



Woody invaders from contrasted climatic origins distribute differently across the urban-to-rural gradient in oceanic Europe – Is it trait-related?

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ABSTRACT

Alien plant species invasion depends on biotic and abiotic conditions that can represent environmental barriers as compared to their native range conditions. Specifically, little is known about how alien plant species distribute along the urban-to-rural gradients based on their native climatic conditions, and how environmental conditions along these gradients could influence intraspecific trait variation. We studied the distribution of eight woody alien plant species from contrasted native range climates along urban-to-rural gradients in European areas with a temperate climate (hereafter termed oceanic Europe). During two consecutive summers and in the Belgian part of oceanic Europe, we then measured their intraspecific trait variation using the nitrogen balance index (NBI), chlorophyll content, flavonols index, specific leaf area (SLA) and internode space. Urban-to-rural gradients were characterized by a system of local climate zones (LCZ), the percentage of artificially sealed surfaces (urbanity) and the sky view factor (SVF). We found that the distribution of studied species in the LCZ classes was highly dependent on the climate of their native range, with species from warm climates occurring more in the most urban areas while the ones from cool climates preferred the more rural or natural areas. However, their intraspecific trait variation was not related to the LCZ class in which they grew, nor to their native climate. Instead, we found a surprisingly consistent effect of shielded environments (low SVF) along the entire urban-to-rural gradient on leaf and development traits. Such environments induced a lower leaf flavonols index and higher NBI and SLA, suggesting a shade response and possibly lower heat and drought stress. Our results show that although woody alien plant species from warmer or cooler native climates distributed differently along the urbanization gradient in oceanic Europe, they did not show contrasted intraspecific trait variation. Nevertheless, our findings highlight that even if the woody alien plant species from cooler native ranges are currently more present in the most natural areas, special attention should be paid to woody alien plant species from warmer native ranges that are yet restricted to the most urban areas and could potentially have severe impacts in the future when the barriers to their spread weaken with climate change.

1. Introduction

The number of alien species worldwide increases and does not show any sign of saturation (Seebens et al., 2017). This is notably due to the continuing steep rise in international trade, travel, and transport, resulting in the biotic homogenization of the world, and suggests that biological invasions will be increasingly problematic in the future (Olden and Rooney, 2006; Pyšek et al., 2010; van Kleunen et al., 2018). However, only a small number of introduced alien plants become naturalized in a new environment after overcoming a series of abiotic and biotic barriers

(Blackburn et al., 2014; Dullinger et al., 2017; Richardson et al., 2000). In Europe, alien plant invasions occur in a wide range of habitats, from the rural outskirts to the city cores (Catford et al., 2011). Specifically, cities contain a higher number and proportion of newly arriving alien plant species than rural areas (Godefroid and Ricotta, 2018; Lambdon et al., 2008). Some previous studies have suggested that a few climate-limited alien species might benefit from the warmer climatic conditions in urban environments, as these would allow them to overcome cold-sensitive life stages (Essl, 2007; Walther et al., 2009). Nevertheless, little is known about whether alien plant species from different native

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climatic conditions distribute differently and have contrasted intraspecific trait variation along the urban-to-rural gradients.

Cities provide plants with unique growing conditions (McKinney, 2002; Schmidt et al., 2014). The low albedo and weak evapotranspiration due to urban structures, the heat storage and release due to buildings and anthropogenic activities, all together lead to higher temperatures in cities than in the rural surroundings (urban heat island (UHI) effects (Dirksen et al., 2019; Oke, 1981)). In western Europe, the effects of the UHI are strongest in summer and in the most impervious areas (Arnds et al., 2017; Oke, 1981; Top et al., 2020). The intensity of the UHI effect is strongly related to the characteristics of each city, such as its 3D structure like the layout and height of buildings, as well as its regional climate conditions (Ward et al., 2016; Zhao et al., 2014).

While the UHI effects operate at the landscape scale, a broad range of cooler and warmer microhabitats occurs at a scale of meters due to the heterogeneity of the urban matrix (Ren et al., 2013). Indeed, the height and spacing of buildings affect energy fluxes and result in micro-scale temperature variations (Grimmond et al., 2001). These temperature differences are strongly linked to the sky view factor (SVF), a measure of the proportion of open sky, which is a proxy for the ratio of the radiation received by a surface from the sky to the radiation emitted at a given location (Tan et al., 2016; Watson and Johnson, 1987). Urban areas characterized by large, densely arranged buildings have low SVF values, and therefore receive less solar radiation and have reduced airflow. However, those areas have greater solar reflectance due to building surfaces and more intense heat-producing anthropogenic activities, which locally enhance UHI effects (Bonamente et al., 2013; Theeuwes et al., 2017). These urban environments with low SVF cool less efficiently and have lower temperature variations than rural environments (Oke, 1981; Steeneveld et al., 2011). Trees and parks also induce low SVF values, but they limit heat storage and mitigate UHI effects through evapotranspiration (Dirksen et al., 2019). For example, locations with low SVF values due to buildings or vegetation do not have the same temperature conditions at the local scale, with cooler temperatures in the case of dense vegetation cover rather than in the case of highly built-up areas (Lindberg et al., 2016; Middel and Krayenhoff, 2019; Oliveira et al., 2011). The complexity of the urban-to-rural gradient from a microclimatic viewpoint has recently been summarized into the local climate zones (LCZ, Anjos et al., 2020; Demuzere et al., 2019; Dian et al., 2020). LCZ classes correspond to areas with uniform urbanization characteristics such as built up percentage, building structure, SVF and land use categories (Stewart and Oke, 2012). The more urban LCZ classes correspond to higher built up percentages and lower SVF values, and have large UHI effects (Anjos et al., 2020; Mandelmlch et al., 2020).

The hot urban air, especially due to the UHI effects, can influence local precipitation (Cosgrove and Berkelhammer, 2018). For example, urbanization has been shown to intensify summer thunderstorms in European cities (Li et al., 2020; Lorenz et al., 2019; Schliunzen et al., 2010). The hydrological system in urban areas must then cope with fluctuating amounts of surface runoff on impervious surfaces (Hamdi et al., 2011). As urban soils are characterized by compacted substrates and anthropogenic materials, they are typically drier than rural ones, most strongly so during the summer months (Fortuniak et al., 2006; Hamdi et al., 2015).

Plants growing along environmental gradients must cope with significant spatial variations in growing conditions, which can be visible by differences in their development and morphology (Chevin et al., 2010; Esperon-Rodriguez et al., 2020; Nicotra et al., 2010). These responses can be assessed by studying physiological or morphological traits variations. This has been widely investigated at the interspecific level, notably along altitudinal or latitudinal gradients (Borowy and Swan, 2020; Francis and Chadwick, 2012). For example, alien plant species reaching high elevations worldwide have a broad tolerance to climatic conditions, which allows them to develop along large sections of the altitudinal gradients (Alexander et al., 2011; Kühn et al., 2021). The native climatic conditions of alien plants introduced to foreign environments strongly determine their capacity to establish and spread (Alexander and Edwards, 2010). The

thermal stress, development and phenology of alien species in the invaded range often depend on their native climatic conditions (Godoy et al., 2011; Iacarella et al., 2015; Ricciardi et al., 2013). For example, the flowering phenology of alien plant species has been found to depend on the climate of origin, with species from tropical native climate flowering later than those from temperate climates in an invaded area with a mediterranean climate (Godoy et al., 2009; Guarino et al., 2021). Additionally, plants from warmer native climates respond more strongly at the intraspecific level to warm and dry growing conditions with greater variations of leaf pigments such as chlorophyll and xanthophyll, than plants from cooler native climates (García-Plazaola et al., 2008). Recent research has suggested that the warmer microclimates and drier growing conditions of cities might affect the distribution of alien plant species. For example, in areas of western Europe with a temperate oceanic climate, alien plant species restricted to urban areas come from native ranges that are warmer and/or drier than climatic conditions in oceanic Europe (Geron et al., 2021). However, we need to get a better understanding of how urban-to-rural gradients influence the distribution and the intraspecific trait variation of alien plant species (McDonnell, 2011). Intraspecific trait variations have been studied and compared between alien plant species having different invasion stages, between native and alien plant species, as well as between growing seasons (Canessa et al., 2018; Milanović et al., 2020; Seabloom et al., 2015; Westerband et al., 2021; Wolkovich et al., 2013). However, studies about alien plant species along urban-to-rural gradients have particularly focused on the species-level traits that are the most present in urban areas, or on the difference in the timing of biological events between cities and rural areas (Alberti et al., 2017; Fisogni et al., 2020). Furthermore, to our knowledge, no study has been done on differences in intraspecific trait variations between alien plant species from contrasted native climates as a function of urbanization. In addition, the use of fine spatiotemporal scales is rare but essential to detect intraspecific trait variations, as urban-to-rural gradients are often studied at scales that are too coarse for plant species (Williams et al., 2015).

Woody alien plants are one of the main plant invader categories worldwide, but also one of the most impactful groups, especially in cities (Potgieter et al., 2017; Richardson and Rejmánek, 2011). Although vegetation is crucial to adapt warming cities to global changes, previous landscaping tendencies have promoted the use of woody alien plant species along urban-to-rural gradients (Paz-Dyderska et al., 2020; Walther et al., 2009). Given the known negative impact of these woody alien plant species, it is then crucial to study how woody alien plant species from contrasted native climatic conditions distribute along urban-to-rural gradients, and if they differ in their intraspecific trait variations. In this paper, we studied eight woody alien plant species, from contrasted native climatic conditions: four from warmer and four from cooler native climates than the invaded study area, during two growing seasons. We addressed the following questions: (i) Are woody alien plants species from warmer and cooler native climates distributed differently in the LCZ classes in oceanic Europe? (ii) Do they show contrasted intraspecific trait variations depending on the growing season, the LCZ classes, or the local microhabitats in which they occur?

2. Methods

2.1. Study area

We delineated our study area as temperate oceanic Europe with warm summers and no dry season as defined by Köppen-Geiger climate classification Cfb (Fig. 1, Beck et al., 2018). This geographic entity was considered to represent the invaded range, and is hereafter referred to as “oceanic Europe”. It includes the scattered small patches of temperate climate in the Alps, Apennines and Balkan. While the alien plant species distribution was studied over the entire study area, the intraspecific trait variation of alien plant species was examined in the Belgian part of oceanic Europe (Fig. 1). This area contains some of the most urbanized parts of Europe, embedded in a rural matrix.

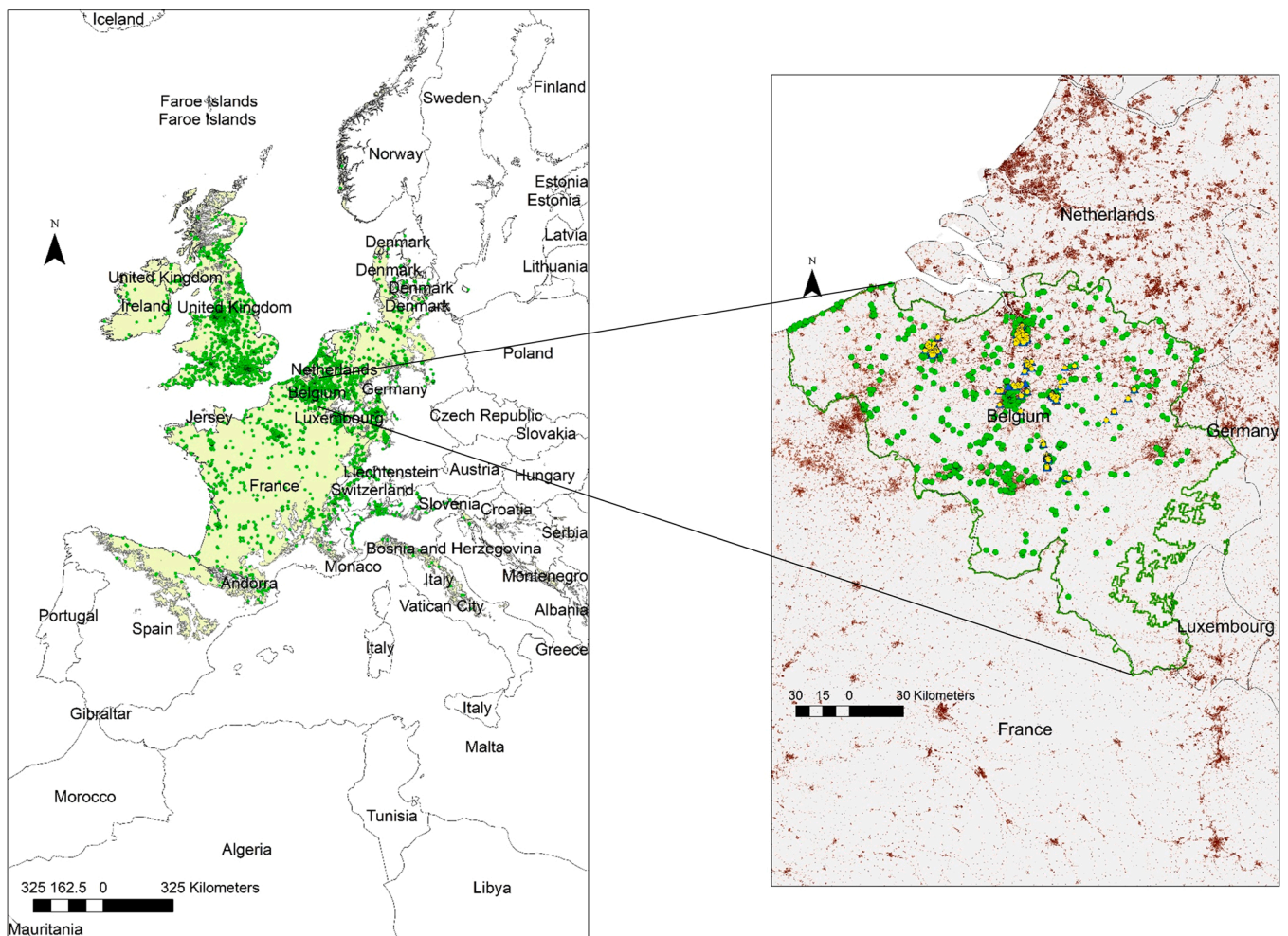


Fig. 1. Maps of the study area. Left panel: data coverage for the eight woody alien plant species in oceanic Europe. The climate zone as a whole is in light green and each processed occurrence – regardless of species - is indicated with a bright green dot. See [Supplementary material 1, Fig. 1](#), for the distributions of each of the species separately. Right panel: the processed occurrences of the eight woody alien plant species in the Belgian part of oceanic Europe are indicated with bright green dots. The studied locations for the eight woody alien plant species are represented by light blue triangles for locations studied in 2019 and bright green pentagons for locations studied in 2020. The Belgian part of oceanic Europe (i.e., only the south of Belgium is not situated in oceanic Europe) is delineated by the green line. The percentage of sealed surfaces (urbanity) is represented at 20×20 m by the gray-dark red gradient, with the gray zones representing rural areas with very low urbanity (~ 0 %) and dark red areas representing the zones with the highest urbanity (~ 100 %).

2.2. Species list

We selected eight woody alien plant species from contrasted native climatic conditions, either warmer or cooler than the study area, based on distribution maps and literature: *Ailanthus altissima* (Mill.) Swingle, *Berberis aquifolium* Pursh, *Buddleja davidii* Franch, *Cornus sericea* L., *Paulownia tomentosa* (Thunb.) Steud., *Prunus laurocerasus* L., *Senecio inaequidens* DC. and *Symphoricarpos albus* (L.) S. F. Blake ([Table 1](#), [Kew Gardens, 2021](#)). The average year of first observation in oceanic Europe was 1860 for the “Warm” native climate group, and 1881 for the “Cool” native climate group ([Table 1](#)). To obtain the native climate preferences of each species, species distribution models (SDMs) were built with their native occurrences from the Global Biodiversity Information Facility (GBIF, 2020), using maximum entropy modeling (Maxent, [Phillips et al., 2017, 2006, 2004](#)). Maxent predictions were transformed into presence cells, and constituted the species modeled native ranges (based on the methods in [Geron et al., 2021](#); see [Supplementary material 1](#) for detailed methods and the modeled native ranges). We used the annual mean temperature and the precipitation of the driest month extracted with a 5×5 km grid over the modeled native ranges of each species (Bioclimatic predictors 1 and 14 respectively, [Fick & Hijmans, 2017](#)). These two bioclimatic predictors have been proven to influence the

distribution of emerging alien plant species in urban environments in oceanic Europe and represent the temperature and drought-affinity of the species ([Geron et al., 2021](#)). We calculated the mean values for the annual mean temperature for each species modeled native range and the mean value for the annual mean temperature over oceanic Europe. This allowed us to situate the “Warm” and “Cool” alien plant species groups in function of the annual mean temperature conditions over oceanic Europe ([Table 1](#)). Woody alien plant species from the “Warm” group came from warmer native ranges and woody alien plant species from the “Cool” group came from cooler native ranges than the study area. Importantly, even if the species of the “Warm” group came from drier native ranges than the species from the “Cool” group in terms of the precipitation of the driest month, all species came from drier native ranges than the study area.

Note that we only used these SDMs to get an estimation of the native climatic conditions of each of the studied alien plant species and did not extrapolate the results of these SDMs to predict their distribution in the introduced range. This exempts us from the issue that predictions of species distribution models in invaded ranges may suffer from low accuracy due, for example, to differences in climatic preferences of species between their native and invaded ranges ([Atwater et al., 2018](#); [Goeckede et al., 2020](#)).

Table 1

Studied species information. If species' information was not retrieved in the global literature, additional local references were added. The mean annual mean temperature and the mean precipitation of the driest month across Oceanic Europe were 9.9 °C and 52.1 mm, respectively. The mean annual mean temperature and the mean precipitation of the driest month for the species from the "Warm" and "Cool" native climate groups were 14 °C and 15.8 mm, and 8.7 °C and 34.1 mm, respectively. The standard deviation of the mean annual mean temperature and of the mean precipitation of the driest month for the species from the "Warm" and "Cool" native climate groups were 1.1 and 1.9, and 0.5 and 3.2, respectively. In comparison with species from the "Warm" group, species from the "Cool" group are thus more homogenous in terms of annual mean temperature but less homogenous in terms of precipitation of the driest month. See Methods for calculation of annual mean temperature and precipitation of the driest month over the modeled native ranges of each species and over oceanic Europe, as well as the species' group determination. Seed dispersal refers to the main means. References used: ⁽⁶⁾Essl (2007); ⁽⁷⁾Gilbert (1995); ⁽⁸⁾Kowarik et al. (1995); ⁽³⁾Monty et al. (2013); ⁽¹⁾POWO (2020); ⁽²⁾Richardson and Rejmánek (2011); ⁽⁵⁾van Valkenburg et al. (2021); ⁽⁴⁾Zieritz et al. (2017). ⁽⁹⁾WFO (2021).

Species ⁽¹⁾	Family ⁽¹⁾	Native range ⁽¹⁾	Annual mean temperature over the modeled native range (°C)	Precipitation of the driest month over the modeled native range (mm)	Native climate group	Vector of introduction ⁽²⁾	Pathway of introduction ⁽⁴⁾	Adult height (m) ⁽⁵⁾	Life form ⁽⁵⁾	Seed dispersal ⁽⁵⁾	Year of first observation in the wild
<i>Ailanthus altissima</i> (Mill.) Swingle	Simaroubaceae DC.	Asia (China)	13.2	19.3	Warm	Ornamental	Deliberate	25–30	Tree	Anemochory	1786 ⁽⁴⁾
<i>Berberis aquifolium</i> Pursh	Berberidaceae Juss.	North America (SW. Canada to N. California)	9.8	25.8	Cool	Ornamental	Deliberate	1	Shrub	Ornithochory	1874 ⁽⁴⁾
<i>Buddleja davidii</i> Franch	Scrophulariaceae Juss.	Asia (Tibet to central and S. China)	12.7	17.7	Warm	Ornamental	Deliberate	1–6	Shrub	Anemochory	1895 ⁽⁴⁾
<i>Cornus sericea</i> L.	Cornaceae Bercht. & J. Presl	North America	8.4	35.4	Cool	Ornamental	Deliberate	1–6	Shrub	Ornithochory	1838 ⁽⁴⁾
<i>Paulownia tomentosa</i> (Thunb.) Steud.	Paulowniaceae Nakai	Asia (Central and E. China, S. Korea)	12.9	15.2	Warm	Ornamental	Deliberate	20 ⁽⁶⁾	Tree ⁽⁶⁾	Anemochory ⁽⁶⁾	1925 ⁽⁶⁾
<i>Prunus laurocerasus</i> L.	Rosaceae Juss.	Eurasia (SE. Europe to Iran)	9.2	41.5	Cool	Ornamental	Deliberate	6–8	Shrub	Ornithochory	1965 ⁽⁸⁾
<i>Senecio inaequidens</i> DC.	Asteraceae Bercht. & Presl	Africa (Mozambique to S. Africa)	17.1	10.8	Warm	Industry ⁽³⁾	Accidental ⁽³⁾	1	Subshrub ⁽⁹⁾	Anemochory	1836 ⁽⁴⁾
<i>Symphoricarpos albus</i> (L.) S. F. Blake	Caprifoliaceae Juss.	North America (Subarctic America to N., W. & Central U.S.A.)	7.5	33.6	Cool	Ornamental	Deliberate	1–3 ⁽⁷⁾	Shrub ⁽⁷⁾	Ornithochory ⁽⁷⁾	1817 ⁽⁷⁾

2.3. Occurrences in LCZ in oceanic Europe

In order to acquire high resolution occurrence data of the eight alien plant species in oceanic Europe, we created an iNaturalist project (<https://www.inaturalist.org/projects/city-invasions>, “iNaturalist”, 2021), for citizens to register those species, capturing all observations within the studied countries. We only kept occurrences considered as “research grade”, that is checked at least one time by other participants, georeferenced, with photos and corresponding to a non-cultivated plant. Occurrences with a precision of less or equal to 50 m were kept (mean precision of 10 m), and the temporal window was limited to the 2011–2020 period. Occurrences were then resampled with a 200 × 200 m resolution raster grid placed over oceanic Europe to reduce sampling bias. In each 200 × 200 m grid cell, and for each species, only a randomly chosen occurrence was kept if several were present. This resulted in a total of 5800 processed occurrences in oceanic Europe (see [Supplementary material 1, Fig. 1](#); number of occurrences ranged from 1956 for *B. davidii* to 116 for *C. sericea*), from which we extracted the local climate zones (LCZ, 100 × 100 m resolution, [Demuzere et al., 2019](#)). To compare the distribution of each species in the LCZ classes with a random distribution, a set of random occurrences according to the number of occurrences of each species was created, from which the LCZ classes were extracted. The “Compact highrise”, “Open highrise” or “Lightweight lowrise” LCZ classes are virtually not present in the study area and were thus excluded, and the water class was not considered ([Demuzere et al., 2019](#)). We observed a very low proportion or no presence of the alien plant species in the “Bush, scrub”, “Bare rock, paved”, and “Bare soil, sand” classes, and these classes were not further analyzed (0.2 % of the total number of occurrences was comprised in these LCZ classes, [Supplementary material 2, Table 2](#)). Finally, for the comparison between the observed and random occurrences for each of the studied species, the observed or random occurrences in a LCZ class in oceanic Europe that accounted for less than 5 % of the total observed or random occurrences for a certain species were set to 0 ([Supplementary material 2, Table 2](#)).

2.4. Location selection in Belgium and field campaigns

We used the Belgian citizen observation platform Waarnemingen.be/Observations.be to acquire high-resolution GPS points of the occurrences of the selected species in Belgium. Due to its local popularity, this platform could provide us with a higher number of occurrences than iNaturalist for that region. Only the validated species identifications were kept ([Natuurpunt and Natuurinformatie, 2018](#), mean precision of 140 m, for the period 1998–2018, number of occurrences ranged from 1989 for *S. inaequidens* to 61 for *P. tomentosa*).

For location selection in the field, the urban-to-rural gradients were characterized using remotely sensed urbanity (percentage of sealed surfaces, original scale: 400 m², ([European Environment Agency \(EEA\), 2019](#))) at two scales: 400 m² (20 × 20 m) and aggregated at 9 km² (3 × 3 km). The use of these two scales allowed to take into account scale-dependent effects of urbanization: UHI effects operate most strongly at a resolution of several kilometers, while at 400 m² resolution more fine-grained urban microclimates are captured ([Brans et al., 2017; Kaiser et al., 2016](#)). The 400 m² scale will later on be referred as the “local scale” urbanity, and the 9 km² scale as the “landscape scale” urbanity.

We conducted a random selection of species’ occurrences, yet maximizing the range of urbanity at both the local and landscape scale as well as the range of possible combinations of the two scales. This was performed by dividing both the local and landscape urbanity scales in classes of 10 % and selecting an equal number of random occurrences from each combination of local and landscape-level classes, if occupied by the species. This way, we obtained the full, crossed spectrum of the two urbanity scales specific to each considered species. Each location selected as such was visited and, if the target alien species was found, one representative individual was chosen (excluding individuals with obvious damages from e.g. management), and its precise location was taken with a handheld GPS. A total of 277 and 287 individuals were visited in July 2019 and 2020, respectively: 52 and 47 for *A. altissima*, 36 and 39 for *B. aquifolium*, 34 and 42 for *B. davidii*, 29 and 27 for *C. sericea*, 37 and 32 for *P. tomentosa*, 33 and 30 for *P. laurocerasus*, 17 and 36 for

Table 2

Distribution in oceanic Europe of the mean observed and random occurrence numbers for each of the LCZ classes, per alien plant species “Warm” or “Cool” native climate group. The mean total number of occurrences for the “Warm” and “Cool” group equals 864 and 604, respectively. In italic, observed occurrence number different from the random ones. The observed proportion in each LCZ class that are significantly higher for one of the two native climate groups in comparison to the other one, are marked with the following code: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. We observed a very low proportion or no presence of the alien plant species from the “Warm” and “Cool” groups in the “Bush, scrub”, “Bare rock, paved”, and “Bare soil, sand” classes, and these classes were not further analyzed and in gray. LCZ classes were reorganized in function of building and vegetation percentages, see [Demuzere et al. \(2019\)](#).

LCZ class	Group	Mean observed number	Mean observed proportion	Mean random number	Mean random proportion
Compact midrise	Warm	37***	0.06	0	0.00
Compact lowrise	Warm	33***	0.04	2	< 0.001
Large lowrise	Warm	95***	0.11	4	< 0.001
Open midrise	Warm	60***	0.08	1	< 0.001
Open lowrise	Warm	337	0.38	42	0.05
Sparsely built	Warm	23	0.03	12	0.01
Low plants	Warm	97	0.10	470	0.54
Scattered trees	Warm	110	0.12	158	0.18
Dense trees	Warm	69	0.08	172	0.20
Bush, scrub	Warm	1	0.002	5	< 0.01
Bare rock, paved	Warm	2	0.004	1	< 0.001
Bare soil, sand	Warm	1	0.002	0	0.00
Compact midrise	Cool	9	0.01	0	0.00
Compact lowrise	Cool	8	0.01	1	< 0.001
Large lowrise	Cool	15	0.03	2	< 0.001
Open midrise	Cool	20	0.03	1	< 0.001
Open lowrise	Cool	253	0.41	34	0.06
Sparsely built	Cool	29***	0.05	9	0.01
Low plants	Cool	66	0.12	328	0.54
Scattered trees	Cool	106***	0.20	107	0.18
Dense trees	Cool	99***	0.15	119	0.20
Bush, scrub	Cool	0	0.00	3	< 0.001
Bare rock, paved	Cool	0	0.00	1	< 0.001
Bare soil, sand	Cool	0	0.00	1	< 0.001

S. inaequidens, and 39 and 34 for *S. albus*. Seventy-one % of the locations of 2019 could be resurveyed in 2020, with the difference due to the removal of some studied alien plants by urban management actions between 2019 and 2020. In those cases, a new location was selected with comparable urbanity values. In addition, new locations were added in 2020 for the species with the lowest spatial coverage in 2019 (mainly for *S. inaequidens*). The months of July 2019 and 2020 in our study area were characterized by unusually dry weather compared with the climatic means of the 1981–2010 period, calculated for the climatic reference station for Belgium, Uccle. The precipitation total was respectively 28 % and 35 % lower than normal. The mean temperature was 1.1 °C higher than normal in July 2019, and 0.5 °C lower than normal in 2020. The total hours of sunshine were 119 % of the normal in 2019, and close to normal in 2020 (RMI, 2020, 2019).

2.5. Field measurements

2.5.1. Environmental variables

To quantify the growing conditions of each alien plant individual, we used the LCZ classes, a proxy of urbanity at 2 spatial scales, the sky view factor (SVF), and the building ratio.

The LCZ class along the urban-to-rural gradients at each of the studied plant locations was extracted, and classes containing less than 5 % of the total studied alien plant observations were pooled with the most comparable LCZ classes. This was done in order to avoid low numbers of plant locations in some of the LCZ classes. To do so, five plant locations were attributed from “Open midrise” to “Compact midrise”, five from “Sparsely built” to “Open lowrise”, 19 from “Dense trees” to “Scattered trees” and 21 from “Low plants” to “Scattered trees” class.

The local scale urbanity (20 × 20 m) was acquired at each plant location. The urbanity of the growing environment of each of the studied alien plants was characterized by visually estimating the percentage of impervious surface in a 40 × 40 cm square centered on the focal organism and will be referred to as the “organism scale” urbanity.

The SVF is the proportion of the sky that is open at a certain location (Johnson and Watson, 1984; Middel et al., 2018). Using a clinometer, we measured the standardized horizon angle (taken at 1 m height) above which the sky was visible in each cardinal direction, without distinguishing between buildings or vegetation: $SVF = \frac{((90-N)+(90-E)+(90-S)+(90-W))}{360}$, with N, E, S, W, standardized horizon angle towards north, east, south and west, at the location of each studied plant. The SVF is directly linked to the solar energy which a place receives due to the local 3-D geometry. As such, an open terrain gets a higher amount of short and long wave radiation from the sky ($SVF \approx 1$) than a shielded terrain ($SVF \approx 0$) (Dirksen et al., 2019; Oke, 1981).

As the SVF does not distinguish between plants and buildings, the building ratio was quantified as the visual estimation of the dominant category, either buildings or vegetation, that induced the SVF in each cardinal direction (values of: 0 for only vegetation, 0.5 in case of both buildings and vegetation, 1 for only buildings). UHI effects are indeed exacerbated by building proportion but reduced through evaporative cooling and/or vegetative shading, and a location with a low SVF value due to buildings results in higher temperature at the very local scale than a location with a low SVF value due to a dense vegetation canopy (Caluwaerts et al., 2020; Middel and Krayenhoff, 2019; Wang et al., 2015). The average building ratio for the four cardinal directions was then calculated as $Building\ ratio = \frac{BN+BE+BS+BW}{4}$, with BN, BE, BS, BW, building ratio towards the north, east, south and west, respectively. Spearman correlations showed that the building ratio was strongly positively correlated with the urbanity at the organism and local scales as well as with the SVF (Supplementary material 2, Table 1).

2.5.2. Intraspecific trait variations

To study the intraspecific trait variations of the studied alien species along the urban-to-rural gradients, we measured the internode space,

and leaf traits such as the chlorophyll content, the flavonols content, the nitrogen balance index (NBI) and the specific leaf area (SLA), for each individual.

Plant internode space responds negatively to drought and positively to shading (Gorton et al., 2018; Nicotra et al., 2010). The SLA relates to shading impact and resource uptake, with higher values in shielded conditions and areas with high nutrient availability (Gregg et al., 2003; Song et al., 2019). SLA and internode space decrease under dry and high temperatures conditions, but increase under high temperatures if water availability is high (Esperon-Rodriguez et al., 2020; Molina-Montenegro et al., 2012). Dry, high UV, and warm conditions lower the chlorophyll content and NBI, but raise the flavonols content (Ballizany et al., 2012; Brossa et al., 2009; Dongyun et al., 2014; Hatier and Gould, 2009). The NBI indicates carbon/nitrogen allocation changes due to nitrogen deficiency, with lower values expected in more stressful growing conditions such as shallower, more drained and limited soil space in highly urbanized areas, despite the fact that cities generally have richer soils (Cerovic et al., 2012; Pavao-Zuckerman, 2008). This measure is non-invasive and less sensitive to leaf age and canopy position than other nitrogen nutrition indices (Cerovic et al., 2015; Diago et al., 2016; Dong et al., 2021). The traits used to study the intraspecific trait variations during summer capture processes happening at different time scales: the internode space reflects the whole-season growing conditions, whereas the SLA and pigments such as chlorophyll or flavonols reflect the response of individuals over a much shorter time period – that of leaf ontogeny and leaf life span (Fernández Honaine et al., 2019; Fusaro et al., 2019; Song et al., 2019).

The internode space just below the youngest fully developed leaf, was measured using a folding meter.

The NBI, the chlorophyll content ($\mu\text{g}/\text{cm}^2$) and the flavonols content were acquired in the field on the three latest developed leaves using the Dualex® Scientific + (Force-A, Orsay, France), and averaged per individual plant. The chlorophyll content is obtained via the transmittance ratio at two different wavelengths, one in the far-red absorbed by chlorophyll and one in the near-infrared as a reference. The Dualex acquires the flavonols index via the screening effect of these polyphenols on chlorophyll fluorescence (called hereafter “flavonols index”, Cerovic et al., 2012). The NBI is calculated as the ratio chlorophyll/flavonols.

The same leaves as measured above were ultimately collected for further processing. The fresh leaf area was measured using a flatbed scanner and later analyzed in ImageJ (Rasband, 2018), and the dry mass was measured after drying the leaves at 60 °C for 48 h. The SLA was calculated following $SLA = \frac{\text{leaf area (cm}^2\text{)}}{\text{dry mass (g)}}$.

2.6. Statistical analyses

2.6.1. Alien plant distribution in LCZ classes

We compared the observed and the random distribution of each species in the LCZ classes in oceanic Europe with the help of chi-squared tests. The same test was used for the pooled distribution in the LCZ classes of the four invaders from either the “Warm” or “Cool” native climate group, with the mean for each class calculated over each group of four species, compared to random distributions. Finally, separate 2-sample proportion z tests were conducted to compare the proportions of “Warm” and “Cool” alien plant species in each of the LCZ classes.

2.6.2. Alien plant intraspecific trait variations

We built linear mixed models to disentangle the main drivers of the intraspecific trait variations across the eight alien plant species at two spatial scales: the LCZ classes (100 × 100 m) and the finer microhabitat effects (containing the local scale urbanity (20 × 20 m), the organism scale urbanity (40 × 40 cm) and the SVF at the plant locations as explanatory variables), taking into account their native climate group (“Warm” or “Cool”). For all linear mixed models, we included a random factor accounting for the location identity. This allowed us to take into

account the fact that 71 % of the locations were resurveyed during the two growing seasons.

We tested if the date of observation within each growing season (20 days in 2019 and 2020) significantly impacted alien plant intraspecific trait variation with linear mixed models for each of the developmental (internode space) and leaf variables (SLA, chlorophyll content, flavonols index and NBI), with species identity and location identity as two separate random factors (package lme4, Bates et al., 2020). We did not find any significant influence of the date of observation on the developmental and leaf variables, and therefore excluded this variable from the following analyses.

Next, the relationships between the variables measuring the intraspecific trait variation (developmental and leaf variables: response variables) and the LCZ classes (resolution of 100×100 m), the species native climate group and the growing season (explanatory variables) were analyzed across all species, again with species identity and location identity as two separate random factors. The full models included the two-way interactions between the LCZ classes, the species native climate group and the growing season. In the finer-resolution linear mixed models (with the urbanity at the local scale (20×20 m) and at the organism scale (40×40 cm)), we analyzed the relationships between the developmental and leaf variables (response variables), and the urbanity at two scales (local and organism), the SVF, the species native climate group and the growing season (explanatory variables), again with species identity and location identity as two separate random factors. The full models included all two-way interactions of the explanatory variables. Quadratic terms for the local and organism urbanity scales and the SVF were included to test for an optimum in conditions along the gradient. Only the SVF² had a significant effect and its interactions with the other explanatory variables were included for the NBI and the flavonols index (Williams et al., 2015). Note that the LCZ classes and the finer-resolution variables (urbanity at the local and organism scales, and the SVF) could not be analyzed with one overarching model due to the complexity of the resulting models.

For both models at each of the spatial scales, the NBI, flavonols index, SLA and internode space were log-transformed to obtain residual normality. We verified if the addition of the species identity as a random intercept increased the fit of the models, for each of the response variables by doing the analysis of variance and calculating the Akaike Information Criterion (AIC) difference between the full models with and without species as a random intercept (Galwey, 2006). For all response variables and at both coarser and finer resolutions, the addition of the species identity as a random intercept decreased the AIC with more than two, and significantly increased the fit of the models. While the addition of the location identity as a random factor did not decrease the AIC (or not much), we decided to keep it in as it reflected the structure of the data.

We checked the variance inflation factors (VIF) for all models, which showed no multicollinearity for any of the explanatory variables ($1 < VIF < 1.14$, package performance, Lüdtke et al., 2020). We used the dredge function (package MuMIn, K. Barton, 2019) to select the “optimal models”, i.e., those with a $\Delta AIC < 2$ (a difference of less than two in the AIC, in comparison with the best model: the one with the lowest AIC). The pseudo-R-squared was calculated for all best models, for each of the response variables (Package MuMIn, K. Barton, 2009). We performed model averaging on these “optimal models” (function model.avg, MuMIn, K. Barton, 2019). We call “final models” either the averaged model or the best model, when only one model was retained (all other models with $\Delta AIC > 2$ in comparison with the best model).

As the building ratio was too strongly correlated with urbanity at the local and organism scale, as well as with the SVF, to be included in the full model, any remaining underlying effects of the building ratio on alien plant intraspecific trait variations was tested in linear models of the residuals of the best models for each of the response variables (R package lme4, Bates et al., 2020).

ArcMap 10.5.1 (ArcGis Desktop, 2017) was used for spatial

processing. All statistical analyses were performed in R, version 4.0.3 (R Core Team, 2018), and $p = 0.05$ was taken as threshold for significance.

3. Results

3.1. Alien plant species distribution in the LCZ classes in Oceanic Europe

The woody alien plant species occurred in all LCZ classes present in oceanic Europe (Table 2, Supplementary material 2, Table 2). The distribution of the species when pooled in the “Warm” and “Cool” native climate groups significantly differed from a random distribution for 90 % of the LCZ classes in oceanic Europe (for all LCZ classes, except for the “Cool” group in the rural LCZ classes, Table 2). When analyzed for each species separately, the alien plant distribution in the LCZ classes in oceanic Europe significantly differed from a random one (Supplementary material 2, Table 2). In oceanic Europe, the proportion of alien plant species from the “Warm” native climate group was significantly higher than the proportion of alien plant species from the “Cool” native climate group in the most urban LCZ classes; whereas the proportion of alien plant species from the “Cool” native climate group was significantly higher than the proportion of alien plant species from the “Warm” native climate group in the most rural/natural LCZ classes (Table 2 and Fig. 2). The highest proportion of alien species occurrences from the two groups was present in the “Open lowrise” class, where their proportion was not significantly different between the “Warm” and “Cool” native climate groups, but was significantly different from random for both groups (Table 2 and Fig. 2). The same distribution pattern was present in the Belgian part of the study area (data not shown).

3.2. Alien plant intraspecific trait variation in function of the LCZ classes in Belgium

Despite a strong impact on alien species distribution, the LCZ classes did not significantly explain the intraspecific trait variation of the alien plant species. Only the chlorophyll content was significantly higher in the most urban LCZ classes. The “Warm” and “Cool” native climate group and the growing season were only retained in the final model of the chlorophyll content, but not significantly (Supplementary material 2, Table 3).

3.3. Alien plant intraspecific trait variation at the finer resolution in Belgium

Across the “Warm” and “Cool” native climate groups and the growing seasons, the SVF and the urbanity at the organism scale appeared as the most important drivers of the intraspecific trait variation of woody alien plant species. Low SVF values significantly increased the NBI and SLA, and decreased the flavonols index, across both native climate groups, while a negative yet non-significant effect of a decreasing SVF on the internode space was also retained in the final model (Table 3, Figs. 3–6, Supplementary material 2, Fig. 1). The chlorophyll content significantly decreased at high urbanity at the organism scale, and during the second growing season for the woody alien plant species from the “Warm” native climate group (Table 3, Fig. 4).

A significant quadratic effect of the SVF was retained for the NBI and the flavonols index (Table 3, Figs. 3 and 5), while quadratic SVF effects were absent for the SLA and the internode space (Table 3, Fig. 6, Supplementary material 2, Fig. 1). No interactions between the SVF and the urbanity at the organism or the local scale were retained in any of the final models (Table 3).

The building ratio did not significantly explain the residuals' variation for any of the best mixed models at the finer resolution.

4. Discussion

Our study showed that the distribution of woody alien plant species

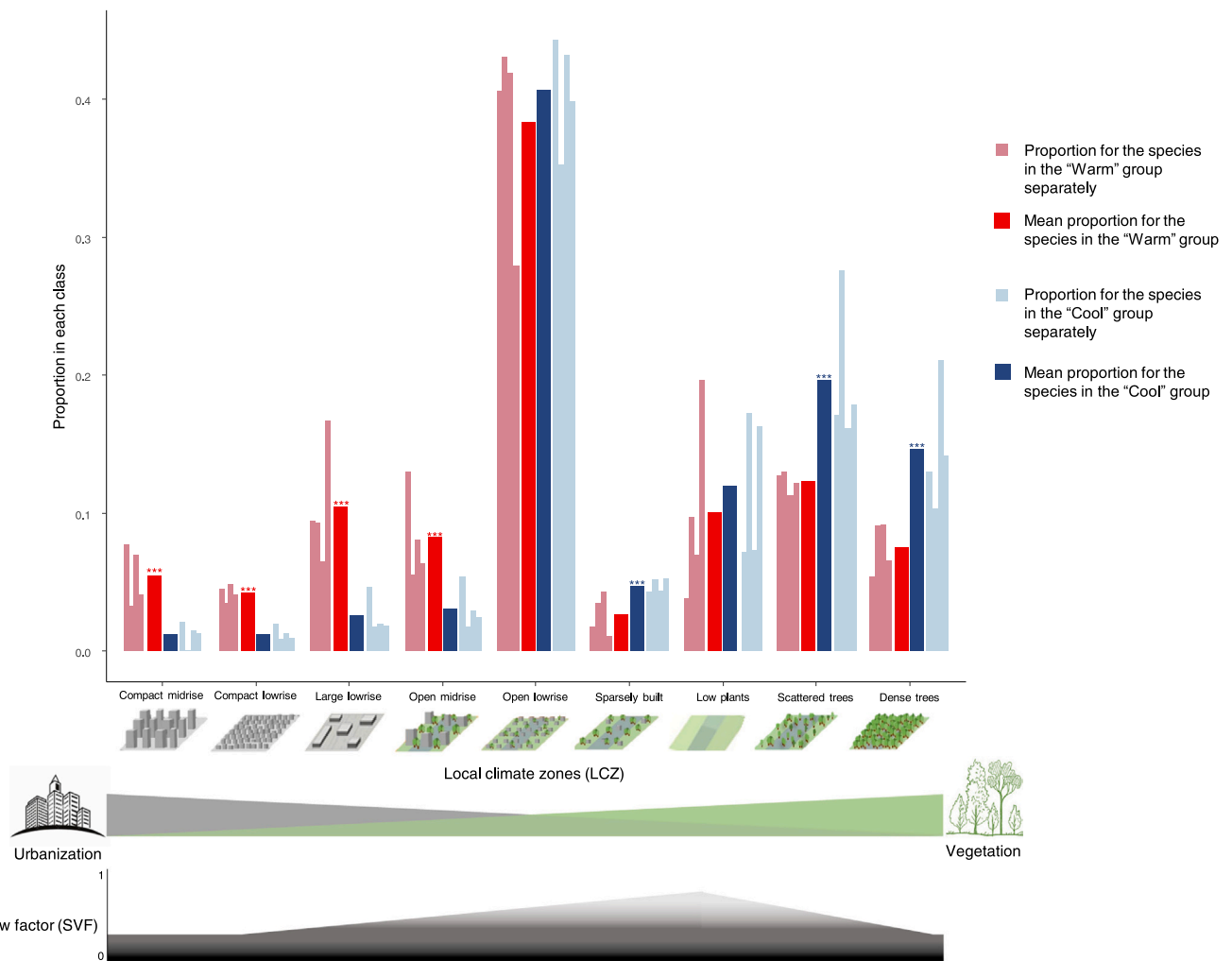


Fig. 2. Proportion of each woody alien plant species, and mean proportion of the species per “Warm” (red) or “Cool” (blue) native climate group in function of the local climate zones (LCZ) in which they grow in oceanic Europe. Proportion bars are organized as follows: *A. altissima*, *B. davidii*, *P. tomentosa* and *S. inaequidens* from the “Warm” native climate group are represented in this order by the light red bars, the bright red bar represents the mean “Warm” native climate group proportion; *B. aquifolium*, *C. sericea*, *P. laurocerasus* and *S. albus* from the “Cool” native climate group are represented in this order by the light blue bars, the dark blue bar represents the mean “Cool” native climate group proportion. The mean proportions that are significantly higher for one of the two groups in comparison to the other one as tested with a 2-sample proportion z test, are marked with the following code: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, in the color of the one that is higher. LCZ classes were ordered in function of the imperviousness and vegetation percentages. The urbanization is represented by the imperviousness percentage represented by the gray gradient that decreases towards the rural end of the urban-to-rural gradient, the vegetation percentage represented by the green gradient that increases towards the rural end of the urban-to-rural gradient, and the sky view factor (SVF) represented by the color gradient from black to gray for low (~ 0) to high values (~ 1), respectively. The imperviousness and vegetation percentages as well as the SVF are diagrammed and based on the values used to determine the LCZ classes.

in oceanic Europe depended on the climatic conditions of their native range, but that their intraspecific trait variations did not differ, at least not for the set of traits under study. On the contrary, all the studied species seemed to benefit from sheltered environments in summer. We found that woody alien plant species from warmer native climates were more present towards the most urban LCZ classes whereas the species from cooler native climates were restricted to the more rural/natural LCZ classes in line with Géron et al. (2021). Nevertheless, the intraspecific trait variation of the woody alien plant species was rarely explained by the LCZ classes in which they grew but was driven by the SVF and the urbanity at the organism scale. Whatever their native climates or the growing season, woody alien plant species had higher NBI and SLA values, but a lower flavonols index and internode space (although not significantly) in areas with low SVF values. Higher SLA and NBI values and lower flavonols index values are typical shade responses, although a corresponding increase in internode space or a reduction in chlorophyll content per unit area in function of decreasing

SVF were not observed (Fernández Honaine et al., 2019; Khalid et al., 2019; Khan et al., 2000; Lichtenthaler et al., 2007; Quero et al., 2006; Weinig and Delph, 2001). Apart from a response to lower UV radiation, the lower flavonols index could also reflect the lower temperature extremes and higher soil moisture in the shade (Bouderias et al., 2020; Brossa et al., 2009). The chlorophyll content was the only trait showing lower values when the woody alien plants were growing in highly urbanized areas at the organism scale. This is in line with other studies that found that plants produced less chlorophyll when growing in urban environments with impervious soils (Rahman et al., 2014; van Geel et al., 2019). Finally, whether the SVF was due to buildings or vegetation had no significant effect on the intraspecific trait variation of the studied species.

Importantly, we did not detect significant effects of the growing season on the measured traits, except for the chlorophyll content which was lower for the “Warm” native climate group during the cooler 2020 summer. Indeed, both summers experienced severe droughts, but

Table 3

Estimates for the final models (averaged or best models, if only one model was retained) testing for the drivers of the nitrogen balance index (NBI), the chlorophyll content, the flavonols index, the specific leaf area (SLA) and the internode space conducted across species with linear mixed models for the effects of the urbanity scales, the SVF, the growing season and the native climate group and their interactions. Only the variables or interactions taken back in the averaged or best models are presented. Standard errors are indicated between brackets, and significant effects are in bold, and coded as follows: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. The number of models in the final model is specified. Information of the best models for each response variable are detailed with marginal R^2 corresponding to the proportion of variance explained by the fixed factors alone, and the conditional R^2 corresponding to the proportion of variance explained by the fixed and random factors together.

	Nitrogen balance index (NBI)	Chlorophyll content	Flavonols index	Specific leaf area (SLA)	Internode space
Number of models in the final model	1	1	3	3	4
(Intercept)	3.59 *** (0.11)	32.15 *** (2.18)	-0.19 * (0.09)	4.10 *** (0.20)	1.21 *** (0.25)
SVF	-1.98 *** (0.44)	-0.31 (3.15)	1.90 *** (0.36)	-0.76 *** (0.19)	0.04 (0.12)
SVF ²	1.33 ** (0.54)		-1.34 ** (0.44)		
“Warm” native climate group		-2.56 (3.12)		0.42 (0.31)	0.21 (0.34)
Urbanity 40 cm		-0.04 *** (0.01)			
Growing season 2020		3.04 * (1.50)	0.03 (0.04)		
“Warm” native climate group × SVF		-0.34 (3.83)		-0.07 (0.20)	
“Warm” native climate group × Growing season 2020		-3.12 * (1.25)			
SVF × Growing season 2020		-1.08 (3.68)			
Best model information					
df	5	9	5	5	3
Log Likelihood	-317.62	-1747.59	-206.54	-451.75	-530
Num. obs.	523	523	523	501	508
Num. groups: species	8	8	8	8	8
Num. groups: location id	176	176	176	173	176
Var: species (Intercept)	0.03	13.01	0.02	0.08	0.28
Var: location id (Intercept)	0.02	1.55	0.01	0.01	0.02
Var: Residual	0.15	45.15	0.11	0.33	0.43
Pseudo marginal R^2	0.11	0.16	0.14	0.13	0
Pseudo conditional R^2	0.33	0.36	0.32	0.32	0.41

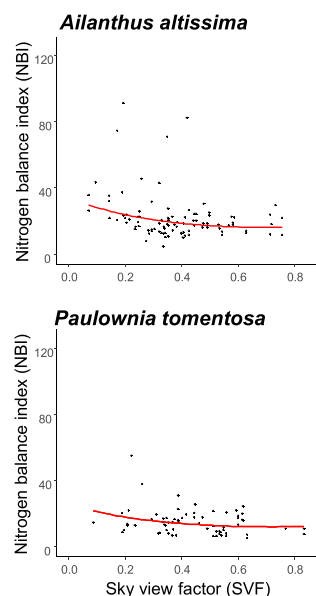
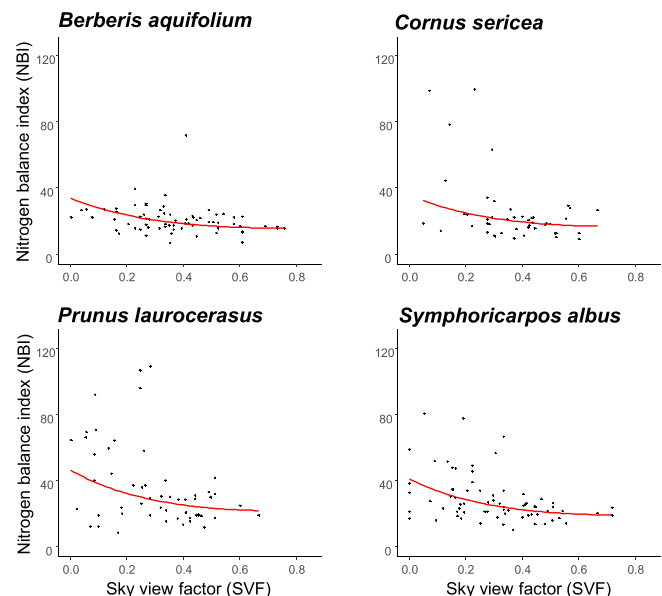
‘Warm’ alien species**‘Cold’ alien species**

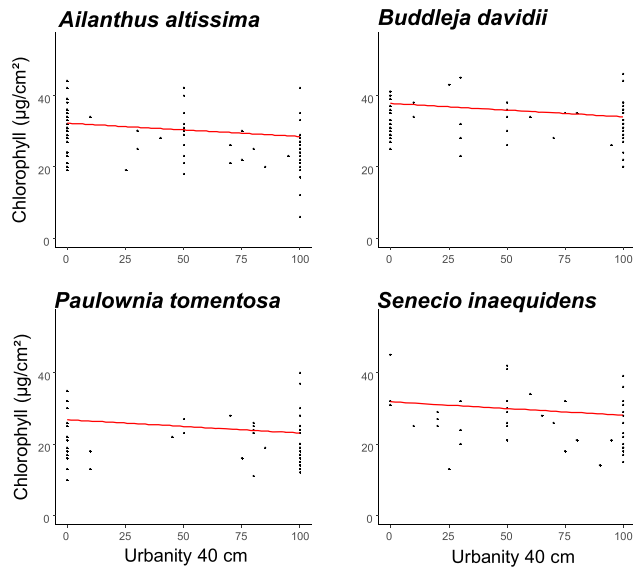
Fig. 3. Nitrogen balance index (NBI) as a function of the sky view factor (SVF, measured at the individual) for each of the alien plant species either from the “Warm” or the “Cool” native climate group. Measured values are represented by the black dots, and the modeled trends are in red.

summer 2019 being warmer and 2020 closer to the climatic average (RMI, 2020, 2019). The lower chlorophyll content for the “Warm” native climate group during the cooler 2020 summer conditions is in line with evidence supporting the fact that plant species from warmer native climatic conditions respond more strongly to temperature variations (García-Plazaola et al., 2008). The lack of response for the other measured traits is surprising as some, such as the flavonols, are known to respond strongly to temperature conditions (Ballizany et al., 2012), yet it strengthens our conclusions that our observed intraspecific trait variation along urban-to-rural gradient is robust for interannual

variation in weather conditions. We also did not find any effect of the interactions between the urbanity at the local and at the organism scale, or between the urbanity at the local or at the organism scale and the SVF, which implies that the patterns we found with the SVF or with the urbanity at the organism scale did not vary along the urban-to-rural gradients. Interestingly, the higher chlorophyll content we found for plants growing in the most urban LCZ classes was not found back at the local or organism urbanity scale, where we found the opposite trend.

Although summer conditions along the urban-to-rural gradients impacted the intraspecific trait variations of all the studied alien species

'Warm' alien species



'Cool' alien species

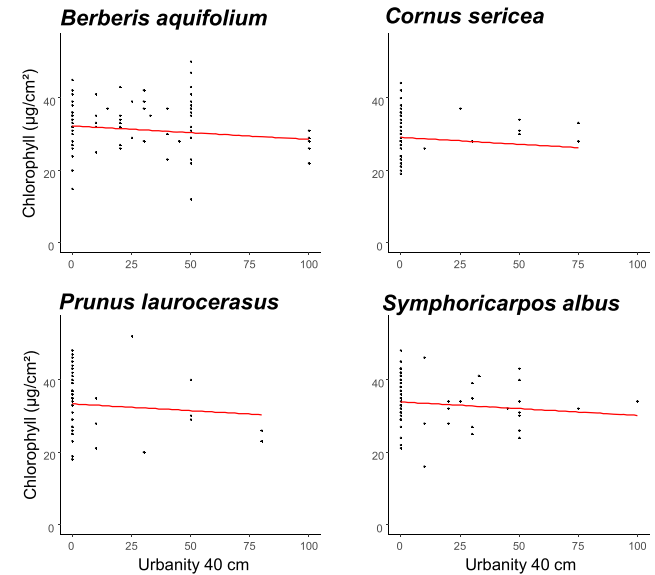
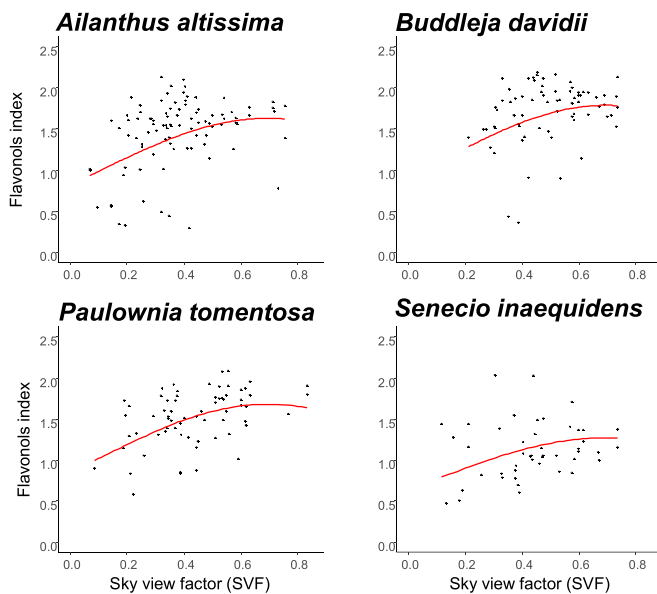


Fig. 4. Chlorophyll content as a function of the urbanity at the organism scale ($40\text{ cm} \times 40\text{ cm}$) for each of the alien plant species either from the “Warm” or the “Cool” native climate group. Measured values are represented by the black dots, and the modeled trends are in red.

'Warm' alien species



'Cool' alien species

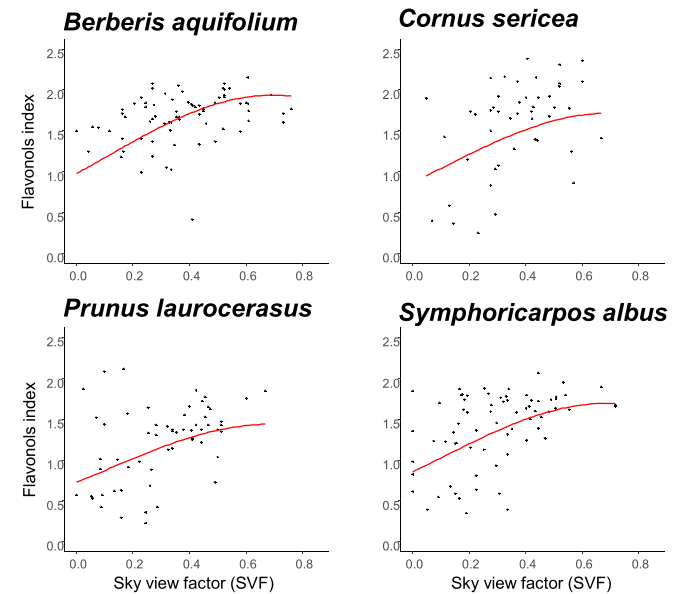


Fig. 5. Flavonols index as a function of the sky view factor (SVF, measured at the individual) for each of the alien plant species either from the “Warm” or the “Cool” native climate group. Measured values are represented by the black dots, and the modeled trends are in red.

at the organism scale, these trait responses were similar between the “Warm” and “Cool” native climate groups. The leaf and growth traits we used were chosen because of their strong response to summer conditions with high UV, elevated temperatures and drought periods (Duan et al., 2016; Mediavilla et al., 2019). However, we cannot exclude that other traits such as stomatal conductance, wood cavitation, water potential or root length would respond differently between the two native range groups along the urbanization gradients. Another reason for the absence of contrasted intraspecific trait variation between the “Warm” and the “Cool” native climate groups may lie in the timing of the study. It is possible that such contrasts occur early or late in the growing season and/or when looking at other traits, when urban environments may reduce the intensity and frequency of freezing events, thus extending the

growing season relative to rural environments (Guilbert et al., 2019). Additionally, different patterns might occur when looking at other life stages. Early life stages or traits such as the reproduction or germination success, have been proven to be decisive for alien plant invasions (Gioria and Pyšek, 2017). For example, the phenology of some alien plant species found in more urban environments in oceanic Europe often involves late flowering and fruiting, which represent crucial stages sensitive to freezing events (Fried et al., 2016). As such, the longer growing season in urban areas might allow alien plant species from warmer native climatic conditions to better reproduce in cities. Indeed, those species often need a longer growing season to complete their reproductive cycle and thus reproduce late in the growing season, at times when freezing events are less likely in urban areas than in rural areas.

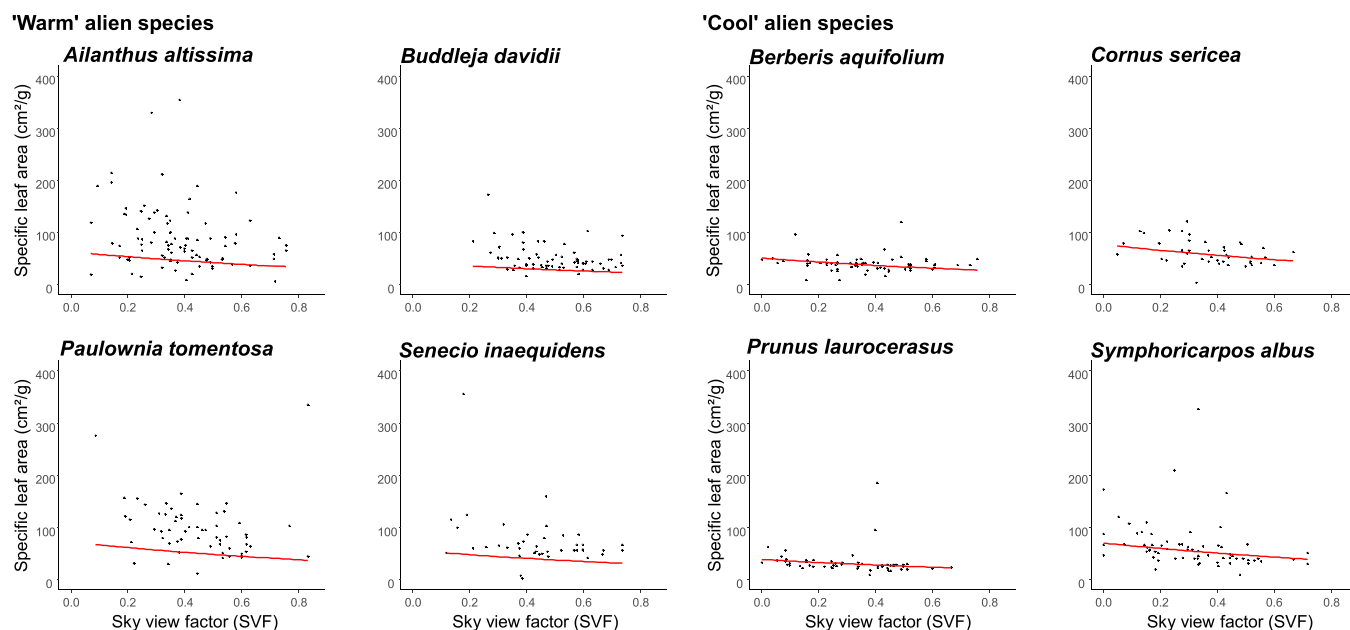


Fig. 6. Specific leaf area (SLA) as a function of the sky view factor (SVF, measured at the individual) for each of the alien plant species either from the “Warm” or the “Cool” native climate group. Measured values are represented by the black dots, and the modeled trends are in red.

Moreover, the urban microclimate has been shown to promote the seedling survival in late winter and early spring of some woody alien plant species of the “Warm” native climate group like *A. altissima* or *P. tomentosa*, which tend to be highly frost-sensitive at the juvenile stage (von der Lippe et al., 2005). This could be the reason why they are mostly restricted to the most favorable urban microhabitats in terms of temperature, in central Europe (Essl, 2007). On the other hand, it has been noted that for some of the woody alien plant species from the “Cool” native climate group such as *P. laurocerasus* or *S. albus*, seedlings or young plants are negatively impacted by warmer microclimate and/or drier soil conditions, which would limit their establishment in cities and restrict them to the rural outskirts (Berger et al., 2007; Gilbert, 1995).

Most common woody alien plant species present in urban environments have been linked to specific dispersal modes such as ornitochory, while anemochory is a dispersal mode that has been negatively associated with urban areas (Richardson and Rejmánek, 2011; Williams et al., 2015). Even if we did not include this parameter in our study, we noted that we found patterns different from those in the literature for the dispersal mode of the alien plant species more present in urban environments. Indeed, alien plant species from the “Warm” group which rely mostly on anemochory were more present in urban areas, while alien plant species from the “Cool” group which rely mostly on ornitochory were more present in rural areas, suggesting that temperature affinity might overrule dispersal traits as driver of species distributions along the urban-to-rural gradient. On the other hand, other factors such as the introduction date can influence the establishment and distribution of alien plant species (Wilson et al., 2007). However, in our case the majority of the studied woody alien plant species has been observed in the wild for more than 100 years, regardless of their affiliation to the “Warm” or “Cool” native climate group. Moreover, a recent study by Géron et al. (2021) found little importance of the year of first observation, but high relevance of native climatic conditions for the distribution of alien plant species along urban-to-rural gradients in western Europe.

Although alien plant species were present in all the LCZ categories, they showed significant differences in proportional distributions between LCZ categories. This is in agreement with other findings that the distribution of alien plant species highly relates to the habitat type, in urban systems but also in other environments (Axmanová et al., 2021;

Campagnaro et al., 2018; Chytrý et al., 2008; Godefroid and Ricotta, 2018). Additionally, the LCZ class that was the most invaded, across both native climate groups of alien plant species, was the one corresponding to detached houses with gardens (“Open lowrise”, Stewart and Oke, 2012). This is in line with previous studies that showed that alien plant species tend to escape from cultivated areas such as gardens where the growing conditions are manipulated by anthropogenic activities and the propagule pressure is high (Botham et al., 2009; van Kleunen et al., 2015). Moreover, all but one of our study species were introduced for ornamental purposes, which links to the growing evidence of the role of planted ornamental woody alien plant species as a source of woody plant invasion (Čeplová et al., 2017; Godefroid and Ricotta, 2018). Importantly, we showed that even though all studied species seemed to be the most present in the “Open lowrise” category, they distinctly distributed towards the most urban or rural ends of the gradient depending on their preferred climatic conditions. While this pattern results in a high proportion of woody alien plant species from warm origins in cities, it also conversely results in relatively higher invasion of “Cool” aliens in the “Dense” and “Scattered trees” categories. Therefore, the contrasted distribution related to the native climates of woody alien plant species in our study could probably be less related to propagule pressure, dispersal patterns in the study region, the time since their introduction or difference in their use, than to possible developmental differences along urban-to-rural gradients. Nevertheless, it remains possible – as in any observational study – that underlying unmeasured processes or parameters, such as biotic interactions, disturbances, soil moisture and/or nutrient levels, or differential adaptation to conditions in the invasive range, to name a few, are behind the observed patterns. Indeed, high levels of disturbances – related to the urbanization gradient in our study –, wetter habitats or soils with higher nutrient levels are for example often linked to higher proportions of alien plant species in diverse environments (Akin-Fajiyé and Akomolafe, 2021; Bazzichetto et al., 2021; Chytrý et al., 2008; Lembrechts et al., 2016; Porté et al., 2011). Moreover, disentangling the role of establishment, development and dispersal patterns, and their interaction with adaptation and plasticity, from that of climatic conditions in alien plant invasions certainly represents research avenues for the future.

The variables we chose to characterize the environment have all been shown to be representative of the temperature variations along

urban-to-rural gradients, either due to the UHI effects or to the microclimatic conditions. Indeed, the LCZ classes and urbanity at local scale correlate with temperature differences between urban and rural environments, while the SVF and the urbanity at the organism scale are linked to variations in light and temperature at a resolution of a few meters (Anjos et al., 2020; Caluwaerts et al., 2020; Dian et al., 2020; Ward et al., 2016). However, as mentioned above, we only noticed effects of variables depicting the urban-to-rural gradients such as the urbanity and the SVF at the organism scale on the intraspecific trait variation and in the same direction for both alien species from “Warm” and “Cool” native climate groups. We argue that in our study the finer-scaled light and temperature variations related to the SVF or the urbanity at the organism scale might have overruled the larger-scale variables such as the LCZ classes or the urbanity at the local scale. For example, it has been found that areas shaded by buildings or vegetation can experience an average decrease in air temperature of approximately 5 °C, when temperature differences between urban and rural areas due to the UHI effects are situated around 2 °C in the study area (Middel and Krayenhoff, 2019; Top et al., 2020; Toparlar et al., 2018). Additionally, the building ratio that we used to further refine the SVF did not further explain the intraspecific trait variation of the studied woody alien plant species, even though it is known that sheltered environments surrounded by either buildings or vegetation show strong differences in temperatures (Lindberg et al., 2016; Middel and Krayenhoff, 2019; Oliveira et al., 2011). This might be due to the fact that the building ratio variable we used was strongly correlated to the urbanity at the local and organism scales. Indeed, the urbanity at the organism scale was already impacting the trait response to summer conditions. High resolution in-situ temperature datasets along urban-to-rural gradients are often lacking due to practical (logistical and cost) challenges. Future studies would clearly benefit from such knowledge on fine-scale spatiotemporal variations responses in microclimatic conditions (Lembrechts et al., 2020).

We argue that it is important to keep an eye on woody alien plant species in cities. Indeed, they can have harmful consequences by damaging anthropogenic structures such as buildings and heritage sites, but also by adversely affecting the native biota in the most natural areas (Campagnaro et al., 2018; Celesti-Grapow and Ricotta, 2020; Richardson and Rejmánek, 2011). We showed that woody alien plant species from cooler native ranges are more present in the most natural areas in oceanic Europe where they can already have serious impact on ecosystems. For example, *P. laurocerasus*, one of the species from the “Cool” native climate group, has been shown to invade forested areas in western Europe where it alters soil characteristics and decreases native plant diversity (Rusterholz et al., 2018). On the other hand, even if woody alien plant species from warmer native ranges seem to be more present in the most urban areas in oceanic Europe at the moment, they could have severe impacts in rural areas in the future when the barriers to their spread weaken with climate change. This is what has been noted for example for *A. altissima*, a species from the “Warm” native climate group, in the warmer climate of Mediterranean Europe. There, this alien species displayed an initial establishment phase in urban areas and a secondary invasion into more rural and/or natural areas. In these Mediterranean areas, this species has adverse impacts in urban areas because of its establishment on historical buildings, but it also decreases the native plant species richness in invaded forests in the rural surroundings (Celesti-Grapow and Ricotta, 2020; Montecchiari et al., 2020; Sladonja et al., 2015). Interestingly, the invasion process of another species from the “Warm” native climate group, *P. tomentosa*, is very similar to the one of *A. altissima* in Europe. Indeed, this species is now mainly present in urban areas but is increasingly found in more natural settings like forest clearings, even if it does not seem to highly impact the native flora (yet), suggesting potential adverse effects in a warmer future (Bindewald et al., 2020; Essl, 2007). Under climate change and urbanization, urban trees and vegetation are essential to accommodate cities for the future, and especially to the increasing intra-urban temperatures

differences (Lindberg et al., 2016; Ziter et al., 2019). However, previous trends in urban greening have promoted the use of fast growing, drought and heat resistant woody alien plant species (McKinney, 2006; Paz-Dyderska et al., 2020; van Kleunen et al., 2018). Thus, global changes might turn drought - and heat - adapted species into a high risk group across the whole urban-to-rural gradient in the future. Indeed, urban areas seem to concentrate alien plant species from warm or dry native ranges and the high propagule pressure due to the plantations in both public and private lawns might turn cities into hotspots for future invasions (Dullinger et al., 2017; Géron et al., 2021).

Authors' contributions

C.G., J.J.L., I.N. and A.M. designed the research, C.G. and J.J.L. conducted the field work, C.G. did the analyses and led paper writing, all authors contributed substantially to revisions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Pre-processed data made available on Figshare <https://doi.org/10.6084/m9.figshare.20452005.v1>.

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Appendix. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ufug.2022.127694](https://doi.org/10.1016/j.ufug.2022.127694).

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