

1 This paper was published in the journal Basic and Applied Ecology.

2 Pedro Pinho, Joan Casanelles-Abella, Ana Catarina Luz, Anna Maria Kubicka, Cristina
3 Branquinho, Lauri Laanisto, Lena Neuenkamp, Marta Alós Ortí, Martin K. Obrist, Nicolas
4 Deguines, Piotr Tryjanowski, Roeland Samson, Ülo Niinemets, Marco Moretti,
5 2021. Research agenda on biodiversity and ecosystem functions and services in European
6 cities, Basic and Applied Ecology, <https://doi.org/10.1016/j.baae.2021.02.014>

7

8 <https://www.sciencedirect.com/science/article/pii/S1439179121000402>

9 PERSPECTIVE

10 **Title:**

11 **Research agenda on biodiversity and ecosystem functions and services in European cities**

12

13 **Keywords**

14 citizen science; habitat mapping; multiple environmental gradients; neglected habitats and niches;
15 species traits; urban ecology;

16

17 **Authors**

18 Pedro Pinho ^{a*}, Joan Casanelles-Abella ^{b,c}, Ana Catarina Luz ^d, Anna Maria Kubicka ^e, Cristina
19 Branquinho ^a, Lauri Laanisto ^f, Lena Neuenkamp ^g, Marta Alós Ortí ^e, Martin K. Obrist ^b, Nicolas
20 Deguines ^h, Piotr Tryjanowski ^d, Roeland Samson ⁱ, Ülo Niinemets ^{f,j}, Marco Moretti ^b

21

22 **Affiliations**

23 ^a Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de
24 Lisboa, Lisbon, Portugal

25 ^b Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow and Landscape
26 Research WSL, Birmensdorf, Switzerland

27 ^c Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland

28 ^d ISEG – Lisbon School of Economics & Management, Universidade de Lisboa, Portugal

29 ^e Institute of Zoology, Poznań University of Life Sciences, Poznan, Poland

30 ^f Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu,
31 Estonia

32 ^g Institute of Plant Science, University of Bern, Bern, Switzerland

33 ^h Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France.

34 ⁱ Laboratory of Environmental and Urban Ecology, University of Antwerp, Antwerp, Belgium

35 ^j Estonian Academy of Sciences, Tallinn, Estonia

36

37 ***Corresponding author. Pedro Pinho, Tel.: +351217500000.**

38 **E-mail address: ppinho@fc.ul.pt**

39

40

Abstract

Cities are challenging environments for human life, because of multiple environmental issues driven by urbanization. These can sometimes be mitigated through ecosystem services provided by different functions supported by biodiversity. However, biodiversity in cities is affected by numerous factors, namely habitat loss, degradation, and fragmentation, as well as pollution, altered climate, and new biotic challenges. To better understand the link between biodiversity and ecosystem functions and services, we need to improve our mechanistic knowledge of these relationships. Trait-based ecology is a promising approach for unravelling the causes and consequences of biodiversity filtering on ecosystem processes and underlying services, but large gaps remain unexplored.

Here, we present a series of research directions that are aimed at extending the current knowledge of the relationship between trait-based biodiversity and ecosystem functions and services in cities. These directions are based on: (1) improving urban habitat mapping; (2) considering often neglected urban habitats and ecological niches; (3) integrating multiple urban gradients; (4) using trait-based approaches to improve our mechanistic understanding of the relationships between biodiversity and ecosystem functions and services; and (5) extending the involvement of citizens.

Pursuing these research directions may support the sustainable management of urban ecosystems and the long-term provision of ecosystem services, ultimately enhancing the well-being of urban populations.

Introduction

Humans and their activities have been transforming the Earth and its ecosystems in multiple ways, including alterations of the landscape, disturbance regimes, species distributions and interactions (Boivin et al. 2016). Urbanization is one such global trend within the Anthropocene, impacting people, biodiversity and consequently ecosystem functions (EF) and services (ES).

Cities are socio-ecological systems mostly dominated by the grey infrastructure (built-up area, including buildings and roads) and the green and blue infrastructure, which include all natural, semi-natural and artificial (i.e. entirely human-made) habitats within a city, such as parks, rivers and green-roofs. Despite their socio-economic benefits, urban areas are a challenging environment for city-dwellers (Engemann et al. 2019). For instance, cities typically have higher temperatures and more air pollution than rural areas (Munzi et al. 2014). To mitigate these urban problems, cities can rely on a mixture of technological and nature-based solutions to provide key services , including climate and water regulation, noise reduction, air filtration and recreational and aesthetic value (Diaz et al. 2018; IPBES 2019; Capotorti et al. 2019). Recently, the added value of green spaces to ameliorate the multiple negative impacts of pandemic situations (such as the CoVid-19) on human well-being is being heightened by a sharp increase in visitation to such green areas (Grima et al., 2020). Nature-based solutions are intended to benefit both people and nature, with the added advantage of promoting biodiversity and fostering cities as socio-ecologically resilient systems (Elmqvist et al. 2019).

Biodiversity faces multiple challenges in cities, including habitat fragmentation and high spatio-temporal disturbances when compared to non-urban areas. Changes in biodiversity and species composition due to these stressors often cascade down to shifts in EF and ES provisioning, including the potential loss of key ES (e.g., Tresch et al. 2019b). These stressors can also impact species composition with knock-on effects on ES provisioning due to species-specific responses depending on species traits, for example causing a decline in pollination service (measured by flower visitation) through favouring Hymenoptera in cities compared to Diptera and Lepidoptera (Theodorou et al.

2020). The need for ES provisioning differs across cities, depending on cultural, political, socio-economical, and historical aspects, as well as topographic, climatic, and geological conditions (Ossola et al. 2019). Nonetheless, biodiversity is universally shaped by a set of factors that filter the regional species pool and select for adapted species that might result in functionally similar species assemblages (Fournier et al. 2020). In this regard, research approaches based on traits, i.e. phenotypic features of organisms that affect their fitness (Violle et al. 2007), have been proposed. Still, the relative contribution of different components of biodiversity and the mechanisms behind the provision of ES remains understudied (Schwarz et al. 2017). Moreover, studies about urban ecology, as in other fields of ecology (Meyer et al. 2016), have some major spatial and taxonomic biases. Many studies can only cover a subset of the existing ecological components (e.g. through targeting specific habitats or times of the day) and taxonomic groups, ultimately limiting the knowledge on the relationship between biodiversity and EF.

Since cities are socio-ecological systems driven by human perceptions and needs, citizen science programs can provide important contributions to biodiversity data and promote awareness among city residents. Citizen science programs could ultimately help fill gaps in the knowledge of species' distributions and their relationships to ES in cities (Serret et al. 2019). To overcome these knowledge gaps a comprehensive overview on trait-based biodiversity EF and ES research in cities is needed as a solid basis for future research agendas including academic and citizen sciences approaches. Building on extensive literature research focussed on the relationships between biodiversity, EF and ES provision, and on the questions raised during the development of the European research project BioVeins (Connectivity of green and blue infrastructures: living veins for biodiverse and healthy cities, BiodivERsA3201510), we identified multiple knowledge gaps for biodiversity, EF and ES research in cities. Acknowledging that these gaps could be tackled using an approach based on the quantification of EF and ES and their relationships with biodiversity, and with the ultimate objective of promoting resilient cities, we present a series of research directions that point towards: (1) improving urban habitat mapping; (2) considering neglected urban habitats and ecological niches; (3) integrating

multiple urban environmental gradients; (4) using trait-based approaches to improve our mechanistic understanding of biodiversity and its relationship with EF and ES; and (5) extending the involvement of citizens in biodiversity, EF and ES research. A conceptual scheme of the research agenda is presented in Fig. 1.

Research agenda to assess biodiversity, EF and ES in cities

Improving urban habitat mapping

Urban biodiversity research needs detailed knowledge of the habitat types and their spatial distribution in cities. Habitat composition in the Natura 2000 network of protected areas is being characterized through a coordinated effort at the European level (EC 2020), but this work remains limited to case studies and does not provide extensive mapping of urban areas. Some cities, such as Zurich or Paris, map their habitats at a very fine spatial resolution, and city-scale studies can make use of these resources. However, thematic and temporal resolutions are not compatible, and standard habitat mapping is currently not available at the European level (Kabisch et al. 2016). Although the European Urban Atlas (EEA 2012) uses a consistent set of rules for mapping, its habitat definition is limited to only three classes: 'Green Urban Areas', 'Forest', and 'Herbaceous Vegetation Association', and it omits key attributes, such as vegetation structure and management, which are critical for linking them to biodiversity (Pinho et al. 2016) and ES provisioning (Mexia et al. 2018). Moreover, small habitat patches, such as green roofs and walls, flower beds and domestic gardens, as well as linear elements, such as green belts and ecotones, are often omitted even though they are novel urban habitats with critical features for biodiversity and ES provision (Hand et al. 2017).

Remote sensing data can be an important source for mapping urban land use. Unlike land-cover maps, remote sensing data is continuous over space, can be continuously updated, and has been used in urban areas to assess e.g. carbon stocks, urban heat island hotspots (Dobbs et al. 2018) and patterns

of urban biodiversity (Pellissier et al. 2017). An added value of remote sensing is that it enables rapid collection of data that can be used for monitoring and as part of an early warning system, i.e. signalling areas that are currently unchanged but that are likely to undergo changes in the future, such as drought-induced tree mortality, based on time-series analysis (Yanlan et al. 2019). This area of research remains unexplored regarding biodiversity changes.

To avoid the pitfalls of using linear city-centre to peri-urban gradients to characterize polycentric cities (Ramalho et al. 2012), future studies should consider the characteristics of each habitat patch and its surroundings, irrespective of its geographical position and distance from the city centre. This can be done, for example, by stratifying sampling to the environmental factor of interest or to a proxy of environmental factors (e.g. dense urban landcover as a proxy for air pollution) (Pinho et al. 2016). Future work using spatially complete analyses (Pinho et al. 2008) could provide further insights into species-specific mechanisms (such as dispersion) or the spatial structure of underlying socio-ecological factors (such as management intensity, urban heat-island effect and equity in the distribution of ES).

Research directions - urban habitat mapping:

1. Create ecologically meaningful habitat-based maps of cities, including the full range of land uses, management strategies and habitat sizes.
2. Use remote sensing data series to create a spatially complete and temporally replicated sampling design, enabling better characterization of urban habitats and long-term processes.

Considering neglected urban habitats and ecological niches

Typically, urban areas contain three main land cover types: artificial built-up area, e.g. houses and roads (grey infrastructure), terrestrial and aquatic habitats (green and blue infrastructures, respectively). Although these land covers are intermingled in cities in space and time, they are often

studied separately regarding: (1) their identity (green, blue, grey); (2) their vertical distribution (above vs. below the surface), (3) the time of day when the investigation occurs (day vs. night) and (4) typology (e.g. green roof vs. meadow). However, urban habitats are perceived and used by most animals as a continuum, since they often depend on more than one habitat to complete their life cycle or to perform important activities, such as reproduction, nesting, and foraging (Colding 2007). Moreover, it is important not to minimize the importance of the below-ground habitat to many organisms, including bacteria, arthropods, fungi, and snails. Belowground biodiversity is tightly connected with the aboveground compartment through processes such as leaf litter decomposition, nutrient exchange, and soil formation. Participating in shaping primary productivity, the roles of belowground biodiversity thus cascades into the next trophic levels, ultimately determining other ES such as pest control, pollination, and food production (Tresch et al. 2019a). Such nutrient and energy transfers across neighbouring habitats are expected to be intense but remain largely unexplored.

Day and night provide two contrasting habitat spaces and ecological niches for nocturnal and diurnal organisms. Nocturnal habitats are key for species such as bats, ground-dwelling arthropods, moths and a myriad of other insects that carry out a range of under-studied ES in cities, such as pollination of night-flowering plants (Knop et al. 2017) and pest control. While other animals such as birds share the same space during the day, only by looking at both, nocturnal and diurnal organisms, we can have a complete perspective on the local food webs (Villarroya-Villalba et al. 2021).

To balance the impossibility of investigating all ecological niches and habitats during the whole life cycle of organisms, we can focus on traits related to daily and annual activity time, voltinism (number of generations an organism completes within a year), and ontogeny (the developmental history of an organism during its lifetime; see Moretti et al. (2017) for terrestrial invertebrates, Pérez-Harguindeguy et al. (2013) for plants, and Dawson et al. (2019) for fungi). Moreover, by investigating trait variation at the individual rather than species level, one could consider phenotypic plasticity and possible adaptations to the particular environmental conditions in cities, thereby shedding light on important

eco-evolutionary mechanisms that need to be explored further at the genetic level (Uchida et al., 2021).

Research directions - neglected habitats and niches:

1. Use trait-based approaches to understand species' responses to unexplored niches and to compare responses across taxa, cities and regions.
2. Investigate intraspecific trait variability to quantify phenotypic plasticity and adaptations to the urban environmental conditions.

Integrating multiple environmental gradients

The processes related to urbanization are associated with a multitude of socio-ecological drivers, such as the management intensity of green areas, air, light, and noise pollution, and climatic conditions (temperature, humidity). Because these drivers act simultaneously with different spatio-temporal dynamics, it is increasingly important to study their effects jointly to identify potential non-additive effects on EF and trade-offs on ES.

Urban green space management (e.g. plant and vegetation composition, configuration, structure, and management) affects biodiversity and EF, and can cause trade-offs on ES provision. For example, slow-growing, open-crowned trees such as oaks and maples can increase the aesthetic value and microclimate regulation more than fast-growing narrow-crowned trees (de Abreu-Harbich et al. 2015), but these effects can be limited during the cold season due to leaf loss, in comparison with evergreen species. Differences among vegetation traits and species composition also affect leaf litter (de)composition, which, in turn, affects environmental conditions for ground-dwelling organisms and their associated ES, such as protection against soil erosion (Li et al. 2014), habitat provision for biodiversity (Smith et al. 2014), organic matter decomposition, and nutrient cycling (Tresch et al. 2019a).

Choices of plant species featuring specific traits by both home gardeners and by managers of public green spaces, has major impacts on biodiversity and multi-trophic interactions. For instance, replacing intensively managed lawns with extensively managed meadows has been shown to enhance pollinator diversity (Baldock et al. 2019) and cultural services (Home et al. 2019), but meadows are less suitable for other recreational activities and may increase a sense of insecurity in people (Home et al. 2019, Fischer et al. 2020). An unintended consequence of plant selection by gardeners and managers of public green spaces is the introduction of exotic and potentially invasive species, and the associated animals (such as herbivore insects) and pathogens (such as fungi and bacteria). While cultivar and exotic species provide ES and may benefit native biodiversity, especially under extensive management and appropriate densities and distributions (Ramírez-Cruz et al. 2019), the risk of species becoming invasive must not be minimized, even if these species are particularly appreciated by people, e.g. for their aesthetic value (Marija et al. 2020). Consequences of invasive species may include e.g. being diseases vectors and homogenizing the biotic communities (see Gaertner et al., 2017). One important open question is whether exotic and invasive species traits ranges fall within the native species ranges (Finerty et al. 2016) and what are the consequences to Es and EF.

Vegetation can mitigate the effects of urban pollution (e.g. air pollution, Grote et al. 2016, Matos et al. 2019) but is simultaneously affected by it. For instance, tree morphological, physiological and phenological traits influence the removal of tropospheric ozone (Manes et al. 2012), while volatile-emitting species can contribute to air pollution, providing an ecosystem disservice (Uan et al. 2020). At the same time, reduced air pollution in European cities (EEA 2018) has positively influenced sensitive taxa, such as lichens, and nitrogen-tolerant species have recolonized cities after the decline in SO₂ (Van Dobben & ter Braak 1998). Nonetheless, water, noise and light pollution are still high in many urban areas (Gaston & Holt 2018), impacting biodiversity by adding additional environmental filters (Aronson et al. 2016). However, we have limited knowledge of how changing pollution levels can affect the assembly of urban species (by modifying extinction and colonization rates) and subsequently the ES provided. For example, the shift towards electric vehicles will likely decrease the

emissions of NO_x in cities. This in turn could potentially reduce acidification and eutrophication, boost the biodiversity of plant communities, and increase the associated ES (Jones et al. 2014).

The urban heat-island effect, i.e. the higher temperature observed in cities than in surrounding rural areas, selects for heat- and drought-tolerant species (Fournier et al. 2020; Piano et al. 2017) and increases primary productivity (Shochat et al. 2006), with possible effects on biotic interactions, leaf litter decomposition (Jochner & Menzel 2015; Tresch et al. 2019a) and tree transpiration (Zölch et al. 2016). There are several open questions regarding the effects of climate change superimposed on local urban heat-island effects (Grilo et al. 2020), with birds and plants showing contrasting responses between species (Wohlfahrt et al. 2019).

All the environmental factors listed above act simultaneously on urban biodiversity and associated EF and ES. Their joint effects remain understudied but could be effectively explored by using both an adequate sampling design (de Keyser et al. 2017) and a trait-based approach. The latter may allow us to identify and predict which socio-ecological filtering mechanisms drive species assembly and key ES in urban areas.

Research directions - multiple environmental gradients:

1. Quantify the multiple environmental drivers of biodiversity and EF, and the trade-offs on ES, considering the ecological, cultural, social, and economic dimensions.
2. Assess the new species assemblages, including exotic species, and individual adaptations resulting from changing environmental conditions, including ongoing climate change superimposed on the urban heat-island effect, and its consequences for ES.

Using trait-based approaches to improve our mechanistic understanding of biodiversity relationships with EF and ES

Trait-based approaches make it possible to identify biotic, abiotic and socio-cultural control mechanisms acting on community assemblages and the resulting consequences for EF within and across trophic levels (Diaz et al. 2007), as well as synergies and trade-offs among ES associated with the traits involved (Lavorel & Grigulis 2012). Syntheses of empirical studies conducted in non-urban systems have shown that both trait dominance and trait complementarity, although not mutually exclusive (Dias et al. 2013), can be important drivers of EF and ES. As socio-ecological systems, cities challenge our traditional understanding of how species assemblages are filtered and how this, in turn, influences ecosystem functioning, stability and service delivery (Aronson et al. 2016). Which traits and functional components of biodiversity drive EF and ES, and how these can be translated into planning and management guidelines that can be implemented in restoration or conservation activities remains unknown (Luederitz et al. 2015, Schwarz et al. 2017). For example, what type of socio-ecological filters are working during a pandemic situation and that lead people to visit more a given green space than other (Grima et al., 2020) remains unexplored. Investigation of the types of filters, traits and functional components (including those related to socio-economic factors) could therefore unravel the mechanisms linking biodiversity with EF and ES in cities. By understanding these mechanisms predictions of ES under global change and restoration strategies could be improved, e.g. by promoting species assemblages that are able to provide the desired ES (Laughlin 2014).

Recent studies have highlighted the importance of long-term research (Weisser et al. 2017). While species composition is temporally variable (e.g. due to stochastic processes), functionally redundant species may be abundant in different years, thereby contributing to the overall stability of EF and ES (Isbell et al. 2011; Winfree et al. 2018). Thus, research conducted over long timescales and multi-service provision is an important research direction, due to their paramount importance to understand ecosystem resilience in ES provisioning.

Research directions - trait-based approaches:

1. Identify relevant socio-environmental filters, species traits and functional components to unravel the mechanisms linking biodiversity and EF with ES.
2. Identify traits that will become important given future global changes and include them in studies and restoration and conservation guidelines.

Involving citizens in biodiversity, EF and ES research

Public participation is the involvement of stakeholders (mostly citizens) in public consultations or scientific inquiries and ranges from information exchanges to active decision-making processes (Ambrose-Oji et al. 2017). Citizen scientists can become involved in management and conservation and often improve their urban ecology knowledge in doing so (Deguines et al. 2018, 2020). Citizen science projects target a broad range of taxa (vertebrates, invertebrates, plants, bacteria, fungi, and protozoa) in many marine and terrestrial ecosystems, many of which are normally inaccessible, such as private gardens. Citizen scientists can also investigate and map the (spatio-temporal dynamics of) urban filters such as air pollution and air temperature (Sauermann et al. 2020). Cities encompass most of the world's human population; consequently, enhancing the collection of data on urban biodiversity in future projects using citizen science will improve the ability of citizens and policy-makers to respond to a wide range of ecological and environmental questions related to e.g. air quality, climate change, invasive species, conservation biology, population ecology, ecosystem functioning, and ecosystem service delivery by increasing the number and size of datasets (Silvertown 2009; Martin et al. 2019). Thus, the involvement of citizens in observing and sampling biodiversity has expanded to the fields of urban governance and planning (Buijs et al. 2016), often driven by global and national policy agendas (e.g. EC 2013, UN-HABITAT 2016).

The usefulness of citizen science projects in science is, however, dependent on the quality of the collected data (Serret et al. 2019) and can be limited by the non-random distribution of sampling effort and poorly classified species (Crall et al. 2011). Future studies in citizen science must ensure that standard protocols developed with statisticians are used (Bird et al. 2014). Another open question regarding citizen science is related to error propagation through complex chains of data collection, because data is collected in very different conditions, by multiple people, and in multiple events. Future research should attempt to identify the main steps of data collection while validating each step along the chain (Snyder et al. 2019).

One way to boost the participation of citizens in future studies is to promote bottom-up initiatives that engage citizens with local green spaces. It is important to ground such initiatives using a combination of social and environmental objectives, rooted in environmental stewardship that goes beyond immediate personal benefit and incorporates wider cultural values (Buijs et al. 2016), thus contributing to science and helping fulfil the aim of monitoring through indicators, as set out in the Sustainable Development Goals (SDG). A powerful tool available to do so is the public participation geographic information system (PPGIS), a method combining spatially explicit data with local knowledge, perceptions and values of individuals or groups of people (Brown & Fagerholm 2015). This method should be used in future studies to map ES (Burkhard & Maes 2017), identify cultural and meaningful green spaces (Rall et al. 2017), model residents' visits to green spaces (Luz et al. 2019), and identify potential land use conflicts (Brown & Raymond, 2014) and environmental justice issues (Raymond et al. 2016), among many other uses (Rall et al. 2018).

Research directions - involving citizens:

1. Use standard sampling protocols, include error reporting and analysis, and frame future work within international initiatives, such as the Sustainable Development Goals.

2. Support bottom-up initiatives of citizen science.

306

307 **Conclusions**

308 Here, we identified five major research gaps in urban ecology research and put forth suggestions for
309 future research directions, including habitat mapping, neglected habitats and ecological niches,
310 multiple urban gradients, trait-based approaches, and citizens engagement. Overall, trait-based
311 approaches emerged as a common ground to integrate all research directions, from remote sensing
312 detection, measuring impacts of disturbance to targets of citizen science. In fact, trait-based metrics
313 are expected to provide the link of biodiversity with ecosystem functions (EF) and thus ecosystem
314 services (ES). Since these approaches remain poorly investigated in urban environments, especially
315 within the identified research directions, focussing on those directions can help overcome the
316 current knowledge gaps and enable us to make cities more resilient for both nature and human life.

317

318 **Acknowledgements**

319 We acknowledge the questions and suggestions made by the anonymous reviews of this manuscript
320 that greatly improved the text.

321

322 **Funding**

323 This work was partially funded by the European ERA Net BiodivERsA project “BioVEINS: Connectivity
324 of green and blue infrastructures: living veins for biodiverse and healthy cities” (H2020
325 BiodivERsA32015104). J. Casanelles-Abella was supported by the Swiss National Science Foundation
326 (project 31BD30_172467). M. Alós Ortí was supported by the European Social Fund’s Dora Plus
327 Programme, A. C. Luz was funded by the Fundação para a Ciência e Tecnologia (FCT) Portugal
328 (SFRH/BPD/108156/2015 fellowship), and A. Kubicka acknowledges Poland funding through
329 NCN/2016/22/Z/NZ8/00004.

References

- Ambrose-Oji B., Buijs A., Geróházi E., Mattijssen T., Száraz L., Van der Jagt A., Hansen R., Rall E., Andersson E., Kronenberg J., Rolf W. (2017). Innovative Governance for Urban Green Infrastructure, A Guide for Practitioners, GREEN SURGE project Deliverable 6.3, University of Copenhagen, Copenhagen, Denmark.
- Aronson M. F. J., Nilon C.H., Lepczyk C. A., Parker T. S., Warren P. S., Cilliers S. S., Goddard M. A., Hahs A. K., Herzog C., Katti M., et al. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology* 97, 2952-s063.
- Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., ... Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B, Biological Sciences*, 281, 20133330.
- Baldock, K. C. R., Goddard, M. A., Hicks, D. M. et al. (2019) A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nat. Ecol. Evol.* 3, 363–373.
- Bird T. J., Bates A. E., Lefcheck J. S., Hill N. A., Thomson R. J., Edgar G. J., Stuart-Smith R. D., Wotherspoon S., Krkosek M., Stuart-Smith J. F., Pecl G. T., Barrett N., Frusher S. (2014). Statistical solutions for error and bias in global citizen science datasets. *Biological Conservation* 173, 144-154.
- Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., ... Petraglia, M. D. (2016). Ecological consequences of human niche construction, Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 6388–6396.
- Brown G., & Fagerholm N. (2015). Empirical PPGIS/PGIS mapping of ecosystem services, A review and evaluation. (2015). *Ecosystem Services* 13, 119–133.

353 Brown G., & Raymond C. M. (2014). Methods for identifying land use conflict potential using
354 participatory mapping. *Landscape and Urban Planning* 122, 196–208.

355 Buijs A. E., Mattijssen T. J. M., Van der Jagt A. P. N., Ambrose-Oji B., Andersson E., Elands B. H. M.,
356 Steen Møller M. (2016). Active citizenship for urban green infrastructure, fostering the diversity
357 and dynamics of citizen contributions through mosaic governance. *Curr. Opin. Environ. Sustain.*
358 22, 1–6.

359 Burkhard B., & Maes J (Eds.). (2017). *Mapping Ecosystem Services*. Pensoft Publishers, Sofia, 374 pp.

360 Capotorti G., Alós Ortí M.M., Copiz R., Fusaro L., Mollo B., Salvatori E., Zavattero L. (2019). Biodiversity
361 and ecosystem services in urban green infrastructure planning, A case study from the
362 metropolitan area of Rome (Italy). *Urban Forestry & Urban Greening* 37, 87-96.

363 Colding, J. (2007). 'Ecological land-use complementation' for building resilience in urban ecosystems.
364 *Landscape and Urban Planning*, 81, 46-55.

365 Crall A. W., Newman G. J., Stohlgren T. J., Holfelder K. A., Graham J., Waller D. M. (2011). Assessing
366 citizen science data quality, an invasive species case study. *Conservation Letters* 4, 433-442.

367 Dawson, S. K., Boddy, L., Halbwachs, H., et al. (2019). Handbook for the measurement of macrofungal
368 functional traits, A start with basidiomycete wood fungi. *Funct Ecol.*; 33, 372– 387.

369 de Abreu-Harbich V., Labak L., Matzarakis A. (2015). Effect of tree planting design and tree species on
370 human thermal comfort in the tropics. *Landscape and Urban Planning* 138, 99-109.

371 de Keyzer, C. W., Rafferty, N.E., Inouye, D. W., Thomson, J.D. (2017). Confounding effects of spatial
372 variation on shifts in phenology. *Global Change Biology* 23, 1783-1791.

373 Deguines N., de Flores M., Loïs G., Julliard R., Fontaine C. (2018). Fostering close encounters of the
374 entomological kind. *Frontiers in Ecology and the Environment*. 16, 202-203.

375 Deguines N., Princé K., Prévot A.-C., Fontaine B. (2020) Assessing the emergence of pro-biodiversity
376 practices in citizen scientists of a backyard butterfly survey. *Science of The Total Environment*,
377 136842.

378 Dias, A. T. C., M. P. Berg, F. de Bello, A. R. Van Oosten, K. Bila, & M. Moretti. (2013). An experimental
379 framework to identify community functional components driving ecosystem processes and
380 services delivery. *Journal of Ecology* 101, 29-37.

381 Diaz S., Lavorel S., de Bello F., Quétier F., Grigulis K., Robson T (2007). Incorporating plant functional
382 diversity effects in ecosystem service assessments. *Proceedings of the National Academy of*
383 *Sciences*, 104, 20684-20689.

384 Diaz, S., & Cabido, M. (2001). Vive la difference, plant functional diversity matters to ecosystem
385 processes. *Trends in Ecology & Evolution*, 16, 646-655.

386 Diaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., ... Shirayama, Y. (2018).
387 Assessing nature's contributions to people. *Science*, 359, 270–272.

388 Dobbs, C., Hernandez-Moreno, A., Reyes-Paecke, S., Miranda, M. D., (2018). Exploring temporal
389 dynamics of urban ecosystem services in Latin America, The case of Bogota (Colombia) and
390 Santiago (Chile). *Ecological Indicators* 85, 1068-1080.

391 EC, 2020. NATURA 2000 in cities. Publications Office of the European Union, Luxembourg, 2020,
392 <https://ec.europa.eu/environment/nature/natura2000>

393 EEA., European Environmental Agency (2018). Air quality in Europe — 2018 report. EC., Copenhagen,
394 Denmark.

395 EEA., European Environmental Agency (2012). European Urban Atlas. EC., Copenhagen, Denmark.

396 Elmqvist, T., Andersson, E., Frantzeskaki, N. et al. Sustainability and resilience for transformation in
397 the urban century (2019). *Nat Sustain* 2, 267–273.

398 Engemann, K., Pedersen, C. B., Arge, L., Tsirogiannis, C., Mortensen, P. B., & Svenning, J. C. (2019).
399 Residential green space in childhood is associated with lower risk of psychiatric disorders from
400 adolescence into adulthood. *Proceedings of the National Academy of Sciences of the United*
401 *States of America*, 116, 5188–5193.

402 Finerty, G.E., de Bello, F., Bílá, K., Berg, M.P., Dias, A.T., Pezzatti, G.B. and Moretti, M. (2016) Exotic or
403 not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter
404 decomposition. *Journal of Ecology*, 104: 1400-1409.

405 Fischer, L. K, Neuenkamp, L., Lampinen, J., ... & Klaus, V. H. (2020). Public attitudes toward
406 biodiversity-friendly greenspace management in Europe. *Conservation Letters*. 13, 13:e12718.

407 Fournier, B., Frey, D. & Moretti, M. (2020). The origin of urban communities, From the regional species
408 pool to community assemblages in city. *J. Biogeogr.*, 47, 615-629.

409 Gaertner, M., Wilson, J. R. U., Cadotte, M. W., MacIvor, J. S., Zenni, R. D., Richardson, D. M. (2017).
410 Non-native species in urban environments: patterns, processes, impacts and challenges.
411 *Biological Invasions* 19, 3461–3469.

412 Gaston K. J. & Holt, L. A. (2018). Nature, extent and ecological implications of night-time light from
413 road vehicles. *Journal of Applied Ecology* 55, 2296-2307.

414 Grilo F, Pinh.o P, Aleixo C., Catita C., Silva P., Lopes N., Freitas C., Santos-Reis M., McPhearson T.,
415 Branquinho C. (2020). Using green to cool the grey: modelling the cooling effect of green spaces
416 with a high spatial resolution. *Science of the Total Environment* 724, 138182.

417 Grima, N., Corcoran, W., Hill-James, C., Langton, B., Sommer, H., Fisher, B. (2020) The importance of
418 urban natural areas and urban ecosystem services during the COVID-19 pandemic. *PLoS ONE*
419 15: e0243344.

420 Grote, R., Samson, R., Alonso, R., Amorim, J. H., Cariñanos, P., Churkina, G., Fares, S., Le-Thiec, D.,
421 Niinemets, U., Mikkelsen, T. N., Paoletti, E., Tiwary, A., Calfapietra, C. (2016) Functional traits of

422 urban trees: air pollution mitigation potential. *Frontiers in Ecology and Environment* 14, 543-
 423 550.

424 Hand, K. L., Freeman, C., Seddon, P. J., Recio, M. R., Stein, A., van Heezik, Y., (2017). The importance
 425 of urban gardens in supporting children's biophilia. *Proceedings of the National Academy of*
 426 *Sciences of the United States of America* 114, 274-279.

427 Home, R., Lewis, O., Bauer, N., Fliessbach, A., Frey, D., Lichtsteiner, S., Moretti, M., Tresch, S., Young,
 428 C., Zanetta, A. & Stolze, M. (2019). Effects of garden management practices, by different types
 429 of gardeners, on human wellbeing and ecological and soil sustainability in Swiss cities. *Urban*
 430 *Ecosystems*, 22, 189-199.

431 IPBES. (2019). *The global assessment report on summary on policymakers of the IPBES global*
 432 *assessment report on biodiversity and ecosystem services*. Retrieved from
 433 [https://ipbes.net/system/tdf/ipbes_global_assessment_report_summary_for_policymakers.p](https://ipbes.net/system/tdf/ipbes_global_assessment_report_summary_for_policymakers.pdf?file=1&type=node&id=35329)
 434 [df?file=1&type=node&id=35329](https://ipbes.net/system/tdf/ipbes_global_assessment_report_summary_for_policymakers.pdf?file=1&type=node&id=35329).

435 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., ... Loreau, M. (2011). High
 436 plant diversity is needed to maintain ecosystem services. *Nature*, 477, 199–202.

437 Jochner, S., & Menzel, A. (2015). Urban phenological studies—past, present, future. *Environmental*
 438 *Pollution*, 203, 250-261.

439 L. Jones, A. Provins, M. Holland, G. Mills, F. Hayes, B. Emmett, J. Hall, L. Sheppard, R. Smith, M. Sutton,
 440 K. Hicks, M. Ashmore, R. Haines-Young, L. Harper-Simmonds. 2014. A review and application of
 441 the evidence for nitrogen impacts on ecosystem services, *Ecosystem Services*, 7, 76-88.

442 Jung, K. & Threlfall, C. G. (2018). Trait-dependent tolerance of bats to urbanization, a global meta-
 443 analysis. *Proceedings of the Royal Society B., Biological Sciences*, 285, 20181222.
 444 10.1098/rspb.2018.1222.

445 Kabisch N., Strohbach M., Haase D., Kronenberg J. (2016). Urban green space availability in European
 446 cities. *Ecological Indicators*, 70, 586-596.

447 Kang W., Minor E. S., Park C R., Lee D. (2015). Effects of habitat structure, human disturbance, and
 448 habitat connectivity on urban forest bird communities. *Urban Ecosystems*, 18, 857-870.

449 Knop, E., Zoller, L., Ryser, R., Erpe, C. G., Horler, M. & Fontaine, C. (2017). Artificial light at night as a
 450 new threat to pollination. *Nature*, 548, 7666, 10.1038/nature23288.

451 Laanisto, L., Tamme, R., Hiiesalu, I., Szava-Kovats, R., Gazol, A., & Pärtel, M. (2013).
 452 Microfragmentation concept explains non-positive environmental heterogeneity–diversity
 453 relationships. *Oecologia*, 171, 217-226.

454 Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven
 455 ecological restoration. *Ecology Letters*, 17, 771-784.

456 Lavorel, S. & Grigulis, K. (2012) How fundamental plant functional trait relationships scale-up to trade-
 457 offs and synergies in ecosystem services. *Journal of Ecology*, 100, 128-140.

458 Liu, Y., Kumar, M., Katul, G. G., & Porporato, A. (2019). Reduced resilience as an early warning signal
 459 of forest mortality. *Nature Climate Change*, 9, 880–885.

460 Luederitz, C., Brink, E., Gralla, F., Hermelingmeier, V., Meyer, M., Niven, L., ... von Wehrden, H. (2015).
 461 A review of urban ecosystem services, six key challenges for future research. *Ecosystem*
 462 *Services*, 14, 98–112.

463 Luz, A. C., Buijs, M., Aleixo, C., Metelo, I., Grilo, F., Branquinho, C., Santos-Reis, M., & Pinho, P. (2019).
 464 Should I stay or should I go? Modelling the fluxes of urban residents to visit green spaces. *Urban*
 465 *Forestry and Urban Greening*, 40, 195–203.

466 Manes, F., Incerti, G., Salvatori, E., Vitale, M., Ricotta, C. & Costanza, R. (2012). Urban ecosystem
 467 services, tree diversity and stability of tropospheric ozone removal. *Ecological Applications*, 22,
 468 349-360.

469 Milanović. M., Knapp, S., Pyšek, P., & Kühn, I. 2020. Linking traits of invasive plants with ecosystem
 470 services and disservices, *Ecosystem Services*, 42, 101072.

471 Martin, G., Devictor, V., Motard, E., Machon, N., & Porcher, E. (2019). Short-term climate-induced
 472 change in French plant communities. *Biology Letters*, 15, 20190280.

473 Matos P., Vieira J., Rocha B., Branquinho C., Pinho P. (2019). Modeling the provision of air-quality
 474 regulation ecosystem service provided by urban green spaces using lichens as ecological
 475 indicators. *Science of the Total Environment*, 654, 705-713.

476 Mexia, T., Vieira, J., Principe, A., Anjos, A., Silva, P., Lopes, N., Freitas, C., Santos-Reis, M., Correia, O.,
 477 Branquinho, C., Pinho, P., (2018). Ecosystem services, Urban parks under a magnifying glass.
 478 *Environmental Research* 160, 469-478.

479 Meyer, C., Weigelt, P., & Kreft, H. (2016). Multidimensional biases, gaps and uncertainties in global
 480 plant occurrence information. *Ecology Letters*, 19, 992–1006.

481 Moretti, M., Dias, A., De Bello, F. et al. (2017). Handbook of protocols for standardized measurements
 482 of terrestrial invertebrate functional traits. *Functional Ecology*, 31, 558–567.

483 Munzi S., Correia O., Silva P., Lopes N., Freitas C., Branquinho C., Pinho P. (2014). Lichens as ecological
 484 indicators in urban areas, beyond the effects of pollutants. *Journal of Applied Ecology* 51, 1750-
 485 1757.

486 Ossola, A., Locke, D., Lin, B. & Minor, E. (2019). Greening in style, Urban form, architecture and the
 487 structure of front and backyard vegetation. *Landscape and Urban Planning*, 185, 141-157.

488 Pellissier, V., Mimet, A., Fontaine, C., Svenning, J.C., Couvet, D., (2017). Relative importance of the
 489 land-use composition and intensity for the bird community composition in anthropogenic
 490 landscapes. *Ecology and Evolution* 7, 10513-10535.

491 Pérez-Harguindeguy N., Díaz S., Vendramini F., Cornelissen J. H. C., Gurvich D. E., Cabido M. (2003).
 492 Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology* 28,
 493 642–650.

494 Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., ... Hendrickx, F. (2017). Urbanization
 495 drives community shifts towards thermophilic and dispersive species at local and landscape
 496 scales. *Global Change Biology*, 23, 2554–2564.

497 Pinho P., Augusto S., Martins-Loucao M. A., Pereira M. J., Soares A., Maguas C., Branquinho C. (2008).
 498 Causes of change in nitrophytic and oligotrophic lichen species in a Mediterranean climate,
 499 Impact of land cover and atmospheric pollutants. *Environmental Pollution* 154, 380-389.

500 Pinho, P., Correia, O., Lecoq, M., Munzi, S., Vasconcelos, S., Goncalves, P., Rebelo, R., Antunes, C., Silva,
 501 P., Freitas, C., Lopes, N., Santos-Reis, M., Branquinho, C., (2016). Evaluating green infrastructure
 502 in urban environments using a multi-taxa and functional diversity approach. *Environmental*
 503 *Research* 147, 601-610.

504 Rall E., Bieling C., Zytynska S., Haase D. (2017). Exploring city-wide patterns of cultural ecosystem
 505 service perceptions and use. *Ecological Indicators* 77, 80–95.

506 Rall E., Hansen R., Stephan P. (2019). The added value of public participation GIS (PPGIS) for urban
 507 green infrastructure planning. *Urban Forestry & Urban Greening*, 40, 264-274.

508 Ramalho, C. E., Hobbs, R. J. (2012). Time for a change, dynamic urban ecology. *Trends in Ecology &*
 509 *Evolution* 27, 179-188.

510 Ramírez-Cruz G. A, Solano-Zavaleta I, Mendoza-Hernández P. E, Méndez-Janovitz M., Suárez-
 511 Rodríguez M., et al. (2019) This town ain't big enough for both of us...or is it? Spatial co-
 512 occurrence between exotic and native species in an urban reserve. *PLOS ONE*, 14, e0211050.

513 Raymond, C. M., Gottwald, S., Kuoppa, J., & Kyttä, M. (2016). Integrating multiple elements of
514 environmental justice into urban blue space planning using public participation geographic
515 information systems. *Landscape and Urban Planning*, 153, 198–208.

516 Sauermann H., Vohland K., Antoniou V., Balázs B., Göbel C., Karatzas K., Mooney P., Perelló J., Ponti
517 M., Samson R., Winter S (2020). Citizen Science and Sustainability Transitions. *Research Policy*,
518 49, 103978.

519 Schwarz N., Moretti M., Bugalho M. N., Davies ZG., Haase D., Hack J., Hof A., Melero Y., Pett T. J.,
520 Knapp S. (2017). Understanding biodiversity-ecosystem service relationships in urban areas, A
521 comprehensive literature review. *Ecosystem Services*, 27, 161-171.

522 Serret, H., Deguines, N., Jang, Y., Lois, G., & Julliard, R. (2019). Data Quality and Participant
523 Engagement in Citizen Science, Comparing Two Approaches for Monitoring Pollinators in France
524 and South Korea. *Citizen Science, Theory and Practice*, 4, 22.

525 Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E. & Hope, D. (2006). From patterns to emerging
526 processes in mechanistic urban ecology. *Trends Ecol. Evol.* 21, 186–191.

527 Silvertown, J., (2009). A new dawn for citizen science. *Trends in Ecology and Evolution* 24, 467–471.

528 Smith, L. S., Broyles, M. E. J., Larzleer, H. K., & Fellowes, M. D. E. (2014). Adding ecological value to the
529 urban lawnscape. Insect abundance and diversity in grass-free lawns. *Biodiversity and*
530 *Conservation*, 24, 47–62.

531 Snyder J. T., Whitney M. M., Dam HG., Jacobs M. W., Baumann H. (2019). Citizen science observations
532 reveal rapid, multi-decadal ecosystem changes in eastern Long Island Sound. *Marine*
533 *Environmental Research* 146, 80-88.

534 Tresch, S., Frey, D., Le Bayon, R. C., Zanetta, A., Rasche, F., Fliessbach, A. & Moretti, M. (2019a). Litter
535 decomposition driven by soil fauna, plant diversity and soil management in urban gardens.
536 *Science of the Total Environment*, 658, 1614-1629.

537 Tresch, S., Frey, D., Le Bayon, R. C., Mader, P., Stehle, B., Fliessbach, A., & Moretti, M. (2019b). Direct
 538 and indirect effects of urban gardening on aboveground and belowground diversity influencing
 539 soil multifunctionality. *Scientific Reports*, 9, 9769.

540 Uchida. K., Blakey, R. V., Burger, J. R., Cooper D. S., Niesner, C. A., Blumstein, D. T. (2021) Urban
 541 Biodiversity and the Importance of Scale. *Trends in Ecology & Evolution*, 36, 123-131.

542 UN. (2017). New Urban Agenda - Habitat III. Page 30 in General Assembly of the United Nations.

543 UN-HABITAT (2016). Goal 11, Make cities inclusive, safe, resilient and sustainable.

544 Van Dobben H. F., & Ter Braak C. J. F. (1998). Effects of atmospheric NH₃ on epiphytic lichens in the
 545 Netherlands, The pitfalls of biological monitoring. *Atmospheric Environment* 32, 551-557.

546 Villarroya-Villalba L., Casanelles-Abella J., Moretti M., Pinho P., van Mensel A., Chiron F., Zellweger F.,
 547 Obrist K.M. (2021). Response of bats and nocturnal insects to urban green areas in Central
 548 Europe. *Basic and Applied Ecology*; in press.

549 Weisser, W. W., Roscher, C., Meyer, S. T., Ebeling, A., Luo, G., Allan, E., ... Eisenhauer, N. (2017).
 550 Biodiversity effects on ecosystem functioning in a 15-year grassland experiment, Patterns,
 551 mechanisms, and open questions. *Basic and Applied Ecology*, 23, 1–73.

552 Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species
 553 turnover promotes the importance of bee diversity for crop pollination at regional scales.
 554 *Science*, 359, 791–793.

555 Wohlfahrt, G., Tomelleri, E. & Hammerle, A. (2019). The urban imprint on plant phenology. *Nat. Ecol.*
 556 *Evol.* 3, 1668–1674.

557 Yuan, Y., Sun, Z., Kännaste, A., Guo, M., Zhou G., Niinemets, U. (2020) Isoprenoid and aromatic
 558 compound emissions in relation to leaf structure, plant growth form and species ecology in 45
 559 East-Asian urban subtropical woody species. *Urban Forestry & Urban Greening*, 53, 126705.

560 Zölch, T., Maderspacher, J., Wamsler, C., & Pauleit, S. (2016). Using green infrastructure for urban
561 climate-proofing: An evaluation of heat mitigation measures at the micro-scale. *Urban Forestry*
562 & *Urban Greening*, 20, 305-316.

563

564 **Fig. 1.** Conceptual research agenda to improve our understanding of relationships between
565 biodiversity and ecosystem functions and services (B-EF/ES) in cities. The five topics highlighted by
566 text sections are discussed in detail in the main text.

567

Research agenda on biodiversity and ecosystem functions and services in European cities

