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► **To cite this version:**

Charly Géron, Jonas Lembrechts, Jan Borgelt, Jonathan Roger Michel Henri Lenoir, Rafiq Hamdi, et al.. Urban alien plants in temperate oceanic regions of Europe originate from warmer native ranges. *Biological Invasions*, 2021, 23 (6), pp.1765-1779. 10.1007/s10530-021-02469-9 . hal-03362904

HAL Id: hal-03362904

<https://hal.science/hal-03362904>

Submitted on 2 Oct 2021

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1 **Alien plants on a city trip: Urban invaders originate from warmer native ranges**

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26 **Short title:** Urban alien plants come from warmer climates

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28 **Acknowledgments:** This work was supported by the Fonds de la Recherche Scientifique (FNRS).

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34 **Abstract**

35 **Aim:** To test the long-expected connection between the native climatic conditions of alien plant species
36 and their preference for urban versus rural conditions, a hypothesis driven by the presence of warmer
37 and drier microclimates in cities due to the urban heat island effect.

38 **Location:** Western Europe.

39 **Time period:** 1950-2018.

40 **Major taxa studied:** Plants.

41 **Methods:** We evaluated the relationship between climate in the native range and occurrence urbanity of
42 24 emerging alien plant species in western Europe, based on land imperviousness data obtained from
43 land.copernicus.eu.

44 **Results:** Alien species growing in more urban environments originated from warmer or drier native
45 ranges than the invaded area.

46 **Main conclusions:** These results have important implications for alien species management as climate
47 warming in oceanic Europe will likely lift climatic barriers that currently constrain numerous alien plant
48 species to cities, boosting the role of cities as points of entry for invasive plants.

49

50 **Keywords:** alien plant species, biological invasions, urbanization, native climate, global changes

51

52 **Introduction**

53 The second half of the twentieth century has been characterized by a steep rise in international trade,
54 travel, and transport, resulting in the biotic homogenization of the world through increased alien species
55 introductions (Olden & Rooney 2006; Pyšek *et al.* 2010; van Kleunen *et al.* 2018). Data from Europe shows
56 that most introductions happened after 1990, during the so-called “globalization era” (Hulme 2009). The
57 success and speed of alien species invasion depend on the propagule pressure of alien species and the
58 lifting of certain barriers, such as lower abiotic or biotic constraints in the introduced range (Dullinger *et al.*
59 *et al.* 2017). Only a small portion of introduced alien species passes all of these barriers (Walther *et al.* 2009)
60 to become invasive, and significantly impacts native biota (Dullinger *et al.* 2017). Alien plant invasions
61 occur in all habitats, extending from rural to urban ones; however, the susceptibility to invasion (i.e.,
62 invasibility) of these habitats varies. **Some land use categories, especially the most anthropogenic ones**
63 **(e.g., urban areas), display higher alien plant invasions and often concentrate newly arrived alien plant**
64 **species, due to high propagule pressure, concentration of transport infrastructure, and recurring**
65 **anthropogenic disturbance (Botham *et al.* 2009; Catford *et al.* 2011; Godefroid & Ricotta 2018). In**
66 particular, climatic conditions are recognized as the first filter that either holds back alien plant species or
67 allows successful establishment and spread in novel regions (Richardson *et al.* 2000). In recent decades,
68 an increasing number of thermophilous (e.g., warm-loving) and drought-resistant alien plant species has
69 been introduced to temperate regions, with some surviving up to 1000 km further north than their natural
70 range limits, at colder latitudes and altitudes, where they are not naturally present (McKinney 2006;
71 Walther *et al.* 2009). The establishment, survival, and spread of such plant species from warmer origins
72 might depend on “heat islands,” such as urban areas; yet, this hypothesis has not been formally assessed
73 (Walther *et al.* 2009). Therefore, urban environments represent useful systems to study climatic
74 constraints on the invasion success of alien plant species (Brans *et al.* 2017; van Kleunen *et al.* 2018).

75 Urban environments provide unique growing conditions for plants. However, the intensity to which
76 environmental conditions are modified by human activities sharply decreases from city centers towards
77 rural peripheries (Alberti *et al.* 2003; Ortega & Pearson 2005; Schmidt *et al.* 2014). One common and well-
78 known aspect of urban environments is their modified microclimate. Indeed, city areas are warmer than
79 the rural surroundings, which is a phenomenon called the urban heat island (UHI) effect (Oke *et al.* 2017;
80 Bader *et al.* 2018). Three main factors contribute to the establishment of urban heat islands: 3-D urban
81 geometry, thermal characteristics of impervious surfaces, and anthropogenic heat release. Local
82 background climate also strongly contributes to the magnitude of the urban heat island (Zhao *et al.* 2014;
83 Ward *et al.* 2016). The proportion of built up area (i.e., imperviousness) is a commonly used proxy to

84 characterize urbanization. Areas with 10% built up surfaces are considered to be urban in western Europe
85 (Kaiser *et al.* 2016; Brans *et al.* 2017). Plant urbanity (i.e., the proportion of built up surface in the plant's
86 vicinity) is used to characterize its growing environment in relation to urbanization (Hill *et al.* 2002). The
87 high percentage of impervious surfaces associated with intense anthropogenic activity modify soil
88 characteristics and disrupt the water cycle, resulting in highly fluctuating amounts of surface runoff water
89 (Hamdi *et al.* 2011). Consequently, urban habitats induce warmer and drier microclimates, broadening
90 regional climatic variation, whereas rural habitats present naturally occurring climatic conditions of a given
91 region. Native niche conditions of alien plants that are newly introduced to foreign environments strongly
92 influence their establishment, and determine their population growth and capacity to spread (Alexander
93 & Edwards 2010). Native niche optimum is often used to characterize climatic suitability for alien plant
94 species (van Kleunen *et al.* 2015). Urban-to-rural gradients show variability in their microclimatic
95 conditions, and might filter alien plant species based on their native niche optimum. For example, the
96 preference of native plants for urban habitats is often related to the level of thermophily; in other words,
97 plants mostly found in cities would be pre-adapted to the warmer and drier urban conditions (McKinney
98 2006; Schmidt *et al.* 2014; Szymura *et al.* 2018).

99 Existing studies have demonstrated that a high number of urbanophile plant species are thermophilous,
100 with the high diversity and proportion of alien plant species in cities being positively coupled to city size
101 and percentage of built-up surface (Schmidt *et al.* 2014; Čeplová *et al.* 2017); however, a comprehensive
102 assessment of the supposed link between climatic conditions in the native range and the level of urbanity
103 in the invaded range of alien plant species remains unproven, to the best of our knowledge. This is a crucial
104 step towards identifying the characteristics of more urban alien species for conserving native species more
105 effectively, as their high number and diversity has already transformed cities into invasion hotspots. This
106 phenomenon will likely be amplified in the future by global changes if urban invasion is, indeed, strongly
107 driven by the microclimate. Since the surrounding landscape will become warmer in parallel, these urban
108 alien plants might subsequently spill over more abundantly to the rural surroundings, using cities as
109 stepping stone for further spread.

110 This study evaluated 24 emerging alien plant species originating from outside western Europe, using
111 oceanic Europe (area of western Europe with a temperate climate, with warm summers but no dry season)
112 as the study zone. The study aimed to: (a) disentangle the relationships between the climatic conditions
113 in the native range (i.e., niche optimum) and the level of urbanity in the invaded range, while taking the
114 first date of observation in the wild into account, and (b) test whether more urban alien plant species
115 originate from native ranges with a warmer climate than that of the invaded range.

116 **Methods**

117 ***Study area, species selection, and native ranges***

118 To delineate our study area, we used the Köppen-Geiger climate classification and focused on the
119 temperate oceanic climate of Europe (Fig. 1): Cfb (i.e., temperate climatic conditions with warm summers
120 and no dry season) (Beck *et al.* 2018). This geographic entity was considered to represent the invaded
121 range in this study, and is referred to as “oceanic Europe” in this study (Fig. 1). This delineation was chosen
122 to keep the background macroclimatic conditions as homogeneous as possible, and to better contrast with
123 the urban heat island (UHI) effect of the main cities occurring in the study area. **We then selected a list of
124 alien plant species growing in terrestrial environments, which stages of invasion are still considered as
125 incipient with distributions that remain restricted in oceanic Europe, but which are also having moderate
126 to high impacts on biodiversity.** This selection was based on the Harmonia database (“Harmonia database”
127 2019) and European Union (EU) Regulation no. 1143/2014. Species with unclear native ranges (e.g.,
128 hybrids) were removed. This led to an initial total of 33 species eligible for inclusion (Fig. 2).

129 ***Alien species distribution data***

130 ***Modelled native ranges***

131 **Native countries and native regions for each of the 33 species were retrieved from Plants of the World
132 Online (POWO 2020) and occurrences were acquired from the Global Biodiversity Information Facility
133 (GBIF 2020) using the R packages rgbif and taxize (Chamberlain *et al.* 2019, 2020). Native regions were
134 reported following the World Geographical Scheme for Recording Plant Distributions (WGSRPD) and range
135 from continental to regional scale (Brummitt *et al.* 2001). In order to minimize variability in number of
136 occurrence points across countries, a maximum of 300 occurrence points was retrieved from GBIF (GBIF
137 Secretariat 2019) for each species per native country. By default, this included only the most recent
138 occurrence points. Then, only the points falling inside reported native WGSRPD regions were kept.
139 Duplicates were removed, as well as outliers that were detected based on Mahalanobis distance (MD) and
140 defined as any points having an MD four times larger than the 0.95 percentile of the entirety (Mahalanobis
141 1936). MD was calculated for each occurrence based on its location and bioclimatic conditions. Since
142 outliers already influence the calculations of MD, we applied this approach again after removing the first
143 set of outliers. Since species distributions hardly follow any administrative boundaries, we define the
144 modelling extent for each studied alien plant species as all ecoregions (Olson *et al.* 2001) containing at
145 least one of its remaining occurrence points. Furthermore, to acknowledge the fact that defining native
146 countries and WGSRPD regions as well as data availability within ecoregions may be suspect to errors and
147 biases, we included all neighboring ecoregions as well. WorldClim bioclimatic predictors and land cover**

148 types were used to predict the possible native range of each species at 30 arcmin resolution across the
149 defined modelling extent using maximum entropy modelling (Maxent) (Phillips *et al.* 2004, 2006, 2017).
150 WorldClim bioclimatic predictors (n = 19, see <https://www.worldclim.com/bioclim> for full list) (Fick &
151 Hijmans 2017) were downloaded in 10 arcmin resolution and aggregated to modelling resolution (30
152 arcmin, approximately 56 km at the equator) by averaging. Land cover classes (n = 22, including different
153 types and mosaics of vegetation, see [http://maps.elie.ucl.ac.be/CCI/viewer/download/CCI-](http://maps.elie.ucl.ac.be/CCI/viewer/download/CCI-LC_Maps_Legend.pdf)
154 [LC_Maps_Legend.pdf](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
155 product (original scale 300 m X 300 m, ESA 2017). Each class was transformed into a binary raster depicting
156 presence (= 1) or absence (= 0) of the land cover type, and then aggregated to modelling resolution by
157 averaging, resulting in one raster for each land cover class. Handling of spatial data was conducted using
158 the R packages raster, rgdal, maptools, rgeos and sp (Bivand *et al.* 2013, 2019; Bivand & Lewin-Koh 2019;
159 Bivand & Rundel 2019; Hijmans 2019). Maxent is a probability density estimation approach suited for
160 predicting species distributions based on presence-only data (Elith *et al.* 2006). In Maxent, environmental
161 variables and transformations thereof are used to predict species distributions. For our spatial predictions,
162 we kept the Maxent default settings for selecting appropriate variables, transformations (out of linear,
163 quadratic, product, hinge and threshold) and regularization values used to reduce overfitting (Elith *et al.*
164 2011; Merow *et al.* 2013). In addition, Maxent requires background information to contrast the
165 environmental background against presence locations, and ultimately, fit response curves (Elith *et al.*
166 2011). We collected background information from each cell across the modelling extent to avoid fitting
167 the model with randomly generated points. Model fitting, prediction and range generation were executed
168 with the R package dismo (Hijmans *et al.* 2017). The Maxent prediction was transformed into presence
169 cells using the cut-off threshold that maximized model sensitivity for each species. This step results in a
170 patchy landscape consisting of suitable and unsuitable habitat patches. We temporarily increased the
171 extent of each patch by 10 % using buffering, to remove patches that would not contain any occurrence
172 points, hence, removing patches that are unlikely being colonized by the species. This gave us a native
173 range area estimation for each of the studied alien plant species, and the 19 WorldClim bioclimatic
174 predictors (Fick & Hijmans, 2017) were further sampled with a 5 km X 5 km grid over each of them. These
175 bioclimatic predictors data were used to depict climatic conditions in the modelled native ranges of species
176 (Fig. 2). Finally, for each of the 24 species, we defined the main Köppen-Geiger climate class (Beck *et al.*
177 2018) for its modelled native range as the class in which most of native range area 5 km X 5 km fishnet
178 points fell.

179

180 *Oceanic Europe*

181 The occurrence of the selected alien plant species, for the invaded ranges, was downloaded from the
182 Global Biodiversity Information Facility (GBIF, see Appendix S1 Table S1.2 in Supporting Information,
183 GBIF.org, 2019), were acquired for 1950–2018, and were handled in ArcMap 10.5.1 (2017). This time
184 period was set because it encompassed 90% of the observations available on GBIF.org across all species.
185 We only included species with at least 50 observations in the invaded range, which led to the removal of
186 9 out of 33 species, and a final list of 24 species (Fig. 2, see Appendix S1 Table S1.2 in Supporting
187 Information). The invaded distribution data of species were processed to correct for variation in the
188 resolution of data in GBIF.org, and to solve high local spatial autocorrelation for example bias towards
189 areas with high occurrence densities. To do so, fishnets of 5 km X 5 km were placed over oceanic Europe.
190 In each cell, and for each species, if several occurrence records were present, only a randomly chosen one
191 was kept. This resulted in a total of 20000 processed occurrence records for oceanic Europe (See Appendix
192 S2 in Supporting Information for details on species occurrence and maps in modelled native ranges and
193 oceanic Europe). The density of impervious areas, representing the percentage of built-up land surface in
194 2015 (land.copernicus.eu, 2018) was used to characterize the level of urbanization throughout the invaded
195 range of each study species (Fig. 2). To do so, the imperviousness layer was aggregated, using the mean,
196 at a spatial resolution of 5 km X 5 km (original scale: 20 m X 20 m), to match the resolution of the
197 occurrence datasets. The proportion of impervious area was extracted for each occurrence cell in the
198 invaded range, and the mean value was calculated for each species. This parameter was subsequently
199 referred to as “mean urbanity” (value between 0 and 1) (Fig. 2). **Moran’s index was calculated for each**
200 **species in ArcMap 10.5.1 (2017), checking for spatial autocorrelation in the processed occurrences of each**
201 **of the alien plant species in oceanic Europe.**

202 ***Statistical analyses***

203 A principal component analysis (PCA) was conducted on the bioclimatic conditions within the modelled
204 native ranges (R package factoextra, Kassambara and Mundt, 2017) to simplify the large set (19) of
205 explanatory variables to a 3-dimensional climatic niche space. The three first PCA axes were retained, with
206 the three bioclimatic predictors that contributed the most to each of these three PCA axes. We extracted
207 the values (i.e., coordinates) along the three first PCA axes for the sampled 5 km X 5 km points over the
208 modelled native ranges of each studied alien species (Fig. 1). **The first three PCA axes explained 39%, 22%,**
209 **and 14% variance, respectively, of the WorldClim bioclimatic data (Table 1).**
210 **The minimum temperature of the coldest month (Bio 6, positively correlated), the mean temperature of**
211 **the coldest quarter (i.e., the coldest four months of the year, Bio 11, positive), and the annual mean**

212 temperature range (Bio 1, positive) contributed the most to PCA axis 1 (Table 1). This first PCA axis, thus,
213 represented the severity of the native winter climate, and the extent of temperature variations throughout
214 the year. High values along this PCA axis indicate a native range climate with milder winter temperatures
215 and little annual variation in temperature. Thus, we called this axis native “winter temperature”
216 conditions.

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

221 The mean temperature of the warmest quarter (Bio 10, positive), maximum temperature of the warmest
222 month (Bio 5, positive), and mean temperature of the wettest quarter (Bio 8, positive) contributed the
223 most to the third PCA axis (Table 1). High values along this PCA axis meant warmer high temperature values
224 in the native range climate. The third PCA axis thus represented native “summer temperature” conditions.

225 The mean position along these three PCA axes was calculated for each focal species separately, to depict
226 niche optimum. This parameter was referred to as “barycenter”.

227 The date of first observation of the studied species in oceanic Europe was derived from Zieritz *et al.* 2017
228 and the “Harmonia database” 2019, and compiled the first observation data in Belgium, France, Great
229 Britain, and the Netherlands, which are the countries having the biggest area in oceanic Europe.

230 The analysis of the relationships for mean urbanity (response variable) with respect to the species
231 barycenter and the date of first observation (explanatory variables) was performed using betaregressions
232 (R package betareg, Cribari-Neto & Zeileis 2010), as we hypothesized that native climatic conditions
233 explained the distribution of alien plant species in urban versus rural areas in oceanic Europe. The response
234 variable, mean urbanity, was continuous, and was derived from proportions and restricted to the unit
235 interval (0, 1), but no values were exactly equal to 0 or 1, thus justifying the use of betaregressions (Douma
236 & Weedon 2019). The full model included all one-way interactions of the explanatory variables. We used
237 the dredge function (package MuMIn, Barton, 2019) to select the models to be averaged. In other words,
238 the best model had the lowest Akaike Information Criterion (AIC) and highest Phi coefficient (model
239 precision), and selected models had a delta AIC lower than 2 relative to the best model. Using this
240 procedure, two candidate models were retained. We then performed model averaging on these selected
241 models (R package MuMIn, Barton, 2019).

242 To characterize the origin of the studied alien plant species in term of native bioclimatic values, baseline
243 values for each of the 19 WorldClim bioclimatic predictors were calculated as their mean value over the

244 species respective native ranges. To compare those values with climatic conditions occurring in the
245 invaded range, baseline values for each of the 19 WorldClim bioclimatic predictors were calculated as their
246 mean value over the oceanic Europe study zone. To define the species as more urban or more rural, a cut-
247 off value of mean urbanity of the studied species was obtained by calculating the mean of the mean
248 urbanity of the 24 studied species (= 8.6%). This mean urbanity cut-off value was used to distinguish
249 species displaying a mean urbanity above this threshold as more urban, and species displaying a mean
250 urbanity below this threshold as more rural, in oceanic Europe. Confusion matrixes were produced for all
251 of the bioclimatic predictors, and only the best is shown here. Following their position along the reference
252 values, species considered as true positive (TP), true negative (TN), false positive (FP), and false negative
253 (FN) were determined. The precision of species placement was calculated as $\frac{TP}{(TP+FP)}$. Finally, a generalised
254 linear model was used to test the relationship of the mean urbanity of the studied species (response
255 variable) with their main native climate, which was described as the main Köppen-Geiger climate class in
256 which they occur in their native range (explanatory variable, treated as factor) (package car, John *et al.*,
257 2019). A binomial family was used, with the response variable being treated as a vector accounting for the
258 urbanity and non-urbanity percentages (i.e. $c(\%urbanity, \%non-urbanity)$) following the method of Crawley, 2013.
259 All statistical analyses were performed in R, version 1.1.463 (RStudio Team 2016).

260

261 **Results**

262 ***Native climatic conditions and invaded urbanity of alien plant species***

263 The 24 studied alien plant species showed high variability in native climatic conditions, with native ranges
264 encompassing a total of 26 out of the 30 Köppen-Geiger climate classes, yet with 87% of occurrences in
265 seven of the 30 climate classes. The urbanity of all occurrence records and species together in oceanic
266 Europe ranged from 0 to 93%; mean species-level urbanity varied between 4 and 17%. **22 of the 24 studied**
267 **alien plant species displayed a high spatial autocorrelation.**

268 ***Alien plant species from warmer and drier origins are more likely to develop in higher urbanity areas in*** 269 ***oceanic Europe***

270 **The averaged betaregression model explaining the mean urbanity in oceanic Europe of a given alien plant**
271 **species included the position of the barycenter of the bioclimatic niche of the species along PCA axes 2**
272 **and 3, and the date of first observation in the wild (Table 2).**

273 **Native climate “precipitation” (PCA axis 2) had a negative effect and “summer temperature” (PCA axis 3)**
274 **had a positive effect on species mean urbanity in oceanic Europe, both displaying the strongest support**

275 overall (Table 2; present in the 2 selected models). Thus, in oceanic Europe, alien plant species from
276 warmer (PCA axis 3) and/or drier (PCA axis 2) native ranges were, on average, found in more urban
277 environments (Fig. 3a and b).

278 The date of first observation in the wild had a weak positive but not significant effect on species mean
279 urbanity, and was only present in one of the selected models (Fig. 3c). Alien plant species present in the
280 wild for a more recent period of time were found in more urban environments.

281 The main native Köppen-Geiger climate class had a non-significant effect on species mean urbanity ($p >$
282 0.05 , $Df = 3$, $LR\ Chisq = 5.79$). However, visualization of the main Köppen-Geiger climate classes (Fig. 3a)
283 showed that more urban alien species primarily originated from subtropical or continental climates in the
284 native range. In comparison, more rural alien species primarily originated from contrasted and/or cooler
285 climates in the native range (e.g., alpine or continental) (Fig. 3, 4).

286 The confusion matrix of mean annual temperature had the strongest correlation with the urbanity of alien
287 species, with the highest estimation precision (0.58). This result highlights the importance of mean annual
288 temperature as a driver of the urbanity of alien species in oceanic Europe. Seven out of the 12 more urban
289 aliens originated from native ranges with warmer mean annual temperatures compared to the mean
290 annual temperature in oceanic Europe (TP, Fig. 4). In addition, ten out of the 12 more rural alien species
291 originated from native ranges with cooler mean temperature compared to oceanic Europe (TN, Fig. 4).

292 **Discussion**

293 The current study showed that the variation in the urbanity of alien plant species was largely explained by
294 the climatic conditions in their modelled native ranges. Native niche optimum, accounted for the PCA axis
295 barycenters in our study, had a preponderant importance. A predominant proportion of more urban and
296 more rural alien species originated from warmer and cooler native ranges, respectively, compared to the
297 studied area, in terms of mean annual temperature. Alien plants that grew in more urban environments
298 primarily originated from two main climate types: subtropical and continental climates. In comparison,
299 alien plants that grew in more rural environments appeared to mainly originate from alpine, continental,
300 and Mediterranean climates. Yet, variation in the native climate was more important for these rural alien
301 species compared to more urban alien species.

302 We acknowledge that the date of first observation in the wild had a slight but not significant effect, and
303 that we could not robustly prove that alien plant species spreading more recently were usually found in
304 more urban environments. Even though the propagule pressure of the studied alien species is not the
305 same everywhere in oceanic Europe; the introduction of plant species tends to happen at higher rates in
306 densely inhabited areas. Alien species also tend to escape from cultivated areas, such as gardens, present

307 in urban and rural areas (Botham *et al.* 2009; Dullinger *et al.* 2017). However, we noticed that the
308 occurrence of the studied alien species exhibited broad variety of urbanity values, showing that they were
309 present in all types of environments, from densely built metropolitan areas (London, Paris, etc.) in highly
310 urbanized regions (Flanders, Netherlands) to extensive rural zones (central France, Wales, etc.). Western
311 Europe has the highest road and rail density of any continent, and is considered to be the world's most
312 urbanized region (Hulme 2009; Terama *et al.* 2019). Consequently, the displacement of propagules is far
313 easier in this region compared to less human-modified parts of the world. Thus, we argue that the
314 preference of some alien species in our study for more urban or more rural environments, could be linked
315 to climatic filtering of urban climate. Indeed, our study indicates that alien plants of various origins do not
316 establish randomly along the imperviousness gradient; rather, alien plant species from warmer and/or
317 drier native ranges tend to establish in more urban environments, visible by the predominant effect of the
318 native climate barycenters.

319 Oceanic Europe has a temperate mild and humid climate; however, urban environments have elevated
320 summer temperatures due to the UHI-effect, and a modified water cycle due to impervious surfaces. These
321 phenomena result in warmer and drier local conditions compared to rural surroundings (Ortega & Pearson
322 2005; Walther *et al.* 2009; Kaiser *et al.* 2016; Szymura *et al.* 2018). Therefore, we hypothesize that it is
323 more likely that alien species from warmer and drier native ranges than those in our study area develop
324 in more urban environments, induced by the presence of warmer and drier microclimates in oceanic
325 European cities.

326 More urban aliens from subtropical climates likely take advantage of the longer growing season and
327 reduced winter freezing events associated with the UHI (Walther *et al.* 2009; Schmidt *et al.* 2014). The first
328 developmental stages of several alien plant species from subtropical climates are particularly sensitive to
329 temperature. For instance, the germination of *Baccharis halimifolia* and *Lonicera japonica* are optimal at
330 around 20–25 °C (Schierenbeck 2004; Fried *et al.* 2016), representing a relatively high temperature range
331 for oceanic Europe. Moreover, seedlings of such species also tend to be highly frost sensitive, as illustrated
332 by the high mortality of *Ailanthus altissima* seedlings after freezing events (von der Lippe *et al.* 2005). The
333 phenology of these species often involves late flowering and fruiting, which represent crucial stages
334 sensitive to the earliness, duration, and intensity of freezing events (e.g., *Baccharis halimifolia*, (Fried *et al.*
335 *et al.* 2016), *Cyperus eragrostis* (Iefländer & Lauerer 2007), and *Potentilla indica* (Dakskobler & Vreš 2009)).
336 In addition, urban environments display more drained and disturbed substrates (Schmidt *et al.* 2014) that
337 might represent conditions with favorable humidity for more urban aliens from drier native ranges that
338 are adapted to either limited and/or seasonal precipitation regimes in an oceanic humid climatic region.

339 Some of the alien species in our study prefer disturbed and/or drained soil conditions (e.g., *Reynoutria*
340 *sachalinensis* (Sukopp & Starfinger 1995)), and germinate better under contrasted temperatures (e.g.
341 *Elaeagnus augustifolia*, (Guilbault *et al.* 2012)). The urban microclimate also promotes the survival of the
342 seedlings of some of these species (e.g., *Acer negundo*, (von der Lippe *et al.* 2005)).

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

349 The separation of more urban aliens from the whole alien species pool indicates that urban conditions
350 could act as a strong filter for warmth and drought-adapted plant species. This phenomenon is of great
351 conservation concern, because many ornamental species introduced to temperate regions originate from
352 dry and warm areas (van Kleunen *et al.* 2018). Moreover, urban environments might enhance alien plant
353 invasions in the future, due to higher environmental disequilibrium caused by enhanced urbanization,
354 trade, and climate change (van Kleunen *et al.* 2018). Because urban areas are highly connected with rural
355 surroundings, they actively export propagules (Hulme 2009; Catford *et al.* 2011). Under climate change,
356 surrounding rural areas will become suitable for drought and warm adapted species, in addition to urban
357 environments (Kendal *et al.* 2012). Cities could act as veritable migration outpost for these climate limited
358 alien plant species, facilitating their escape to newly suitable rural areas (Hulme 2009; Dullinger *et al.* 2017;
359 Pyšek *et al.* 2017).

360 This study demonstrated that global databases (such as GIBF.org, WorldClim, Copernicus Imperviousness
361 Density), if cautiously used, are relevant for analyses at a continental scale. The strong relationship
362 between urbanity in the invaded range and climatic conditions in the modelled native range, at a
363 continental scale, suggests that even stronger microclimatic effects might be at play at local scales, as
364 suggested by previous studies (Botham *et al.* 2009; Walther *et al.* 2009; Lembrechts *et al.* 2018). Even if
365 we acknowledge variability within species and limited number of studied species, the strong pattern found
366 in the current study confirmed that this global relationship with climatic conditions of origin is consistent,
367 and highlighted that multi-species studies are essential for comprehending invasion processes and urban
368 invasion ecology (Catford *et al.* 2011).

369 In an era of biotic homogenization (Pyšek *et al.* 2010; Terama *et al.* 2019), urban environments could
370 represent hotspots for invasion by new alien plant species. Therefore, emphasis should be placed on

371 invasion processes and monitoring invasion in urban environments to advance our understanding on what
372 drives the early stages of invasion, when it might still be controlled. Furthermore, this phenomenon might
373 be compounded by the fact that warmer and drier climates might become more common across the whole
374 urban-to-rural gradient under climate change (Hamdi *et al.* 2015; Brans *et al.* 2017). Therefore, it is
375 important to raise the awareness of public institutions and private property owners, especially since
376 massive urban plantations, such as public and/or private gardens, which could help cities adapt to climate
377 change, might otherwise represent potential sites for the “seeding” of future plant invasions (Essl 2007;
378 Gaertner *et al.* 2017).

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559 **Data accessibility statement:** no new data were used.

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566 **Tables**567 **Table 1: Results of the Principal Component Analysis (PCA) for the 19 WorldClim bioclimatic predictors.**

PCA Dimension	Predictor number	Name short	Contribution (%)	Correlation
Dimension 1	Bio 6	Minimum temperature coldest	12.3	0.96
	Bio 7	Mean temperature Coldest Quarter	12.2	0.95
	Bio 11	Annual mean temperature	10.9	0.90
Dimension 2	Bio 3	Annual precipitation	15.4	0.81
	Bio 14	Precipitation driest quarter	14.9	0.80
	Bio 17	Precipitation driest month	13.9	0.77
Dimension 3	Bio 10	Mean temperature warmest	1.95	0.72
	Bio 5	Maximum temperature warmest	1.73	0.68
	Bio 8	Mean temperature wettest	1.58	0.64

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569 Table 2: Estimates and corresponding p-values of the total mean urbanity variance explained by the averaged model. Significant effects are
 570 displayed in bold. N = number of species. Variables contained in each model of the selection used in the model averaging are represented by the
 571 following numbers: 1 = PCA axis 2 barycenter; 2 = PCA axis 3 barycenter; 3 = Date of first observation. The variables, pseudo R², Log-likelihood, and
 572 corresponding AICc are detailed for each model. The pseudo R² of the best model of all (Model 1) indicates that 43% of the variance in the data
 573 was explained by the model.

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	mean	precision
(Intercept)	-2.231*** (0.06)	
PCA axis 2 barycenter	-0.173** (0.055)	
PCA axis 3 barycenter	0.119** (0.045)	
Date of first observation	0.05 (0.068)	
(phi)		171.093** (51.13)
Significance: *** = p < 0.001; ** = p < 0.01; * = p < 0.05		

N = 24

Averaged models:	Variables	Pseudo R ²	Log-likelihood	AICc
Model 1	1,2,3	0.43	59.66 on 5 Df	-106.0
Model 2	1,2	0.36	57.94 on 4 Df	-105.8

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576 **Figures**

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

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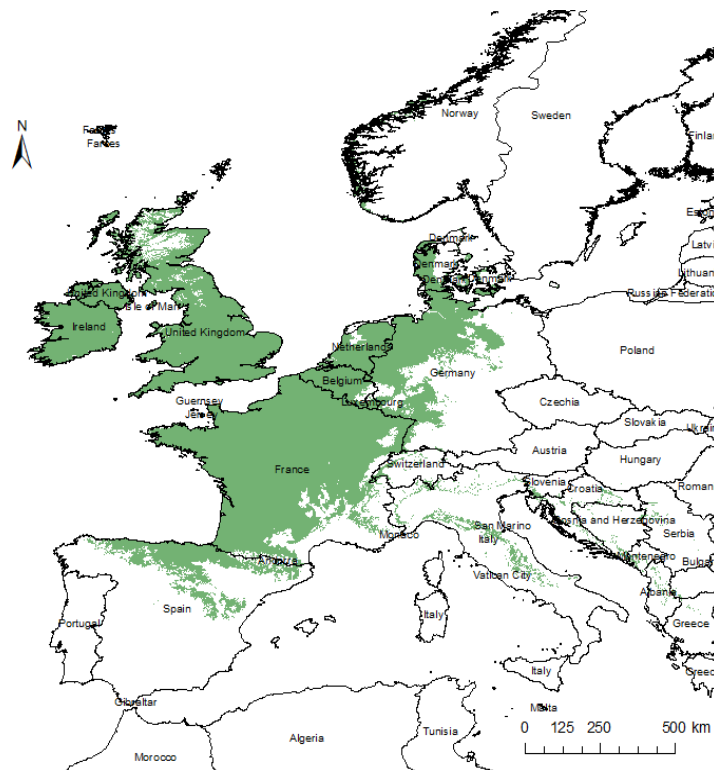
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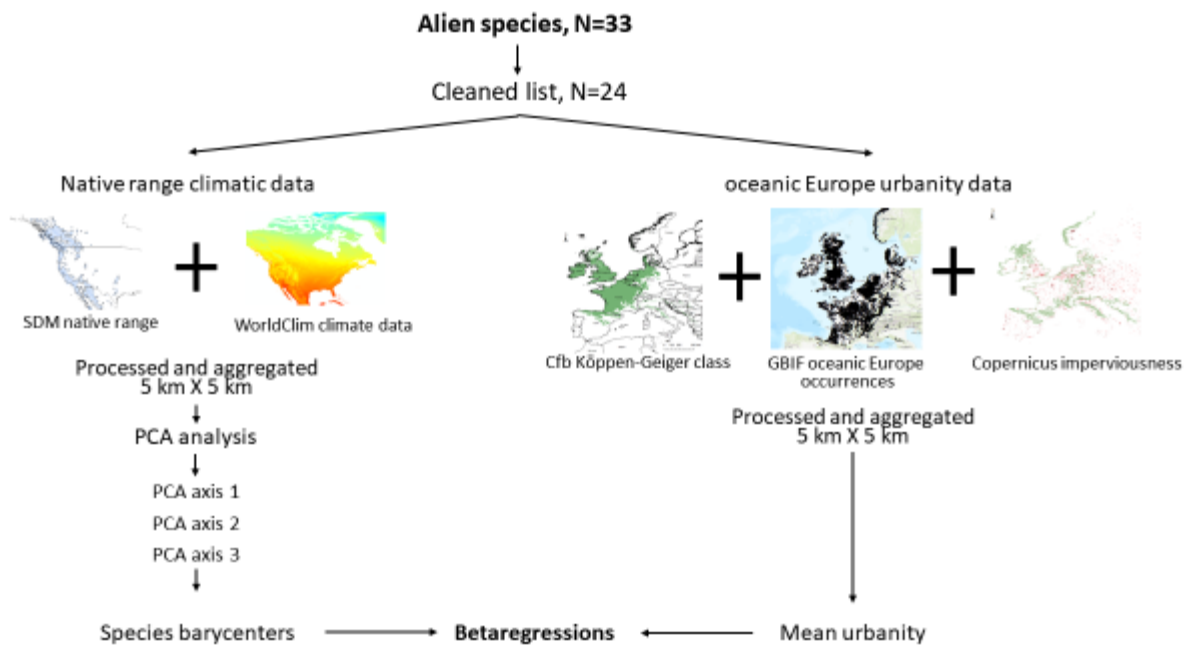
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601 Figure 2: Organizational chart of data acquisition, treatment, and analyses.



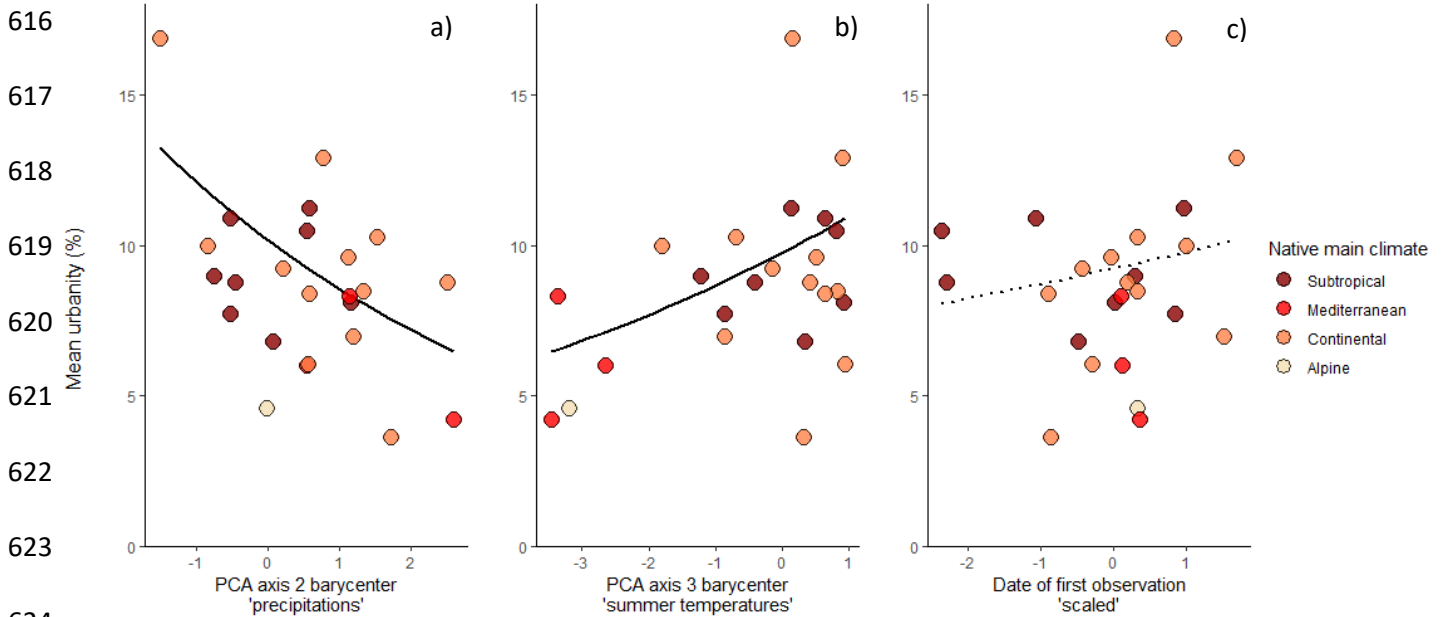
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605 Figure 3: Mean urbanity (in %) of the studied alien plant species as a function of their native range barycenter
606 calculated from the three first dimensions of the PCA conducted with WoldrClim bioclimatic predictors. Mean
607 urbanity of alien plant species: a) as a function of the barycenter of species for PCA axis 2, mainly associated
608 with the bioclimatic predictors of “precipitation”; b) as a function of the barycenter of species for PCA axis 3,
609 mainly associated with the bioclimatic predictors of “summer temperature”, and c) as a function of the scaled
610 date of first observation in the wild. Each point corresponds to a species, colored as a function of the main
611 Köppen-Geiger climate class in which it was observed the most in its modelled native range. Lines correspond
612 to the averaged model output (predicted mean urbanity, %) in oceanic Europe. Full lines correspond to
613 significant effect in the full averaged model, and dashed line corresponds to a non-significant effect in the full
614 averaged model.

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631 Figure 4: Mean urbanity of alien plant species in oceanic Europe as a function of their native range mean
 632 annual temperature (°C). Each point corresponds to a different species. The full vertical line represents the
 633 mean annual temperature (°C), considered as the reference in oceanic Europe: 9.9 °C. The dashed horizontal
 634 line corresponds with the mean urbanity value for the set of studied species: 8.6; species with lower mean
 635 urbanity than this value were considered to be more rural aliens in oceanic Europe (i.e. 12 out of the 24
 636 studied species); with higher urbanity than this value were considered as more urban aliens in oceanic Europe
 637 (i.e. 12 out of the 24 studied alien species). Species are colored following their native main Köppen-Geiger
 638 climate class. Species represented with squares correspond to either true negative or true positive in the
 639 confusion matrix, and species represented with circles are either false negatives or false positives.

