BIODIVERSITY RESEARCH



Projecting potential future shifts in species composition of **European urban plant communities**

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Abstract

Aim: Urban floras are composed of species of different origin, both native and alien, and with various traits and niches. It is likely that these species will respond to the ongoing climate change in different ways, resulting in future species compositions with no analogues in current European cities. Our goal was to estimate potential shifts in plant species composition in European cities under different scenarios of climate change for the 21st century.

Location: Europe.

Methods: Potential changes in the distribution of 375 species currently growing in 60 large cities in Southern, Central and Western Europe were modelled using generalized linear models and four climate change projections for two future periods (2041–2060 and 2061-2080). These projections were based on two global climate models (CCSM4 and MIROC-ESM) and two Representative Concentration Pathways (2.6 and 8.5).

Results: Results were similar across all climate projections, suggesting that the composition of urban plant communities will change considerably due to future climate change. However, even under the most severe climate change scenario, native and alien species will respond to climate change similarly. Many currently established species will decline and others, especially annuals currently restricted to Southern Europe, will spread to northern cities. In contrast, perennial herbs, woody plants and most species with temperate continental and oceanic distribution ranges will make up a smaller proportion of future European urban plant communities in comparison with the present communities.

Main conclusions: The projected 21st century climate change will lead to considerable changes in the species composition of urban floras. These changes will affect the structure and functioning of urban plant communities.

CCSM4, climate change, plant functional types, plant invasion, urban ecology, vegetation modelling

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1 | INTRODUCTION

Understanding species responses to climate change is very important for nature conservation and management in the context of current global changes (Hannah, Midgley, & Millar, 2002; Heller & Zavaleta, 2009; Sala et al., 2000). Shifts in the distribution and abundance of plant species caused by climate change will have important effects on ecosystem processes, including net primary production and nutrient cycling (Eviner & Chapin, 2003). These shifts are not only restricted to natural or semi-natural ecosystems but also occur in urban and other human-made ecosystems (Millennium Ecosystem Assessment, 2005).

To some extent, urban ecosystems can be viewed as projections of future ecosystems; already today, their temperatures are as high as the temperatures that the surrounding rural areas will experience in the coming decades (Grimm et al., 2008; Sukopp & Wurzel, 2003). Novel plant communities develop in such dynamic ecosystems due to both urbanization and climate change (Knapp, Winter, & Klotz, 2017; Nobis, Jaeger, & Zimmermann, 2009; Walther et al., 2009). These plant communities and their formation processes are very important because they may impact the health and well-being of urban citizens. In particular, urban ecosystems provide services such as air purification, noise reduction, urban cooling and runoff mitigation (Aronson et al., 2017; Gómez-Baggethun et al., 2013). Changes in the species composition of urban communities due to global change might affect their functions, ecosystem services and ultimately urban residents.

Projecting responses of species composition of urban plant communities to future climate change can be easier and more reliable than in other ecosystem types for a variety of reasons. Over large distances and even in different macroclimatic regions, the same urban habitats can be found in nearly all cities (Rebele, 1994; Savard, Clergeau, & Mennechez, 2000). Each city contains a central square with paved areas, an urban park, residential areas and disturbed, largely unmanaged plots. These habitats are comparable between cities regarding their management, which makes them an ideal model for exploring their macroclimatic effects on species composition in comparative studies across multiple cities (Lososová et al., 2012b). Moreover, urbanization likely has a stronger effect on the species composition at the habitat level than at the city level (see e.g., Čeplová, Kalusová, & Lososová, 2017; Piano et al., 2017). In the future, even if cities differ in terms of their management and environmental policies, projections of future changes in species composition based on comparable urban habitats will be less affected by these policy differences between cities than the projections based on the whole urban floras.

Future species establishment requires not only suitable macroclimate but also the capacity of species to disperse to areas with favourable environmental conditions and, if possible, empty niches, limited competition and low incidence of other negative biotic interactions (Ehrlén & Morris, 2015; Thuiller et al., 2013). All the species currently occurring in urban areas have overcome environmental filters imposed by urbanization (Aronson et al., 2016; Williams et al., 2009); therefore, we may suppose that species with similar dispersal strategies will have similar chances of reaching similar habitats in other cities during

a period of climate change. Migration barriers or less effective dispersal strategies may prevent or delay species from reaching new cities (Ehrlén & Morris, 2015). For instance, seed dispersal may be less effective in long-lived plants such as shrubs and trees, causing timelags between climate change and population responses. However, the dispersal limitation of a plant species is probably much weaker in urban areas than in other environments due to human-mediated intercity transport (Knapp et al., 2008; von der Lippe & Kowarik, 2007; Williams et al., 2009; but see Cheptou, Carrue, Rouifed, & Cantarel, 2008). Negative effects of biotic interactions on the establishment of newly arriving species are also limited in urban environments because cities provide heterogeneous mosaics of various habitat types occupied by many species with contrasting requirements. In highly urbanized areas, species usually occur in small isolated patches of suitable habitats with small interspecific competition (Kowarik, 2011), which is further minimized by frequent disturbances.

Urban floras are species-rich and consist of both native and alien species originating from different parts of the world (Aronson et al., 2014; Kühn & Klotz, 2006; Lososová et al., 2012a; Pyšek, 1998; Williams et al., 2009). Urban floras are composed of various life-forms, including annual, biennial and perennial herbs, and woody plants. European cities are located in different climatic regions with different regional species pools: for instance, while annual herbs prevail in Southern Europe, perennial species dominate in Central Europe (Tutin et al., 1968–1980, 1993). It is therefore likely that species of different origin or different life-forms will respond to future climate change in different ways (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010).

Our goal was to estimate the future changes in the species composition of European urban plant communities based on an original standardized sample of species composition in 60 cities in Southern, Central and Western Europe. Using two climate change scenarios for two future periods, we develop projections of the shifts in the distribution of 375 urban plant species and the resulting diversity changes in European cities. We hypothesize that future climate change will change the species composition of European urban flora and the proportions of species of different origin or different life-forms.

2 | METHODS

2.1 | Datasets

This study is based on a dataset of the species composition of urban habitats sampled across a broad climatic range in 2009–2015. We recorded plant species occurrences using a standardized protocol (for details see Lososová et al., 2012a) in 60 European cities with more than 100,000 inhabitants (Figure 1). The studied cities are distributed across Southern, Central and Western Europe, spanning a large macroclimatic gradient with mean annual temperatures from 7.9 to 18.6°C and annual precipitation from 229 to 1,289 mm (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The current and future climatic conditions for these cities are summarized in Tables 1 and S2.

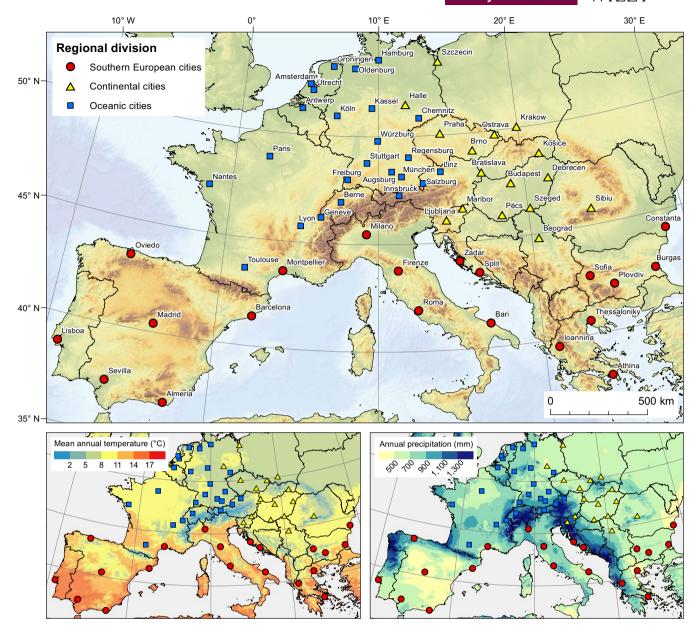


FIGURE 1 Studied cities classified based on their current climate to Southern European, Continental and Oceanic. The classification is based on macroclimatic variables as shown on the small maps below [Colour figure can be viewed at wileyonlinelibrary.com]

We recorded all spontaneously occurring vascular plant species, including ornamental species that escaped from cultivation with the exception of those deliberately planted or vegetative clones derived from planted individuals, in seven 1-ha plots in each city, with each plot representing one habitat. The sampled habitats included (1) historical city square, (2) boulevard, (3) residential area with open building pattern, (4) residential area with compact building pattern, (5) Englishstyle urban park where old mostly deciduous trees are dominant, (6) early successional site and (7) mid-successional site. The areas of these habitats were found using city plans and aerial photographs, and a representative 1-ha plot was sampled in each habitat of each city, which resulted in 420 sampled plots (7 habitats × 60 cities).

Plant taxa were identified using mainly national floras. Their taxonomy and nomenclature follow the Euro+Med PlantBase (www.emplantbase.org, accessed on July 2016) and Flora Europaea (Tutin et al., 1968–1980, 1993) for families not yet included in the Euro+Med PlantBase. For all cities, a cumulative list of the 1,948 species occurring in at least one of the seven sampled 1-ha plots was prepared and used for further analyses (Table S1). We divided the species into two groups according to their origin: native species (all European species including archaeophytes, i.e., species introduced to Europe before 1500) and alien species (all non-European neophytes, i.e., species introduced after 1500; Pyšek et al., 2004). Species native to some part of Europe and occurring as aliens in another part of Europe were considered as native. Species were further assigned to three life-form categories: annuals, perennial herbs and woody plants, following the LEDA database (Kleyer et al., 2008). Based on their macroclimatic characteristics, the studied cities were divided into Southern European, continental (eastern Central Europe and northern Balkans) and oceanic (Western Europe and western Central Europe) regions (Figure 1). The species

CCSM4 model 2050 2070 RCP 8.5 RCP 2.6 **RCP 8.5 RCP 2.6** Current climate Southern European cities Mean annual temperature (°C) Min. 10.2 11.9 13.0 11.9 14.1 Mean 14.8 16.2 17.2 16.2 18.2 Max. 18.6 20.2 21.3 20.2 22.2 Annual precipitation (mm/year) Min. 229 181 214 177 216 660 636 612 655 608 Mean Max. 1,081 1,051 1,012 1,074 999 Continental cities Mean annual temperature (°C) Min. 8.2 9.9 10.4 9.9 11.4 Mean 9.7 11.3 121 11.3 13 2 Max. 12.3 13.8 14.9 13.8 16.0 Annual precipitation (mm/year) Min. 483 488 481 480 487 Mean 659 661 657 667 654 1.289 1.284 1.309 1.319 1.267 Max. Oceanic cities Annual precipitation (mm/year) 603 601 598 596 603 Min. 793 788 791 Mean 784 791 Mean annual temperature (°C) Min. 7.9 9.5 9.8 9.4 10.8 Mean 9.5 10.9 11.5 10.9 12.4 Мах. 12.7 14.2 15.3 14.2 16.3 1,192 1,218 1,221 Мах. 1,221 1,212

TABLE 1 Climatic conditions in the surveyed European cities according to the WorldClim datasets

that significantly (p < .05) prevailed in the cities of one of these regions were identified using Fisher's exact test as available in the Juice 7.0 program (Tichý, 2002).

2.2 | Climatic data

To model current and future species distributions in European cities, we used interpolated macroclimate data at the ~1 km² resolution available in the WorldClim database (Hijmans et al., 2005; Version 1.4). Current climatic conditions were expressed using bioclimatic variables derived from the monthly temperature and precipitation values for the period 1960–1990. Future conditions were expressed using bioclimatic variables calculated based on the IPCC Fifth Assessment Report (IPCC, 2014) climate projections from two global climate models: the Community Climate System Model 4.0 (CCSM4) and the MIROC-based Earth System Model (MIROC-ESM). The CCSM4 is a general circulation climate model consisting of atmosphere, land, ocean and sea ice components that are linked through a coupler that

exchanges state information and fluxes between the components (Gent et al., 2011). The MIROC-ESM consists of three components including a comprehensive atmospheric general circulation model (GCM), an ocean GCM and a land surface model, which are coupled by a flux coupler (Watanabe et al., 2011). For both models, we considered only extreme greenhouse gas concentration scenarios as described by two Representative Concentration Pathways (RCPs). The RCP 2.6 scenario assumes the peak in global annual greenhouse gas emissions to occur between 2010 and 2020 with a slow decline after this time frames. The RCP 8.5 scenario assumes that emissions will continuously rise throughout the 21st century (Meinshausen et al., 2011). These two scenarios respectively represent the smallest and the largest future change in global climate considered by the IPCC.

To project changes in species distributions under future climate change, we considered two periods, 2041–2060 and 2061–2080, hereafter referred to as 2050 and 2070. We obtained eight bioclimatic datasets describing climatic conditions in European cities for the two future periods as projected by the two global climate models

TABLE 2 Percentage of species modelled to occur in the studied cities in the future relative to the current number of species occurring in these cities. The CCSM4 global climatic model and two extreme Representative Concentration Pathways (RCP) are considered. Mean number of species per city is calculated from all 1,948 recorded species. Number of modelled species is a subset of the total number of species that occur in 6–54 cities

				2050		2070	
Species	Current climate Mean no. of species/city	Total no. of species	No. of modelled species	RCP 2.6	RCP 8.5	RCP 2.6	RCP 8.5
Native species	240.4	1,559	579	95	93	95	92
Alien species	39.9	388	102	98	97	98	96
Annual herb	107.6	751	256	105	109	105	114
Perennial herb	130.4	907	322	92	86	91	82
Woody plant	42.4	290	103	91	84	90	79
Southern European	36.8	252	152	125	142	124	161
Continental	34.2	91	85	93	91	94	86
Oceanic	82.8	208	195	85	76	85	68

and two RCPs. All climatic data were processed in ArcGIS 10.2.2 (ESRI, Redlands, CA).

2.3 | Analyses

To estimate the patterns of future changes in the distribution of vascular plant species across European cities, we first established species distribution models for each species of urban flora based on current climatic conditions and tested the performance of the following modelling algorithms: generalized linear models (GLM), multiple adaptive regression splines (MARS), support vector machines (SVM) and random forests (RF). As all these models of current species distributions showed a similar over-fitting pattern due to the low frequency of many species across the studied cities, we decided to use binomial GLM with a regularization technique, also known as Lasso regression. This method shrinks the magnitude of each regression coefficient by adding a penalty into the cost function to avoid over-fitting problems (for details see Friedman, Hastie, & Tibshirani, 2010). The degree of regularization is controlled by λ parameter. To select the most appropriate λ , we used a 10-fold cross-validation test as implemented in the cv.glmnet function in the glmnet package (Friedman et al., 2010) of R software (R Core Team, 2014). This function selects the λ value with the lowest cross-validated binomial deviance. Models of current species distributions fitted using this technique showed very good predictive power in most cases. However, the method was able to model only species that occurred in more than five and less than 55 cities because of the low number of presence or absence data available for the model fitting procedure. Therefore, we removed these very rare and very common species from our dataset of 1,948 species and fitted GLM models only for the other 681 (35%) species. Thus, we modelled distributions of only those species for which we were able to fit reliable models. The distributions of 375 of these 681 (55%) species were significantly influenced by climate, while the other species were distributed independently of climate; thus, we were not able to model their distributions with climatic predictors. All the final models were fitted with five bioclimatic variables from the WorldClim database: annual mean temperature (BIO1), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation seasonality (coefficient of variation; BIO15) and precipitation of the warmest quarter (BIO18). These variables were identified using GLM as the most important bioclimatic variables significantly driving current distributions of most plant species recorded in the studied European cities.

The probability of species occurrence in each studied European city under future climate change was estimated based on the abovementioned species distribution models and eight sets of five climatic variables describing climatic conditions in the two future periods (2050 and 2070) as projected by the two global climate models (CCSM4 and MIROC-ESM) under two RCPs scenarios (2.6 and 8.5). For each species, the modelled occurrence probabilities for current and future climatic conditions in each city were summed, and the overall distribution change was calculated as the difference between these two models. Finally, we plotted the number of current occurrences for species belonging to different groups (native and alien species; annual herbs, perennial herbs and woody plants; Southern European, continental and oceanic species) against their predicted distribution changes to explore whether different species groups show different relationships between current distributions and predicted distributions change under future climate change.

3 | RESULTS

Our records from the studied cities cumulatively contained 1,948 species. The most common species, occurring in nearly all cities, were Ochlopoa annua, Polygonum aviculare, Sonchus oleraceus and Plantago major. Of the 375 species that were used for distribution modelling, 141 were annuals (e.g., Lapsana communis, Rumex pulcher

and Sherardia arvensis), 178 perennial herbs (e.g., Alcea rosea and Armoracia rusticana) and 56 shrubs and trees (e.g., Euonymus europaeus and Morus alba); 52 were alien (extra-European neophytes; e.g., Buddleja davidii, Oxalis pes-caprae and Sorghum halepense) and 323 were native European species (including archaeophytes). Of the 323

native species, 117 species were classified as Southern European (e.g., Andryala integrifolia, Bellardia trixago and Catapodium rigidum), 55 as continental (e.g., Chenopodiastrum hybridum and Sclerochloa dura) and 151 as oceanic (e.g., Persicaria maculosa; for more details see the species list in Table S1).

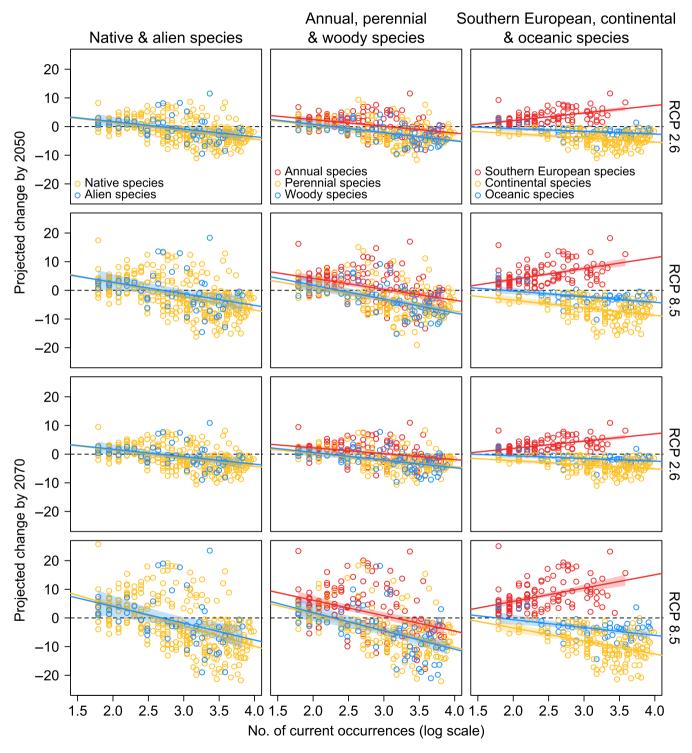


FIGURE 2 The relationships between log-transformed current occurrence frequency of each modelled species in the studied cities and its projected absolute change between the present and two future periods (2050 and 2070). Results for climatic model CCSM4 and two extreme Representative Concentration Pathways (RCP 2.6 and RCP 8.5) are shown. Linear regressions and their 0.1 and 0.9 confidence intervals show differences and their significance between species groups [Colour figure can be viewed at wileyonlinelibrary.com]

The results presented here are based on the climate model CCSM4. Both scenarios, the minimum (RCP 2.6) or the maximum (RCP 8.5) climate change projections in 2050 and 2070, suggested very similar trends in terms of the projected changes in urban plant species compositions. Our models suggest that under a warmer climate, the overall number of urban species will decrease (Table 2). The only groups of species that are likely to increase their extent are annuals and Southern European species.

Even though the general projected future trend shows the spread of relatively rare species and the decline of common ones (apart from those currently confined to Southern Europe), particular species groups are likely to respond to climate change differently (Figure 2). The models indicate future decreases in the frequencies of both native and alien species with no significant differences between these two groups, but the models also indicate significant differences in the responses to climate change between different life-forms and species of different European regions (Figure 2).

The models for annual herbs suggest an increase in the number of cities occupied by them under future climate change, whereas models for perennial herbs and woody plants suggest a decrease in occurrence. Separating species according to their regional origin suggests that Southern European species would benefit from climate change, especially after the longer time period (2070) and under the most severe climate change scenario (RCP 8.5). In contrast, continental species are likely to slowly decrease in number, while species growing in oceanic cities would be most affected by this climate change and vanish faster than continental species from the studied cities. The results for the MIROC-ESM climatic projections suggested very similar patterns but with even more pronounced species distribution shifts (Figure S1).

4 | DISCUSSION

4.1 | Current urban flora

The studied cities are distributed across Southern, Central and Western Europe spanning a large macroclimatic gradient. Despite the differences in species composition among these cities (Lososová et al., 2012a), native species prevail over alien species, and annual and perennial herbs prevail over woody plants in all the cities. Similar patterns could also be found in other large cities of the world (La Sorte et al., 2014; McKinney, 2008; Ricotta et al., 2014; Schmidt, Poppendieck, & Jensen, 2014).

4.2 | Species composition of future urban floras

According to the considered climate change scenarios, mean annual temperature in the studied area of Europe could rise by 1.5–3.3°C °C by 2070, while precipitation patterns will be more diverse, with drier summers in the Mediterranean and wetter winters in Northern Europe (IPCC, 2014; van Engelen, Klein Tank, van der Schrier, & Klok, 2008). These changes may lead to more favourable conditions for some species and less favourable conditions for

others. The structure and composition of urban plant communities will thus be considerably altered by future climate change. Many European urban species could decline (Figure 2), whereas some currently rare species (or alien species that will be introduced in the future), whose distribution we could not model, would spread. It is likely that under future climate change, the empty niches created by the decline of some currently established species will be filled by species that will be able to cope with higher temperatures and periods of drought. Such species might include those of African or Middle Eastern origins. However, some species may be less sensitive to climate changes, as indicated by approximately 45% of our studied species for which we found no relationship between their geographic distribution and climate.

Thuiller, Lavorel, Araújo, Sykes, and Prentice (2005) showed for the whole European flora that species from Southern Europe, which can tolerate high temperatures and dry summers, are well adapted to future conditions and are likely to migrate to the more northern areas in Europe. We found similar trends for urban floras, which are subsets of regional floras lacking most of the rare native species but containing a large proportion of alien species. Under the most severe climate change scenario (RCP 8.5), mainly annual herbs of Southern European origin are likely to increase their occurrence in European urban floras by 2070. In contrast, perennial herbs, woody plants and most species in the cool-temperate zone will probably be less represented in future European urban plant communities in comparison with their representation in current communities. Predicted changes in species distributions are weaker, but still obvious, for the other climate change scenarios.

Our models assume climate to be the major factor driving species distributions. We are aware that other factors are also important, especially dispersal constraints on species being able to spread, population persistence of locally established species after the climate becomes unsuitable for them, local site conditions, land use and biotic interactions (Araújo & Luoto, 2007; Svenning & Skov, 2007; Thuiller et al., 2008; Wisz et al., 2013). However, dispersal limitations are probably lessened by human-assisted dispersal in urban areas (Knapp et al., 2008; von der Lippe & Kowarik, 2007; Williams et al., 2009). Similarly, biotic interactions seem to be rather unimportant at the spatial resolution of our study, because in the seven 1-ha plots sampled in a heterogeneous environment of each city, plants with similar niches may occur in different places, therefore avoiding direct interactions (Kowarik, 2011; Pearson & Dawson, 2003).

4.3 | Alien species under climate change

Surprisingly, even under the most severe climate change scenario, no differences were found between the projected future distributions of native and alien species. However, it is likely that some of the already present or naturalized alien species could enter the invasive stage and spread quickly to new sites (Richardson et al., 2000; Williamson & Fitter, 1996).

Although our models project a decrease in the frequency of alien species under climate change, there are still many alien species

with small ranges that may potentially spread in the future, but we could not model their future distribution because of the low number of their occurrences. Several of them may have been introduced to Europe recently, not yet filling their climatic niches in Europe (Lambdon et al., 2008) and spreading under the current climate, while others are limited by the current climate but may spread under a changed climate in the future (see Carboni et al., 2017; Walther et al., 2009).

Urban areas are the centres of introduction and cultivation of ornamental plants. Most alien species in urban areas are ornamental plants that escape from cultivation (Čeplová, Lososová, & Kalusová, 2017; Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007; Haeuser, Dawson, & van Kleunen, 2017; Lambdon et al., 2008). It is likely that warmer climate together with urban sprawl will increase the invasion risk mainly for ornamental plant species in a large part of Europe, as these species are often cultivated beyond the climatic limits of their natural populations, and their survival in urban areas is also supported by irrigation or the lower risk of damage from frost due to urban heat island effects (Dullinger et al., 2016; Walther et al., 2009).

Our results suggest that mainly alien species from regions with warm climates, currently limited to Southern Europe, are likely to increase their rate of spread and colonize the cities of Central and Western Europe. Because of the globally increasing rate and extent of biological invasions (Seebens et al., 2017), new alien species from outside Europe will also appear in European cities in the future.

4.4 | Life-forms and European regions

Our models indicate that there will be different responses to future climate change among plant life-forms. However, even if there were no differences between the climatic limitations of individual life-forms, fast-spreading annuals would respond to climate change more rapidly than perennial herbs or woody plants. Annual herbs are highly dynamic plants and respond quickly to environmental change (Grime, 2001). Many annuals also possess a ruderal life strategy, producing large numbers of propagules and often being selfers (Aarssen, 1998). These traits make them able to track changing environment more quickly and effectively than other life-forms. Annual herbs of Southern European origin are especially likely to extend their range in the future. These species will be the likely winners of future climate change. Our models predict that perennial herbs and woody plants will respond to climate change more slowly.

With predicted warming, species currently occurring in warmer areas are likely to shift northwards and to higher elevations, as has been already documented for some species (Jurasinski & Kreyling, 2007; Walther et al., 2009). The number of suitable cities will increase for species that are currently restricted to Southern Europe. Species now common in Southern Europe will, on average, probably spread northwards more rapidly than rare species, which may lead to increasing homogenization of European urban flora. Nevertheless, some species currently occurring in Southern European cities may not be able to persist in increasingly arid

conditions that are expected to develop in this region (Mariotti et al., 2008). This would result in future impoverishment of the Southern European urban floras unless other species, for example, from Northern Africa or the Middle East, would fill the gap. We also expect changes in species composition in temperate parts of Europe; for example, temperate trees may be gradually replaced by trees and shrubs better adapted to warmer conditions. Species of oceanic Europe may also decline because most of the studied cities may become too dry for them.

5 | CONCLUSIONS

Using two global climate models and two scenarios of future climate change, we project significant changes in the composition of European urban floras during the 21st century. While the majority of species, mostly perennial and woody plants currently occurring in the oceanic and continental parts of Europe, will tend to decrease their geographic ranges, annual herbs of Southern European origin could expand to cities in more northern parts of Europe. Among those species that will decline, our models suggest comparable magnitudes of decline in the distribution ranges for both native and currently occurring alien species. However, it is likely that newly arriving alien species will increase the invasion risk in cities.

Our projections of future changes of urban floras have important implications for urban planners and decision makers. Increasing proportion of annual herbs in the urban habitats over the Southern, Central and Western European cities will lead to changes in ecosystem services. Plant communities dominated by annual herbs will be less effective at air purification and urban cooling than communities dominated by perennial or woody plants. Management of urban green areas should therefore focus on minimizing the decline of native perennial and woody plants while maintaining a heterogeneous mosaic of diverse urban habitats.

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DATA ACCESSIBILITY

Species data (alien status, life span and currently preferred geographic region) are archived as Supporting Information (Table S1), which may be found in the online version of this article. Climatic data (Hijmans et al., 2005) are accessible at http://www.world-clim.org/.

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REFERENCES

- Aarssen, L. W. (1998). Why are most selfers annuals? A new hypothesis for the fitness benefit of selfing. Oikos, 98, 606–612.
- Araújo, M. B., & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, 16, 743–753. https://doi.org/10.1111/j.1466-8238.2007.00359.x
- 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*, 281, 20133330. https://doi. org/10.1098/rspb.2013.3330
- Aronson, M. F. J., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., ... Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. Frontiers in Ecology and the Environment, 15, 189–196. https://doi.org/10.1002/fee.1480
- Aronson, M. F. J., Nilon, C. H., Lepczyk, C. A., Parker, T. S., Warren, P. G., Cilliers, S. S., ... Zipperer, W. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology*, 97, 2952–2963. https://doi.org/10.1002/ecy.1535
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x
- Carboni, M., Guéguen, M., Barros, C., Georges, D., Boulangeat, I., Douzet, R., ... Thuiller, W. (2017). Simulating plant invasion dynamics in mountain ecosystems under global change scenarios. *Global Change Biology*, 24, e289–e302. https://doi.org/10.1111/gbc.13879
- Čeplová, N., Kalusová, V., & Lososová, Z. (2017). Effects of settlement size, urban heat island and habitat type on urban plant biodiversity. *Landscape and Urban Planning*, 159, 15–22.
- Čeplová, N., Lososová, Z., & Kalusová, V. (2017). Urban ornamental trees: A source of current invaders; a case study from a European city. *Urban Ecosystems*, 20, 1135–1140.
- Cheptou, P.-O., Carrue, O., Rouifed, S., & Cantarel, A. (2008). Rapid evolution of seed dispersal in an urban environment in the weed Crepis sancta. Proceedings of the National Academy of Sciences of the United States of America, 105, 3796–3799. https://doi.org/10.1073/ pnas.0708446105
- Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007). A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, 13, 527–534. https://doi.org/10.1111/j.1472-4642.2007.00359.x
- Dullinger, I., Wessely, J., Bossdorf, O., Dawson, W., Essl, F., Gattringer, A., ... Dullinger, S. (2016). Climate change will increase the naturalization risk from garden plants in Europe. Global Ecology and Biogeography, 26, 43-53
- Ehrlén, J., & Morris, W. F. (2015). Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, 18, 303–314. https://doi.org/10.1111/ele.12410
- Eviner, V. T., & Chapin, F. S. (2003). Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology, Evolution, and Systematics, 34, 455–485. https://doi.org/10.1146/annurev.ecolsys.34.011802.132342
- Friedman, J., Hastie, T., & Tibshirani, R. (2010). Regularization paths for generalized linear models via coordinate descent. *Journal of Statistical Software*, 33, 1–22.
- Gent, P. R., Danabasoglu, G., Donner, L. J., Holland, M. M., Hunke, E. C., Jayne, S. R., ... Zhang, M. (2011). The community climate system model version 4. *Journal of Climate*, 24, 4973–4991. https://doi.org/10.1175/2011JCLI4083.1
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, 25, 325–331. https://doi.org/10.1016/j. tree.2010.03.002

- Gómez-Baggethun, E., Gren, Á., Barton, D. N., Langemeyer, J., McPhearson, T., O'Farrell, P., ... Kremer, P. (2013). Urban ecosystem services. In T. Elmqvist, M. Fragkias, J. Goodness, B. Güneralp, P. J. Marcutollio, R. I. McDonald, & C. Wilkinson (Eds.), *Urbanization*, biodiversity and ecosystem services: Challenges and opportunities (pp. 175–251). Dordrecht, The Netherlands: Springer. https://doi.org/10.1007/978-94-007-7088-1
- Grime, J. P. (2001). Plant strategies, vegetation processes, and ecosystem properties. Chichester, UK: Wiley.
- Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, 309, 756–760. https://doi.org/10.1126/science.1150195
- Haeuser, E., Dawson, W., & van Kleunen, M. (2017). The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. *Journal of Ecology*, 105, 1698–1708. https://doi. org/10.1111/1365-2745.12798
- Hannah, L., Midgley, G. F., & Millar, D. (2002). Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, 11, 485–495. https://doi.org/10.1046/j.1466-822X.2002.00306.x
- Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, 142, 14–32. https://doi.org/10.1016/j. biocon.2008.10.006
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. https://doi. org/10.1002/(ISSN)1097-0088
- IPCC (2014). Climate change 2014: Synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC.
- Jurasinski, G., & Kreyling, J. (2007). Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science*, 18, 711–718. https://doi.org/10.1111/j.1654-1103.2007. tb02585 x
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., ... Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of Northwest European flora. *Journal of Ecology*, 96, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x
- Knapp, S., Kühn, I., Wittig, R., Ozinga, W. A., Poschlod, P., & Klotz, S. (2008). Urbanization causes shifts in species' trait state frequencies. *Preslia*, 80, 375–388.
- Knapp, S., Winter, M., & Klotz, S. (2017). Increasing species richness but decreasing phylogenetic richness and divergence over a 320-year period of urbanization. *Journal of Applied Ecology*, 54, 1152–1160. https://doi.org/10.1111/1365-2664.12826
- Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. Environmental Pollution, 159, 1974–1983. https://doi.org/10.1016/j. envpol.2011.02.022
- Kühn, I., & Klotz, S. (2006). Urbanization and homogenization— Comparing the floras of urban and rural areas in Germany. Biological Conservation, 127, 292–300. https://doi.org/10.1016/j.biocon.2005.06.033
- La Sorte, F. A., Aronson, M. F. J., Williams, S. G., Celesti-Grapow, L., Cilliers, S., Clarkson, B. D., ... Winter, M. (2014). Beta diversity of urban floras among European and non-European cities. Global Ecology and Biogeography, 23, 769-779. https://doi.org/10.1111/geb.12159
- Lambdon, P. W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., ... Hulme, P. (2008). Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. *Preslia*, 80, 101–149.
- Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., ... Řehořek, V. (2012a). Native and alien floras in urban habitats: A comparison across 32 cities of central Europe. *Global Ecology and Biogeography*, 21, 545–555. https://doi.org/10.1111/j.1466-8238.2011.00704.x

- Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., ... Řehořek, V. (2012b). Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation*, 145, 179–184. https://doi.org/10.1016/j. biocon.2011.11.003
- Mariotti, A., Zeng, N., Yoon, J. H., Artale, V., Navarra, A., Alpert, P., & Li, L. Z. X. (2008). Mediterranean water cycle changes: Transition to drier 21st century conditions in observations and CMIP3 simulations. *Environmental Research Letters*, 3, 044001. https://doi.org/10.1088/1748-9326/3/4/044001
- McKinney, M. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11, 161–176. https://doi.org/10.1007/s11252-007-0045-4
- Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J.-F., ... van Vuuren, D. P. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. Climatic Change, 109, 213–241. https://doi.org/10.1007/s10584-011-0156-z
- Millennium Ecosystem Assessment (2005). *Urban systems*. Washington, DC: World Resources Institute.
- Nobis, M. P., Jaeger, J. A. G., & Zimmermann, N. E. (2009). Neophyte species richness at the landscape scale under urban sprawl and climate warming. *Diversity and Distributions*, 15, 928–939. https://doi. org/10.1111/j.1472-4642.2009.00610.x
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12, 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x
- Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., ... Hendrickx, F. (2017). Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, 23, 2554–2564. https://doi.org/10.1111/gcb.13606
- Pyšek, P. (1998). Alien and native species in Central European urban floras: A quantitative comparison. *Journal of Biogeography*, 25, 155–163.
- Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G., Williamson, M., & Kirschner, J. (2004). Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon*, 53, 131–143.
- R Core Team (2014). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rebele, F. (1994). Urban ecology and special features of urban ecosystems. *Global Ecology and Biogeography Letters*, 4, 173–187. https://doi.org/10.2307/2997649
- Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions*, 6, 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x
- Ricotta, C., Celesti-Grapow, L., Kühn, I., Rapson, G., Pyšek, P., La Sorte, F. A., & Thompson, K. (2014). Geographical constraints are stronger than invasion patterns for European urban floras. *PLoS ONE*, 9(1), e85661. https://doi.org/10.1371/journal.pone.0085661
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. Science, 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770
- Savard, J. P. L., Clergeau, P., & Mennechez, G. (2000). Biodiversity concepts and urban ecosystems. Landscape and Urban Planning, 4, 131–142. https://doi.org/10.1016/S0169-2046(00)00037-2
- Schmidt, K. J., Poppendieck, H. H., & Jensen, K. (2014). Effects of urban structure on plant species richness in a large European

- city. Urban Ecosystems, 17, 427-444. https://doi.org/10.1007/s11252-013-0319-v
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 14435. https://doi. org/10.1038/ncomms14435
- Sukopp, H., & Wurzel, A. (2003). The effects of climate change on the vegetation of central European cities. *Urban Habitats*, 1, 65–86.
- Svenning, J. C., & Skov, F. (2007). Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, 10, 453-460. https://doi.org/10.1111/j.1461-0248. 2007.01038.x
- Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., ... Zimmermann, N. E. (2008). Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics, 9, 137–152. https://doi.org/10.1016/j. ppees.2007.09.004
- Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005).
 Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America, 102, 8245–8250. https://doi.org/10.1073/pnas.0409902102
- Thuiller, W., Münkemüller, T., Lavergne, S., Mouillot, D., Schiffers, K., & Gravel, D. (2013). A road map for integrating eco-evolutionary processes into biodiversity models. *Ecology Letters*, 16, 94–105. https://doi.org/10.1111/ele.12104
- Tichý, L. (2002). JUICE, software for vegetation classification. Journal of Vegetation Science, 13, 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x
- Tutin, T. G., Burges, N. A., Chater, O. A., Edmondson, J. R., Heywood, V. H., Moore, D. M., ... Webb, D. A. (1993). Flora Europaea, Vol. 1., 2 ed. Cambridge, UK: Cambridge University Press.
- Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., & Walters, S. M. (1968–1980). Flora Europaea, Vols 2–5. Cambridge, UK: Cambridge University Press.
- van Engelen, A., Klein Tank, A., van der Schrier, G., & Klok, L. (2008). European Climate assessment & dataset (ECA&D). Report 2008 'Towards an operational system for assessing observed changes in climate extremes'. De Bilt, The Netherlands: KNMI.
- von der Lippe, M., & Kowarik, I. (2007). Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, 21, 986–996. https://doi.org/10.1111/j.1523-1739.2007.00722.x
- Walther, G. R., Roques, A., Hulme, P. E., Pyšek, P., Kühn, I., Zobel, M., ... Settele, J. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology and Evolution*, 24, 686–693. https://doi.org/10.1016/j.tree.2009.06.008
- Watanabe, S., Hajima, T., Sudo, K., Nagashima, T., Takemura, T., Okajima, H., ... Sato, H. (2011). MIROC-ESM: Model description and basic results of CMIP5-20c3m experiments. Geoscientific Model Development Discussions, 4, 845-872. https://doi.org/10.5194/ gmd-4-845-2011
- Williams, N. S. G., Schwartz, M. W., Vesk, P. A., McCarthy, M. A., Hahs, A. K., Clemants, S. E., ... McDonnell, M. J. (2009). A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology*, 97, 4–9. https://doi.org/10.1111/j.1365-2745.2008.01460.x
- Williamson, M., & Fitter, A. (1996). The varying success of invaders. *Ecology*, 77, 1661–1666. https://doi.org/10.2307/2265769
- Wisz, M. S., Pottie, J., Kissling, W. D., Pellisier, L., Lenoir, J., Damgaard, C. F., ... Svenning, J.-C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88, 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

BIOSKETCH

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SUPPORTING INFORMATION

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