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Characteristics of novel urban vegetation in two Portuguese urban regions

Estêvao Portela-Pereira[a,b,c], Carlos Neto[a,b], Eduardo Brito-Henriques[a,b], Ana Luísa Soares[c] and Sónia Talhé Azambuja[c]

[a]Centre of Geographical Studies, Institute of Geography and Spatial Planning, University of Lisbon, Edifício IGOT, Rua Branca Edmée Marques, Cidade Universitária, 1600-276 Lisboa, Portugal; [b]Associated Laboratory Terra, Portugal; [c]Centre for Applied Ecology "Prof. Baeta Neves" (CEABN-InBIO), School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal

ABSTRACT

Urban novel ecosystems were sampled across vacant sites in two Portuguese urban regions. The flora were studied with a focus on species' origin, life form, ecological, chorological and naturalisation types. A multivariate constrained ordination technique was used to identify relationships between plant composition and environmental factors. The vegetation of the two urban regions shows differences, highlighting biome influence, as well as due to climatic variables and (to a lesser degree) soil characteristics and lithology. Although native species are clearly dominant, the frequency of non-native species is high and most are potentially or effectively invasive. In the ecological spectrum, the dominance of opportunistic ruderal species suggests a risk of biotic homogenisation in these ecosystems, which is also noticeable in the analysis of life form, but less in chorological and nativeness spectra. Portuguese novel urban ecosystems are, therefore, simultaneously an opportunity, since spontaneous vegetation management is more cost effective and can bring wilderness to cities; and a hazard, because invasive species must be controlled to support biodiversity conservation efforts.

KEYWORDS
Biotic homogenisation; invasion risk; non-native plants; novel urban ecosystems; ruderal plants; urban biodiversity

Introduction

Vacant land has traditionally been overlooked by urban planning or urban governance (Bowman & Pagano, 2004). However, in recent years, with shrinking cities becoming more common around the world due to the epidemic foreclosure of companies and the collapse of real estate investments due to the global financial crisis, interest in wastelands and derelict has increased, and a new generation of studies on this topic has emerged (Anderson & Minor, 2017; Burkholder, 2012; Deng & Ma, 2015; Dubeaux & Sabot, 2018; Gandy, 2013). Several recent studies draw attention to the social and environmental value/services of wastelands (Anderson & Minor, 2017; Botzat et al., 2016; Burkholder, 2012; Carlet et al., 2017; Kim et al., 2016; Threlfall & Kendal, 2018; Zefferman et al., 2018). Nowadays, vacant land is progressively being regarded as part of the city's green infrastructure (Kim et al., 2016; Lokman, 2017), serving as spontaneous or unplanned

CONTACT Estêvão Portela-Pereira estevao@campus.ul.pt
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green areas and providing cultural services, such as vital exposure to wilderness, with reduced or zero costs (Botzat et al., 2016; Heckert & Kondo, 2018; Kim & Kim, 2016; Rupprecht et al., 2015; Threlfall & Kendal, 2018; Zefferman et al., 2018). In fact, aesthetic and affective qualities may be attributed to the crude authenticity of 'novel urban ecosystems' (hereinafter 'NUE'), with their naturalistic appearance (Gandy, 2013; Lokman, 2017).

However, using wastelands as unplanned green spaces implies knowledge of their vegetation. Still, research on NUE is relatively recent (compared to other more natural ecosystems) and has mainly been conducted in Temperate cities (Celesti-Grapow et al., 2006; Godefroid et al., 2007; Rupprecht et al., 2015), with some exceptions. Some studies on this topic have been developed, for instance, in Southern Europe (Celesti-Grapow & Blasi, 1998; Celesti-Grapow et al., 2006; Dana et al., 2002). In Portugal, particularly, these studies are limited to some floristic relevés within the ruderal vegetation classification (Costa et al., 1997, 2012; Mouga et al., 1995). Although old walls or roofs are recognised as secondary habitats (Mouga et al., 1995), only recently has urban biodiversity begun to be studied from a new perspective by Portuguese researchers (Farinha-Marques et al., 2017; Graça et al., 2018).

Furthermore, as urbanisation is arguably a major cause of biotic homogenisation (Müller et al., 2013; Olden et al., 2005), one might be tempted to believe that the spontaneous vegetation of cities will not display much regional variability. However, research suggests that the species composition of NUE is influenced by several biotic and abiotic environmental conditions, which may vary according to region, biome and city history (Bonthoux et al., 2014; Müller et al., 2013; Muratet et al., 2007; Rupprecht et al., 2015). Cities are deeply altered environments where temperature, water availability, and soil nutrients differ from those of the surrounding regions. These conditions provide both opportunities and challenges for organisms, creating a unique biosphere where anthropophilic species are favoured (Burkholder, 2012). Cities have many disturbed habitats and an altered ecosystem functionality (Sandström et al., 2006), which makes invasion ecology a particularly relevant feature (Richardson & Ricciardi, 2013; Penone et al., 2012). Due to the presence of human-introduced species, NUE are expected to have a great diversity of species. However, opinions differ on whether this variety is positive for the environment (Müller et al., 2013). Studies already conducted on NUE show that in some cases they can have rare-endangered native species (Dana et al., 2002; Kowarik, 2011; Müller et al., 2013; Muratet et al., 2007), but tend mainly to favour generalist species (Müller et al., 2013).

Moreover, although urban biodiversity is reasonably well understood, there is still some controversy surrounding what should be prioritised for conservation and management (Farinha-Marques et al., 2011; Given & Meurk, 2000; Hamilton, 2005; Kowarik, 2011; MEA, 2005; Müller et al., 2013; Müller & Werner, 2010; Puppim de Oliveira et al., 2011). A consensual definition of urban biodiversity was attained in the UN Biodiversity Convention (CBD, 2012) but some authors exclude non-native species or managed ecosystems from biodiversity (Sala et al., 2000), highlighting 'true biodiversity' (Olden et al., 2005). They argue that the aforementioned urban habitat variety is not necessarily synonymous with biodiversity (Müller & Werner, 2010), since it can make cities a hub for non-native species dispersion and invasion, affecting the surrounding ecosystems (Godefroid et al., 2007; Kowarik, 2011; Müller & Werner, 2010; Sukopp, 2002). Furthermore, non-native species can promote new taxa, but hybridisation is a major contemporary extinction force (Richardson & Ricciardi, 2013), especially for rare native species (Müller et al., 2013). Conversely, other authors consider the biocentric approaches to biodiversity and the defense of species origin a prejudice (Davis et al., 2011; Simberloff, 2016) and a menace to the future of novel urban wilderness (Gandy, 2016; Kowarik, 2018; Threlfall & Kendal, 2018).

The aims of this study on Portuguese NUE vegetation are to analyse: (a) plant communities' diversity, composition and traits; (b) regional variability/homogenisation of flora; (c) explanatory environmental conditions; and (d) non-native and invasive species.

Methods

Study area

The NUE of four cities (administratively distinct municipalities) in two urban areas of mainland Portugal were studied: Lisbon and Barreiro in the Lisbon Metropolitan Area (LMA) in the southwest central region, and Guimarães and Vizela in the Ave Intermunicipal Community (AIC), in northwest Portugal. These two urban territories have different natural and urban contexts. The LMA is the main Portuguese urban area (2.8 million inhabitants, according to the 2021 preliminary census results). Bordered by the Atlantic Ocean, it is divided by the Tagus River. Lisbon, on the north bank, is the centre of this urban region, boasting an area of 100 km^2 and 544,851 inhabitants (2021 census preliminary results). Barreiro is a former industrial suburb (awaiting renovation) on the south bank. Its development dates to the late 19th century, when the railway was established, and the first manufacturing plants emerged. Over the decades, the city became a prosperous industrial centre (cork, agrochemicals, electrical, metallurgical, and heavy steel sectors). After the 1970s, Barreiro experienced severe de-industrialisation and a population decrease. In the last census (2021), the number of inhabitants in the municipality stood at 78,362. Framed in the Mediterranean biome, with a Mediterranean pluviseasonal oceanic climate (Monteiro-Henriques et al., 2016), forests of *Olea europaea* var. *sylvestris* in volcanic vertic soils, *Quercus faginea* subsp. *broteroi* in marlstones and *Quercus suber* in siliceous sandstones or volcanic rocks (Capelo et al., 2007) are the potential natural vegetation.

Conversely, with a population of 418,586 in 2021, the AIC is characterised by urban sprawl associated with diffuse industrialisation (textile and clothes industry). Guimarães, a medieval and touristic city, with 156,852 inhabitants in the municipality (2021 census preliminary results), is the most important urban centre in this region; Vizela is a small town known for its Roman baths which has become an industrial centre with 23,903 inhabitants in the municipality. Both have experienced deindustrialisation in recent decades and ruins and urban derelicts populate their municipalities. The AIC region is characterised by a Mediterranean pluviseasonal oceanic climate in the lower areas and a Temperate (sub-Mediterranean) oceanic climate in the higher areas (Monteiro-Henriques et al., 2016). The potential vegetation is a thermophilous *Quercus robur* forest with *Q. suber* (Capelo et al., 2007), with Temperate features. The soils and lithology are mostly silicicolous, deriving from granites and schist.

Site selection

The site selection was based on the results of an exhaustive inventory of ruins and vacant lands in the four cities, combining remote sensing techniques and fieldwork (Brito-Henriques et al., 2018). A sample from that inventory set was chosen. 16 sites were studied in the two urban areas, five in each of the main cities and three in the secondary ones. The site areas vary from the simple ruins of a house and its curtilage to industrial complexes with different types of ruins and vacant lots. The sites were selected to cover these different (and representative) types as well as scattered locations across the urban fabric of the four cities, and also on the basis of their easy and safe access. They included the vacant lands of former agricultural fields close to streets (four), remnants of forest edges (one), industrial ruins and demolitions and their vacant surroundings (five), abandoned railways (one), and derelicts of houses, yards and unfinished constructions and allotments, including old roofs and walls (five).

Vegetation survey

Only vascular plants were surveyed. The nomenclature of the taxa was mainly in line with Castroviejo (1986/2015) and Franco & Rocha Afonso (1971/2003), while the syntaxa followed

Costa et al. (2012). The plant composition of the sites was sampled through 60 relevés, 28 in the LMA and 32 in the AIC, between early May and June. Floristic relevés were performed based on the phytosociological method, with the distribution and number of samples were defined by the vegetation patterns found on the sites. The sample areas were defined within these patterns randomly (size depended on vegetation type – a few square metres when herbaceous, around a hundred square metres when arboreal) and all the species were identified and their cover-abundance registered by means of the Braun-Blanquet scale (then converted to the average percentage) (Godefroid et al., 2007).

Flora

The list of species was classified using different plant typologies: taxonomic, geographical origin of the species, Raunkiaer life form, ecological (preferential ecology of each species according to the vegetation types of Costa et al., 2012), the adapted Pignatti chorological type and naturalisation status of Richardson et al., as reported by Portela-Pereira (2013) (Supplementary Appendix 2).

Environmental survey

The environmental characteristics, which can influence the flora of these sites, were also recorded. For each sample, some parameters were measured on site, such as elevation, soil and substrate characteristics (depth, texture), and others were later typified, such as types of habitat (topographic features), vegetation (plant community structure), vacantness (ruin or vacant origin) and age and degree of disturbance. Bioclimatic indicators (Itc – compensated thermicity index – and Io – ombrothermic index – of the Rivas Martinez classification system, 2011 version) were also used (Monteiro-Henriques et al., 2016) (Supplementary Appendix 1).

Statistical analysis

Floristic and environmental surveys were analysed in Canoco 5, through a CCA (Canonical Correspondence Analysis) multivariate constrained ordination (Šmilauer & Lepš, 2014) (dataset: 60 samples, 339 species and 12 environmental explanatory variables). The response data were log-transformed ($1*Y+1$) and the rare species in the dataset were downweighted (Šmilauer & Lepš, 2014). Of the initial environmental variables, only 8 variables were accepted by the CCA, using a forward selection approach (Supplementary Appendix 1).

The flora were also analysed by comparing the lists of the two urban areas through descriptive statistics.

Results

Plant communities' diversity, composition and traits

Seventy-nine botanical families are represented in the NUE flora catalogue, including *Poaceae* (15%), *Asteraceae* (14%) and *Fabaceae* (13%). The LMA and AIC spectra are similar, however in the AIC, *Asteraceae* is the most represented family.

In the NUE sampled, 73% of the species are interpreted as native. The identified flora include species such as *Quercus suber*, a protected national tree, 26% are non-native, and the cryptogenic species only represent 1%. Comparatively, the LMA and AIC catalogues are similar, pointing to the same proportion of around 75% native and 25% non-native species (Figure 1). Among the LMA native species, the rocky West Iberian endemism *Antirrhinum linkianum* may be noted,

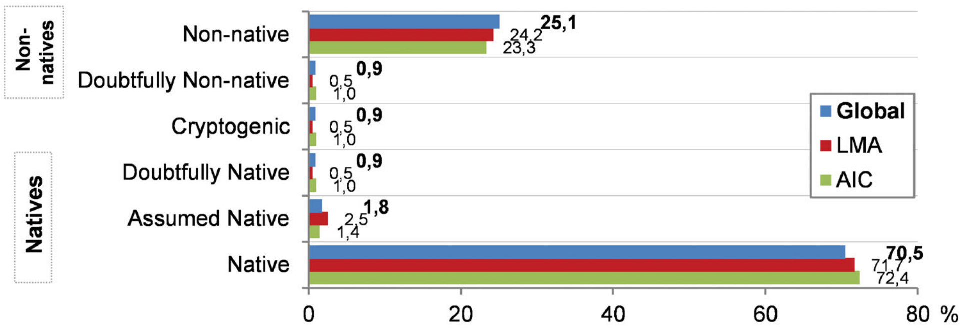

Figure 1. Nativeness spectrum of Portuguese NUE plant species. Species origin. *Note*: Global: both urban areas; LMA: Lisbon Metropolitan Area; AIC: Ave Intermunicipal Community.

occurring close to calcareous ruins. In the AIC, five Iberian endemisms were identified: *Carex elata* subsp. *reuteriana*, from rocky river channels; *Echium rosulatum*, nitrophilous in siliceous soils; *Dactylis glomerata* subsp. *lusitanica*, from grasslands; *Adenocarpus lainzii* and *Ulex europaeus* subsp. *latebracteatus*, from north-west Iberian shrubland. However, none of these endemisms or protected species are rare or threatened.

The NUE flora is clearly composed of herbaceous plants (77%), dominated by terophyte (44%) and hemicryptophyte (28%) life forms. The third dominant life form consists of trees (including arborescent shrubs) (15%), while shrubs represent only 5% (divided equally by camephytes and nanophanerophytes) (Supplementary Appendix 3).

Most of the species find their ecological optimum in synanthropic vegetation (Figure 2), and some non-native species have their optimum in (semi-) natural habitats that are disturbed, such as coastal dunes (*Carpobrotus edulis*), rock crevices (e.g. *Erigeron karvinskianus*) or anthropized riparian forests. Thus, 58% of the species have ecological preferences for vegetation disturbed by human activities. Given their importance, several subtypes were distinguished of which species with synanthropic sunny annual vegetation preferences (25.7%) were noted. However, some species with their optimum in non-ruderal habitats are also worthy of mention, such as plants from terophytic grasslands (7.4%), meadows (6.8%) and native forests (5.6%).

In the species distribution range (chorotypes) there is a clear predominance of Mediterranean elements (31%) and Paleotemperates (17%), followed by American species (10%) (Figure 3).

(Homogenisation and) flora regional variability

As mentioned with regard to nativeness, but with greater biotic homogenisation, the flora of the two LMA and AIC urban areas also have similar life form spectra, although some differences may be noted: in the LMA, terophytes are more prevalent (52%) than hemicryptophytes (22%), whereas in the AIC, terophytes (39%) and hemicryptophytes (33%) are more balanced (Supplementary Appendix 3).

A similar picture is also found in the ecological spectrum. In the LMA, there are more synanthropic vegetation species (66%) than in the AIC (53%). This difference is mainly due to increasing annual ruderal vegetation species in the LMA (34%), which were also the most representative in the AIC, albeit amounting to only 21% (Figure 2).

In the chorotypes, apart from some homogenisation indicated by the presence of non-native (American) elements (10% LMA, 9% AIC), there is evidence of regional differences. In the LMA, the Mediterranean elements are clearly the most dominant (38%), with less expression of Paleotemperates (13%) and other European and Mediterranean elements, namely Mediterranean-Iranian-Turanian (9%) and Subcosmopolitan elements (8%) (Figure 3). In the AIC, the Mediterranean (23%) and Paleotemperate (22%) elements are co-dominant. Other European and

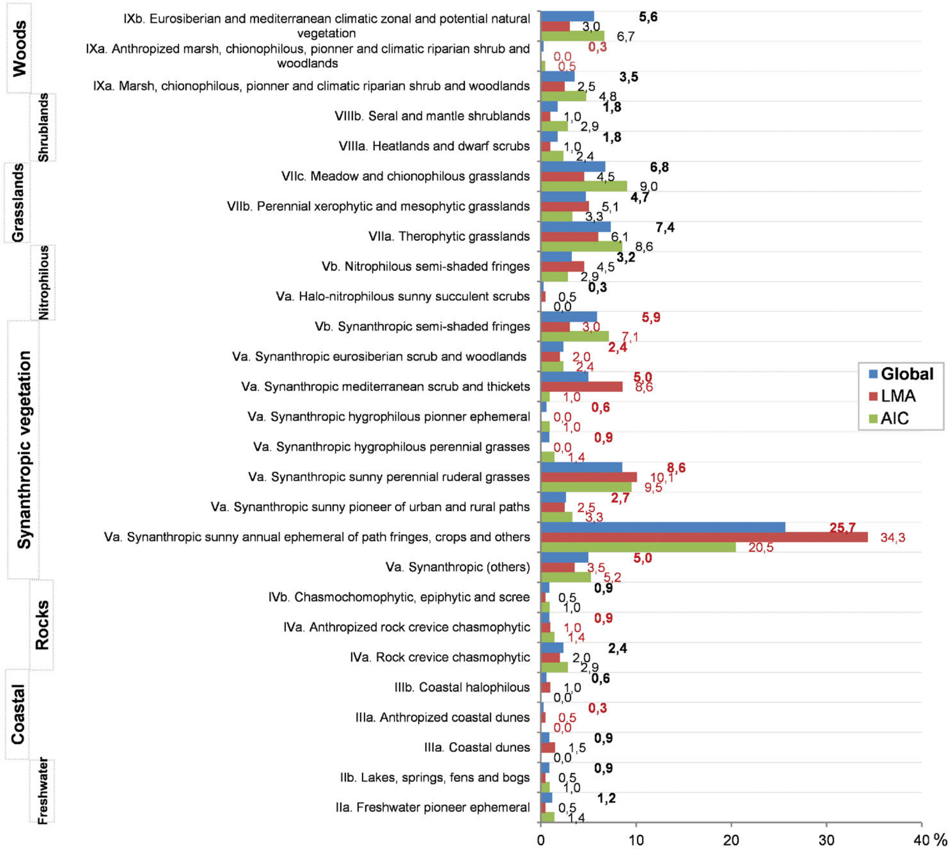

Figure 2. Ecological spectrum of Portuguese NUE plant species. Vegetation (sub)types, based on plant species' ecological (syntaxonomical) optimum in Portugal. *Note (to online version)*: Values in black identify natural vegetation types; in red synanthropic vegetation or anthropized natural vegetation types. Global: both urban areas; LMA: Lisbon Metropolitan Area; AIC: Ave Intermunicipal Community.

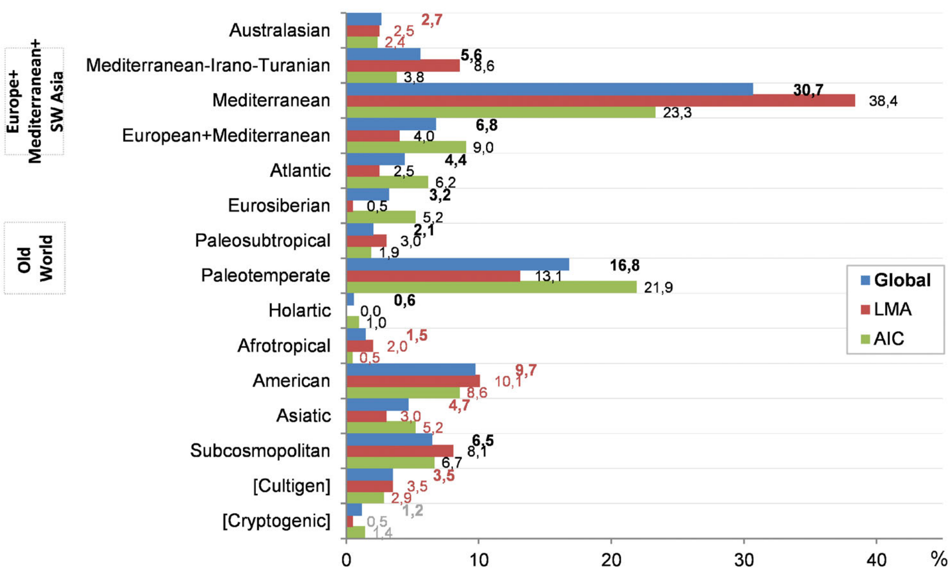

Figure 3. Chorological spectrum of Portuguese NUE plant species. Chorotypes. *Note (to online version)*: Values in black identify chorotypes mainly with native species, in red those with non-native, and cryptogenic in grey. Global: both urban areas; LMA: Lisbon Metropolitan Area; AIC: Ave Intermunicipal Community.

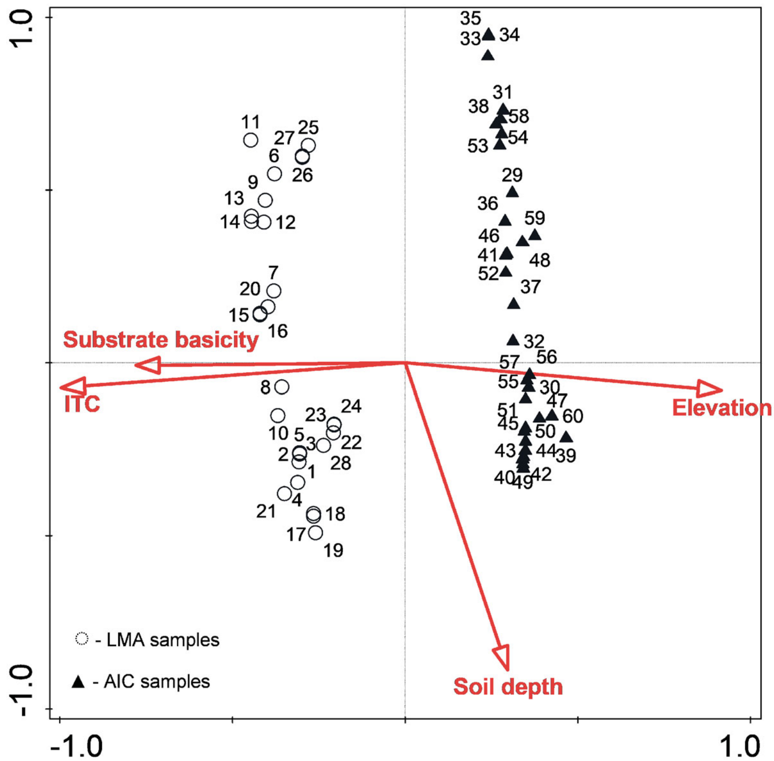

Figure 4. CCA biplot, sample sites and environmental variables. *Note*: LMA: Lisbon Metropolitan Area; AIC: Ave Intermunicipal Community.

Mediterranean elements enrich the flora (European + Mediterranean (9%), Atlantic (6%) and Eurosiberian (5%), which are residual in the LMA). Subcosmopolitan elements were also found to have some expression (7%).

A comparison of all NUE relevé samples pointed to the main vegetation difference being an evident floristic distinction between the LMA (CCA biplot left half) and AIC (right half) plant communities (Figure 4). This difference was mainly due to the urban areas only sharing 20% of the species, with 42% being exclusive to the AIC and 38% to the LMA. This is partly because the species matrix only represents a part of the flora of these territories. Furthermore, biogeographically, some native species that are characteristic of northwestern Portugal do not naturally occur in the LMA and vice-versa. *Carex reuteriana* or *Adenocarpus lainzii*, for instance, are Iberian Atlantic endemisms (Figure 5). On the other hand, *Reichardia picroides*, *Olea sylvestris* and *Blackstonia acuminata* subsp. *aestiva*, are Mediterranean elements, mainly basophilous, which do not occur in the AIC.

Environmental conditions

The CCA also showed that environmental variables respond to this differentiation (the accumulated variance of two main variables was only 7.85%) (Table 1). The selected response variables were temperature (analysed through Itc) and soil depth. Itc is higher in the LMA, reflecting a more termophilous climate, with little occurrence of winter frost. The artificial urbanscape features of the NUE are not directly highlighted in the multivariate analysis. Nevertheless, it is possible to detect some individualisation of rocky plant species in concrete and ruins through a soil depth gradient (biplot upper half) (Figure 5). Elevation and substrate basicity are not such important response variables (Table 2). The explained cumulative variance for all four variables

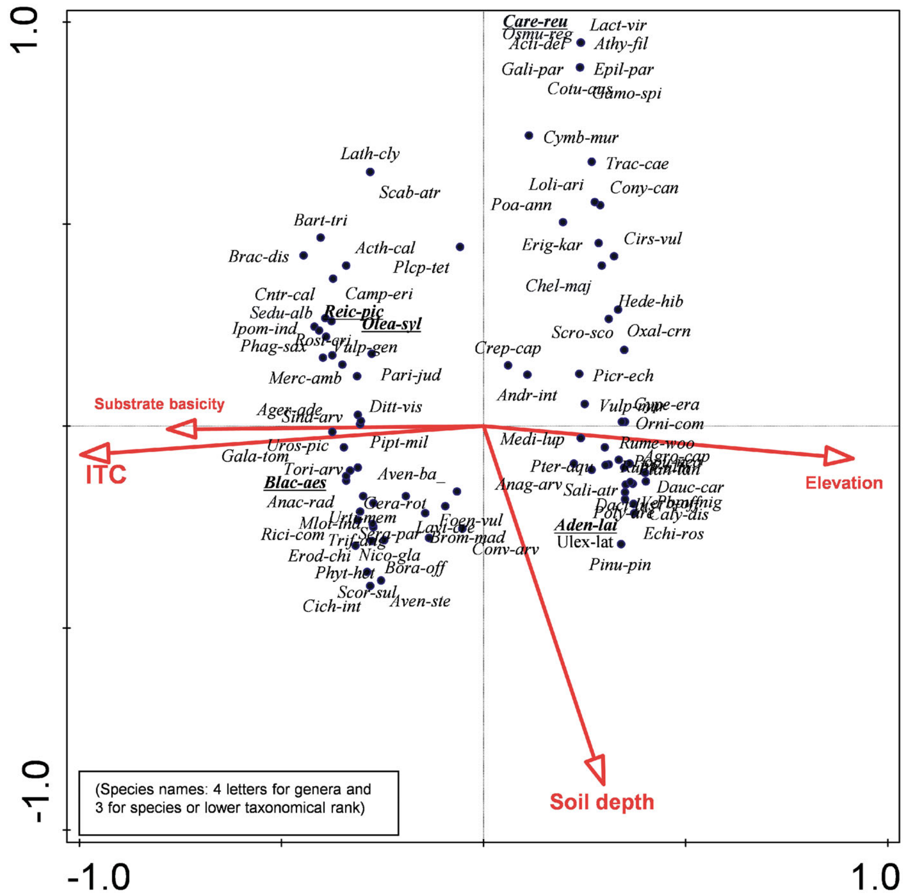

Figure 5. CCA biplot species and environmental variables.

Table 1. Summary of 'constrained-P' analysis, method CCA (Canoco 5).

Analysed data summary				
Cases	60 relevés			
Response variables	339 species			
Explanatory variables	8 environmental variables [DF = 4]			
Summary of results				
Total variation is 12.41877, explanatory variables account for 12.2% (adjusted explained variation is 5.8%)				
Summary table				
Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.6313	0.3432	0.2872	0.2516
Explained variation (cumulative)	5.08	7.85	10.16	12.19
Pseudo-canonical correlation	0.9754	0.9095	0.8862	0.8795
Explained fitted variation (cumulative)	41.72	64.40	83.38	100.00

Table 2. Forward selection results of 'constrained-P' analysis, method CCA (Canoco 5).

Name	Explains %	Contribution %	Pseudo-F	p
ITC	5.1	22.7	3.1	0.0001
Soil depth	2.7	12.2	1.7	0.0001
Elevation	2.3	10.4	1.4	0.0017
Substrate basicity	2.1	9.4	1.3	0.0127

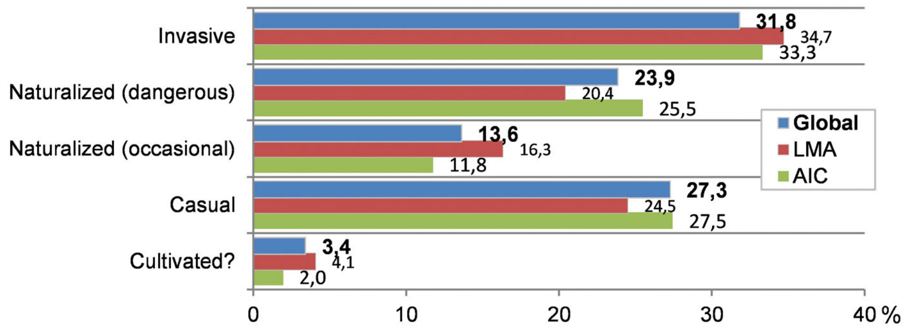

Figure 6. Naturalisation spectrum of Portuguese NUE plant species. Naturalisation status. *Note*: Global: both urban areas; LMA: Lisbon Metropolitan Area; AIC: Ave Intermunicipal Community.

accepted by the model was 12.2% (Table 1). Other variables such as age and degree of disturbance or biotope type are of no statistical significance.

Non-native and invasive species

Evaluating only non-native flora (88 out of 339) in the naturalisation spectrum, most species carry both an effective and potential ecological risk. Of these, 32% (or 8% in the Portuguese NUE total flora) had an invader status in Portugal (Figure 6). If naturalised-dangerous species are added, 56% of non-native species have a serious potential risk of invasiveness, representing 14% of the total flora found in the NUE. Comparing the two regions, it is worth noting that the percentage of effective and potential invasive species was slightly higher in the AIC (59%) than in the LMA (55%).

Discussion

Novel urban ecosystems – richness or invasion of species?

Species richness is often higher in cities and may be even higher in NUE than in formal green spaces, due to the combination of natural and anthropic processes in the introduction and dissemination of the flora (Bonthoux et al., 2014; Rupprecht et al., 2015). The findings of this survey corroborate this conclusion. The species richness of NUE is attested by the fact that around 9% of the entire spontaneous Portuguese flora (i.e. including native and non-native naturalised species) is present in the sampled urban areas. The wide diversity of species in the NUE is also related to the fact that urban ecosystems are more cosmopolitan than more natural ecosystems, with a higher frequency of non-native species. In Central Europe, cities have 14% more non-native species than the surroundings areas, and in the centre of Berlin the non-native frequency is as high as 54% (Muratet et al., 2007). Despite being clearly dominated by native species, the NUE sampled were observed to have a higher non-native species percentage (26%) than the mainland Portuguese territory (18%) (Morais et al., 2017) or the riparian forests of the Portuguese Tagus River basin (21%) (Portela-Pereira, 2013). This relative frequency is also higher than in other Mediterranean NUE, such as Almeria (Spain) (17%) (Dana et al., 2002), but similar to the non-native species frequency observed in cities (global average) (28%) (Aronson et al., 2014), such as in Brussels (28%) (Godefroid et al., 2007) and Plzen (Czech Republic) (29%) (Müller et al., 2013). Normally, conservation examples of sensitive-endemic and rare or threatened species in NUE occur in remnants of native ecosystems, namely in rare or declining habitats (Kowarik, 2011; Muratet et al., 2007), such as the case of the halophilous habitats of Almeria (Dana et al., 2002). Although not all the native species are capable of tolerating the challenging conditions of cities (Rupprecht et al., 2015), important species may still emerge in NUE (Aronson et al., 2014), for example in Paris (Muratet et al., 2007). In most cases, these species occur mainly when the NUE mimic natural habitats (Rupprecht et al., 2015), such as the old walls in Almeria (Dana et al., 2002) and the disused German railway lines, and can even include self-sustaining populations (Farinha-Marques et al., 2011; Kowarik, 2011). In the Portuguese NUE some endemics are found in native vegetation remnants and secondary habitats, e.g. the nitrophilous *Echium rosulatum* is well adapted in the AIC.

However, urbanisation reduces previously abundant native species to boost the number and extent of invaders by increasing the introduction of new species for ornamental purposes, and creating disturbed habitats (Kowarik, 2011; McDonald et al., 2013). Proportionately, Portuguese NUE also foster far more potential and effective invaders than mainland Portugal (at least 17% according to Morais et al. (2017)) and the Portuguese Tagus riparian forests (33% according to Portela-Pereira (2013)).

Plant species traits – regional variability and risks of biotic homogenization in novel urban ecosystems

The chorological origin of non-native species does not really differ between the NUE in the two urban regions, with the American species constituting the main group. Moreover, at the national level, Portugal's naturalised flora is dominated by plants of American origin (Almeida & Freitas, 2001). Although this indicates some biotic homogenisation – a pre-state of biodiversity and (bio)-cultural loss (Ignatieva, 2010; Olden et al., 2005) – in the Portuguese NUE species, their origins are not yet completely homogenised.

Portugal's position between the Mediterranean and Atlantic has produced a diversified flora that differs considerably from region to region. Despite the small size of the country, the Portuguese landscape is naturally diverse, and the native identity of the flora is also perceived in the Portuguese NUE. Mediterranean elements are dominant in both the urban regions under study, however northern AIC displays a higher influence of a Temperate biome than the LMA. In fact, beyond this analysis of the flora through the species' corotypes, and also in the multivariate analysis of Portuguese NUE relevés, the main pattern results from the influence of the biome on the species' assemblage (Aronson et al., 2014; Müller et al., 2013), due to Portugal's border position. Although not dominant, native regional species give identity to Portuguese NUE vegetation. These results, taken with those found in the ecological spectrum, point to the importance of controlling non-native species to maintain the biological diversity and regional identity (and therefore the nativeness) of NUE, contrary to what is defended by other authors (Threlfall & Kendal, 2018).

The Portuguese NUE ecological spectrum is dominated by opportunistic species, with ecological optimum in vegetation disturbed by human activities. Although they may contain some important species for conservation, urban ecosystems cannot substitute natural ecosystems' functioning for species that are sensitive to fragmentation (Bonthoux et al., 2014; Farinha-Marques et al., 2011; Kowarik, 2011). NUE foster generalist species which tolerate a greater range of environmental conditions (Bonthoux et al., 2014; Farinha-Marques et al., 2011; McDonald et al., 2013). Species' richness may increase but make NUE particularly susceptible to biotic homogenisation (Bonthoux et al., 2014; McDonald et al., 2013), and contribute to a loss of global species' richness and biodiversity (Aronson et al., 2014). In Temperate European cities, besides ruderal nitrophilous perennials, natural grassland species may also be dominant (Maurer et al., 2000; Muratet et al., 2007). Curiously, the ecological optimum of native non-synanthropic species in Portuguese NUE also highlights (Figure 2) some common apophyte species in northern hemisphere cities. These native species originate from natural therophytic grasslands and meadow-riparian habitats (Müller & Werner, 2010), which are also (semi-)natural disturbed habitats.

The differences detected in the NUE ecological spectrum in the two Portuguese urban regions may be explained by the fact that AIC cities are smaller than those in the LMA and have undergone a more recent urban expansion (Müller et al., 2013). Elements of non-ruderal native vegetation penetrate further in the AIC, since more natural landscape remnants are available, enabling more native propagules for 'rewilderness'. Hence, it may be said that the NUE of the AIC are more connected to the countryside surroundings than those of the LMA. This may also explain the slightly higher frequency of non-native species with an invasion risk, since connectivity works for both florae (Muratet et al., 2007).

Disturbance in urban ecosystems also enhances annual and biennial species (Kowarik, 2011; Maurer et al., 2000). These are characteristics of 'urbanophytes', besides their other broad ecological assets (Müller & Werner, 2010; Muratet et al., 2007). Many of today's cosmopolitan weeds, mainly having evolved in European cities (Müller & Werner, 2010), represent biotic homogenisation in life forms. The Portuguese NUE life form spectrum does not differ from this reality and, as already mentioned, is also dominated by this type of herbaceous plant species.

Novel urban ecosystems' environmental predictors

The evaluation of the relative influence of ecological variables on species in urban areas is more complex than in natural areas due to the fact that these variables are mixed with (and subject to) anthropogenic variables (Aronson et al., 2014; Müller et al., 2013; Muratet et al., 2007) and this is also a more recent type of assessment (Godefroid et al., 2007; Müller et al., 2013) with several limitations (e.g. large variability, geographical bias) (Aronson et al., 2014; Bonthoux et al., 2014; Rupprecht et al., 2015). In Portuguese NUE, vegetation responds to environmental factors, yet the amount of generalist species and the variety of human intervention can make such relations inconspicuous (perhaps the justification for the particularly low cumulative variance explained by the CCA), more than in natural ecosystems. Nonetheless, temperature (Itc, and correlated Io) was the most important variable for the Portuguese NUE vegetation distribution, reflecting the climatic differences between the LMA and the AIC (Monteiro-Henriques et al., 2016). The importance of temperature for the NUE vegetation has already been documented in the literature. Gradients in the local air temperature and humidity pointed to a significant influence on species' composition in Brussels, as well as the temperature in Berlin's railway wastelands (Bonthoux et al., 2014). In Central Europe, different relationships between temperature and neophytes (i.e. non-native species introduced after 1492) were found in urban florae (Godefroid et al., 2007). Temperature, soil moisture and nutrients are environmental filters that explain the higher frequencies of invasive and non-native species in urbanised landscapes (Penone et al., 2012).

The influence of lithology in the NUE vegetation is not direct since it may vary with the scale of analysis. In Portuguese NUE, both lithology and elevation are related to the CCA climatic gradient. Substrate basicity is higher in the LMA (more calcareous lithology), but this gradient is overshadowed by the climatic differences between the two urban regions. In Germany, city lithological heterogeneity was the most important factor found to explain the number of native species (Kowarik, 2011). Nonetheless, in the highly urbanised *départment* Hauts-de-Seine, no evidence of the effect of lithology or geomorphology on floristic wasteland was detected (Muratet et al., 2007). Original lithology and geomorphology may be unimportant factors in disturbed and fragmented urbanscape (Bonthoux et al., 2014; Muratet et al., 2007). In Brussels, various types of anthropogenic substrates had different effects on species' composition and the frequency of neophytes (Godefroid et al., 2007).

Moreover, soil moisture, nitrogen and pH, in addition to light intensity were the most powerful predictors of NUE species' composition studies, as in many other plant communities (Bonthoux et al., 2014; Godefroid et al., 2007; Muratet et al., 2007). In Portuguese NUE, similar ecological spectra results were attained – in both NUE the nitrophilous and heliophilous plants were dominant, and a soil depth gradient was also highlighted as a second axis in the CCA analysis.

In the present research on the Portuguese NUE, age and degree of disturbance was included in the CCA model, but not retained due to a lack of statistical significance. The age of the wasteland (Bonthoux et al., 2014) and previous land use (Godefroid et al., 2007) are related to soil parameters. Urban vegetation succession is subject to extremely variable anthropogenic influences, linked to the site's history (Sukopp, 2002). Also, plants that develop extensively, as invaders, can influence soil parameters and consequently modify species' composition (Bonthoux et al., 2014). In general, older urban landscapes have more non-native species than recently settled landscapes (Müller et al., 2013), but old wastelands are significantly less diverse than intermediate aged sites (Muratet et al., 2007), providing conditions for both early and mid-succession species (Bonthoux et al., 2014). Therefore, NUE vegetation could be deemed a non-equilibrium system, and the stochastic considered to be more important than the deterministic processes (Sukopp, 2002).

Implications for novel urban ecosystems management

Failure to appreciate various components of biodiversity, including the multifaceted process of biotic homogenisation, could well undermine the efforts to fight invasive species and sustain biodiversity (Olden & Rooney, 2006). Our results suggest that NUE have both advantages and disadvantages. If managed integrally within the scope of the sustainable daily routine and strategy of the urban fabric, they can function as temporary (or permanent) connection spaces – that is, NUE are an opportunity. Vegetation management using large amounts of money, labour and herbicides to suit abstract notions of aesthetics and social norms has proven to be ecologically and economically inefficient (Rupprecht et al., 2015). NUE may provide an ecological alternative to planned gardens if they are integrated in green corridors and sustainable management practices are applied, including ecological restorations, as suggested by some authors (Bonthoux et al., 2014; Kowarik, 2011; Rupprecht et al., 2015). Cities would benefit from NUE being managed as public spaces or commons (Zefferman et al., 2018). NUE can also be used as study labs for invasiveness, vegetation classification (Franceschi, 1996; Godefroid et al., 2007) and other eco-sociological research (Botzat et al., 2016), thus contributing to the environmental education and nature connection of dwellers (Threlfall & Kendal, 2018).

Even ruin aesthetics may be permitted, but as with every ruin, measures should be taken to ensure it does not become a hazard and risk to people (education) and (natural) heritage preservation - in other words, NUE have many opportunistic species which can have disadvantages if they are not managed and controlled. In particular, the negative impact of invaders on biodiversity should not be underestimated. Urban managers should be aware of the risks that their presence represents in NUE biodiversity management (Zefferman et al., 2018) and for the surrounding ecosystems (Graça et al., 2018).

Conclusions

In the Portuguese NUE, native species are far more frequent than non-native species. Although no rare or sensitive species were detected in the sampled Portuguese NUE, the biogeographical indicator species and Iberian endemics are diverse in the two different urban regions.

The environmental factor analysis confirms the importance of species' origins, revealing the relative influence of the biome on species' assemblages, which, in turn, are also related to climate factors, and other features, such as soil or lithology. As also seen in the chorological spectrum, the 'identity' of the two regional Portuguese NUE is characterised by native species, more Mediterranean in the LMA and less in the AIC.

Notwithstanding, Portuguese NUE are dominated by opportunistic species that contribute to biotic homogenisation, more clearly so in ecological or life form spectra than in nativeness or chorological spectra analysis. Even some of the perceived 'Americanization' does not surpass the Mediterranean and Paleotemperate elements, which have different frequencies as far as the biogeographical features of Portuguese NUE are concerned. These differences appear to confirm that smaller cities have a lower frequency of generalist species, thus pointing to a stronger connection with the surrounding native landscapes. However, connectivity may also explain the presence of more ecological risk species.

Portuguese NUE are, therefore, both an opportunity, since spontaneous vegetation management is more cost effective, contributing to bringing wilderness to cities, and a hazard, as opportunistic invasive species must be controlled to ensure that biodiversity conservation efforts are not undermined.

Geolocation information

Cities where vacant sites were studied (WGS 84): AIC – Ave Intermunicipal Community (in Portuguese 'Comunidade Intermunicipal do Ave'), Guimarães 41.44082, -8.28275 and Vizela 41.37347, -8.30972. LMA – Lisbon Metropolitan Area (in Portuguese 'Área Metropolitana de Lisboa'), Lisbon 38.71795, -9.13637 and Barreiro 38.66007, -9.08556.

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Notes on contributors

Estêvão Portela-Pereira is a geobotanist, with a degree in geography and a PhD in physical geography, on the geobotany of riparian forests. His interests are the study, classification and management of both native and non-native (invaders) flora, vegetation and habitats. Phytosociology and invasion ecology are his chosen subjects, as well as hydrogeomorphology, salicology and biogeography. Currently, his work is divided between management and restoration of protected species and habitats, flora and habitats consultancy, and research projects with the Centre of Geographical Studies (CEG) of the Universidade de Lisboa.

Carlos Neto is a biogeographer, vegetation ecologist and vascular plant taxonomist. His main areas of interest and research are biogeography, plant ecology, phytosociology and physical geography. The flora studies follow the components of taxonomy, auto-ecology, chorology, cartography, conservation policies and molecular studies. The vegetation studies have guided his research to focus on the interpretation and description of new communities and the relations with biotope characteristics and anthropic impact. The impact of environmental changes on flora and vegetation is another area of interest, especially: (1) the impact of the sea rise in the salt marshes of coastal lagoons and coastal sand dunes; (2) the importance of land cover and land use changes in natural plant communities and their floristic composition; (3) modelling the impact of environmental changes (especially climate changes) on the future spatial distribution of plant populations; (4) management policies to mitigate the impacts on natural ecosystems especially in coastal areas.

Eduardo Brito-Henriques is a human geographer whose research and publications are geared towards tourism geographies, global connections, heritage and urban natures, and devastated landscapes (post-industrial and shrinking cities, ruins, wastelands). He is Associate Professor at the Universidade de Lisboa (Institute of Geography and Spatial Planning), and within the R&D Unit — the Centre of Geographical Studies — he is head of the TERRITUR Research Group (Tourism, Heritage and Space research group).

Ana Luísa Soares has been Professor at ISA/ULisboa since 1998. She holds a degree in landscape architecture (1995) and was awarded her doctoral degree in 2007, both from ISA. She is a researcher at CEABN-InBIO/ISA/ULisboa (1998-present) where her contribution to the following may be highlighted: restoration of the Botanical Garden of Ajuda (1993-1997); and restoration of gardens' hydraulic systems, walls and trails (2007-2010), funded by EEA Grants. She has participated in several research projects, most noteworthy as Principal Investigator of the project LX GARDENS - Lisbon Historic Gardens and Parks: landscape heritage study and inventory(FCT); and as a team member for Landscape Phytosociology and Sustainable Gardens, funded by PRODER (2011-2014); NativeScapeGR, Green roofing with native species alternative urban landscape areas to enhance water use and sustainability in Mediterranean conditions (FCT) (2014-2015); NoVOID-Ruins and vacant lands in Portuguese cities (FCT). She was national delegate of COST E39: Forests, trees and human health and wellbeing (2004-2008). In 2016, she was member of the Management Commission of the Botanical Garden of Lisbon and Tropical Botanical Garden of the University of Lisbon. Since 2019 she has been the coordinator of the Botanical Garden of Ajuda, ISA/ULisbon. She is also the author of several book chapters and scientific papers.

Sónia Talhé Azambuja obtained a degree in landscape architecture from the School of Agriculture (ISA) of the Technical University of Lisbon (2000), and pursued studies at the School of Arts and Humanities of the University of Lisbon (FL/ULisboa), concluding her Master's in art, heritage and restoration (2006) and Ph.D. in history (art, heritage, and restoration, 2015) with the classification of *summa cum laude*. She currently holds the position of Invited Assistant Professor of Landscape Architecture at the University of Lisbon ISA/ULisboa and at the University of Algarve (FCT/UAlg). She lectures in the areas of history and theory of landscape architecture and art, and rendering in landscape architecture. She is author of two books on the symbolism of plants, animals, and landscape in Portuguese Painting of the 15th–17th centuries [(Lisbon: Scribe, 2021), (Lisbon: Nova Vega, 2009)]. She is also author of several book chapters and scientific papers. She is a researcher at CEABN-InBIO/ISA/ULisboa (2011-present) and Secretary-General of the Board of the Portuguese Association of Landscape Architects-APAP (2016–2018). As President of the Association of Friends of the Botanical Garden of Ajuda-AAJBA since 2010, she coordinates the conservation/restoration works of the Botanical Garden of Ajuda. International Member of ICOMOS-IFLA International Scientific Committee on Cultural Landscapes (2009–2019).

ORCID

Estêvao Portela-Pereira http://orcid.org/0000-0001-6161-0492
Carlos Neto http://orcid.org/0000-0003-0912-0255
Eduardo Brito-Henriques http://orcid.org/0000-0002-2225-869X
Ana Luísa Soares http://orcid.org/0000-0003-2108-826X
Sónia Talhé Azambuja http://orcid.org/0000-0002-4880-808X

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