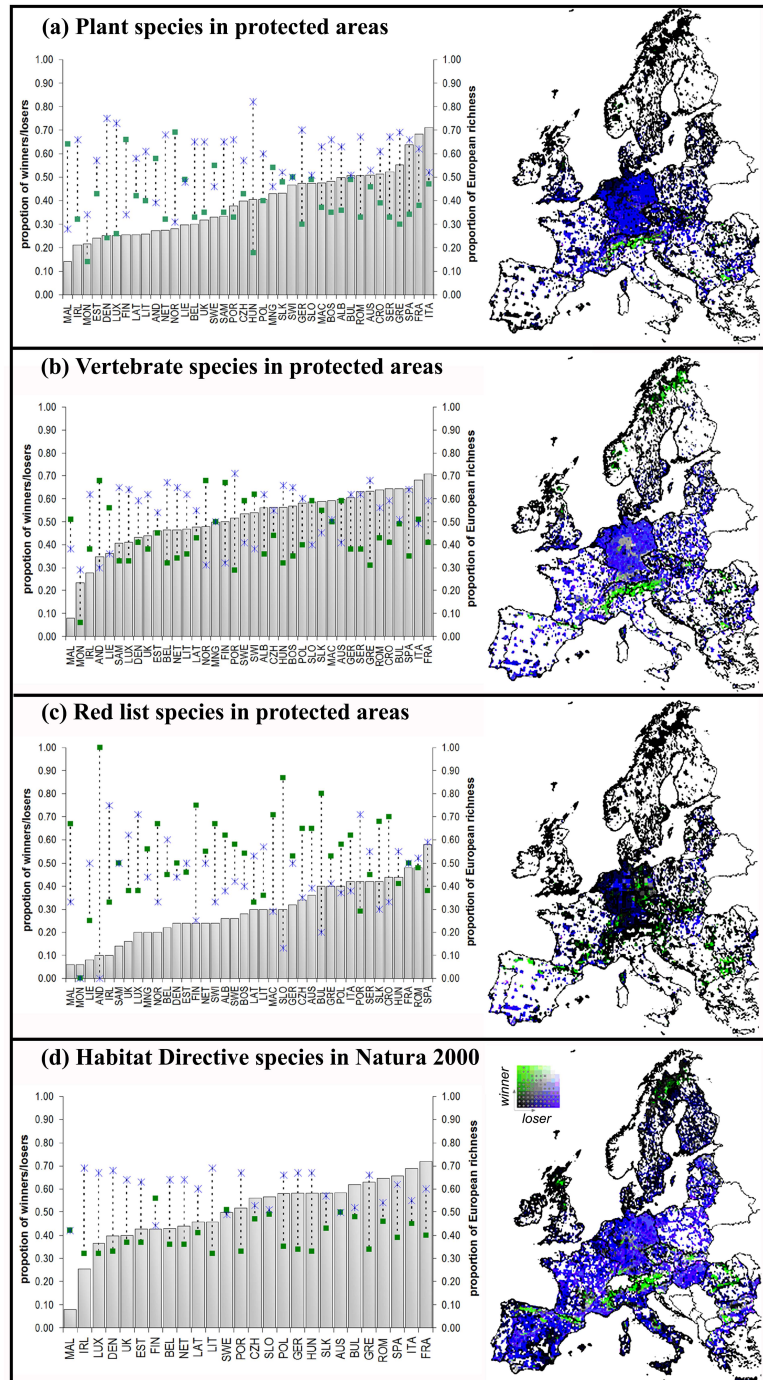


Fig. 2. Geographical distribution of winners and losers. Left - The proportion of European species that occur in each individual country (bars, left axis) against the proportion of projected loser (blue asterisks, right axis) and winner species (green squares, right axis) as projected for 2080 with the A1FI scenario: (A) plant species occurring in protected areas; (B) vertebrate species occurring in protected areas; (C) IUCN Red data vertebrate and plant species occurring in protected areas (n=52); (D) Bird & Habitat directive vertebrate and plant species occurring in Natura 2000 sites (n=317). Notice that countries on the x axis are ordered by the proportion of European species that occur in them. Right - Overlay between richness of species losing and winning suitable climate in conservation areas. Scores are divided into 10 equal-interval colour classes, where increasing intensities of blue represent increasing numbers of species losing suitable climate in conservation areas and increasing intensities of green represent increasing numbers of species winning suitable climate; shades of grey represent linearly covarying scores between winners and losers. All 10' latitude and longitude cells with >0% coverage with conservation areas are coloured. Regions with several small-sized conservation areas appear to have greater degree of protection but for the analyses, the percentage of grid-cell coverage by conservation areas was computed (Fig. S1) and combined with modelled climatic suitabilities for each species. Country abbreviations are as follows: ALB – Albania; AND – Andorra; AUS – Austria; BEL – Belgium; BOS – Bosnia & Herzegovina; BUL – Bulgaria; CRO – Croatia; CZH – Czech Republic; DEN – Denmark; EST – Estonia; FIN – Finland; FRA – France; GER – Germany; GRE – Greece; HUN – Hungary; IRL – Ireland; ITA – Italy; LAT – Latvia; LIE – Liechtenstein; LIT – Lithuania; LUX – Luxembourg; MAC – Macedonia; MAL – Malta; MNG – Montenegro; MON – Monaco; NET – Netherlands; NOR – Norway; POL – Poland; POR – Portugal; ROM – Romania; SAM – San Marino; SER – Serbia; SLK – Slovakia; SLO – Slovenia; SPA – Spain; SWE – Sweden; SWI – Switzerland; UK – United Kingdom.

DISCUSSION

This study provides the most comprehensive analysis of climate change impacts and their uncertainties, on protected biodiversity anywhere in the world. However, not all uncertainties were accounted for. For example, population dynamics causing non-linear responses to climate change (e.g., Keith *et al.* 2008; Anderson *et al.* 2009) were not modelled. The same can be said about interdependencies between species, some of which may have cascading effects and cause secondary extinctions when key species are removed (e.g., Ebenman & Jonsson 2005; Tylianakis *et al.* 2008). In fact, given the extent of the study region and the sheer number of species, simplifications are inevitable. The question is whether such

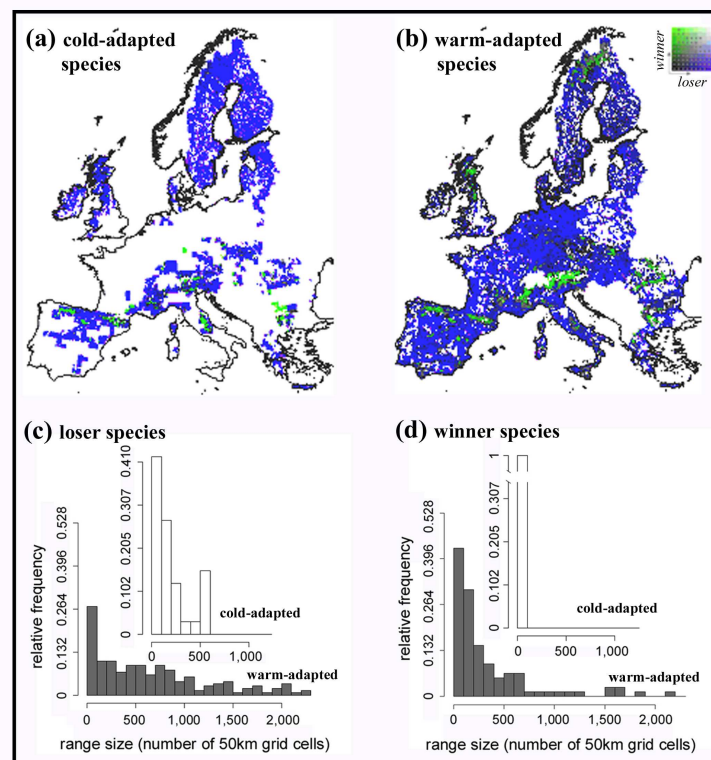


Fig. 3. Vulnerability of cold-adapted versus warm-adapted Bird & Habitat Directive species occurring in Natura 2000 areas: (A) overlay between richness of cold-adapted loser and winner species; (B) overlay between richness of warm-adapted loser and winner species. Scores on the maps are divided into 10 equal-interval colour classes, where increasing intensities of blue represent increasing numbers of loser species and increasing intensities of green represent increasing number of winner species; shades of grey represent linearly covarying scores between winners and losers; (C) Frequency distribution of the range sizes (number of grid cells occupied) of cold-adapted (empty bars) and warm-adapted loser species (dark bars) ($W=1530$, $p<0.001$); (D) Frequency distribution of range sizes of cold-adapted (empty bars) and warm-adapted winner species (dark bars) ($W=3$, $p=0.100$).

simplifications enable useful projections under climate change. A number of studies have empirically demonstrated that carefully implemented bioclimatic models can recover the broad-scale direction of species range changes under climate change (Araújo *et al.* 2005b; Green *et al.* 2008; Rodríguez-Sánchez & Arroyo 2008; Kearney *et al.* 2010; Dobrowski *et al.* 2011) and others have demonstrated the usefulness of models for uncovering deep-time biological processes, such as extinction and speciation (e.g., Raxworthy *et al.* 2003; Nogués-Bravo *et al.* 2008; Carnaval *et al.* 2009). There are important uncertainties with regards to the magnitude of modelled range changes, since these are contingent on several unmeasured factors. However, evidence shows that models can recover the tendency of range increase or decrease with reasonable accuracy. Thus, one possible approach to limit uncertainty is to interpret

model projections conservatively. By quantifying whether species are expected to win or lose climate suitability under climate change we avoid making quantitative inferences about population parameters, such as changes in range, abundance or extinction risk, that are not explicitly modelled (e.g., Brook *et al.* 2009). Our ensemble forecasting strategy also surmounts familiar shortcomings of bioclimatic envelope models, particularly their potential to yield very different projections under future scenarios. Of particular relevance is the use of weighted-majority criterion to generate consensus among projections (Araújo *et al.* 2005b; Marmion *et al.* 2009), the restriction of analysis to areas with known records of occurrence for species, thus removing commission errors, and the use of a probabilistic-based approach to match conservation areas with climate suitability scores for species (Alagador *et al.* 2011). We also show that the risk of models extrapolating beyond the baseline climate is small, as non-analogue climates are restricted to southern Europe and impacts are projected for conservation areas throughout Europe. Despite methodological advances, any study using models needs to exercise caution when deriving conclusions with relevance for policy making. We argue that by examining changes in climatic suitability rather than making inferences about species range changes, we focus on what models truly deliver and substantially reduce uncertainties arising from simplification of complex ecological processes. Despite restricting our assessment to statistics of winners and losers, results have profound consequences for policy making.

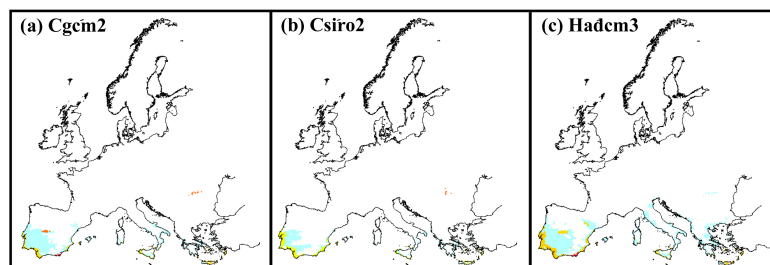


Fig. 4. Distribution of non-analogue climates in 2080 under the A1FI emission scenario. For each variable (mean temperature of the coldest month, mean annual summed precipitation, mean annual growing degree days, and the ratio of mean annual actual evapotranspiration over mean annual potential evapotranspiration), non-analogue climates are defined as those exceeding the highest and lowest values recorded for the baseline. Colours indicate 'richness' of non-analogue climates, i.e., the summed occurrence of non-analogue climates for each variable, where increasing gradients of red indicate increased richness of non-analogue climates and white cells indicate absence of non-analogue climates.

Using analysis of 21st century climate change impacts on terrestrial vertebrate and plant species diversity in conservation areas, we demonstrate that climate change presents a challenge to the view that species' distributions change relatively slowly unless they are directly affected by human activities. Specifically, we show that during the 21st century climate conditions are likely to become less suitable for species in European conservation areas. Nationally designated protected areas would preserve species better than unprotected areas, probably because they tend to occur in mountains, which act as climate refugia. Species in the Natura 2000 network are more vulnerable since more flatlands are included in the network and proportional range losses under climate impacts are greater there (Peterson 2003; Loarie *et al.* 2009). Our analysis does not provide quantitative estimates of extinction risk for species, because such estimates are beyond current data and modelling capabilities. However, future conservation efforts should be fully aware that the distribution of biodiversity, and species of concern, will be dramatically altered by climate change and that increased extinctions risk is one of the possible outcomes. Although reduction of greenhouse gas emissions would help mitigating climate impacts on biodiversity, conserving biodiversity will require approaches above and beyond those that are currently implemented in Europe. Such approaches might include the reclassification of existing conservation areas (Fuller *et al.* 2010) and the designation of new areas, as well as the implementation of mechanisms for integrated management of the countryside to facilitate movement of species between conservation areas. Making such moves implies a major paradigm shift in current conservation policies.

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Supporting Online Material for
CLIMATE CHANGE THREATENS EUROPEAN CONSERVATION AREAS

- S1. Figures

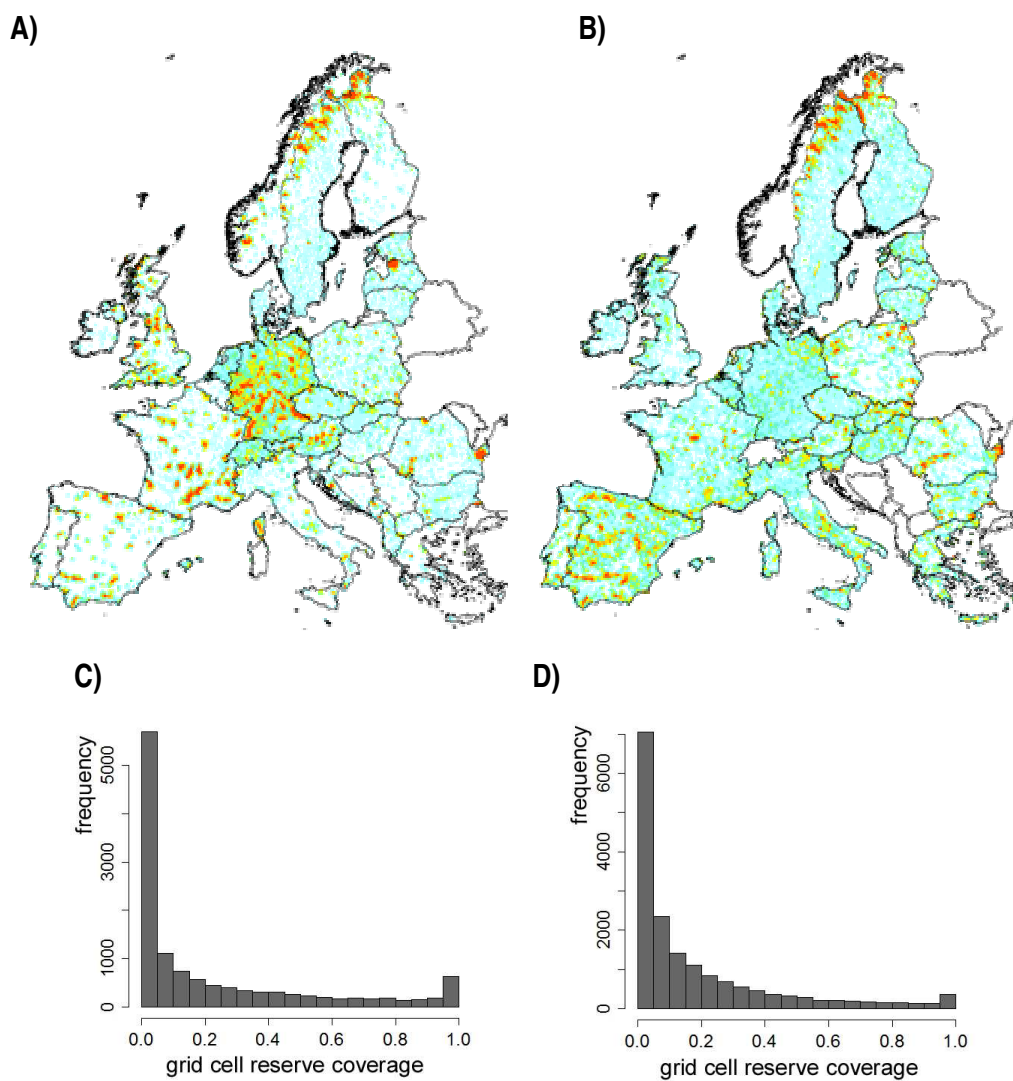


Fig S1 – Proportion of 10' grid cells that are covered by protected areas (A) and Natura 2000 (B), and the respective frequency distribution values of the proportion of coverage of protected areas (C) and Natura 2000 (D).

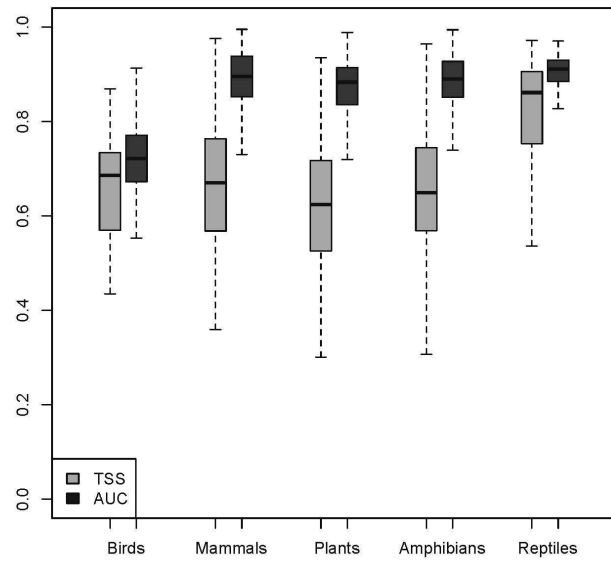


Fig S2 –Predictive modelling accuracy for the five species groups. Each box represents the extreme of the lower whisker, the lower hinge, the median, the upper hinge and the extreme of the upper whisker for the True Skill Statistic (TSS), and the Area Under the Curve (AUC). The boxes represent the metrics estimated during the cross-validation phase (on the testing data not used for calibrating the models) and across the 7 different models retained.

- S2. Tables

Table S1a - Numbers of species projected to gain (win) and lose (los) climatic suitability in protected areas (in parenthesis is the expected value outside protected areas), for different combinations of emission scenarios and time periods. Projections are provided for IUCN Red-Listed species (RL species), and for the complete pool of vertebrate and plant species considered (all). Protected areas retaining more loser species than 95% of a set of similar sized random selected areas are marked with *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$).

	A1FI				A2				B1				B2			
	RL species		all		RL species		all		RL species		all		RL species		all	
	win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Amphibians																
2020	8 (2) ***	0 (6)	32 (19) ***	10 (23)	8 (2) ***	0 (6)	32 (19) ***	10 (23)	7 (3) ***	1 (5)	32 (21) ***	10 (21)	8 (3) ***	0 (5)	34 (21) ***	8 (21)
2050	3 (2) *	5 (6)	21 (18) ***	21 (24)	3 (2) **	5 (6)	24 (19) ***	18 (23)	5 (2) ***	3 (6)	27 (19) ***	15 (23)	4 (2) ***	4 (6)	25 (19) ***	17 (23)
2080	2 (2)	6 (6)	14 (14)	28 (28)	2 (2)	6 (6)	16 (14)	26 (28)	3 (2) *	5 (6)	25 (13) ***	17 (29)	5 (2) ***	3 (6)	27 (14) ***	15 (28)
Reptiles																
2020	5 (3) ***	2 (4)	46 (40) ***	18 (24)	5 (3) ***	2 (4)	48 (41) ***	16 (23)	5 (3) ***	2 (4)	45 (40) ***	19 (24)	5 (3) ***	2 (4)	49 (41) ***	15 (23)
2050	3 (2) ***	4 (5)	41 (36) ***	23 (28)	3 (2) ***	4 (5)	41 (34) ***	23 (30)	2 (2) ***	5 (5)	41 (37) ***	23 (27)	3 (2) ***	4 (5)	41 (36) ***	23 (28)
2080	3 (2) **	4 (5)	41 (38) ***	23 (26)	3 (2) **	4 (5)	41 (38) ***	23 (26)	4 (2) **	3 (5)	43 (37) ***	21 (27)	6 (2) ***	1 (5)	46 (38) ***	18 (26)
Birds																
2020	6 (4) ***	8 (10)	157 (132) ***	185 (211)	6 (4) ***	8 (10)	156 (135) ***	186 (208)	5 (3)	9 (11)	153 (128) **	189 (215)	5 (3)	9 (11)	155 (130) ***	187 (213)
2050	5 (6)	9 (8) *	154 (130) ***	188 (213)	6 (6)	8 (8) *	157 (128) ***	185 (215)	5 (6)	9 (8) *	158 (130) ***	184 (213)	4 (5)	10 (9) *	154 (128) ***	188 (215)
2080	5 (4)	9 (10)	130 (101) ***	212 (242)	5 (4)	9 (10)	141 (111) ***	201 (232)	4 (3)	10 (11)	148 (120) ***	194 (223)	4 (4)	10 (10)	147 (118) ***	195 (225)
Mammals																
2020	12 (10)	9 (11)	65 (51) ***	70 (84)	12 (11)	9 (10)	65 (52) ***	70 (83)	11 (11)	10 (10)	64 (55) ***	71 (80)	11 (11)	10 (10)	64 (57) ***	71 (78)
2050	11 (8) ***	10 (13)	56 (37) ***	79 (98)	11 (9) ***	10 (12)	57 (39) ***	78 (96)	11 (9) ***	10 (12)	59 (39) ***	76 (96)	11 (9) ***	10 (12)	58 (40) ***	77 (95)
2080	9 (7) ***	12 (14)	43 (35) ***	92 (100)	11 (7) ***	10 (14)	51 (36) ***	84 (99)	11 (7) ***	10 (14)	58 (37) ***	77 (98)	10 (7) **	11 (14)	58 (37) ***	77 (98)
Plants																
2020	1 (1)	2 (2)	663 (565) ***	641 (740)	1 (1)	2 (2)	678 (567) ***	626 (738)	1 (1)	2 (2)	668 (554) ***	636 (751)	1 (1)	2 (2)	676 (557) ***	629 (748)
2050	3 (2)	0 (1)	613 (469) ***	692 (836)	3 (2)	0 (1)	631 (489) ***	674 (816)	3 (2)	0 (1)	630 (490) ***	675 (815)	3 (2)	0 (1)	633 (498) ***	672 (807)
2080	2 (1) ***	1 (2)	497 (324) ***	808 (981)	2 (1) ***	1 (2)	542 (355) ***	763 (950)	2 (1) ***	1 (2)	538 (368) ***	767 (937)	2 (1) ***	1 (2)	563 (387) ***	742 (918)

Table S1a (continued)

A1F1				A2				B1				B2				
RL species		all		RL species		all		RL species		all		RL species		all		
win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los	
All taxa																
2020	32	21	963	924	32	21	979	908	29	24	962	925	30	23	978	910
	(20)	(33)	(807)	(1082)	(21)	(32)	(814)	(1075)	(21)	(32)	(798)	(1091)	(21)	(32)	(806)	(1083)
	***		***		***		***		**		***		***		***	
2050	25	28	885	1003	26	27	910	978	26	27	915	973	25	28	911	977
	(20)	(33)	(690)	(1199)	(21)	(32)	(709)	(1180)	(21)	(32)	(715)	(1174)	(20)	(33)	(721)	(1168)
	**		***		**		***		***		***		***		***	
2080	21	32	725	1163	23	30	791	1097	24	29	812	1076	27	26	841	1047
	(16)	(47)	(512)	(1377)	(16)	(37)	(554)	(1335)	(15)	(38)	(575)	(1314)	(16)	(37)	(594)	(1295)
	***		***		***		***		***		***		***		***	

Table S1b – Numbers of species projected to gain (win) and lose (los) climatic suitability in Natura 2000 areas (in parenthesis is the expected value outside the Natura 2000), for different combinations of emission scenarios and time periods. Projections are provided for Habitat Directive species (HD species), and for the complete pool of vertebrate and plant species considered (all). Protected areas retaining more loser species than 95% of a set of similar sized random selected areas are marked with *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$).

	A1FI				A2				B1				B2			
	HD species		All		HD species		all		HD species		all		HD species		all	
	win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Amphibians																
2020	23 (17) ***	9 (15)	28 (19) ***	14 (23)	23 (17) ***	9 (15)	28 (19) ***	14 (23)	24 (17) ***	8 (15)	31 (21) ***	11 (21)	24 (18) ***	8 (14)	31 (21) ***	11 (21)
2050	17 (14) **	15 (18)	20 (17) **	22 (25)	17 (16) **	15 (16)	20 (19) **	22 (23)	17 (16) **	15 (16)	20 (19) **	22 (23)	18 (17) **	14 (15)	21 (20) **	21 (22)
2080	11 (9)	21 (23)	13 (10) **	29 (32)	11 (11)	21 (21)	13 (12) **	29 (30)	12 (11)	20 (21)	14 (11) **	28 (31)	15 (11) ***	17 (21)	18 (13) **	24 (29)
Reptiles																
2020	23 (22)	13 (14)	40 (37) *	24 (27)	23 (22)	13 (14)	40 (38) *	24 (26)	22 (21)	14 (15)	41 (36) *	23 (28)	24 (23)	12 (13)	42 (39) **	22 (25)
2050	25 (25)	11 (11)	36 (35)	28 (29)	26 (25)	10 (11)	36 (35)	28 (29)	25 (25)	11 (11)	37 (38)	27 (26)	25 (25)	11 (11)	37 (36)	27 (28)
2080	25 (22)	11 (14)	39 (35) *	25 (29)	25 (23)	11 (13)	39 (36) *	25 (28)	25 (23)	11 (13)	38 (35)	26 (29)	28 (24) **	8 (12)	41 (37) **	23 (27)
Birds																
2020	61 (58) *	111 (114)	130 (124) *	212 (219)	63 (58) **	109 (114)	134 (125) ***	208 (218)	59 (54)	113 (118)	131 (120) *	211 (223)	61 (54) *	111 (118)	134 (120) ***	208 (223)
2050	66 (64)	106 (108)	128 (124)	214 (219)	67 (64)	105 (108)	129 (124)	213 (219)	65 (64)	107 (108)	128 (125)	214 (218)	64 (64)	108 (108)	126 (125)	216 (218)
2080	49 (42) ***	123 (130)	106 (97) ***	236 (246)	51 (48) ***	121 (124)	111 (105) ***	231 (238)	52 (50) ***	120 (122)	117 (114) ***	225 (229)	52 (49) ***	120 (123)	117 (112) ***	225 (231)
Mammals																
2020	29 (23) ***	25 (31)	63 (50) ***	72 (85)	29 (23) ***	25 (31)	63 (50) ***	72 (85)	28 (23) ***	26 (31)	62 (48) ***	73 (87)	29 (23) ***	25 (31)	63 (51) ***	72 (84)
2050	20 (17) ***	34 (37)	43 (37) ***	92 (98)	20 (17) ***	34 (37)	46 (38) ***	89 (97)	23 (17) ***	31 (37)	49 (40) ***	86 (95)	23 (17) ***	31 (37)	49 (42) ***	86 (93)
2080	14 (13)	40 (41)	33 (31)	102 (104)	15 (12)	39 (42)	36 (30) ***	99 (105)	19 (15) ***	35 (39)	43 (35) ***	92 (100)	18 (15) ***	36 (39)	42 (35) ***	93 (100)
Plants																
2020	13 (13)	15 (15) ***	581 (535) ***	724 (770)	13 (13)	15 (15) ***	585 (535) ***	720 (770)	13 (13)	15 (15) ***	571 (511) ***	734 (794)	14 (13)	14 (15) **	586 (519) ***	719 (786)
2050	13 (13)	15 (15) ***	512 (448) ***	793 (857)	13 (13)	15 (15) ***	523 (458) ***	782 (847)	13 (13)	15 (15) ***	531 (456) ***	774 (849)	15 (15)	13 (13) **	537 (476) ***	768 (829)
2080	11 (11)	17 (17) ***	363 (316) ***	942 (989)	11 (13)	17 (15) ***	398 (350) ***	907 (955)	12 (13)	16 (15) ***	407 (356) ***	897 (949)	13 (14)	15 (14) **	432 (382) ***	873 (923)

Table S1b (continued)

	A1F1				A2				B1				B2			
	HD species		all		HD species		all		HD species		all		HD species		all	
	win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
<i>All taxa</i>																
2020	149 (133) *	173 (189)	842 (765) ***	1046 (1124)	151 (133) *	171 (189)	850 (767) ***	1038 (1122)	146 (128) *	176 (194)	836 (736) ***	1052 (1153)	152 (131) *	170 (191)	856 (750) ***	1032 (1139)
2050	141 (133) *	181 (189)	739 (661) ***	1149 (1228)	143 (135) *	179 (187)	754 (674) ***	1134 (1215)	143 (135) *	179 (187)	765 (678) ***	1123 (1211)	145 (138) *	177 (184)	770 (699) ***	1118 (1190)
2080	110 (97) *	212 (225)	554 (489) ***	1334 (1400)	113 (107)	209 (215)	597 (533) ***	1291 (1356)	121 (112) *	202 (210)	619 (551) ***	1268 (1338)	126 (113) *	196 (209)	650 (579) ***	1238 (1310)

Table S2 - Percentage of projected loser species. Values are provided for different combinations of suites of species, conservation areas, emission scenarios and years. Significant pairwise differences between means were assessed with McNemar tests for the complete pool of species in protected areas as well as for the Habitat Directive species in NATURA sites. Wilcoxon-signed rank tests are provided for Red-listed species in protected areas. Letters *a* to *e* code the pairs of emission scenarios with proportions of loser species projected to be different with the following levels of significance *** $p<0.001$, ** $p<0.01$, * $p<0.05$. For the all-species in protected areas set, the A1FI scenario for 2020 differs from the A2 scenario (*a*, $p<0.01$), the A2 scenario differs from the B1 scenario (*b*, $p<0.05$), and the B1 scenario differs from the B2 scenario (*c*, $p<0.05$).

		A1FI	A2	B1	B2	mean±SD
<i>all species</i>						
Protected areas	2020	48.91 <i>a**</i>	48.07 <i>a**,b*</i>	48.97 <i>b*,c*</i>	48.17 <i>c*</i>	48.53±0.48
	2050	53.10 <i>a***,b***,c***</i>	51.77 <i>a***</i>	51.51 <i>B***</i>	51.72 <i>c***</i>	52.02±0.72
	2080	61.57 <i>a***,b***,c***</i>	58.07 <i>a***,d***</i>	56.96 <i>b***,e***</i>	55.43 <i>c***,d***,e***</i>	58.01±2.61
<i>priority species</i>						
Protected areas	2020	39.62	39.62	45.28	43.40	41.98±2.83
	2050	52.83	50.94	50.94	52.83	51.89±1.09
	2080	60.38 <i>a*</i>	56.60 <i>b*</i>	54.72	49.06 <i>a*, b*</i>	55.19±4.72
Natura 2000	2020	53.56	52.94	54.49	52.63	53.41±0.82
	2050	56.04	55.42	55.42	54.80	55.42±0.51
	2080	65.63 <i>a**</i>	64.71 <i>b**</i>	62.54 <i>c*</i>	60.68 <i>a**,b**,c*</i>	63.39±2.22

Table S3a – Number of species projected to gain (win) and lose (los) climatic suitability in protected areas (in parenthesis: outside protected areas), for the different countries, climatic storylines and analysed years. Projections are provided for Red-List species (RL species) and for all species (all).

		A1FI				A2				B1				B2			
		all species		RL species		all species		RL species		all species		RL species		all species		RL species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Amphibians																	
Albania	2020	7 (7)	8 (8)	0 (0)	0 (0)	7 (7)	8 (8)	0 (0)	0 (0)	7 (6)	8 (9)	0 (0)	0 (0)	7 (7)	8 (8)	0 (0)	0 (0)
	2050	10 (10)	5 (5)	0 (0)	0 (0)	10 (10)	5 (5)	0 (0)	0 (0)	10 (10)	5 (5)	0 (0)	0 (0)	10 (10)	5 (5)	0 (0)	0 (0)
	2080	6 (5)	9 (10)	0 (0)	0 (0)	6 (5)	9 (10)	0 (0)	0 (0)	6 (3)	9 (12)	0 (0)	0 (0)	6 (5)	9 (10)	0 (0)	0 (0)
Andorra	2020	7 (8)	1 (0)	1 (1)	0 (0)	7 (8)	1 (0)	1 (1)	0 (0)	7 (8)	1 (0)	1 (1)	0 (0)	7 (8)	1 (0)	1 (1)	0 (0)
	2050	7 (7)	1 (1)	1 (1)	0 (0)	8 (8)	0 (0)	1 (1)	0 (0)	8 (8)	0 (0)	1 (1)	0 (0)	8 (7)	0 (0)	1 (1)	0 (0)
	2080	7 (7)	1 (1)	1 (1)	0 (0)	6 (7)	2 (1)	1 (1)	0 (0)	7 (6)	1 (2)	1 (1)	0 (0)	7 (6)	1 (2)	1 (1)	0 (0)
Austria	2020	13 (12)	7 (8)	0 (0)	0 (0)	13 (12)	7 (8)	0 (0)	0 (0)	13 (12)	7 (8)	0 (0)	0 (0)	12 (12)	8 (8)	0 (0)	0 (0)
	2050	14 (13)	6 (7)	0 (0)	0 (0)	16 (15)	4 (5)	0 (0)	0 (0)	14 (14)	5 (5)	0 (0)	0 (0)	14 (15)	5 (5)	0 (0)	0 (0)
	2080	14 (10)	6 (10)	0 (0)	0 (0)	14 (12)	6 (8)	0 (0)	0 (0)	14 (15)	4 (5)	0 (0)	0 (0)	14 (14)	4 (5)	0 (0)	0 (0)
Belgium	2020	14 (13)	4 (6)	0 (0)	0 (0)	13 (13)	4 (6)	0 (0)	0 (0)	14 (13)	4 (6)	0 (0)	0 (0)	13 (12)	5 (7)	0 (0)	0 (0)
	2050	12 (5)	7 (14)	0 (0)	0 (0)	12 (5)	7 (14)	0 (0)	0 (0)	12 (5)	7 (14)	0 (0)	0 (0)	12 (5)	7 (14)	0 (0)	0 (0)
	2080	5 (3)	14 (16)	0 (0)	0 (0)	8 (4)	11 (15)	0 (0)	0 (0)	8 (7)	11 (12)	0 (0)	0 (0)	6 (6)	13 (13)	0 (0)	0 (0)
Bosnia and Herzeg	2020	10 (6)	9 (13)	1 (1)	0 (0)	10 (7)	9 (12)	1 (1)	0 (0)	7 (6)	11 (13)	1 (1)	0 (0)	8 (6)	10 (13)	1 (1)	0 (0)
	2050	11 (9)	8 (10)	1 (1)	0 (0)	12 (9)	7 (10)	1 (1)	0 (0)	12 (8)	7 (11)	1 (1)	0 (0)	12 (9)	7 (10)	1 (1)	0 (0)
	2080	7 (7)	12 (12)	0 (1)	1 (0)	11 (8)	8 (11)	1 (1)	0 (0)	8 (8)	10 (11)	0 (1)	0 (0)	10 (8)	9 (11)	1 (1)	0 (0)
Bulgaria	2020	10 (7)	7 (10)	0 (0)	0 (0)	11 (7)	6 (10)	0 (0)	0 (0)	11 (7)	6 (10)	0 (0)	0 (0)	11 (7)	6 (10)	0 (0)	0 (0)
	2050	12 (10)	5 (7)	0 (0)	0 (0)	12 (11)	5 (6)	0 (0)	0 (0)	13 (10)	4 (7)	0 (0)	0 (0)	13 (11)	4 (6)	0 (0)	0 (0)
	2080	9 (9)	8 (8)	0 (0)	0 (0)	9 (9)	8 (8)	0 (0)	0 (0)	11 (9)	6 (8)	0 (0)	0 (0)	10 (10)	7 (7)	0 (0)	0 (0)
Croatia	2020	6 (4)	13 (15)	2 (2)	0 (0)	6 (4)	13 (15)	2 (2)	0 (0)	4 (4)	15 (15)	1 (2)	1 (0)	6 (4)	13 (15)	2 (2)	0 (0)
	2050	6 (6)	13 (13)	2 (2)	0 (0)	6 (6)	13 (13)	2 (2)	0 (0)	6 (6)	13 (13)	2 (2)	0 (0)	6 (6)	13 (13)	2 (2)	0 (0)
	2080	5 (5)	14 (14)	2 (2)	0 (0)	7 (6)	12 (13)	2 (2)	0 (0)	5 (5)	14 (14)	2 (2)	0 (0)	5 (5)	14 (14)	2 (2)	0 (0)
Czech Republic	2020	17 (11)	2 (8)	0 (0)	0 (0)	17 (11)	2 (8)	0 (0)	0 (0)	17 (13)	2 (6)	0 (0)	0 (0)	17 (13)	2 (6)	0 (0)	0 (0)
	2050	13 (10)	6 (9)	0 (0)	0 (0)	14 (13)	5 (6)	0 (0)	0 (0)	14 (13)	5 (6)	0 (0)	0 (0)	14 (13)	5 (6)	0 (0)	0 (0)
	2080	11 (7)	8 (12)	0 (0)	0 (0)	13 (10)	6 (9)	0 (0)	0 (0)	14 (12)	5 (7)	0 (0)	0 (0)	14 (12)	5 (7)	0 (0)	0 (0)
Denmark	2020	10 (10)	4 (4)	0 (0)	0 (0)	10 (10)	4 (4)	0 (0)	0 (0)	10 (10)	4 (4)	0 (0)	0 (0)	10 (10)	4 (4)	0 (0)	0 (0)
	2050	9 (10)	5 (4)	0 (0)	0 (0)	10 (10)	4 (4)	0 (0)	0 (0)	9 (10)	5 (4)	0 (0)	0 (0)	9 (9)	5 (5)	0 (0)	0 (0)
	2080	6 (7)	8 (8)	0 (0)	0 (0)	7 (7)	7 (7)	0 (0)	0 (0)	7 (8)	7 (6)	0 (0)	0 (0)	7 (7)	7 (7)	0 (0)	0 (0)
Estonia	2020	11 (11)	0 (0)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)
	2050	11 (11)	0 (0)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)	11 (10)	0 (1)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)
	2080	11 (11)	0 (0)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)	11 (11)	0 (0)	0 (0)	0 (0)
Finland	2020	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)
	2050	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)
	2080	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)	5 (4)	0 (1)	0 (0)	0 (0)
France	2020	15 (9)	12 (18)	2 (1)	0 (1)	15 (9)	12 (18)	2 (1)	0 (1)	15 (9)	12 (18)	2 (1)	0 (1)	14 (9)	13 (18)	2 (1)	0 (1)
	2050	11 (6)	16 (21)	2 (1)	0 (1)	11 (4)	16 (23)	2 (1)	0 (1)	13 (3)	14 (24)	2 (1)	0 (1)	13 (5)	14 (22)	2 (1)	0 (1)
	2080	13 (8)	15 (20)	1 (1)	1 (1)	12 (7)	16 (20)	1 (1)	1 (1)	13 (5)	15 (22)	2 (1)	0 (1)	13 (7)	15 (20)	2 (1)	0 (1)
Germany	2020	12 (10)	8 (10)	0 (0)	0 (0)	12 (10)	8 (10)	0 (0)	0 (0)	12 (11)	8 (9)	0 (0)	0 (0)	12 (11)	8 (9)	0 (0)	0 (0)
	2050	10 (9)	10 (11)	0 (0)	0 (0)	10 (10)	10 (10)	0 (0)	0 (0)	11 (11)	9 (9)	0 (0)	0 (0)	10 (9)	10 (11)	0 (0)	0 (0)
	2080	3 (3)	17 (17)	0 (0)	0 (0)	5 (4)	15 (16)	0 (0)	0 (0)	8 (6)	12 (14)	0 (0)	0 (0)	6 (5)	14 (15)	0 (0)	0 (0)
Greece	2020	4 (2)	10 (13)	0 (0)	0 (0)	4 (2)	9 (13)	0 (0)	0 (0)	4 (2)	10 (13)	0 (0)	0 (0)	4 (2)	10 (13)	0 (0)	0 (0)
	2050	9 (7)	6 (8)	0 (0)	0 (0)	10 (9)	5 (6)	0 (0)	0 (0)	10 (9)	5 (6)	0 (0)	0 (0)	10 (10)	5 (5)	0 (0)	0 (0)
	2080	3 (2)	11 (13)	0 (0)	0 (0)	4 (2)	10 (13)	0 (0)	0 (0)	3 (1)	12 (14)	0 (0)	0 (0)	4 (2)	10 (13)	0 (0)	0 (0)
Hungary	2020	1 (1)	15 (15)	0 (0)	0 (0)	1 (2)	15 (14)	0 (0)	0 (0)	2 (1)	14 (15)	0 (0)	0 (0)	2 (2)	14 (14)	0 (0)	0 (0)
	2050	4 (4)	12 (12)	0 (0)	0 (0)	4 (5)	12 (11)	0 (0)	0 (0)	5 (6)	11 (10)	0 (0)	0 (0)	6 (6)	10 (10)	0 (0)	0 (0)
	2080	6 (7)	10 (9)	0 (0)	0 (0)	5 (8)	11 (8)	0 (0)	0 (0)	5 (8)	11 (8)	0 (0)	0 (0)	5 (8)	11 (8)	0 (0)	0 (0)
Ireland	2020	2 (2)	1 (1)	0 (0)	0 (0)	2 (2)	1 (1)	0 (0)	0 (0)	2 (2)	1 (1)	0 (0)	0 (0)	2 (2)	1 (1)	0 (0)	0 (0)
	2050	3 (1)	0 (2)	0 (0)	0 (0)	3 (1)	0 (2)	0 (0)	0 (0)	3 (1)	0 (2)	0 (0)	0 (0)	3 (1)	0 (2)	0 (0)	0 (0)

	2080	1 (1)	2 (2)	0 (0)	0 (0)	3 (1)	0 (2)	0 (0)	0 (0)	3 (1)	0 (2)	0 (0)	0 (0)	3 (1)	0 (2)	0 (0)	0 (0)
	2020	20 (16)	7 (12)	1 (2)	1 (0)	20 (15)	7 (13)	1 (2)	1 (0)	20 (15)	6 (12)	1 (2)	1 (0)	20 (15)	7 (13)	1 (2)	1 (0)
Italy	2050	21 (17)	6 (11)	2 (2)	0 (0)	20 (17)	7 (11)	2 (2)	0 (0)	19 (17)	8 (11)	2 (2)	0 (0)	20 (17)	7 (11)	2 (2)	0 (0)
	2080	17 (14)	10 (14)	2 (2)	0 (0)	17 (15)	10 (13)	2 (2)	0 (0)	19 (15)	8 (13)	2 (1)	0 (1)	19 (15)	8 (13)	2 (2)	0 (0)
Latvia	2020	12 (12)	0 (0)	0 (0)	0 (0)	12 (12)	0 (0)	0 (0)	0 (0)	12 (12)	0 (0)	0 (0)	0 (0)	12 (12)	0 (0)	0 (0)	0 (0)
	2050	12 (12)	0 (0)	0 (0)	0 (0)	12 (12)	0 (0)	0 (0)	0 (0)	12 (12)	0 (0)	0 (0)	0 (0)	12 (12)	0 (0)	0 (0)	0 (0)
	2080	10 (9)	2 (3)	0 (0)	0 (0)	12 (11)	0 (1)	0 (0)	0 (0)	12 (11)	0 (1)	0 (0)	0 (0)	12 (11)	0 (1)	0 (0)	0 (0)
Liechten-stein	2020	7 (8)	6 (6)	0 (0)	0 (0)	8 (8)	6 (6)	0 (0)	0 (0)	8 (8)	6 (6)	0 (0)	0 (0)	7 (8)	6 (6)	0 (0)	0 (0)
	2050	9 (9)	5 (5)	0 (0)	0 (0)	14 (14)	0 (0)	0 (0)	0 (0)	14 (14)	0 (0)	0 (0)	0 (0)	14 (14)	0 (0)	0 (0)	0 (0)
	2080	11 (11)	3 (3)	0 (0)	0 (0)	13 (13)	1 (1)	0 (0)	0 (0)	13 (13)	1 (1)	0 (0)	0 (0)	13 (13)	1 (1)	0 (0)	0 (0)
Lithuania	2020	12 (12)	1 (1)	0 (0)	0 (0)	12 (12)	1 (1)	0 (0)	0 (0)	12 (12)	1 (1)	0 (0)	0 (0)	12 (12)	1 (1)	0 (0)	0 (0)
	2050	12 (12)	1 (1)	0 (0)	0 (0)	12 (12)	1 (1)	0 (0)	0 (0)	12 (12)	1 (1)	0 (0)	0 (0)	12 (12)	1 (1)	0 (0)	0 (0)
	2080	9 (8)	4 (5)	0 (0)	0 (0)	10 (10)	3 (3)	0 (0)	0 (0)	12 (12)	1 (1)	0 (0)	0 (0)	12 (11)	1 (2)	0 (0)	0 (0)
Luxembourg	2020	14 (15)	2 (4)	0 (0)	0 (0)	14 (15)	2 (4)	0 (0)	0 (0)	14 (15)	2 (4)	0 (0)	0 (0)	14 (15)	2 (4)	0 (0)	0 (0)
	2050	10 (9)	7 (10)	0 (0)	0 (0)	10 (11)	7 (8)	0 (0)	0 (0)	10 (11)	7 (8)	0 (0)	0 (0)	9 (9)	8 (10)	0 (0)	0 (0)
	2080	4 (3)	15 (16)	0 (0)	0 (0)	8 (4)	10 (15)	0 (0)	0 (0)	9 (8)	9 (11)	0 (0)	0 (0)	9 (8)	9 (11)	0 (0)	0 (0)
Macedonia	2020	8 (9)	6 (5)	0 (0)	0 (0)	8 (9)	6 (5)	0 (0)	0 (0)	8 (10)	6 (4)	0 (0)	0 (0)	8 (10)	6 (4)	0 (0)	0 (0)
	2050	10 (8)	4 (6)	0 (0)	0 (0)	10 (8)	4 (6)	0 (0)	0 (0)	10 (8)	4 (6)	0 (0)	0 (0)	10 (8)	4 (6)	0 (0)	0 (0)
	2080	9 (7)	5 (7)	0 (0)	0 (0)	10 (7)	4 (7)	0 (0)	0 (0)	10 (8)	4 (6)	0 (0)	0 (0)	10 (9)	4 (5)	0 (0)	0 (0)
Malta	2020	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)
	2050	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)
	2080	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)
Monaco	2020	0 (2)	1 (3)	0 (0)	0 (0)	0 (2)	1 (3)	0 (0)	0 (0)	0 (2)	1 (3)	0 (0)	0 (0)	0 (2)	1 (3)	0 (0)	0 (0)
	2050	0 (1)	1 (4)	0 (0)	0 (0)	0 (1)	1 (4)	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)	0 (0)	0 (1)	1 (4)	0 (0)	0 (0)
	2080	0 (1)	1 (4)	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)	0 (0)
Montenegro	2020	9 (10)	5 (4)	0 (0)	0 (0)	9 (10)	5 (4)	0 (0)	0 (0)	6 (10)	8 (4)	0 (0)	0 (0)	8 (10)	6 (4)	0 (0)	0 (0)
	2050	9 (9)	5 (5)	0 (0)	0 (0)	9 (9)	5 (5)	0 (0)	0 (0)	8 (9)	6 (5)	0 (0)	0 (0)	9 (9)	5 (5)	0 (0)	0 (0)
	2080	7 (8)	7 (6)	0 (0)	0 (0)	8 (9)	6 (5)	0 (0)	0 (0)	7 (9)	7 (5)	0 (0)	0 (0)	7 (9)	7 (5)	0 (0)	0 (0)
Netherlands	2020	9 (9)	9 (9)	0 (0)	0 (0)	9 (9)	9 (9)	0 (0)	0 (0)	9 (9)	9 (9)	0 (0)	0 (0)	8 (8)	10 (10)	0 (0)	0 (0)
	2050	7 (7)	11 (11)	0 (0)	0 (0)	8 (8)	10 (10)	0 (0)	0 (0)	9 (9)	9 (9)	0 (0)	0 (0)	9 (8)	9 (10)	0 (0)	0 (0)
	2080	5 (5)	13 (13)	0 (0)	0 (0)	5 (5)	13 (13)	0 (0)	0 (0)	6 (6)	12 (12)	0 (0)	0 (0)	6 (6)	12 (12)	0 (0)	0 (0)
Norway	2020	4 (6)	1 (0)	0 (0)	0 (0)	4 (6)	1 (0)	0 (0)	0 (0)	4 (6)	1 (0)	0 (0)	0 (0)	4 (6)	1 (0)	0 (0)	0 (0)
	2050	5 (6)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)
	2080	4 (5)	1 (1)	0 (0)	0 (0)	4 (5)	1 (1)	0 (0)	0 (0)	4 (5)	1 (1)	0 (0)	0 (0)	4 (5)	1 (1)	0 (0)	0 (0)
Poland	2020	15 (15)	3 (3)	0 (0)	0 (0)	15 (15)	3 (3)	0 (0)	0 (0)	15 (15)	3 (3)	0 (0)	0 (0)	15 (15)	3 (3)	0 (0)	0 (0)
	2050	10 (9)	8 (9)	0 (0)	0 (0)	11 (10)	7 (8)	0 (0)	0 (0)	12 (11)	6 (7)	0 (0)	0 (0)	11 (11)	7 (7)	0 (0)	0 (0)
	2080	8 (7)	10 (11)	0 (0)	0 (0)	8 (8)	10 (10)	0 (0)	0 (0)	10 (9)	8 (9)	0 (0)	0 (0)	10 (9)	8 (9)	0 (0)	0 (0)
Portugal	2020	9 (5)	10 (14)	2 (1)	3 (4)	8 (5)	11 (14)	2 (1)	3 (4)	9 (6)	10 (13)	2 (1)	3 (4)	10 (6)	9 (13)	2 (1)	3 (4)
	2050	0 (2)	19 (17)	0 (1)	5 (4)	1 (2)	18 (17)	1 (1)	4 (4)	2 (2)	17 (17)	2 (1)	3 (4)	3 (3)	16 (16)	2 (1)	3 (4)
	2080	2 (2)	17 (17)	1 (0)	4 (5)	2 (2)	17 (17)	1 (0)	4 (5)	2 (3)	17 (16)	1 (1)	4 (4)	2 (3)	17 (16)	1 (1)	4 (4)
Romania	2020	12 (9)	6 (9)	0 (0)	0 (0)	12 (9)	6 (9)	0 (0)	0 (0)	11 (9)	7 (9)	0 (0)	0 (0)	11 (9)	7 (9)	0 (0)	0 (0)
	2050	14 (9)	4 (9)	0 (0)	0 (0)	13 (8)	5 (10)	0 (0)	0 (0)	14 (9)	4 (9)	0 (0)	0 (0)	14 (9)	4 (9)	0 (0)	0 (0)
	2080	10 (7)	8 (11)	0 (0)	0 (0)	10 (8)	8 (10)	0 (0)	0 (0)	11 (8)	7 (10)	0 (0)	0 (0)	11 (8)	7 (10)	0 (0)	0 (0)
San Marino	2020	5 (5)	9 (10)	0 (0)	0 (0)	5 (6)	9 (9)	0 (0)	0 (0)	5 (4)	9 (11)	0 (0)	0 (0)	5 (6)	9 (9)	0 (0)	0 (0)
	2050	5 (7)	9 (8)	0 (0)	0 (0)	5 (8)	9 (7)	0 (0)	0 (0)	5 (8)	9 (7)	0 (0)	0 (0)	5 (9)	9 (6)	0 (0)	0 (0)
	2080	4 (5)	10 (10)	0 (0)	0 (0)	6 (5)	8 (10)	0 (0)	0 (0)	4 (5)	10 (10)	0 (0)	0 (0)	5 (5)	9 (10)	0 (0)	0 (0)
Serbia	2020	5 (6)	14 (14)	0 (0)	0 (0)	5 (6)	14 (14)	0 (0)	0 (0)	5 (7)	14 (13)	0 (0)	0 (0)	5 (7)	14 (13)	0 (0)	0 (0)
	2050	7 (8)	11 (12)	0 (0)	0 (0)	10 (8)	9 (12)	0 (0)	0 (0)	10 (8)	9 (12)	0 (0)	0 (0)	9 (8)	10 (12)	0 (0)	0 (0)
	2080	7 (8)	12 (12)	0 (0)	0 (0)	8 (8)	11 (12)	0 (0)	0 (0)	9 (8)	10 (12)	0 (0)	0 (0)	10 (11)	9 (9)	0 (0)	0 (0)
Slovakia	2020	16 (8)	2 (10)	0 (0)	0 (0)	16 (8)	2 (10)	0 (0)	0 (0)	16 (8)	2 (10)	0 (0)	0 (0)	16 (9)	2 (9)	0 (0)	0 (0)
	2050	15 (8)	3 (10)	0 (0)	0 (0)	15 (8)	3 (10)	0 (0)	0 (0)	16 (7)	2 (11)	0 (0)	0 (0)	15 (7)	3 (11)	0 (0)	0 (0)
	2080	12 (6)	5 (12)	0 (0)	0 (0)	14 (6)	4 (12)	0 (0)	0 (0)	14 (8)	4 (10)	0 (0)	0 (0)	14 (8)	4 (10)	0 (0)	0 (0)
Slovenia	2020	9 (5)	10 (14)	2 (2)	0 (0)	9 (5)	10 (14)	2 (2)	0 (0)	9 (5)	10 (14)	2 (2)	0 (0)	9 (5)	10 (14)	2 (2)	0 (0)
	2050	12 (7)	7 (12)	2 (2)	0 (0)	13 (7)	6 (12)	2 (2)	0 (0)	12 (7)	7 (12)	2 (2)	0 (0)	12 (7)	7 (12)	2 (2)	0 (0)
	2080	10 (5)	9 (14)	2 (2)	0 (0)	11 (6)	8 (13)	2 (2)	0 (0)	9 (5)	10 (14)	2 (2)	0 (0)	9 (5)	10 (14)	2 (2)	0 (0)
Spain	2020	21 (7)	4 (18)	6 (2)	0 (4)	20 (6)	5 (19)	6 (2)	0 (4)	20 (6)	5 (19)	6 (2)	0 (4)	21 (8)	4 (17)	6 (2)	0 (4)
	2050	9 (4)	15 (21)	2 (0)	4 (6)	10 (4)	15 (21)	3 (0)	3 (6)	10 (5)	14 (20)	3 (0)	3 (6)	12 (5)	13 (20)	3 (1)	3 (5)
	2080	8 (5)	17 (20)	1 (0)	5 (6)	8 (7)	17 (18)	2 (2)	4 (4)	9 (7)	16 (18)	2 (2)	4 (4)	10 (7)	15 (18)	2 (2)	4 (4)

Sweden	2020	9 (10)	3 (2)	0 (0)	0 (0)	9 (10)	3 (2)	0 (0)	0 (0)	9 (11)	3 (1)	0 (0)	0 (0)	9 (11)	3 (1)	0 (0)	0 (0)
	2050	9 (11)	3 (1)	0 (0)	0 (0)	9 (11)	3 (1)	0 (0)	0 (0)	9 (11)	3 (1)	0 (0)	0 (0)	9 (11)	3 (1)	0 (0)	0 (0)
	2080	8 (7)	4 (5)	0 (0)	0 (0)	9 (8)	3 (4)	0 (0)	0 (0)	9 (10)	3 (2)	0 (0)	0 (0)	9 (10)	3 (2)	0 (0)	0 (0)
Switzerland	2020	16 (16)	4 (4)	0 (0)	0 (0)	16 (16)	4 (4)	0 (0)	0 (0)	16 (16)	4 (4)	0 (0)	0 (0)	16 (16)	4 (4)	0 (0)	0 (0)
	2050	16 (15)	4 (5)	0 (0)	0 (0)	16 (16)	4 (4)	0 (0)	0 (0)	16 (16)	4 (4)	0 (0)	0 (0)	16 (16)	4 (4)	0 (0)	0 (0)
	2080	12 (8)	8 (12)	0 (0)	0 (0)	14 (10)	6 (10)	0 (0)	0 (0)	14 (11)	6 (9)	0 (0)	0 (0)	14 (10)	6 (10)	0 (0)	0 (0)
UK	2020	5 (3)	3 (5)	0 (0)	0 (0)	5 (3)	3 (5)	0 (0)	0 (0)	5 (4)	3 (4)	0 (0)	0 (0)	5 (3)	3 (5)	0 (0)	0 (0)
	2050	4 (3)	4 (5)	0 (0)	0 (0)	3 (3)	5 (5)	0 (0)	0 (0)	3 (3)	5 (5)	0 (0)	0 (0)	3 (3)	5 (5)	0 (0)	0 (0)
	2080	3 (4)	5 (4)	0 (0)	0 (0)	4 (4)	4 (4)	0 (0)	0 (0)	4 (4)	4 (4)	0 (0)	0 (0)	4 (3)	4 (5)	0 (0)	0 (0)

		A1FI				A2				B1				B2			
		all species		RL species		all species		RL species		all species		RL species		all species		RL species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Reptiles																	
Albania	2020	18 (16)	13 (17)	1 (1)	0 (1)	22 (18)	10 (15)	1 (1)	0 (1)	18 (17)	13 (16)	1 (1)	0 (1)	23 (18)	9 (15)	1 (1)	0 (1)
	2050	23 (23)	10 (10)	1 (1)	1 (1)	23 (23)	10 (10)	1 (1)	1 (1)	24 (23)	9 (10)	2 (1)	0 (1)	23 (23)	10 (10)	1 (1)	1 (1)
	2080	25 (26)	8 (7)	2 (2)	0 (0)	26 (27)	7 (6)	2 (2)	0 (0)	27 (27)	6 (6)	2 (2)	0 (0)	28 (27)	5 (6)	2 (2)	0 (0)
Andorra	2020	8 (13)	1 (0)	0 (0)	0 (0)	8 (12)	1 (0)	0 (0)	0 (0)	9 (12)	1 (0)	0 (0)	0 (0)	9 (11)	1 (1)	0 (0)	0 (0)
	2050	9 (12)	1 (2)	0 (0)	0 (0)	10 (13)	0 (2)	0 (0)	0 (0)	9 (13)	1 (2)	0 (0)	0 (0)	10 (13)	0 (1)	0 (0)	0 (0)
	2080	15 (15)	0 (0)	0 (0)	0 (0)	15 (15)	0 (0)	0 (0)	0 (0)	13 (14)	1 (1)	0 (0)	0 (0)	14 (14)	1 (1)	0 (0)	0 (0)
Austria	2020	12 (10)	1 (3)	1 (0)	0 (1)	12 (10)	1 (3)	1 (0)	0 (1)	12 (10)	1 (3)	1 (0)	0 (1)	12 (10)	1 (3)	1 (0)	0 (1)
	2050	11 (10)	1 (3)	1 (0)	0 (1)	11 (10)	1 (3)	0 (0)	0 (1)	10 (10)	2 (3)	0 (0)	0 (1)	10 (10)	3 (3)	0 (0)	1 (1)
	2080	11 (10)	2 (3)	1 (0)	0 (1)	12 (10)	1 (3)	1 (0)	0 (1)	12 (10)	1 (3)	1 (0)	0 (1)	12 (10)	1 (3)	1 (0)	0 (1)
Belgium	2020	4 (2)	2 (5)	0 (1)	0 (0)	3 (2)	3 (5)	0 (1)	0 (0)	3 (1)	3 (5)	0 (0)	0 (0)	3 (1)	3 (6)	0 (0)	0 (1)
	2050	1 (2)	5 (5)	0 (0)	1 (1)	2 (2)	5 (5)	0 (0)	1 (1)	1 (2)	6 (5)	0 (0)	1 (1)	3 (3)	4 (4)	0 (0)	1 (1)
	2080	3 (3)	4 (4)	1 (1)	0 (0)	3 (2)	4 (5)	1 (0)	0 (1)	3 (2)	4 (5)	1 (0)	0 (1)	3 (2)	4 (5)	1 (0)	0 (1)
Bosnia and Herzeg	2020	16 (23)	5 (2)	0 (1)	0 (0)	16 (23)	5 (2)	0 (1)	0 (0)	15 (23)	6 (2)	0 (1)	0 (0)	15 (23)	5 (2)	0 (1)	0 (0)
	2050	18 (21)	4 (5)	1 (2)	0 (0)	17 (20)	4 (6)	0 (2)	0 (0)	17 (21)	4 (5)	0 (2)	0 (0)	17 (21)	4 (5)	0 (2)	0 (0)
	2080	18 (22)	5 (4)	2 (2)	0 (0)	18 (22)	5 (4)	2 (2)	0 (0)	16 (22)	5 (4)	0 (2)	0 (0)	17 (22)	5 (4)	1 (2)	0 (0)
Bulgaria	2020	25 (25)	4 (4)	2 (2)	0 (0)	23 (24)	6 (5)	2 (2)	0 (0)	24 (25)	5 (4)	2 (2)	0 (0)	24 (25)	5 (4)	2 (2)	0 (0)
	2050	21 (20)	8 (9)	2 (2)	0 (0)	21 (20)	8 (9)	2 (2)	0 (0)	22 (20)	7 (9)	2 (2)	0 (0)	21 (21)	8 (8)	2 (2)	0 (0)
	2080	25 (24)	4 (5)	2 (2)	0 (0)	25 (24)	4 (5)	2 (2)	0 (0)	25 (24)	4 (5)	2 (2)	0 (0)	25 (24)	4 (5)	2 (2)	0 (0)
Croatia	2020	24 (24)	2 (4)	0 (1)	0 (0)	24 (24)	2 (4)	0 (1)	0 (0)	24 (25)	3 (3)	1 (1)	0 (0)	25 (25)	2 (3)	1 (1)	0 (0)
	2050	24 (23)	3 (5)	1 (1)	0 (0)	24 (23)	3 (5)	1 (1)	0 (0)	24 (23)	3 (5)	1 (1)	0 (0)	24 (23)	3 (5)	1 (1)	0 (0)
	2080	24 (24)	3 (4)	1 (1)	0 (0)	24 (23)	3 (5)	1 (1)	0 (0)	24 (25)	3 (3)	1 (1)	0 (0)	24 (24)	3 (4)	1 (1)	0 (0)
Czech Republic	2020	10 (10)	0 (0)	1 (1)	0 (0)	10 (10)	0 (0)	1 (1)	0 (0)	10 (10)	0 (0)	1 (1)	0 (0)	10 (10)	0 (0)	1 (1)	0 (0)
	2050	7 (6)	3 (4)	0 (0)	1 (1)	7 (7)	3 (3)	0 (0)	1 (1)	7 (7)	3 (3)	0 (0)	1 (1)	7 (7)	3 (3)	0 (0)	1 (1)
	2080	7 (7)	3 (3)	0 (0)	1 (1)	7 (7)	3 (3)	0 (0)	1 (1)	8 (7)	2 (3)	0 (0)	1 (1)	8 (6)	2 (4)	0 (0)	1 (1)
Denmark	2020	5 (6)	2 (1)	1 (1)	0 (0)	5 (6)	2 (1)	1 (1)	0 (0)	5 (6)	2 (1)	1 (1)	0 (0)	5 (6)	2 (1)	1 (1)	0 (0)
	2050	5 (5)	2 (2)	1 (1)	0 (0)	5 (6)	2 (1)	1 (1)	0 (0)	5 (6)	2 (1)	1 (1)	0 (0)	5 (6)	2 (1)	1 (1)	0 (0)
	2080	5 (5)	2 (2)	1 (1)	0 (0)	5 (5)	2 (2)	1 (1)	0 (0)	5 (5)	2 (2)	1 (1)	0 (0)	5 (5)	2 (2)	1 (1)	0 (0)
Estonia	2020	4 (4)	0 (1)	0 (1)	0 (0)	4 (5)	0 (0)	0 (1)	0 (0)	4 (4)	0 (1)	0 (1)	0 (0)	4 (5)	0 (0)	0 (1)	0 (0)
	2050	4 (3)	0 (1)	0 (0)	0 (0)	3 (3)	1 (1)	0 (0)	0 (0)	3 (3)	1 (1)	0 (0)	0 (0)	3 (3)	1 (1)	0 (0)	0 (0)
	2080	4 (4)	0 (0)	0 (0)	0 (0)	4 (4)	0 (0)	0 (0)	0 (0)	4 (4)	0 (0)	0 (0)	0 (0)	4 (4)	0 (0)	0 (0)	0 (0)
Finland	2020	3 (4)	0 (1)	0 (1)	0 (0)	3 (4)	0 (1)	0 (1)	0 (0)	3 (4)	0 (1)	0 (1)	0 (0)	3 (4)	0 (1)	0 (1)	0 (0)
	2050	3 (4)	0 (1)	0 (1)	0 (0)	3 (3)	0 (1)	0 (0)	0 (0)	3 (3)	0 (2)	0 (0)	0 (1)	3 (3)	0 (2)	0 (0)	0 (1)
	2080	4 (4)	0 (1)	1 (1)	0 (0)	3 (4)	0 (1)	0 (1)	0 (0)	3 (4)	0 (1)	0 (1)	0 (0)	3 (4)	0 (1)	0 (1)	0 (0)
France	2020	21 (20)	10 (13)	3 (3)	0 (1)	21 (20)	11 (13)	3 (3)	0 (1)	21 (20)	10 (13)	3 (3)	0 (1)	21 (20)	10 (13)	3 (3)	0 (1)
	2050	21 (19)	12 (15)	2 (2)	1 (2)	20 (18)	12 (15)	2 (2)	1 (2)	20 (18)	12 (14)	2 (2)	1 (2)	20 (18)	12 (14)	2 (2)	1 (2)
	2080	22 (20)	13 (15)	2 (1)	2 (3)	23 (19)	12 (15)	3 (1)	1 (3)	24 (20)	11 (14)	3 (2)	1 (2)	23 (19)	12 (15)	2 (1)	2 (3)
Germany	2020	6 (6)	6 (6)	1 (1)	0 (0)	6 (6)	6 (6)	1 (1)	0 (0)	6 (6)	6 (6)	1 (1)	0 (0)	6 (6)	6 (6)	1 (1)	0 (0)
	2050	8 (8)	4 (4)	0 (0)	1 (1)	7 (8)	5 (4)	0 (0)	1 (1)	8 (7)	4 (5)	0 (0)	1 (1)	7 (7)	5 (5)	0 (0)	1 (1)
	2080	8 (8)	4 (4)	1 (1)	0 (0)	8 (8)	4 (4)	1 (1)	0 (0)	9 (9)	3 (3)	1 (1)	0 (0)	8 (8)	4 (4)	1 (1)	0 (0)
Greece	2020	15 (13)	19 (24)	1 (1)	1 (1)	19 (13)	16 (24)	1 (1)	1 (1)	17 (13)	18 (24)	1 (1)	1 (1)	23 (17)	12 (20)	1 (1)	1 (1)
	2050	21 (22)	14 (15)	1 (1)	1 (1)	21 (23)	14 (14)	1 (1)	1 (1)	21 (22)	14 (15)	1 (1)	1 (1)	21 (23)	14 (14)	1 (1)	1 (1)

	2080	24 (23)	11 (14)	1 (1)	1 (1)	24 (24)	11 (13)	1 (1)	1 (1)	25 (25)	10 (12)	1 (2)	1 (0)	25 (25)	10 (12)	1 (1)	1 (1)
	2020	10 (11)	4 (3)	1 (1)	0 (0)	10 (11)	4 (3)	1 (1)	0 (0)	10 (11)	4 (3)	1 (1)	0 (0)	10 (11)	4 (3)	1 (1)	0 (0)
Hungary	2050	9 (9)	5 (5)	1 (1)	0 (0)	8 (9)	5 (5)	0 (1)	0 (0)	8 (10)	6 (4)	0 (1)	1 (0)	8 (9)	5 (5)	0 (0)	0 (1)
	2080	11 (11)	3 (3)	1 (1)	0 (0)	11 (12)	3 (2)	1 (1)	0 (0)	12 (12)	2 (2)	1 (1)	0 (0)	12 (12)	2 (2)	1 (1)	0 (0)
Ireland	2020	1 (2)	0 (0)	0 (0)	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)
	2050	1 (1)	1 (1)	0 (0)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)
	2080	1 (1)	1 (1)	0 (0)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)
	2020	24 (23)	14 (17)	2 (2)	2 (2)	25 (23)	13 (17)	2 (2)	2 (2)	26 (24)	12 (17)	2 (2)	2 (2)	25 (24)	13 (16)	2 (2)	2 (2)
Italy	2050	25 (28)	13 (13)	3 (3)	1 (1)	25 (28)	13 (13)	3 (3)	1 (1)	25 (28)	13 (13)	3 (3)	1 (1)	27 (27)	11 (14)	3 (3)	1 (1)
	2080	29 (27)	10 (14)	3 (2)	1 (2)	27 (27)	11 (14)	2 (2)	2 (2)	26 (26)	12 (15)	2 (2)	2 (2)	28 (26)	10 (15)	2 (2)	2 (2)
	2020	5 (6)	0 (0)	0 (1)	0 (0)	5 (6)	0 (0)	0 (1)	0 (0)	5 (6)	0 (0)	0 (1)	0 (0)	5 (6)	0 (0)	0 (1)	0 (0)
	2050	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)
Latvia	2080	4 (4)	1 (1)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)
	2020	5 (7)	0 (0)	0 (1)	0 (0)	5 (7)	0 (0)	0 (1)	0 (0)	5 (7)	0 (0)	0 (1)	0 (0)	5 (7)	0 (0)	0 (1)	0 (0)
Liechten-stein	2050	4 (4)	1 (1)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)
	2080	5 (6)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)
	2020	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)
	2050	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)
Lithuania	2080	5 (4)	0 (1)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	5 (6)	0 (0)	0 (0)	0 (0)
	2020	4 (5)	1 (3)	0 (1)	0 (0)	5 (5)	1 (3)	0 (1)	0 (0)	4 (5)	1 (3)	0 (1)	0 (0)	4 (5)	1 (3)	0 (1)	0 (0)
Luxembourg	2050	4 (5)	3 (3)	0 (1)	0 (0)	5 (6)	2 (2)	0 (1)	0 (0)	5 (6)	2 (2)	0 (1)	0 (0)	5 (6)	2 (2)	0 (1)	0 (0)
	2080	4 (5)	3 (3)	0 (1)	0 (0)	4 (5)	3 (3)	0 (1)	0 (0)	4 (5)	3 (3)	0 (1)	0 (0)	4 (5)	3 (3)	0 (1)	0 (0)
	2020	21 (21)	8 (8)	1 (1)	1 (1)	21 (22)	8 (7)	1 (1)	1 (1)	22 (23)	7 (5)	1 (1)	1 (1)	22 (24)	6 (5)	1 (1)	1 (1)
	2050	23 (21)	7 (9)	1 (1)	1 (1)	22 (21)	8 (9)	1 (1)	1 (1)	23 (22)	7 (8)	1 (1)	1 (1)	22 (21)	7 (9)	1 (1)	1 (1)
Macedonia	2080	25 (27)	5 (3)	1 (2)	1 (0)	25 (25)	5 (5)	1 (1)	1 (1)	25 (26)	5 (4)	1 (1)	1 (1)	25 (25)	5 (5)	1 (1)	1 (1)
	2020	7 (9)	0 (0)	1 (1)	0 (0)	7 (9)	0 (0)	1 (1)	0 (0)	7 (9)	0 (0)	1 (1)	0 (0)	7 (9)	0 (0)	1 (1)	0 (0)
Malta	2050	8 (8)	1 (1)	1 (1)	0 (0)	8 (8)	1 (1)	1 (1)	0 (0)	8 (8)	1 (1)	1 (1)	0 (0)	8 (7)	1 (1)	1 (1)	0 (0)
	2080	8 (9)	1 (0)	1 (1)	0 (0)	8 (9)	1 (0)	1 (1)	0 (0)	9 (9)	1 (0)	1 (1)	0 (0)	8 (9)	1 (0)	1 (1)	0 (0)
	2020	2 (12)	0 (5)	1 (1)	0 (1)	2 (11)	0 (4)	1 (1)	0 (1)	2 (11)	0 (6)	1 (1)	0 (1)	2 (11)	0 (5)	1 (1)	0 (1)
	2050	3 (9)	0 (8)	1 (1)	0 (1)	3 (9)	0 (8)	1 (1)	0 (1)	3 (9)	0 (8)	1 (1)	0 (1)	3 (9)	0 (8)	1 (1)	0 (1)
Monaco	2080	3 (6)	2 (11)	0 (0)	0 (2)	3 (9)	2 (8)	1 (1)	0 (1)	3 (9)	1 (7)	1 (1)	0 (1)	4 (9)	0 (8)	1 (1)	0 (1)
	2020	25 (25)	5 (5)	0 (0)	0 (0)	25 (24)	5 (6)	0 (0)	0 (0)	25 (23)	5 (7)	0 (0)	0 (0)	25 (23)	5 (7)	0 (0)	0 (0)
Montenegro	2050	24 (24)	7 (7)	1 (1)	0 (0)	23 (24)	7 (7)	0 (1)	0 (0)	23 (24)	7 (7)	0 (1)	0 (0)	24 (24)	7 (7)	1 (1)	0 (0)
	2080	25 (24)	6 (7)	1 (1)	0 (0)	25 (24)	6 (7)	1 (1)	0 (0)	23 (25)	7 (6)	0 (1)	0 (0)	23 (24)	7 (7)	0 (1)	0 (0)
	2020	4 (3)	3 (4)	1 (1)	0 (0)	4 (3)	3 (4)	1 (1)	0 (0)	4 (2)	3 (5)	1 (0)	0 (1)	3 (2)	4 (5)	1 (0)	0 (1)
	2050	3 (3)	4 (4)	0 (0)	1 (1)	3 (3)	4 (4)	0 (0)	1 (1)	3 (3)	4 (4)	0 (0)	1 (1)	3 (3)	4 (4)	0 (0)	1 (1)
Netherlands	2080	3 (3)	4 (4)	0 (0)	1 (1)	3 (3)	4 (4)	0 (0)	1 (1)	3 (3)	4 (4)	0 (0)	1 (1)	3 (3)	4 (4)	0 (0)	1 (1)
	2020	4 (6)	1 (0)	1 (1)	0 (0)	4 (6)	1 (0)	1 (1)	0 (0)	4 (6)	1 (0)	1 (1)	0 (0)	4 (6)	1 (0)	1 (1)	0 (0)
Norway	2050	5 (6)	0 (0)	1 (1)	0 (0)	5 (6)	0 (0)	1 (1)	0 (0)	5 (6)	0 (0)	1 (1)	0 (0)	5 (6)	0 (0)	1 (1)	0 (0)
	2080	5 (6)	0 (0)	1 (1)	0 (0)	5 (6)	0 (0)	1 (1)	0 (0)	5 (6)	0 (0)	1 (1)	0 (0)	5 (6)	0 (0)	1 (1)	0 (0)
	2020	8 (8)	1 (1)	1 (1)	0 (0)	8 (8)	1 (1)	1 (1)	0 (0)	8 (8)	1 (1)	1 (1)	0 (0)	8 (8)	1 (1)	1 (1)	0 (0)
	2050	7 (6)	3 (4)	0 (0)	1 (1)	7 (7)	3 (3)	0 (0)	1 (1)	7 (7)	3 (3)	0 (0)	1 (1)	6 (5)	4 (5)	0 (0)	1 (1)
Poland	2080	7 (7)	3 (3)	1 (1)	0 (0)	7 (7)	3 (3)	1 (1)	0 (0)	5 (6)	4 (4)	0 (0)	1 (1)	6 (7)	4 (3)	0 (1)	1 (0)
	2020	11 (10)	17 (18)	0 (0)	4 (4)	11 (10)	17 (18)	0 (0)	4 (4)	11 (10)	16 (18)	0 (0)	4 (4)	11 (10)	17 (18)	0 (0)	4 (4)
Portugal	2050	10 (10)	18 (18)	1 (0)	3 (4)	10 (11)	18 (17)	1 (0)	3 (4)	12 (12)	16 (16)	1 (1)	3 (3)	12 (11)	16 (17)	1 (0)	3 (4)
	2080	10 (9)	18 (19)	0 (0)	4 (4)	10 (10)	18 (18)	0 (0)	4 (4)	10 (10)	18 (18)	0 (0)	4 (4)	10 (10)	18 (18)	0 (0)	4 (4)
	2020	19 (19)	3 (3)	2 (2)	0 (0)	19 (19)	3 (3)	2 (2)	0 (0)	19 (19)	3 (3)	2 (2)	0 (0)	19 (19)	3 (3)	2 (2)	0 (0)
	2050	19 (17)	3 (5)	2 (2)	0 (0)	19 (17)	3 (5)	2 (2)	0 (0)	19 (17)	3 (5)	2 (2)	0 (0)	19 (17)	3 (5)	2 (2)	0 (0)
Romania	2080	20 (18)	2 (4)	2 (2)	0 (0)	20 (18)	2 (4)	2 (2)	0 (0)	19 (18)	3 (4)	2 (2)	0 (0)	19 (18)	3 (4)	2 (2)	0 (0)
	2020	8 (8)	3 (5)	0 (0)	0 (0)	7 (8)	4 (5)	0 (0)	0 (0)	9 (8)	3 (5)	0 (0)	0 (0)	9 (9)	3 (4)	0 (0)	0 (0)
San Marino	2050	9 (8)	3 (5)	0 (0)	0 (0)	9 (8)	3 (5)	0 (0)	0 (0)	9 (8)	3 (5)	0 (0)	0 (0)	9 (9)	3 (4)	0 (0)	0 (0)
	2080	9 (9)	3 (4)	0 (0)	0 (0)	9 (9)	3 (4)	0 (0)	0 (0)	9 (9)	3 (4)	0 (0)	0 (0)	9 (9)	3 (4)	0 (0)	0 (0)
	2020	21 (23)	2 (6)	1 (2)	0 (0)	20 (24)	2 (5)	1 (2)	0 (0)	22 (24)	2 (5)	1 (2)	0 (0)	20 (23)	2 (6)	1 (2)	0 (0)
	2050	22 (26)	3 (4)	1 (2)	0 (0)	21 (26)	4 (4)	1 (2)	0 (0)	23 (27)	2 (3)	1 (2)	0 (0)	23 (25)	2 (4)	1 (2)	0 (0)
Serbia	2080	22 (26)	4 (4)	1 (2)	0 (0)	22 (26)	4 (4)	1 (2)	0 (0)	22 (26)	3 (4)	1 (2)	0 (0)	22 (26)	3 (4)	1 (2)	0 (0)
	2020	10 (8)	0 (3)	0 (1)	0 (0)	10 (8)	0 (3)	0 (1)	0 (0)	10 (9)	0 (2)	0 (1)	0 (0)	10 (9)	0 (2)	0 (1)	0 (0)
Slovakia	2050	9 (8)	1 (3)	0 (1)	0 (0)	9 (7)	1 (3)	0 (1)	0 (0)	8 (8)	2 (3)	0 (1)	0 (0)	9 (6)	1 (5)	0 (1)	0 (0)
	2080	9 (8)	1 (3)	0 (1)	0 (0)	9 (9)	1 (2)	0 (1)	0 (0)	10 (9)	0 (2)	0 (1)	0 (0)	9 (9)	1 (2)	0 (1)	0 (0)

Slovenia	2020	17 (22)	2 (4)	1 (1)	0 (0)	18 (22)	2 (4)	1 (1)	0 (0)	17 (22)	3 (4)	1 (1)	0 (0)	17 (22)	2 (4)	1 (1)	0 (0)
	2050	20 (22)	2 (4)	0 (1)	0 (0)	20 (22)	2 (4)	0 (1)	0 (0)	20 (22)	2 (4)	0 (1)	0 (0)	20 (22)	2 (4)	0 (1)	0 (0)
	2080	21 (22)	3 (4)	1 (1)	0 (0)	20 (22)	3 (4)	0 (1)	0 (0)	20 (22)	3 (4)	1 (1)	0 (0)	20 (22)	3 (4)	1 (1)	0 (0)
Spain	2020	23 (18)	13 (18)	3 (2)	2 (3)	23 (18)	13 (18)	3 (2)	2 (3)	22 (17)	14 (19)	3 (2)	2 (3)	24 (18)	12 (18)	3 (2)	2 (3)
	2050	17 (15)	19 (21)	3 (1)	2 (4)	19 (15)	17 (21)	3 (1)	2 (4)	17 (15)	19 (21)	2 (1)	3 (4)	21 (15)	15 (21)	4 (1)	1 (4)
	2080	18 (16)	18 (20)	2 (1)	3 (4)	20 (16)	16 (20)	4 (1)	1 (4)	20 (16)	16 (20)	3 (1)	2 (4)	21 (17)	15 (19)	4 (2)	1 (3)
Sweden	2020	6 (6)	0 (0)	1 (1)	0 (0)	6 (6)	0 (0)	1 (1)	0 (0)	6 (6)	0 (0)	1 (1)	0 (0)	6 (6)	0 (0)	1 (1)	0 (0)
	2050	4 (5)	1 (1)	0 (0)	1 (1)	5 (5)	1 (1)	0 (0)	1 (1)	5 (5)	1 (1)	0 (0)	1 (1)	5 (5)	1 (1)	0 (0)	1 (1)
	2080	6 (5)	0 (1)	1 (1)	0 (0)	6 (6)	0 (0)	1 (1)	0 (0)	6 (6)	0 (0)	1 (1)	0 (0)	6 (6)	0 (0)	1 (1)	0 (0)
Switzerland	2020	15 (14)	0 (1)	1 (1)	0 (0)	15 (14)	0 (1)	1 (1)	0 (0)	15 (13)	0 (2)	1 (1)	0 (0)	15 (13)	0 (2)	1 (1)	0 (0)
	2050	11 (12)	4 (3)	0 (1)	1 (0)	11 (12)	4 (3)	0 (1)	1 (0)	12 (12)	3 (3)	1 (1)	0 (0)	12 (12)	3 (3)	1 (1)	0 (0)
	2080	11 (12)	4 (3)	1 (1)	0 (0)	11 (12)	4 (3)	1 (1)	0 (0)	11 (12)	4 (3)	1 (1)	0 (0)	11 (12)	4 (3)	1 (1)	0 (0)
UK	2020	3 (2)	3 (4)	1 (1)	0 (0)	3 (2)	3 (4)	1 (1)	0 (0)	2 (2)	4 (4)	1 (1)	0 (0)	3 (2)	3 (4)	1 (1)	0 (0)
	2050	3 (2)	3 (4)	1 (0)	0 (1)	3 (2)	3 (4)	1 (0)	0 (1)	3 (3)	3 (3)	1 (1)	0 (0)	3 (2)	3 (4)	1 (0)	0 (1)
	2080	3 (3)	3 (3)	1 (1)	0 (0)	3 (3)	3 (3)	1 (1)	0 (0)	3 (3)	3 (3)	1 (1)	0 (0)	3 (3)	3 (3)	1 (1)	0 (0)

A1FI				A2				B1				B2			
all species		RL species		all species		RL species		all species		RL species		all species		RL species	
win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los

Birds

Albania	2020	87 (111)	101 (92)	2 (1)	1 (2)	88 (111)	101 (92)	2 (1)	1 (2)	87 (109)	102 (94)	2 (1)	1 (2)	87 (108)	102 (95)	2 (1)	1 (2)
	2050	77 (90)	114 (113)	3 (3)	0 (0)	78 (90)	115 (112)	3 (3)	0 (0)	77 (88)	115 (115)	3 (3)	0 (0)	77 (89)	115 (114)	3 (3)	0 (0)
	2080	65 (74)	129 (130)	3 (3)	0 (0)	63 (76)	130 (128)	3 (3)	0 (0)	64 (74)	128 (130)	3 (3)	0 (0)	67 (75)	125 (129)	3 (3)	0 (0)
Andorra	2020	70 (78)	41 (40)	1 (1)	0 (0)	71 (78)	41 (40)	1 (1)	0 (0)	71 (78)	39 (41)	1 (1)	0 (0)	71 (78)	39 (41)	1 (1)	0 (0)
	2050	77 (81)	41 (44)	1 (1)	0 (0)	86 (85)	33 (37)	1 (1)	0 (0)	84 (83)	36 (40)	1 (1)	0 (0)	82 (82)	35 (41)	1 (1)	0 (0)
	2080	86 (89)	37 (38)	1 (1)	0 (0)	79 (81)	42 (44)	1 (1)	0 (0)	80 (79)	39 (45)	1 (1)	0 (0)	79 (79)	42 (46)	1 (1)	0 (0)
Austria	2020	118 (114)	104 (113)	3 (4)	7 (6)	121 (113)	103 (113)	3 (4)	7 (6)	118 (112)	105 (115)	3 (4)	7 (6)	118 (112)	106 (114)	3 (4)	7 (6)
	2050	137 (126)	89 (100)	6 (6)	4 (4)	140 (125)	86 (101)	6 (6)	4 (4)	138 (123)	88 (103)	5 (5)	5 (5)	139 (124)	87 (103)	6 (5)	4 (5)
	2080	125 (113)	102 (114)	5 (4)	5 (6)	130 (118)	98 (109)	5 (4)	5 (6)	131 (117)	95 (110)	4 (4)	6 (6)	130 (115)	96 (112)	4 (4)	6 (6)
Belgium	2020	55 (60)	116 (122)	2 (2)	1 (2)	54 (55)	118 (127)	2 (2)	1 (2)	53 (56)	119 (126)	2 (2)	1 (2)	52 (50)	119 (133)	1 (2)	2 (2)
	2050	73 (75)	97 (108)	2 (1)	2 (3)	73 (73)	97 (109)	2 (1)	2 (3)	73 (74)	98 (109)	1 (1)	3 (3)	67 (69)	105 (114)	2 (2)	2 (2)
	2080	56 (57)	120 (126)	1 (1)	3 (3)	57 (60)	116 (123)	1 (1)	3 (3)	60 (59)	113 (124)	0 (1)	3 (3)	56 (61)	118 (122)	0 (1)	3 (3)
Bosnia and Herzeg	2020	67 (89)	117 (118)	1 (2)	2 (2)	65 (92)	117 (115)	1 (2)	2 (2)	64 (90)	119 (117)	1 (2)	2 (2)	65 (90)	117 (117)	1 (2)	2 (2)
	2050	70 (88)	117 (121)	2 (3)	1 (1)	74 (91)	114 (118)	2 (3)	1 (1)	72 (89)	115 (119)	2 (3)	1 (1)	72 (89)	116 (120)	2 (3)	1 (1)
	2080	53 (78)	135 (132)	3 (3)	1 (1)	59 (83)	128 (127)	2 (3)	1 (1)	57 (86)	128 (124)	2 (3)	1 (1)	63 (84)	122 (126)	2 (3)	1 (1)
Bulgaria	2020	133 (116)	112 (128)	5 (4)	4 (5)	131 (120)	114 (124)	5 (5)	4 (4)	129 (114)	116 (130)	5 (3)	4 (6)	129 (115)	116 (129)	5 (3)	4 (6)
	2050	132 (106)	112 (138)	8 (6)	1 (3)	134 (108)	111 (136)	8 (5)	1 (4)	135 (110)	110 (134)	8 (5)	1 (4)	132 (109)	113 (135)	8 (5)	1 (4)
	2080	104 (91)	141 (153)	7 (6)	2 (3)	118 (97)	127 (147)	6 (5)	3 (4)	117 (99)	128 (145)	4 (5)	5 (4)	112 (99)	133 (145)	5 (5)	4 (4)
Croatia	2020	101 (91)	132 (147)	3 (3)	5 (6)	104 (91)	129 (147)	3 (3)	5 (6)	105 (90)	126 (148)	2 (3)	5 (6)	103 (90)	127 (148)	3 (3)	5 (6)
	2050	104 (88)	129 (151)	5 (5)	3 (4)	104 (94)	129 (145)	5 (5)	3 (4)	104 (92)	128 (147)	5 (5)	3 (4)	101 (85)	131 (154)	4 (5)	4 (4)
	2080	84 (74)	149 (165)	5 (4)	3 (5)	89 (80)	143 (159)	5 (5)	3 (4)	94 (84)	138 (155)	3 (4)	5 (5)	90 (81)	141 (158)	3 (4)	5 (5)
Czech Republic	2020	105 (100)	112 (118)	8 (5)	1 (4)	104 (99)	113 (119)	7 (5)	2 (4)	102 (99)	113 (119)	7 (5)	2 (4)	101 (99)	116 (119)	7 (5)	2 (4)
	2050	98 (95)	118 (123)	7 (6)	2 (3)	97 (95)	120 (123)	7 (6)	2 (3)	93 (90)	124 (128)	7 (6)	2 (3)	93 (86)	123 (132)	7 (5)	2 (4)
	2080	90 (90)	128 (128)	6 (5)	3 (4)	98 (89)	120 (129)	7 (5)	2 (4)	99 (90)	118 (128)	6 (5)	3 (4)	92 (85)	125 (133)	6 (4)	3 (5)
Denmark	2020	110 (105)	63 (72)	2 (2)	1 (3)	111 (105)	62 (72)	2 (2)	1 (3)	108 (105)	65 (72)	2 (2)	1 (3)	111 (106)	63 (71)	3 (2)	1 (3)
	2050	107 (110)	66 (68)	3 (3)	1 (2)	108 (110)	65 (68)	3 (3)	1 (2)	107 (109)	66 (69)	3 (3)	1 (2)	104 (107)	67 (71)	3 (3)	1 (2)
	2080	65 (72)	109 (106)	1 (2)	3 (3)	73 (77)	101 (101)	2 (2)	3 (3)	78 (79)	97 (99)	2 (2)	3 (3)	78 (78)	97 (100)	2 (2)	3 (3)
Estonia	2020	76 (79)	120 (120)	2 (2)	5 (5)	76 (78)	121 (121)	2 (2)	5 (5)	77 (77)	120 (122)	2 (2)	5 (5)	78 (79)	119 (120)	2 (2)	5 (5)
	2050	95 (94)	102 (105)	3 (3)	4 (4)	94 (92)	103 (107)	3 (3)	4 (4)	93 (95)	102 (104)	3 (3)	4 (4)	97 (96)	100 (103)	3 (3)	4 (4)
	2080	79 (80)	119 (119)	3 (3)	4 (4)	84 (83)	114 (116)	4 (3)	3 (4)	91 (90)	107 (109)	4 (4)	3 (3)	92 (93)	106 (106)	4 (4)	3 (3)
Finland	2020	160 (129)	53 (91)	4 (3)	1 (3)	160 (128)	54 (92)	4 (3)	1 (3)	158 (128)	56 (92)	4 (4)	1 (2)	158 (128)	56 (92)	4 (3)	1 (3)
	2050	147 (119)	67 (101)	3 (4)	2 (2)	147 (119)	67 (101)	3 (4)	2 (2)	147 (122)	67 (98)	4 (4)	2 (2)	146 (119)	67 (101)	3 (4)	2 (2)
	2080	140 (110)	75 (110)	4 (4)	2 (2)	146 (118)	69 (102)	4 (4)	2 (2)	146 (123)	69 (97)	4 (4)	2 (2)	147 (122)	68 (98)	4 (4)	2 (2)
France	2020	96 (72)	154 (182)	2 (2)	3 (4)	98 (72)	153 (182)	3 (2)	3 (4)	94 (69)	156 (185)	2 (2)	3 (4)	93 (68)	157 (186)	2 (2)	3 (4)
	2050	114 (95)	137 (160)	3 (3)	3 (3)	116 (99)	135 (156)	3 (3)	3 (3)	118 (98)	134 (157)	3 (3)	3 (3)	115 (98)	137 (157)	3 (3)	3 (3)
	2080	94 (80)	157 (175)	3 (3)	3 (3)	103 (84)	147 (171)	3 (3)	3 (3)	105 (86)	145 (169)	3 (3)	3 (3)	103 (83)	147 (172)	3 (3)	3 (3)
Germany	2020	80 (78)	150 (153)	3 (2)	5 (6)	77 (78)	153 (153)	3 (2)	5 (6)	76 (77)	154 (154)	3 (2)	5 (6)	75 (76)	155 (155)	3 (2)	5 (6)

Greece	2050	89 (89)	142 (142)	3 (3)	5 (5)	86 (86)	142 (145)	3 (3)	5 (5)	86 (84)	143 (147)	2 (3)	6 (5)	86 (85)	142 (146)	3 (3)	5 (5)
	2080	90 (84)	143 (149)	4 (4)	4 (4)	93 (88)	140 (145)	4 (4)	4 (4)	104 (96)	129 (137)	3 (3)	5 (5)	101 (92)	132 (141)	4 (4)	4 (4)
	2020	85 (67)	138 (173)	4 (6)	1 (2)	87 (71)	136 (169)	4 (6)	1 (2)	83 (69)	141 (171)	4 (6)	1 (2)	87 (72)	137 (168)	4 (6)	1 (2)
Hungary	2050	91 (75)	138 (165)	4 (6)	1 (2)	89 (77)	139 (164)	4 (6)	1 (2)	88 (75)	140 (165)	4 (6)	1 (2)	89 (76)	138 (164)	4 (6)	1 (2)
	2080	66 (60)	164 (181)	4 (5)	1 (3)	71 (61)	159 (180)	4 (5)	1 (3)	72 (53)	157 (188)	4 (5)	1 (3)	76 (61)	153 (180)	4 (5)	1 (3)
	2020	69 (64)	138 (144)	6 (5)	5 (6)	69 (64)	137 (144)	6 (5)	5 (6)	68 (64)	138 (144)	6 (3)	5 (8)	69 (67)	136 (141)	6 (3)	5 (8)
Ireland	2050	75 (66)	132 (142)	4 (4)	7 (7)	78 (69)	128 (139)	5 (4)	6 (7)	79 (69)	127 (139)	4 (4)	7 (7)	76 (71)	128 (137)	3 (4)	8 (7)
	2080	57 (57)	150 (151)	4 (4)	7 (7)	60 (61)	147 (147)	4 (4)	7 (7)	69 (67)	138 (141)	4 (2)	7 (9)	68 (70)	139 (138)	4 (3)	7 (8)
	2020	43 (48)	74 (81)	0 (0)	2 (3)	44 (48)	73 (81)	0 (0)	2 (3)	45 (48)	73 (81)	0 (0)	2 (3)	43 (48)	74 (81)	0 (0)	2 (3)
Italy	2050	46 (49)	74 (80)	0 (0)	2 (3)	48 (50)	72 (79)	0 (0)	2 (3)	46 (50)	75 (79)	0 (0)	2 (3)	46 (50)	75 (79)	0 (0)	2 (3)
	2080	46 (47)	78 (82)	0 (0)	2 (3)	47 (49)	76 (80)	0 (0)	2 (3)	50 (49)	72 (80)	0 (0)	2 (3)	48 (49)	72 (80)	0 (0)	2 (3)
	2020	119 (69)	114 (167)	4 (1)	2 (5)	118 (67)	114 (169)	4 (1)	2 (5)	120 (67)	113 (169)	4 (1)	2 (5)	117 (66)	116 (170)	4 (1)	2 (5)
Latvia	2050	125 (71)	108 (165)	4 (3)	2 (3)	124 (71)	109 (165)	4 (3)	2 (3)	125 (69)	108 (167)	4 (3)	2 (3)	125 (71)	107 (165)	4 (3)	2 (3)
	2080	105 (62)	128 (173)	4 (2)	2 (4)	106 (64)	126 (172)	4 (2)	2 (4)	110 (61)	123 (174)	5 (2)	1 (4)	108 (59)	124 (176)	4 (2)	2 (4)
	2020	77 (82)	120 (117)	2 (2)	8 (8)	78 (84)	119 (115)	2 (3)	8 (7)	78 (85)	119 (114)	2 (3)	8 (7)	77 (84)	120 (115)	2 (2)	8 (8)
Liechten-stein	2050	96 (99)	101 (100)	4 (4)	6 (6)	94 (99)	103 (100)	4 (4)	6 (6)	99 (101)	98 (98)	4 (5)	6 (5)	99 (99)	98 (100)	4 (4)	6 (6)
	2080	77 (81)	120 (118)	3 (4)	7 (6)	81 (83)	115 (116)	3 (3)	7 (7)	88 (88)	109 (111)	4 (4)	6 (6)	88 (91)	109 (108)	3 (4)	7 (6)
	2020	64 (68)	59 (60)	1 (1)	0 (0)	64 (68)	58 (59)	1 (1)	0 (0)	64 (69)	58 (60)	1 (1)	0 (0)	64 (69)	58 (59)	1 (1)	0 (0)
Lithuania	2050	73 (79)	51 (54)	1 (1)	0 (0)	85 (89)	41 (45)	1 (1)	0 (0)	85 (89)	40 (45)	1 (1)	0 (0)	85 (88)	43 (44)	1 (1)	0 (0)
	2080	75 (79)	53 (57)	0 (0)	1 (1)	66 (68)	65 (66)	0 (0)	1 (1)	81 (88)	44 (47)	1 (1)	0 (0)	83 (89)	43 (46)	1 (1)	0 (0)
	2020	86 (87)	99 (105)	2 (3)	7 (7)	86 (87)	100 (105)	2 (3)	7 (7)	88 (89)	98 (103)	2 (3)	7 (7)	86 (89)	100 (103)	2 (3)	7 (7)
Luxembourg	2050	68 (67)	121 (125)	4 (4)	6 (6)	71 (68)	119 (124)	4 (4)	6 (6)	70 (68)	119 (124)	4 (4)	6 (6)	68 (67)	122 (125)	4 (4)	6 (6)
	2080	57 (59)	134 (134)	3 (3)	7 (7)	61 (62)	130 (131)	4 (3)	6 (7)	68 (71)	122 (121)	3 (2)	7 (8)	63 (65)	128 (128)	4 (3)	6 (7)
	2020	58 (67)	76 (86)	1 (1)	1 (2)	57 (65)	75 (88)	1 (1)	1 (2)	53 (64)	78 (88)	1 (1)	1 (2)	54 (63)	78 (89)	1 (1)	1 (2)
Macedonia	2050	74 (86)	63 (68)	0 (1)	2 (2)	81 (86)	54 (68)	0 (1)	2 (2)	73 (83)	61 (69)	0 (1)	2 (2)	69 (75)	70 (78)	0 (1)	2 (2)
	2080	48 (51)	93 (103)	0 (1)	2 (2)	55 (57)	81 (96)	0 (1)	2 (2)	60 (65)	76 (89)	0 (1)	2 (2)	56 (60)	79 (94)	0 (1)	2 (2)
	2020	128 (114)	67 (103)	3 (4)	0 (1)	134 (117)	62 (103)	3 (4)	0 (1)	131 (115)	64 (104)	3 (4)	0 (1)	132 (116)	62 (103)	3 (4)	0 (1)
Malta	2050	108 (96)	90 (125)	3 (4)	1 (1)	108 (96)	90 (124)	3 (4)	1 (1)	111 (96)	88 (124)	3 (4)	1 (1)	107 (98)	91 (123)	3 (4)	1 (1)
	2080	95 (81)	106 (140)	3 (3)	1 (2)	97 (83)	101 (138)	3 (3)	1 (2)	107 (86)	92 (135)	3 (3)	1 (2)	103 (88)	96 (133)	3 (3)	1 (2)
	2020	7 (7)	5 (12)	1 (1)	0 (0)	7 (7)	6 (12)	1 (1)	0 (0)	7 (7)	6 (11)	1 (1)	0 (0)	6 (6)	7 (13)	1 (1)	0 (0)
Monaco	2050	8 (11)	8 (8)	1 (1)	0 (0)	8 (11)	7 (8)	1 (1)	0 (0)	6 (11)	7 (7)	1 (1)	0 (0)	9 (12)	7 (8)	1 (1)	0 (0)
	2080	8 (9)	10 (11)	1 (1)	0 (0)	8 (9)	10 (11)	1 (1)	0 (0)	7 (9)	10 (11)	1 (1)	0 (0)	8 (8)	9 (12)	1 (1)	0 (0)
	2020	3 (33)	6 (51)	0 (0)	0 (0)	3 (32)	6 (50)	0 (0)	0 (0)	3 (32)	6 (52)	0 (0)	0 (0)	3 (32)	6 (51)	0 (0)	0 (0)
Montenegro	2050	6 (33)	6 (56)	0 (0)	0 (0)	6 (32)	6 (59)	0 (0)	0 (0)	5 (32)	6 (58)	0 (0)	0 (0)	6 (34)	6 (55)	0 (0)	0 (0)
	2080	3 (18)	24 (71)	0 (0)	0 (0)	2 (29)	16 (58)	0 (0)	0 (0)	3 (25)	12 (63)	0 (0)	0 (0)	3 (32)	9 (56)	0 (0)	0 (0)
	2020	84 (90)	76 (91)	3 (2)	0 (2)	85 (91)	75 (90)	3 (2)	0 (2)	82 (85)	75 (94)	3 (2)	0 (2)	83 (85)	77 (94)	3 (2)	0 (2)
Netherlands	2050	79 (79)	82 (102)	2 (2)	1 (2)	79 (80)	81 (101)	2 (2)	1 (2)	76 (77)	85 (104)	2 (2)	1 (2)	78 (75)	83 (105)	2 (2)	1 (2)
	2080	69 (70)	93 (112)	2 (2)	1 (2)	70 (71)	90 (111)	2 (2)	1 (2)	75 (67)	86 (114)	2 (2)	1 (2)	74 (66)	87 (115)	2 (2)	1 (2)
	2020	37 (37)	146 (147)	0 (0)	4 (4)	37 (37)	146 (147)	0 (0)	4 (4)	37 (38)	146 (146)	0 (0)	4 (4)	37 (37)	146 (147)	0 (0)	4 (4)
Norway	2050	68 (64)	115 (120)	0 (0)	3 (4)	63 (63)	119 (121)	0 (0)	3 (4)	63 (64)	121 (120)	0 (0)	4 (4)	65 (64)	118 (120)	0 (1)	3 (3)
	2080	60 (61)	124 (123)	1 (1)	3 (3)	62 (63)	121 (121)	1 (1)	3 (3)	61 (61)	122 (123)	0 (0)	4 (4)	61 (63)	121 (121)	0 (0)	4 (4)
	2020	118 (116)	87 (97)	2 (2)	2 (3)	119 (116)	87 (97)	2 (2)	2 (3)	120 (120)	86 (93)	2 (2)	2 (3)	124 (122)	82 (91)	2 (2)	2 (3)
Poland	2050	143 (127)	65 (86)	3 (3)	1 (2)	142 (125)	65 (88)	3 (3)	1 (2)	142 (131)	66 (82)	2 (3)	2 (2)	141 (128)	66 (85)	2 (3)	2 (2)
	2080	136 (122)	70 (91)	2 (3)	2 (2)	137 (122)	69 (91)	2 (3)	2 (2)	143 (132)	65 (81)	2 (3)	2 (2)	142 (125)	65 (88)	2 (3)	2 (2)
	2020	81 (78)	138 (148)	3 (3)	7 (9)	81 (77)	139 (149)	3 (3)	7 (9)	81 (80)	139 (146)	3 (3)	7 (9)	79 (79)	140 (147)	3 (3)	7 (9)
Portugal	2050	77 (74)	144 (152)	5 (5)	6 (7)	74 (77)	147 (149)	3 (4)	7 (8)	74 (79)	147 (147)	3 (3)	7 (9)	74 (73)	147 (153)	3 (4)	7 (8)
	2080	75 (70)	146 (157)	5 (6)	5 (6)	81 (79)	141 (148)	5 (6)	5 (6)	80 (84)	141 (143)	5 (5)	5 (7)	79 (82)	142 (145)	5 (5)	5 (7)
	2020	59 (53)	125 (142)	1 (0)	4 (5)	55 (52)	130 (142)	1 (0)	4 (5)	55 (53)	131 (141)	1 (0)	4 (5)	58 (53)	127 (140)	1 (0)	4 (5)
Romania	2050	61 (59)	127 (136)	4 (2)	1 (3)	65 (59)	124 (136)	4 (2)	1 (3)	63 (61)	124 (134)	4 (2)	1 (3)	64 (58)	124 (136)	4 (2)	1 (3)
	2080	56 (58)	133 (137)	3 (2)	2 (3)	58 (55)	131 (139)	3 (2)	2 (3)	58 (55)	131 (140)	3 (2)	2 (3)	57 (53)	132 (142)	3 (1)	2 (4)
	2020	119 (111)	124 (136)	2 (5)	8 (6)	122 (109)	121 (138)	2 (5)	8 (6)	118 (113)	125 (134)	2 (5)	8 (6)	124 (112)	119 (135)	2 (5)	8 (6)
San Marino	2050	92 (86)	150 (161)	4 (6)	5 (5)	96 (85)	147 (162)	4 (6)	6 (5)	92 (83)	151 (163)	3 (6)	7 (5)	95 (84)	148 (163)	4 (5)	6 (6)
	2080	87 (76)	156 (171)	3 (5)	7 (6)	93 (82)	150 (165)	2 (5)	8 (6)	98 (86)	145 (161)	2 (3)	8 (8)	101 (91)	142 (156)	2 (4)	8 (7)
	2020	58 (59)	63 (89)	0 (1)	0 (0)	58 (59)	63 (89)	0 (1)	0 (0)	58 (59)	65 (88)	0 (1)	0 (0)	57 (59)	64 (89)	0 (1)	0 (0)
Serbia	2050	53 (51)	76 (97)	0 (1)	0 (0)	56 (52)	72 (96)	0 (1)	0 (0)	53 (50)	74 (98)	0 (1)	0 (0)	52 (51)	75 (97)	0 (1)	0 (0)
	2080	36 (38)	94 (110)	0 (1)	0 (0)	40 (41)	89 (107)	0 (1)	0 (0)	39 (44)	90 (104)	0 (1)	0 (0)	43 (45)	85 (103)	0 (1)	0 (0)
	2020	113 (100)	105 (129)	2 (2)	8 (8)	110 (98)	109 (131)	2 (2)	8 (8)	110 (103)	109 (126)	2 (2)	8 (8)	112 (101)	104 (128)	2 (2)	8 (8)
	2050	93 (92)	127 (139)	3 (3)	7 (7)	95 (92)	125 (139)	3 (3)	7 (7)	93 (88)	127 (143)	3 (3)	7 (7)	94 (92)	126 (139)	3 (3)	7 (7)

	2080	70 (75)	150 (156)	3 (3)	7 (7)	80 (80)	139 (151)	3 (3)	7 (7)	81 (83)	137 (148)	1 (2)	9 (8)	87 (83)	133 (148)	3 (2)	7 (8)
	2020	128 (90)	82 (127)	7 (7)	3 (3)	127 (90)	83 (127)	7 (7)	3 (3)	127 (91)	84 (126)	6 (7)	4 (3)	125 (92)	85 (125)	6 (7)	4 (3)
Slovakia	2050	118 (84)	94 (133)	7 (6)	3 (4)	115 (85)	97 (132)	7 (6)	3 (4)	114 (81)	98 (136)	7 (5)	3 (5)	111 (80)	101 (137)	7 (5)	3 (5)
	2080	102 (71)	111 (146)	4 (4)	6 (6)	107 (81)	106 (136)	5 (5)	5 (5)	104 (79)	108 (138)	4 (3)	6 (7)	103 (80)	110 (137)	4 (3)	6 (7)
Slovenia	2020	113 (99)	88 (115)	4 (4)	1 (1)	113 (100)	87 (114)	4 (4)	1 (1)	117 (96)	85 (118)	4 (4)	1 (1)	113 (96)	88 (118)	4 (4)	1 (1)
	2050	127 (115)	76 (101)	5 (4)	0 (1)	130 (120)	73 (96)	5 (4)	0 (1)	122 (114)	80 (102)	5 (4)	0 (1)	124 (114)	79 (102)	5 (4)	0 (1)
2080		114 (95)	90 (121)	4 (4)	1 (1)	117 (102)	85 (114)	5 (4)	0 (1)	119 (103)	85 (113)	5 (4)	0 (1)	118 (103)	86 (113)	5 (4)	0 (1)
	2020	102 (59)	131 (178)	5 (3)	2 (5)	106 (63)	127 (174)	5 (3)	2 (5)	104 (59)	129 (178)	5 (2)	2 (6)	101 (60)	132 (177)	5 (3)	2 (5)
Spain	2050	107 (68)	125 (170)	4 (3)	3 (5)	110 (68)	122 (170)	4 (3)	3 (5)	105 (67)	127 (171)	4 (3)	3 (5)	105 (70)	127 (168)	4 (4)	3 (4)
	2080	80 (58)	152 (180)	4 (1)	3 (7)	86 (61)	146 (177)	4 (1)	3 (7)	94 (62)	138 (176)	4 (1)	3 (7)	91 (63)	141 (175)	4 (2)	3 (6)
2020		134 (111)	89 (115)	2 (3)	4 (3)	134 (109)	90 (117)	2 (3)	4 (3)	135 (112)	88 (114)	2 (3)	4 (3)	140 (111)	84 (115)	2 (3)	4 (3)
	2050	143 (119)	79 (106)	3 (4)	3 (2)	144 (121)	79 (104)	3 (4)	3 (2)	145 (121)	77 (104)	3 (4)	3 (2)	143 (120)	80 (105)	3 (4)	3 (2)
Sweden	2080	124 (102)	100 (124)	2 (2)	4 (4)	130 (109)	94 (117)	2 (2)	4 (4)	141 (117)	83 (109)	3 (4)	3 (2)	137 (114)	87 (112)	3 (3)	3 (3)
	2020	127 (121)	70 (76)	3 (2)	0 (2)	124 (122)	73 (76)	2 (2)	1 (2)	125 (121)	73 (77)	2 (2)	1 (2)	125 (120)	73 (78)	2 (2)	1 (2)
Switzerland	2050	137 (130)	61 (69)	2 (3)	2 (1)	140 (131)	57 (67)	2 (3)	1 (1)	144 (132)	54 (67)	3 (3)	1 (1)	140 (131)	58 (68)	2 (2)	2 (2)
	2080	120 (112)	80 (89)	2 (2)	2 (2)	122 (118)	78 (83)	2 (2)	2 (2)	121 (120)	76 (82)	1 (2)	2 (2)	123 (119)	75 (83)	1 (2)	3 (2)
2020		72 (70)	117 (123)	2 (1)	2 (3)	71 (69)	118 (124)	2 (1)	2 (3)	72 (68)	117 (125)	2 (1)	2 (3)	71 (70)	118 (123)	2 (1)	2 (3)
	2050	82 (78)	108 (115)	1 (1)	3 (3)	78 (75)	112 (116)	1 (1)	3 (3)	79 (77)	110 (115)	1 (1)	3 (3)	80 (78)	110 (115)	1 (1)	3 (3)
UK	2080	71 (69)	120 (124)	1 (1)	3 (3)	73 (72)	117 (121)	1 (1)	3 (3)	77 (76)	112 (117)	1 (1)	3 (3)	76 (74)	113 (119)	1 (1)	3 (3)

		A1FI				A2				B1				B2			
		all species		RL species		all species		RL species		all species		RL species		all species		RL species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Mammals																	
Albania	2020	32 (37)	39 (36)	5 (5)	2 (2)	30 (37)	41 (36)	4 (5)	3 (2)	30 (36)	41 (37)	4 (5)	3 (2)	30 (35)	41 (38)	4 (5)	3 (2)
	2050	24 (28)	47 (45)	4 (5)	3 (2)	27 (28)	46 (45)	4 (4)	3 (3)	26 (27)	47 (46)	4 (4)	3 (3)	25 (28)	46 (45)	4 (4)	3 (3)
	2080	20 (21)	52 (52)	4 (4)	3 (3)	20 (21)	52 (52)	4 (4)	3 (3)	20 (23)	53 (50)	3 (3)	4 (4)	20 (21)	53 (52)	3 (3)	4 (4)
Andorra	2020	41 (43)	7 (9)	5 (6)	0 (0)	39 (41)	8 (11)	4 (5)	1 (1)	39 (41)	8 (10)	4 (5)	1 (1)	40 (41)	8 (11)	4 (5)	0 (1)
	2050	35 (36)	16 (17)	5 (4)	1 (2)	44 (40)	6 (13)	6 (5)	0 (1)	39 (39)	12 (14)	4 (5)	1 (1)	44 (39)	7 (13)	6 (5)	0 (1)
	2080	38 (39)	14 (14)	5 (5)	1 (1)	35 (37)	17 (16)	4 (5)	2 (1)	34 (35)	17 (18)	3 (4)	2 (2)	36 (36)	16 (17)	4 (5)	1 (1)
Austria	2020	57 (48)	29 (39)	5 (4)	3 (4)	57 (50)	29 (37)	5 (4)	3 (4)	58 (50)	28 (37)	5 (4)	3 (4)	58 (50)	28 (37)	5 (4)	3 (4)
	2050	56 (49)	31 (37)	6 (5)	2 (3)	59 (50)	28 (36)	7 (5)	1 (3)	59 (49)	28 (38)	6 (5)	2 (3)	60 (49)	27 (37)	6 (5)	2 (3)
	2080	53 (39)	33 (48)	5 (5)	3 (3)	54 (44)	32 (43)	5 (5)	3 (3)	55 (45)	31 (42)	5 (4)	3 (4)	55 (45)	31 (42)	4 (4)	4 (4)
Belgium	2020	35 (31)	28 (32)	4 (3)	4 (5)	35 (30)	28 (33)	4 (3)	4 (5)	35 (31)	28 (32)	5 (3)	3 (5)	33 (30)	29 (33)	4 (3)	3 (5)
	2050	34 (22)	29 (41)	5 (3)	3 (5)	32 (25)	31 (38)	4 (5)	4 (3)	32 (25)	30 (38)	4 (5)	4 (3)	29 (22)	34 (41)	4 (4)	4 (4)
	2080	19 (16)	44 (47)	4 (5)	4 (3)	23 (19)	40 (44)	4 (5)	4 (3)	23 (22)	39 (41)	4 (5)	4 (3)	20 (19)	43 (44)	4 (4)	4 (4)
Bosnia and Herzeg	2020	23 (36)	42 (41)	4 (8)	1 (1)	25 (35)	41 (42)	4 (7)	1 (2)	24 (36)	41 (41)	4 (8)	1 (1)	25 (36)	42 (41)	4 (8)	1 (1)
	2050	24 (37)	43 (40)	3 (7)	2 (2)	27 (37)	42 (40)	2 (7)	3 (2)	26 (37)	43 (40)	3 (7)	2 (2)	27 (37)	42 (40)	3 (7)	2 (2)
	2080	20 (34)	49 (43)	2 (7)	3 (2)	20 (35)	48 (42)	2 (7)	3 (2)	22 (36)	46 (41)	3 (7)	2 (2)	23 (34)	46 (43)	3 (7)	2 (2)
Bulgaria	2020	59 (46)	26 (40)	11 (12)	1 (0)	58 (46)	28 (40)	10 (12)	2 (0)	59 (46)	27 (40)	11 (12)	1 (0)	59 (48)	27 (38)	11 (12)	1 (0)
	2050	47 (33)	39 (53)	10 (10)	2 (2)	47 (35)	39 (51)	10 (10)	2 (2)	50 (35)	36 (50)	10 (10)	2 (2)	50 (35)	36 (51)	10 (10)	2 (2)
	2080	47 (29)	39 (57)	10 (7)	2 (5)	50 (35)	36 (51)	10 (8)	2 (4)	48 (33)	38 (53)	9 (7)	3 (5)	49 (37)	37 (49)	10 (7)	2 (5)
Croatia	2020	35 (31)	48 (57)	7 (5)	4 (7)	34 (31)	49 (57)	6 (5)	5 (7)	36 (31)	47 (57)	8 (5)	3 (7)	33 (30)	50 (58)	6 (5)	5 (7)
	2050	38 (32)	45 (56)	8 (7)	4 (5)	38 (32)	45 (55)	8 (7)	4 (5)	36 (31)	47 (57)	8 (6)	4 (6)	37 (31)	47 (57)	8 (7)	4 (5)
	2080	31 (25)	52 (63)	7 (5)	4 (7)	33 (26)	50 (62)	7 (5)	4 (7)	32 (27)	53 (61)	6 (6)	6 (6)	33 (25)	50 (63)	7 (5)	4 (7)
Czech Republic	2020	55 (43)	25 (36)	6 (4)	3 (5)	53 (43)	27 (37)	6 (4)	3 (5)	53 (44)	27 (36)	6 (4)	3 (5)	50 (43)	30 (37)	6 (4)	3 (5)
	2050	43 (36)	37 (44)	6 (4)	3 (5)	42 (39)	38 (41)	6 (4)	3 (5)	40 (37)	40 (43)	4 (4)	5 (5)	40 (39)	39 (41)	4 (4)	5 (5)
	2080	37 (31)	43 (49)	4 (5)	5 (4)	42 (34)	38 (46)	4 (4)	5 (5)	48 (44)	32 (36)	4 (4)	5 (5)	48 (42)	32 (38)	4 (4)	5 (5)
Denmark	2020	37 (39)	14 (14)	3 (4)	0 (0)	39 (39)	14 (14)	4 (4)	0 (0)	38 (39)	14 (14)	3 (4)	0 (0)	38 (39)	14 (14)	3 (4)	0 (0)
	2050	35 (35)	18 (18)	4 (3)	0 (1)	35 (35)	18 (18)	4 (3)	0 (1)	35 (34)	18 (19)	4 (3)	0 (1)	35 (33)	18 (20)	4 (3)	0 (1)
	2080	23 (22)	30 (31)	3 (2)	1 (2)	26 (25)	27 (28)	2 (2)	2 (2)	27 (28)	26 (25)	2 (2)	2 (2)	26 (26)	26 (27)	2 (2)	2 (2)
Estonia	2020	26 (26)	28 (28)	1 (1)	4 (4)	26 (26)	28 (28)	1 (1)	4 (4)	26 (26)	28 (28)	1 (1)	4 (4)	26 (26)	28 (28)	1 (1)	4 (4)
	2050	27 (27)	27 (27)	1 (1)	4 (4)	26 (27)	28 (27)	0 (1)	5 (4)	27 (27)	27 (27)	0 (1)	5 (4)	27 (26)	27 (28)	0 (0)	5 (5)
	2080	19 (20)	35 (34)	1 (1)	4 (4)	21 (22)	33 (32)	1 (1)	4 (4)	23 (24)	31 (30)	1 (1)	4 (4)	22 (22)	32 (32)	1 (1)	4 (4)
Finland	2020	40 (31)	16 (27)	3 (2)	2 (3)	39 (31)	17 (27)	3 (2)	2 (3)	39 (31)	17 (27)	3 (2)	2 (3)	39 (31)	17 (27)	3 (2)	2 (3)

France	2050	40 (30)	16 (28)	2 (2)	3 (3)	40 (31)	16 (27)	2 (2)	3 (3)	40 (31)	16 (27)	2 (2)	3 (3)	40 (31)	16 (27)	2 (2)	3 (3)
	2080	33 (27)	23 (31)	2 (2)	3 (3)	35 (28)	21 (30)	2 (2)	3 (3)	35 (30)	21 (28)	2 (2)	3 (3)	35 (30)	21 (28)	2 (2)	3 (3)
	2020	34 (25)	58 (68)	7 (6)	6 (7)	34 (28)	58 (65)	7 (7)	6 (6)	36 (27)	56 (66)	8 (6)	5 (7)	35 (28)	57 (65)	7 (7)	6 (6)
Germany	2050	36 (20)	56 (72)	7 (2)	6 (11)	36 (21)	56 (71)	7 (2)	6 (11)	38 (22)	54 (70)	7 (3)	6 (10)	38 (22)	54 (70)	7 (3)	6 (10)
	2080	30 (18)	63 (75)	6 (2)	7 (11)	34 (19)	58 (74)	8 (2)	5 (11)	38 (20)	54 (72)	8 (3)	5 (10)	38 (21)	54 (71)	8 (3)	5 (10)
	2020	35 (33)	49 (50)	4 (4)	4 (4)	35 (33)	49 (50)	4 (4)	4 (4)	35 (33)	49 (50)	4 (4)	4 (4)	35 (32)	49 (51)	4 (4)	4 (4)
Greece	2050	31 (31)	53 (52)	4 (4)	4 (4)	31 (30)	53 (53)	5 (4)	3 (4)	30 (29)	54 (54)	5 (4)	3 (4)	28 (29)	56 (54)	4 (4)	4 (4)
	2080	23 (23)	61 (60)	3 (3)	5 (5)	28 (27)	55 (55)	2 (2)	6 (6)	35 (31)	49 (52)	3 (2)	5 (6)	30 (30)	54 (53)	2 (2)	6 (6)
	2020	21 (8)	54 (70)	5 (2)	5 (9)	24 (7)	52 (71)	5 (2)	5 (9)	22 (8)	53 (70)	5 (2)	5 (9)	25 (9)	49 (69)	6 (2)	4 (9)
Hungary	2050	25 (22)	52 (56)	7 (4)	4 (7)	26 (24)	51 (54)	7 (5)	4 (6)	27 (23)	50 (55)	7 (5)	4 (6)	26 (29)	51 (49)	7 (7)	4 (4)
	2080	19 (16)	58 (62)	5 (2)	6 (9)	22 (17)	55 (61)	5 (3)	6 (8)	22 (17)	55 (61)	5 (3)	6 (8)	25 (19)	52 (59)	5 (4)	6 (7)
	2020	29 (24)	54 (62)	5 (5)	7 (7)	29 (23)	54 (63)	5 (4)	7 (8)	29 (26)	54 (60)	5 (4)	7 (8)	30 (28)	53 (58)	5 (5)	7 (7)
Ireland	2050	33 (31)	50 (55)	6 (5)	6 (7)	34 (34)	51 (52)	6 (5)	6 (7)	37 (37)	48 (49)	7 (5)	5 (7)	38 (39)	47 (47)	7 (5)	5 (7)
	2080	27 (26)	57 (60)	7 (5)	5 (7)	28 (30)	55 (56)	7 (6)	5 (6)	33 (35)	52 (51)	6 (6)	6 (6)	36 (36)	49 (50)	7 (6)	5 (6)
	2020	14 (19)	13 (9)	1 (2)	1 (0)	14 (19)	13 (9)	1 (2)	1 (0)	13 (18)	14 (10)	1 (2)	1 (0)	13 (18)	13 (10)	1 (2)	1 (0)
Italy	2050	14 (15)	13 (13)	1 (2)	1 (0)	15 (15)	13 (13)	1 (2)	1 (0)	13 (15)	15 (13)	1 (2)	1 (0)	13 (15)	14 (13)	1 (2)	1 (0)
	2080	11 (11)	17 (17)	1 (2)	1 (0)	13 (12)	14 (16)	1 (2)	1 (0)	15 (14)	13 (14)	1 (2)	1 (0)	15 (14)	12 (14)	1 (2)	1 (0)
	2020	58 (35)	32 (56)	5 (4)	5 (6)	59 (35)	31 (55)	5 (4)	5 (6)	57 (35)	33 (56)	5 (4)	5 (6)	59 (35)	31 (56)	5 (4)	5 (6)
Latvia	2050	50 (29)	40 (62)	3 (3)	7 (7)	52 (28)	38 (63)	3 (3)	7 (7)	52 (27)	38 (64)	3 (3)	7 (7)	53 (31)	37 (60)	3 (3)	7 (7)
	2080	42 (21)	48 (70)	3 (2)	7 (8)	42 (23)	48 (68)	3 (2)	7 (8)	44 (24)	46 (67)	3 (3)	7 (7)	46 (25)	44 (66)	4 (3)	6 (7)
	2020	30 (29)	30 (32)	2 (2)	3 (4)	30 (29)	30 (32)	2 (2)	3 (4)	30 (29)	30 (32)	2 (2)	3 (4)	30 (30)	30 (31)	2 (2)	3 (4)
Lithuania	2050	33 (33)	27 (28)	2 (2)	3 (4)	32 (33)	28 (28)	2 (2)	3 (4)	32 (33)	28 (28)	2 (2)	3 (4)	32 (34)	28 (27)	2 (2)	3 (4)
	2080	24 (24)	36 (37)	2 (2)	3 (4)	24 (23)	36 (38)	2 (2)	3 (4)	29 (25)	31 (36)	2 (2)	3 (4)	26 (24)	34 (37)	2 (2)	3 (4)
	2020	28 (29)	22 (23)	3 (3)	0 (0)	28 (28)	22 (23)	3 (3)	0 (0)	28 (28)	22 (22)	3 (3)	0 (0)	28 (28)	23 (23)	3 (3)	0 (0)
Luxembourg	2050	34 (34)	19 (19)	1 (1)	2 (2)	42 (43)	10 (10)	2 (3)	0 (0)	41 (41)	11 (11)	2 (2)	0 (0)	42 (42)	11 (11)	3 (3)	0 (0)
	2080	31 (31)	19 (20)	2 (2)	1 (1)	38 (38)	15 (15)	2 (2)	1 (1)	40 (40)	11 (13)	3 (3)	0 (0)	40 (40)	12 (12)	3 (3)	0 (0)
	2020	35 (33)	24 (26)	2 (2)	3 (3)	35 (33)	24 (26)	2 (2)	3 (3)	36 (34)	23 (25)	2 (2)	3 (3)	36 (34)	23 (25)	2 (2)	3 (3)
Malta	2050	28 (26)	31 (33)	3 (2)	2 (3)	30 (28)	29 (31)	3 (3)	2 (2)	30 (29)	29 (30)	3 (3)	2 (2)	30 (25)	29 (34)	3 (2)	2 (3)
	2080	20 (20)	39 (39)	2 (2)	3 (3)	21 (21)	38 (38)	2 (2)	3 (3)	22 (22)	35 (37)	2 (2)	3 (3)	21 (21)	37 (38)	2 (2)	3 (3)
	2020	41 (37)	18 (24)	6 (4)	1 (3)	39 (36)	20 (25)	5 (4)	2 (3)	40 (37)	19 (24)	6 (4)	1 (3)	39 (35)	20 (26)	5 (4)	2 (3)
Macedonia	2050	37 (32)	21 (29)	5 (5)	2 (2)	38 (37)	21 (24)	5 (5)	2 (2)	37 (37)	21 (24)	5 (5)	2 (2)	35 (33)	24 (28)	5 (5)	2 (2)
	2080	16 (17)	42 (44)	3 (4)	4 (3)	24 (22)	35 (39)	3 (4)	4 (3)	31 (27)	28 (34)	4 (4)	3 (3)	29 (26)	30 (35)	5 (4)	2 (3)
	2020	45 (29)	30 (48)	6 (7)	3 (2)	46 (28)	30 (49)	7 (7)	2 (2)	45 (30)	30 (47)	6 (6)	3 (3)	46 (33)	30 (44)	6 (7)	3 (2)
Monaco	2050	41 (27)	35 (50)	7 (6)	2 (3)	41 (29)	35 (48)	7 (6)	2 (3)	43 (30)	33 (47)	8 (6)	1 (3)	43 (31)	33 (46)	8 (6)	1 (3)
	2080	36 (22)	40 (55)	7 (4)	2 (5)	38 (23)	38 (54)	7 (5)	2 (4)	42 (25)	34 (52)	7 (5)	2 (4)	42 (27)	34 (50)	7 (6)	2 (3)
	2020	4 (7)	7 (8)	0 (0)	0 (0)	4 (6)	7 (8)	0 (0)	0 (0)	4 (7)	7 (8)	0 (0)	0 (0)	4 (6)	7 (8)	0 (0)	0 (0)
Montenegro	2050	8 (10)	5 (5)	0 (0)	0 (0)	8 (10)	5 (5)	0 (0)	0 (0)	8 (10)	5 (5)	0 (0)	0 (0)	8 (10)	5 (5)	0 (0)	0 (0)
	2080	8 (10)	5 (5)	0 (0)	0 (0)	6 (8)	6 (6)	0 (0)	0 (0)	8 (9)	5 (5)	0 (0)	0 (0)	9 (9)	5 (6)	0 (0)	0 (0)
	2020	3 (14)	0 (6)	1 (1)	0 (0)	3 (14)	1 (6)	1 (1)	0 (0)	3 (14)	1 (7)	1 (1)	0 (0)	3 (14)	1 (6)	1 (1)	0 (0)
Netherlands	2050	1 (4)	2 (16)	1 (1)	0 (0)	1 (4)	2 (17)	1 (1)	0 (0)	1 (4)	2 (17)	1 (1)	0 (0)	1 (5)	2 (14)	1 (1)	0 (0)
	2080	0 (5)	5 (15)	0 (0)	0 (1)	1 (9)	4 (12)	1 (1)	0 (0)	1 (9)	3 (12)	1 (1)	0 (0)	1 (9)	3 (11)	1 (1)	0 (0)
	2020	36 (38)	25 (26)	3 (5)	2 (0)	35 (37)	26 (27)	3 (4)	2 (1)	35 (35)	25 (29)	3 (3)	2 (2)	35 (38)	26 (26)	3 (5)	2 (0)
Norway	2050	40 (39)	22 (25)	4 (5)	1 (0)	40 (40)	21 (24)	5 (5)	0 (0)	40 (39)	22 (25)	5 (5)	0 (0)	39 (39)	23 (25)	5 (5)	0 (0)
	2080	33 (33)	29 (31)	4 (5)	1 (0)	35 (36)	27 (28)	4 (5)	1 (0)	36 (36)	26 (28)	4 (4)	1 (1)	36 (35)	26 (29)	4 (5)	1 (0)
	2020	19 (19)	41 (41)	2 (2)	5 (5)	20 (18)	40 (41)	3 (2)	4 (5)	20 (19)	40 (41)	3 (2)	4 (5)	20 (19)	40 (41)	3 (2)	4 (5)
Poland	2050	23 (20)	37 (40)	4 (4)	3 (3)	22 (22)	38 (38)	5 (5)	2 (2)	23 (23)	37 (37)	5 (5)	2 (2)	21 (21)	39 (39)	4 (5)	3 (2)
	2080	17 (16)	43 (44)	5 (4)	2 (3)	18 (17)	42 (43)	5 (4)	2 (3)	22 (21)	38 (39)	5 (5)	2 (2)	20 (19)	39 (40)	4 (4)	2 (2)
	2020	23 (27)	29 (26)	1 (1)	3 (3)	23 (27)	29 (26)	1 (1)	3 (3)	23 (27)	29 (26)	1 (1)	3 (3)	23 (29)	29 (24)	1 (1)	3 (3)
Portugal	2050	35 (34)	17 (19)	2 (1)	2 (3)	35 (34)	17 (19)	2 (1)	2 (3)	35 (35)	17 (18)	2 (1)	2 (3)	35 (35)	17 (18)	2 (1)	2 (3)
	2080	33 (31)	19 (22)	2 (1)	2 (3)	33 (32)	19 (21)	2 (1)	2 (3)	35 (33)	17 (20)	2 (2)	2 (2)	35 (34)	17 (19)	2 (2)	2 (2)
	2020	46 (43)	34 (37)	5 (5)	3 (3)	46 (44)	34 (36)	5 (5)	3 (3)	47 (45)	33 (35)	5 (5)	3 (3)	46 (44)	34 (36)	5 (5)	3 (3)
Romania	2050	35 (31)	45 (49)	4 (4)	4 (4)	37 (34)	43 (46)	4 (4)	4 (4)	37 (34)	43 (46)	4 (4)	4 (4)	37 (33)	43 (47)	4 (4)	4 (4)
	2080	30 (23)	50 (57)	4 (4)	4 (4)	34 (25)	46 (55)	4 (4)	4 (4)	34 (31)	46 (49)	4 (4)	4 (4)	34 (30)	46 (50)	4 (4)	4 (4)
	2020	20 (12)	39 (48)	3 (1)	6 (8)	19 (12)	40 (48)	3 (1)	6 (8)	19 (12)	40 (48)	3 (1)	6 (8)	20 (13)	39 (47)	3 (1)	6 (8)
Spain	2050	9 (5)	50 (55)	0 (0)	9 (9)	8 (6)	51 (54)	0 (0)	9 (9)	9 (5)	50 (55)	0 (0)	9 (9)	9 (7)	50 (53)	0 (0)	9 (9)
	2080	8 (8)	51 (52)	1 (1)	8 (8)	8 (8)	51 (52)	0 (1)	9 (8)	8 (8)	51 (52)	0 (0)	9 (9)	8 (10)	51 (50)	0 (1)	9 (8)
	2020	48 (41)	36 (44)	8 (11)	7 (4)	46 (41)	38 (44)	7 (11)	8 (4)	48 (43)	36 (42)	9 (11)	6 (4)	47 (43)	37 (42)	8 (11)	7 (4)
Sweden	2050	41 (25)	43 (60)	10 (8)	5 (7)	42 (25)	42 (60)	10 (8)	5 (7)	42 (32)	42 (53)	10 (9)	5 (6)	44 (30)	40 (55)	10 (9)	5 (6)

	2080	33 (26)	52 (59)	8 (9)	7 (6)	38 (27)	47 (58)	8 (9)	7 (6)	44 (35)	39 (50)	8 (10)	7 (5)	44 (36)	40 (49)	9 (10)	6 (5)
	2020	16 (27)	34 (35)	1 (3)	2 (3)	16 (28)	33 (34)	1 (3)	1 (3)	16 (26)	33 (36)	1 (3)	1 (3)	18 (28)	33 (34)	1 (3)	1 (3)
San Marino	2050	15 (23)	37 (39)	1 (2)	2 (4)	15 (23)	37 (39)	1 (2)	2 (4)	15 (23)	37 (39)	1 (2)	2 (4)	16 (23)	36 (39)	1 (2)	2 (4)
	2080	14 (15)	37 (47)	1 (2)	2 (4)	14 (17)	38 (45)	1 (2)	2 (4)	13 (20)	38 (42)	1 (2)	2 (4)	14 (21)	37 (41)	1 (2)	2 (4)
	2020	41 (35)	45 (52)	7 (7)	3 (3)	41 (37)	45 (50)	7 (7)	3 (3)	40 (37)	46 (50)	7 (7)	3 (3)	42 (36)	44 (51)	7 (7)	3 (3)
Serbia	2050	42 (35)	44 (52)	7 (7)	3 (3)	43 (35)	43 (52)	7 (7)	3 (3)	42 (37)	44 (50)	7 (7)	3 (3)	42 (38)	44 (49)	7 (7)	3 (3)
	2080	30 (31)	56 (56)	5 (6)	5 (4)	31 (34)	54 (53)	5 (7)	5 (3)	37 (34)	49 (52)	5 (5)	5 (5)	36 (35)	49 (52)	5 (5)	5 (5)
	2020	68 (44)	16 (47)	9 (7)	2 (5)	67 (44)	17 (47)	9 (7)	2 (5)	66 (46)	18 (45)	9 (7)	2 (5)	66 (46)	18 (45)	9 (7)	2 (5)
Slovakia	2050	63 (35)	23 (56)	10 (7)	2 (5)	65 (37)	23 (54)	10 (7)	2 (5)	65 (39)	21 (52)	10 (7)	2 (5)	64 (39)	23 (52)	10 (7)	2 (5)
	2080	56 (31)	31 (60)	10 (8)	2 (4)	56 (36)	30 (55)	10 (8)	2 (4)	62 (37)	24 (54)	10 (7)	2 (5)	62 (39)	25 (52)	10 (8)	2 (4)
	2020	50 (32)	26 (47)	6 (5)	0 (2)	51 (32)	25 (47)	6 (5)	0 (2)	47 (32)	28 (47)	6 (5)	0 (2)	48 (31)	27 (48)	6 (5)	0 (2)
Slovenia	2050	57 (34)	20 (45)	6 (4)	0 (3)	57 (35)	20 (44)	6 (4)	0 (3)	56 (35)	21 (44)	6 (4)	0 (3)	56 (35)	21 (44)	6 (4)	0 (3)
	2080	48 (30)	30 (49)	6 (4)	1 (3)	54 (32)	24 (47)	6 (4)	1 (3)	54 (33)	22 (46)	6 (4)	0 (3)	54 (33)	24 (46)	6 (4)	1 (3)
	2020	37 (13)	42 (66)	9 (4)	3 (8)	37 (13)	42 (66)	9 (4)	3 (8)	35 (13)	44 (66)	9 (4)	3 (8)	37 (13)	42 (66)	9 (4)	3 (8)
Spain	2050	29 (13)	50 (66)	7 (3)	5 (9)	33 (12)	46 (67)	7 (2)	5 (10)	32 (11)	47 (68)	7 (2)	5 (10)	33 (13)	46 (66)	7 (3)	5 (9)
	2080	20 (12)	59 (67)	3 (2)	9 (10)	22 (11)	57 (68)	5 (2)	7 (10)	27 (12)	52 (67)	7 (2)	5 (10)	28 (14)	51 (65)	7 (2)	5 (10)
	2020	39 (36)	25 (28)	4 (4)	3 (3)	39 (36)	25 (28)	4 (4)	3 (3)	40 (36)	24 (28)	4 (4)	3 (3)	40 (36)	24 (28)	4 (4)	3 (3)
Sweden	2050	43 (39)	21 (25)	5 (4)	2 (3)	43 (40)	21 (24)	5 (4)	2 (3)	43 (42)	21 (22)	5 (5)	2 (2)	43 (39)	21 (25)	5 (4)	2 (3)
	2080	40 (34)	24 (30)	5 (2)	2 (5)	41 (37)	23 (27)	5 (4)	2 (3)	44 (38)	20 (26)	6 (4)	1 (3)	42 (38)	22 (26)	5 (4)	2 (3)
	2020	55 (50)	24 (28)	6 (5)	2 (2)	55 (50)	24 (29)	6 (6)	2 (2)	55 (51)	24 (28)	6 (6)	2 (2)	54 (51)	25 (28)	6 (6)	2 (2)
Switzerland	2050	58 (50)	21 (29)	6 (5)	2 (3)	61 (55)	18 (24)	6 (6)	2 (2)	61 (57)	18 (22)	6 (7)	2 (1)	62 (54)	17 (25)	6 (5)	2 (3)
	2080	50 (40)	28 (39)	5 (5)	3 (3)	52 (43)	27 (36)	5 (5)	3 (3)	52 (46)	27 (33)	5 (5)	3 (3)	51 (45)	28 (34)	5 (5)	3 (3)
	2020	21 (18)	26 (30)	2 (2)	1 (1)	20 (18)	27 (29)	2 (2)	1 (1)	20 (19)	27 (29)	2 (2)	1 (1)	21 (19)	26 (29)	2 (2)	1 (1)
UK	2050	21 (19)	27 (29)	2 (2)	1 (1)	21 (20)	27 (28)	2 (2)	1 (1)	21 (20)	27 (28)	2 (2)	1 (1)	21 (20)	27 (28)	2 (2)	1 (1)
	2080	15 (14)	33 (34)	1 (1)	2 (2)	18 (15)	30 (33)	3 (1)	0 (2)	21 (19)	27 (29)	3 (3)	0 (0)	20 (19)	28 (29)	3 (3)	0 (0)

		A1FI				A2				B1				B2			
		all species		RL species		all species		RL species		all species		RL species		all species		RL species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Plants																	
Albania	2020	265 (269)	355 (381)	1 (1)	1 (2)	266 (273)	356 (376)	1 (1)	1 (2)	270 (262)	356 (387)	1 (1)	1 (2)	267 (272)	357 (377)	1 (1)	1 (2)
	2050	329 (300)	297 (349)	3 (2)	0 (1)	332 (313)	295 (337)	3 (2)	0 (1)	328 (307)	297 (342)	3 (2)	0 (1)	330 (312)	298 (338)	3 (2)	0 (1)
	2080	229 (204)	399 (445)	1 (1)	1 (2)	248 (223)	380 (426)	1 (1)	1 (2)	244 (214)	385 (436)	1 (1)	1 (2)	260 (225)	368 (425)	1 (1)	1 (2)
Andorra	2020	198 (223)	118 (127)	0 (0)	0 (0)	197 (222)	122 (129)	0 (0)	0 (0)	200 (227)	118 (121)	0 (0)	0 (0)	198 (222)	120 (124)	0 (0)	0 (0)
	2050	186 (192)	144 (162)	0 (0)	0 (0)	216 (214)	111 (135)	0 (0)	0 (0)	209 (214)	117 (136)	0 (0)	0 (0)	213 (213)	116 (139)	0 (0)	0 (0)
	2080	208 (206)	140 (151)	0 (0)	0 (0)	200 (205)	144 (152)	0 (0)	0 (0)	187 (194)	153 (159)	0 (0)	0 (0)	191 (196)	151 (158)	0 (0)	0 (0)
Austria	2020	350 (302)	300 (356)	0 (0)	0 (0)	348 (302)	303 (356)	0 (0)	0 (0)	348 (300)	301 (358)	0 (0)	0 (0)	347 (297)	304 (360)	0 (0)	0 (0)
	2050	392 (318)	261 (341)	0 (0)	0 (0)	396 (327)	257 (331)	0 (0)	0 (0)	394 (318)	257 (339)	0 (0)	0 (0)	390 (321)	264 (336)	0 (0)	0 (0)
	2080	303 (242)	352 (419)	0 (0)	0 (0)	331 (272)	326 (388)	0 (0)	0 (0)	340 (285)	313 (375)	0 (0)	0 (0)	333 (282)	320 (378)	0 (0)	0 (0)
Belgium	2020	131 (118)	240 (271)	0 (0)	0 (0)	130 (116)	240 (273)	0 (0)	0 (0)	131 (117)	245 (272)	0 (0)	0 (0)	129 (114)	243 (275)	0 (0)	0 (0)
	2050	147 (139)	227 (252)	0 (0)	0 (0)	137 (133)	235 (258)	0 (0)	0 (0)	145 (132)	227 (258)	0 (0)	0 (0)	140 (125)	235 (266)	0 (0)	0 (0)
	2080	127 (125)	253 (266)	0 (0)	0 (0)	141 (133)	240 (258)	0 (0)	0 (0)	146 (129)	234 (261)	0 (0)	0 (0)	138 (130)	240 (261)	0 (0)	0 (0)
Bosnia and Herzeg	2020	232 (337)	296 (293)	1 (1)	0 (0)	237 (343)	292 (288)	1 (1)	0 (0)	233 (330)	299 (301)	1 (1)	0 (0)	237 (340)	296 (291)	1 (1)	0 (0)
	2050	271 (335)	276 (296)	1 (1)	0 (0)	274 (344)	266 (286)	1 (1)	0 (0)	268 (334)	275 (297)	1 (1)	0 (0)	275 (336)	269 (294)	1 (1)	0 (0)
	2080	194 (275)	359 (356)	1 (1)	0 (0)	215 (293)	335 (338)	1 (1)	0 (0)	211 (304)	333 (327)	1 (1)	0 (0)	222 (305)	323 (326)	1 (1)	0 (0)
Bulgaria	2020	385 (276)	262 (384)	1 (1)	0 (0)	381 (276)	269 (384)	1 (1)	0 (0)	372 (265)	275 (394)	1 (1)	0 (0)	377 (279)	269 (381)	1 (1)	0 (0)
	2050	336 (229)	316 (431)	1 (1)	0 (0)	335 (234)	315 (426)	1 (1)	0 (0)	337 (236)	312 (424)	1 (1)	0 (0)	340 (243)	311 (417)	1 (1)	0 (0)
	2080	320 (170)	334 (490)	1 (0)	0 (1)	341 (195)	313 (465)	1 (0)	0 (1)	310 (190)	344 (470)	1 (0)	0 (1)	334 (206)	320 (454)	1 (0)	0 (1)
Croatia	2020	292 (265)	343 (406)	1 (1)	0 (0)	298 (269)	338 (401)	1 (1)	0 (0)	285 (257)	350 (414)	1 (1)	0 (0)	287 (261)	347 (410)	1 (1)	0 (0)
	2050	317 (287)	325 (384)	1 (1)	0 (0)	329 (291)	317 (379)	1 (1)	0 (0)	319 (284)	323 (386)	1 (1)	0 (0)	318 (287)	327 (384)	1 (1)	0 (0)
	2080	252 (191)	398 (480)	1 (1)	0 (0)	267 (212)	380 (458)	1 (1)	0 (0)	266 (211)	380 (460)	1 (1)	0 (0)	264 (214)	381 (457)	1 (1)	0 (0)
Czech Republic	2020	304 (263)	214 (258)	0 (0)	0 (0)	304 (262)	214 (259)	0 (0)	0 (0)	302 (270)	215 (251)	0 (0)	0 (0)	299 (269)	219 (252)	0 (0)	0 (0)
	2050	272 (241)	247 (279)	0 (0)	0 (0)	283 (251)	235 (269)	0 (0)	0 (0)	275 (247)	243 (273)	0 (0)	0 (0)	272 (246)	247 (273)	0 (0)	0 (0)
	2080	221 (200)	298 (320)	0 (0)	0 (0)	232 (217)	286 (303)	0 (0)	0 (0)	252 (235)	266 (286)	0 (0)	0 (0)	247 (232)	272 (289)	0 (0)	0 (0)
Denmark	2020	186 (186)	133 (141)	0 (0)	0 (0)	183 (185)	139 (142)	0 (0)	0 (0)	182 (184)	138 (143)	0 (0)	0 (0)	183 (185)	138 (143)	0 (0)	0 (0)

	2050	135 (139)	190 (189)	0 (0)	0 (0)	134 (145)	189 (183)	0 (0)	0 (0)	132 (141)	191 (187)	0 (0)	0 (0)	123 (130)	201 (198)	0 (0)	0 (0)
	2080	78 (83)	247 (245)	0 (0)	0 (0)	84 (89)	240 (239)	0 (0)	0 (0)	96 (100)	230 (228)	0 (0)	0 (0)	91 (94)	235 (234)	0 (0)	0 (0)
	2020	216 (216)	97 (98)	0 (0)	0 (0)	213 (213)	101 (101)	0 (0)	0 (0)	208 (210)	106 (104)	0 (0)	0 (0)	211 (212)	103 (102)	0 (0)	0 (0)
Estonia	2050	181 (181)	132 (133)	0 (0)	0 (0)	182 (181)	132 (133)	0 (0)	0 (0)	177 (178)	137 (135)	0 (0)	0 (0)	180 (182)	134 (132)	0 (0)	0 (0)
	2080	136 (137)	178 (177)	0 (0)	0 (0)	147 (148)	167 (166)	0 (0)	0 (0)	159 (158)	155 (156)	0 (0)	0 (0)	151 (154)	163 (160)	0 (0)	0 (0)
	2020	249 (223)	69 (108)	0 (0)	0 (0)	249 (223)	69 (108)	0 (0)	0 (0)	246 (221)	72 (110)	0 (0)	0 (0)	248 (224)	70 (107)	0 (0)	0 (0)
Finland	2050	228 (196)	91 (135)	0 (0)	0 (0)	228 (198)	91 (133)	0 (0)	0 (0)	226 (195)	94 (136)	0 (0)	0 (0)	225 (195)	95 (136)	0 (0)	0 (0)
	2080	209 (171)	110 (160)	0 (0)	0 (0)	212 (179)	107 (152)	0 (0)	0 (0)	219 (185)	101 (146)	0 (0)	0 (0)	214 (183)	105 (148)	0 (0)	0 (0)
	2020	372 (310)	511 (578)	0 (0)	0 (0)	378 (309)	504 (580)	0 (0)	0 (0)	379 (299)	505 (589)	0 (0)	0 (0)	370 (303)	513 (586)	0 (0)	0 (0)
France	2050	344 (270)	542 (618)	0 (0)	0 (0)	349 (275)	535 (612)	0 (0)	0 (0)	342 (268)	540 (618)	0 (0)	0 (0)	348 (266)	534 (621)	0 (0)	0 (0)
	2080	335 (244)	555 (649)	0 (0)	0 (0)	350 (261)	537 (630)	0 (0)	0 (0)	360 (274)	522 (616)	0 (0)	0 (0)	358 (273)	528 (617)	0 (0)	0 (0)
	2020	197 (189)	418 (426)	0 (0)	0 (0)	195 (189)	420 (426)	0 (0)	0 (0)	195 (187)	420 (428)	0 (0)	0 (0)	192 (189)	423 (426)	0 (0)	0 (0)
Germany	2050	190 (183)	424 (433)	0 (0)	0 (0)	193 (183)	422 (433)	0 (0)	0 (0)	193 (180)	422 (434)	0 (0)	0 (0)	192 (183)	424 (433)	0 (0)	0 (0)
	2080	183 (176)	432 (440)	0 (0)	0 (0)	189 (182)	425 (433)	0 (0)	0 (0)	199 (187)	417 (428)	0 (0)	0 (0)	191 (189)	423 (426)	0 (0)	0 (0)
	2020	187 (175)	474 (547)	0 (0)	3 (3)	191 (178)	472 (544)	0 (0)	3 (3)	180 (178)	475 (544)	0 (0)	3 (3)	189 (182)	470 (540)	0 (0)	3 (3)
Greece	2050	272 (247)	398 (475)	2 (2)	1 (1)	275 (256)	395 (465)	2 (2)	1 (1)	270 (248)	399 (474)	2 (2)	1 (1)	283 (266)	388 (455)	2 (2)	1 (1)
	2080	205 (207)	473 (515)	2 (1)	1 (2)	215 (204)	463 (518)	2 (1)	1 (2)	223 (203)	451 (519)	2 (1)	1 (2)	242 (212)	433 (510)	2 (1)	1 (2)
	2020	174 (159)	333 (370)	0 (0)	0 (0)	178 (159)	331 (370)	0 (0)	0 (0)	180 (165)	328 (363)	0 (0)	0 (0)	186 (176)	323 (352)	0 (0)	0 (0)
Hungary	2050	143 (137)	367 (392)	0 (0)	0 (0)	149 (140)	361 (388)	0 (0)	0 (0)	170 (162)	341 (367)	0 (0)	0 (0)	175 (168)	334 (361)	0 (0)	0 (0)
	2080	94 (93)	420 (436)	0 (0)	0 (0)	111 (108)	402 (421)	0 (0)	0 (0)	133 (137)	377 (392)	0 (0)	0 (0)	136 (141)	374 (388)	0 (0)	0 (0)
	2020	132 (111)	133 (166)	0 (0)	0 (0)	131 (111)	134 (166)	0 (0)	0 (0)	130 (110)	137 (167)	0 (0)	0 (0)	129 (111)	139 (166)	0 (0)	0 (0)
Ireland	2050	106 (76)	164 (201)	0 (0)	0 (0)	110 (79)	160 (198)	0 (0)	0 (0)	107 (77)	162 (200)	0 (0)	0 (0)	107 (77)	164 (200)	0 (0)	0 (0)
	2080	87 (62)	181 (215)	0 (0)	0 (0)	94 (69)	177 (208)	0 (0)	0 (0)	101 (75)	170 (202)	0 (0)	0 (0)	102 (73)	169 (204)	0 (0)	0 (0)
	2020	569 (317)	324 (609)	0 (1)	0 (0)	564 (318)	325 (608)	0 (1)	0 (0)	564 (303)	325 (623)	0 (1)	0 (0)	566 (317)	323 (609)	0 (1)	0 (0)
Italy	2050	482 (293)	421 (633)	0 (1)	0 (0)	487 (298)	413 (629)	0 (1)	0 (0)	483 (293)	420 (634)	0 (1)	0 (0)	490 (297)	411 (629)	0 (1)	0 (0)
	2080	430 (267)	470 (659)	0 (1)	0 (0)	449 (272)	450 (655)	0 (1)	0 (0)	461 (263)	440 (664)	0 (1)	0 (0)	478 (276)	424 (651)	0 (1)	0 (0)
	2020	204 (214)	125 (117)	0 (0)	0 (0)	206 (215)	124 (116)	0 (0)	0 (0)	207 (214)	123 (117)	0 (0)	0 (0)	206 (215)	124 (116)	0 (0)	0 (0)
Latvia	2050	185 (189)	146 (142)	0 (0)	0 (0)	188 (192)	143 (139)	0 (0)	0 (0)	182 (182)	149 (149)	0 (0)	0 (0)	187 (188)	144 (143)	0 (0)	0 (0)
	2080	139 (141)	192 (190)	0 (0)	0 (0)	153 (149)	178 (182)	0 (0)	0 (0)	166 (163)	163 (168)	0 (0)	0 (0)	164 (167)	167 (164)	0 (0)	0 (0)
	2020	192 (198)	181 (183)	0 (0)	0 (0)	191 (200)	181 (181)	0 (0)	0 (0)	194 (199)	180 (182)	0 (0)	0 (0)	189 (198)	181 (182)	0 (0)	0 (0)
Liechten-stein	2050	220 (225)	152 (161)	0 (0)	0 (0)	241 (245)	132 (138)	0 (0)	0 (0)	240 (242)	134 (140)	0 (0)	0 (0)	237 (242)	135 (141)	0 (0)	0 (0)
	2080	191 (193)	187 (191)	0 (0)	0 (0)	211 (216)	170 (172)	0 (0)	0 (0)	230 (233)	143 (150)	0 (0)	0 (0)	223 (226)	156 (159)	0 (0)	0 (0)
	2020	225 (219)	107 (118)	0 (0)	0 (0)	224 (221)	108 (116)	0 (0)	0 (0)	222 (220)	109 (117)	0 (0)	0 (0)	224 (221)	108 (116)	0 (0)	0 (0)
Lithuania	2050	173 (168)	160 (169)	0 (0)	0 (0)	179 (178)	153 (159)	0 (0)	0 (0)	177 (174)	155 (163)	0 (0)	0 (0)	173 (171)	159 (166)	0 (0)	0 (0)
	2080	133 (136)	203 (201)	0 (0)	0 (0)	142 (142)	192 (195)	0 (0)	0 (0)	161 (158)	173 (179)	0 (0)	0 (0)	152 (153)	182 (184)	0 (0)	0 (0)
	2020	128 (138)	169 (191)	0 (0)	0 (0)	122 (133)	173 (196)	0 (0)	0 (0)	120 (133)	181 (196)	0 (0)	0 (0)	120 (131)	179 (197)	0 (0)	0 (0)
Luxembourg	2050	115 (120)	191 (209)	0 (0)	0 (0)	127 (128)	181 (200)	0 (0)	0 (0)	124 (131)	181 (198)	0 (0)	0 (0)	124 (123)	186 (206)	0 (0)	0 (0)
	2080	81 (79)	229 (250)	0 (0)	0 (0)	95 (95)	216 (234)	0 (0)	0 (0)	99 (105)	208 (224)	0 (0)	0 (0)	98 (98)	211 (231)	0 (0)	0 (0)
	2020	281 (203)	283 (415)	0 (0)	1 (1)	285 (216)	278 (400)	0 (0)	1 (1)	284 (216)	280 (401)	0 (0)	1 (1)	289 (230)	280 (387)	0 (0)	1 (1)
Macedonia	2050	317 (247)	268 (371)	1 (0)	0 (1)	319 (252)	264 (367)	1 (0)	0 (1)	324 (250)	257 (369)	1 (0)	0 (1)	326 (259)	261 (359)	1 (0)	0 (1)
	2080	220 (173)	371 (446)	0 (0)	1 (1)	254 (201)	333 (418)	0 (0)	1 (1)	271 (201)	315 (418)	0 (0)	1 (1)	280 (214)	306 (405)	0 (0)	1 (1)
	2020	97 (125)	44 (56)	0 (0)	0 (0)	98 (124)	45 (56)	0 (0)	0 (0)	99 (125)	43 (56)	0 (0)	0 (0)	94 (123)	44 (57)	0 (0)	0 (0)
Malta	2050	120 (136)	45 (46)	0 (0)	0 (0)	119 (135)	46 (47)	0 (0)	0 (0)	122 (135)	43 (47)	0 (0)	0 (0)	120 (134)	45 (48)	0 (0)	0 (0)
	2080	117 (122)	52 (59)	0 (0)	0 (0)	117 (121)	51 (62)	0 (0)	0 (0)	119 (125)	46 (54)	0 (0)	0 (0)	124 (131)	43 (51)	0 (0)	0 (0)
	2020	19 (139)	23 (138)	0 (0)	0 (0)	19 (144)	26 (134)	0 (0)	0 (0)	20 (135)	26 (143)	0 (0)	0 (0)	20 (144)	26 (134)	0 (0)	0 (0)
Monaco	2050	17 (96)	49 (184)	0 (0)	0 (0)	17 (98)	49 (185)	0 (0)	0 (0)	17 (98)	45 (183)	0 (0)	0 (0)	17 (100)	49 (182)	0 (0)	0 (0)
	2080	27 (89)	81 (192)	0 (0)	0 (0)	27 (96)	70 (186)	0 (0)	0 (0)	24 (102)	56 (178)	0 (0)	0 (0)	28 (108)	55 (175)	0 (0)	0 (0)
	2020	336 (331)	199 (227)	2 (1)	0 (1)	337 (331)	201 (230)	2 (1)	0 (1)	328 (324)	209 (237)	2 (1)	0 (1)	331 (329)	207 (231)	2 (1)	0 (1)
Montenegro	2050	355 (343)	194 (218)	2 (2)	0 (0)	355 (347)	193 (214)	2 (2)	0 (0)	348 (346)	200 (215)	2 (2)	0 (0)	353 (344)	195 (217)	2 (2)	0 (0)
	2080	295 (267)	252 (294)	2 (2)	0 (0)	315 (294)	233 (267)	2 (2)	0 (0)	315 (295)	232 (266)	2 (2)	0 (0)	318 (298)	229 (263)	2 (2)	0 (0)
	2020	102 (98)	255 (259)	0 (0)	0 (0)	101 (97)	255 (261)	0 (0)	0 (0)	99 (100)	258 (258)	0 (0)	0 (0)	98 (98)	259 (260)	0 (0)	0 (0)
Netherlands	2050	103 (105)	251 (253)	0 (0)	0 (0)	101 (99)	256 (259)	0 (0)	0 (0)	105 (105)	252 (253)	0 (0)	0 (0)	102 (102)	255 (256)	0 (0)	0 (0)
	2080	113 (112)	245 (246)	0 (0)	0 (0)	114 (111)	244 (247)	0 (0)	0 (0)	106 (107)	249 (251)	0 (0)	0 (0)	107 (107)	247 (251)	0 (0)	0 (0)
	2020	258 (249)	91 (119)	0 (0)	0 (0)	256 (249)	93 (119)	0 (0)	0 (0)	256 (251)	94 (117)	0 (0)	0 (0)	255 (252)	95 (116)	0 (0)	0 (0)
Norway	2050	256 (244)	95 (124)	0 (0)	0 (0)	258 (245)	93 (123)	0 (0)	0 (0)	255 (244)	94 (124)	0 (0)	0 (0)	256 (243)	95 (125)	0 (0)	0 (0)
	2080	243 (212)	109 (156)	0 (0)	0 (0)	245 (226)	107 (142)	0 (0)	0 (0)	253 (234)	98 (134)	0 (0)	0 (0)	250 (233)	101 (135)	0 (0)	0 (0)
	2020	290 (253)	232 (276)	0 (0)	0 (0)	283 (253)	240 (276)	0 (0)	0 (0)	287 (256)	236 (273)	0 (0)	0 (0)	285 (255)	238 (274)	0 (0)	0 (0)
Poland	2050	236 (206)	288 (323)	0 (0)	0 (0)	238 (209)	285 (320)	0 (0)	0 (0)	249 (218)	273 (311)	0 (0)	0 (0)	246 (218)	277 (311)	0 (0)	0 (0)

Portugal	2080	209 (190)	317 (339)	0 (0)	0 (0)	226 (205)	299 (324)	0 (0)	0 (0)	248 (221)	275 (308)	0 (0)	0 (0)	242 (214)	283 (314)	0 (0)	0 (0)
	2020	223 (200)	253 (289)	0 (0)	0 (0)	224 (201)	253 (290)	0 (0)	0 (0)	229 (208)	244 (282)	0 (0)	0 (0)	232 (211)	245 (280)	0 (0)	0 (0)
	2050	153 (141)	322 (349)	0 (0)	0 (0)	158 (147)	315 (343)	0 (0)	0 (0)	160 (149)	314 (341)	0 (0)	0 (0)	167 (151)	308 (339)	0 (0)	0 (0)
Romania	2080	161 (151)	319 (340)	0 (0)	0 (0)	163 (152)	318 (337)	0 (0)	0 (0)	171 (153)	309 (337)	0 (0)	0 (0)	171 (166)	309 (324)	0 (0)	0 (0)
	2020	373 (332)	278 (330)	0 (0)	0 (0)	373 (330)	278 (332)	0 (0)	0 (0)	370 (343)	280 (319)	0 (0)	0 (0)	374 (347)	276 (315)	0 (0)	0 (0)
	2050	272 (212)	377 (450)	0 (0)	0 (0)	281 (216)	368 (446)	0 (0)	0 (0)	286 (231)	369 (431)	0 (0)	0 (0)	285 (234)	367 (428)	0 (0)	0 (0)
San Marino	2080	219 (170)	438 (492)	0 (0)	0 (0)	238 (197)	418 (464)	0 (0)	0 (0)	259 (221)	397 (441)	0 (0)	0 (0)	265 (227)	390 (435)	0 (0)	0 (0)
	2020	153 (184)	196 (252)	0 (0)	0 (0)	150 (181)	197 (254)	0 (0)	0 (0)	152 (178)	198 (257)	0 (0)	0 (0)	152 (181)	198 (254)	0 (0)	0 (0)
	2050	152 (141)	206 (295)	0 (0)	0 (0)	157 (143)	201 (293)	0 (0)	0 (0)	152 (137)	207 (299)	0 (0)	0 (0)	157 (144)	200 (292)	0 (0)	0 (0)
Serbia	2080	126 (116)	233 (320)	0 (0)	0 (0)	134 (123)	224 (313)	0 (0)	0 (0)	141 (123)	218 (313)	0 (0)	0 (0)	147 (131)	212 (305)	0 (0)	0 (0)
	2020	319 (298)	310 (384)	1 (0)	0 (1)	320 (297)	312 (385)	1 (0)	0 (1)	315 (301)	315 (381)	1 (0)	0 (1)	313 (307)	317 (374)	1 (0)	0 (1)
	2050	284 (281)	357 (401)	1 (1)	0 (0)	295 (292)	345 (390)	1 (1)	0 (0)	293 (289)	348 (393)	1 (1)	0 (0)	295 (296)	345 (386)	1 (1)	0 (0)
Slovakia	2080	215 (211)	429 (471)	1 (0)	0 (1)	229 (231)	412 (451)	1 (1)	0 (0)	245 (242)	399 (440)	1 (0)	0 (1)	250 (252)	392 (430)	1 (0)	0 (1)
	2020	379 (278)	162 (285)	0 (0)	0 (0)	381 (277)	161 (286)	0 (0)	0 (0)	379 (276)	163 (287)	0 (0)	0 (0)	376 (277)	164 (286)	0 (0)	0 (0)
	2050	356 (249)	194 (314)	0 (0)	0 (0)	361 (252)	190 (311)	0 (0)	0 (0)	357 (258)	193 (304)	0 (0)	0 (0)	355 (252)	194 (311)	0 (0)	0 (0)
Slovenia	2080	263 (161)	286 (401)	0 (0)	0 (0)	300 (189)	250 (374)	0 (0)	0 (0)	323 (217)	223 (346)	0 (0)	0 (0)	322 (215)	227 (348)	0 (0)	0 (0)
	2020	277 (236)	281 (382)	1 (1)	0 (0)	278 (236)	279 (381)	1 (1)	0 (0)	274 (234)	285 (384)	1 (1)	0 (0)	274 (233)	286 (385)	1 (1)	0 (0)
	2050	354 (299)	220 (319)	1 (1)	0 (0)	357 (305)	214 (312)	1 (1)	0 (0)	343 (295)	230 (323)	1 (1)	0 (0)	343 (298)	232 (320)	1 (1)	0 (0)
Spain	2080	284 (227)	298 (391)	1 (1)	0 (0)	312 (259)	266 (359)	1 (1)	0 (0)	306 (253)	268 (365)	1 (1)	0 (0)	306 (252)	273 (366)	1 (1)	0 (0)
	2020	381 (271)	441 (561)	0 (0)	0 (0)	387 (272)	436 (560)	0 (0)	0 (0)	390 (274)	434 (558)	0 (0)	0 (0)	384 (275)	439 (557)	0 (0)	0 (0)
	2050	318 (223)	505 (608)	0 (0)	0 (0)	340 (221)	485 (610)	0 (0)	0 (0)	331 (222)	494 (610)	0 (0)	0 (0)	335 (228)	491 (604)	0 (0)	0 (0)
Sweden	2080	284 (235)	543 (598)	0 (0)	0 (0)	299 (238)	527 (594)	0 (0)	0 (0)	315 (250)	510 (581)	0 (0)	0 (0)	322 (245)	504 (586)	0 (0)	0 (0)
	2020	278 (270)	144 (159)	0 (0)	0 (0)	279 (270)	144 (159)	0 (0)	0 (0)	281 (269)	142 (159)	0 (0)	0 (0)	280 (268)	144 (161)	0 (0)	0 (0)
	2050	272 (247)	152 (181)	0 (0)	0 (0)	270 (247)	153 (181)	0 (0)	0 (0)	274 (250)	149 (179)	0 (0)	0 (0)	268 (248)	155 (181)	0 (0)	0 (0)
Switzerland	2080	232 (210)	194 (219)	0 (0)	0 (0)	242 (225)	184 (204)	0 (0)	0 (0)	257 (230)	168 (199)	0 (0)	0 (0)	247 (229)	178 (200)	0 (0)	0 (0)
	2020	311 (286)	286 (316)	0 (0)	0 (0)	309 (283)	286 (319)	0 (0)	0 (0)	310 (287)	287 (315)	0 (0)	0 (0)	307 (289)	289 (314)	0 (0)	0 (0)
	2050	364 (311)	239 (291)	0 (0)	0 (0)	373 (322)	230 (282)	0 (0)	0 (0)	367 (321)	235 (282)	0 (0)	0 (0)	369 (315)	234 (289)	0 (0)	0 (0)
UK	2080	305 (264)	300 (341)	0 (0)	0 (0)	313 (278)	290 (329)	0 (0)	0 (0)	313 (274)	290 (329)	0 (0)	0 (0)	310 (269)	293 (337)	0 (0)	0 (0)
	2020	176 (168)	236 (246)	0 (0)	0 (0)	175 (167)	237 (247)	0 (0)	0 (0)	175 (168)	238 (246)	0 (0)	0 (0)	169 (168)	242 (246)	0 (0)	0 (0)
	2050	157 (148)	256 (267)	0 (0)	0 (0)	158 (150)	255 (265)	0 (0)	0 (0)	157 (149)	256 (266)	0 (0)	0 (0)	157 (148)	256 (267)	0 (0)	0 (0)
	2080	143 (137)	270 (278)	0 (0)	0 (0)	153 (146)	261 (269)	0 (0)	0 (0)	155 (146)	258 (269)	0 (0)	0 (0)	155 (143)	259 (272)	0 (0)	0 (0)

Table S3b - Numbers of species projected to gain (win) and lose (los) climatic suitability in Natura 2000 areas (in parenthesis is expected value outside the Natura 2000), for different combinations of countries, emission scenarios and time periods. Projections are provided for Habitat Directive species (HD species), and for the complete pool of vertebrate and plant species considered (all).

		A1FI				A2				B1				B2			
		all species		HD species		all species		HD species		all species		HD species		all species		HD species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Amphibians																	
Austria	2020	12 (12)	8 (8)	9 (9)	5 (5)	12 (12)	8 (8)	9 (9)	5 (5)	12 (11)	8 (9)	9 (8)	5 (6)	12 (12)	8 (8)	9 (9)	5 (5)
	2050	14 (13)	6 (7)	10 (9)	4 (5)	14 (14)	5 (6)	10 (9)	4 (5)	13 (13)	6 (6)	9 (9)	5 (5)	13 (15)	6 (5)	9 (10)	5 (4)
	2080	14 (12)	6 (8)	9 (8)	5 (6)	14 (12)	6 (8)	9 (8)	5 (6)	14 (15)	4 (5)	9 (10)	4 (4)	13 (14)	5 (5)	9 (10)	4 (4)
Belgium	2020	13 (13)	6 (6)	8 (8)	4 (4)	13 (13)	6 (6)	8 (8)	4 (4)	13 (13)	6 (6)	8 (8)	4 (4)	12 (12)	7 (7)	7 (7)	5 (5)
	2050	7 (5)	12 (14)	4 (3)	8 (9)	6 (5)	13 (14)	3 (3)	9 (9)	7 (5)	12 (14)	4 (3)	8 (9)	5 (5)	14 (14)	3 (3)	9 (9)
	2080	5 (3)	14 (16)	3 (1)	9 (11)	7 (4)	12 (15)	4 (2)	8 (10)	8 (6)	11 (13)	4 (4)	8 (8)	7 (6)	12 (13)	4 (4)	8 (8)
Bulgaria	2020	8 (6)	9 (13)	5 (6)	6 (8)	8 (7)	9 (12)	5 (6)	6 (8)	8 (6)	9 (13)	5 (6)	6 (8)	8 (6)	9 (13)	5 (6)	6 (8)
	2050	12 (9)	5 (10)	9 (8)	2 (6)	12 (9)	5 (10)	9 (8)	2 (6)	12 (8)	5 (11)	9 (7)	2 (7)	12 (9)	5 (10)	9 (8)	2 (6)
	2080	8 (7)	9 (12)	6 (6)	5 (8)	8 (8)	9 (11)	6 (7)	5 (7)	10 (8)	7 (11)	6 (7)	5 (7)	11 (8)	6 (11)	7 (7)	4 (7)
Czech Republic	2020	16 (7)	3 (10)	10 (4)	3 (7)	17 (7)	2 (10)	11 (4)	2 (7)	17 (7)	2 (10)	11 (4)	2 (7)	17 (8)	2 (9)	11 (5)	2 (6)
	2050	14 (10)	5 (7)	10 (7)	3 (4)	14 (11)	5 (6)	10 (8)	3 (3)	15 (10)	4 (7)	10 (7)	3 (4)	14 (11)	5 (6)	10 (8)	3 (3)
	2080	13 (9)	6 (8)	8 (5)	5 (6)	14 (9)	5 (8)	9 (6)	4 (5)	14 (9)	5 (8)	9 (5)	4 (6)	14 (10)	5 (7)	9 (6)	4 (5)
Denmark	2020	9 (11)	5 (8)	7 (8)	3 (5)	9 (12)	5 (7)	7 (8)	3 (5)	9 (13)	5 (6)	7 (8)	3 (5)	9 (13)	5 (6)	7 (8)	3 (5)
	2050	9 (11)	5 (8)	6 (9)	4 (4)	9 (13)	5 (6)	6 (9)	4 (4)	9 (13)	5 (6)	6 (9)	4 (4)	9 (13)	5 (6)	6 (9)	4 (4)
	2080	7 (7)	8 (12)	4 (5)	6 (8)	7 (10)	7 (9)	5 (7)	5 (6)	7 (12)	7 (7)	5 (8)	5 (5)	7 (12)	7 (7)	5 (8)	5 (5)
Estonia	2020	10 (10)	1 (4)	8 (7)	0 (3)	10 (10)	1 (4)	8 (7)	0 (3)	11 (10)	0 (4)	8 (7)	0 (3)	11 (10)	0 (4)	8 (7)	0 (3)
	2050	11 (10)	0 (4)	8 (7)	0 (3)	11 (10)	0 (4)	8 (7)	0 (3)	11 (10)	0 (4)	8 (7)	0 (3)	11 (9)	0 (5)	8 (6)	0 (4)
	2080	9 (8)	2 (7)	6 (5)	2 (5)	11 (7)	0 (7)	8 (5)	0 (5)	11 (8)	0 (6)	8 (6)	0 (4)	11 (7)	0 (7)	8 (5)	0 (5)
Finland	2020	4 (11)	1 (0)	2 (8)	1 (0)	4 (11)	1 (0)	2 (8)	1 (0)	5 (11)	0 (0)	3 (8)	0 (0)	5 (11)	0 (0)	3 (8)	0 (0)
	2050	5 (11)	0 (0)	3 (8)	0 (0)	5 (11)	0 (0)	3 (8)	0 (0)	5 (11)	0 (0)	3 (8)	0 (0)	5 (11)	0 (0)	3 (8)	0 (0)
	2080	5 (11)	0 (0)	3 (8)	0 (0)	5 (11)	0 (0)	3 (8)	0 (0)	5 (11)	0 (0)	3 (8)	0 (0)	5 (11)	0 (0)	3 (8)	0 (0)
France	2020	10 (4)	17 (1)	8 (2)	11 (1)	11 (4)	16 (1)	9 (2)	10 (1)	10 (4)	17 (1)	8 (2)	11 (1)	10 (4)	17 (1)	8 (2)	11 (1)
	2050	8 (4)	19 (1)	6 (2)	13 (1)	9 (4)	18 (1)	7 (2)	12 (1)	9 (4)	18 (1)	7 (2)	12 (1)	9 (4)	18 (1)	7 (2)	12 (1)
	2080	8 (4)	20 (1)	6 (2)	14 (1)	8 (4)	20 (1)	6 (2)	14 (1)	9 (4)	19 (1)	7 (2)	13 (1)	9 (4)	19 (1)	7 (2)	13 (1)
Germany	2020	11 (9)	9 (18)	7 (8)	7 (11)	11 (10)	9 (17)	7 (9)	7 (10)	13 (9)	7 (18)	9 (8)	5 (11)	13 (10)	7 (17)	9 (9)	5 (10)
	2050	10 (6)	10 (21)	8 (4)	6 (15)	12 (6)	8 (21)	8 (4)	6 (15)	12 (4)	8 (23)	8 (3)	6 (16)	12 (6)	8 (21)	8 (4)	6 (15)
	2080	4 (8)	16 (19)	3 (6)	11 (13)	5 (7)	15 (20)	3 (5)	11 (14)	7 (6)	13 (21)	5 (5)	9 (14)	5 (7)	15 (20)	3 (5)	11 (14)
Greece	2020	2 (10)	13 (10)	1 (6)	8 (8)	2 (11)	13 (9)	1 (7)	8 (7)	2 (11)	13 (9)	1 (7)	8 (7)	2 (11)	13 (9)	1 (7)	8 (7)
	2050	10 (9)	5 (11)	7 (7)	2 (7)	10 (10)	5 (10)	7 (8)	2 (6)	10 (11)	5 (9)	7 (8)	2 (6)	10 (10)	5 (10)	7 (8)	2 (6)
	2080	2 (3)	13 (17)	1 (2)	8 (12)	3 (5)	12 (15)	1 (3)	8 (11)	2 (6)	13 (14)	0 (4)	9 (10)	4 (6)	11 (14)	2 (4)	7 (10)
Hungary	2020	1 (2)	15 (13)	1 (1)	10 (8)	1 (2)	15 (13)	1 (1)	10 (8)	1 (2)	15 (13)	1 (1)	10 (8)	1 (2)	15 (13)	1 (1)	10 (8)
	2050	5 (7)	11 (8)	3 (5)	8 (4)	5 (8)	11 (7)	3 (5)	8 (4)	6 (7)	10 (8)	4 (5)	7 (4)	6 (9)	10 (6)	4 (6)	7 (3)
	2080	7 (2)	9 (13)	4 (1)	7 (8)	7 (2)	9 (13)	4 (1)	7 (8)	7 (1)	9 (14)	4 (0)	7 (9)	7 (1)	8 (14)	4 (0)	6 (9)
Ireland	2020	2 (2)	1 (14)	2 (1)	0 (10)	2 (2)	1 (14)	2 (1)	0 (10)	2 (2)	1 (14)	2 (2)	0 (9)	2 (2)	1 (14)	2 (2)	0 (9)
	2050	1 (4)	2 (12)	1 (2)	1 (9)	1 (4)	2 (12)	1 (2)	1 (9)	1 (6)	2 (10)	1 (4)	1 (7)	1 (6)	2 (10)	1 (4)	1 (7)
	2080	1 (7)	2 (9)	1 (4)	1 (7)	1 (8)	2 (8)	1 (5)	1 (6)	1 (8)	2 (8)	1 (5)	1 (6)	1 (8)	2 (8)	1 (5)	1 (6)
Italy	2020	20 (2)	7 (1)	16 (2)	4 (0)	20 (2)	7 (1)	16 (2)	4 (0)	20 (2)	7 (1)	16 (2)	4 (0)	20 (2)	7 (1)	16 (2)	4 (0)
	2050	20 (1)	8 (2)	16 (1)	5 (1)	21 (1)	7 (2)	16 (1)	5 (1)	21 (1)	7 (2)	17 (1)	4 (1)	23 (1)	5 (2)	18 (1)	3 (1)
	2080	18 (1)	10 (2)	15 (1)	6 (1)	19 (1)	9 (2)	16 (1)	5 (1)	18 (1)	10 (2)	15 (1)	6 (1)	19 (1)	9 (2)	16 (1)	5 (1)
Latvia	2020	12 (16)	0 (12)	9 (13)	0 (8)	12 (15)	0 (13)	9 (13)	0 (8)	12 (15)	0 (12)	9 (13)	0 (7)	12 (15)	0 (13)	9 (13)	0 (8)
	2050	12 (17)	0 (11)	9 (14)	0 (7)	12 (17)	0 (11)	9 (14)	0 (7)	12 (17)	0 (11)	9 (14)	0 (7)	12 (17)	0 (11)	9 (14)	0 (7)
	2080	10 (14)	2 (14)	7 (12)	2 (9)	11 (14)	1 (14)	8 (12)	1 (9)	11 (15)	1 (13)	8 (12)	1 (9)	11 (15)	1 (13)	8 (13)	1 (8)
Lithuania	2020	12 (12)	1 (0)	9 (9)	1 (0)	12 (12)	1 (0)	9 (9)	1 (0)	12 (12)	1 (0)	9 (9)	1 (0)	12 (12)	1 (0)	9 (9)	1 (0)
	2050	12 (12)	1 (0)	9 (9)	1 (0)	12 (12)	1 (0)	9 (9)	1 (0)	12 (12)	1 (0)	9 (9)	1 (0)	12 (12)	1 (0)	9 (9)	1 (0)
	2080	7 (9)	6 (3)	5 (6)	5 (3)	10 (11)	3 (1)	7 (8)	3 (1)	12 (11)	1 (1)	9 (8)	1 (1)	11 (11)	2 (1)	8 (8)	2 (1)
Luxembourg	2020	15 (12)	4 (1)	9 (9)	3 (1)	15 (12)	4 (1)	9 (9)	3 (1)	15 (12)	4 (1)	9 (9)	3 (1)	15 (12)	4 (1)	9 (9)	3 (1)

Malta	2050	11 (12)	8 (1)	7 (9)	5 (1)	11 (12)	8 (1)	7 (9)	5 (1)	11 (12)	8 (1)	7 (9)	5 (1)	9 (12)	10 (1)	5 (9)	7 (1)
	2080	3 (8)	16 (5)	2 (5)	10 (5)	8 (10)	11 (3)	4 (7)	8 (3)	8 (12)	11 (1)	4 (9)	8 (1)	8 (11)	11 (2)	4 (8)	8 (2)
	2020	2 (15)	0 (4)	1 (9)	0 (3)	2 (15)	0 (4)	1 (9)	0 (3)	2 (15)	0 (4)	1 (9)	0 (3)	2 (15)	0 (4)	1 (9)	0 (3)
Netherlands	2050	2 (11)	0 (8)	1 (7)	0 (5)	2 (11)	0 (8)	1 (7)	0 (5)	2 (11)	0 (8)	1 (7)	0 (5)	2 (9)	0 (10)	1 (5)	0 (7)
	2080	2 (3)	0 (16)	1 (2)	0 (10)	2 (7)	0 (12)	1 (3)	0 (9)	2 (8)	0 (11)	1 (4)	0 (8)	2 (8)	0 (11)	1 (4)	0 (8)
	2020	10 (2)	8 (0)	6 (1)	6 (0)	9 (2)	9 (0)	6 (1)	6 (0)	9 (2)	9 (0)	6 (1)	6 (0)	8 (2)	10 (0)	5 (1)	7 (0)
Poland	2050	8 (2)	10 (0)	5 (1)	7 (0)	8 (2)	10 (0)	5 (1)	7 (0)	8 (2)	10 (0)	5 (1)	7 (0)	8 (2)	10 (0)	5 (1)	7 (0)
	2080	5 (2)	13 (0)	3 (1)	9 (0)	5 (2)	13 (0)	3 (1)	9 (0)	7 (2)	11 (0)	4 (1)	8 (0)	5 (2)	13 (0)	3 (1)	9 (0)
	2020	16 (9)	2 (9)	11 (6)	2 (6)	16 (8)	2 (10)	11 (5)	2 (7)	16 (9)	2 (9)	11 (6)	2 (6)	16 (7)	2 (11)	11 (4)	2 (8)
Portugal	2050	11 (7)	7 (11)	7 (4)	6 (8)	12 (8)	6 (10)	8 (5)	5 (7)	12 (9)	6 (9)	8 (6)	5 (6)	12 (8)	6 (10)	8 (5)	5 (7)
	2080	8 (5)	10 (13)	5 (3)	8 (9)	8 (6)	10 (12)	5 (3)	8 (9)	10 (6)	8 (12)	6 (4)	7 (8)	10 (6)	8 (12)	6 (4)	7 (8)
	2020	5 (15)	14 (3)	4 (10)	8 (3)	6 (15)	13 (3)	4 (10)	8 (3)	7 (15)	12 (3)	5 (10)	7 (3)	7 (15)	12 (3)	5 (10)	7 (3)
Romania	2050	1 (9)	18 (9)	0 (6)	12 (7)	1 (10)	18 (8)	0 (7)	12 (6)	1 (11)	18 (7)	0 (7)	12 (6)	3 (11)	16 (7)	1 (7)	11 (6)
	2080	1 (7)	18 (11)	1 (5)	11 (8)	1 (8)	18 (10)	1 (5)	11 (8)	2 (9)	17 (9)	1 (6)	11 (7)	2 (9)	17 (9)	1 (6)	11 (7)
	2020	11 (5)	7 (14)	6 (3)	7 (9)	11 (4)	7 (15)	6 (2)	7 (10)	11 (6)	7 (13)	6 (4)	7 (8)	11 (6)	7 (13)	6 (4)	7 (8)
Slovakia	2050	13 (2)	5 (17)	11 (1)	2 (11)	13 (2)	5 (17)	11 (1)	2 (11)	14 (2)	4 (17)	11 (1)	2 (11)	14 (3)	4 (16)	11 (1)	2 (11)
	2080	10 (2)	8 (17)	7 (1)	6 (11)	11 (2)	7 (17)	7 (1)	6 (11)	12 (3)	6 (16)	7 (1)	6 (11)	11 (3)	7 (16)	7 (1)	6 (11)
	2020	12 (9)	6 (9)	8 (6)	5 (7)	12 (9)	6 (9)	8 (6)	5 (7)	12 (9)	6 (9)	8 (6)	5 (7)	12 (9)	6 (9)	8 (6)	5 (7)
Slovenia	2050	11 (7)	7 (11)	8 (5)	5 (8)	12 (8)	6 (10)	8 (6)	5 (7)	12 (9)	6 (9)	8 (7)	5 (6)	12 (9)	6 (9)	8 (7)	5 (6)
	2080	8 (7)	10 (11)	6 (5)	7 (8)	9 (8)	9 (10)	6 (6)	7 (7)	11 (8)	7 (10)	7 (6)	6 (7)	10 (8)	8 (10)	6 (6)	7 (7)
	2020	5 (7)	14 (11)	5 (6)	9 (7)	5 (7)	14 (11)	5 (6)	9 (7)	5 (7)	14 (11)	5 (5)	9 (8)	5 (7)	14 (11)	5 (5)	9 (8)
Spain	2050	8 (7)	11 (11)	7 (5)	7 (8)	9 (8)	10 (10)	8 (6)	6 (7)	8 (7)	11 (11)	7 (5)	7 (8)	9 (7)	10 (11)	8 (5)	6 (8)
	2080	6 (6)	13 (12)	5 (5)	9 (8)	6 (6)	13 (12)	5 (5)	9 (8)	5 (8)	14 (10)	5 (6)	9 (7)	5 (9)	14 (9)	5 (6)	9 (7)
	2020	17 (5)	8 (14)	11 (5)	6 (9)	17 (5)	8 (14)	11 (5)	6 (9)	19 (4)	6 (15)	13 (4)	4 (10)	20 (4)	5 (15)	14 (4)	3 (10)
Sweden	2050	6 (7)	19 (12)	4 (6)	13 (8)	8 (7)	17 (12)	6 (6)	11 (8)	7 (7)	18 (12)	5 (6)	12 (8)	9 (7)	16 (12)	7 (6)	10 (8)
	2080	8 (5)	17 (14)	6 (4)	11 (10)	8 (5)	17 (14)	6 (4)	11 (10)	9 (5)	16 (14)	6 (5)	11 (9)	9 (5)	16 (14)	6 (5)	11 (9)
	2020	10 (6)	2 (19)	7 (5)	2 (12)	10 (6)	2 (19)	7 (5)	2 (12)	10 (6)	2 (19)	7 (5)	2 (12)	10 (8)	2 (17)	7 (6)	2 (11)
UK	2050	10 (3)	2 (22)	7 (2)	2 (15)	10 (3)	2 (22)	7 (2)	2 (15)	10 (3)	2 (22)	7 (2)	2 (15)	10 (4)	2 (21)	7 (3)	2 (14)
	2080	8 (5)	4 (20)	6 (3)	3 (14)	8 (6)	4 (19)	6 (4)	3 (13)	10 (7)	2 (18)	7 (5)	2 (12)	10 (7)	2 (18)	7 (5)	2 (12)
	2020	5 (10)	3 (2)	3 (7)	2 (2)	5 (10)	3 (2)	3 (7)	2 (2)	5 (11)	3 (1)	3 (8)	2 (1)	5 (11)	3 (1)	3 (8)	2 (1)
	2050	4 (11)	4 (1)	2 (8)	3 (1)	4 (11)	4 (1)	2 (8)	3 (1)	4 (11)	4 (1)	2 (8)	3 (1)	5 (11)	3 (1)	3 (8)	2 (1)
	2080	3 (7)	5 (5)	1 (5)	4 (4)	4 (8)	4 (4)	2 (6)	3 (3)	4 (10)	4 (2)	2 (7)	3 (2)	4 (10)	4 (2)	2 (7)	3 (2)

		A1FI				A2				B1				B2			
		all species		HD species		all species		HD species		all species		HD species		all species		HD species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Reptiles																	
Austria	2020	10 (10)	3 (3)	6 (6)	1 (1)	10 (10)	3 (3)	6 (6)	1 (1)	10 (10)	3 (3)	6 (6)	1 (1)	10 (10)	3 (3)	6 (6)	1 (1)
	2050	9 (10)	4 (3)	6 (7)	1 (0)	10 (10)	3 (3)	7 (7)	0 (0)	10 (10)	3 (3)	7 (7)	0 (0)	10 (10)	3 (3)	7 (7)	0 (0)
	2080	11 (10)	2 (3)	6 (6)	1 (1)	10 (10)	3 (3)	6 (6)	1 (1)	10 (10)	3 (3)	6 (6)	1 (1)	10 (10)	3 (3)	6 (6)	1 (1)
Belgium	2020	3 (2)	4 (5)	1 (0)	2 (3)	3 (2)	4 (5)	1 (0)	2 (3)	3 (2)	4 (5)	1 (0)	2 (3)	2 (2)	5 (5)	0 (0)	3 (3)
	2050	2 (2)	5 (5)	1 (1)	2 (2)	2 (2)	5 (5)	1 (1)	2 (2)	2 (2)	5 (5)	1 (1)	2 (2)	3 (3)	4 (4)	2 (2)	1 (1)
	2080	3 (3)	4 (4)	1 (1)	2 (2)	3 (2)	4 (5)	1 (1)	2 (2)	2 (2)	5 (5)	1 (1)	2 (2)	3 (2)	4 (5)	1 (1)	2 (2)
Bulgaria	2020	24 (23)	5 (2)	14 (14)	2 (1)	24 (23)	5 (2)	14 (14)	2 (1)	22 (23)	7 (2)	11 (14)	5 (1)	25 (23)	4 (2)	14 (14)	2 (1)
	2050	20 (21)	9 (5)	15 (13)	1 (2)	21 (20)	8 (6)	15 (13)	1 (2)	20 (21)	9 (5)	15 (13)	1 (2)	21 (21)	8 (5)	15 (13)	1 (2)
	2080	24 (22)	5 (4)	14 (13)	2 (2)	24 (22)	5 (4)	14 (13)	2 (2)	24 (22)	5 (4)	14 (13)	2 (2)	24 (22)	5 (4)	14 (13)	2 (2)
Czech Republic	2020	10 (25)	0 (4)	6 (14)	0 (2)	10 (25)	0 (4)	6 (14)	0 (2)	10 (26)	0 (3)	6 (14)	0 (2)	10 (25)	0 (4)	6 (14)	0 (2)
	2050	7 (20)	3 (9)	6 (15)	0 (1)	7 (20)	3 (9)	6 (15)	0 (1)	7 (20)	3 (9)	6 (15)	0 (1)	7 (21)	3 (8)	6 (15)	0 (1)
	2080	7 (24)	3 (5)	5 (14)	1 (2)	7 (24)	3 (5)	5 (14)	1 (2)	8 (24)	2 (5)	6 (14)	0 (2)	8 (24)	2 (5)	6 (14)	0 (2)
Denmark	2020	5 (10)	2 (0)	1 (6)	2 (0)	5 (10)	2 (0)	1 (6)	2 (0)	5 (10)	2 (0)	1 (6)	2 (0)	5 (10)	2 (0)	1 (6)	2 (0)
	2050	6 (6)	1 (4)	3 (5)	0 (1)	6 (7)	1 (3)	3 (6)	0 (0)	6 (7)	1 (3)	3 (6)	0 (0)	6 (7)	1 (3)	3 (6)	0 (0)
	2080	4 (7)	3 (3)	2 (5)	1 (1)	5 (7)	2 (3)	2 (5)	1 (1)	5 (8)	2 (2)	2 (6)	1 (0)	5 (6)	2 (4)	2 (5)	1 (1)
Estonia	2020	5 (6)	0 (1)	2 (2)	0 (1)	5 (6)	0 (1)	2 (2)	0 (1)	5 (6)	0 (1)	2 (2)	0 (1)	5 (6)	0 (1)	2 (2)	0 (1)
	2050	4 (5)	0 (2)	2 (2)	0 (1)	3 (6)	1 (1)	2 (2)	0 (1)	3 (6)	1 (1)	2 (2)	0 (1)	3 (5)	1 (2)	2 (2)	0 (1)
	2080	4 (5)	0 (2)	2 (2)	0 (1)	4 (5)	0 (2)	2 (2)	0 (1)	4 (5)	0 (2)	2 (2)	0 (1)	4 (5)	0 (2)	2 (2)	0 (1)

Finland	2020	2 (4)	2 (1)	1 (2)	0 (0)	2 (5)	2 (0)	1 (2)	0 (0)	2 (4)	2 (1)	1 (2)	0 (0)	2 (5)	2 (0)	1 (2)	0 (0)
	2050	3 (3)	1 (1)	1 (2)	0 (0)	3 (3)	1 (1)	1 (2)	0 (0)	3 (3)	1 (1)	1 (2)	0 (0)	3 (3)	1 (1)	1 (2)	0 (0)
	2080	5 (4)	0 (0)	1 (2)	0 (0)	4 (4)	1 (0)	1 (2)	0 (0)	3 (4)	1 (0)	1 (2)	0 (0)	3 (4)	1 (0)	1 (2)	0 (0)
France	2020	21 (4)	11 (1)	10 (1)	7 (0)	21 (4)	11 (1)	10 (1)	7 (0)	21 (4)	11 (1)	10 (1)	7 (0)	21 (4)	11 (1)	10 (1)	7 (0)
	2050	21 (4)	13 (1)	12 (1)	6 (0)	20 (4)	13 (1)	12 (1)	6 (0)	19 (3)	14 (2)	12 (1)	6 (0)	19 (3)	14 (1)	12 (1)	6 (0)
	2080	21 (4)	14 (1)	11 (1)	8 (0)	21 (4)	13 (1)	11 (1)	7 (0)	21 (4)	13 (1)	11 (1)	7 (0)	21 (4)	13 (1)	11 (1)	7 (0)
Germany	2020	6 (20)	6 (13)	2 (11)	4 (7)	5 (20)	6 (14)	2 (11)	4 (8)	5 (20)	6 (13)	2 (11)	4 (7)	5 (20)	6 (13)	2 (11)	4 (7)
	2050	8 (22)	4 (12)	5 (13)	1 (5)	8 (20)	4 (13)	5 (13)	1 (5)	8 (20)	4 (13)	5 (13)	1 (5)	7 (19)	5 (14)	5 (12)	1 (6)
	2080	8 (20)	4 (15)	5 (10)	1 (9)	8 (21)	4 (14)	5 (11)	1 (8)	9 (21)	3 (14)	5 (11)	1 (8)	8 (21)	4 (14)	5 (11)	1 (8)
Greece	2020	12 (6)	25 (6)	6 (2)	15 (4)	14 (5)	23 (7)	8 (2)	13 (4)	15 (6)	22 (6)	7 (3)	14 (3)	16 (6)	21 (6)	10 (3)	11 (3)
	2050	23 (8)	14 (4)	16 (5)	5 (1)	23 (8)	14 (4)	16 (5)	5 (1)	23 (8)	14 (4)	16 (5)	5 (1)	23 (7)	14 (5)	16 (5)	5 (1)
	2080	27 (8)	10 (4)	16 (5)	5 (1)	27 (8)	10 (4)	17 (5)	4 (1)	27 (9)	10 (3)	16 (5)	5 (1)	26 (8)	11 (4)	17 (5)	4 (1)
Hungary	2020	11 (12)	3 (25)	7 (7)	1 (14)	11 (12)	3 (25)	7 (7)	1 (14)	11 (12)	3 (25)	7 (7)	1 (14)	10 (16)	4 (21)	7 (11)	1 (10)
	2050	9 (22)	5 (15)	7 (16)	1 (5)	9 (22)	5 (15)	7 (16)	1 (5)	10 (22)	4 (15)	7 (16)	1 (5)	10 (22)	4 (15)	7 (16)	1 (5)
	2080	11 (22)	3 (15)	7 (13)	1 (8)	12 (23)	2 (14)	7 (14)	1 (7)	12 (23)	2 (14)	7 (14)	1 (7)	12 (25)	2 (12)	7 (16)	1 (5)
Ireland	2020	2 (11)	0 (3)	1 (7)	0 (1)	2 (11)	0 (3)	1 (7)	0 (1)	2 (11)	0 (3)	1 (7)	0 (1)	2 (11)	0 (3)	1 (7)	0 (1)
	2050	1 (10)	1 (4)	1 (7)	0 (1)	1 (10)	1 (4)	1 (7)	0 (1)	1 (9)	1 (5)	1 (7)	0 (1)	1 (9)	1 (5)	1 (7)	0 (1)
	2080	1 (11)	1 (3)	1 (7)	0 (1)	1 (12)	1 (2)	1 (7)	0 (1)	1 (12)	1 (2)	1 (7)	0 (1)	1 (12)	1 (2)	1 (7)	0 (1)
Italy	2020	26 (2)	14 (0)	14 (1)	9 (0)	26 (2)	14 (0)	14 (1)	9 (0)	28 (2)	12 (0)	14 (1)	9 (0)	27 (2)	13 (0)	14 (1)	9 (0)
	2050	29 (1)	12 (1)	19 (1)	5 (0)	29 (1)	12 (1)	18 (1)	6 (0)	30 (1)	11 (1)	19 (1)	5 (0)	30 (1)	11 (1)	19 (1)	5 (0)
	2080	28 (1)	13 (1)	18 (1)	6 (0)	28 (1)	13 (1)	18 (1)	6 (0)	28 (1)	13 (1)	18 (1)	6 (0)	28 (1)	13 (1)	18 (1)	6 (0)
Latvia	2020	5 (21)	0 (19)	3 (10)	0 (13)	5 (22)	0 (18)	3 (11)	0 (12)	5 (22)	0 (19)	3 (11)	0 (13)	5 (23)	0 (17)	3 (12)	0 (11)
	2050	5 (27)	0 (14)	3 (19)	0 (5)	5 (26)	0 (15)	3 (18)	0 (6)	5 (26)	0 (15)	3 (18)	0 (6)	5 (26)	0 (15)	3 (18)	0 (6)
	2080	4 (26)	1 (15)	3 (16)	0 (8)	5 (26)	0 (15)	3 (16)	0 (8)	5 (25)	0 (16)	3 (15)	0 (9)	5 (26)	0 (15)	3 (16)	0 (8)
Lithuania	2020	5 (6)	0 (0)	3 (3)	0 (0)	5 (6)	0 (0)	3 (3)	0 (0)	5 (6)	0 (0)	3 (3)	0 (0)	5 (6)	0 (0)	3 (3)	0 (0)
	2050	5 (5)	0 (0)	3 (3)	0 (0)	5 (5)	0 (0)	3 (3)	0 (0)	5 (5)	0 (0)	3 (3)	0 (0)	5 (5)	0 (0)	3 (3)	0 (0)
	2080	5 (4)	0 (1)	3 (3)	0 (0)	5 (6)	0 (0)	3 (3)	0 (0)	5 (5)	0 (0)	3 (3)	0 (0)	5 (5)	0 (0)	3 (3)	0 (0)
Luxembourg	2020	5 (5)	3 (0)	2 (3)	1 (0)	5 (5)	3 (0)	2 (3)	1 (0)	4 (5)	3 (0)	2 (3)	1 (0)	4 (6)	3 (0)	2 (3)	1 (0)
	2050	4 (5)	3 (0)	2 (3)	1 (0)	5 (5)	2 (0)	2 (3)	1 (0)	5 (5)	2 (0)	2 (3)	1 (0)	5 (5)	2 (0)	2 (3)	1 (0)
	2080	5 (4)	3 (1)	2 (3)	1 (0)	5 (6)	3 (0)	2 (3)	1 (0)	5 (5)	3 (0)	2 (3)	1 (0)	5 (6)	3 (0)	2 (3)	1 (0)
Malta	2020	8 (5)	0 (3)	3 (2)	0 (1)	8 (5)	0 (3)	3 (2)	0 (1)	8 (5)	0 (3)	3 (2)	0 (1)	8 (5)	0 (3)	3 (2)	0 (1)
	2050	8 (5)	1 (3)	3 (2)	0 (1)	8 (6)	1 (2)	3 (2)	0 (1)	8 (6)	1 (2)	3 (2)	0 (1)	7 (6)	1 (2)	3 (2)	0 (1)
	2080	8 (5)	1 (3)	2 (2)	1 (1)	8 (5)	1 (3)	2 (2)	1 (1)	9 (5)	0 (3)	3 (2)	0 (1)	8 (5)	0 (3)	2 (2)	0 (1)
Netherlands	2020	3 (9)	4 (0)	1 (3)	2 (0)	2 (9)	5 (0)	1 (3)	2 (0)	2 (9)	5 (0)	1 (3)	2 (0)	2 (9)	5 (0)	1 (3)	2 (0)
	2050	3 (8)	4 (1)	2 (3)	1 (0)	3 (8)	4 (1)	2 (3)	1 (0)	3 (8)	4 (1)	2 (3)	1 (0)	3 (8)	4 (1)	2 (3)	1 (0)
	2080	3 (9)	4 (0)	2 (3)	1 (0)	3 (9)	4 (0)	2 (3)	1 (0)	3 (9)	4 (0)	2 (3)	1 (0)	3 (9)	4 (0)	2 (3)	1 (0)
Poland	2020	8 (3)	1 (4)	4 (1)	1 (2)	8 (3)	1 (4)	4 (1)	1 (2)	8 (3)	1 (4)	4 (1)	1 (2)	8 (3)	1 (4)	4 (1)	1 (2)
	2050	8 (3)	2 (4)	6 (2)	0 (1)	7 (3)	2 (4)	6 (2)	0 (1)	7 (3)	3 (4)	6 (2)	0 (1)	7 (3)	3 (4)	6 (2)	0 (1)
	2080	7 (3)	3 (4)	5 (2)	1 (1)	7 (3)	3 (4)	5 (2)	1 (1)	6 (3)	4 (4)	5 (2)	1 (1)	7 (3)	3 (4)	5 (2)	1 (1)
Portugal	2020	10 (8)	18 (1)	7 (4)	8 (1)	9 (8)	19 (1)	7 (4)	8 (1)	11 (8)	17 (1)	8 (4)	7 (1)	12 (8)	16 (1)	8 (4)	7 (1)
	2050	10 (6)	18 (4)	8 (5)	7 (1)	10 (7)	18 (3)	8 (6)	7 (0)	12 (6)	16 (4)	9 (6)	6 (0)	12 (5)	16 (5)	9 (5)	6 (1)
	2080	8 (7)	20 (3)	7 (5)	8 (1)	9 (7)	19 (3)	7 (5)	8 (1)	9 (5)	19 (4)	7 (4)	8 (1)	10 (7)	18 (3)	8 (5)	7 (1)
Romania	2020	19 (10)	3 (18)	12 (7)	1 (8)	19 (10)	3 (18)	12 (7)	1 (8)	19 (10)	3 (18)	12 (7)	1 (8)	19 (10)	3 (18)	12 (7)	1 (8)
	2050	17 (10)	5 (18)	12 (7)	1 (8)	17 (11)	5 (17)	12 (8)	1 (7)	18 (12)	4 (16)	12 (9)	1 (6)	17 (11)	5 (17)	12 (8)	1 (7)
	2080	20 (9)	2 (19)	12 (7)	1 (8)	20 (10)	2 (18)	12 (7)	1 (8)	19 (10)	3 (18)	12 (7)	1 (8)	19 (10)	3 (18)	12 (7)	1 (8)
Slovakia	2020	10 (19)	1 (3)	6 (12)	0 (1)	10 (19)	1 (3)	6 (12)	0 (1)	10 (19)	1 (3)	6 (12)	0 (1)	10 (19)	1 (3)	6 (12)	0 (1)
	2050	8 (17)	3 (5)	5 (12)	1 (1)	8 (17)	3 (5)	5 (12)	1 (1)	8 (17)	3 (5)	5 (12)	1 (1)	7 (17)	4 (5)	5 (12)	1 (1)
	2080	9 (18)	2 (4)	5 (12)	1 (1)	9 (18)	2 (4)	5 (12)	1 (1)	9 (18)	2 (4)	5 (12)	1 (1)	9 (18)	2 (4)	5 (12)	1 (1)
Slovenia	2020	23 (8)	3 (3)	12 (5)	1 (1)	23 (8)	3 (3)	12 (5)	1 (1)	22 (9)	3 (2)	12 (5)	1 (1)	23 (9)	3 (2)	12 (5)	1 (1)
	2050	22 (8)	4 (3)	12 (5)	1 (1)	20 (7)	5 (3)	12 (5)	1 (1)	22 (8)	4 (3)	12 (5)	1 (1)	21 (6)	5 (5)	12 (5)	1 (1)
	2080	23 (8)	3 (3)	12 (5)	1 (1)	23 (9)	3 (2)	12 (5)	1 (1)	23 (9)	3 (2)	12 (5)	1 (1)	23 (9)	3 (2)	12 (5)	1 (1)
Spain	2020	20 (22)	16 (4)	13 (12)	7 (1)	22 (22)	14 (4)	14 (12)	6 (1)	23 (22)	13 (4)	14 (12)	6 (1)	22 (21)	14 (4)	14 (12)	6 (1)
	2050	15 (22)	21 (4)	13 (12)	7 (1)	15 (22)	20 (4)	13 (12)	6 (1)	14 (22)	22 (4)	12 (12)	8 (1)	15 (22)	21 (4)	13 (12)	7 (1)
	2080	17 (22)	19 (4)	14 (12)	6 (1)	18 (22)	18 (4)	15 (12)	5 (1)	20 (22)	16 (4)	16 (12)	4 (1)	21 (22)	15 (4)	16 (12)	4 (1)
Sweden	2020	5 (17)	1 (19)	2 (12)	0 (8)	5 (17)	1 (19)	2 (12)	0 (8)	5 (17)	1 (19)	2 (12)	0 (8)	5 (17)	1 (19)	2 (12)	0 (8)
	2050	5 (15)	1 (21)	2 (13)	0 (7)	5 (15)	1 (21)	2 (13)	0 (7)	5 (15)	1 (21)	2 (13)	0 (7)	5 (15)	1 (21)	2 (13)	0 (7)
	2080	6 (16)	0 (20)	2 (13)	0 (7)	6 (16)	0 (20)	2 (13)	0 (7)	6 (16)	0 (20)	2 (13)	0 (7)	6 (17)	0 (19)	2 (14)	0 (6)
UK	2020	3 (6)	3 (0)	1 (2)	1 (0)	3 (6)	3 (0)	1 (2)	1 (0)	3 (6)	3 (0)	1 (2)	1 (0)	3 (6)	3 (0)	1 (2)	1 (0)

2050	3 (5)	3 (1)	1 (2)	1 (0)	3 (5)	3 (1)	1 (2)	1 (0)	3 (5)	3 (1)	1 (2)	1 (0)	3 (5)	3 (1)	1 (2)	1 (0)
2080	3 (5)	3 (1)	1 (2)	1 (0)	3 (6)	3 (0)	1 (2)	1 (0)	3 (6)	3 (0)	1 (2)	1 (0)	3 (6)	3 (0)	1 (2)	1 (0)

		A1FI				A2				B1				B2			
		all species		HD species		all species		HD species		all species		HD species		all species		HD species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Birds																	
Austria	2020	114 (113)	109 (114)	50 (51)	62 (62)	115 (116)	110 (110)	52 (53)	61 (60)	117 (112)	107 (115)	51 (50)	61 (63)	118 (113)	106 (114)	53 (51)	60 (62)
	2050	130 (129)	96 (98)	64 (65)	48 (48)	134 (128)	91 (98)	67 (65)	45 (48)	132 (130)	93 (97)	64 (64)	48 (49)	131 (129)	95 (98)	63 (63)	49 (50)
	2080	118 (118)	110 (109)	53 (53)	60 (60)	125 (122)	103 (105)	57 (56)	56 (57)	125 (121)	101 (106)	57 (56)	55 (57)	120 (116)	105 (111)	55 (53)	57 (60)
Belgium	2020	59 (58)	121 (124)	23 (23)	61 (61)	57 (51)	122 (133)	22 (20)	62 (64)	57 (51)	123 (131)	21 (20)	63 (64)	56 (48)	123 (136)	20 (18)	63 (66)
	2050	77 (74)	103 (110)	34 (34)	50 (50)	74 (72)	106 (112)	33 (33)	51 (51)	72 (73)	108 (111)	31 (33)	53 (51)	66 (69)	113 (115)	30 (33)	54 (51)
	2080	58 (57)	124 (127)	26 (25)	58 (59)	60 (59)	121 (125)	27 (26)	57 (58)	64 (60)	116 (124)	27 (28)	56 (56)	61 (59)	120 (125)	28 (27)	56 (57)
Bulgaria	2020	119 (115)	125 (128)	57 (56)	58 (59)	122 (118)	123 (126)	60 (59)	55 (56)	114 (114)	131 (130)	54 (55)	61 (60)	119 (116)	125 (128)	57 (55)	58 (60)
	2050	115 (107)	130 (137)	62 (59)	53 (56)	114 (108)	131 (136)	59 (60)	56 (55)	112 (111)	133 (133)	60 (60)	55 (55)	110 (107)	135 (137)	59 (58)	56 (57)
	2080	97 (91)	148 (153)	54 (49)	61 (66)	102 (96)	143 (148)	54 (52)	61 (63)	103 (100)	141 (144)	51 (48)	64 (67)	102 (100)	143 (144)	51 (48)	64 (67)
Czech Republic	2020	108 (101)	108 (117)	53 (49)	56 (62)	109 (98)	107 (120)	53 (48)	56 (63)	104 (98)	110 (120)	52 (47)	56 (64)	106 (98)	109 (120)	53 (47)	56 (64)
	2050	102 (91)	115 (127)	54 (46)	56 (65)	99 (95)	118 (123)	50 (46)	60 (65)	96 (87)	121 (131)	47 (43)	63 (68)	94 (86)	122 (132)	46 (43)	63 (68)
	2080	92 (88)	126 (130)	48 (43)	63 (68)	96 (90)	122 (128)	48 (44)	63 (67)	101 (90)	117 (128)	49 (42)	62 (69)	98 (84)	120 (134)	47 (41)	64 (70)
Denmark	2020	105 (106)	72 (71)	47 (48)	35 (34)	106 (106)	71 (71)	49 (48)	33 (34)	106 (105)	71 (72)	49 (47)	33 (35)	106 (104)	70 (73)	49 (47)	33 (35)
	2050	107 (111)	71 (67)	49 (52)	34 (31)	106 (110)	70 (67)	50 (52)	33 (31)	106 (110)	72 (68)	49 (52)	34 (31)	101 (106)	76 (72)	46 (49)	37 (34)
	2080	65 (72)	113 (106)	23 (27)	60 (56)	76 (77)	102 (101)	30 (31)	53 (52)	78 (79)	99 (99)	32 (32)	51 (51)	77 (78)	101 (100)	31 (32)	52 (51)
Estonia	2020	77 (78)	122 (120)	34 (35)	68 (67)	76 (80)	122 (119)	33 (36)	69 (66)	75 (78)	124 (121)	33 (35)	69 (67)	79 (80)	120 (119)	34 (36)	68 (66)
	2050	93 (95)	106 (104)	39 (41)	63 (61)	93 (95)	106 (104)	39 (41)	63 (61)	90 (96)	109 (103)	37 (42)	65 (60)	95 (96)	104 (103)	40 (41)	62 (61)
	2080	78 (79)	121 (119)	32 (33)	70 (68)	83 (83)	116 (116)	36 (36)	66 (66)	87 (93)	112 (106)	38 (40)	64 (62)	90 (93)	109 (106)	39 (41)	63 (61)
Finland	2020	152 (129)	67 (91)	73 (60)	37 (50)	152 (128)	67 (92)	73 (59)	37 (51)	151 (127)	68 (93)	72 (59)	38 (51)	152 (126)	67 (94)	73 (58)	37 (52)
	2050	141 (119)	78 (101)	65 (55)	45 (55)	140 (119)	79 (101)	65 (55)	45 (55)	139 (122)	80 (98)	64 (55)	46 (55)	138 (120)	81 (100)	63 (55)	47 (55)
	2080	129 (110)	90 (110)	56 (49)	54 (61)	133 (118)	86 (102)	58 (53)	52 (57)	137 (120)	82 (100)	62 (54)	48 (56)	136 (121)	83 (99)	61 (55)	49 (55)
France	2020	79 (79)	174 (175)	34 (38)	90 (87)	81 (78)	172 (177)	35 (37)	89 (88)	78 (71)	174 (183)	32 (33)	92 (92)	77 (71)	176 (184)	32 (33)	92 (92)
	2050	102 (98)	152 (157)	51 (51)	74 (74)	104 (100)	150 (155)	52 (52)	73 (73)	102 (98)	151 (157)	51 (51)	73 (74)	105 (99)	148 (156)	52 (51)	72 (74)
	2080	86 (80)	169 (175)	49 (43)	76 (82)	92 (86)	163 (169)	50 (44)	75 (81)	89 (87)	164 (168)	46 (44)	78 (81)	88 (86)	165 (169)	45 (44)	79 (81)
Germany	2020	84 (77)	146 (154)	40 (34)	72 (79)	79 (74)	150 (157)	37 (33)	75 (80)	81 (76)	148 (155)	39 (34)	73 (79)	79 (76)	150 (155)	37 (34)	75 (79)
	2050	88 (91)	142 (141)	40 (42)	72 (72)	91 (87)	139 (144)	40 (38)	72 (75)	90 (87)	140 (144)	40 (37)	72 (76)	90 (86)	140 (145)	41 (37)	71 (76)
	2080	84 (87)	149 (146)	36 (38)	79 (77)	91 (93)	142 (140)	40 (42)	75 (73)	100 (100)	131 (133)	42 (44)	71 (71)	96 (96)	135 (137)	39 (43)	74 (72)
Greece	2020	84 (67)	155 (173)	42 (38)	74 (78)	82 (70)	157 (170)	42 (39)	74 (77)	82 (67)	157 (173)	40 (36)	76 (80)	85 (71)	154 (168)	43 (40)	73 (76)
	2050	86 (74)	153 (166)	51 (47)	65 (69)	88 (76)	151 (165)	53 (49)	63 (68)	87 (76)	152 (164)	51 (48)	65 (68)	86 (75)	153 (165)	52 (48)	64 (68)
	2080	61 (56)	179 (185)	37 (35)	80 (82)	65 (59)	175 (182)	40 (35)	77 (82)	62 (52)	178 (189)	35 (29)	82 (88)	68 (61)	172 (180)	40 (36)	77 (81)
Hungary	2020	65 (64)	141 (143)	39 (38)	71 (73)	67 (65)	140 (142)	40 (39)	71 (72)	69 (66)	139 (141)	39 (37)	72 (74)	67 (68)	141 (139)	39 (38)	72 (73)
	2050	67 (68)	140 (139)	42 (42)	69 (69)	72 (69)	136 (138)	44 (43)	67 (68)	74 (70)	134 (137)	43 (41)	68 (70)	77 (71)	131 (136)	45 (43)	66 (68)
	2080	57 (57)	151 (150)	34 (34)	77 (77)	62 (61)	146 (146)	38 (38)	73 (73)	66 (69)	142 (138)	39 (41)	72 (70)	68 (70)	140 (137)	39 (40)	72 (71)
Ireland	2020	44 (50)	80 (79)	17 (16)	44 (45)	45 (49)	79 (80)	17 (16)	44 (45)	44 (49)	79 (80)	16 (16)	44 (45)	45 (50)	79 (79)	17 (16)	44 (45)
	2050	49 (50)	77 (79)	16 (15)	45 (46)	50 (50)	76 (79)	17 (15)	44 (46)	48 (50)	78 (79)	15 (15)	46 (46)	47 (50)	79 (79)	14 (15)	47 (46)
	2080	48 (47)	79 (82)	15 (14)	46 (47)	50 (49)	76 (80)	15 (15)	46 (46)	50 (49)	76 (80)	16 (15)	45 (46)	47 (50)	77 (79)	14 (14)	46 (47)
Italy	2020	95 (64)	139 (172)	46 (27)	64 (83)	95 (66)	140 (170)	46 (27)	64 (83)	95 (66)	140 (170)	45 (28)	65 (82)	95 (66)	138 (170)	45 (29)	64 (81)
	2050	87 (68)	149 (168)	45 (35)	65 (75)	90 (71)	145 (165)	48 (38)	61 (72)	88 (68)	148 (168)	46 (35)	64 (75)	88 (70)	148 (166)	46 (37)	64 (73)
	2080	74 (62)	160 (173)	38 (36)	72 (74)	77 (62)	158 (174)	40 (34)	70 (76)	79 (60)	156 (175)	37 (30)	73 (80)	78 (60)	156 (175)	36 (31)	73 (79)
Latvia	2020	80 (83)	118 (116)	37 (36)	67 (69)	81 (83)	116 (116)	37 (36)	66 (69)	84 (84)	114 (115)	38 (37)	66 (68)	85 (83)	112 (115)	38 (36)	65 (68)
	2050	99 (102)	99 (97)	46 (46)	58 (59)	98 (99)	100 (100)	46 (44)	58 (61)	96 (99)	101 (100)	45 (45)	58 (60)	97 (99)	100 (100)	45 (44)	59 (61)
	2080	78 (82)	121 (117)	35 (36)	70 (69)	82 (83)	117 (116)	38 (37)	67 (68)	88 (88)	111 (111)	41 (40)	64 (65)	87 (89)	112 (110)	40 (41)	65 (64)
Lithuania	2020	83 (87)	107 (105)	36 (40)	64 (61)	83 (87)	107 (104)	37 (40)	63 (60)	84 (89)	106 (103)	37 (42)	63 (59)	85 (89)	103 (103)	37 (42)	62 (59)
	2050	68 (66)	123 (126)	32 (31)	68 (70)	70 (68)	121 (124)	33 (31)	67 (70)	69 (68)	122 (124)	33 (32)	67 (69)	68 (66)	123 (126)	32 (30)	68 (71)
	2080	60 (60)	132 (133)	26 (26)	75 (76)	61 (62)	131 (131)	25 (26)	76 (76)	68 (71)	123 (121)	29 (31)	71 (70)	61 (66)	131 (127)	26 (30)	75 (72)
Luxembourg	2020	62 (68)	85 (85)	25 (29)	40 (37)	62 (68)	85 (85)	25 (29)	40 (37)	60 (64)	86 (89)	23 (27)	40 (39)	59 (63)	87 (89)	23 (26)	41 (39)
	2050	84 (87)	62 (67)	34 (35)	28 (31)	85 (88)	63 (66)	36 (37)	28 (29)	82 (85)	64 (67)	34 (35)	29 (30)	74 (78)	72 (76)	31 (32)	34 (34)

Malta	2080	49 (53)	101 (101)	18 (18)	47 (48)	57 (57)	89 (97)	20 (20)	45 (46)	64 (65)	82 (89)	20 (19)	43 (47)	59 (60)	86 (94)	19 (19)	44 (47)
	2020	8 (7)	6 (12)	2 (1)	3 (5)	8 (7)	6 (12)	2 (1)	3 (5)	8 (7)	6 (11)	2 (1)	3 (5)	7 (6)	6 (13)	2 (1)	3 (5)
	2050	10 (11)	7 (8)	4 (4)	3 (3)	10 (11)	7 (8)	4 (4)	3 (3)	10 (12)	7 (7)	4 (4)	3 (3)	10 (12)	7 (8)	4 (4)	3 (3)
	2080	8 (9)	10 (11)	2 (2)	5 (5)	8 (9)	10 (11)	2 (2)	5 (5)	8 (9)	9 (11)	2 (3)	3 (4)	8 (8)	8 (12)	2 (2)	4 (5)
Netherlands	2020	40 (38)	141 (146)	17 (14)	72 (76)	40 (38)	142 (146)	17 (14)	73 (76)	39 (37)	143 (147)	16 (14)	74 (76)	39 (37)	143 (147)	16 (14)	74 (76)
	2050	70 (64)	113 (119)	32 (28)	58 (61)	65 (62)	117 (122)	29 (28)	61 (62)	67 (64)	116 (120)	29 (28)	61 (62)	67 (63)	115 (120)	29 (28)	60 (62)
	2080	60 (60)	124 (124)	28 (28)	62 (62)	61 (63)	122 (121)	28 (29)	62 (61)	61 (61)	122 (123)	25 (25)	65 (65)	61 (63)	121 (121)	28 (28)	62 (62)
	2020	80 (78)	143 (148)	36 (35)	79 (82)	81 (77)	143 (149)	37 (35)	78 (82)	83 (79)	141 (147)	37 (37)	78 (80)	80 (79)	144 (147)	36 (36)	79 (81)
Poland	2050	71 (75)	154 (151)	35 (38)	81 (79)	71 (79)	153 (147)	35 (38)	80 (79)	72 (79)	153 (147)	36 (37)	81 (80)	72 (75)	154 (151)	35 (35)	82 (82)
	2080	73 (71)	153 (156)	33 (34)	85 (84)	79 (78)	147 (149)	36 (35)	81 (83)	79 (86)	147 (141)	35 (40)	82 (78)	82 (85)	145 (142)	38 (39)	80 (79)
	2020	52 (54)	139 (141)	31 (34)	61 (60)	52 (53)	139 (141)	32 (33)	60 (60)	51 (54)	140 (140)	31 (34)	61 (60)	53 (52)	138 (141)	32 (32)	60 (61)
	2050	58 (61)	135 (134)	36 (38)	57 (56)	58 (60)	135 (135)	36 (38)	57 (56)	58 (60)	135 (134)	35 (36)	58 (57)	55 (57)	138 (137)	33 (35)	60 (58)
Portugal	2080	54 (58)	139 (137)	33 (35)	60 (59)	53 (55)	140 (140)	33 (34)	60 (60)	55 (55)	138 (140)	34 (33)	59 (61)	52 (54)	141 (141)	30 (31)	63 (63)
	2020	123 (111)	123 (134)	63 (57)	62 (68)	123 (108)	123 (137)	63 (53)	62 (72)	121 (111)	125 (134)	60 (55)	65 (70)	123 (111)	123 (134)	62 (55)	63 (70)
	2050	100 (85)	146 (160)	55 (48)	70 (77)	104 (86)	142 (159)	57 (48)	68 (77)	105 (82)	141 (163)	55 (45)	70 (80)	103 (84)	142 (161)	55 (47)	69 (78)
	2080	93 (75)	154 (170)	47 (40)	78 (85)	100 (78)	147 (167)	51 (42)	74 (83)	105 (84)	139 (161)	51 (43)	72 (82)	102 (89)	143 (156)	50 (43)	74 (82)
Romania	2020	105 (86)	111 (131)	51 (44)	62 (69)	104 (87)	113 (130)	50 (44)	63 (69)	106 (90)	111 (127)	50 (44)	63 (69)	108 (88)	109 (129)	52 (42)	61 (71)
	2050	93 (83)	124 (134)	51 (46)	62 (67)	94 (85)	123 (132)	52 (48)	61 (65)	91 (81)	126 (136)	50 (44)	63 (69)	90 (81)	127 (136)	50 (45)	63 (68)
	2080	86 (70)	131 (147)	45 (37)	68 (76)	92 (80)	125 (137)	47 (41)	66 (72)	91 (78)	126 (139)	44 (36)	69 (77)	91 (79)	126 (138)	45 (38)	68 (75)
	2020	105 (94)	107 (118)	49 (44)	48 (52)	107 (94)	105 (118)	51 (44)	46 (52)	104 (94)	108 (118)	48 (45)	49 (51)	102 (93)	110 (119)	47 (45)	50 (51)
Slovakia	2050	119 (115)	94 (101)	55 (54)	42 (45)	123 (117)	90 (99)	56 (55)	41 (44)	119 (114)	94 (102)	54 (53)	43 (46)	119 (113)	94 (103)	54 (52)	43 (47)
	2080	101 (96)	114 (120)	46 (45)	52 (54)	110 (103)	104 (113)	50 (48)	48 (51)	111 (102)	103 (113)	49 (47)	49 (51)	113 (104)	101 (110)	49 (49)	49 (49)
	2020	83 (60)	153 (177)	43 (33)	73 (84)	87 (63)	149 (174)	45 (35)	71 (82)	82 (59)	154 (178)	41 (32)	75 (85)	81 (59)	154 (178)	43 (32)	72 (85)
	2050	85 (65)	153 (172)	48 (39)	69 (78)	88 (65)	150 (172)	50 (39)	67 (78)	85 (65)	153 (172)	48 (40)	69 (77)	86 (63)	152 (174)	48 (38)	69 (79)
Spain	2080	71 (58)	167 (179)	40 (34)	77 (83)	76 (60)	161 (177)	45 (35)	72 (82)	76 (59)	161 (178)	43 (35)	74 (82)	76 (61)	162 (176)	41 (36)	76 (81)
	2020	130 (110)	93 (116)	56 (47)	56 (65)	129 (109)	93 (117)	55 (47)	56 (65)	134 (112)	90 (114)	59 (48)	53 (64)	134 (111)	90 (115)	59 (47)	53 (65)
	2050	139 (118)	84 (107)	61 (51)	51 (61)	138 (120)	84 (105)	60 (51)	51 (61)	140 (120)	82 (105)	62 (52)	49 (60)	138 (117)	85 (108)	60 (51)	51 (61)
	2080	123 (102)	103 (124)	51 (44)	62 (69)	128 (109)	98 (117)	54 (46)	59 (67)	137 (117)	88 (109)	59 (52)	53 (61)	135 (113)	90 (113)	57 (50)	55 (63)
Sweden	2020	80 (69)	109 (124)	38 (30)	50 (62)	77 (68)	112 (125)	37 (29)	51 (63)	80 (67)	109 (126)	37 (28)	51 (64)	78 (70)	110 (123)	36 (30)	52 (62)
	2050	89 (76)	102 (117)	37 (30)	53 (62)	87 (75)	103 (117)	37 (30)	53 (61)	86 (74)	106 (118)	35 (29)	56 (62)	88 (75)	104 (118)	36 (30)	55 (62)
	2080	76 (69)	117 (124)	30 (27)	62 (65)	83 (72)	109 (121)	34 (26)	57 (66)	86 (76)	106 (117)	36 (28)	55 (64)	84 (74)	108 (119)	35 (26)	56 (66)

		A1FI				A2				B1				B2			
		all species		HD species		all species		HD species		all species		HD species		all species		HD species	
		win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Mammals																	
Austria	2020	49 (50)	37 (37)	21 (21)	17 (17)	50 (51)	36 (36)	21 (21)	17 (17)	49 (51)	36 (36)	21 (21)	17 (17)	49 (50)	37 (37)	21 (21)	17 (17)
	2050	50 (51)	36 (36)	20 (22)	18 (16)	53 (51)	33 (36)	22 (23)	16 (15)	53 (49)	33 (37)	23 (22)	15 (16)	53 (51)	33 (36)	23 (22)	15 (16)
	2080	44 (42)	42 (45)	18 (16)	20 (22)	51 (47)	35 (40)	22 (19)	16 (19)	55 (48)	31 (39)	23 (21)	15 (17)	53 (49)	33 (38)	22 (21)	16 (17)
Belgium	2020	39 (31)	24 (31)	19 (15)	7 (11)	38 (30)	25 (33)	19 (15)	7 (11)	38 (30)	25 (33)	18 (15)	8 (11)	36 (29)	27 (34)	18 (15)	8 (11)
	2050	26 (23)	37 (40)	9 (9)	17 (17)	29 (25)	34 (38)	10 (10)	16 (16)	29 (25)	34 (38)	10 (10)	16 (16)	26 (21)	37 (42)	10 (9)	16 (17)
	2080	16 (16)	47 (47)	8 (8)	18 (18)	20 (19)	43 (44)	9 (9)	17 (17)	21 (19)	42 (44)	8 (9)	18 (17)	20 (19)	43 (44)	8 (8)	18 (18)
Bulgaria	2020	53 (46)	33 (40)	27 (20)	13 (20)	54 (46)	32 (40)	27 (20)	13 (20)	55 (46)	31 (39)	28 (20)	12 (20)	54 (48)	32 (38)	28 (22)	12 (18)
	2050	40 (33)	46 (53)	22 (18)	18 (22)	40 (35)	46 (51)	21 (18)	19 (22)	43 (36)	43 (50)	23 (18)	17 (22)	45 (35)	41 (51)	23 (18)	17 (22)
	2080	32 (29)	54 (57)	15 (13)	25 (27)	39 (35)	47 (51)	19 (16)	21 (24)	38 (32)	48 (54)	18 (14)	22 (26)	40 (36)	46 (50)	19 (15)	21 (25)
Czech Republic	2020	52 (43)	28 (37)	24 (19)	12 (17)	50 (43)	30 (37)	24 (19)	12 (17)	51 (44)	29 (36)	24 (19)	12 (17)	50 (44)	30 (36)	24 (19)	12 (17)
	2050	44 (36)	36 (44)	21 (17)	15 (19)	43 (39)	37 (41)	22 (18)	14 (18)	41 (38)	39 (42)	20 (18)	16 (18)	41 (39)	39 (41)	21 (19)	15 (17)
	2080	41 (31)	39 (49)	18 (13)	18 (23)	44 (34)	36 (46)	18 (13)	18 (23)	48 (44)	32 (36)	22 (20)	14 (16)	46 (42)	34 (38)	20 (19)	16 (17)
Denmark	2020	36 (39)	17 (14)	13 (14)	6 (5)	37 (39)	16 (14)	14 (14)	5 (5)	36 (39)	17 (14)	13 (14)	6 (5)	36 (39)	16 (14)	13 (14)	5 (5)
	2050	32 (35)	21 (18)	12 (13)	7 (6)	33 (35)	20 (18)	13 (13)	6 (6)	34 (35)	19 (18)	14 (13)	5 (6)	33 (34)	20 (19)	13 (13)	6 (6)
	2080	21 (22)	32 (31)	6 (6)	13 (13)	26 (25)	27 (28)	8 (8)	11 (11)	27 (28)	26 (25)	8 (8)	11 (11)	26 (26)	27 (27)	8 (8)	11 (11)
Estonia	2020	25 (26)	29 (28)	10 (10)	11 (11)	25 (26)	29 (28)	10 (10)	11 (11)	25 (26)	29 (28)	10 (10)	11 (11)	25 (26)	29 (28)	10 (10)	11 (11)
	2050	27 (27)	27 (27)	9 (9)	12 (12)	27 (27)	27 (27)	9 (9)	12 (12)	27 (27)	26 (27)	9 (9)	12 (12)	26 (26)	28 (28)	9 (9)	12 (12)
	2080	20 (20)	34 (34)	7 (7)	14 (14)	22 (21)	32 (33)	8 (8)	13 (13)	22 (24)	32 (30)	8 (8)	13 (13)	22 (22)	32 (32)	8 (8)	13 (13)
Finland	2020	38 (31)	20 (27)	13 (11)	6 (8)	38 (31)	20 (27)	13 (11)	6 (8)	39 (31)	19 (27)	13 (11)	6 (8)	39 (31)	19 (27)	13 (11)	6 (8)

France	2050	38 (30)	20 (28)	12 (11)	7 (8)	38 (31)	20 (27)	12 (11)	7 (8)	37 (31)	21 (27)	12 (11)	7 (8)	37 (31)	21 (27)	12 (11)	7 (8)
	2080	34 (27)	24 (31)	12 (10)	7 (9)	34 (28)	24 (30)	12 (10)	7 (9)	34 (30)	24 (28)	12 (11)	7 (8)	34 (30)	24 (28)	12 (11)	7 (8)
	2020	30 (27)	63 (65)	13 (13)	30 (29)	33 (27)	60 (65)	14 (13)	29 (29)	31 (27)	62 (65)	13 (13)	30 (29)	33 (27)	60 (65)	15 (13)	28 (29)
Germany	2050	26 (21)	66 (71)	15 (12)	27 (30)	26 (22)	66 (70)	15 (12)	27 (30)	24 (23)	68 (69)	14 (13)	28 (29)	25 (24)	67 (68)	14 (13)	28 (29)
	2080	20 (20)	73 (73)	13 (13)	30 (30)	22 (22)	71 (70)	14 (13)	29 (29)	24 (24)	68 (68)	14 (13)	28 (29)	25 (23)	67 (69)	14 (13)	28 (29)
	2020	35 (35)	48 (49)	15 (15)	21 (21)	35 (35)	48 (49)	15 (15)	21 (21)	35 (36)	48 (48)	15 (16)	21 (20)	35 (35)	48 (49)	15 (16)	21 (20)
Greece	2050	31 (31)	52 (53)	12 (11)	24 (25)	30 (30)	52 (54)	12 (11)	24 (25)	29 (29)	53 (55)	12 (11)	24 (25)	30 (28)	53 (56)	12 (11)	24 (25)
	2080	26 (24)	57 (60)	9 (10)	27 (26)	28 (27)	54 (56)	8 (8)	28 (28)	33 (32)	50 (52)	10 (9)	26 (27)	31 (30)	52 (54)	9 (9)	27 (27)
	2020	13 (7)	65 (71)	7 (3)	31 (35)	16 (7)	62 (71)	8 (3)	30 (35)	14 (8)	64 (70)	7 (3)	31 (35)	16 (7)	62 (71)	8 (3)	30 (35)
Hungary	2050	29 (22)	49 (56)	11 (6)	27 (32)	29 (23)	49 (55)	11 (6)	27 (32)	29 (23)	49 (55)	11 (6)	27 (32)	29 (28)	49 (50)	11 (9)	27 (29)
	2080	19 (16)	59 (62)	8 (6)	30 (32)	21 (16)	57 (62)	9 (6)	29 (32)	19 (16)	59 (62)	10 (7)	28 (31)	22 (18)	56 (60)	10 (8)	28 (30)
	2020	28 (24)	57 (61)	10 (6)	30 (33)	28 (24)	56 (61)	10 (6)	30 (33)	28 (25)	57 (60)	10 (7)	30 (32)	29 (26)	56 (59)	10 (7)	30 (32)
Ireland	2050	33 (31)	52 (54)	13 (13)	27 (26)	35 (33)	51 (52)	14 (12)	26 (27)	36 (38)	50 (48)	13 (16)	27 (24)	40 (39)	45 (46)	17 (16)	22 (23)
	2080	26 (26)	60 (59)	11 (11)	29 (28)	30 (29)	56 (56)	12 (13)	28 (26)	36 (36)	50 (50)	15 (16)	25 (24)	37 (37)	49 (49)	16 (16)	24 (24)
	2020	12 (19)	16 (9)	6 (9)	7 (4)	11 (19)	17 (9)	6 (9)	7 (4)	11 (19)	17 (9)	6 (9)	7 (4)	11 (19)	17 (9)	6 (9)	7 (4)
Italy	2050	13 (15)	15 (13)	6 (8)	7 (5)	13 (15)	15 (13)	6 (8)	7 (5)	13 (15)	15 (13)	6 (8)	7 (5)	13 (15)	15 (13)	6 (8)	7 (5)
	2080	10 (11)	18 (17)	4 (5)	9 (8)	11 (12)	17 (16)	5 (6)	8 (7)	13 (14)	15 (14)	6 (7)	7 (6)	12 (14)	16 (14)	6 (7)	7 (6)
	2020	49 (34)	41 (57)	25 (16)	15 (25)	52 (33)	39 (58)	26 (16)	15 (25)	49 (31)	42 (60)	25 (16)	16 (25)	51 (34)	40 (57)	26 (16)	15 (25)
Latvia	2050	40 (26)	51 (65)	20 (12)	21 (29)	40 (26)	51 (65)	19 (11)	22 (30)	39 (26)	52 (65)	20 (12)	21 (29)	44 (28)	47 (63)	22 (12)	19 (29)
	2080	30 (19)	61 (72)	14 (7)	27 (34)	33 (19)	58 (72)	17 (7)	24 (34)	34 (24)	57 (67)	18 (12)	23 (29)	35 (23)	56 (68)	19 (11)	22 (30)
	2020	29 (29)	32 (32)	13 (13)	12 (12)	29 (29)	32 (32)	13 (13)	12 (12)	29 (29)	32 (32)	13 (13)	12 (12)	29 (29)	32 (32)	13 (13)	12 (12)
Lithuania	2050	33 (33)	28 (28)	12 (12)	13 (13)	33 (33)	28 (28)	12 (12)	13 (13)	33 (33)	28 (28)	12 (12)	13 (13)	33 (34)	28 (27)	12 (12)	13 (13)
	2080	24 (24)	37 (37)	10 (10)	15 (15)	23 (23)	38 (38)	10 (10)	15 (15)	28 (24)	33 (37)	11 (10)	14 (15)	25 (24)	36 (37)	11 (10)	14 (15)
	2020	34 (33)	25 (26)	15 (14)	8 (9)	35 (33)	24 (26)	16 (14)	7 (9)	34 (33)	25 (26)	15 (14)	8 (9)	36 (33)	23 (26)	16 (14)	7 (9)
Luxembourg	2050	26 (26)	32 (33)	13 (13)	10 (10)	29 (28)	29 (31)	14 (14)	9 (9)	29 (28)	29 (31)	13 (14)	10 (9)	26 (25)	32 (34)	12 (12)	11 (11)
	2080	19 (20)	40 (39)	7 (8)	16 (15)	21 (21)	38 (38)	8 (8)	15 (15)	21 (22)	37 (37)	8 (9)	15 (14)	22 (21)	37 (38)	8 (8)	15 (15)
	2020	38 (37)	23 (24)	20 (19)	5 (6)	37 (36)	23 (25)	19 (19)	5 (6)	38 (38)	23 (23)	20 (19)	5 (6)	37 (36)	24 (25)	19 (19)	6 (6)
Malta	2050	34 (32)	27 (29)	12 (11)	13 (14)	38 (37)	23 (24)	16 (15)	9 (10)	37 (37)	24 (24)	16 (16)	9 (9)	35 (34)	25 (27)	14 (13)	10 (12)
	2080	17 (17)	44 (44)	8 (8)	17 (17)	22 (22)	39 (39)	9 (9)	16 (16)	28 (27)	33 (34)	10 (9)	15 (16)	27 (26)	34 (35)	9 (9)	16 (16)
	2020	5 (7)	5 (8)	2 (3)	3 (5)	5 (6)	5 (9)	2 (3)	3 (5)	5 (7)	5 (8)	2 (3)	3 (5)	5 (6)	5 (9)	2 (3)	3 (5)
Netherlands	2050	7 (10)	4 (5)	3 (6)	2 (2)	7 (10)	4 (5)	3 (6)	2 (2)	9 (10)	4 (5)	5 (6)	2 (2)	8 (10)	5 (5)	4 (6)	2 (2)
	2080	8 (10)	4 (5)	3 (4)	3 (4)	6 (8)	4 (6)	2 (3)	3 (4)	8 (10)	3 (5)	3 (4)	2 (4)	8 (9)	5 (6)	3 (4)	3 (4)
	2020	18 (19)	42 (41)	10 (10)	15 (15)	19 (19)	41 (41)	11 (10)	14 (15)	19 (19)	41 (41)	11 (10)	14 (15)	19 (19)	41 (41)	11 (10)	14 (15)
Poland	2050	23 (20)	37 (40)	10 (9)	15 (16)	21 (22)	38 (38)	10 (11)	14 (14)	22 (23)	38 (37)	11 (11)	14 (14)	22 (21)	38 (39)	11 (11)	14 (14)
	2080	17 (16)	43 (44)	8 (7)	17 (18)	17 (17)	43 (43)	8 (7)	17 (18)	21 (21)	39 (39)	9 (9)	16 (16)	20 (19)	39 (40)	8 (8)	16 (16)
	2020	44 (43)	36 (37)	23 (23)	13 (13)	45 (44)	35 (36)	23 (24)	13 (12)	46 (45)	34 (35)	24 (24)	12 (12)	46 (44)	34 (36)	24 (24)	12 (12)
Portugal	2050	35 (32)	45 (48)	18 (16)	18 (20)	36 (33)	44 (47)	18 (17)	18 (19)	35 (34)	45 (46)	18 (18)	18 (18)	35 (33)	45 (47)	18 (17)	18 (19)
	2080	27 (25)	53 (55)	14 (12)	22 (24)	30 (26)	50 (54)	15 (14)	21 (22)	34 (31)	46 (49)	17 (16)	19 (20)	32 (30)	48 (50)	17 (16)	19 (20)
	2020	11 (13)	49 (47)	5 (5)	25 (25)	12 (13)	48 (47)	5 (5)	25 (25)	11 (12)	49 (48)	5 (4)	25 (26)	15 (15)	45 (45)	7 (7)	23 (23)
Romania	2050	8 (6)	52 (54)	2 (2)	28 (28)	7 (6)	53 (54)	2 (2)	28 (28)	7 (5)	53 (55)	2 (1)	28 (29)	10 (8)	50 (52)	4 (3)	26 (27)
	2080	8 (7)	52 (53)	4 (4)	26 (26)	8 (8)	52 (52)	4 (4)	26 (26)	6 (7)	54 (53)	3 (3)	27 (27)	6 (8)	54 (52)	3 (4)	27 (26)
	2020	57 (39)	27 (46)	30 (22)	10 (18)	55 (39)	29 (46)	29 (22)	11 (18)	56 (43)	28 (42)	29 (24)	11 (16)	56 (42)	27 (43)	29 (23)	10 (17)
Slovakia	2050	50 (26)	34 (59)	23 (15)	17 (25)	49 (26)	35 (59)	23 (15)	17 (25)	49 (31)	35 (54)	24 (17)	16 (23)	49 (31)	35 (54)	22 (17)	18 (23)
	2080	37 (26)	48 (59)	16 (13)	24 (27)	43 (27)	42 (58)	20 (13)	20 (27)	51 (33)	33 (52)	24 (17)	16 (23)	51 (35)	33 (50)	25 (18)	15 (22)
	2020	53 (44)	37 (47)	23 (16)	15 (23)	53 (42)	37 (48)	23 (16)	15 (23)	54 (45)	36 (46)	23 (16)	16 (23)	56 (45)	35 (46)	24 (16)	15 (23)
Slovenia	2050	49 (33)	42 (58)	21 (16)	18 (23)	51 (34)	40 (57)	23 (16)	16 (23)	49 (37)	41 (54)	21 (17)	17 (22)	51 (38)	40 (53)	23 (17)	16 (22)
	2080	41 (30)	50 (61)	17 (12)	22 (27)	42 (35)	48 (56)	18 (14)	21 (25)	47 (37)	43 (54)	19 (15)	19 (24)	48 (39)	42 (52)	20 (16)	19 (23)
	2020	34 (30)	45 (49)	12 (13)	27 (26)	34 (29)	45 (50)	12 (13)	27 (26)	31 (31)	47 (48)	12 (13)	27 (26)	34 (31)	45 (48)	12 (13)	27 (26)
Spain	2050	40 (32)	39 (47)	16 (14)	23 (25)	42 (34)	37 (45)	17 (15)	22 (24)	40 (33)	39 (46)	15 (13)	24 (26)	39 (32)	40 (47)	15 (13)	24 (26)
	2080	32 (30)	47 (49)	14 (13)	25 (26)	35 (32)	44 (47)	14 (13)	25 (26)	36 (31)	43 (48)	14 (13)	25 (26)	35 (30)	43 (49)	14 (13)	25 (26)
	2020	29 (11)	50 (68)	18 (4)	18 (32)	27 (10)	52 (69)	16 (4)	20 (32)	27 (10)	52 (69)	15 (3)	21 (33)	29 (12)	50 (67)	17 (6)	19 (30)
Sweden	2050	22 (9)	57 (70)	13 (4)	23 (32)	21 (9)	58 (70)	12 (4)	24 (32)	19 (10)	60 (69)	11 (4)	25 (32)	23 (12)	56 (67)	14 (6)	22 (30)
	2080	16 (10)	63 (69)	10 (5)	26 (31)	16 (10)	63 (69)	10 (5)	26 (31)	24 (11)	55 (68)	16 (6)	20 (30)	26 (13)	53 (66)	16 (7)	20 (29)
	2020	40 (36)	24 (28)	18 (17)	8 (9)	40 (36)	24 (28)	18 (17)	8 (9)	40 (36)	24 (28)	18 (17)	8 (9)	40 (36)	24 (28)	18 (17)	8 (9)
UK	2050	44 (39)	20 (25)	19 (18)	7 (8)	44 (40)	20 (24)	19 (18)	7 (8)	44 (41)	20 (23)	19 (18)	7 (8)	44 (39)	20 (25)	19 (18)	7 (8)
	2080	38 (35)	26 (29)	15 (15)	11 (11)	41 (36)	23 (28)	17 (16)	9 (10)	43 (38)	21 (26)	18 (17)	8 (9)	42 (37)	22 (27)	17 (17)	9 (9)
	2020	26 (18)	21 (30)	14 (11)	7 (10)	26 (18)	21 (29)	14 (11)	7 (10)	26 (20)	21 (28)	14 (11)	7 (10)	26 (20)	21 (28)	14 (11)	7 (10)
	2050	23 (20)	25 (28)	11 (10)	10 (11)	24 (20)	23 (28)	12 (10)	8 (11)	24 (20)	24 (28)	12 (10)	9 (11)	24 (20)	24 (28)	12 (10)	9 (11)

		2080	19 (14)	29 (34)	8 (5)	13 (16)	20 (15)	28 (33)	9 (5)	12 (16)	20 (19)	28 (29)	9 (9)	12 (12)	21 (19)	27 (29)	9 (9)	12 (12)
			A1FI				A2				B1				B2			
			all species		HD species		all species		HD species		all species		HD species		all species		HD species	
			win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Plants																		
	2020	338 (312)	316 (348)	6 (8)	8 (7)	337 (310)	318 (350)	6 (8)	8 (7)	333 (306)	323 (353)	6 (8)	8 (7)	337 (302)	319 (358)	6 (8)	8 (7)	
Austria	2050	368 (332)	284 (328)	7 (6)	7 (9)	380 (347)	275 (312)	8 (8)	6 (7)	372 (326)	279 (332)	8 (7)	6 (8)	378 (334)	277 (324)	8 (7)	6 (8)	
	2080	281 (258)	376 (401)	6 (6)	9 (9)	313 (278)	344 (380)	6 (6)	8 (9)	328 (290)	328 (370)	6 (6)	8 (9)	325 (288)	332 (373)	6 (6)	8 (9)	
Belgium	2020	119 (121)	269 (269)	6 (5)	2 (3)	120 (120)	267 (270)	6 (5)	2 (3)	121 (119)	268 (271)	6 (5)	2 (3)	117 (117)	271 (273)	6 (5)	2 (3)	
	2050	133 (135)	257 (256)	7 (7)	1 (1)	131 (132)	259 (259)	7 (7)	1 (1)	129 (130)	260 (261)	7 (7)	1 (1)	127 (122)	263 (269)	6 (6)	1 (2)	
	2080	128 (122)	263 (269)	6 (5)	2 (3)	134 (132)	256 (259)	6 (6)	2 (2)	134 (129)	256 (262)	7 (6)	1 (2)	135 (129)	256 (262)	7 (6)	1 (2)	
Bulgaria	2020	293 (336)	363 (293)	6 (8)	8 (5)	295 (343)	359 (288)	6 (8)	8 (5)	282 (331)	374 (300)	4 (8)	10 (5)	296 (340)	359 (291)	5 (8)	8 (5)	
	2050	259 (335)	397 (296)	5 (9)	9 (4)	266 (345)	391 (285)	5 (9)	9 (4)	269 (333)	388 (297)	4 (9)	10 (4)	280 (335)	378 (296)	5 (9)	9 (4)	
	2080	208 (275)	451 (356)	4 (9)	10 (4)	222 (292)	437 (339)	5 (9)	9 (4)	224 (304)	435 (327)	3 (9)	11 (4)	241 (305)	417 (326)	5 (9)	9 (4)	
Czech Republic	2020	312 (279)	205 (381)	7 (4)	5 (10)	306 (278)	210 (382)	7 (5)	5 (9)	310 (272)	206 (386)	7 (4)	5 (10)	309 (282)	207 (378)	7 (4)	5 (10)	
	2050	284 (231)	234 (429)	8 (4)	4 (10)	290 (234)	226 (426)	8 (4)	4 (10)	293 (234)	222 (425)	8 (4)	4 (10)	288 (241)	228 (418)	8 (4)	4 (10)	
	2080	221 (169)	296 (491)	5 (4)	7 (10)	245 (191)	271 (469)	6 (4)	6 (10)	255 (190)	263 (469)	6 (4)	6 (10)	252 (205)	265 (455)	6 (4)	6 (10)	
Denmark	2020	186 (262)	142 (259)	2 (6)	4 (6)	186 (263)	142 (258)	2 (5)	4 (7)	181 (269)	147 (252)	2 (6)	4 (6)	182 (270)	146 (251)	2 (6)	4 (6)	
	2050	130 (238)	198 (282)	2 (7)	4 (5)	135 (249)	193 (271)	2 (7)	4 (5)	132 (245)	195 (275)	2 (7)	4 (5)	126 (248)	201 (272)	2 (7)	4 (5)	
	2080	83 (201)	245 (320)	2 (6)	4 (6)	87 (218)	240 (302)	2 (6)	4 (6)	94 (238)	233 (283)	1 (6)	5 (6)	90 (229)	237 (292)	1 (6)	5 (6)	
Estonia	2020	207 (188)	106 (139)	3 (2)	2 (4)	204 (185)	109 (142)	3 (2)	2 (4)	205 (185)	109 (143)	3 (2)	2 (4)	206 (185)	108 (143)	3 (2)	2 (4)	
	2050	173 (141)	140 (187)	4 (2)	1 (4)	175 (146)	137 (182)	4 (2)	1 (4)	172 (143)	141 (185)	4 (2)	1 (4)	173 (132)	141 (196)	4 (2)	1 (4)	
	2080	130 (83)	184 (245)	1 (2)	4 (4)	140 (88)	174 (240)	1 (1)	4 (5)	149 (100)	165 (228)	3 (1)	2 (5)	147 (94)	167 (234)	3 (1)	2 (5)	
Finland	2020	243 (216)	86 (98)	5 (3)	1 (2)	241 (213)	88 (101)	5 (3)	1 (2)	237 (211)	93 (103)	5 (3)	1 (2)	237 (212)	92 (102)	5 (3)	1 (2)	
	2050	223 (181)	107 (133)	5 (5)	1 (0)	223 (181)	107 (132)	5 (5)	1 (0)	223 (179)	107 (134)	5 (5)	1 (0)	222 (182)	108 (132)	5 (5)	1 (0)	
	2080	202 (137)	128 (177)	5 (1)	1 (4)	207 (149)	123 (165)	5 (1)	1 (4)	212 (159)	118 (155)	5 (3)	1 (2)	209 (157)	120 (157)	5 (2)	1 (3)	
France	2020	331 (224)	556 (107)	9 (5)	11 (1)	333 (224)	553 (107)	9 (5)	11 (1)	327 (222)	560 (109)	8 (5)	12 (1)	332 (224)	555 (107)	9 (5)	11 (1)	
	2050	298 (196)	586 (135)	7 (5)	13 (1)	295 (196)	589 (135)	8 (5)	12 (1)	294 (195)	591 (136)	8 (5)	12 (1)	292 (195)	592 (136)	8 (5)	12 (1)	
	2080	272 (171)	620 (160)	9 (5)	11 (1)	285 (180)	604 (151)	9 (5)	11 (1)	300 (185)	588 (146)	9 (5)	11 (1)	296 (181)	593 (150)	9 (5)	11 (1)	
Germany	2020	206 (312)	408 (576)	4 (9)	9 (11)	200 (308)	413 (579)	4 (9)	9 (11)	200 (307)	413 (581)	4 (9)	9 (11)	199 (307)	415 (581)	4 (9)	9 (11)	
	2050	193 (281)	422 (607)	5 (9)	8 (11)	190 (280)	425 (607)	5 (9)	8 (11)	192 (275)	422 (612)	5 (9)	8 (11)	196 (279)	418 (608)	5 (9)	8 (11)	
	2080	181 (257)	434 (635)	6 (10)	7 (10)	188 (267)	428 (623)	5 (9)	8 (11)	193 (282)	420 (607)	4 (9)	9 (11)	194 (278)	419 (611)	5 (9)	8 (11)	
Greece	2020	189 (190)	525 (425)	5 (4)	11 (9)	188 (187)	527 (428)	5 (4)	11 (9)	195 (186)	519 (428)	5 (4)	11 (9)	194 (185)	520 (430)	5 (4)	11 (9)	
	2050	261 (185)	458 (431)	8 (5)	8 (8)	267 (186)	453 (430)	8 (5)	8 (8)	257 (184)	463 (432)	7 (5)	9 (8)	267 (185)	451 (431)	7 (5)	9 (8)	
	2080	214 (178)	506 (437)	7 (6)	9 (7)	222 (188)	498 (427)	7 (5)	9 (8)	212 (190)	505 (426)	6 (4)	10 (9)	229 (188)	490 (427)	6 (5)	10 (8)	
Hungary	2020	176 (169)	353 (552)	6 (6)	9 (10)	175 (177)	354 (545)	7 (6)	8 (10)	177 (174)	351 (548)	7 (7)	8 (9)	181 (183)	348 (537)	8 (7)	7 (9)	
	2050	148 (247)	379 (474)	7 (9)	8 (7)	151 (254)	376 (468)	7 (8)	8 (8)	171 (252)	356 (470)	7 (9)	8 (7)	177 (268)	349 (454)	8 (9)	7 (7)	
	2080	104 (207)	425 (515)	4 (7)	11 (9)	113 (206)	415 (516)	5 (7)	10 (9)	142 (202)	384 (520)	5 (6)	10 (10)	145 (210)	382 (512)	5 (6)	9 (10)	
Ireland	2020	99 (155)	177 (374)	3 (6)	1 (9)	99 (158)	178 (371)	3 (6)	1 (9)	98 (166)	179 (363)	3 (6)	1 (9)	98 (177)	179 (352)	3 (7)	1 (8)	
	2050	81 (137)	195 (392)	4 (6)	0 (9)	83 (140)	193 (388)	4 (5)	0 (10)	82 (159)	194 (370)	4 (6)	0 (9)	80 (166)	196 (363)	4 (5)	0 (10)	
	2080	73 (93)	203 (436)	4 (3)	0 (12)	78 (107)	199 (422)	4 (3)	0 (12)	79 (134)	195 (395)	4 (4)	0 (11)	79 (140)	196 (389)	4 (4)	0 (11)	
Italy	2020	488 (112)	434 (165)	12 (3)	10 (1)	490 (112)	433 (164)	12 (3)	10 (1)	478 (110)	443 (167)	12 (3)	10 (1)	489 (111)	432 (166)	13 (3)	9 (1)	
	2050	421 (76)	503 (201)	12 (4)	9 (0)	421 (79)	504 (198)	12 (4)	10 (0)	418 (77)	508 (200)	12 (4)	10 (0)	428 (77)	498 (200)	13 (4)	9 (0)	
	2080	347 (62)	579 (215)	11 (3)	11 (1)	362 (69)	564 (208)	11 (4)	11 (0)	370 (75)	555 (202)	11 (4)	11 (0)	370 (73)	556 (204)	11 (4)	11 (0)	
Latvia	2020	214 (318)	117 (609)	2 (10)	4 (12)	213 (313)	116 (613)	2 (10)	4 (12)	214 (299)	117 (628)	2 (9)	4 (13)	215 (311)	116 (616)	2 (10)	4 (12)	
	2050	189 (276)	141 (651)	3 (10)	3 (12)	192 (278)	138 (649)	3 (10)	3 (12)	185 (273)	145 (654)	3 (10)	3 (12)	189 (287)	141 (640)	3 (10)	3 (12)	
	2080	143 (263)	188 (664)	2 (10)	4 (12)	157 (265)	174 (661)	2 (11)	4 (11)	169 (258)	162 (668)	2 (9)	4 (13)	169 (268)	162 (659)	2 (11)	4 (11)	
Lithuania	2020	224 (211)	110 (120)	2 (2)	4 (4)	222 (212)	112 (119)	2 (2)	5 (4)	222 (212)	113 (119)	2 (2)	5 (4)	222 (213)	113 (118)	2 (2)	5 (4)	
	2050	167 (189)	167 (142)	4 (3)	3 (3)	177 (193)	157 (138)	4 (3)	3 (3)	175 (183)	159 (148)	4 (3)	3 (3)	168 (189)	166 (142)	4 (3)	3 (3)	
	2080	135 (141)	201 (190)	2 (2)	5 (4)	141 (149)	195 (182)	2 (2)	5 (4)	160 (165)	175 (166)	2 (2)	5 (4)	150 (167)	185 (164)	2 (2)	5 (4)	
Luxembourg	2020	137 (220)	190 (117)	2 (2)	3 (5)	133 (222)	194 (115)	2 (2)	4 (5)	135 (220)	194 (117)	2 (2)	4 (5)	132 (220)	193 (117)	2 (2)	4 (5)	
	2050	121 (167)	206 (170)	3 (4)	3 (3)	133 (178)	195 (159)	3 (4)	3 (3)	134 (174)	194 (163)	3 (4)	3 (3)	125 (171)	203 (166)	3 (4)	3 (3)	
	2080	81 (136)	246 (201)	3 (2)	3 (5)	102 (143)	226 (194)	5 (2)	1 (5)	111 (158)	218 (179)	5 (2)	1 (5)	103 (152)	225 (185)	5 (2)	1 (5)	
Malta	2020	98 (141)	41 (188)	2 (3)	1 (3)	100 (133)	40 (195)	2 (2)	1 (4)	99 (134)	39 (194)	2 (2)	1 (4)	95 (134)	40 (194)	2 (3)	1 (3)	

Netherlands	2050	119 (119)	43 (210)	2 (3)	1 (3)	121 (131)	43 (198)	2 (3)	1 (3)	120 (131)	44 (198)	2 (3)	1 (3)	116 (125)	45 (203)	2 (3)	1 (3)
	2080	115 (82)	49 (247)	1 (3)	1 (3)	112 (97)	49 (231)	2 (4)	1 (2)	116 (107)	44 (222)	2 (4)	1 (2)	119 (97)	42 (232)	2 (4)	1 (2)
	2020	104 (125)	251 (56)	4 (3)	2 (1)	103 (124)	252 (55)	4 (3)	2 (1)	102 (125)	252 (55)	4 (3)	2 (1)	99 (123)	255 (56)	4 (3)	2 (1)
Poland	2050	104 (135)	250 (46)	5 (3)	1 (1)	98 (134)	256 (47)	5 (3)	1 (1)	103 (135)	251 (47)	5 (4)	1 (0)	102 (133)	255 (48)	5 (3)	1 (1)
	2080	111 (122)	246 (58)	5 (3)	1 (1)	114 (120)	242 (61)	5 (3)	1 (1)	106 (127)	249 (53)	5 (3)	1 (1)	105 (131)	250 (51)	5 (3)	1 (1)
	2020	264 (98)	263 (260)	4 (5)	8 (1)	263 (98)	264 (260)	4 (5)	8 (1)	270 (99)	258 (259)	4 (5)	8 (1)	267 (98)	260 (260)	4 (5)	8 (1)
Portugal	2050	211 (105)	317 (253)	6 (5)	6 (1)	215 (99)	312 (259)	6 (5)	6 (1)	225 (106)	303 (252)	6 (5)	6 (1)	223 (102)	304 (256)	6 (5)	6 (1)
	2080	202 (112)	327 (246)	5 (5)	7 (1)	212 (111)	316 (247)	5 (5)	7 (1)	227 (107)	299 (251)	5 (5)	7 (1)	223 (106)	306 (252)	5 (5)	7 (1)
	2020	202 (252)	285 (277)	5 (4)	3 (8)	199 (253)	284 (276)	5 (4)	3 (8)	207 (256)	278 (273)	5 (4)	3 (8)	212 (256)	275 (273)	5 (4)	3 (8)
Romania	2050	148 (207)	340 (322)	5 (6)	4 (6)	151 (213)	335 (314)	4 (6)	4 (6)	157 (219)	331 (310)	5 (6)	4 (6)	166 (221)	322 (308)	5 (6)	4 (6)
	2080	157 (191)	334 (338)	5 (5)	4 (7)	158 (206)	332 (323)	5 (5)	4 (7)	164 (226)	324 (303)	5 (5)	4 (7)	170 (217)	319 (312)	5 (5)	4 (7)
	2020	383 (201)	278 (289)	6 (6)	9 (3)	380 (203)	281 (288)	7 (6)	8 (3)	382 (209)	278 (281)	6 (6)	9 (3)	384 (213)	275 (278)	6 (6)	9 (3)
Slovakia	2050	288 (140)	371 (350)	7 (4)	8 (5)	291 (146)	370 (344)	7 (4)	8 (5)	292 (147)	369 (342)	8 (3)	7 (6)	306 (150)	355 (340)	9 (4)	6 (5)
	2080	228 (152)	433 (338)	7 (5)	8 (4)	247 (151)	412 (338)	7 (5)	8 (4)	275 (155)	386 (335)	7 (4)	8 (5)	275 (166)	386 (324)	7 (4)	8 (5)
	2020	324 (330)	237 (331)	7 (7)	6 (8)	324 (325)	237 (336)	7 (7)	6 (8)	327 (335)	234 (326)	7 (7)	6 (8)	328 (340)	234 (321)	7 (7)	6 (8)
Slovenia	2050	277 (210)	286 (452)	8 (6)	5 (9)	281 (212)	282 (450)	8 (6)	5 (9)	289 (221)	271 (441)	8 (7)	5 (8)	287 (225)	276 (437)	8 (7)	5 (8)
	2080	201 (166)	360 (495)	6 (3)	7 (12)	233 (186)	330 (475)	7 (4)	6 (11)	251 (212)	310 (450)	7 (6)	6 (9)	248 (217)	315 (445)	7 (6)	6 (9)
	2020	264 (269)	349 (293)	8 (7)	9 (6)	270 (271)	343 (291)	8 (7)	9 (6)	261 (267)	352 (296)	8 (7)	9 (6)	260 (266)	355 (297)	8 (7)	9 (6)
Spain	2050	329 (240)	287 (323)	11 (6)	6 (7)	335 (244)	281 (318)	12 (6)	5 (7)	326 (252)	290 (310)	11 (6)	6 (7)	324 (246)	292 (316)	11 (6)	6 (7)
	2080	254 (151)	364 (410)	10 (4)	7 (9)	284 (178)	334 (385)	10 (5)	7 (8)	279 (207)	339 (356)	10 (5)	7 (8)	277 (209)	341 (354)	10 (6)	7 (7)
	2020	332 (234)	499 (382)	5 (8)	8 (9)	335 (234)	495 (382)	5 (8)	8 (9)	331 (228)	500 (387)	5 (8)	8 (9)	342 (229)	488 (386)	5 (8)	8 (9)
Sweden	2050	276 (292)	555 (326)	6 (10)	7 (7)	287 (299)	544 (319)	6 (10)	7 (7)	274 (287)	557 (331)	6 (10)	7 (7)	283 (289)	548 (328)	6 (10)	7 (7)
	2080	262 (219)	571 (399)	7 (10)	6 (7)	276 (245)	555 (373)	7 (10)	6 (7)	280 (241)	550 (376)	7 (9)	6 (8)	286 (247)	545 (370)	7 (9)	6 (8)
	2020	278 (259)	147 (573)	5 (4)	4 (9)	279 (259)	147 (573)	5 (4)	4 (9)	281 (263)	146 (569)	5 (5)	4 (8)	282 (268)	146 (564)	5 (5)	4 (8)
UK	2050	267 (217)	160 (614)	6 (5)	3 (8)	269 (212)	159 (619)	6 (5)	3 (8)	272 (219)	154 (613)	7 (5)	2 (8)	265 (221)	160 (610)	6 (5)	3 (8)
	2080	227 (232)	202 (600)	5 (7)	4 (6)	239 (228)	189 (604)	5 (6)	4 (7)	253 (243)	175 (588)	5 (6)	4 (7)	250 (237)	178 (594)	5 (6)	4 (7)
	2020	186 (270)	226 (159)	4 (5)	1 (4)	183 (269)	229 (160)	4 (5)	1 (4)	187 (270)	225 (159)	4 (5)	1 (4)	187 (268)	225 (161)	4 (5)	1 (4)
	2050	172 (247)	240 (181)	4 (6)	1 (3)	178 (247)	233 (181)	4 (6)	1 (3)	177 (249)	234 (180)	4 (7)	1 (2)	174 (248)	237 (181)	4 (6)	1 (3)
	2080	149 (208)	263 (221)	4 (5)	1 (4)	158 (224)	254 (204)	4 (5)	1 (4)	174 (230)	238 (199)	4 (5)	1 (4)	169 (229)	242 (200)	4 (5)	1 (4)

Table S4a – Variability in the numbers of species projected to gain (win) and lose (los) climatic suitability in European protected areas. Values are provided for different combinations of emission scenarios and time periods and using projections made with ensembles from seven bioclimatic modelling techniques and three general circulation models. Results for Red-List species (RL species) and for the complete pool of vertebrate and plant species considered (all). For each year, the winner and loser values in the first line refers to minimum and maximum values projected from the ensemble; second line refers to median value; and third line to standard deviation of values from the ensemble of forecasts.

A1FI				A2				B1				B2				
RL species		all		RL species		all		RL species		all		RL species		all		
win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los	
Amphibians																
2020	2;8	0;6	9;41	1;33	2;8	0;6	8;41	1;34	2;8	0;6	8;41	1;34	2;8	0;6	7;41	1;35
	6	2	30	12	6	2	31	11	6	2	30	12	7	1	32	10
	(2.05)	(2.05)	(8.8)	(8.91)	(2.12)	(2.12)	(9.39)	(9.49)	(1.93)	(1.93)	(9.01)	(9.11)	(1.88)	(1.88)	(9.53)	(9.63)
2050	1;8	0;7	12;41	1;30	1;8	0;7	14;42	0;28	1;8	0;7	11;41	1;31	2;8	0;6	13;42	0;29
	5	3	28	14	5	3	27	15	5	3	28	14	5	3	28	14
	(1.94)	(1.94)	(7.76)	(7.82)	(1.86)	(1.86)	(7.4)	(7.47)	(1.94)	(1.94)	(7.69)	(7.75)	(1.88)	(1.88)	(6.93)	(7.01)
2080	1;8	0;7	9;40	2;33	2;8	0;6	12;41	1;30	1;8	0;7	11;41	1;31	2;8	0;6	16;42	0;26
	4	4	24	18	4	4	24	18	4	4	25	17	4	4	25	17
	(2.18)	(2.18)	(8.41)	(8.54)	(2.13)	(2.13)	(7.84)	(7.95)	(2.16)	(2.16)	(7.45)	(7.56)	(2.09)	(2.09)	(6.95)	(7.09)
Reptiles																
2020	1;7	0;6	35;63	1;29	1;7	0;6	35;63	1;29	1;6	1;6	35;63	1;29	1;6	1;6	34;63	1;30
	5	2	49	15	5	2	50	14	5	2	49	15	5	2	50	14
	(1.53)	(1.53)	(8.87)	(8.87)	(1.51)	(1.51)	(8.39)	(8.39)	(1.66)	(1.66)	(8.81)	(8.81)	(1.47)	(1.47)	(8.48)	(8.48)
2050	2;5	2;5	30;53	11;33	2;5	2;5	31;54	10;33	1;5	2;6	27;55	9;37	2;5	2;5	31;55	9;33
	3	4	44	20	3	4	43	21	3	4	45	19	3	4	42	22
	(0.93)	(0.93)	(6.77)	(6.68)	(0.89)	(0.89)	(6.82)	(6.82)	(1.05)	(1.05)	(7.56)	(7.55)	(0.94)	(0.94)	(6.92)	(6.92)
2080	1;6	1;6	25;57	7;39	1;6	1;6	28;59	5;36	2;6	1;5	30;58	6;34	1;7	0;6	31;60	4;33
	3	4	42	22	3	4	43	21	4	3	45	19	4	3	45	19
	(1.23)	(1.23)	(9.09)	(9.09)	(1.54)	(1.54)	(8.76)	(8.76)	(1.34)	(1.34)	(7.75)	(7.75)	(1.6)	(1.6)	(7.72)	(7.72)
Birds																
2020	4;8	6;9	111;191	134;205	3;8	6;10	112;192	133;204	4;8	6;9	111;192	133;205	3;8	6;10	111;193	132;205
	5	9	144	172	5	9	142	174	5	9	140	179	5	9	143	176
	(1.2)	(0.98)	(25.03)	(23.51)	(1.24)	(1.03)	(24.32)	(22.51)	(1.28)	(1.08)	(25.11)	(23.42)	(1.33)	(1.12)	(25.67)	(23.9)
2050	2;9	5;11	109;206	110;208	2;9	5;11	108;190	132;209	2;9	5;11	103;189	133;214	2;9	5;11	104;193	130;213
	7	7	160	168	7	7	162	165	7	7	157	162	7	7	162	166
	(1.99)	(1.61)	(23.4)	(22.58)	(2.18)	(1.79)	(22.59)	(20.81)	(2.01)	(1.65)	(24.65)	(22.92)	(2.1)	(1.71)	(24.48)	(22.68)
2080	4;8	6;10	121;190	128;213	4;9	5;10	120;204	112;202	3;9	5;11	125;220	96;200	4;9	5;10	124;211	105;202
	6	8	162	164	6	8	163	159	5	8	168	158	5	8	166	159
	(1.38)	(1.24)	(24.33)	(25)	(1.48)	(1.33)	(26.03)	(26.93)	(1.73)	(1.54)	(28.72)	(29.89)	(1.5)	(1.34)	(27.39)	(28.21)
Mammals																
2020	7;13	4;10	54;103	36;84	7;13	4;10	56;103	36;82	6;13	4;11	55;101	38;83	6;13	4;11	55;103	36;83
	9	8	71	68	9	8	72	67	9	8	72	67	9	8	72	67
	(1.98)	(1.98)	(14.85)	(14.96)	(1.93)	(1.93)	(14.64)	(14.73)	(2.14)	(2.14)	(14.65)	(14.74)	(1.83)	(1.83)	(14.73)	(14.79)
2050	5;12	5;12	40;104	35;99	6;12	5;11	43;105	34;96	4;11	6;13	33;102	37;106	6;13	4;11	42;106	33;97
	8	9	73	66	8	9	70 (16.1)	69	8	9	71	68	8	9	70	69
	(1.99)	(1.99)	(17.54)	(17.61)	(1.83)	(1.83)	(16.15)	(16.15)	(2.25)	(2.25)	(19.05)	(19.12)	(2.06)	(2.06)	(17.89)	(17.95)
2080	4;13	4;13	33;102	37;106	5;13	4;12	38;103	36;101	5;13	4;12	35;102	37;104	5;13	4;12	38;102	37;101
	8	9	64	75	9	8	72	66	8	9	73	64	9	8	74	65
	(2.31)	(2.31)	(18.58)	(18.84)	(2.12)	(2.12)	(18.26)	(18.51)	(1.87)	(1.87)	(19.13)	(19.49)	(2.01)	(2.01)	(17.74)	(18.06)
Plants																
2020	0;3	0;3	527;1012	282;778	0;3	0;3	518;1032	262;787	0;3	0;3	514;1030	267;791	0;3	0;3	516;1036	258;789
	1	1	630	675	1	2	635	670	1	2	630	674	1	1	635	670
	(0.85)	(1.03)	(163.62)	(167.86)	(0.86)	(1.03)	(165.28)	(169.45)	(0.83)	(1.03)	(172.47)	(176.39)	(0.86)	(1.03)	(176.56)	(181.13)
2050	0;3	0;3	495;880	417;809	0;3	0;3	493;893	403;812	1;3	0;2	487;878	418;817	0;3	0;3	481;900	396;824
	2	1	658	647	2	1	649	656	2	1	659	646	2	1	654	651
	(0.89)	(1)	(108.5)	(111.16)	(1.04)	(1.14)	(107.95)	(111.03)	(0.81)	(0.92)	(116.19)	(119.33)	(0.96)	(1.05)	(116.5)	(119.79)
2080	0;3	0;3	373;911	386;932	0;3	0;3	445;933	363;860	0;2	0;3	460;916	381;845	0;3	0;3	459;937	359;846
	1	2	521	784	1	2	559	746	1	2	571	734	1	2	566	739
	(0.8)	(0.98)	(149.95)	(154.01)	(0.85)	(1.03)	(140.84)	(144.69)	(0.77)	(1.00)	(151.87)	(155.08)	(0.83)	(1.02)	(144.03)	(147.74)

Table S4b – Variability in the numbers of species projected to gain (win) and lose (los) climatic suitability in the Natura 2000 areas. Values are provided for different combinations of emission scenarios and time periods and using projections made with ensembles from seven bioclimatic modelling techniques and three general circulation models. Results for Habitat-directive species (HD species) and for the complete pool of vertebrate and plant species considered (all). For each year, the winner and loser values in the first line refers to minimum and maximum values projected from the ensemble; second line refers to median value; and third line to standard deviation of values from the ensemble of forecasts.

	A1FI				A2				B1				B2			
	HD species		all		HD species		all		HD species		all		HD species		all	
	win	los	win	los	win	los	win	los	win	los	win	los	win	los	win	los
Amphibians																
2020	7:31	1:25	9:41	1:33	5:31	1:27	7:41	1:35	5:31	1:27	7:41	1:35	6:31	1:26	8:41	1:34
	21	11	28	14	21	11	28	14	21	11	28	14	22	10	28	14
	(6.47)	(6.59)	(8.89)	(9.01)	(6.7)	(6.82)	(9.25)	(9.37)	(6.72)	(6.84)	(9.09)	(9.2)	(6.79)	(6.91)	(9.2)	(9.31)
2050	2:30	2:30	3:40	2:39	2:32	0:30	2:42	0:40	3:29	3:29	3:39	3:39	2:32	0:30	2:42	0:40
	18	14	21	21	18	14	22	20	18	14	23	19	19	13	23	19
	(6.54)	(6.62)	(8.89)	(8.97)	(6.95)	(7.02)	(9.29)	(9.36)	(7.17)	(7.24)	(9.75)	(9.83)	(7.03)	(7.11)	(9.37)	(9.44)
2080	0:30	2:32	0:39	3:42	1:31	1:31	2:41	1:40	5:30	2:27	6:39	3:36	6:32	0:26	7:42	0:35
	14	18	17	25	15	17	18	24	16	16	19	23	17	15	21	21
	(8.07)	(8.16)	(10.83)	(10.93)	(7.65)	(7.75)	(10.43)	(10.53)	(6.8)	(6.9)	(9.56)	(9.66)	(6.33)	(6.42)	(8.97)	(9.08)
Reptiles																
2020	15:35	1:21	25:62	2:39	18:35	1:18	25:62	2:39	14:35	1:22	26:63	1:38	14:35	1:22	26:63	1:38
	22	14	42	22	24	12	42	22	23	13	42	22	25	11	44	20
	(5.96)	(5.81)	(11.36)	(11.28)	(5.52)	(5.39)	(11.21)	(11.15)	(6.24)	(6.15)	(11.76)	(11.72)	(5.8)	(5.67)	(11.01)	(10.94)
2050	4:32	4:32	7:52	12:57	5:32	4:31	8:54	10:56	4:32	4:32	7:54	10:57	5:32	4:31	8:54	10:56
	27	9	40	24	27	9	39	25	27	9	41	23	27	9	40	24
	(8.03)	(8.03)	(13.12)	(13.12)	(8.29)	(8.29)	(13.54)	(13.54)	(8.2)	(8.21)	(13.46)	(13.47)	(8.24)	(8.24)	(13.65)	(13.65)
2080	1:35	1:35	1:57	7:63	2:35	1:34	2:58	6:62	4:35	1:32	8:58	6:56	3:35	1:33	6:58	6:58
	23	13	35	29	24	12	36	28	24	12	38	26	25	11	40	24
	(9.91)	(9.91)	(15.64)	(15.64)	(9.53)	(9.53)	(15.02)	(15.02)	(8.54)	(8.54)	(14)	(14)	(8.96)	(8.96)	(14.24)	(14.24)
Birds																
2020	54:94	72:111	109:190	136:217	56:97	69:109	112:192	134:214	55:97	69:111	110:196	130:214	54:97	69:109	110:195	131:213
	76	87	145	174	76	87	144	176	72	91	143	179	72	91	142	179
	(14.8)	(14.44)	(27.16)	(26.33)	(14.15)	(13.7)	(26.61)	(25.71)	(14.82)	(14.39)	(28.48)	(27.58)	(15.01)	(14.41)	(28.15)	(27.07)
2050	57:96	69:104	109:183	138:210	58:96	69:103	108:184	137:211	57:96	69:104	99:182	139:220	58:97	68:103	100:183	138:219
	73	89	141	180	73	91	143	182	73	92	141	182	71	93	138	186
	(12.28)	(11.09)	(22.18)	(21.1)	(12.43)	(11.12)	(23.3)	(21.87)	(12.55)	(11.28)	(24.97)	(23.54)	(13.07)	(11.86)	(25.45)	(24.03)
2080	47:95	70:114	107:186	140:214	47:96	69:114	112:188	138:210	47:98	67:114	111:190	136:211	46:96	69:115	111:189	137:212
	68	96	128	194	68	93	130	190	78	87	150	175	76	86	143	175
	(16.31)	(15.22)	(26.6)	(25.76)	(15.51)	(14.41)	(25.94)	(24.93)	(16.9)	(16.16)	(27.38)	(26.91)	(16.13)	(15.29)	(26.7)	(25.94)
Mammals																
2020	9:44	5:40	39:97	40:99	9:44	5:40	46:98	39:92	9:44	5:40	43:101	37:95	8:44	5:41	42:101	37:96
	31	19	70	69	31	19	69	70	32	18	71	68	31	19	70	69
	(10.51)	(10.44)	(16.13)	(16.25)	(10.17)	(10.11)	(15.63)	(15.72)	(10.23)	(10.19)	(15.51)	(15.59)	(10.35)	(10.28)	(16.08)	(16.03)
2050	4:43	7:45	29:101	38:109	5:43	7:44	32:100	39:106	3:42	8:46	30:100	39:108	3:45	5:46	38:104	35:99
	22	27	58	81	23	26	55	83	25	24	63	75	26	24	61	77
	(10.27)	(10.09)	(19.52)	(19.35)	(10.2)	(10.09)	(19.6)	(19.45)	(10.57)	(10.43)	(20.45)	(20.25)	(10.28)	(10.12)	(19.17)	(18.96)
2080	3:43	7:46	14:102	37:123	4:43	7:45	24:101	38:114	10:44	6:39	25:103	36:113	8:43	7:41	31:101	38:107
	18	32	43	95	17	32	44	94	20	29	53	86	21	29	52	87
	(10.76)	(10.63)	(23.32)	(23.2)	(10.5)	(10.35)	(21.37)	(21.28)	(9.7)	(9.55)	(21.07)	(21.07)	(9.61)	(9.44)	(20.12)	(20.06)
Plants																
2020	7:24	4:21	471:998	298:833	8:24	4:20	460:1008	289:844	6:25	3:22	453:1002	294:850	6:24	4:22	448:1015	280:856
	13	15	577	727	13	15	575	729	13	15	565	739	13	15	565	739
	(4.92)	(4.86)	(181.34)	(185.13)	(4.82)	(4.76)	(183.85)	(187.64)	(5.15)	(5.08)	(183.91)	(187.79)	(5.13)	(5.07)	(188.67)	(192.67)
2050	3:24	4:25	280:848	449:1024	4:24	4:24	284:860	437:1020	4:24	4:24	271:844	453:1033	4:24	4:24	267:874	423:1037
	15	13	543	762	15	13	554	751	15	13	582	723	15	13	568	737
	(5.84)	(5.83)	(159.47)	(162.35)	(6.04)	(6.03)	(162.21)	(165.06)	(5.88)	(5.88)	(169.36)	(172.39)	(5.75)	(5.72)	(172.1)	(174.93)
2080	0:24	4:28	80:897	400:1224	0:23	5:28	161:901	396:1143	1:24	4:27	246:895	401:1058	0:24	4:28	223:921	376:1081
	10	17	350	949	11	17	408	896	12	16	415	885	12	15	417	886
	(6.32)	(6.27)	(215.55)	(219.22)	(6.28)	(6.23)	(202.28)	(205.94)	(6.18)	(6.15)	(191.94)	(195.83)	(6.04)	(6.02)	(196.48)	(200.28)

Table S5 - Species projected to win and lose climate suitability in (in) and outside (out) protected areas (PA) and Natura 2000 areas RN), for 2020, 2050 and 2080 under different emission scenarios. W stands for projected winners, whereas L stands for projected loser species.

Given the extent of this information and the adopted format (Excel files), these tables can be freely accessed at:
<http://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2011.01610.x/supinfo> within the file: *ELE_1610_sm_tS5.zip*.

CHAPTER VI

Dynamic selection of dispersal pathways for species persistence under climate change

Diogo Alagador, Jorge Orestes Cerdeira, Miguel Bastos Araújo

*"In the end ... success or failure will
come down to an ethical decision, one
on which those now living will be judged
for generations to come."*

E.O. Wilson, 2002

Alagador, D.; Cerdeira, J.O. & Araújo, M.B. 2011. Dynamic selection of dispersal pathways for species persistence under climate change. *Proceedings of the Global Conference on Global Warming 2011*

DYNAMIC SELECTION OF DISPERSAL PATHWAYS FOR SPECIES PERSISTENCE UNDER CLIMATE CHANGE

ABSTRACT

Ongoing climate change is already affecting distributions of many species. Future impacts of climate change are expected to be even greater. Conservation planning methodologies are usually based on the assumption that species distributions change relatively slowly unless they are directly affected by human activities, but this assumption is inappropriate under climate change. To address this problem we develop a model that, assuming a fixed budget limiting the selection of areas devoted to conservation, selects areas for each of different periods of time, and indicates how species disperse between selected areas on successive periods. These areas are termed dispersal pathways. Their effectiveness is assessed based on the performance to retain species suitable climates over time, and on the ability of species to disperse between the areas. The model identifies maximum effective dispersal pathways, limited to some given budget. We applied the model to nine Iberian species and considered four climate change and budgetary scenarios. Climate change scenarios assuming reductions of greenhouse gas emissions had relatively modest gains in species retention areas. But larger budgets for area selection translate in significantly better retention levels. Nevertheless, our model identified species that, regardless the high conservation investment attained with unlimited budget, have a very limited ability to disperse to climatically suitable areas. Connectivity enhancement and assisted colonization could be considered for such cases.

INTRODUCTION

There is an urgent need to assess the impact of climate change on biodiversity (Parmesan & Yohe 2003; Thuiller *et al.* 2011) in order to delineate measures to mitigate the expected negative consequences of such changes (e.g., species' range shifts and consequent loss of species representation within conservation areas) (Hannah *et al.* 2002; Araújo *et al.* 2004; Araújo *et al.* 2011).

Implicit in assessing species range adjustments over time is the requirement that climatically suitable habitats are sufficiently connected through time and that species can disperse to remain in suitable environmental conditions. In such regard, a few modelling attempts have been proposed (Williams *et al.* 2005; Phillips *et al.* 2008; Graham *et al.* 2010) to select a minimum number of areas assuring that a certain number of species populations persist as climate changes. These approaches have been especially dedicated to obtain solutions that achieve predefined conservation targets at minimum cost. A reversed approximation, where conservation targets are maximized for a given cost, can help quantifying the return-on-investment of conservation actions. Under such framework the following questions can be raised: How likely do targeted areas, whose selection is constrained by a given budget, retain species distributions within suitable climates under climate change? To what extent is a given budget sufficient to ensure retention of suitable climates across species distributions? Is species retention at all achievable?

We present a model to identify maximum effective dispersal pathways, subject to a given budget, that permits to addresses these questions. Dispersal pathways are collections of areas selected for each of different time periods, together with a indication on how species disperse between selected areas on successive periods. The model uses the species modelled climatic suitability of each area in different times in the future, and species specific dispersal ability to determine, given some budget that limits the selection of areas, dispersal pathways of maximum effectiveness. Effectiveness is assessed based on the performance of areas to retain species suitable climates over time, and on the ability of species to disperse between the areas. In order to build future dispersal pathways preferentially from areas that are already being targeted for conservation, we penalize the selection of dispersal pathways away from existing protected areas. We thus assign a *cost* to every area, reflecting the unprotected surface area, and consider different budgets to limit area selection. Contrary to other approaches, that whenever an area is selected the corresponding cost is accounted regardless of its (previous and) later use, our model assesses, in each time period, if the conservation investments in the preceded periods are still required to

achieve conservation targets and, if they are not, it deselects areas and transfers resources to other better valued areas.

Here we apply the proposed model in the study of retention levels of nine species with distinct climate tolerances in the Iberian Peninsula, using three global circulation models (CSIRO2, CGCM2 and HadCM3) averaged across two emission scenarios (e.g., A1FI, and B1). The model also explores two assumptions regarding the available budget for conservation (minimum required for non-null effectiveness level for every species, and unlimited budget).

METHODOLOGY

Data

We conducted the analysis for nine Iberian species (Table 1) listed as threatened by the European Habitats Directive (European Council 1992) and/or World Conservation Union (IUCN 2010). Records of presence and absence of species on a UTM 50x50 km grid resolution were obtained from European atlases of vertebrates (Gasc *et al.* 1997; Hagemeijer & Blair 1997; Mitchell-Jones *et al.* 1999) and plants (Jalas & Suominen 1972-1996) (for more details on the data see Williams *et al.* (Williams *et al.* 2000) and Araújo *et al.* (Araújo *et al.* 2011)).

Table 1. Studied species and their taxonomic, conservation and dispersal characteristics.

Species	Common name	Taxa	List ¹	Dispersal ² (km)
<i>Marsilea quadrifolia</i>	Four Leaf Clover	Plant	HD	40
<i>Herniaria lusitanica</i>	Hairy rupturewort	Plant	HD	30
<i>Dianthus cintronus</i>	-	Plant	HD	30
<i>Paeonia officinalis</i>	Common Peony	Plant	HD	20
<i>Pleurodeles waltl</i>	Iberian ribbed newt	Amphibian	RLVS	5
<i>Lacerta schreiberi</i>	Schreiber's lizard	Reptile	RLVS	20
<i>Otis tarda</i>	Great bustard	Bird	RLVS	60
<i>Galemys pyrenaicus</i>	Pyrenean Desman	Mammal	RLVS	30
<i>Mustela lutreola</i>	European Mink	Mammal	RLVS	40

¹ RLVS – Red List of Vertebrate Species; HD – Habitats Directive

² The maximum distance a species disperse in 30 years (Dmax)

We derived four different climate parameters from original monthly-average climate data recorded from 1961-1991 (referred to as 1990) and mapped at a 10' grid cell resolution. The variables were chosen to reflect major drivers of species distributions and include mean temperature of the coldest month, mean annual summed precipitation, mean annual growing degree days and a moisture index. We obtained future projections for the same variables using three global circulation models (CSIRO2, CGCM2 and HadCM3) for the periods of 1991-2020 (referred to as 2020), 2021-2050 (2050), and 2051-2080 (2080), and averaged results across two emission scenarios: A1FI and B1 (Nakicenovic *et al.* 2000: 167).

An ensemble forecasting strategy (Araújo & New 2007) was applied to combine projections from the different bioclimatic models and global circulation models. The climatic suitability, $S(u,sp,t)$, of each grid cell u for each species, sp , was obtained from bioclimatic suitability projections into four time periods, $t \in \{1990,2020,2050,2080\}$, at the resolution of the climate data. To avoid predicting species occurrences in the baseline period (1990) in grid cells where the species were not recorded, we converted all downscaled non-zero climate suitability scores to zero if they coincided with a grid cell where the species has not been recorded.

In order to focus the identification of suitable pathways for species dispersal in areas that are not directly exposed to anthropogenic threats, we used the human footprint index (Sanderson *et al.* 2002) as a measure of human pressure. "Footprint" values range from 0 to 100. Higher values correspond to greater levels of pressure. Here, we assumed that grid cells with a "footprint" above 50 would be unsuitable for the establishment of dispersal pathways for species.

A digital map of Iberian Peninsula protected areas was prepared from the World Database on Protected Areas (IUCN & UNEP 2005). We selected protected areas under the I-VI IUCN management categories and recorded the proportion of each grid cell covered by protected areas. For a more detailed description of the data and the modelling procedures see Araújo *et al.* (Araújo *et al.* 2011).

In order to encourage the selection dispersal pathways within existing protected areas a cost value, $C(u,t)$, was assigned to each grid cell u and time t corresponding to the fraction of the grid cell area not covered by protected areas. Thus, if a grid cell is totally within protected areas, $C(u,t)=0$, for all time periods t .

We assumed for every species a maximum dispersal distance in each time period (Table 1), thus excluding the possibility for long-distance dispersal events. Since the time periods that were considered are of fixed length (30 years), we denote the maximum dispersal distance of species sp simply by $D_{max}(sp)$ (without referring to t). For distances shorter than the maximum dispersal distance, we considered that the species ability to disperse from grid cell u to v , $D(u,v,sp)$, is a function of the Euclidean distance between u and v , $dist(u,v)$:

$$D(u,v,sp) = \begin{cases} \exp(-\alpha \cdot dist(u,v)) & \text{if } dist(u,v) \leq D_{max}(sp) \\ 0 & \text{if } dist(u,v) > D_{max}(sp) \end{cases} \quad (1)$$

We chose α values so that the decay rate of dispersal ability decreases as D_{max} gets larger.

The model

We term dispersal pathway any ordered chain of four grid cells $P=(u,v,w,z)$ that links grid cell u in 1990 to grid cell z in 2080, passing by grid cells v and w in 2020 and 2050, respectively. The effectiveness of dispersal pathways in retaining species, depends on the grid cells' climatic suitability and on the species' ability to move between the grid cells in a given time interval. To measure effectiveness we propose a species retention index for pathway P , which is defined as:

$$R(P,sp) = S(u,sp,1990) \times D(u,v,sp) \times S(v,sp,2020) \times D(w,z,sp) \times S(z,sp,2080) \quad (2)$$

which ranges between 0 and 1. The maximum retention, $R(P,sp)=1$ occurs when species sp remains in the same cell u during all periods and $S(u,sp,t)=1$ (for all time periods t). The minimum retention, $R(P,sp)=0$, occurs if a grid cell in the pathway is unsuitable for the species $S(u,sp,t)=0$, or if the distance between some pair of consecutive grid cells in pathway P exceeds the dispersal capacity of the species, $D_{max}(sp)$.

Two or more dispersal pathways are said to non-overlap (in the same time period) when the grid cells used in the same period are distinct. A solution is a collection of a given number, $k(sp)$, of non-overlapping dispersal pathways for each species sp . The cost of a solution is the sum of the costs of the grid cells used in each period. As we have defined the cost of a grid cell as the fraction not covered by protected areas, the cost of a solution surrogates the amount of allocated resources outside existing protected areas network, counted only during the periods that they are used. The efficiency of a solution increases as more grid cells are used for multiple pathways. Since the pathways required for the same species are non-overlapping, efficient solutions tend to include grid cells for several species during the same time periods.

A solution is feasible if its cost does not exceed a given budget. Our model seeks to find a feasible solution that maximizes the sum of the retention indices across dispersal pathways. Note that optimal solutions for large budgets are likely to be less constrained since a large budget decreases the need for finding sets of pathways that overlap for different species. If there is no budget constraint, an optimal solution can be obtained by maximizing the sum of the retention capabilities of the $k(sp)$ dispersal pathways for each species sp , independently. Optimal solutions retrieve, for a given budget, the best retention opportunities for each species, regarding the number of pathways required for the species. Pathways with low retention values represent areas where species persistence through time is unlikely.

Pathways with high retention values represent areas where species persistence under climate change is more likely.

We designed a mixed integer linear programming formulation for the above model, which fits in the multi-commodity flow setting (Ahuja *et al.* 1993: 649) devised by Philips *et al.* (Phillips *et al.* 2008) for the problem, initially proposed by Williams *et al.* (Williams *et al.* 2005), of finding efficient sets of dispersal pathways for species under climate change. In our model, we define the sum of the retentions indices of the pathways as the objective to be maximized, and we treat efficiency as a constraint bounded by a given budget. In our approach efficiency is evaluated differently than by Philips *et al.* (Phillips *et al.* 2008). While these authors assume that once an area is selected in some time period, its cost is added even if the area is not used in all time periods, our model enables deselecting areas selected in previous time periods, only incorporating costs during the periods they are used. Saved costs from area deselecting are then applied in better-valued areas.

We used CPLEX 11.0 to run the model with the chosen nine species. The climatic suitability of species, $S(u, sp, t)$, were obtained from the distribution projections under the A1FI and B1 scenarios. We required $k(sp)=10$ dispersal pathways for each species and. for each climatic scenario we considered two alternative budgets: (i) minimum budget, i.e., letting the budget to be equal to the minimum value that guarantees the selection of $k(sp)=10$ non-zero retention pathways for each species sp ; and (ii) unlimited budget, i.e., no budget constraint.

RESULTS

The model generates a sequence of areas to acquire (and release) across time that maximizes species retention for a given budget (Fig. 1). Solutions produced for the different emission scenarios overlap extensively (see overlap numbers in Table 2) but, augmenting the budget from the minimum (i.e., only assuring the selection of 10 non-zero retention dispersal pathways per species) to unlimited budget, causes more areas selected, especially along the western regions of Iberian Peninsula (Fig. 1). Indeed, solutions obtained with no budgetary limitations presented twice the number of grid cells when compared with the minimum budget approach. Under this latter scenario the turnover of selected/deselected grid cells is higher and it decreases with time, as the number of selected grid cells (Table 2).

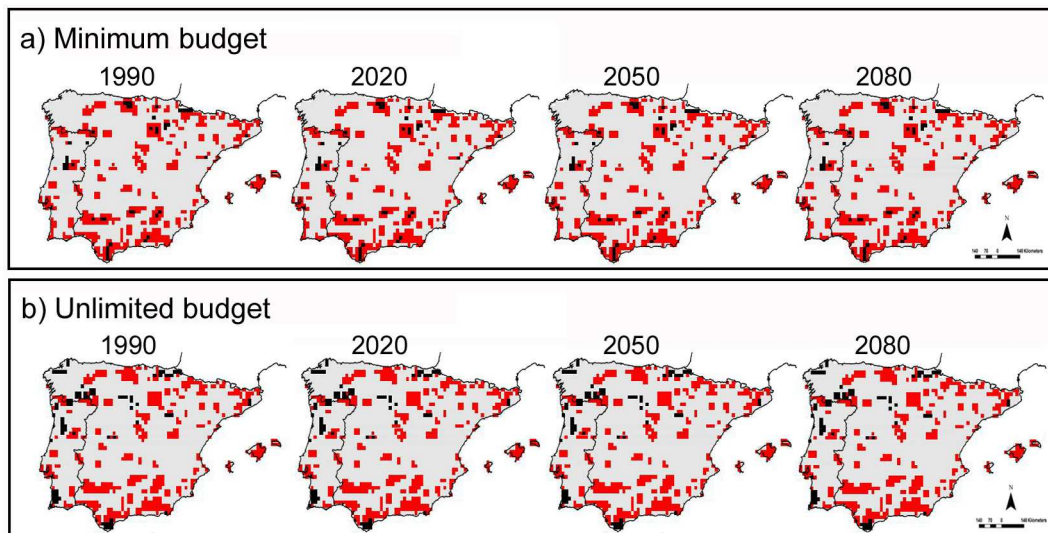


Fig. 1. The selected dispersal pathways (black grid cells) for the retention of nine species in the Iberian Peninsula, under the B1 climate scenario, using **a)** the minimum feasible budget and **b)** unlimited budget. Red grid cells (including more than 1% protected areas coverage) are favored regions for the selection of pathways.

Solutions obtained with no budgetary limitations present twice the number of grid cells when compared with the minimum budget approach. Under the former scenario there are few deselected grid cells across all time periods and the number of selected grid cells maintain constant. Under the latter scenario the

number of deselected grid cells is higher while decreasing with time, like the number of selected grid cells (Table 2).

Although solutions produced under A1FI and B1, using the same budget, are similar in size, average retention success of dispersal pathways for the B1 scenario is higher for all nine species (Fig. 2). Nonetheless, the differences between the two scenarios are less marked when using the minimum budget. For each species, retention indices of the 10 dispersal pathways show important variability, especially under the minimum budget.

Table 2. Number of selected (Sel) and deselected (Desel) grid cells in each time period under two climate scenarios (A1FI and B1). In 1990, the number of deselected grid cells with more than 1% protected area coverage is indicated parenthetically. The spatial agreement of A1FI and B1 solutions is evaluated by the number of grid cells entering both solutions (Overlap).

	1990		2020		2050		2080
	Sel	Desel	Sel	Desel	Sel	Desel	Sel
Minimum budget							
A1FI	46	17(5)	44	8	41	2	39
B1	45	17(5)	43	8	40	2	38
Overlap	45		43		40		37
Unlimited budget							
A1FI	81	0(0)	81	2	81	2	81
B1	80	1(0)	80	3	80	0	80
Overlap	69		69		67		65

Changes in retention are mostly determined from budget availability. The average retention success of pathways increases markedly from minimum to unlimited budget. Major increments are expected for *Lacerta schreberi* (c. 22 times higher) and *Mustela lutreola* (c. 21 times higher), while *Herniaria lusitanica* and *Pleurodeles waltl*, are less favoured (c. 3 times higher) (Fig. 2). However, even with no budgetary limitations, *Marsilea quadrifolia*, and *Mustela lutreola* appear not to be able to track the expected climatic shifts, as their retention indices are close to zero.

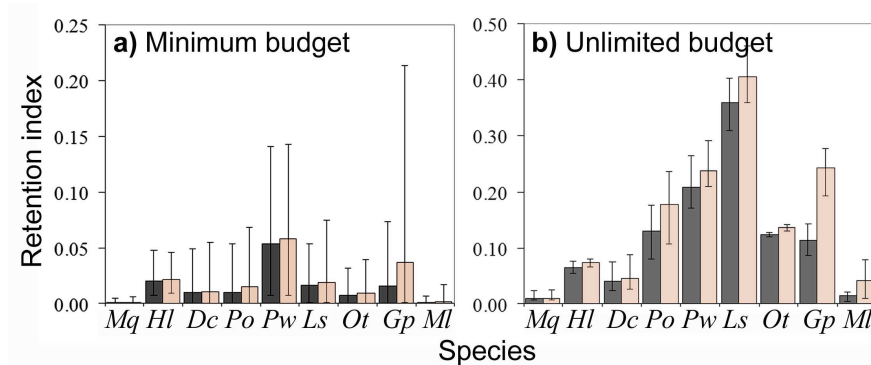


Fig. 2. Average retention of the 10 temporal corridors obtained with the **a)** minimum feasible budget and **b)** with unlimited budget for two climatic scenarios: A1FI (dark grey bars) and B1 (rose bars). Whiskers mark maximum and minimum retention values. Mq: *Marsilea quadrifolia*; Hl: *Herniaria lusitanica*; Dc: *Dianthus cintranus*; Po: *Paeonia officinalis*; Pw: *Pleurodeles waltl*; Ls: *Lacerta schreberi*; Ot: *Otis tarda*; Gp: *Galemys pyrenaicus*; Ml: *Mustela lutreola*.

Adopting the minimum budget approach restricts the potential success of species retention. By favouring grid cells predicted to be reasonable suitable for several species simultaneously, climatic suitability of the selected grid cells is considerably lower than when using unbounded budget (Fig. 3). It should be mentioned that for the majority of species, the average grid cell's suitability with no budgetary constraint is not very different from what occurs if species could disperse freely between every two grid cells (i.e., $D(u,v,sp)=1$ and $Dmax(sp)=+\infty$). An exception is *Marsilea quadrifolia*, for which (the absolute values of)

these differences are significantly increasing with time (Fig. 3). Under the B1 climatic scenario, the climatic suitability for this species is predicted to increase (at least in some regions in Iberian Peninsula), but the species is not able to reach them.

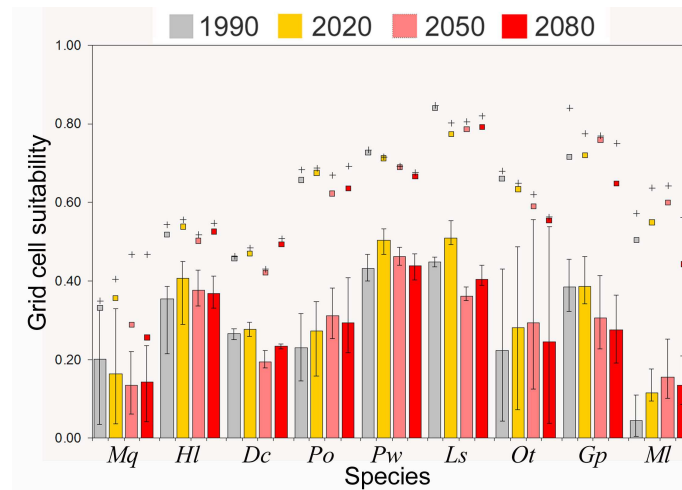


Fig. 3. Average suitability scores of the ten targeted grid cells to be used as dispersal pathways under the B1 climatic scenario, in different time periods. Bars refer to the minimum budget solution (whiskers mark the minimum and maximum scores). Filled squares refer to the unlimited budget solution and crossings refer to universal dispersal, $D_{max}(sp)=+\infty$, with unlimited budget solution. Mq: *Marsilea quadrifolia*; Hl: *Herniaria lusitanica*; Dc: *Dianthus cintronus*; Po: *Paeonia officinalis*; Pw: *Pleurodeles waltl*; Ls: *Lacerta schreberi*; Ot: *Otis tarda*; Gp: *Galemys pyrenaicus*; Ml: *Mustela lutreola*.

DISCUSSION

Spatial conservation planning when based simply on current needs of species risks wasting opportunities for achieving more effective and efficient conservation outcomes (Spring *et al.* 2007; Drechsler *et al.* 2011). This is particularly true under climate change since species will need to move in and out of protected areas in order to track climate suitability. Here, we present a model that anticipates the identification of regions required to facilitate species' range shifts under climate change. The model uses assessments of changes of climatic suitability across space and time and makes assumptions of species' dispersal to determine the location of the candidate areas for the establishment of dispersal pathways. Final outcomes of the model are solutions to maximize species range retention in the future for a given budget. A dynamic mechanism of selection and deselection of areas for species dispersal is explored; the approach implements principles of adaptive management and enables a more efficient allocation of scarce resources for conservation when priorities are bound to change through time and space.

In our implementation of the model, we found that albeit distinct emission scenarios are likely to inflict impacts of varying degrees on species potential distributions, the dispersal pathways required to enable adaptation of the nine species studied, have a significant degree of overlap between the A1FI and B1 scenarios. In other words, with climate changes of different magnitudes, the distribution of the different dispersal pathways does not differ markedly. However, as the two emission scenarios will impose different levels of local suitability, species retention within the selected pathways are likely to differ. For example, our study reports that the average corridor retention index increases c. 2% (for *Marsilea quadrifolia*) to c. 89% (*Mustela lutreola*) when comparing the more severe emission scenario (A1FI; lower values) with the less severe scenario (B1; higher values). Nonetheless, this tendency is veiled by the considerable within-species variation in the retention achieved by different pathways (ex. *Pleurodeles waltl* and *Galemys pyrenaicus* in Fig. 3a), denoting that the persistence of species is mostly dependent on a few critical pathways, to which prioritization should be given.

Our results also demonstrate that, more than reducing greenhouse gas emissions, it is the available budget for area acquisition the main factor determining conservation success (i.e., species retention). The available budget permits to select, in each time period, the areas most climatically suitable for each

species. When budget is reduced the model is forced to select areas capable to support more species but with lower suitability. There are, however, species whose traits (e.g., low climatic tolerance, low dispersal rate) make them unequipped to follow the pace of climate change, even when dispersal pathways are selected with no budgetary constraints. This was the case of *Marsilea quadrifolia* and *Mustela lutreola* (Fig. 2), for which the targeted areas exhibit small retention expectancies. Under situations like these, three conservation mechanisms may rescue the species from regional extinction. First, averting habitat fragmentation and increasing landscape connectivity (e.g., decreasing the human footprint index in our case-study) could increase the chance that species tracks climate suitability as it changes (Opdam & Wascher 2004; Spring *et al.* 2010). Second, increasing carrying capacity and 'in situ' adaptation (e.g., increasing suitability values in our case-study) have been suggested to improve species resilience and recovery to change (Jones & Monaco 2009; Sgrò *et al.* 2010). Third, using assisted colonization, a manipulative mechanism to physically relocate species in locations outside their existing or historical range that are predicted to be favourable for species persistence (Carroll *et al.* 2009; Loss *et al.* 2011). In our analysis this option could be viable for species *Marsilea quadrifolia* and *Mustela lutreola* as suitable climate conditions are predicted to occur in some areas in Iberian Peninsula (Fig. 3). Whether this is worth doing depends on the magnitude of the potential gains for conservation and the required investment (McLachlan *et al.* 2007; Bottrill *et al.* 2008).

Additionally, the model presented here allows to plan (in advance) the areas to be selected as dispersal pathways making possible to avoid unnecessary conflicts with competing land-uses. This anticipative planning allows conservationists to engage society in the efforts to conserve biodiversity while preparing integrative management schemes to maintain the conservation value of the areas to be selected in the future. This requires new on-the-ground conservation instruments including the acquisition of development rights such as logging concessions, agri-environmental schemes and positive or negative incentives to landowners (Araújo 2009: 14; Garcia & Araújo 2010). Conversely, there can be financial gains by trading areas whose conservation status reversed. These gains can be allocated to target better conservation-valued areas. If available, such kind of information can be easily incorporated in the here presented model (Fuller *et al.* 2010; Mascia & Pailler 2011).

Nonetheless, the use of coarse scale predictive data makes this kind of modelling prone to integrate uncertainties. Probabilistic data are the natural way to deal with uncertainties (Colyvan 2008) and can enter directly into our model. Indeed, grid cell climatic suitability values could be directly substituted by probabilities of species occurrences (given the grid cell's climate) and dispersal abilities could be replaced by probabilities of a species to disperse to each grid cell in a given time interval. In such a case the retention index characterizing a pathway would inform on the probability of a species to persist across time if it occurs and disperses through that pathway.

Once identified the coarse-grain dispersal pathways with a model like the one herein proposed, finer-scale assessments based on much refined field data should be performed.

CONCLUSION

The combination of habitat suitability modelling with advanced reserve selection techniques allows the identification of dispersal pathways, which hold great promise for the adaptation of species under climate change. We have presented a spatially conservation prioritization approach that delineates cost-efficient dispersal pathways with the aim of maximizing retention of species ranges under a dynamic scenario of climate change. Unlike previous approaches, where conservation targets are met at minimum cost, our model operates maximizing conservation targets subject to some given cost. The model explicitly integrates an acquisition/ release procedure whereby the possibility of trading-off of areas selected in previous periods by new areas is allowed. This more realistically favors adaptive management schemes and the dynamic reallocation of the scarce resources into new areas as priorities change.

Our findings show that climate change mitigation efforts (reductions of greenhouse gas concentrations) have to be complemented with conservation planning strategies aimed at increasing the retention of species ranges in the landscapes. The approach proposed herein allows researchers and planners alike the identification of cost-effective dispersal pathways for species that enable species to track suitable climates as it changes. The approach is potentially useful to assist conservation prioritization schemes and guide policies aimed at promoting connectivity and assisted colonization under a changing climate.

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CHAPTER VII

Conclusion and outlook

"Equipped with his five senses, man explores the universe around him and calls the adventure Science."

Edwin Powell Hubble, 1954

"Science is the topography of ignorance"

Oliver Wendell Holmes, 1883

7.1 CONCLUSION AND OUTLOOK

Creative approaches at the interface of ecology, statistics, mathematics, informatics, and computational science are essential for improving our understanding of complex ecological systems, and consequently, their protection. For example, mathematics, statistics and computational techniques are emerging as potentially revolutionary tools for studying ecological phenomena. These technologies can play an important role in developing and testing detailed models to support spatially-explicit decisions in conservation planning

This thesis employed mixed-integer programming, graph theory, probability theory and network flows to address three conceptual challenges:

- 1) How to promote spatial coherence of conservation areas accounting for ecological connectivity?;
- 2) How to accommodate specific types of uncertainty in spatial conservation assessments?;
- 3) How to integrate 1) and 2) within a time-changing biodiversity perspective, like the one characterizing climate change impacts, that imposes conservation decisions being predictive and acting proactively?

In the following, it is presented a summarized overview of the research results in the light of these three questions, with possible alternative implementations along with prospects to extend the here presented research.

7.1.1 Spatial coherence for connectivity

In the absence of species specific information, simple rules can be used to assist conservation planners to devise adequate strategies for species persistence. At coarse scales, where global environmental gradients determine biodiversity patterns, general ecological principles may prove profitable for preliminary assessments within Spatial Conservation Planning.

Chapter II follows the study-line of classical reserve design studies. It delivers a spatially-explicit set covering formulation where the location of mandatory areas is used to guide the selection of species-complementary areas ensuring the achievement of species' representation targets. The utility of this approach results from the fact that range-restricted species are natural priorities of spatial conservation assessments. As such, the areas where these species occur are mandatory for their adequate representation. Other scenario, broadening the applicability of the model, emerges when current established protected areas need to be complemented by other areas. In such circumstance, using current protected areas as mandatory, the areas to be selected will be guided by their position. Besides the pure theoretical grounds where this study stands, other limitation of the presented approach concerns the intrinsic complexity of the problem, which makes optimal solutions difficult (or even impossible) to obtain for medium-sized data. Heuristic approaches deserve future attention.

In **chapter III**, it was presented a perspective for spatial arrangements differing from the previous. It starts with fixed patches (e.g., protected areas), where species are considered sufficiently represented and restricts conservation decisions to formally unprotected areas serving as facilitators of species' movements for different patch typologies. The most important achievement of the proposed strategy centres in the way cost-optimization is obtained. Considering that spatial (Euclidean) systems are ruled by the principle of suboptimization (i.e., "the whole is more than the sum of its parts"), the presented framework differs from the common applied "least-cost paths". That is saying that an optimized cost is obtained for the entire network of linkages and not through the sum of optimized pieces derived from multiple pairwise applications of "least cost paths". For the illustrative example reported in **chapter III**, the network of linkages for four climatic protected area types only covered approximately 1% of Iberian Peninsula surface area and 30 to 55% of linkage area were placed within Natura 2000 sites. This gives a

clear message for the importance of Natura 2000 areas to be used as movement paths for the species inhabiting Iberian protected areas.

In this thesis, the typologies of patches, movement suitability values and movement barriers were demonstrated using climatic predictors under the assumption that similar climates support similar pools of species. This is a debatable issue, but served to illustrate one out of a variety of applications the framework has the potential to deal with. Indeed, this framework has the potential to integrate any type of data considered to be relevant for patch classification and for delivering suitability surfaces for each patch type where linkages are to be optimized. Moreover, besides operating with environmental surrogate data, the framework may employ occurrence data for a small set of species with metapopulation structure. This would allow that (if affordable) each population of a species be linked with all the others populations of that species, using suitable areas for the species to move (e.g., obtained through predictive species distribution models or resource selection models).

For the cases where patches are considered fixed through time (e.g., protected areas) there is the opportunity to upgrade the proposed framework to respond to dynamic scenarios as the ones derived from climate change,

7.1.2 Uncertain species' distributions

An important component of decision-analytic approaches is the recognition and treatment of uncertainty. This thesis has dealt mainly with uncertainty concerning species' distributions (and suitable areas) across space (**chapters IV-VI**) and time (**chapter V and VI**). In **chapters IV-VI** algebraic operations were used to combine grid cell-scaled probabilities of species occurrence (or suitability) into a global (averaged) measure of species (suitable areas) range extent (**chapters V and VI**) and species (suitable areas) representation within protected areas (**chapters IV and V**). However, given the inherent data complexity derived from correlative models, this thesis did not afford to explicitly operate with local (grid cell's) stochastic variability of probabilistic predictions for species' occurrences (or suitability indices). Indeed, as species' distributions are characterized by spatial autocorrelation, the way non-independent predictions are integrated to retrieve a confidence interval respecting species' (suitable areas) range extent (globally and within protected areas) is not straightforward to develop, although there are several modelling strategies explicitly designed to account for spatial autocorrelation (e.g., Segurado *et al.* 2006). Therefore, how to combine non-independent data to derive an overall picture of the variability encompassing predictions of species' range (suitable areas) extent may be a relevant theoretical task to explore.

In parallel, future research investments should look to reduce uncertainty. This may require an integrated effort to improve sampling strategies and apply reliable predictive tools where dispersal, biotic interactions and land-cover complement climatic factors in determining more precise species' distributions. Because such responses are species-specific and because such data are hard and expensive to get functional groups of species with similar "ecologies" may be a relevant unit to focus conservation on.

There is also the opportunity to analyse in what levels some management type (e.g., formal protection) favour or disfavour the occurrence of species. Well designed null models may enable such information to be obtained (e.g., Joppa & Pfaff 2011) and contribute for fine-tune broad-scale gap analysis (e.g., **chapter IV**).

7.1.3 Spatio-temporal assessments and climate change

Once researchers recognize the fundamentally dynamic nature of spatial conservation planning, some important new considerations emerge. For example, it is important to assess in what degree past investments in protected area designation translates into adequate species representation across time. As found in **chapter V**, two European conservation area systems are expected to remain relevant conservation tools as climate changes, provided that new areas are added to help counter the reduction of suitable climate space for several listed species. Additional areas, properly sized and placed, can compensate for the loss of suitable climates within European conservation areas expected under distinct socioeconomic storylines. Future attention of European conservation planners should be on the

identification of such areas. **Chapter VI** presents a network flow approach responding to these demands and goes a step further with the recognition that a more dynamic land purchase system may render investments more effective. This is a challenging issue and may constitute a specific research topic in the future (e.g., Fuller *et al.* 2010; Mascia & Pailler 2011). In parallel, queuing theory and dynamic programming have the potential to support analysis verifying the impacts that postponing a decision or advancing a decision (e.g., area acquisition, area release) present over species' retention success and over total conservation expenditures.

Once the important areas assisting spatial adjustments of species ranges have been identified subsequent advances should permit to analyse which management schemes, from a set of possible conservation actions (e.g., habitat restoration, control of invasive species, predator control, disturbance regulation, monitoring, etc.), deliver the major species' retention achievements while being robust to a set of possible future scenarios. New research is revealing innovative approaches to systematically planning multiple actions for multiple species (James *et al.* 2001; Wilson *et al.* 2007) and new versions of custom-made software (e.g., *Marxan with Zones*, *Zonation*: version 3) already enable introducing this analysis.

Given data scarcity and software limitations in handling large datasets, most predictions of species suitable climates in the future are made for a small number of periods. Consequently, the obtained trajectories of species range adjustments are discrete with lengthy information lags in-between predictions. Future implementations should look to obtain time-resolute climatic data to be used as predictors of species' distributions.

7.2 EPISTEMOLOGIC PROSPECT

Biodiversity conservation constitutes a difficult task since it is influenced by a multitude of complex relationships (political, cultural, and economic), by the difficulty to reflect economic gains and by the inherent neutrality that society considers conservation. Immediate actions are needed before opportunities fade away and these should be supported by the best possible science, in order to use the paucity of financial resources for the most conservation valuation.

The examples given in this thesis show how imaginative approaches at the interface of ecology, statistics, mathematics, informatics, and computational science can be used within decision support tools in conservation planning. Significant progress has been made, but further advances will demand shifting the way that society approach research and education. Research institutions and funding agencies must invest more resources in developing and sustaining cross disciplinary research collaborations to generate more generally applicable research. Educational institutions need to invest in programs that provide biologists with robust quantitative and informational skills, and that provide computer scientists, mathematicians, and statisticians with biological expertise. The combination of mathematical and computational advances, sophisticated informatics technologies, and synergistic ties across disciplines may well lead to the most fundamental advances in biodiversity conservation.

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