



Considering urban uses at a fine spatial resolution to understand the distribution of invasive plant species in cities

Muriel Deparis · Nicolas Legay · Francis Isselin-Nondedeu · Sébastien Bonthoux

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Abstract

Context Cities are heterogeneous landscapes, composed of different urban uses with diverse histories. A thorough description of these urban landscapes is required to understand ecological patterns, particularly concerning high-stakes species such as invasive alien plants (IAP) which are abundant in cities.

Objectives We assessed the effects of urban uses and linear structural elements on the distributions of seven IAP in a medium-sized French city (Blois). We examined how the relative contributions of these variables vary between three spatial scales of analysis (100 m, 200 m and 400 m) and three urban classifications.

Methods We characterized the use and age of urban neighborhoods through three classifications with different levels of details and described road and

rail networks of Blois. We analyzed their effects on the distribution of seven invasive plants recorded throughout the whole city using GLM models.

Results Urban use was the most significant variable in explaining IAP distribution. This variable was especially important at the finest spatial scale which allowed a detailed urban classification. Individual residential neighborhoods of different ages explained the distribution of *Buddleja davidii*, *Berberis aquifolium* and *Acer negundo*, whereas industrial areas explained *Ailanthus altissima* distribution. The effects of linear structural elements were lower and differed between species.

Conclusions We show that combining fine-scale spatial analyses with detailed characterization of urban use diversity is critical to understanding ecological patterns at the city scale. Investigating planting choices and dispersal process of IAP could complete our results. Urban descriptions based on explicit urban forms could also contribute to understanding species distribution in cities.

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M. Deparis (✉) · N. Legay · F. Isselin-Nondedeu · S. Bonthoux
UMR 7324, CNRS CITERES, 33 allée Ferdinand de Lesseps, 37200, Tours, INSA Centre Val de Loire, 8 rue de la chocolaterie, 41000 Blois, France
e-mail: muriel.deparis@insa-cvl.fr

F. Isselin-Nondedeu
Institut Méditerranéen de Biodiversité Et Ecologie,
UMR CNRS-IRD, Avignon Université, Aix-Marseille
Université, IUT d'Avignon, 337 chemin des Meinajariés,
Site Agroparc BP 61207, 84911 Avignon, Cedex 09,
France

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Introduction

Urban landscapes are composed of a high spatial heterogeneity of forms and human uses (Larkham 2006). This is particularly true in European cities which

have had a long history of urban modifications. Linear axes that ensure the transport of people and goods are inserted between spaces with diverse uses such as residential areas, industrial and commercial zones, and parks and recreational areas. These landscapes are very dynamic. New neighborhoods appear on the outskirts of cities and existing urban neighborhoods are renewed according to contemporary uses. Certain uses have been diversified in line with new lifestyles. This is the case of residential areas which have developed from the dense housing of old city centers, to collective housing zones with collective green spaces and individual housing zones with privatized houses and gardens. Capturing this spatial and temporal heterogeneity of urban use seems important to understand ecological processes and patterns that take place in cities (Fratarcangeli et al. 2019; Marcus et al. 2020).

However, characterization of urban landscapes often remains very limited in ecological studies. It is mainly based on broad land use classification such as “urban”, “peri-urban” and “rural” (see for example Aronson et al. 2015; Ariori et al. 2017). Such an over-simplistic classification ignores some critical structural and social components such as road and rail networks, and human use and history of the different neighborhoods which can impact ecological patterns. A finer description of urban landscapes is needed to improve understanding of ecological processes in cities (Ramalho and Hobbs 2012; Cadotte et al. 2017). For example, a study of tree communities in the city of Peel, Canada, shows that communities of industrial or vacant blocks are less diverse and richer in invasive plants than those of residential blocks, due to the high variety of horticultural choices and landscaping in residential blocks and the lower management of vacant lots (Bourne and Conway 2014). Štajerová et al. (2017) showed that the diversity of invasive plants increases with the diversity of urban land use in a Czech Republic city.

Considering the variety of urban land use involves analyzing ecological patterns at relevant spatial scales in order to capture urban heterogeneity. The analysis of flora patterns at the city scale has often been carried out at large spatial resolutions ($\geq 1 \text{ km}^2$), making it possible to assess the effects of the main land uses but obscuring the fine spatial variation in urban use and building periods (Godefroid and Koedam 2007; Schmidt et al. 2014; Fratarcangeli et al. 2019). Other

studies have detected differences in alpha diversity or community traits between different land uses that are considered at fine scales (1 ha or smaller) enabling their history to be taken into account (Lososová et al. 2011; Johnson et al. 2018). In order to understand the diverse processes at work in ecological patterns in cities, a multi scale approach could enable the respective contributions of urban components to be assessed across scales.

Cities are recognized as potential sources of invasive alien plants (IAP) which threaten indigenous biodiversity in the surrounding natural environment (Padayachee et al. 2017). Understanding how urban landscape features modulate IAP patterns can help provide planning and management avenues to mitigate the spread of these species. IAP patterns result from both the introduction and dispersal processes, which are linked to various human practices and urban structural elements. Sources of urban plant invasion can be associated with planted ornamental species in gardens or parks, which can escape and colonize adjacent areas according to certain ecological traits (e.g. high rates of reproduction, dispersal or growth, or high tolerance to disturbance and pollution, Catford et al. 2009; Marco et al. 2010). Planting practices and potential sources of invasion vary between neighborhoods according to plant use (i.e. street-side trees, delineating hedges and isolated decorative shrubs) and plant characteristics (e.g. height, shape and color). Planting practices also vary according to the age of the neighborhood linked to changes in horticultural and aesthetic fashions (Mathis and Pépy 2017). For example, before the 1970s in France hedges of individual residential neighborhoods consisted only of thuja or laurel and were then gradually diversified to incorporate colorful shrubs (Frieux et al. 2008). Dispersal of IAP through cities can be linked to different structural vectors of the urban landscape. Linear elements such as roads and railway lines have been demonstrated to facilitate seed dispersal (Ansong and Pickering 2013). For example, air flow created by trains and vehicles are vectors of dispersal for *B. davidii* (Tallent-Halsell and Watt 2009) and rivers can promote IAP dispersion within the city and to the surrounding natural environment (Säumel and Kowarik 2013; Wagner et al. 2020). Besides this influence on dispersal, the ruderal conditions of roadsides, railway lines, riverbanks and more generally of urban soils can favor the establishment

and persistence of pioneer IAP and become sources of invasion (Catford et al. 2012; Dyderski and Jagodziński 2016). Hence, the distribution patterns of IAP in cities depend on human use of each area where IAP could potentially establish and on the structural elements linking them. Thus, to understand IAP patterns in cities it seems crucial to explore the relative effects of both the diverse human uses and the structural elements at multiple scales.

In this study, we characterized the uses and ages of urban neighborhoods and also the structural elements of a medium-sized French city to analyze how they affect the distribution of seven invasive trees and shrubs. We explored these effects at three levels of urban classification and on three spatial scales of analysis. We hypothesized that major structuring urban elements such as roads and railways would have a significant relative effect on a large scale of analysis, while the uses and ages of neighborhoods, which are locally very heterogeneous would have a greater effect at a fine scale. We also hypothesized that the effects of urban factors would depend on IAP characteristics. Colorful flowering plants were expected to be present more in residential areas than in industrial areas. Moreover, by creating dispersion vectors, linear urban elements (roads, railway lines and rivers) should explain the majority of the distribution of species with winged seeds.

Materials and methods

City description

The city of Blois is located in central-western France (47°34'59"N, 1°19'59"E). The mean temperature is 11.6 °C and annual rainfall 640 mm. The surrounding landscape is dominated by agriculture land, with two large forested massifs, to the west and to the south. The river Loire crosses the city from east to west (Appendix 1a). Almost 50,000 people live in Blois and the urban area is about 22 km². The historical center dates from the medieval and Renaissance periods. In the middle of the nineteenth century the railway line was built and the city was reorganized. Strong urban expansion of the city started with reconstruction after World War II and spanned from the end of the 50s (28,190 inhabitants in 1954) to the end of the 80s. This was followed by a densification period

from the 90 s up to the present day (46,086 inhabitants in 2017—Appendix 2). An industrial area was built to the north of the city following the construction of the A10 motorway in the 60s and its expansion slowed down in the 2010s. Most of the residential blocks were built in the 70s, notably the zone for priority urban development (ZUP), created in 1959 and housing 10,000 residents in 2013. The construction of individual housing spanned over 40 years, from the 50s to the 90s. As a result, the city of Blois currently consists of numerous neighborhoods of contrasting uses and ages.

We described the urban landscape of Blois using three grids of different spatial resolutions: a 2198-cell grid of 100×100 m, a 561-cell grid of 200×200 m and a 134-cell grid of 400×400 m (Fig. 1). These spatial resolutions allowed us to describe the city in detail, particularly in terms of the neighborhood main use (NMU), while maintaining a sufficient number of cells for statistical analysis. All urban variables were measured in these three grids.

Neighborhood main use (NMU) variable

Neighborhood main use (NMU) was a qualitative explanatory variable related to the main uses of the city: residential, work, recreation and shopping. It was also related to land cover such as forest and agricultural land. Based on aerial pictures from 2018, pre-exploration in the field and maps of the city, we identified nine classes of NMU: individual residential, collective residential, industrial, public space, parks, riverbanks, vacant, forest and agricultural. This 9-class NMU forms our “middle” classification (Table 1). Parks, riverbanks and vacant spaces which are unbuilt urban classes and forest and agricultural which are non-urban uses were aggregated into two classes to form a 6-class NMU classification (coarse classification, Table 1). Industrial and individual housing areas of Blois have recently diversified greatly, as explained above. NMU was subdivided according to construction date to form the 19-class NMU classification (fine classification, Table 1). This temporal sub-division enabled age variability effects to be investigated at the 100×100 m scale of analysis. Construction dates for 80% of the buildings were collected from data of the National Institute for Geographical and Forest Information (IGN, French public

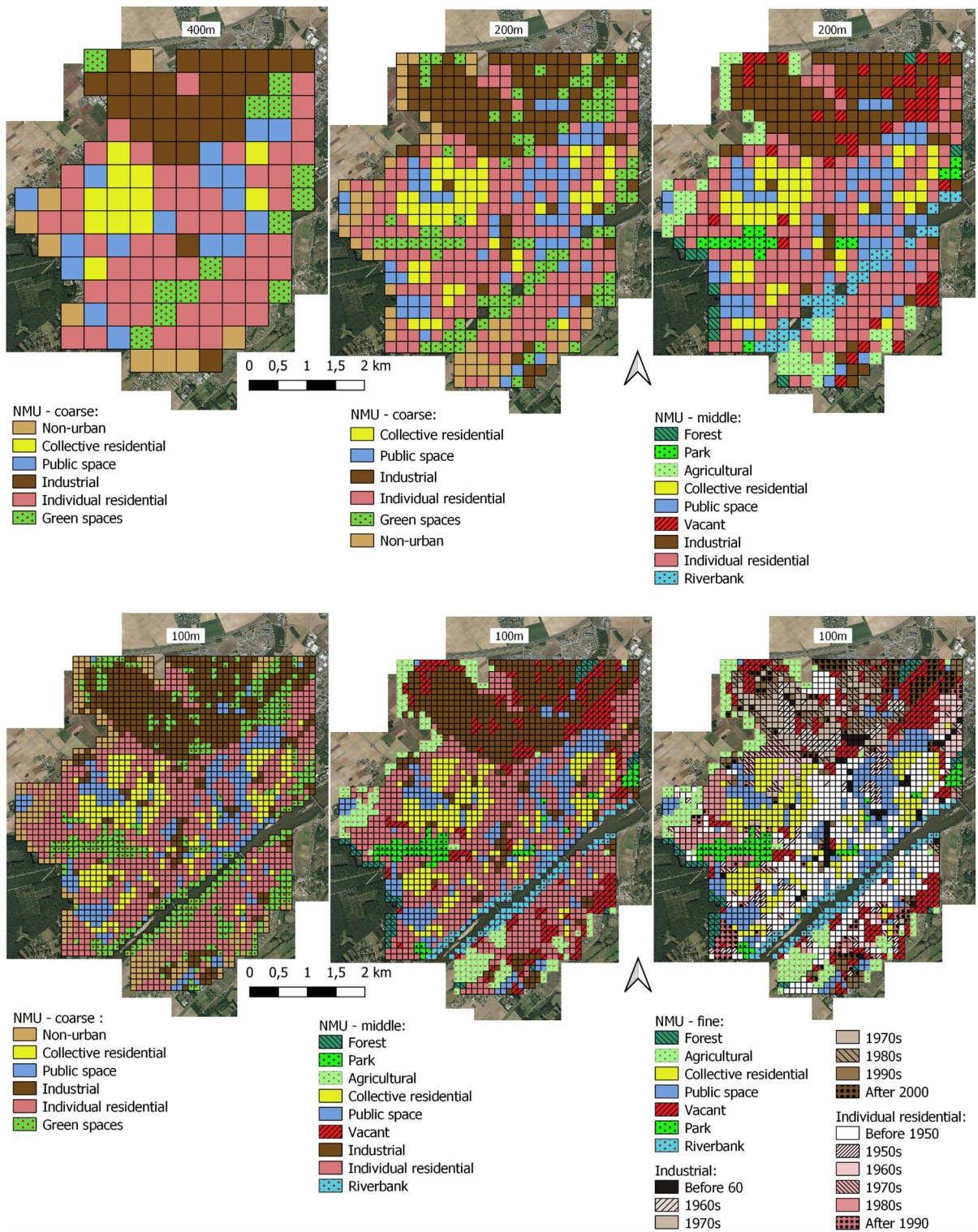


Fig. 1 Maps of the six descriptions of Blois city: 400 m grid with coarse NMU, 200 m grid with coarse and middle NMU and 100 m grid with fine, middle and coarse NMU

Table 1 Description of the neighborhoods main use (NMU) classifications associated to each grain grid



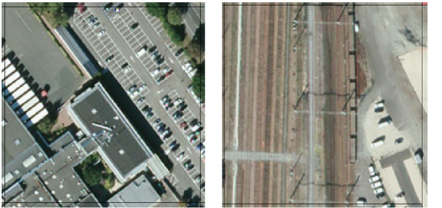

Coarse classification	Middle classification	Fine classification	NMU description and pictures (middle classification—100 m cell)
Individual residential	Individual residential	Residential individual before 50 50–60 60–70 70–80 80–90 After 90	 <p>Individual housing, house with or without garden</p>
Collective residential	Collective residential	Collective residential	 <p>Collective housing, apartment buildings and associated green spaces</p>
Industrial	Industrial	Industrial before 60 60–70 70–80 80–90 90–2000 After 2000	 <p>Built-up areas for industrial (business, parking) and commercial purposes (supermarkets, shopping areas). Also included, train station and railroad. Presumed private management</p>
Public space	Public space	Public space	 <p>Built-up areas with public buildings (town hall, prefecture), schools, cemeteries. Also unbuilt areas under municipal management: sports ground, roundabout</p>

Table 1 (continued)

Coarse classification	Middle classification	Fine classification	NMU description and pictures (middle classification—100 m cell)
Green spaces	Park	Park	 <p>Parks, unbuilt areas maintained for leisure activities. Management assumed by municipal departments</p>
	Riverbanks	Riverbanks	 <p>Unbuilt, permeable areas in contact with the Loire River. Management assumed by regional services</p>
	Vacant	Vacant	 <p>Unbuilt areas, unknown use or no specific destination, maintenance assumed to be null or very punctual. All unbuilt areas that do not correspond to any of the other categories</p>
Non-urban	Forest	Forest	 <p>Urban forest and woods</p>
	Agricultural	Agricultural	 <p>Cultivated areas, including allotments</p>

institute dedicated to the geographic description of French territory, <http://www.ign.fr/institut/>). For

the remaining, old aerial photographs from 1949, 1958, 1964, 1972, 1986, 1996, 2008 and 2011 were

compared manually. To keep a certain number of cells per class of NMU for analysis, the finest NMU classification was only tested for the 100×100 m scale, the middle classification was used at 100×100 m and 200×200 m scales and the coarse classification was used at the three scales (Fig. 1).

Structural urban variables

For each of the three spatial scales, the following urban components were characterized: impervious surfaces relating to the quantity of soil available; areas of primary and secondary roads, and railway lines; distance to primary roads or railway lines which are used as a proxy of dispersal vectors in the city (Appendix 1b–1g). These variables should affect the spatial distribution of species through their influences on dispersal opportunities and habitat conditions (Appendix 3).

The impervious surface index was calculated using a cloud-free Landsat 8 image (spatial resolution 30×30 m) from 19 June 2017. From red and near infra-red channels of satellite images, we calculated the VrNIR-BI index which has been shown to identify built up areas accurately (Estoque and Murayama 2015). This index was calculated for each image pixel and the average value per cell was then calculated for each grid size. With this method, water appears as a highly impervious area and so for cells containing water bodies we calculated the impervious surface index from the pixels without water.

The area of different roads and railway lines in each cell and the distance from the cells to the roads and railway lines were calculated with IGN data using Qgis (Qgis Development Team 2017, version 3.4). These distances inform about the proximity of a linear element that can favor species dispersal. They were calculated between the centroid of each cell to the railway line and primary road using R software (R Core Team 2019) with the *rgeos* package (Bivand and Rundel 2019). Areas of roads and railway lines could be a proxy for quantity of dispersal events or could be linked to the availability of ruderal habitat for species. We considered two types of roads (based on IGN classification), either primary roads that constitute the large road network between cities with heavy high-speed traffic, or secondary roads located within the city with moderate traffic.

Plants of interest

We recorded the distribution of seven IAP: four shrubs, *Buddleja davidii* (Franch 1887), *Berberis aquifolium* (Pursh, 1814), *Cortaderia selloana* (Schult. & Schult.f., Asch. & Graebn., 1900), *Reynoutria japonica* (Houtt., 1777) and three trees *Ailanthus altissima* (Mill, Swingle 1916), *Acer negundo* (Linné, 1753), and *Robinia pseudoacacia* (Linné, 1753). These species are recognized as invasive at a regional and also at national and international scales (Global Invasive Database, Cordier et al. 2016, Méheust and Varray 2020). These species are common in cities, where they have been planted for a long time. For instance in western European cities, *A. altissima* and *A. negundo* have been planted since the end of the eighteenth century along streets because of their fast growth and *R. pseudoacacia* because of its showy fragrant flowers. *B. davidii* and *B. aquifolium* have been planted in gardens for their abundant and colorful flowers and *C. selloana* has been planted on traffic roundabouts and urban parks for its large plumes (Sheppard et al. 2006; Kowarik and Säumel 2007; Sladonja et al. 2015; Straigytė et al. 2015; Tarabon et al. 2018). These species are easily identifiable in the field and are thus of interest in the study of IAP patterns at a city scale. Moreover, they have contrasting dispersal capacities and habitat features, and are thus expected to be influenced differently by the urban variables considered here (Appendix 3).

Plant data collection

Species observations were carried out from 3 April 2018 to 17 July 2018 by walking through different neighborhoods throughout the city, taking streets, paths, parks and interstitial spaces to obtain the most complete view of all public and private urban places (total time of observation 178 h). Each observer had a pair of binoculars to look at remote and inaccessible areas and facilitate species identification. We recorded and located on a city map all individuals and groves of our seven species of interest. These precise distribution maps were then aggregated to create presence-absence grids at the 100 m, 200 m and 400 m-cell resolutions (Appendix 5 for the presence-absence map of each species on the 100 m grid). At each time period, we carried out observations in several types of neighborhoods to avoid any correlations



◀**Fig. 2** Results of the GLM analysis for the spatial distribution for the six IAP species across the three spatial resolutions. All variables except Julian day are shown. The horizontal bars represent the relative importance of each variable. For significant variables, the value of relative importance is written near the bar. Total explained deviance was calculated for the model containing the variables which were significant in the average model. A green bar indicates a significant and positive effect, a red bar indicates a significant and negative effect and a gray bar indicates a non-significant variable. For detailed effects of each NMU, Table 2. Coarse/middle/fine NMU: respective neighborhood main cover and use classification of the grid considered; impervious: impervious surface index; 1st road area: area of primary roads in each cell; distance 1st road: distance from the center of the cell to the nearest section of primary road; 2nd road area: area of secondary road in each cell; rail area: area of railway line in each cell; distance rail: distance from the center of the cell to the nearest section of railway line

between urban use and the ability to detect the presence of a species based on phenology or stages of plant development. For all species identification issues disappeared rapidly with complete leaf bloom, however, to take into account this potential problem the date of observation in Julian days (from 93 to 198, Appendix 1 h) was recorded and included in models.

The spatial configuration of streets and buildings differs greatly between neighborhoods, the least visible areas being individual residential areas (some gardens at the back of houses were sometimes completely invisible from the street) or industrial areas. For example, on the 200 m grid, 211 cells (37%) were partially invisible. However, as the median value of the non-visible area in these cells was 12%, we estimated that the probability of false absences was limited.

Statistical analyses

We investigated the effects of NMU and structural variables on the distribution of the seven IAP based on their presence-absence with generalized linear models (GLM) and binomial distribution. We only analyzed presence-absence of IAP to limit potential bias in the estimation of the area covered. For each species we computed a GLM for each combination of spatial scale and NMU classification, resulting in six models per species (1 model at 400 m grid with coarse NMU; 2 models at 200 m grid with coarse and middle NMU; 3 models at 100 m with coarse, middle and fine NMU) for a total of 36 models. All

correlations of each pair of explanatory variables were low ($r < 0.71$, Dormann et al. 2013, Appendix 4) so all the explanatory variables were kept in the models. As explained before, we added the Julian day of observation as a quantitative explanatory variable to take into account the potential effect of date on species detectability.

We used a model averaging approach to take into account the uncertainty in the model selection process (Burnham and Anderson 2002). With the *MuMIn* package (Barton 2019), we fitted all possible models nested within the full model, ranked them based on AICc and assigned them Aikake weights (w_i). The Julian day was fixed in all candidate models. We then averaged the parameters of the 95% confidence set of models (sum of $w_i > 0.95$) weighted by their w_i . We computed post-hoc comparisons using the *emmeans* package (Lenth 2020) to compare relative effects of NMU classes. We tested the spatial autocorrelation of residuals for GLM with all variables by computing non-parametric spline correlograms with the *ncf* package (Bjornstad 2020). We observed no or very small autocorrelations (for the majority of models, $r < 0.3$ under 300 m) and considered the potential effect as negligible. We calculated the percentage of explained deviance for the model containing the variables which were significant in the average model. We then compared the relative contribution of explanatory variables using a hierarchical partitioning approach (Chevan and Sutherland 1991) with the *hier.part* package (Mac Nally and Walsh 2004). All statistical analyses were computed using R version 3.6.1 (R Core Team 2019).

Results

On the 200 m grid, the IAP encountered the most were *B. davidii* (45% of the cells), *B. aquifolium* (38%), and *R. pseudoacacia* (35%), whereas *R. japonica* was the rarest species (8%). *C. selleana* was present in 9% of the cells, but only in private gardens with no evidence of spontaneous dispersal, so we decided to exclude this species from the analysis. Maps of species distribution are in Appendix 5.

Models of explained deviance of distribution varied from 1% (for *R. japonica* at 100 m grid/middle NMU) to 25% (for *A. negundo* at 100 m grid/fine NMU, Fig. 2). The Julian day variable was significant

for 15 models and its relative contribution was moderate and comprised between 2 and 29% (for *B. davidii* at 100 m grid/middle NMU and *A. negundo* at 100 m grid/coarse NMU respectively—Appendix 6).

Relative contribution of urban variables across spatial scales

Overall, the deviance explained by models declined from the 400 m to the 100 m grid for the coarse NMU classification, except for *A. negundo* (Fig. 2). The relative contribution of NMU increased as the classification for the 100 m grid was refined for all species, except *R. japonica* for which NMU was not significant (Fig. 2). Relative contributions of roads, railway lines and impervious surface variables decreased from 400 to 100 m grids at coarse NMU for all species (except for the impervious variable for *R. pseudoacacia* and distance to railway lines for *A. altissima*, Fig. 2).

Neighborhood main use effects

The NMU was the most significant explanatory variable among the IAP (25 models out of 36, 69% of those tested, Fig. 3) except for *R. japonica*. With one exception (*R. pseudoacacia* for the coarse NMU),

NMU had the highest relative contribution (between 16 and 71%, Fig. 2) whatever the grid, NMU classification or species.

The forest NMU class caused problems of model convergence, so we decided to exclude it from analyses. As very few IAP were observed in the field in this NMU class, its suppression had no effect on the results.

Post-hoc comparisons showed that NMU classes explained IAP distributions differently (Table 2). Looking at the finest classification of NMU at the 100 m grid scale, the individual residential classes were significantly related to four species positively, with differences between age classes: the individual residential class of all decades before the 1990s explained *B. aquifolium* and *B. davidii* distributions, individual residential of 1970s explained *A. negundo* and individual residential before 1950 explained *A. altissima* (Table 2). Collective residential and public space were associated with the presence of *B. davidii*. Before the 1960s, the industrial class explained *A. altissima*, the newest and oldest industrial class and parks explained *R. pseudoacacia*. Riverbanks were linked to the presence of *A. altissima* and *A. negundo* (Table 2). It should be noted that no relationships were established between NMU and the presence of *R. japonica*. This species was encountered in only

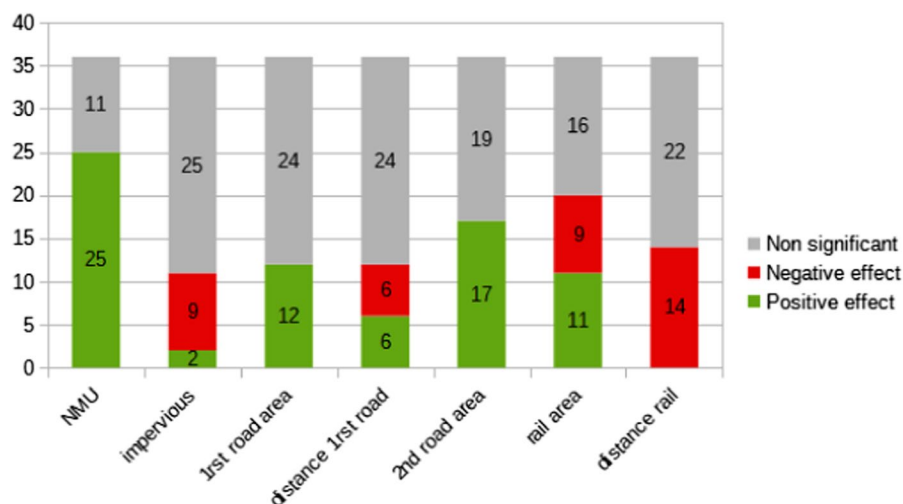


Fig. 3 Among the 36 models, number of times each variable had a positive significant effect, a negative significant effect or had not a significant effect in explaining IAP species distribution. NMU: neighborhood main cover and use; impervious: impervious surface index; 1st road area: area of primary road

in each cell; distance 1st road: distance from the center of the cell to the nearest section of primary road; 2nd road area: area of secondary road in each cell; rail area: area of railway line in each cell; distance rail: distance from the center of the cell to the nearest section of railway line

Table 2 Synthesis of post-hoc comparison of NMU classes

		<i>Ailanthus altissima</i>	<i>Acer negundo</i>	<i>Berberis aquifolium</i>	<i>Buddleja davidii</i>	<i>Robinia pseudoacacia</i>
400 m	Coarse	NS	NS	Green spaces	NS	Individual residential
200 m	Coarse	NS	NS	Individual residential	Individual residential	Individual residential Collective residential Industrial Public space Green spaces
	Middle	Park Riverbanks	Public space	Collective residential	Public space	Agricultural Industrial Park Individual residential
100 m	Coarse	Individual residential	Public space Green spaces	Public space Industrial Individual residential Collective residential	Individual residential Collective residential Industrial Public space	
	Middle	Park Riverbanks	Public space Park	Collective residential Park	Collective residential Industrial Vacant Riverbanks	Individual residential Industrial
	Fine	Individual residential before 1950 Industrial before 1960 Riverbanks	Individual residential 1970 Riverbanks	Individual residential before 1950 Individual residential 1950's Individual residential 1960's Individual residential 1970's Individual residential 1980's	Public space Collective residential Individual residential before 1950 Individual residential 1950's Individual residential 1970's Individual residential 1980's	Industrial after 2000 Industrial before 1960 Park

All NMU classes in this table correspond to neighborhoods associated to a higher presence probability than other NMU. For that reason, blank cell for *R. pseudoacacia* at 100 m grid/coarse NMU does not correspond to non-significant relation, but the only NMU class highlighted in the pairwise comparison is associated to a lower presence probability than other. NS indicates that NMU is not a significant variable in GLM. NMU is not a significant variable in the spatial distribution of *Reynoutria japonica*

8% of 200 m cells, which could explain the lack of results. Distribution maps of each species are available in Appendix 5.

Effects of structural urban variables

Some structural variables had significant and constant effects whatever the species, whereas others had contrasting effects (Fig. 2). The area of secondary roads had a significant positive impact in 17 models (out of 36, 42% of models, Fig. 3) for four species: *A. negundo*, *B. aquifolium*, *B. davidii* and *R. pseudoacacia*. This variable was mainly important for *B. davidii* (from 20 to 55% of relative contribution depending on the grid and the NMU classification, Fig. 2) and *B. aquifolium* (from 21 to 47%, Fig. 2). Distance to railway lines had a significant negative impact on

the presence of species (i.e. the presence increased in proximity to railway lines) for 14 models (Fig. 3, 38% of models) for all species except *R. japonica*. This variable was the second most important after NMU for *A. altissima* (from 15 to 24% of relative contribution, Fig. 2). The area of primary roads had a significant positive effect for 12 models (Fig. 3, 33% of models) for four species: *A. altissima*, *B. aquifolium*, *R. japonica* and *R. pseudoacacia*. For *R. japonica*, this variable explained 21% or 25% of deviance, depending on the NMU classification for the 200 m grid. The distance to primary roads was significant for 12 models (Fig. 3, 33% of models) and rail lines for 20 models (Fig. 3, 55% of models), but the effects differed depending on the species considered. The distance to primary roads had a negative effect on the presence of *A. negundo* and *R. japonica* and a

positive effect on *B. aquifolium* and *R. pseudoacacia* (except at 400 m grid/coarse NMU). For *R. japonica*, the distance to primary roads was the only significant variable at the 100 m grid scale. Except for this species and *R. pseudoacacia* at the 400 m grid /coarse NMU, its relative contribution was low. Railway line areas had significant positive effects on *A. altissima*, *B. davidii* and *R. pseudoacacia* and negative effects on *A. negundo* and *B. aquifolium*. This variable was the second most important after NMU for *A. negundo* (from 5 to 21% of relative contribution, Fig. 2). The value of impervious surface was significant for 11 models out of 36 (Fig. 3, 30% of models) for four species. Its effect was negative for *A. altissima*, *A. negundo* and *R. pseudoacacia* and positive for *B. davidii*. This variable was important for *R. pseudoacacia* (from 13 to 40% of relative contribution) which made it the first variable of importance regarding coarse NMU and the second after NMU for middle and fine NMU classification.

Discussion

This study underlines the need to improve our characterization of urban landscapes to understand ecological patterns at the city scale. Particularly, we showed that detailing urban uses and ages that reflect various human activities and practices at a fine spatial scale is determinant in explaining IAP distribution. Road and railway areas also explained the presence of some IAP, especially at large scales.

Urban use is related to IAP patterns

Our results show that adopting fine spatial scales of analyses (e.g. 1 ha) allows high spatial variability of urban uses to be considered when studying ecological patterns in cities (Fig. 1). Urban uses were the main determinant of IAP distribution, and their importance was reduced and obscured at the coarsest classification level. Urban use explained IAP patterns differently according to plant characteristics. In individual residential neighborhoods, where aesthetic choices are important (Cook et al. 2012), we found two colorful shrub species: *B. aquifolium* with its yellow flowers at the beginning of spring followed by bright green foliage, and *B. davidii* appreciated for its colorful blooming in summer (Tallent-Halsell and Watt

2009). In the field, these species were noticed inside private gardens and not in interstitial public spaces (e.g. streets and pavements). Nevertheless, these species were not predominant in individual residential neighborhoods after 1990, suggesting changes in planting fashions. The effect of this neighborhood on the distribution of these species was probably underestimated because observers' views were obscured by hedges making detection of plants difficult. In individual residential areas of the 1970s, we also found *A. negundo*. During field exploration, we noticed that this species was often planted by the municipality in interstitial public places (e.g. small public squares), suggesting dispersal of spontaneous individuals observed near private borders or gardens. Collective residential areas only explained the presence of *B. davidii*, which was also found in public spaces. We can assume that planting practices and motivations of collective housing managers (the municipal authority of Blois is in charge of 60% of collective housing areas) are not exactly the same as those of individual house owners, explaining the differences in IAP distribution between the two kinds of residential areas in Blois. In addition, *B. davidii* was associated with public spaces, which like collective housing, are managed by the municipality of Blois. This might suggest that the presence of this species is facilitated by municipal staff choices and management.

In industrial areas, human uses are very different from residential areas. These are non-residential areas without domestic or public gardens. Industrial areas were positively correlated with *A. altissima* as in other studies (Sladonja and Poljuha 2018). We mainly observed spontaneous individuals of this species. In the 1980s, the municipality of Blois planted several rows of *A. altissima* in public spaces before cutting them down to limit invasion (personal communication). It is possible that this species that tolerates ruderal soils has dispersed and established under the environmental ruderal conditions of industrial areas (Kowarik and Säumel 2007). Two species were encountered on the riverbanks of the Loire: *A. negundo* and *A. altissima*. These riverbanks are floodable, made of ruderal soils and rarely managed (annual or two-yearly mowing, personal communication). There is little deliberate planting in this expansive and recreational urban place. Both species are known to invade riparian vegetation through their winged seeds which facilitate dispersal by water flow

(Saccone et al. 2010; Säumel and Kowarik 2013; Constán-Nava et al. 2015; Straigytė et al. 2015). Moreover, *A. negundo* being particularly linked to riparian vegetation, moist soil is important for its establishment and growth (Dumas 2019). *A. negundo* is established along the river Loire throughout the region (regional atlas of IAP, Conservatoire Botanique National du Bassin Parisien 2021). Its presence on the riverbanks of Blois is probably partly due to a spontaneous dispersal along the river. On the other hand, *A. altissima* is not associated with the river at the regional scale and its presence in numerous individual residential areas near the riverbanks suggests dispersal originating from the city.

Interestingly, there was no urban use explaining *R. japonica*, and so it was restricted to derelict land, like road embankments, which could also be linked to its dispersal.

All these results provide guidelines to understand how urban uses and social mechanisms of planting practices could explain the distribution of IAP at the city scale. To understand the determinants of planting choice and identify social and economic factors to limit sources of invasion, this study should be combined with social surveys of urban stakeholders (garden owners, municipal managers and horticulturalists).

Linear urban transport elements favor some IAP

We found that road and railway areas mainly explained the presence of some IAP at large spatial scales. This could indicate that these linear elements are suitable habitats and/or corridors of dispersion for these species (Christen and Matlack 2006). For example, the area of and distance to primary roads explained the distribution of *R. japonica*. Road embankments are made of degraded soils and are mowed once or twice a year. This creates ruderal conditions which favor the establishment of that species, but it also results in leaf and stem fragments which can be dispersed along roads by vehicles (Sheppard et al. 2006). The positive impact of railway lines on *R. pseudoacacia* can be explained by the fact that its anemochorous seeds can be dispersed by airflows created by the passage of trains. *B. davidii*, an anemochorous species, is sometimes dispersed by vehicles (Tallent-Halsell and Watt 2009), which could explain the positive link

between secondary roads and that species in the city. Thus, primary roads and railway lines could act as corridors of dispersal, but also provide suitable habitat for different IAP in the city.

In order to investigate further ecological processes resulting from these linear transport elements more functional studies are needed to supplement our pattern approach. Comparing city and regional scale maps showing species distribution could also be valuable. Moreover, some precise information can be lost when using classic grids in pattern studies. For example, based on field observations, individuals of *R. pseudoacacia* were specifically located on railway embankments, which can be considered as suitable habitat for that species. Adopting survey methods that explicitly take into account urban forms would be necessary to examine further the relationships between urban and ecological patterns (Marcus et al. 2020).

Conclusion

In urban landscapes, a critical challenge is to understand the complex relationships between human and ecological factors. We show that combining fine spatial scales of analysis with detailed characterization of the diversity of urban uses is determinant in understanding ecological patterns at the city scale. For example, we found that residential and industrial urban uses are associated with various IAP species according to their morphological characteristics (i.e. color and shape features). To complete our overall exploratory study, social studies are needed to refine underlying processes of planting choices and to find social and economic factors to limit the introduction of IAP in cities. Linear transport corridors and ruderal habitats also explained the distribution of several IAP, but their effects were weaker than urban uses, especially at fine scales. These linear elements probably act both as suitable habitats and dispersal vectors, but further functional studies are needed to explain these mechanisms. Finally, we observed that the classic use of grids in pattern studies results in information loss regarding the spatial organization of urban use and thus blurs our understanding of ecological and urban relationships. Urban description explicitly integrating

urban forms could also contribute to an improved understanding of species distribution in cities.

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Author contributions MD performed the experiment, undertook all Qgis work, analyzed the data and wrote the manuscript. SB and NL conceived, designed and performed the experiment. SB, NL and FI co-wrote and reviewed the manuscript.

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Declarations

Conflict of interest All Authors declare that they have no conflict of interest.

Consent to participate Not applicable.

Consent for publication Not applicable.

Ethical approval.
Not applicable.

Availability of data and material We will provide the localization of our species, likely on a data repository.

Code availability We will provided the R code for test, likely on a data repository.

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