

Functional connectivity in replicated urban landscapes in the land snail (Cornu aspersum)

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Abstract

Urban areas are highly fragmented and thereby exert strong constraints on individual dispersal. Despite this, some species manage to persist in urban areas, such as the garden snail, *Cornu aspersum*, which is common in cityscapes despite its low mobility. Using landscape genetic approaches, we combined study area replication and multi-scale analysis to determine how landscape composition, configuration, and connectivity influence snail dispersal across urban areas. At the overall landscape scale, areas with a high percentage of roads decreased genetic differentiation between populations. At the population scale, genetic differentiation was positively linked with building surface, the proportion of borders where wooded patches and roads appeared side-by-side and the proportion of borders combining wooded patches and other impervious areas. Analyses based on pairwise genetic distances validated the isolation-by-distance and isolation-by-resistance models for this land snail, with an equal fit to least-cost paths and circuit-theory-based models. Each of the 12 landscapes analyzed separately yielded specific relations to environmental features,

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whereas analyses integrating all replicates highlighted general common effects. Our results suggest that urban transport infrastructures facilitate passive snail dispersal. At a local scale, corresponding to active dispersal, unfavorable habitats (wooded and impervious areas) isolate populations. This work upholds the use of replicated landscapes to increase the generalizability of landscape genetics results, and shows how multi-scale analyses provide insight to scale-dependent processes.

Keywords

gene flow, resistance-based models, urban, landscape genetics, Gastropoda, isolation by distance

Introduction

Cities are growing around the world, and they contain an increasing proportion of the human population (United Nations, 2015). Urbanization is regarded as a major threat to global biodiversity (Grimm et al., 2008; McKinney, 2006). Urban areas are characterized by their high degree of fragmentation, where habitat patches are generally restricted to small vegetated areas isolated from each other by an inhospitable matrix (Cadenasso, Pickett, & Schwarz, 2007; Forman, 2014). Habitat patches are also altered by multiple anthropic disturbances and frequent habitat transformation (Ramalho & Hobbs, 2012). Habitat fragmentation affects population genetic structure and dynamics, with potential deleterious effects on population persistence (Keyghobadi, 2007). To limit fragmentation effects, maintaining landscape connectivity (i.e. the degree to which the landscape facilitates or impedes movement, Taylor, Fahrig, Henein, & Merriam, 1993) is an important tool in

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conservation biology. Landscape connectivity is influenced by structural (referring to the physical relationships of landscape elements) and functional (based on the movement of organisms through the landscape, Taylor, Fahrig, & With, 2006) components. Functional landscape connectivity can be assessed by associating genetic population structure with landscape features (Baguette, Blanchet, Legrand, Stevens, & Turlure, 2013; Manel, Schwartz, Luikart, & Taberlet, 2003). When applied to urban areas, landscape genetics approaches have shown that urbanization limits gene flow among populations and thus increases genetic differentiation (M. T. J. Johnson & Munshi-South, 2017). Urban areas act as barriers between non-urban populations located around cities (e.g. bobcats, *Lynx rufus*, Lee et al., 2012; pine marten, *Martes martes,* Ruiz-González et al., 2014; solitary bee, *Colletes floralis*, Davis, Murray, Fitzpatrick, Brown, & Paxton, 2010) and between intra-urban populations (e.g. white-footed mouse, *Peromyscus leucopus*, Munshi-South, 2012; Munshi-South & Kharchenko, 2010; Munshi-South, Zolnik, & Harris, 2016). Such barrier effects were linked to particular urban features such as major transport infrastructures (Holderegger & Di Giulio, 2010; Lee et al., 2012), buildings, bodies of water (common wall lizard, *Podarcis muralis*, Beninde et al., 2016, European hedgehog, *Erinaceus europaeus*, Braaker, Kormann, Bontadina, & Obrist, 2017). Moreover, features favoring gene flow, such as urban green spaces or canopy cover (M. T. J. Johnson & Munshi-South, 2017; Munshi-South, 2012), have also been identified. However, studies that focus on intra-urban populations are under-represented and knowledge is lacking on the way particular urban landscape features and connectivity influence genetic exchange, especially for organisms with restricted mobility (La Point, Balkenhol, Hale, Sadler, & van der Ree, 2015; Storfer, Murphy, Spear, Holderegger, & Waits, 2010).

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Major challenges remain in understanding dispersal processes across landscapes using landscape genetics approaches. These approaches are not always generalizable because they neglect two main issues, (1) landscapes replication and (2) multi-scale landscape analyses (Holderegger & Wagner, 2008; Pflüger & Balkenhol, 2014; Richardson, Brady, Wang, & Spear, 2016; Segelbacher et al., 2010). Landscape replication is necessary to expand the scope of inference of landscape genetics. Multiple and independent landscapes need to be evaluated (Segelbacher et al., 2010), with the landscape itself as a study unit. Replication offers the opportunity to extract general landscape effects across all replicates but also to focus on the specific contribution of each landscape. The few studies using replicated landscapes show that generalization was not straightforward and that extrapolating from one landscape to another could be misleading (Castillo et al., 2016; Hand et al., 2016; Richardson et al., 2016; Villemey et al., 2016). For example, by comparing twelve landscapes, Short Bull et al. (2011) found that the features influencing American black bear gene flow were different between landscapes and were those with the highest variation within each landscape. Landscape replicates should be homogeneous in terms of landscape characteristics when seeking generalization. At least, post-hoc statistical controls can justify that landscape metrics vary in the same way across landscapes. Urban landscapes are good candidates for keeping a certain level of homogeneity among replicates because cities broadly share similar compositions and fragmentation levels due to similarly altered environmental conditions (Groffman et al., 2017; Parris, 2016). However, to date no studies of urban gene flow have used replicated landscapes across multiple cities (M. T. J. Johnson & Munshi-South, 2017).

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Central to landscape ecology is the idea that landscape patterns and processes are scale dependent (Wiens, 1989). Multiple spatial scale approaches are thus recommended to obtain a thorough picture of landscape effects on the genetic structure of populations (Pflüger & Balkenhol, 2014; Wagner & Fortin, 2013), with recent research documenting how multiple scale analysis supports distinct and scale dependent landscape effects (e.g. Angelone, Kienast, & Holderegger, 2011; Dionne, Caron, Dodson, & Bernatchez, 2008; Hand et al., 2016; Millette & Keyghobadi, 2015). However, most studies still evaluate landscape – genetic relationships at a single spatial scale (Manel & Holderegger, 2013; Waits, Cushman, & Spear, 2016), which might result in the lack of a particular landscape effect because of limited scale and/or inferential power. An additional difficulty is that landscape genetic inferences made at one scale are difficult to extrapolate to another scale and may lead to erroneous management recommendations (Dudaniec et al., 2013). For example, Murphy, Evans, & Storfer (2010) showed that the landscape variables in association with genetic structure of the western toad (*Anaxyrus boreas*) were different when they considered several scales (or hierarchical levels, i.e. within or between genetic clusters). Within clusters, significant landscape variables corresponded to localized processes (e.g. growing season precipitation) whereas connectivity between clusters was explained by more general, broad-scale metrics (e.g. topography). Only the proportion of impervious surfaces (including roads) was significant both within and between clusters, showing the effect of fragmentation at different scales. Different hierarchical levels of analysis can be used, but so far most landscape genetic studies have focused on pairwise distance analysis (i.e. matrix quality effect between population pairs), so that the effects of overall landscape or local environmental conditions are most often ignored (DiLeo & Wagner, 2016).

Analysis at the overall landscape scale is rare because it requires replicated landscapes and

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integrating these landscapes into a single analysis. Consideration of the overall landscape scale provides an opportunity to assess the intensity of gene flow and to compare it among landscapes, using metrics of landscape composition and configuration. The degree of homogeneity among landscapes can be assessed and associated with specific effects on the overall genetic structure. Moreover, it provides clues to interpret potential overall landscape effects, e.g. urban green spaces or green waste management, which may influence the probability of passive dispersal events and lead to overall population homogenization.

At a finer spatial scale**,** local conditions such as habitat amount and habitat spatial structure (respectively linked to resource availability and fragmentation) play a major role in population ecology (DiLeo & Wagner, 2016). For example, local conditions can influence population size (and consequently genetic drift) and dispersal through density-dependent processes (Baguette & Van Dyck, 2007; Dahirel, Vardakis, Ansart, & Madec, 2016; Pflüger & Balkenhol, 2014).

Pairwise F_{ST} approaches classically compare genetic differentiation indices to different scenarios testing the effects of matrix quality on dispersal success (Pflüger & Balkenhol, 2014). The simplest scenario is the isolation-by-distance model (IBD), which refers to limited dispersal across space based on Euclidean distances between populations. Based on functional connectivity concepts, isolation-by-resistance (IBR) models hypothesize that low resistant areas exchange a greater number of individuals (McRae, 2006). The classically used resistance-based models are least-cost-path (LCP, Adriaensen et al., 2003) and circuit-theory- (CT-) based analyses (McRae, Dickson, Keitt, & Shah, 2008). The different scenarios

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based on these two models can vary according to the resistance value sets, habitat types, and environmental conditions, which support assessing of their relative performances (e.g. Braaker et al., 2017; Dupont, Torres-Leguizamon, René-Corail, & Mathieu, 2017; Fenderson et al., 2014).

The effects of landscape fragmentation vary depending on organism mobility (Concepción, Moretti, Altermatt, Nobis, & Obrist, 2015). Low-mobility organisms can survive in relatively small habitat patches (Braaker, Ghazoul, Obrist, & Moretti, 2014). However, they tend to be intensively affected by fragmentation (and habitat loss, Öckinger et al., 2010; Piano et al., 2017) when they move among distant habitat patches to disperse or move away from disturbances. Despite their low degree of mobility, organisms such as terrestrial Gastropods can persist and are largely spread across urban landscapes (Barbato, Benocci, Caruso, & Manganelli, 2017). The garden snail *Cornu aspersum* (Gastropoda, Helicidae, formely *Helix aspersa*) is a widespread, synanthropic species (Ansart, Madec, & Guiller, 2009; Barbato et al., 2017; Kerney, Cameron, & Bertrand, 2006). It has poor mobility (a maximum of 10-50 meters per month during activity periods, Dahirel, Vardakis, et al., 2016; Dan, 1978) due to the extremely high cost associated with movement, in energy (foot muscle contraction) and water (mucus production, Denny, 1980). *C. aspersum* lives in aggregated colonies connected by low ongoing gene flow. Spatial distances between populations strongly influence genetic differentiation (Arnaud, 2003; Arnaud et al., 1999; Selander & Kaufman, 1975). Moreover, snails are very sensitive to the type of substrate they are moving through, so their movements can be facilitated by road verges and hedgerows (Arnaud, 2003), while roads drastically limit them (Baur & Baur, 1990).

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We used methodological approaches which aim at identifying the diversity of landscape effects on dispersal, based on landscape replication and multi-scale analyses. Landscape composition and configuration were characterized in each landscape and local environments, and functional connectivity scenarios were applied between population pairs. Resistance-based models (LCP and CT analyses) were compared in association with different sets of resistance values varying in distribution functions. For each scale, population differentiation was quantified using landscape, population, and pairwise $F_{ST,}$ respectively. Based on a replicated study design, the effects of overall landscape, local environment, and functional connectivity were assessed across and among twelve distinct urban landscapes. We expected the amount of favorable habitats (i.e. vegetation) to decrease population divergence whereas unfavorable land cover (roads, buildings) would increase it through fragmentation and barrier effects. We also expected IBR scenarios to better explain population structure than simple IBD models as snails have restricted dispersal capacities and are sensitive to landscape composition.

Materials and methods

Study sites and sampling design

The sampled sites were located in 3 different French urban agglomerations: Angers (Long-Term Ecological Research site [LTER] Zone Atelier Loire - 47°28'N, 0°33'W), Rennes (LTER Zone Atelier Armorique - 48°06'N, 1°40'W), and Lens (50°25'N, 2°49'W). In each urban agglomeration, we selected 4 landscape windows, named "landscapes". The 12 landscapes measured 1.3 km in diameter (SD=0.3 – Fig. 1) with land cover consisting of 43% (SD=12) of green infrastructures (wooded and herbaceous areas), while all the other surfaces were artificial (buildings, roads, asphalt surfaces, detailed in Fig. 2).

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In each of the 12 landscapes, 10 snail populations were collected. *C. aspersum* discrete colonies have been estimated as panmictic units of 25 - 70 m in diameter (Arnaud et al., 1999; Madec, 1989; Selander & Kaufman, 1975). In this study, a population referred to individuals spatially aggregated across a maximum distance of 50m. Populations were on average 580 m (SD = 125) apart in each landscape. We sampled 21 individuals (SD = 3) in each population. Sampling took place from June to October 2015 in Angers and Rennes, and from April to November 2014 in Lens. Snails were found on lawns, at the base of hedgerows, along walls or sidewalks. A total of 2,600 snails was sampled.

Genetic data

DNA extraction, locus amplification and genotyping were performed as described in Arnaud, Madec, Guiller, & Deunff (2003) and Guiller, Arnaud, Vautrin, & Solignac (2000), with slight modifications. Garden snails were genotyped at seven microsatellite loci (Table S1).
Total genomic DNA was extracted from foot muscle tissue (of fresh snails) mixed with 500 µL of 10% Chelex-100 suspension preheated to 60°C and 15 µL of Proteinase K (10 mg/mL). Samples were incubated overnight at 55°C. Then they were mixed twice at 100°C for 15 minutes.
The seven microsatellite loci were multiplexed in three distinct PCR reactions ([Ha6, Ha8], [Ha2, Ha10, Ha11], [Ha14, Ha16]). PCR amplifications were carried out in a total volume of 15 µL containing 7 µL of MyTaq ^{TM} Mix (Bioline), 0.5 µL of each primer (0.2 µM concentration), 1.25 µL of extracted DNA sample, and completed with sterilized water. Cycling was performed with one 5-min step at 94°C, 35 cycles of 30 s at 94°C, 30 s at 51.4°C for [Ha6, Ha8] and [Ha14, Ha16] loci or at 54 °C for [Ha2, Ha10, Ha11], 30 s at 72°C, and one final 5-min step at 72°C before incubation at 4°C. Prior to genotyping with an ABI 3130 XL

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automated DNA sequencer (Applied Biosystems), 1.25 µL of amplified DNA were mixed with 0.25 µL of GeneScan™ 500 ROX™ dye size standard (Applied Biosystems) and 10 µL of Hi-Di™ Formamide for 5 min at 95°C.

Alleles were scored using GeneMapper 4.1 (Applied Biosystems). Genotypic linkage disequilibrium and departures from Hardy Weinberg (HW) equilibrium were tested in each population using Fstat 2.9 (Goudet, 2001). Genotypic (linkage) disequilibrium was altogether non-significant (except for one test in LF1 – adjusted p-value <0.05), so all markers were considered as independent. Significant departures from HW equilibrium (adjusted p-value <0.05) were found in 10% of the 834 tests, with two loci showing the greatest deviations from HW equilibrium in Rennes landscapes (Ha16 and Ha11 - Table S2). We suspected null alleles, whose frequencies were mostly low (mean = 0.067; SD = 0.064, Table S3), but occasionally reached >0.2 in Rennes landscapes. We thus computed landscape $F_{ST,}$ population $F_{ST,}$ and pairwise F_{ST} values by correcting for the presence of null alleles with an expectation maximization method using FreeNA software (Chapuis & Estoup, 2007). Landscape F_{ST} was estimated including all sampled populations in each landscape. Population-specific F_{ST} was estimated between the focal population and all other populations in each landscape, reflecting the genetic differentiation of a population as compared to all other populations (Gaggiotti & Foll, 2010; Pflüger & Balkenhol, 2014). Pairwise F_{ST} was estimated between population pairs in each landscape. Allele frequencies and heterozygosities were computed with R (R Core Team, 2015) and hierfstat R package (Goudet & Jombart, 2015). Mean expected heterozygosity ranged from 0.69 to 0.85 (depending on landscape). The mean number of alleles was 7.7, and ranged between 5.7 and 10.3 (Table 2).

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Landscape metrics and connectivity map modeling

For each city, a high resolution (5 × 5 m) land cover map was produced from GIS Data from the National Geographic Institute of France (BD TOPO (c) IGN - 2010). The maps distinguished 6 land cover classes: building, wooded areas, herbaceous areas, water bodies, transport infrastructures (roads and railways), and other impervious asphalt surfaces (e.g. parking lots, sidewalks – Fig. 1, Fig. 2, and Table 1). We computed simple landscape metrics applied to each land cover class (except water surfaces, which were rare) using two spatial pattern analysis programs, Fragstat v.4 (Mcgarigal, Cushman, Neel, & Ene, 2002) and Chloé2012 (Boussard & Baudry, 2014). The percentage of landscape occupied by each characterized landscape composition (PLAND) and the mean area of patches for each land cover class (AREA (MN)) reported the landscape fragmentation level. As *Cornu aspersum* can detect boundaries between land cover types during exploration (Dahirel, Séguret, Ansart, & Madec, 2016), we quantified another fragmentation metric that was the proportion of borders combining two different specified adjacent land cover classes (RATE COUPLE, Fig. S1). These 20 landscape metrics (i.e. 5 land cover classes each for PLAND and AREA metrics, 10 combinations for RATE COUPLE) were computed at the landscape (the 12 landscapes - 1.3 km diameter) and population scales, with a buffer radius of 70 m around each population location, corresponding to the estimated panmictic unit size for the population scale (Fig. 1).

Regarding pairwise F_{ST} analysis, landscape connectivity was estimated with two different resistance-based models. These models are based on landscape resistance values that reflect the energetic cost for an individual to move, its willingness to move, and/or the risk of moving across each habitat class (Zeller, McGarigal, & Whiteley, 2012). Populations are linked to each other across resistance maps (on which resistance values are applied to each

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land cover class) by different algorithms, searching for optimal (less resistant) pathways. Least-cost-path (LCP) analyses predict the optimal path with the lowest cumulated resistance, whereas circuit-theory- (CT-) based models integrate all available pathways (McRae et al., 2008). To determine resistance values, hierarchization of land cover classes was adapted from the 4-level fuzzy coding system used by Falkner, Obrdlík, Castella, & Speight (2001) to describe the degree of association of molluscan species to habitat types. Herbaceous areas were the most favorable habitat. Wooded and impervious areas were less favorable, followed by transport infrastructure. Building and water bodies were the least permeable areas (Table 1). Resistance-based model performance is known to vary with the transformation function applied to resistance values (Chardon, Adriaensen, & Matthysen, 2003; Rayfield, Fortin, & Fall, 2010). We created three sets of resistance values varying in transformation function: linear, exponential, and logarithmic functions, bounded from 1 to 100 (Table 1). LCP lengths were extracted with Graphab software (Foltête, Clauzel, & Vuidel, 2012) and cumulated resistance (from CT-based analysis) with Circuitscape (McRae et al., 2008). Geographic Euclidean distances were also computed (ArcGIS, ESRI, and R-package g-distance, van Etten, 2017). All Euclidean and resistance distances were log-transformed and used in distinct regression analyses.

Statistical analyses

We first described the overall genetic structure of our data set by means of a hierarchical analysis of molecular variance using the R package hierfstat (Goudet & Jombart, 2015).
At the landscape scale, we tested whether landscape F_{ST} was related to any landscape metrics with linear models by frequentist hypothesis testing (F statistics in ANOVA). Because of the small sample size (12 landscapes), landscape metrics were tested one after the other

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in the linear model.

For both population and pairwise F_{ST} analyses, the whole dataset (i.e. the 120 populations and 574 pairs included in the 12 landscapes) was used in linear mixed models integrating landscape identity as a random factor. Despite the hierarchical sampling design, landscape identity could not be nested within the three cities because of model overfitting considerations. The number of levels would be too small (four landscapes) per random factor (city; Bolker et al., 2009).

At the population scale, the relation between population F_{ST} and local landscape metrics was analyzed in two steps. First, we used automated model selection (R package MuMin, Bartoń, 2016) to compare additive mixed models that included a maximum of 10 variables (the number of 20 landscape metrics was too large for our sample size: 12×10 populations, Forstmeier, Wagenmakers, & Parker, 2017). We retained all variables included in models that were within 2 AICc units from the best model (Burnham & Anderson, 2002) and computed the model-averaged importance of these variables. Then, we focused on landscape-specific effects by analyzing models built with each of the retained variables (fixed factor) and including a random slope to the random factor (Bates, Mächler, Bolker, & Walker, 2014). Random effect variations were highlighted by likelihood ratio tests (LRT) by comparing models with and without random slopes (see Jaffé et al., 2016).

Pairwise F_{ST} (standardized with a logit function, Rousset, 1997) were used as the dependent variable, and resistance-based (least-cost lengths or cumulated resistances) or Euclidean distances were used as the independent variable in linear mixed models (random intercept and slope). Linear mixed models were compared based on their AICc values (J. B. Johnson & Omland, 2004; Row, Knick, Oyler-McCance, Lougheed, & Fedy, 2017). The correlation structure of the maximum likelihood population effect (MLPE, Clarke, Rothery, & Raybould,

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2002; Jaffé et al., 2016; Peterman, Connette, Semlitsch, & Eggert, 2014; Van Strien, Keller, & Holderegger, 2012) was added to the pairwise F_{ST} models. MLPE parameterization accounted for the covariate structure of allelic frequencies between populations in each landscape, corresponding to the proportion of the variance linked to the correlation between pairwise distances. The R package nmle (Pinheiro, Bates, DebRoy, Sarkar, & R-core Team, 2016) was used with corMLPE R function (https://github.com/nspope/corMLPE). The contribution of landscape-specific effects was highlighted by LRT, comparing models with and without a random slope (Jaffé et al., 2016).

Moreover, landscape-specific effects were analyzed by linear models computed for each landscape (as classically done in non-replicated landscape studies – e.g. Dupont, Torres-Leguizamon, René-Corail, & Mathieu, 2017). This one-by-one landscape approach was applied to population and pairwise F_{ST} analyses. Metrics were separately tested in each model by hypothesis testing (F statistics in ANOVA). Focusing on population F_{ST}, we tried to determine why some landscape metrics were relevant as fixed factors in the whole dataset linear mixed model whereas they performed satisfactorily only in a few landscapes when landscapes were analyzed separately. We compared landscape metric values with permutation tests between the group of landscapes with relevant metrics and the group of remaining landscapes (see Short Bull et al., 2011).

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Results

Landscape F_{ST}

Landscape F_{ST} values varied among landscapes (range: 0.035- 0.15; Fig. 3, Table 2; see also the Supplementary text for a global overview of the genetic structure across cities, landscapes and populations and Fig. S2). The percentage of transport infrastructure was the only landscape metric (from a total of 20) with a significant relationship with landscape F_{ST} (slope estimate (SE) = -0.011 (0.004); F value = 8.2 on 1 and 10 DF; p-value = 0.017; R^2 = 0.43 – Fig. 3). Globally, populations were genetically more differentiated when landscapes comprised a low percentage of transport infrastructure (mainly roads).

Population F_{ST}

Model selection retained three metrics included in models within 2 AICc units from the best model. Population F_{ST} values were positively correlated with the average surface of buildings (AREA building), the proportion of wooded/transport infrastructure borders (RATE COUPLE w/t) and wooded/impervious borders (RATE COUPLE w/i – Table 3). We focused on models associating one of the three retained metrics as a fixed factor and the landscape random factor with random intercept and slope. Variability among landscapes (random effects) was detected for these three models (LRT and random estimate ranges – Table 3). When each landscape was analyzed separately, the links between population F_{ST} and landscape metrics were not consistent across landscapes (fixed factor p-value <0.05 in less than three landscapes out of the 12 landscapes for each of the 20 landscape metrics: PLAND, AREA, RATE_COUPLE for each land cover class). Only the average surface of buildings (AREA

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building) and proportion of wooded/ transport infrastructure borders (RATE COUPLE w/t) were positively related with population F_{ST} in 3 different landscapes ([AF2, AF4, RF2] and [LF2, RF2, RF3], respectively). We tested whether the non-significance of the average surface of buildings in some landscapes was linked with a reduced surface occupied by buildings, which may have been non-limiting for individual dispersal. AREA building was higher in the group of significant landscapes (mean (SD) = 437 (288) sq.m *vs*. mean (SD) = 315 (297) sq.m – permutation test, p = 0.04). No difference was detected for RATE COUPLE w/t values.

Pairwise F_{ST}

Regarding pairwise analysis with the whole dataset (landscapes as a random factor), several models had lower AICc values than the null model (i.e. without any fixed factor – Table 4). These models included Euclidean distances or LCP distances for exponential, linear and logarithmic distributions of resistance values, and CT distances for all distributions of resistance values. Among those, three models equally outperformed the model with Euclidean distances: two models with LCP distances (logarithmic and exponential distributions) and one model with CT distances (exponential distribution - Table 4). We focused on the Euclidean distance model (i.e. the isolation by distance [IBD] model) to study variability among landscape random effects because among satisfactory models it was the most parsimonious model (regarding its intrinsic simplicity relative to resistance-based models). The likelihood ratio test of this IBD model with or without a random slope was significant (LR = 7.98; p = 0.018). The magnitude of the landscape-specific IBD effect varied across landscapes. The mean IBD slope for all landscapes (fixed effect estimate) was 0.010,

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while landscape-specific IBD slopes (random effect estimates) ranged from -0.010 (AF2) to 0.014 (LF1, Fig. 4). When landscapes were analyzed separately (one linear model per landscape), null models (without any fixed effect) had the lowest AICc values in 11 landscapes. Only landscape LF3 had LCP distance models (all distributions of resistance values) better than the null model (delta AICc >2).

Discussion

We studied the population genetic structure of the garden snail (*Cornu aspersum*), an organism with restricted dispersal, across 12 fragmented urban landscapes. We aimed to generalize our results across landscapes and highlight the diversity of relationships between landscape and genetic patterns, by means of landscape replication and multi-scale analyses. Three different scales of analysis yielded diverse relationships between landscape structure, composition, functional connectivity, and population differentiation. We showed at the landscape scale that transport infrastructures decreased genetic differentiation, suggesting these infrastructures facilitate passive dispersal events across cityscapes in the land snail. At the population scale, building surfaces, the proportion of borders combining wooded areas and roads or wooded areas and impervious surfaces increased genetic differentiation. These local factors may reduce (short) active dispersal movements. We also documented isolation by distance and isolation by resistance for the species in urban matrices. Relationships between genetic differentiation and landscape characteristics were highly variable among landscapes, supporting the necessity to replicate landscapes.

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Landscape structure and scales

At the landscape scale, populations were genetically more differentiated when roads were in low proportion. Roads are mainly recognized to act as barriers to dispersal (Balkenhol & Waits, 2009; M. T. J. Johnson & Munshi-South, 2017). However, in our case, no barrier effect was detected at the landscape scale. Instead, we detected a positive effect of roads on gene flow, meaning that roads were not only permeable but also facilitated gene flow. The potential role of roads as dispersal corridors has already been documented in the alpine newt (*Ichthyosaura alpestris*, Prunier et al., 2014) and is often linked with road verge effects. Gene flow can be favored by the presence of vegetated road verges known to facilitate animal dispersal (Holderegger & Di Giulio, 2010) and favor snail dispersal movements (Arnaud, 2003; Baur & Baur, 1990). Another interpretation could be that roads increase events of passive dispersal. Snails have a great potential for passive dispersal associated with human activities (e.g. Aubry, Labaune, Magnin, Roche, & Kiss, 2006): some of their biological traits favor passive dispersal events, such as easily transported dormant stages or human-associated habitat requirements (Medley, Jenkins, & Hoffman, 2015).

At the local environment scale, populations located close to large (enough) building areas were genetically different from the others. Based on these results, buildings can be considered as local fragmenting elements that impede gene exchange between the focal population and the others, and limit population size. Despite the wide acceptance that buildings fragment cityscapes, this effect has rarely been precisely identified (but see Beninde et al., 2016) and is more often included in a general effect attributed to urban infrastructure (associated with roads and impervious areas, e.g. Davis et al., 2010; Delaney,

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Riley, & Fisher, 2010; Munshi-South et al., 2016; Ruiz-González et al., 2014; Watts, Rouquette, Saccheri, Kemp, & Thompson, 2004). The amount of borders associating wooded areas and roads or wooded and impervious areas was related to increased population differentiation, and by consequence showed a barrier effect. Wooded areas are not an optimal habitat for *Cornu aspersum* (Falkner et al., 2001) or other land snails (Rosin, Lesicki, Kwieciński, Skórka, & Tryjanowski, 2017). At this local scale, the proximity of wooded areas to roads (or other impervious areas) resulted in fragmented wooded patches and may have decreased habitat quality. A typical case was street trees associated with asphalt, covering the ground under the tree canopy (e.g. Fernández-Juricic, 2000). We could also hypothesize that garden snails present in these wooded/road borders ran higher risks of mortality due to the negative effects of roads (e.g. crushing, dehydration, pollution, Balkenhol & Waits, 2009; Forman, 2003).

Landscape- and population-related analyses extracted different significant landscape effects, adding to the scale-dependent effects that have been documented in a few studies (Angelone et al., 2011; Keller, Holderegger, & van Strien, 2013; Razgour et al., 2014; Worthington Wilmer et al., 2008). An intriguing result of our study was that roads had contrasting effects depending on scale, facilitating dispersal at large distances and impeding it at shorter distances. Scale-dependent effects are easily understood when accounting for different dispersal mechanisms, such as passive and active dispersal (Worthington Wilmer et al., 2008). These authors have documented that passive and active dispersal can be influenced by different landscape features in an aquatic snail. We suggest here that the same landscape feature can have contrasting effects depending on the dispersal

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mechanism, with roads increasing passive dispersal but impeding active dispersal in the land snail. Our results also show that extrapolation across spatial scales can be misleading, and we encourage the study of multiple scales in landscape genetic studies (Keller et al., 2013).

Relevance of resistance-based models

IBD was validated as expected for a species with limited and highly costly dispersal movements (Bohonak, 1999). Few resistance-based models outperformed the IBD model (LCP associated with logarithmic and exponential resistance value distribution and CT with exponential distribution). It was difficult to determine which distribution of resistance values performed best. Basically, the difference between distributions was the classification of intermediate-quality habitat classes, considered as rather favorable and similar to a secondary habitat (exponential distribution) or largely costly and risky (logarithmic distribution). The exponential distribution has been illustrated as a better distribution to apply to resistance values (e.g. Braaker, Moretti, et al., 2014; Driezen, Adriaensen, Rondinini, Doncaster, & Matthysen, 2007; Trainor, Walters, Morris, Sexton, & Moody, 2013). However, the best transformation may depend on the type of biological data used to calculate resistance values (e.g. genetic distance or daily movement, Braaker et al., 2017). In our study, LCP and CT performed equally well with the exponential distribution, and it was not possible to resolve competing assumptions (e.g. single or multiple optimal paths). Circuit-theory-based analysis is commonly highlighted as more informative than LCP about gene flow (Coulon et al., 2004; Garrido-Garduño, Téllez-Valdés, Manel, & Vázquez-Domínguez, 2016; La Point, Gallery, Wikelski, & Kays, 2013; McRae et al., 2008), but comparisons have seldom been made in urban landscapes. Urban landscape characteristics

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could lead to different relative performance between LCP and CT-based models. Highly contrasted land cover, restricted habitat, or high landscape fragmentation may indeed reduce the number of potential pathways and movement success probability and thereby limit the added value of CT analysis.

Landscape replication

We showed that single landscape analyses led to various (sometimes opposite) conclusions about the effects of landscape on genetic structure. Gathering several landscape data in linear mixed models increased statistical power and provided more robust conclusions: for example, we validated the IBD model and identified landscape characteristics that influence dispersal that would not have been detected otherwise. Moreover, the mixed model offered the opportunity to study specific effects of landscape through random effect analysis. However, this opportunity to study the whole dataset of replicated landscapes with a mixed model seems to be rarely used (Castillo et al., 2016; Short Bull et al., 2011; Villemey et al., 2016; but see Jaffé et al., 2016, who did not replicate landscapes but species).

The correspondence between our general conclusions and landscape-specific contributions (single landscape analyses) was not straightforward. For example, at the population F_{ST} scale, landscape metrics that were significant in at least 3 landscapes were also significant in the analysis of the whole dataset. Variability in landscape-specific results illustrates the difficulty of generalizing results from single-landscape studies. Several arguments can be advanced to explain this variability across landscapes (Richardson et al., 2016). First,

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landscapes influence organisms in a heterogeneous way (e.g. Short Bull et al., 2011). In the case of the garden snail, the average surface occupied by buildings was a significant and positive predictor of population differentiation only in the three landscapes in which building surface was the highest. Second, statistical power may be too low to detect and quantify landscape effects when analyzing single landscapes (Jaquiéry, Broquet, Hirzel, Yearsley, & Perrin, 2011). For example, analyses of pairwise distances in single landscape sorted the null model as the best one although a highly significant IBD was found when analyzing the whole dataset. Disentangling the relative importance of these and other factors on the differences expressed across landscapes is an interesting topic linked to replicated study designs that would deserve further investigations.

Genetic differentiation using F_{ST}

F_{ST} is a robust metric widely used to describe population genetic structure (Holsinger & Weir, 2009) and indirectly measures effective dispersal (successful gene flow) across evolutionary time scales (Broquet & Petit, 2009). It is important to keep in mind that patterns of genetic differentiation result from a dynamic equilibrium between drift and dispersal, which are forces with opposite effects on population divergence. Genetic drift induces lower genetic differentiation between large populations compared to small ones independently of dispersal rate (Jaquiéry et al., 2011). However, the contribution of genetic drift is rarely determined (but see Prunier, Dubut, Chikhi, & Blanchet, 2015). Moreover, certain amount of time is required to reach an equilibrium after a landscape transformation or a disturbance. This time lag is difficult to assess because it depends on multiple demographic and landscape factors (Epps & Keyghobadi, 2015). A time lag between

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landscape and genetic patterns may be frequent in urban landscapes due to high rates of area transformation and disturbance (Ramalho & Hobbs, 2012).

We studied three different scales separately with three F_{ST} computing variations (landscape, population, and pairwise F_{ST}). It could be interesting to integrate data from each scale analysis into one model to quantify the relative contribution of each scale. The use of gravity models may be promising in explaining gene flow as a function of landscape predictors measured at both population and pairwise levels (DiLeo & Wagner, 2016; Murphy, Dezzani, Pilliod, & Storfer, 2010; Pflüger & Balkenhol, 2014).

Conclusion

We used landscape replication to highlight the effects of landscape composition, configuration and connectivity models on genetic differentiation of garden snail populations. Replication gave access to robust conclusions about the overall effects of landscape on population structure by linear mixed model analysis and the consideration of different scales of analysis. Relationships between landscape and genetic structure were also partly landscape- and scale-dependent.

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Data accessibility

The datasets with *C.aspersum* microsatellite genotypes are available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.p9f13

Authors' Contributions

E.J.P., A.E., L.M. initiated and designed the study. M.B., A.E., P.P., L.M., V.B., E.J.P. collected the data, and M.C.M, A.G., M.B., P.P. performed molecular analyses. J.N. and V.B. provided maps. M.B. and P.P. conducted connectivity and landscape genetics analyses. M.B. performed statistical analyses and wrote the manuscript, supervised by E.J.P., A.E. and L.M..

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Tables and Figures

Table 1: Habitat classes, description, hierarchization (Hier) and resistance value sets; Exp : exponential, Log: logarithmic, Lin: linear

Habitat class	Description	Hier	Exp	Log	Lin
Herbaceous	Garden, lawn, grassland, ruderal area, herbaceous plant, bush, hedge, isolated trees	1	1	1	1
Wooded	Grove, tree, wood	2	13	50	33
Impervious	Asphalt surfaces other than roads, parking lots, sidewalks	2	13	50	33
Transport infrastructure	Road, railway	3	37	80	67
Building	Building, construction site	4	100	100	100
Water	Canal, ditch, pond	4	100	100	100

Table 2: Genetic statistics for each landscape: Number of sampled individuals (Tot nb), Mean Fis, mean observed heterozygosities (Ho), mean expected heterozygosities (He), mean number of alleles per locus, landscape FST ($F_{ST}g$).

Study area	Tot nb	Mean Fis	Ho	He	Mean allele nb	$F_{ST}g$
AF1	224	0.047	0.803	0.843	10.20	0.048
AF2	229	0.091	0.775	0.852	10.33	0.041
AF3	211	0.124	0.736	0.840	9.73	0.035
AF4	212	0.104	0.750	0.838	9.25	0.052
LF1	198	0.103	0.622	0.693	5.88	0.124
LF2	210	0.080	0.669	0.727	5.88	0.116

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LF3	174	0.076	0.701	0.759	6.24	0.098
LF4	191	0.065	0.717	0.766	6.68	0.059
RF1	235	0.219	0.596	0.764	8.14	0.081
RF2	233	0.250	0.548	0.731	7.13	0.151
RF3	232	0.289	0.529	0.743	6.94	0.115
RF4	244	0.293	0.509	0.720	5.71	0.110
Grand mean	216	0.145	0.663	0.773	7.68	0.086

Table 3: Population F_{ST} analysis, regressions summarized according to landscape metrics associated with model-averaged importance, fixed estimate, standard error and range of the random estimates from random slope models; LRT ratio and level of significance, p-value: ***<0.001; *<0.05.

Landscape metrics	Model-averaged importance	Fixed estimate	Fixed SE	Random estimate range	LRT
RATE COUPLE wooded/ impervious	0.74	0.63	0.32	[-0.68; 0.88]	4.7 *
RATE COUPLE wooded / transport infr.	0.56	0.61	0.49	[-1.82; 2.78]	24.4 ***
AREA building	0.51	0.27	0.17	[-0.53; 1.13]	30.1 ***

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Table 4: Pairwise F_{ST} analyses with distances as a fixed factor, fixed estimate and standard error, AICc, and ΔAICc. Distances were extracted from least-cost-path (LCP) or circuit-theory (CT) analyses based on different distributions of resistance values: exponential (exp), logarithmic (log), linear (lin), and Euclidean distance (Euc)

Distance	Fixed estimate	Fixed SE	AICc	ΔAICc
LCP.log	0.0094	0.0035	-2287.6	0
CT.exp	0.0272	0.0090	-2287.1	0.5
LCP.exp	0.0096	0.0032	-2286.9	0.7
Euc	0.0099	0.0035	-2284.3	3.3
LCP.lin	0.0091	0.0032	-2284.1	3.5
CT.lin	0.0223	0.0074	-2283.0	4.6
CT.log	0.0203	0.0068	-2281.4	6.2
null	NA	NA	-2270.5	17.1

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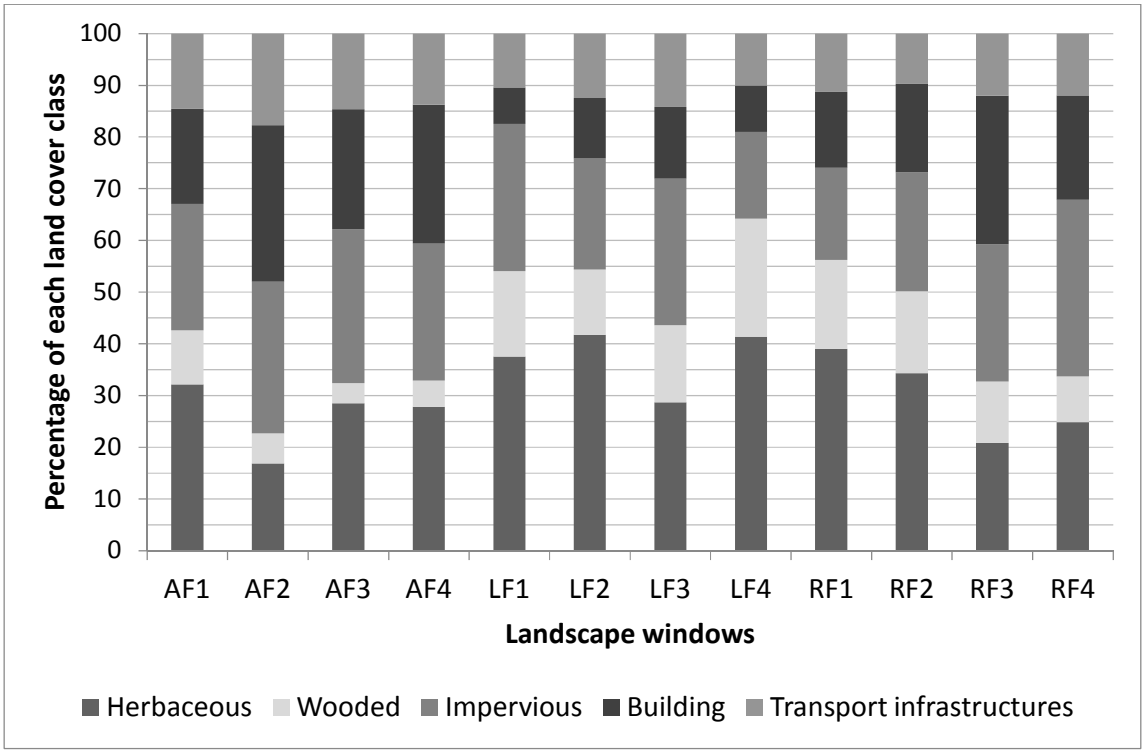


Figure 2: Percentage of each land cover class in the 12 landscapes. AF: Angers, LF: Lens, RF: Rennes.

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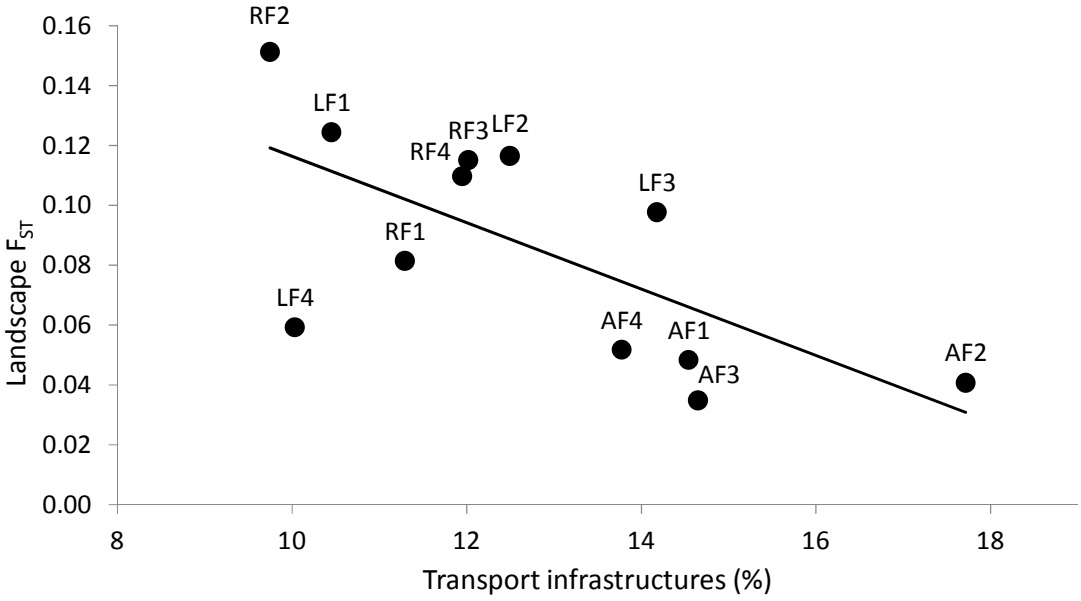


Figure 3: Landscape F_{ST} and percentage of surfaces occupied by transport infrastructures in each landscape; linear regression (line): $R^2 = 0.43$; slope estimate = -0.011

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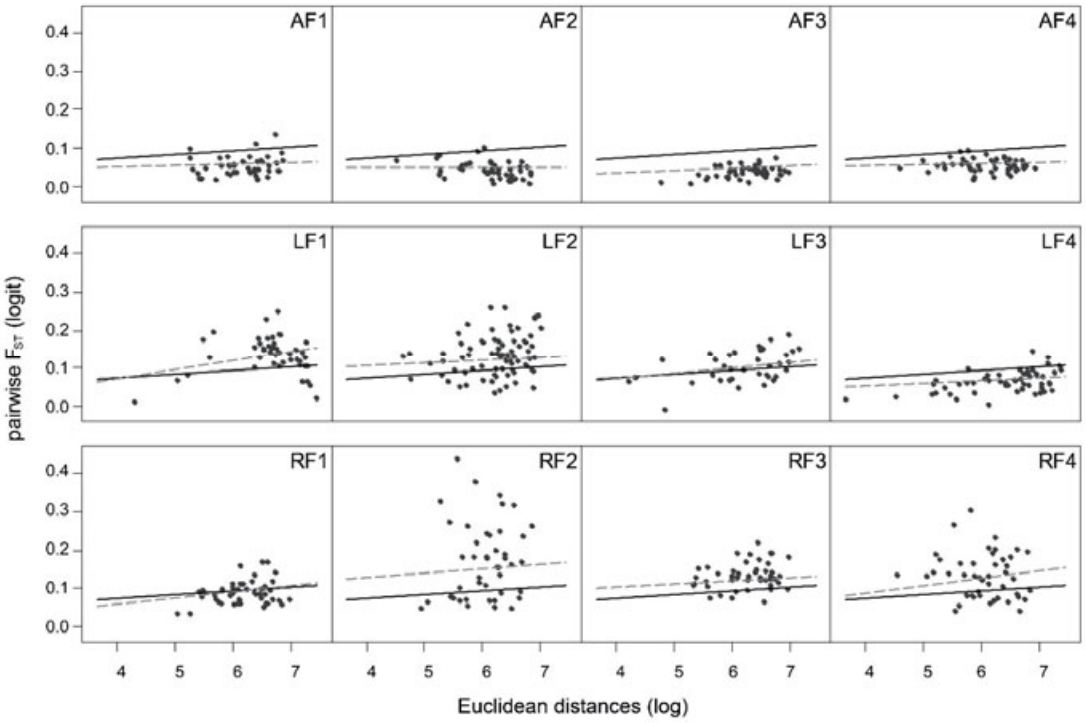


Figure 4: Isolation by Euclidean distance (IBD) in the 12 landscapes, fixed effect (black line) and landscape-specific random effect (grey dotted lines).

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