RESEARCH ARTICLE

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The observed link between urbanization and invasion can depend on how invasion is measured

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Abstract

Aim: Cities are thought to promote biological invasions because invasive species are more often introduced in urban areas and because they are more successful in disturbed environments. However, the association is not as strongly supported by the literature as is generally assumed and might depend on how urbanization and invasion are measured. In this study, we test if the type of data used to assess the link between urbanization and invasion can affect a study's conclusions.

Location: Europe and middle Rhône valley (~5000 km^2 in south-eastern France).

Method: We studied the spatial distribution of the invasive garden ant *Lasius neglectus* in its current introduced range in Europe and tested its association with urbanization using three measures of invasion (presence-only, presence–absence and population area) and two measures of urbanization (urban/nonurban land cover classification and proportion of impervious surfaces (buildings, road) per spatial unit).

Results: Based on presence-only data across Europe, *L. neglectus* occurred in urban areas 10 times more often than expected from a random geographical distribution. However, when controlling for spatial bias in sampling effort with presence–absence data (1870 sampling locations in the middle Rhône valley, France), the occurrence of the species was independent of urbanization. Moreover, the surface occupied by *L. neglectus* populations was negatively correlated with urbanization.

Main conclusions: These findings show that the type of occurrence data used to test the link between urbanization and invasion can strongly affect the conclusion of a study. This is particularly concerning because invasion studies often use presence-only data that are likely biased towards cities. Future urban invasions studies must be carefully designed to avoid this pitfall.

KEYWORDS
biological invasions, *Lasius neglectus*, sampling bias, secondary spread, urbanization

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1 | INTRODUCTION

It is generally assumed that urbanization promotes biological invasions (Borden & Flory, 2021; Gaertner et al., 2017). This assumption is supported by multiple studies that show that invasive species richness increases along urbanization gradients (Kühn et al., 2017), that invasive populations reach higher densities in urban areas (Cadotte et al., 2017), and that invasive species have better physical conditions and greater reproductive output in urban than in nonurban areas (Marques et al., 2020). Two nonexclusive processes can lead to these positive associations between urbanization and invasion. First, invasive species are more often introduced in urban areas because cities concentrate human activities and thus introduction events (Padayachee et al., 2017). Second, invasive species are more successful in cities because urban-modified environmental conditions increase their probability of surviving and reproducing as well as their secondary spread through landscapes (Kowarik & von der Lippe, 2011; Marques et al., 2020).

However, the positive relationship between urbanization and biological invasions might not be as systematic, nor as strongly supported by the literature as is generally assumed. For instance, the abundance (i.e. number of individuals) of invasive species increases with urbanization in invertebrates but not in plants and vertebrates (Cadotte et al., 2017). In addition, the proportion of urban invasions might be overestimated because the detection of invasive populations is likely biased towards urban areas as they contain higher densities of people and, thus, more opportunities for detection (Adams et al., 2020; Fithian et al., 2015; Hughes et al., 2021). More generally, wildlife is recorded more often in areas that are easily accessible to humans (Petersen et al., 2021). For example, among over 700 million animal occurrences on GBIF (www.gbif.org), Hughes et al. (2021) found that only 11% of Earth's land surface was sampled, 80% of records were within 2.5 km of roads, and that 22%–47% of records were within urban areas. Finally, urbanization gradients are often poorly defined, sometimes as the distance to a city centre, or grouped in broad urban versus nonurban classes (Cadotte et al., 2017). Therefore, the general link between urbanization and biological invasions is still unclear and the type of data used to assess invasive species distribution across urbanization gradients might affect our ability to characterize this link.

Assessing how the type of data used to measure invasion shapes our comprehension of the link between urbanization and invasion is important to better model invasive species distribution at local to global spatial scale. Presence–absence data are generally (but not always; Gormley et al., 2011) better than the presence-only data for modelling species distributions because presence-only data often suffer from a strong, and difficult to correct, spatial bias in sampling effort (Leroy et al., 2018; Phillips et al., 2009). Furthermore, presence-only and presence–absence data might misrepresent the spatial distribution of species by exaggerating the importance of small marginal sink populations, contrarily to not only more accurate but also more costly and geographically limited data such as abundance data (Ashcroft et al., 2017; Jarnevich et al., 2021). Thus, the type of data used to measure species occurrence might affect our ability to not only model and predict species distributions but also to understand species–environment relationships (Inman et al., 2021). So far, it remains unknown whether different measures of invasion (e.g. presence-only, presence–absence or abundance) lead to different conclusions about the link between urbanization and invasion.

To address this issue, we studied how different measures of invasive species occurrence influence the association between invasion and urbanization. Using the ongoing invasion of the ant *Lasius neglectus* in Europe as a model system, we tested the link between invasion and urbanization using three measures of invasion (i.e. presence only, presence–absence and population area) and two measures of urbanization (i.e. urban/nonurban land cover classification and proportion of impervious surfaces (e.g. building, roads) per spatial unit). First, we tested whether *L. neglectus* occurrences were more frequently recorded in urban environments throughout Europe using 180 presence-only data. Second, we tested whether *L. neglectus* populations were detected more often in urban environments while controlling for sampling effort using a 1870 presence–absence dataset across the Rhône Valley, France. Finally, by measuring 33 populations occurring along an urbanization gradient, we tested whether the area invaded by *L. neglectus* populations (hereafter "population area") was positively associated with urbanization.

2 | METHODS

2.1 | Study species

The ant (Hymenoptera, Formicidae), *L. neglectus*, is thought to originate from Asia Minor and is a widespread invader in Europe (Blatrix et al., 2018; Ugelvig et al., 2008). It is the least climatically limited invasive ant in central and northern Europe (Bertelsmeier & Courchamp, 2014). Unlike most other ant species invasive in Europe (e.g. *Linepithema humile*, *Paratrechina longicornis*, *Wasmannia auropunctata*), the genus *Lasius* occurs naturally throughout Europe, which might partially explain why *L. neglectus* is not climatically limited in this region (Charrier et al., 2020; Espadaler et al., 2018; Janicki et al., 2016; Rabitsch, 2011). Like most invasive ant species, *L. neglectus* has limited natural dispersal abilities because its winged reproductive females do not perform nuptial flights (Espadaler et al., 2007). Natural dispersal occurs through an incremental expansion of colonies (20–100 m per year; Espadaler et al., 2007) often resulting in large populations of interconnected nests with numerous queens and low intraspecific aggression. These colonies are often referred to as "supercolonies" (Espadaler et al., 2004). However, to simplify the terminology throughout the manuscript, we have chosen to use the term "population" to refer to a colony. Finally, in *L. neglectus* (as in most other invasive ants; Rabitsch, 2011), regional spread occurs via human-mediated dispersal when contaminated materials such as soil or potted plants are transported for landscaping, construction or horticultural trade (Schultz & Seifert, 2005; Van Loon et al., 1990).

2.2 | Indices of urbanization

We compared two commonly used measures of urbanization: urban/nonurban land cover classification and proportion of impervious surfaces. The European land cover classification (i.e. categorical: urban/nonurban) was obtained from the Corine Land Cover (CLC) classification 2018 (100-m resolution cells; from land.copernicus.eu). Corine Land Cover was simplified into two categories: urban (CLC class 1) and nonurban (CLC classes 2 and 3; nonurban areas are composed of agricultural (CLC class 2) and forests and seminatural areas (CLC class 3)). Land cover classifications are frequently used to characterize urbanization but, as a coarse discrete variable, it might oversimplify the urbanization gradient. To have a more precise and continuous representation of the urbanization gradient, we used the proportion of impervious surfaces (calculated as the percentage of soil sealing with impervious materials such as asphalt and cement per spatial unit) from the European Settlement Map 2015 (20-m resolution cells; from land.copernicus.eu).

2.3 | Presence-only data

We obtained 230 occurrence locations of *L. neglectus* across its current introduced range in Europe from the CREAF database (Espadaler & Bernal, 2020). *Lasius neglectus* occurrences located outside of the area covered by Corine Land Cover (50 out of 230) were removed from the dataset before the analysis (180 remaining occurrences; Figure 1a). In addition, to characterize urbanization in the area where *L. neglectus* can occur, we constrained our analyses to the smallest rectangular area including all 180 *L. neglectus*

occurrences and ignored areas with obvious unsuitable climatic conditions (such as extremely cold, high elevation areas). We, therefore, excluded areas with minimal temperature of coldest month (bio06) and maximum temperature of warmest month (bio05) that were more than 1°C outside of the range of values of *L. neglectus* occurrences for these two climatic variables (from worldclim.org). We extracted the land cover information for Europe ($N \sim 350$ million of pixels at 100 m resolution) and for locations where *L. neglectus* occurs ($N = 180$ locations; Figure 1b). We also calculated the proportion of impervious surfaces (averaged at 100-m resolution, because *L. neglectus* populations often spread over several hundred square meters; Espadaler et al., 2007; Gippet et al., 2021) for the 180 locations where *L. neglectus* occurs and for 9999 sets of 180 randomly selected locations (Data S1–S3). Finally, we tested if *L. neglectus* occurrences were more often located in urban areas than expected from a random distribution across Europe using a two-sample test for equality of proportions (function "prop.test" from the *stats* package in R v.3.6.2, R Core Team, 2019). We tested if *L. neglectus* occurred in more urbanized locations than randomly sampled locations across Europe by comparing the median proportion of impervious surfaces between the 180 *L. neglectus* occurrences and each of the 9999 sets of 180 random locations with Wilcoxon rank sum tests (function "wilcox.test" from the *stats* package in R; Figure S1).

2.4 | Presence–absence data

We performed a detection survey at a regional scale (~ 5000 km^2) in south-eastern France between 2011 and 2019. The area includes the city of Lyon (second-largest French metropolitan area after Paris)
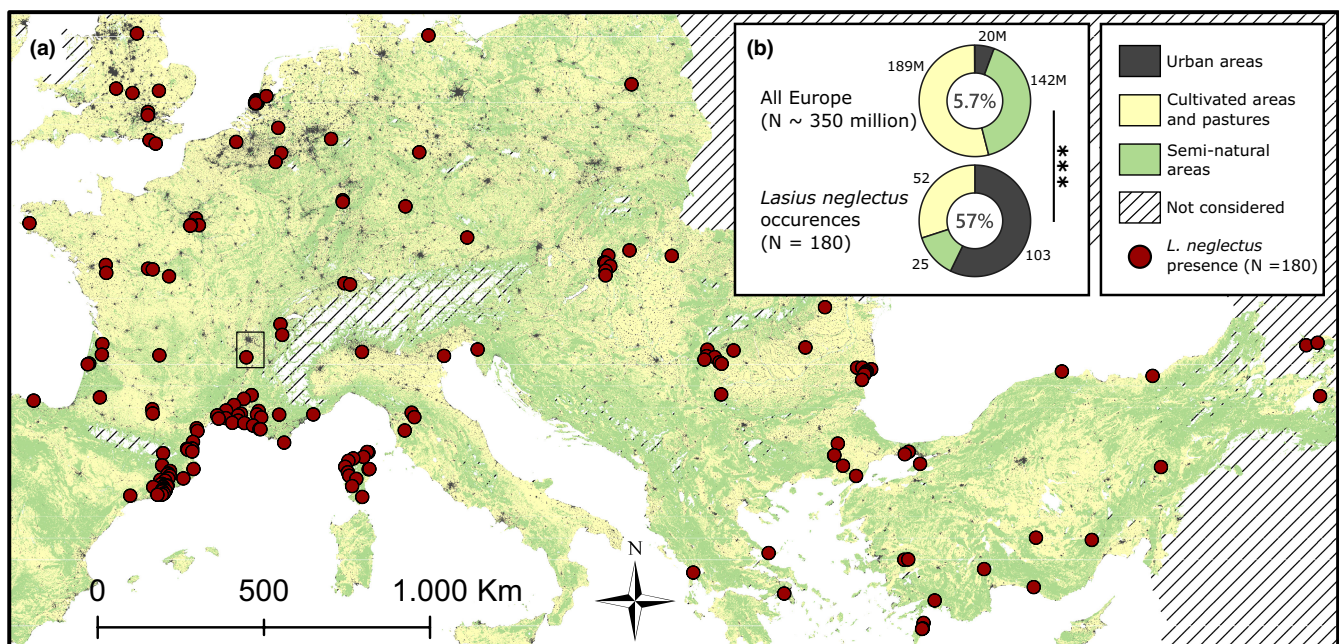

FIGURE 1 (a) Occurrences of *Lasius neglectus* in Europe (180 locations: red dots). Background map represents Corine Land Cover classification (2012) across *L. neglectus* range: cultivated areas and pastures (yellow), grassland, forest and other seminatural areas (green) and urbanized areas (dark grey). The black rectangle indicates the regional sampling area (Figure 2a). (b) Comparison of the proportion of urban land cover between *L. neglectus* occurrence locations and the background map (Proportion test, $p < .0001$)

and is characterized by a temperate climate with Mediterranean and continental influences. In this area, a total of 1870 locations were sampled between May and September in 2011, 2012, 2013, 2015 and 2019. Sampling locations were selected on public land with vegetation (an essential requirement for ant nests and foraging) wherever access was possible. To select sampling locations, two zones were determined in the study landscape: "within city centres" and "outside city centres." "Within city centres" corresponded to the urban core of the main cities in the area (Lyon, Vienne, Bourgoin-Jallieu, Annonay) where it was not possible to park with a car (samplers were thus progressing on foot) and "outside city centres" corresponded to suburban, industrial, agricultural and semi-natural areas surrounding city centres as well as the main valleys linking the cities (along the highways A7, A43 and A47) where site to site progression could be made by car. Outside city centres, sampling locations were selected along road transects and separated by at least 500 m (~70% of sampling locations). Inside city centres, sampling locations were selected along street transects and separated by at least 200 m (~30% of sampling locations). Road and street transects were chosen to cover as homogenously as possible the study landscape. The exact sampling locations were determined in the field, depending on the availability of suitable habitats and on various unforeseeable constraints (e.g. construction works, green space maintenance, high density of people or potential dangers). These surveys were designed to detect *L. neglectus* and, because it was assumed that urbanization promoted the ant invasion, sampling locations were more often located inside urban areas (*sensus* Corine Land Cover) than expected if they had been randomly sampled throughout the landscape (even in the "outside city centres" zone). Still, 38% of sampled locations were located outside urban areas, in agricultural or semi-natural lands (Figure 2a,b), therefore, covering the entire urbanization gradient. Sampling was performed by teams of two to five persons for a combined search time of 40 min (sampling time depended on the number of samplers, for example, four samplers took 10 min per site; two samplers, 20 min per site) within a radius of 15–20 m, and only when air temperatures were comprised between 16 and 28°C (i.e. best detection condition according to Seifert, 2007). Sampling consisted of a direct search of ant nests and trails on the ground, trees and shrubs, followed by hand collecting using an entomological aspirator. *L. neglectus*, like most other invasive ant species, forms large conspicuous populations of interconnected nests and, in spring and summer, thousands of workers are recruited on foraging trails that are easy to detect on trees, shrubs and on the ground, even by nonspecialist observers (Espadaler & Bernal, 2020; Gippet et al., 2018). In addition, to make sure that small *L. neglectus* populations were not confused with native *Lasius* species (typically *L. alienus*), all ants from the genus *Lasius* were sampled (one sample corresponds to one nest or one foraging trail) and stored in 96% ethanol at −20°C. Ants were then identified to the species level using morphological criteria (Seifert, 2007) and, for morphologically ambiguous *Lasius* individuals, molecular identifications were performed by sequencing the Cytochrome Oxydase I (COI) mitochondrial gene (one individual per population; see Gippet et al., 2017). Thus, we were confident in our ability to determine whether *L. neglectus* was present or absent at sampled sites. Land cover information and proportion of impervious surfaces were extracted for each sampling location ($N = 1870$), and for the study landscape using a minimum bounding polygon ($N \sim 400{,}000$ pixels at 100-m resolution; Figure 2a, Data S4–S6). Using two-sample tests for equality of proportions (function "prop. test" from the *stats* package in R), we tested (i) if locations invaded by *L. neglectus* ($N = 94$) were located more often in urban areas compared to all sampled locations ($N = 1870$), (ii) if the 1870 sampled locations were located more often in urban areas than expected from a random distribution across the surveyed area, and (iii) if locations invaded by *L. neglectus* ($N = 94$) were more often located in urban areas than expected from a random distribution across the surveyed area. Additionally, because agricultural areas share with urban areas a higher likelihood of human introduction and highly modified environments, we tested if locations invaded by *L. neglectus* ($N = 94$) were rarer in seminatural areas than in anthropized areas (i.e. urban and agricultural) using a two-sample tests for equality of proportions ($N = 1870$; function "prop.test" from the *stats* package in R). We finally compared the proportion of impervious surfaces between invaded and noninvaded locations ($N = 94$ and 1776 respectively) using a Wilcoxon rank sum test (function "wilcox.test" from the *stats* package in R).

2.5 | Population area

We measured the surface occupied by 33 *L. neglectus* populations found by the regional survey (i.e. middle Rhône valley, France; Figure 2a) and by previous opportunistic detections (8 populations out of 33). Selected populations covered the whole urbanization gradient, from urban core to semi-natural areas (Figure S2). Population measurements were performed between May and August in 2012 and 2013, by teams of two to five persons by direct search of ant nests and trails on the ground, trees and shrubs in every direction from the initial point of detection. Ants sampled were taken every 20–40 m and precisely georeferenced. Population boundaries were defined and search stopped when, in every direction, no more *L. neglectus* were found for more than 50 m from the last location where *L. neglectus* was detected. Native *Lasius* ants were sampled whenever there was a doubt on their identity based on field observation. All samples were identified with a stereomicroscope using morphological criteria (Seifert, 2007). All mapped *L. neglectus* occurrences were then imported into ArcGIS 10.1 (ESRI, Environmental Systems Research Institute, Redlands, 2012) and the surface occupied by each population (hereafter "population area") was calculated as the area of the polygon obtained from mapped locations by minimum bounding geometry. Measured populations were classified as urban if more than 50% of their extent was composed of urban land cover, and as nonurban otherwise. The proportion of impervious surfaces for each measured population was computed as the average proportion of impervious surfaces of pixels located in a 100-m-radius circle around the population centre (Data S7). We chose a 100-m-radius

circle because its surface (31,000 m²) is in the same order of magnitude than the average surface occupied by the populations in our study landscape (mean ± SE = 26,629 ± 10,440 m²). Finally, we tested if population areas differed among urban (N = 24) and nonurban (N = 9) populations using a linear model (function "lm" from the *stats* package in R) with population area (log-transformed) as the response variable and land cover classification (categorical: urban/nonurban) as the explanatory variable. We also tested if population area (log-transformed) was correlated with the proportion of impervious surfaces using a linear model (N = 33). Model validity was verified using diagnostic plots and Shapiro–Wilk's residuals normality tests (function "shapiro.test" from the *stats* package in R). All statistical analyses and visualizations can be reproduced using the available R code (SI_1).

3 | RESULTS

3.1 | Presence-only data

Urban areas covered 5.7% of Europe (excluding areas that are nonsuitable for *L. neglectus*), however, they made up 57% of the 180 *L. neglectus* European occurrences. *L. neglectus* has thus been detected 10 times more frequently in urban areas than expected from a random distribution across Europe (Proportion test: X^2 = 888.8, p < .0001; Figure 1b). The average proportion of impervious surfaces was 14 times greater in locations invaded by *L. neglectus* (27.1%) than in randomly selected locations (1.9%) (Average Wilcoxon tests' statistics over 9999 random samplings: W = 7503, p < .0001).

3.2 | Presence–absence data

Urban areas covered 16% of our sampling area. Among the 1870 locations sampled in this area, 63% were in urban areas, indicating that our sampling survey was biased towards urban areas (3.9 times more frequent than random; Proportion test: X^2 = 2871.3, p < .0001; Figure 2b). Among sampled locations, 94 were invaded by *L. neglectus* (5%), including 65 in urban areas (i.e. 5.6% of urban areas were invaded) and 29 in nonurban areas (i.e. 4% of nonurban areas were invaded). When ignoring the sampling effort, *L. neglectus* was 4.3 times more frequent in urban areas than expected from a random geographical distribution (69% of invaded locations were in urban areas; X^2 = 188.3, p < .0001; Figure 2b) However, when accounting for the sampling effort, *L. neglectus* was not overrepresented in urban areas (Proportion test: X^2 = 1.4, p = .23; Figure 2b). In addition, *L. neglectus* was not rarer in seminatural than in anthropized areas (Proportion test: X^2 < 0.0001, p = 1) as 4.9% (5 out of 103) of seminatural areas and 5% (89 out of 1767) of anthropized areas (i.e. agricultural and urban areas) were invaded. Finally, the proportion of impervious surfaces did not differ among invaded and noninvaded locations (W = 75,650, p = .12; Figure 2c).

3.3 | Population area

The surface occupied by the 33 measured *L. neglectus* populations ranged from 362 to 254,311 m² (Figure 3). Population area did not differ among urban and nonurban populations (Linear model: Estimate ± SE = 0.08 ± 0.7, t = 0.1, p = .92) but was negatively correlated with the proportion of impervious surfaces (Linear model: Estimate ± SE = −0.03 ± 0.01, t = −2.4, p = .024, R^2 = .13; Figure 3).

4 | DISCUSSION

We have shown that the type of data used to measure invasive species distribution can easily bias our understanding of the link between invasion and urbanization. In *L. neglectus*, this link was positive according to the presence-only data, nonexistent according to the presence–absence data and negative according to the population area data.

Our findings support the idea that presence-only data overestimate the presence of invasive species in cities and thus tend to show a false positive association between invasion and urbanization. Studies testing the effect of urbanization and more generally of land cover on invasive species distribution using presence-only data should, therefore, account for this bias to avoid flawed conclusions. The importance of accounting for sampling bias when modelling species distribution with presence-only data has been extensively documented in the last decade (Johnston et al., 2020; Kramer-Schadt et al., 2013; Phillips et al., 2009; Stolar & Nielsen, 2015), yet, only a minority of modelling studies apply control methods (14% as of 2013; Yackulic et al., 2013). An increasing number of methods are developed to correct sampling bias in presence-only data (Chauvier et al., 2021; Inman et al., 2021; Phillips et al., 2009), such as the utilization of biased background data (i.e. occurrences of other species sharing similar sampling biases as the target species; Phillips et al., 2009) or of nonrandom pseudo-absences that consider the spatial distribution of occurrences in the different land cover categories (Hertzog et al., 2014). The consequences of not accounting for sampling bias in species distribution models is generally assessed in terms of model performance (Chauvier et al., 2021; Leroy et al., 2018; Milanesi et al., 2020; Phillips et al., 2009) but the effect of sampling bias on species–environment relationships is rarely investigated (Inman et al., 2021). Therefore, this study provides valuable empirical evidence that the type of occurrence data used to study species–environment relationships can have profound impact on the conclusions of a study.

Presence–absence data could also be used to better assess the link between urbanization and invasion because they can account for unbalanced sampling effort. However, compared to presence-only data, these types of data are much more expensive to collect and generally limited geographically. In this study, we only sampled one region (i.e. the middle Rhône valley, France) and found that *L. neglectus* was equally present in urban and nonurban areas, but it is possible that the link between urbanization and the invasion of
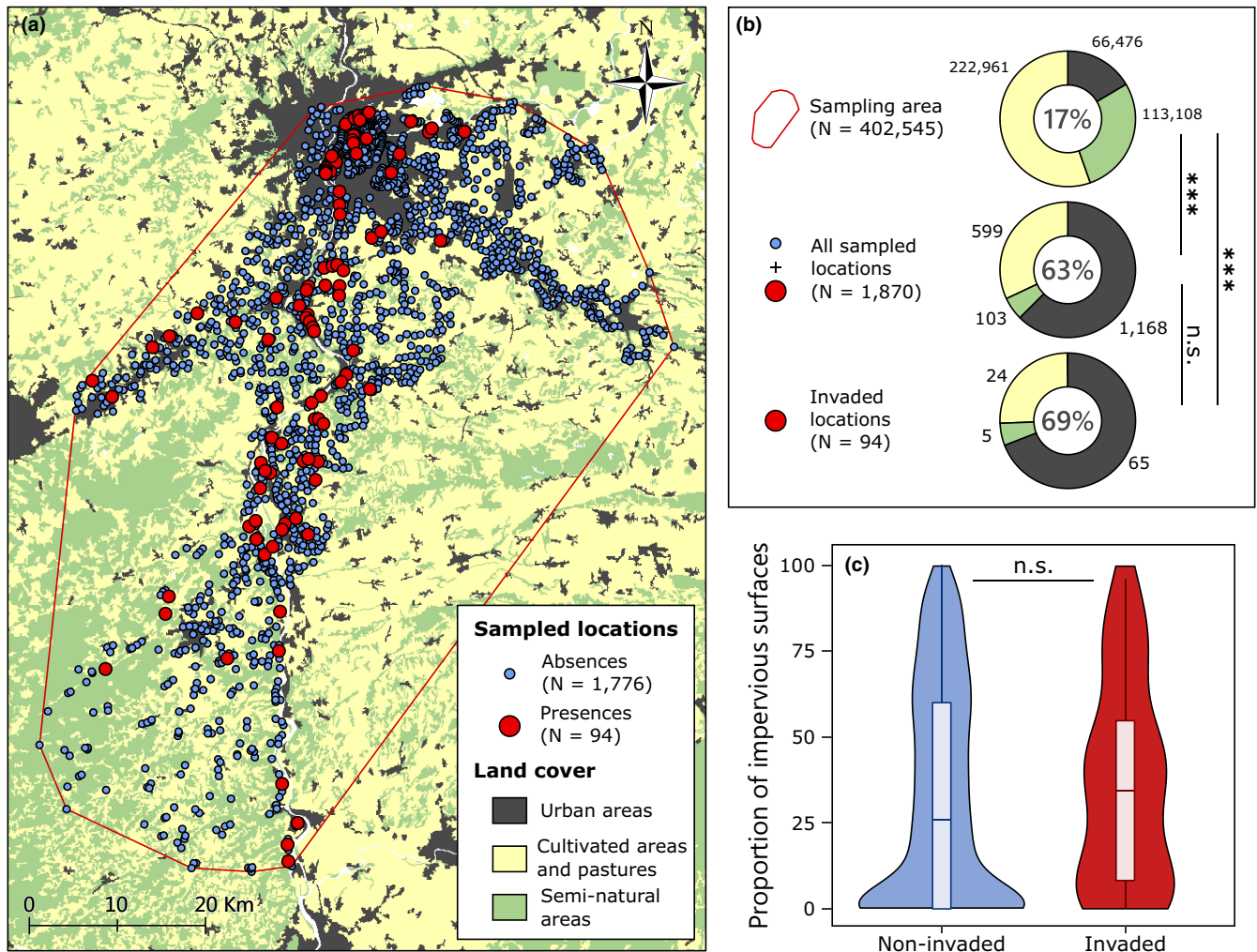
FIGURE 2 (a) Regional distribution of *Lasius neglectus* (middle Rhône valley, France). The presence and absence of *L. neglectus* across 1870 sampled locations. Background map features Corine Land Cover classification: cultivated areas and pastures (yellow), grassland, forest and other seminatural areas (green) and urbanized areas (grey). (b) Proportion of urban and nonurban land covers in the sampling area (dashed red polygon), in all sampled locations (red: invaded and blue: noninvaded sampling sites) and in invaded locations only (n.s.: nonsignificant, ***p < .001). (c) Proportion of impervious surfaces (i.e. percentage of artificially sealed surface per spatial unit) at sampling locations invaded (red; N = 94) or not (blue; N = 1776) by *L. neglectus* (p = .12). Violin plots represent the distribution of the proportion of impervious surfaces in each group. Coloured shapes show the density of data points per units on the y-axis. For associated boxplots, boxes contain 50% of the data (central thick horizontal line is the median) and whiskers contain the lowest and highest 25% of the data

L. neglectus differs in other regions. The climatic context could, for instance, greatly affect the suitability of urban areas relative to adjacent nonurban areas (Pyšek et al., 2020). For example, the invasive ant *Tetramorium immigrans* is found only in urban areas at high latitudes while it is distributed across the urban–rural gradient at lower latitudes, most likely because the species benefits from urban heat island effects in colder environments (Cordonnier et al., 2020; Gippet et al., 2017). Our regional presence/absence dataset showed that *L. neglectus* was not affected by urbanization in our study region, contrary to what could have been concluded from uncorrected presence-only continental data. However, we observed that *L. neglectus* populations were smaller in more urbanized areas. This is not unexpected because, in highly urbanized areas, patches of habitable open vegetation are small and isolated from each other, which might strongly limit the maximum spatial extent that an invasive population

can reach. The negative correlation between the proportion of impervious surfaces and *L. neglectus* population area could also be linked to population age, with urban populations being smaller because they were introduced later than nonurban populations. This scenario is possible but unlikely because *L. neglectus* occurred across the urbanization gradient, suggesting that the temporal dynamic of the invasion is not linked to urbanization. Finally, it is also interesting to notice that we found no difference in *L. neglectus* population area between urban and nonurban areas (based on Corine Land Cover classification), suggesting that broad urban versus nonurban classes (100 m resolution) are too coarse to detect the effect of urbanization on the surface occupied by *L. neglectus* populations.

Interestingly, the negative association between urbanization and invasion found in the population area data was not detected using the presence–absence data. This is consistent with the idea
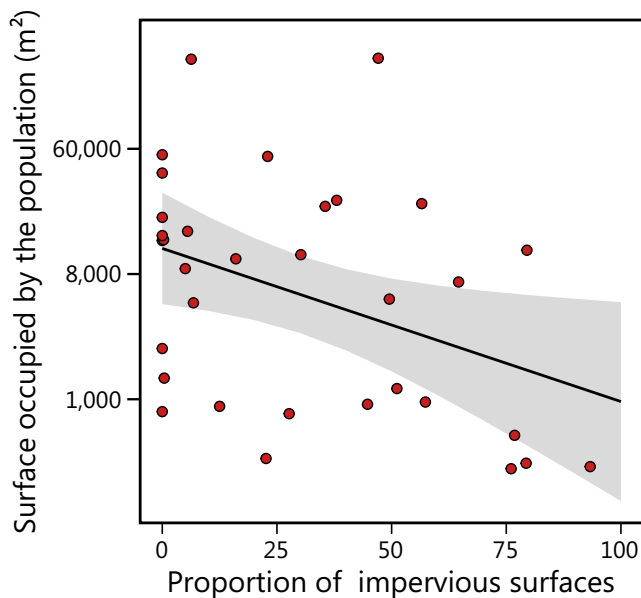
FIGURE 3 Correlation between urbanization and *Lasius neglectus* population area (*n* = 33). Black line and shaded area represent the slope ±95% CI estimation of the relationship (Linear model, R^2 = .13). The *y*-axis is log-scaled

that presence–absence data might overestimate the importance of small marginal populations (Ashcroft et al., 2017). Thus, this result is particularly important because it suggests that even studies using high-quality presence–absence data might miss important species–environment relationships. This is particularly problematic when studying invasive species because abundance is strongly linked to the survival (e.g. Allee effect; Taylor & Hastings, 2005) and impacts of invasive species (Bradley et al., 2019).

Overall, our findings do not contradict the idea that cities and their surroundings are hotspots for the introduction of invasive species, but they challenge the assumption that urbanized environments are systematically more suitable for invasive species. Furthermore, in our study landscape, *L. neglectus* was as likely to occur in seminatural areas as in anthropized areas (i.e. agricultural and urban areas), suggesting that its distribution (in the middle Rhône valley) is completely independent of land use and that most suitable habitats can be colonized, most likely by local human-mediated dispersal events (Espadaler et al., 2007; Gippet et al., 2019). *Lasius neglectus* might, therefore, be a serious threat to local biodiversity hotspots (Liu et al., 2020) and its impacts in these habitats should be further assessed as existing evidence is limited to disturbed habitats in an urbanized area of Budapest, Hungary (Nagy et al., 2009).

It is possible that most invasions start inside or near cities as the direct result of increased human density and activity, but the subsequent spread of invasive species might often be independent of, or even negatively affected by urban environments. The link between urbanization and invasion differs among invasive species and cities (Gippet et al., 2017; Perez & Diamond, 2019) and future research is needed to quantify the proportion of invasive species that are favoured by urban conditions and the ecological traits associated with it.

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BIOSKETCH

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Author contributions: JMWG, CR, NM and BK designed the study. JMWG, TC, JG, HT and BK did the field work and ant morphological identifications. AD and BK performed the molecular identifications. JMWG processed the data and performed statistical analyses and data visualization. JMWG, CR, TC and BK wrote the first draft of the manuscript, and all co-authors participated in improving the subsequent versions.

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