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► **To cite this version:**

Muriel Deparis, Nicolas Legay, Francis Isselin-Nondedeu, Sébastien Bonthoux. Considering urban uses at a fine spatial resolution to understand the distribution of invasive plant species in cities. *Landscape Ecology*, 2022, 37, pp.1145-1159. 10.1007/s10980-022-01415-x . hal-03613607

HAL Id: hal-03613607

<https://hal.science/hal-03613607>

Submitted on 18 Mar 2022

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

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11 Abstract

12 Context

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

17 Objectives

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

22 Methods

23 We characterized the use and age of urban neighborhoods through three classifications with
24 different levels of details and described road and rail networks of Blois. We analyzed their effects on
25 the distribution of seven invasive plants recorded throughout the whole city using GLM models.

26 Results

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

32 Conclusions

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

37 Keywords: neighborhoods, railways, roads, spatial resolution, urban description, urban uses.

38 Introduction

39 Urban landscapes are composed of a high spatial heterogeneity of forms and human uses (Larkham
40 2006). This is particularly true in European cities which have had a long history of urban
41 modifications. Linear axes that ensure the transport of people and goods are inserted between
42 spaces with diverse uses such as residential areas, industrial and commercial zones, and parks and
43 recreational areas. These landscapes are very dynamic. New neighborhoods appear on the outskirts
44 of cities and existing urban neighborhoods are renewed according to contemporary uses. Certain
45 uses have been diversified in line with new lifestyles. This is the case of residential areas which have
46 developed from the dense housing of old city centers, to collective housing zones with collective
47 green spaces and individual housing zones with privatized houses and gardens. Capturing this spatial
48 and temporal heterogeneity of urban use seems important to understand ecological processes and
49 patterns that take place in cities (Fratarcangeli et al. 2019; Marcus et al. 2020).

50 However, characterization of urban landscapes often remains very limited in ecological studies. It is
51 mainly based on broad land use classification such as “urban”, “peri-urban” and “rural” (see for
52 example Aronson et al. 2015; Ariori et al. 2017). Such an over-simplistic classification ignores some
53 critical structural and social components such as road and rail networks, and human use and history
54 of the different neighborhoods which can impact ecological patterns. A finer description of urban
55 landscapes is needed to improve understanding of ecological processes in cities (Ramalho and Hobbs
56 2012; Cadotte et al. 2017). For example, a study of tree communities in the city of Peel, Canada,
57 shows that communities of industrial or vacant blocks are less diverse and richer in invasive plants
58 than those of residential blocks, due to the high variety of horticultural choices and landscaping in
59 residential blocks and the lower management of vacant lots (Bourne and Conway 2014). Štajerová et
60 al. (2017) showed that the diversity of invasive plants increases with the diversity of urban land use
61 in a Czech Republic city.

62 Considering the variety of urban land use involves analyzing ecological patterns at relevant spatial
63 scales in order to capture urban heterogeneity. The analysis of flora patterns at the city scale has

64 often been carried out at large spatial resolutions ($\geq 1 \text{ km}^2$), making it possible to assess the effects of
65 the main land uses but obscuring the fine spatial variation in urban use and building periods
66 (Godefroid and Koedam 2007; Schmidt et al. 2014; Fratarcangeli et al. 2019). Other studies have
67 detected differences in alpha diversity or community traits between different land uses that are
68 considered at fine scales (1ha or smaller) enabling their history to be taken into account (Lososová et
69 al. 2011; Johnson et al. 2018). In order to understand the diverse processes at work in ecological
70 patterns in cities, a multi scale approach could enable the respective contributions of urban
71 components to be assessed across scales.

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

90 can promote IAP dispersion within the city and to the surrounding natural environment (Säumel and
91 Kowarik 2013; Wagner et al. 2020). Besides this influence on dispersal, the ruderal conditions of
92 roadsides, railway lines, riverbanks and more generally of urban soils can favor the establishment
93 and persistence of pioneer IAP and become sources of invasion (Catford et al. 2012; Dyderski and
94 Jagodziński 2016). Hence, the distribution patterns of IAP in cities depend on human use of each area
95 where IAP could potentially establish and on the structural elements linking them. Thus, to
96 understand IAP patterns in cities it seems crucial to explore the relative effects of both the diverse
97 human uses and the structural elements at multiple scales.

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

108 **Materials and methods**

109 **City description**

110 The city of Blois is located in central-western France (47°34'59"N, 1°19'59"E). The mean temperature
111 is 11.6°C and annual rainfall 640 mm. The surrounding landscape is dominated by agriculture land,
112 with two large forested massifs, to the west and to the south. The river Loire crosses the city from
113 east to west (see Appendix 1a). Almost 50,000 people live in Blois and the urban area is about 22
114 km². The historical center dates from the medieval and Renaissance periods. In the middle of the 19th
115 century the railway line was built and the city was reorganized. Strong urban expansion of the city

116 started with reconstruction after World War II and spanned from the end of the 50s (28,190
117 inhabitants in 1954) to the end of the 80s. This was followed by a densification period from the 90s
118 up to the present day (46,086 inhabitants in 2017 - see Appendix 2). An industrial area was built to
119 the north of the city following the construction of the A10 motorway in the 60s and its expansion
120 slowed down in the 2010s. Most of the residential blocks were built in the 70s, notably the zone for
121 priority urban development (ZUP), created in 1959 and housing 10,000 residents in 2013. The
122 construction of individual housing spanned over 40 years, from the 50s to the 90s. As a result, the
123 city of Blois currently consists of numerous neighborhoods of contrasting uses and ages.

124 We described the urban landscape of Blois using three grids of different spatial resolutions: a 2,198-
125 cell grid of 100×100m, a 561-cell grid of 200×200m and a 134-cell grid of 400×400m (Fig. 1). These
126 spatial resolutions allowed us to describe the city in detail, particularly in terms of the neighborhood
127 main use (NMU), while maintaining a sufficient number of cells for statistical analysis. All urban
128 variables were measured in these three grids.

129 Neighborhood main use (NMU) variable

130 Neighborhood main use (NMU) was a qualitative explanatory variable related to the main uses of the
131 city: residential, work, recreation and shopping. It was also related to land cover such as forest and
132 agricultural land. Based on aerial pictures from 2018, pre-exploration in the field and maps of the
133 city, we identified nine classes of NMU: individual residential, collective residential, industrial, public
134 space, parks, riverbanks, vacant, forest and agricultural. This 9-class NMU forms our “middle”
135 classification (Table 1). Parks, riverbanks and vacant spaces which are unbuilt urban classes and
136 forest and agricultural which are non-urban uses were aggregated into two classes to form a 6-class
137 NMU classification (coarse classification, Table 1). Industrial and individual housing areas of Blois
138 have recently diversified greatly, as explained above. NMU was subdivided according to construction
139 date to form the 19-class NMU classification (fine classification, Table 1). This temporal sub-division
140 enabled age variability effects to be investigated at the 100X100m scale of analysis. Construction

141 dates for 80% of the buildings were collected from data of the National Institute for Geographical
142 and Forest Information (IGN, French public institute dedicated to the geographic description of
143 French territory, <http://www.ign.fr/institut/>). For the remaining, old aerial photographs from 1949,
144 1958, 1964, 1972, 1986, 1996, 2008 and 2011 were compared manually. To keep a certain number of
145 cells per class of NMU for analysis, the finest NMU classification was only tested for the 100X100m
146 scale, the middle classification was used at 100X100m and 200X200m scales and the coarse
147 classification was used at the three scales (Fig. 1).

148 Structural urban variables

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

154 The impervious surface index was calculated using a cloud-free Landsat 8 image (spatial resolution
155 30 x 30m) from 19 June 2017. From red and near infra-red channels of satellite images, we calculated
156 the VrNIR-BI index which has been shown to identify built up areas accurately (Estoque and
157 Murayama 2015). This index was calculated for each image pixel and the average value per cell was
158 then calculated for each grid size. With this method, water appears as a highly impervious area and
159 so for cells containing water bodies we calculated the impervious surface index from the pixels
160 without water.

161 The area of different roads and railway lines in each cell and the distance from the cells to the roads
162 and railway lines were calculated with IGN data using Qgis (version 3.4). These distances inform
163 about the proximity of a linear element that can favor species dispersal. They were calculated
164 between the centroid of each cell to the railway line and primary road using R software (R Core
165 Team, 2018) with the *rgeos* package (Bivand and Rundel 2019). Areas of roads and railway lines could

166 be a proxy for quantity of dispersal events or could be linked to the availability of ruderal habitat for
167 species. We considered two types of roads (based on IGN classification), either primary roads that
168 constitute the large road network between cities with heavy high-speed traffic, or secondary roads
169 located within the city with moderate traffic.

170 Plants of interest

171 We recorded the distribution of seven IAP: four shrubs, *Buddleja davidii* (Franch 1887), *Berberis*
172 *aquifolium* (Pursh, 1814), *Cortaderia selloana* (Schult. & Schult.f., Asch. & Graebn., 1900), *Reynoutria*
173 *japonica* (Houtt., 1777) and three trees *Ailanthus altissima* (Mill, Swingle 1916), *Acer negundo* (Linné,
174 1753), and *Robinia pseudoacacia* (Linné, 1753). These species are recognized as invasive at a regional
175 and also at national and international scales (Global Invasive Database, Cordier et al. 2016, Méheust
176 et al. 2020). These species are common in cities, where they have been planted for a long time. For
177 instance in western European cities, *A. altissima* and *A. negundo* have been planted since the end of
178 the 18th century along streets because of their fast growth and *R. pseudoacacia* because of its showy
179 fragrant flowers. *B. davidii* and *B. aquifolium* have been planted in gardens for their abundant and
180 colorful flowers and *C. selloana* has been planted on traffic roundabouts and urban parks for its large
181 plumes (Sheppard et al. 2006; Kowarik and Säumel 2007; Sladonja et al. 2015; Straigytė et al. 2015;
182 Tarabon et al. 2018). These species are easily identifiable in the field and are thus of interest in the
183 study of IAP patterns at a city scale. Moreover, they have contrasting dispersal capacities and habitat
184 features, and are thus expected to be influenced differently by the urban variables considered here
185 (Appendix 3).

186 Plant data collection

187 Species observations were carried out from 3 April 2018 to 17 July 2018 by walking through different
188 neighborhoods throughout the city, taking streets, paths, parks and interstitial spaces to obtain the
189 most complete view of all public and private urban places (total time of observation 178h). Each
190 observer had a pair of binoculars to look at remote and inaccessible areas and facilitate species

191 identification. We recorded and located on a city map all individuals and groves of our seven species
192 of interest. These precise distribution maps were then aggregated to create presence-absence grids
193 at the 100m, 200m and 400m-cell resolutions (see Appendix 5 for the presence-absence map of each
194 species on the 100m grid). At each time period, we carried out observations in several types of
195 neighborhoods to avoid any correlations between urban use and the ability to detect the presence of
196 a species based on phenology or stages of plant development. For all species identification issues
197 disappeared rapidly with complete leaf bloom, however, to take into account this potential problem
198 the date of observation in Julian days (from 93 to 198, Appendix 1h) was recorded and included in
199 models.

200 The spatial configuration of streets and buildings differs greatly between neighborhoods, the least
201 visible areas being individual residential areas (some gardens at the back of houses were sometimes
202 completely invisible from the street) or industrial areas. For example, on the 200m grid, 211 cells
203 (37%) were partially invisible. However, as the median value of the non-visible area in these cells was
204 12%, we estimated that the probability of false absences was limited.

205 **Statistical analyses**

206 We investigated the effects of NMU and structural variables on the distribution of the seven IAP
207 based on their presence-absence with generalized linear models (GLM) and binomial distribution. We
208 only analyzed presence-absence of IAP to limit potential bias in the estimation of the area covered.
209 For each species we computed a GLM for each combination of spatial scale and NMU classification,
210 resulting in six models per species (1 model at 400m grid with coarse NMU; 2 models at 200m grid
211 with coarse and middle NMU; 3 models at 100m with coarse, middle and fine NMU) for a total of 36
212 models. All correlations of each pair of explanatory variables were low ($r < |0.7|$, Dormann et al.
213 2013, Appendix 4) so all the explanatory variables were kept in the models. As explained before, we
214 added the Julian day of observation as a quantitative explanatory variable to take into account the
215 potential effect of date on species detectability.

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

230 Results

231 On the 200m grid, the IAP encountered the most were *B. davidii* (45% of the cells), *B. aquifolium*
232 (38%), and *R. pseudoacacia* (35%), whereas *R. japonica* was the rarest species (8%). *C. selloana* was
233 present in 9% of the cells, but only in private gardens with no evidence of spontaneous dispersal, so
234 we decided to exclude this species from the analysis. Maps of species distribution are in Appendix 5.

235 Models of explained deviance of distribution varied from 1% (for *R. japonica* at 100m grid/middle
236 NMU) to 25% (for *A. negundo* at 100m grid/fine NMU, Fig. 2). The Julian day variable was significant
237 for 15 models and its relative contribution was moderate and comprised between 2% and 29% (for
238 *B. davidii* at 100m grid/middle NMU and *A. negundo* at 100m grid/coarse NMU respectively -
239 Appendix 6).

240 Relative contribution of urban variables across spatial scales

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

247 Neighborhood main use effects

248 The NMU was the most significant explanatory variable among the IAP (25 models out of 36, 69% of
249 those tested, Fig. 3) except for *R. japonica*. With one exception (*R. pseudoacacia* for the coarse
250 NMU), NMU had the highest relative contribution (between 16% and 71%, Fig. 2) whatever the grid,
251 NMU classification or species.

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

255 Post-hoc comparisons showed that NMU classes explained IAP distributions differently (Table 2).
256 Looking at the finest classification of NMU at the 100m grid scale, the individual residential classes
257 were significantly related to four species positively, with differences between age classes: the
258 individual residential class of all decades before the 1990s explained *B. aquifolium* and *B. davidii*
259 distributions, individual residential of 1970s explained *A. negundo* and individual residential before
260 1950 explained *A. altissima* (Table 2). Collective residential and public space were associated with the
261 presence of *B. davidii*. Before the 1960s, the industrial class explained *A. altissima*, the newest and
262 oldest industrial class and parks explained *R. pseudoacacia*. Riverbanks were linked to the presence
263 of *A. altissima* and *A. negundo* (Table 2). It should be noted that no relationships were established
264 between NMU and the presence of *R. japonica*. This species was encountered in only 8% of 200m

265 cells, which could explain the lack of results. Distribution maps of each species are available in
 266 Appendix 5.

267 Effects of structural urban variables

268 Some structural variables had significant and constant effects whatever the species, whereas others
 269 had contrasting effects (Fig. 2). The area of secondary roads had a significant positive impact in 17
 270 models (out of 36, 42% of models, Fig. 3) for four species: *A. negundo*, *B. aquifolium*, *B. davidii* and
 271 *R. pseudoacacia*. This variable was mainly important for *B. davidii* (from 20% to 55% of relative
 272 contribution depending on the grid and the NMU classification, Fig. 2) and *B. aquifolium* (from 21% to
 273 47%, Fig. 2). Distance to railway lines had a significant negative impact on the presence of species
 274 (i.e. the presence increased in proximity to railway lines) for 14 models (Fig. 3, 38% of models) for all
 275 species except *R. japonica*. This variable was the second most important after NMU for *A. altissima*
 276 (from 15% to 24% of relative contribution, Fig. 2). The area of primary roads had a significant positive
 277 effect for 12 models (Fig. 3, 33% of models) for four species: *A. altissima*, *B. aquifolium*, *R. japonica*
 278 and *R. pseudoacacia*. For *R. japonica*, this variable explained 21% or 25% of deviance, depending on
 279 the NMU classification for the 200m grid. The distance to primary roads was significant for 12 models
 280 (Fig. 3, 33% of models) and rail lines for 20 models (Fig. 3, 55% of models), but the effects differed
 281 depending on the species considered. The distance to primary roads had a negative effect on the
 282 presence of *A. negundo* and *R. japonica* and a positive effect on *B. aquifolium* and *R. pseudoacacia*
 283 (except at 400m grid/coarse NMU). For *R. japonica*, the distance to primary roads was the only
 284 significant variable at the 100m grid scale. Except for this species and *R. pseudoacacia* at the 400m
 285 grid /coarse NMU, its relative contribution was low. Railway line areas had significant positive effects
 286 on *A. altissima*, *B. davidii* and *R. pseudoacacia* and negative effects on *A. negundo* and *B. aquifolium*.
 287 This variable was the second most important after NMU for *A. negundo* (from 5% to 21% of relative
 288 contribution, Fig. 2). The value of impervious surface was significant for 11 models out of 36 (Fig. 3,
 289 30% of models) for four species. Its effect was negative for *A. altissima*, *A. negundo* and
 290 *R. pseudoacacia* and positive for *B. davidii*. This variable was important for *R. pseudoacacia* (from

291 13% to 40% of relative contribution) which made it the first variable of importance regarding coarse
292 NMU and the second after NMU for middle and fine NMU classification.

293 Discussion

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

299 Urban use is related to IAP patterns

300 Our results show that adopting fine spatial scales of analyses (e.g. 1 ha) allows high spatial variability
301 of urban uses to be considered when studying ecological patterns in cities (Fig. 1). Urban uses were
302 the main determinant of IAP distribution, and their importance was reduced and obscured at the
303 coarsest classification level. Urban use explained IAP patterns differently according to plant
304 characteristics. In individual residential neighborhoods, where aesthetic choices are important (Cook
305 et al. 2012), we found two colorful shrub species: *B. aquifolium* with its yellow flowers at the
306 beginning of spring followed by bright green foliage, and *B. davidii* appreciated for its colorful
307 blooming in summer (Tallent-Halsell and Watt 2009). In the field, these species were noticed inside
308 private gardens and not in interstitial public spaces (e.g. streets and pavements). Nevertheless, these
309 species were not predominant in individual residential neighborhoods after 1990, suggesting changes
310 in planting fashions. The effect of this neighborhood on the distribution of these species was
311 probably underestimated because observers' views were obscured by hedges making detection of
312 plants difficult. In individual residential areas of the 1970s, we also found *A. negundo*. During field
313 exploration, we noticed that this species was often planted by the municipality in interstitial public
314 places (e.g. small public squares), suggesting dispersal of spontaneous individuals observed near
315 private borders or gardens. Collective residential areas only explained the presence of *B. davidii*,

316 which was also found in public spaces. We can assume that planting practices and motivations of
317 collective housing managers (the municipal authority of Blois is in charge of 60% of collective housing
318 areas) are not exactly the same as those of individual house owners, explaining the differences in IAP
319 distribution between the two kinds of residential areas in Blois. In addition, *B. davidii* was associated
320 with public spaces, which like collective housing, are managed by the municipality of Blois. This might
321 suggest that the presence of this species is facilitated by municipal staff choices and management.

322 In industrial areas, human uses are very different from residential areas. These are non-residential
323 areas without domestic or public gardens. Industrial areas were positively correlated with *A.*
324 *altissima* as in other studies (Sladonja and Poljuha 2018). We mainly observed spontaneous
325 individuals of this species. In the 1980s, the municipality of Blois planted several rows of *A. altissima*
326 in public spaces before cutting them down to limit invasion (personal communication). It is possible
327 that this species that tolerates ruderal soils has dispersed and established under the environmental
328 ruderal conditions of industrial areas (Kowarik and Säumel 2007). Two species were encountered on
329 the riverbanks of the Loire: *A. negundo* and *A. altissima*. These riverbanks are floodable, made of
330 ruderal soils and rarely managed (annual or two-yearly mowing, personal communication). There is
331 little deliberate planting in this expansive and recreational urban place. Both species are known to
332 invade riparian vegetation through their winged seeds which facilitate dispersal by water flow
333 (Saccone et al. 2010; Säumel and Kowarik 2013; Constán-Nava et al. 2015; Straigytė et al. 2015).
334 Moreover, *A. negundo* being particularly linked to riparian vegetation, moist soil is important for its
335 establishment and growth (Dumas 2019). *A. negundo* is established along the river Loire throughout
336 the region (regional atlas of IAP, CBNBP). Its presence on the riverbanks of Blois is probably partly
337 due to a spontaneous dispersal along the river. On the other hand, *A. altissima* is not associated with
338 the river at the regional scale and its presence in numerous individual residential areas near the
339 riverbanks suggests dispersal originating from the city.

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

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

347 Linear urban transport elements favor some IAP

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

360 In order to investigate further ecological processes resulting from these linear transport elements
361 more functional studies are needed to supplement our pattern approach. Comparing city and
362 regional scale maps showing species distribution could also be valuable. Moreover, some precise
363 information can be lost when using classic grids in pattern studies. For example, based on field
364 observations, individuals of *R. pseudoacacia* were specifically located on railway embankments,

365 which can be considered as suitable habitat for that species. Adopting survey methods that explicitly
366 take into account urban forms would be necessary to examine further the relationships between
367 urban and ecological patterns (Marcus et al. 2020).

368 **Conclusion**

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

383 **Declarations**

384 Acknowledgments

385 This work was performed within the framework of the ZAL (LTSER Zone Atelier Loire). We also thank
386 the referees for their constructive comments which substantially improved the manuscript.

387 Funding

388 Funding of the M2 internship by CITERES laboratory and the PhD project by Ministère de
389 l'Enseignement Supérieur et de la Recherche (France).

390 Conflicts of interest/Competing interests - No conflicts of interest

391 Ethics approval - Not applicable

392 Consent to participate - Not applicable

393 Consent for publication - Not applicable

394 Availability of data and material (data transparency): we will provide the localization of our species,
395 likely on a data repository.

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

397 Authors' contributions

398 Muriel Deparis performed the experiment, undertook all Qgis work, analyzed the data and wrote the
399 manuscript.

400 Sebastien Bonthoux and Nicolas Legay conceived, designed and performed the experiment.

401 Sebastien Bonthoux, Nicolas Legay and Francis Isselin co-wrote and reviewed the manuscript.

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520 **Figure captions**

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

523 **Fig. 2** Results of the GLM analysis for the spatial distribution for the six IAP species across the three
 524 spatial resolutions. All variables except Julian day are shown. The horizontal bars represent the

525 relative importance of each variable. For significant variables, the value of relative importance is
526 written near the bar. Total explained deviance was calculated for the model containing the variables
527 which were significant in the average model. A green bar indicates a significant and positive effect, a
528 red bar indicates a significant and negative effect and a gray bar indicates a non-significant variable.
529 For detailed effects of each NMU, see Table 2. Coarse/middle/fine NMU: respective neighborhood
530 main cover and use classification of the grid considered; impervious: impervious surface index; 1st
531 road area: area of primary roads in each cell; distance 1st road: distance from the center of the cell
532 to the nearest section of primary road; 2nd road area: area of secondary road in each cell; rail area:
533 area of railway line in each cell; distance rail: distance from the center of the cell to the nearest
534 section of railway line.

535 **Fig 3** Among the 36 models, number of times each variable had a positive significant effect, a
536 negative significant effect or had not a significant effect in explaining IAP species distribution.
537 NMU: neighborhood main cover and use; impervious: impervious surface index; 1st road area: area
538 of primary road in each cell; distance 1st road: distance from the center of the cell to the nearest
539 section of primary road; 2nd road area: area of secondary road in each cell; rail area: area of railway
540 line in each cell; distance rail: distance from the center of the cell to the nearest section of railway
541 line.