

Urban alien plants in temperate oceanic regions of Europe originate from warmer native ranges

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Abstract When colonizing new areas, alien plant species success can depend strongly on local environmental conditions. Microclimatic barriers might be the reason why some alien plant species thrive in urban areas, while others prefer rural environments. We tested the hypothesis that the climate in the native range is a good predictor of the urbanity of alien species in the invaded range. The relationship between climate in the native range and the percentage of artificially sealed surfaces (urbanity) at the

occurrences of 24 emerging alien plant species, in European areas with a temperate climate (termed oceanic Europe) was evaluated. We found that alien species growing in more urban environments originated from warmer or drier native ranges than found in oceanic Europe. These results have strong conservation implications as climate-warming will likely lift climatic barriers that currently constrain numerous alien plant species to cities, boosting the role of cities as points of entry for invasive plants.

Keywords Alien plant species · Biological invasions · Urbanization · Native climate · Global changes

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Introduction

The second half of the twentieth century has been characterized by a steep rise in international trade, travel, and transport, resulting in the biotic homogenization of the world through increased alien species introductions (Olden and Rooney 2006; Pyšek et al. 2010; van Kleunen et al. 2018). Data from Europe shows that most recorded introductions happened after 1990, during the so-called “globalization era” (Hulme 2009). The success and speed of alien species invasion depend on the propagule pressure of alien species and the lifting of certain barriers, such as lower abiotic or biotic constraints in the introduced range (Dullinger et al. 2017). Only a small portion of introduced alien species passes all of these barriers (Walther et al. 2009) to become invasive, and significantly impacts native biota (Dullinger et al. 2017). Alien plant invasions occur in all habitats, extending from rural-to-urban ones. However, some land use categories, especially the most anthropogenic ones (e.g., urban areas), display higher numbers and a higher proportion of alien plant species, while also providing a hotspot for newly arriving alien plant species (Catford et al. 2011; Godefroid and Ricotta 2018). These patterns result from the high propagule pressure, concentration of transport infrastructure, and recurring anthropogenic disturbance in these habitats (Botham et al. 2009).

Climatic conditions are recognized as the first filter that either holds back alien plant species or allows successful establishment and spread in novel regions (Richardson et al. 2000). In recent decades, however, an increasing number of thermophilous (e.g., warm-loving) and drought-resistant alien plant species have been introduced to temperate regions, with some surviving up to 1000 km further north than their natural range limits, at colder latitudes and altitudes, where they are not naturally present (McKinney 2006; Walther et al. 2009). The establishment, survival, and spread of such plant species from warmer origins might depend on “heat islands” such as urban areas; yet, this hypothesis has so far not been formally assessed (Walther et al. 2009). Therefore, urban environments represent useful systems to study climatic constraints on the invasion success of alien plant species (Brans et al. 2017; van Kleunen et al. 2018).

Urban environments provide unique growing conditions for plants, with high human population

densities, a large proportion of impervious surfaces, high road concentration and rapid disturbance changes, as well as air and soil pollution, to name a few (McKinney 2002; Schmidt et al. 2014). The intensity of these anthropogenic factors sharply decreases from city centers towards rural peripheries (Alberti et al. 2003; Ortega and Pearson 2005; Schmidt et al. 2014). One common and well-known aspect of urban environments are their modified microclimates. Indeed, city areas have higher mean annual land surface temperatures due to the lower albedo of sealed surfaces and anthropogenic heat emission (Geletič et al. 2019). Raised air temperatures in cities relative to the rural surroundings result in the formation of urban heat islands (UHI) (Oke 1981; Oke et al. 2017; Bader et al. 2018). The magnitude and extent of the UHI depend strongly on 3-D urban geometry, wind speed and cloud cover, and often also vary between seasons. UHI intensity is more distinctive in the most impervious areas, in calm, summer evenings (Oke 1981; Arnds et al. 2017). Local background climate also strongly contributes to the magnitude of the UHI (Zhao et al. 2014; Ward et al. 2016). Furthermore, hot urban air, due to the UHI-effects, forms a heat plume which can locally influence weather (Cosgrove and Berkelhammer 2018). Indeed, a maximum precipitation intensification around 30 km downwind of urban areas has been proven for some European cities, especially for high intensity summertime precipitation events (Schlünzen et al. 2010; Lorenz et al. 2019). Additionally, because of impervious surfaces, the hydrological system in urban areas must cope with fluctuating amounts of surface runoff (Hamdi et al. 2011). Nevertheless, urban soils in Europe are typically drier than rural ones in all months, and particularly during the summer months (Fortuniak et al. 2006; Hamdi et al. 2015), due to increased compaction and the greater presence of sealed surfaces and anthropogenic materials (Schmidt et al. 2014; Godefroid and Ricotta 2018). Urban habitats thus tend to induce warmer microclimates and drier growing conditions, broadening regional climatic variation, whereas rural habitats present naturally occurring climatic conditions of a given region. Native niche conditions of alien plants that are newly introduced to foreign environments strongly influence their establishment, and determine their population growth and capacity to spread (Alexander and Edwards 2010). Rural-to-urban gradients show variability in their

microclimatic conditions, and might filter alien plant species based on their native niche optimum. For example, the preference of native plants for urban habitats is often related to the level of thermophily; in other words, plants mostly found in cities would be pre-adapted to the warmer and drier urban conditions (McKinney 2006; Schmidt et al. 2014; Szymura et al. 2018). However, a comprehensive assessment of the supposed link between climatic conditions in the native range and the level of urbanity in the invaded range of alien plant species remains unproven, to the best of our knowledge.

This is a crucial step towards identifying the characteristics of more urban alien species for conserving native species more effectively, as their high number and diversity has already transformed cities into invasion hotspots. If urban invasion is indeed strongly driven by the microclimate, this phenomenon will likely be amplified in the future by global changes. Since the surrounding landscape will become warmer in parallel, these urban alien plants might subsequently spill over more abundantly to the rural surroundings, using cities as stepping stones for further spread.

This study evaluated 24 emerging alien plant species in oceanic Europe (areas of Europe with a temperate climate, with warm summers but no dry season). The study aimed to: (a) disentangle the relationships between the climatic conditions in the native range (i.e., niche optimum) and the level of urbanity in the invaded range, while taking introduction history into account, and (b) test whether more urban alien plant species originate from native ranges with a warmer climate than that of the invaded range.

Methods

Study area, species selection, and native ranges

To delineate our study area, we used the Köppen-Geiger climate classification and focused on the temperate oceanic climate areas (Fig. 1): Cfb (i.e., temperate climatic conditions with warm summers and no dry season (Beck et al. 2018)) in Europe which was coarsely considered as all land areas comprised in a rectangular extent of top left corner 64°0'34"N 11°44'43"W, and of bottom right corner 41°23'31"N 28°3'5"E. This geographic entity was considered to

represent the invaded range in this study, and is referred to as “oceanic Europe” (Fig. 1). This climate-based delineation was chosen to keep the background macroclimatic conditions as homogeneous as possible, so to have a better contrast with the UHI-effects of the main cities occurring in the study area. Note that small patches of temperate climate occur in the Alps, Apennines and Balkan areas, these are also included in the study.

Next, we selected all alien plant species growing in terrestrial environments with distributions restricted in oceanic Europe, but which are also considered to have moderate to high impacts on biodiversity in the region. This selection was based on the Harmonia database (“Harmonia database” 2019) and European Union (EU) Regulation no. 1143/2014 which together include all species currently considered at risk of having biodiversity impacts in the region. Four species with uncertain native ranges (e.g., hybrids) were removed. This led to an initial total of 33 species eligible for inclusion (Fig. 2).

Alien species distribution data

Modelled native ranges

Native ranges of the 33 studied species were modelled to find their mean native climate preferences with a species distribution model framework.

Countries and regions within the native range for each of the 33 species were retrieved from Plants of the World Online (POWO 2020) and occurrences were acquired from the Global Biodiversity Information Facility (GBIF 2020) using the R packages *rgbif* and *taxize* (Chamberlain et al. 2019, 2020). Native regions were reported following the World Geographical Scheme for Recording Plant Distributions (WGSRPD) (Brummitt et al. 2001). In order to minimize spatial autocorrelation, the variability in number of occurrence points across different reporting countries was minimized by taking a maximum of 300 occurrence points retrieved from GBIF (GBIF Secretariat 2019) for each species per country within their respective native range. By default, this included the 300 most recent occurrence points for each of the countries considered as in the native range. Then, only the points falling inside reported native regions were kept. Duplicates were removed, as well as outliers that were detected based on Mahalanobis distance (MD)



Fig. 1 Map of the Cfb climate zones in Europe (i.e., temperate climate with warm summers but no dry season, Beck et al. 2018), displayed in green, and here called “oceanic Europe”.

and defined as any points having an MD four times larger than the 0.95 percentile of the entirety (Mahalanobis 1936). MD was calculated for each occurrence based on its location and bioclimatic conditions. Since outliers already influence the calculations of MD, we

applied this approach again after removing the first set of outliers. Since species distributions hardly follow any administrative boundaries, we define the modelling extent for each studied alien plant species as all ecoregions (Olson et al. 2001) containing at least one

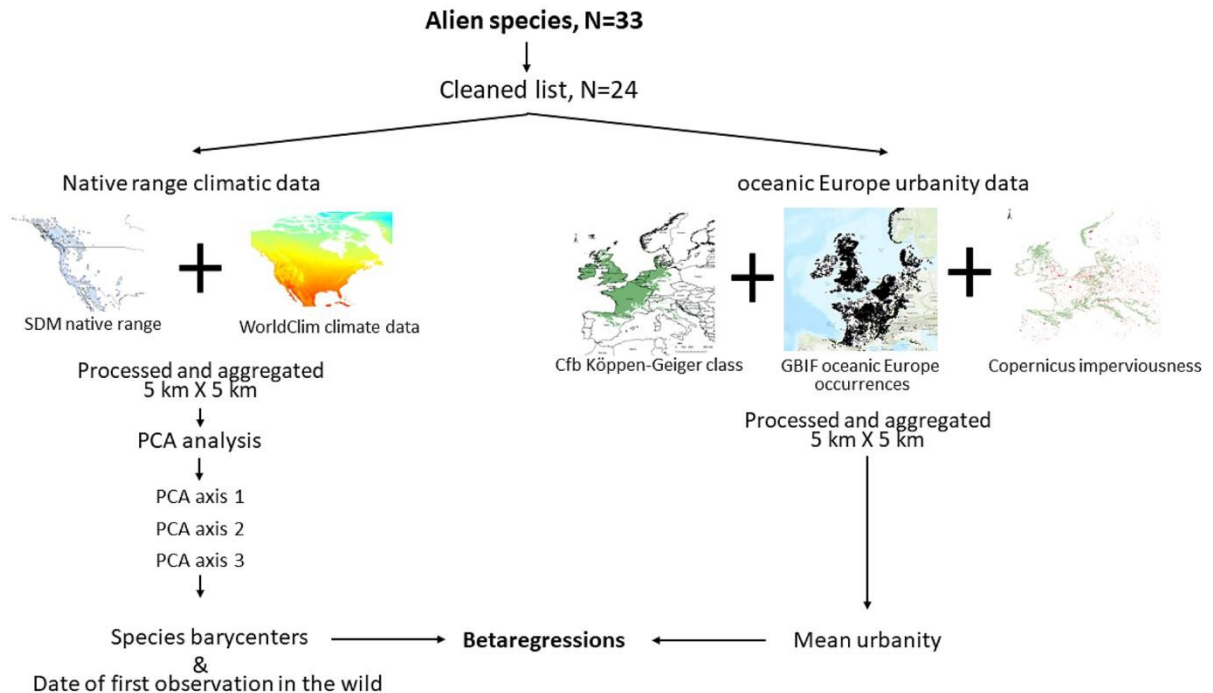


Fig. 2 Organizational chart of data acquisition, treatment, and analyses. For details, see Methods

of its remaining occurrence points plus all neighboring ecoregions, to acknowledge the fact that defining native countries and regions as well as data availability within ecoregions may be subject to errors and biases.

WorldClim bioclimatic predictors and fractions of land cover types were used to predict the possible native range of each species at 30 arcmin resolution across the defined modelling extent using maximum entropy modelling (Maxent) (Phillips et al. 2004, 2006, 2017). WorldClim bioclimatic predictors ($n = 19$, see <https://www.worldclim.com/bioclim> for full list) (Fick and Hijmans 2017) were downloaded in 10 arcmin resolution and aggregated to modelling resolution (30 arcmin, approximately 56 km at the equator) by averaging. Fractions of land cover classes ($n = 22$, including different types and mosaics of vegetation, see http://maps.elie.ucl.ac.be/CCI/viewer/download/CCI-LC_Maps_Legend.pdf for full list) were calculated based on the European Space Agency's land cover product (original scale 300 m \times 300 m, ESA 2017). Each class was transformed into a binary raster depicting presence (= 1) or absence (= 0) of the land cover type, and then aggregated to modelling resolution by averaging, resulting in one raster for each land cover class. Handling of

spatial data was conducted using the R packages raster, rgdal, maptools, rgeos and sp (Bivand et al. 2013, 2019; Bivand and Lewin-Koh 2019; Bivand and Rundel 2019; Hijmans 2019).

Maxent is a probability density estimation approach suited for predicting species distributions based on presence-only data (Elith et al. 2006). In Maxent, environmental variables and transformations thereof are used to predict species distributions. For our spatial predictions, we kept the Maxent default settings for selecting appropriate variables, transformations (out of linear, quadratic, product, hinge and threshold) and regularization values used to reduce overfitting (Elith et al. 2011; Merow et al. 2013). In addition, Maxent requires background information to contrast the environmental background against presence locations, and ultimately, fit response curves (Elith et al. 2011). We collected this background information (WorldClim bioclimatic predictors and land cover classes) from each cell across the modelling extent to avoid fitting the model with randomly generated points. Model fitting, prediction and range generation were executed with the R package dismo (Hijmans et al. 2017). The Maxent prediction was transformed into presence cells using the cut-off threshold that maximized model

sensitivity for each species. This step resulted in a patchy landscape consisting of suitable and unsuitable habitat. We then selected all suitable habitat patches that contained or were in the proximity of at least one occurrence point (i.e. at a distance from the closest occurrence point of up to 10% of the total extent of the suitable patch), hence, removing patches that are unlikely being colonized by the species. This gave us a native range area estimation for each of the studied alien plant species (See Supplementary information 1 for modelled native ranges of the studied species).

Next, the 19 WorldClim bioclimatic predictors (Fick and Hijmans 2017) were further extracted with a 5 km × 5 km fishnet over each studied species' modelled native range. These bioclimatic predictors data were used to depict the native niche optimum in the modelled native ranges, which is often used to characterize climatic suitability for alien plant species (van Kleunen et al. 2015). A principal component analysis (PCA) was conducted on the bioclimatic conditions within the modelled native ranges (R package factextra, Kassambara and Mundt 2017) to simplify the large set (19) of explanatory variables to a 3-dimensional climatic niche space, after standardizing them following the default settings of the R package FactoMineR, so that each of the variables has a standard deviation of one and a mean of zero (Husson et al. 2020). The three first PCA axes were retained, with the three bioclimatic predictors that contributed the most to each of these three PCA axes. We extracted the values (i.e., coordinates) along the first three PCA axes for each of the sampled 5 × 5 km

fishnet points over the studied alien species modelled native ranges (Fig. 1). The first three PCA axes explained respectively 39%, 22%, and 14% of the variance in the WorldClim bioclimatic data (Table 1). For each focal species separately, we then calculated the mean values as extracted using the fishnet points along the three PCA axes to depict their niche optimum along these axes. These parameters were referred to as the “barycenter” for each specific axis.

The minimum temperature of the coldest month (Bio 6, positively correlated), the mean temperature of the coldest quarter (i.e., the coldest three months of the year, Bio 11, positive), and the annual mean temperature (Bio 1, positive) contributed the most to PCA axis 1 (Table 1). This first PCA axis, thus, represented the severity of the native winter climate, and the annual mean temperature. High values along this PCA axis indicated a native range climate with milder winter temperatures and a higher annual mean temperature. Thus, we called this axis native “winter temperature” conditions.

The annual precipitation (Bio 12, positive), the precipitation of the driest quarter (Bio 17, positive), and the precipitation of the driest month (Bio 14, positive) contributed the most to PCA axis 2 (Table 1). The second PCA axis thus represented the precipitation amount of the native range climate, with high values indicating more precipitation. The second PCA axis thus reflected native “precipitation” conditions.

The mean temperature of the warmest quarter (Bio 10, positive), the maximum temperature of the warmest month (Bio 5, positive), and the mean temperature of the wettest quarter (Bio 8, positive)

Table 1 Results of the principal component analysis (PCA) for the 19 WorldClim bioclimatic predictors, extracted in the modelled native ranges of the studied species

PCA axis	Predictor	Full name	Contribution (%)	Correlation
Axis 1	Bio 6	Minimum temperature of the coldest month	12.3	0.96
	Bio 11	Mean temperature of the coldest quarter	12.2	0.95
	Bio 1	Annual mean temperature	10.9	0.90
Axis 2	Bio 12	Annual precipitation	15.4	0.81
	Bio 17	Precipitation of the driest quarter	14.9	0.80
	Bio 14	Precipitation of the driest month	13.9	0.77
Axis 3	Bio 10	Mean temperature of the warmest quarter	1.95	0.72
	Bio 5	Maximum temperature of the warmest month	1.73	0.68
	Bio 8	Mean temperature of the wettest quarter	1.58	0.64

contributed the most to the third PCA axis (Table 1). High values along this PCA axis meant warmer high temperature values in the native range climate. The third PCA axis thus represented native “summer temperature” conditions.

Finally, for each of the 33 species, we defined the main Köppen-Geiger climate class (Beck et al. 2018) for its modelled native range as the class in which most of its native range area 5 km × 5 km fishnet points fell.

Occurrence data in Oceanic Europe

The proportion of built up area (i.e., imperviousness) is a commonly used proxy to characterize urbanization. Plant urbanity (i.e., the proportion of built up surface in the plant’s vicinity) is used to characterize its growing environment in relation to urbanization (Hill et al. 2002). Following Kaiser et al. (2016) and Brans et al. (2017), we considered 5 km × 5 km resolution (25 km²) areas with at least 10% built up surfaces as urbanized. Note that urbanity percentages are lower at a coarser resolution, hence this value is lower than reported in other studies at a higher resolution (e.g. MacGregor-Fors 2011, 66% at a 0.01 km² resolution).

The occurrence data of the selected alien plant species in the invaded range was also downloaded from the Global Biodiversity Information Facility (GBIF, see Table S2.1 in Supplementary information 2, GBIF.org, 2019), acquired for 1950–2018, and handled in ArcMap 10.5.1 (2017). This time period was set because it encompassed 90% of the observations available on GBIF.org across all species. We only included species with at least 50 observations in the invaded range, which led to the removal of 9 out of 33 species, and a final list of 24 species (Fig. 2, see Table S2.2 in Supplementary information 2). The distribution data were processed to correct for variation in the resolution of data in GBIF.org, and to solve high local spatial autocorrelation, for example through a bias towards areas with high occurrence densities. To do so, fishnets of 5 km × 5 km were placed over oceanic Europe. In each cell, and for each species, if several occurrence records were present, only a randomly chosen one was kept. This resulted in a total of 20,000 processed occurrence records for oceanic Europe (See Supplementary information 1 for details on species occurrence in oceanic Europe).

The density of impervious areas, representing the percentage of built-up land surface in 2015 (land-copernicus.eu, 2018) was used to characterize the level of urbanization throughout the invaded range of each study species (Fig. 2). To do so, the imperviousness layer was aggregated, using the mean, at a spatial resolution of 5 km × 5 km (original scale: 20 m × 20 m), to match the resolution of the occurrence datasets. In doing so, we worked with the large-scale rural-to-urban gradients, but not the fine-grained variation in urbanity, which can be caused by urban parks for example. The proportion of impervious area was extracted for each occurrence cell in the invaded range, and the mean value was calculated for each species. This parameter was subsequently referred to as “mean urbanity” (value between 0 and 1) (Fig. 2).

The year of first observation of the studied alien plant species in oceanic Europe was derived from Zieritz et al. (2017) and the “Harmonia database” (2019), and allowed us to account for their time since introduction, a factor often related to plant invasion success (Lambdon and Hulme 2006). These data compiled the first observation years in Belgium, France, Great Britain, and the Netherlands, which are the countries contributing to the largest part of oceanic Europe, and spanned from 1683 to 2008.

Statistical analyses

The analysis of the relationships for mean urbanity (response variable) with respect to the species barycenter along the three PCA axes and the year of first observation (scaled for modelling purposes following: $\frac{x_i - \text{mean}(x)}{\text{sd}(x)}$ with x_i the year of first observation, mean (x) its mean, and sd (x) its standard deviation, lower values of scaled year of first observation corresponded to the most ancient observations) (explanatory variables) was performed using betaregressions (R package betareg, Cribari-Neto and Zeileis 2010). We hypothesized that native climatic conditions explained the distribution of alien plant species in urban versus rural areas in oceanic Europe. The response variable, mean urbanity, was continuous, and was derived from proportions and restricted to the unit interval (0, 1), but no values were exactly equal to 0 or 1, thus justifying the use of betaregressions (Douma and Weedon 2019). The full model included all two-way interactions between the species

barycenter along the three PCA axes. We used the dredge function (package MuMIn, Barton 2009) to select the models to be averaged: the best model had the lowest Akaike Information Criterion (AIC) and highest Phi coefficient (model precision), and selected models had a delta AIC lower than 2 relative to this best model. Using this procedure, two candidate models were retained. We then performed model averaging on these selected models (R package MuMIn, Barton 2009).

To characterize the origin of the studied alien plant species in terms of native bioclimatic values, baseline values for each of the 19 WorldClim bioclimatic predictors were calculated as their mean value over the species respective modelled native ranges. To compare those values with climatic conditions occurring in the invaded range, oceanic Europe baseline values for each of the 19 WorldClim bioclimatic predictors were also calculated as their mean value over the oceanic Europe study zone. To define the species as more urban or more rural, a cut-off value of mean urbanity of the studied species was obtained by calculating the mean of the mean urbanity of the 24 studied species (= 8.6%). This mean urbanity cut-off value was used to distinguish species displaying a mean urbanity above this threshold as more urban, and species displaying a mean urbanity below this threshold as more rural, in oceanic Europe. Using the previously calculated baseline values in the modelled native ranges and in oceanic Europe, confusion matrices were produced for all of the bioclimatic predictors, and the best one was retained. Following their position along the reference values, species considered as true positive (TP), true negative (TN), false positive (FP), and false negative (FN) were determined. The precision of species placement was calculated as $\frac{TP}{(TP+FP)}$.

Finally, a generalized linear model was used to test the relationship of the mean urbanity of the studied species (response variable) with their main native climate, which was described as the main Köppen-Geiger climate class in which they occur in their native range (explanatory variable, treated as factor) (package car, John et al. 2019). A binomial family was used, with the response variable being treated as a vector accounting for the urbanity and non-urbanity percentages (i.e. $c(\%_{\text{urbanity}}, \%_{\text{non-urbanity}})$) following the method of Crawley (2013).

All statistical analyses were performed in RStudio, version 1.1.463 (RStudio Team 2016).

Results

Native climatic conditions and invaded urbanity of alien plant species

The 24 studied alien plant species showed high variability in native climatic conditions, with native ranges encompassing a total of 27 out of the 30 Köppen-Geiger climate classes, yet with 87% of occurrences in seven of the 30 climate classes (see Table S3 in Supplementary information 3). The urbanity of all occurrence records and species together in oceanic Europe ranged from 0 to 93%; mean species-level urbanity varied between 4 and 17% (see Table S4 in Supplementary information 4).

Alien plant species from warmer and drier origins are more likely to develop in higher urbanity areas in oceanic Europe

Native climate “precipitation” (PCA axis 2) had a significant negative effect and “summer temperature” (PCA axis 3) had a significant positive effect on species mean urbanity in oceanic Europe, both displaying the strongest support overall (Table 2; present in the 2 selected models). Thus, in oceanic Europe, alien plant species from warmer (PCA axis 3) or drier (PCA axis 2) native ranges were, on average, found in more urban environments (Fig. 3a and b).

The year of first observation in the wild had a weak positive but non-significant effect on species mean urbanity, and was only present in one of the two selected models (Fig. 3c). This suggested that alien plant species present in the wild for a shorter period of time were found in more urban environments.

The main native Köppen-Geiger climate class had a non-significant effect on species mean urbanity ($p = 0.12$, $Df = 3$, $LR \text{ Chisq} = 5.79$). However, visualization of the main Köppen-Geiger climate classes (Fig. 3a) showed that more urban alien species primarily tended to originate from subtropical or continental climates in the native range. In comparison, more rural alien species primarily originated from contrasted and/or cooler climates in the native range (e.g., alpine or continental) (Figs. 3, 4).

Table 2 Estimates and corresponding p-values of the total mean urbanity variance explained by the averaged model. Significant effects are displayed in bold: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. Number of species = 24. Standard errors are indicated between brackets. Variables contained in each model of the selection used in the model

	Mean	Precision		
(Intercept)	-2.231*** (0.06)			
PCA axis 2 barycenter	-0.173** (0.055)			
PCA axis 3 barycenter	0.119** (0.045)			
Year of first observation 'scaled'	0.05 (0.068)			
(phi)		171.093** (51.13)		
Averaged models:	Variables	Pseudo R ²	Log-likelihood	AICc
Model 1	1,2,3	0.43	59.66 on 5 Df	-106
Model 2	1,2	0.36	57.94 on 4 Df	-105.8

averaging are represented by the following numbers: 1 = PCA axis 2 barycenter; 2 = PCA axis 3 barycenter; 3 = Year of first observation 'scaled'. The variables, pseudo R^2 , Log-likelihood, and corresponding AICc are detailed for each model. The pseudo R^2 of the best model of all (Model 1) indicates that 43% of the variance in the data was explained by the model

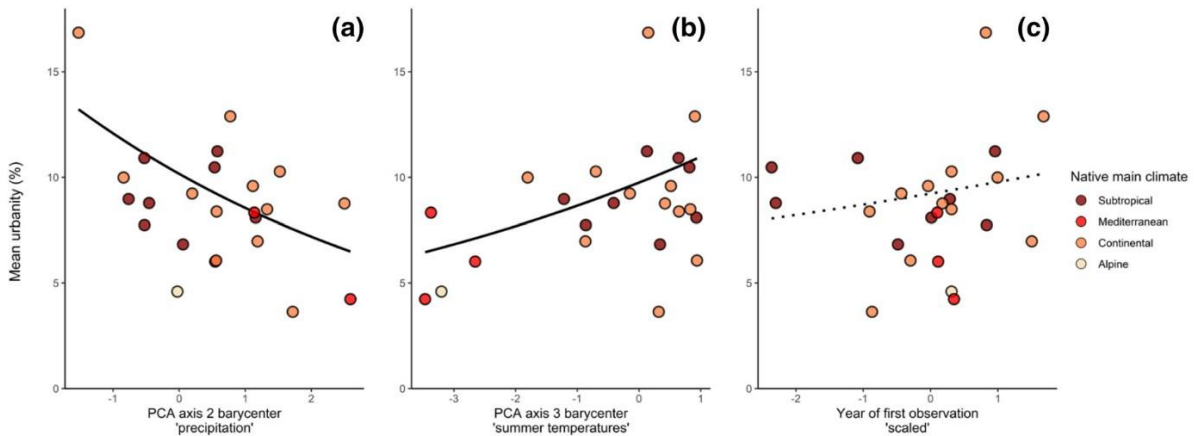


Fig. 3 Mean urbanity (in %) of the studied alien plant species as a function of their native range barycenter calculated for the three first dimensions of the PCA conducted with WorldClim bioclimatic predictors. Mean urbanity of alien plant species as a function of: **a** the barycenter of a species for PCA axis 2, mainly associated with the bioclimatic predictors of “precipitation” with high values indicating more precipitation; **b** the barycenter of a species for PCA axis 3, mainly associated with the bioclimatic predictors of “summer temperature” with high values indicating higher temperatures, and **c** the scaled year of

first observation in the wild, ranging from 1683 (low values) to 2008 (high values). Each point corresponds to a species, colored following the main Köppen-Geiger climate class in which it was observed the most in its modelled native range. Lines correspond to the averaged model output (predicted mean urbanity, %) in oceanic Europe. Full lines correspond to significant effects in the full averaged model, and dashed line corresponds to a non-significant effect in the full averaged model

The confusion matrix of annual mean temperature had the strongest correlation with the urbanity of alien species, with the highest estimation precision (0.58).

Seven out of the 12 more urban aliens originated from native ranges with warmer annual mean temperatures compared to the annual mean temperature in oceanic

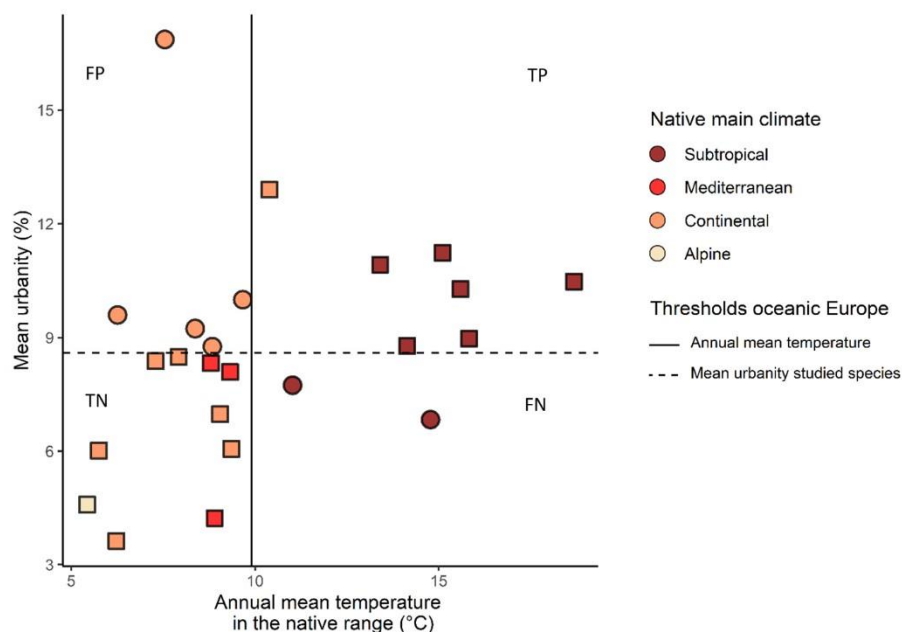


Fig. 4 Mean urbanity (in %) of alien plant species in oceanic Europe as a function of their native range annual mean temperature (°C). Each point corresponds to a different species. The full vertical line represents the annual mean temperature (°C) over the Cfb climate zones in western Europe, considered as the reference in oceanic Europe: 9.9 °C. The dashed horizontal line corresponds with the mean urbanity value for the set of studied species: 8.6%; half of the studied species

displayed a lower mean urbanity than this value and were considered to be more rural aliens in oceanic Europe, and vice versa. Species are colored following their native main Köppen-Geiger climate class. Species represented with squares correspond to either true negative (TN) or true positive (TP) in the confusion matrix, and species represented with circles are either false negatives (FN) or false positives (FP)

Europe (TP, Fig. 4). In addition, ten out of the 12 more rural alien species originated from native ranges with cooler annual mean temperatures compared to oceanic Europe (TN, Fig. 4).

Discussion

The underlying study showed that the variation in the urbanity of alien plant species in oceanic Europe was partly explained by the climatic conditions in their modelled native ranges. Indeed, a predominant proportion of more urban and more rural alien species originated from warmer and cooler native ranges, respectively, compared to the studied area. Alien plants that grew in more urban environments primarily originated from two main climate types: subtropical and continental climates. In comparison, alien plants that grew in more rural environments appeared to mainly originate from alpine, continental, and Mediterranean climates. Yet, variation in the native

climate was more important for these rural alien species compared to more urban alien species.

Alien species that established more recently in oceanic Europe tended to be more restricted to more urban environments, albeit not significantly so. Thus, we argue that the preference of some alien species in our study for more urban or more rural environments could be linked to climatic filtering of urban climate. Indeed, our study indicates that alien plants of various origins do not establish randomly along the imperviousness gradient; rather, alien plant species from warmer or drier native ranges tend to establish in more urban environments, visible by the significant effect of the native climate barycenters. However, the contrasted development in more rural vs more urban environments of the studied species cannot be attributed solely to their native range climatic conditions. Variables such as the frequency of anthropogenic disturbances, alien species propagule pressure, the availability of bare ground, garden and green space density, are known to contribute as well to

the complex processes that determine alien plant distribution in urban environments (McKinney 2006; Botham et al. 2009; Čeplová et al. 2017). Yet, most of these factors would likely apply similarly to species from warmer or cooler origins, and our results thus suggest a substantial role of UHI-effects as driver. Moreover, even if the introduction of plant species tends to happen at higher rates in densely inhabited areas, alien species often escape from cultivated areas, such as gardens, which are present in both urban and rural areas (Botham et al. 2009; Dullinger et al. 2017). We also noticed that the occurrence of all the studied alien species exhibited a broad variety of urbanity values, showing that they were present in all types of environments, from densely built metropolitan areas (London, Paris, etc.) in highly urbanized regions (Flanders, Netherlands) to extensive rural zones (central France, Wales, etc.). Western Europe has the highest road and rail density of any continent, and is considered to be the world's most urbanized region (Hulme 2009; Terama et al. 2019). Consequently, the displacement of propagules is far easier in this region compared to less human-modified parts of the world, implying that most of the studied species had a fair opportunity to establish along the whole urban–rural gradient.

Oceanic Europe has a temperate mild and humid climate; however, urban environments have elevated summer temperatures due to the UHI-effects, and a modified water cycle due to impervious surfaces. These phenomena result in local warmer microclimates and drier growing conditions in cities compared to rural surroundings (Ortega and Pearson 2005; Scalenghe and Ajmone-Marsan 2009; Walther et al. 2009; Kaiser et al. 2016; Szymura et al. 2018). Therefore, we hypothesize that it is more likely that alien species from warmer and drier native ranges than those in our study area develop in more urban environments, induced by the presence of warmer microclimates and drier soils in oceanic European cities.

More urban aliens from subtropical climates likely take advantage of the longer growing season and reduced winter freezing events associated with the UHI-effects (Walther et al. 2009; Schmidt et al. 2014). The first developmental stages of several alien plant species from subtropical climates are particularly sensitive to temperature. For instance, the germination of *Baccharis halimifolia* and *Lonicera japonica* is

optimal at around 20–25 °C (Schierenbeck 2004; Fried et al. 2016), representing a relatively high temperature range for oceanic Europe. Moreover, seedlings of such species also tend to be highly frost sensitive, as illustrated by the high mortality of *Ailanthus altissima* seedlings after freezing events (von der Lippe et al. 2005). The phenology of these species often involves late flowering and fruiting, which represent crucial stages sensitive to the timing, duration, and intensity of freezing events (e.g., *Baccharis halimifolia* (Fried et al. 2016), *Cyperus eragrostis* (Iefländer and Lauerer 2007), and *Potentilla indica* (Dakskobler and Vreš 2009)). In addition, urban environments display more drained and disturbed substrates (Schmidt et al. 2014) that might represent conditions with favorable humidity for more urban aliens from drier native ranges that are adapted to either limited and/or seasonal precipitation regimes than in this oceanic humid climatic region. Some of the alien species in our study prefer disturbed and/or drained soil conditions (e.g., *Reynoutria sachalinensis* (Sukopp and Starfinger 1995)), and germinate better under contrasted temperatures (e.g. *Elaeagnus angustifolia*, (Guilbault et al. 2012)). The urban microclimate also promotes the survival of the seedlings of some of these species (e.g., *Acer negundo*, (von der Lippe et al. 2005)).

Conversely, alien plant species associated with lower urbanity in oceanic Europe tend to originate from cooler ranges, and thus might perform less well in warmer and drier urban environments. Warmer temperatures inhibit the development abilities of some of these species, especially for young individuals (e.g., *Lupinus polyphyllus* (Elliott et al. 2011) and *Lysichiton americanus* (Schrader and Klingenstein 2006)), whereas drier substrates negatively impact the development of species, such as *Prunus laurocerasus* (Berger et al. 2007) and *Spiraea alba* (Stanton and Mickelbart 2014).

This study demonstrated that global databases (such as GBIF.org, WorldClim, Copernicus Imperviousness Density), if cautiously used, are relevant for analyses at a continental scale. The relationship between urbanity in the invaded range and climatic conditions in the modelled native range observed here at a continental scale, suggests that even stronger microclimatic effects might be at play at local scales (Botham et al. 2009; Walther et al. 2009; Lembrechts et al. 2018). Even if we acknowledge variability within

species, the pattern found in the current study confirmed that this global relationship with climatic conditions of origin is consistent, and highlights that multi-species studies are essential for comprehending invasion processes and urban invasion ecology (Catford et al. 2011).

The separation of more urban aliens from the whole alien species pool indicates that urban conditions could act as a filter for warmth and drought-adapted plant species. This phenomenon is of great conservation concern, because many ornamental species introduced to temperate regions originate from dry and warm areas (van Kleunen et al. 2018). Furthermore, urban environments might enhance alien plant invasions in the future, due to a higher environmental disequilibrium resulting from enhanced urbanization, trade, and climate change (van Kleunen et al. 2018). Because urban areas are highly connected with rural surroundings, they actively export propagules (Hulme 2009; Catford et al. 2011). Under the current projections of climate change, some surrounding rural areas in oceanic Europe could also increasingly become suitable for drought and warm adapted species (Kendal et al. 2012). Cities could then, for some time, act as migration outpost for these so far climate-limited alien plant species, facilitating their escape to newly suitable rural areas (Hulme 2009; Dullinger et al. 2017; Pyšek et al. 2017). Indeed, climate change in the region is expected to bring warmer mean annual temperatures, and more contrasted precipitation regimes, with drier summers but wetter winters (Kovats et al. 2014; Miller and Hutchins 2017). At the same time, however, the warming climate might amplify the UHI-effects and thus perhaps render urban environments less suitable for many alien species. For example, higher frequencies of extreme climatic events such as prolonged and stronger heatwaves forecasted under climate change might have disproportionate impacts on plant species in urban environments because of increased heat stress leading to higher evapotranspirative demands (Kovats et al. 2014; Zipper et al. 2017). Still, while the UHI-effects depend on both local weather conditions and background climate, it has been shown in European cities such as Brussels that climate change will only have limited impact on the UHI by 2050 (Oke 1981; Hamdi et al. 2015).

In an era of biotic homogenization and climate change (Pyšek et al. 2010; Terama et al. 2019), urban

environments could represent hotspots for invasion by new alien plant species. Therefore, emphasis should be placed on invasion processes and monitoring invasion in urban environments to advance our understanding of what drives the early stages of invasion, when they might still be controlled. Furthermore, this phenomenon might be compounded by the fact that warmer and drier climates might become more common across the whole rural-to-urban gradient under climate change (Hamdi et al. 2015; Brans et al. 2017). Therefore, it is important to raise the awareness of public institutions and private property owners regarding the use of such warm- and drought-adapted alien species. The latter could prevent urban plantations such as public and/or private gardens, which are critical for cities to adapt to climate change, to unintentionally represent potential sites for the “seeding” of future plant invasions (Essl 2007; Gaertner et al. 2017).

Author contributions C.G., J.J.L., I.N. and A.M. designed the research, J.B. and C.G. performed the native range modelling, C.G. did the analyses and led paper writing, all authors contributed substantially to revisions. We thank two anonymous reviewers for their suggestions and comments.

Funding This work was supported by the Fonds de la Recherche Scientifique (FNRS).

Code availability All code made available on Figshare.

Compliance with ethical standards

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Availability of data and material No new data were used, pre-processed data made available on Figshare.

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