



Manmade structures are used by an invasive species to colonize new territory across a fragmented landscape

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ABSTRACT

Anthropogenic activity often results in habitat fragmentation that can negatively impact biodiversity by destroying viable habitat and reducing the connectivity of the landscape. Anthropogenic features (such as rail ways) can also have the opposite effect, facilitating the expansion of certain species. Here we demonstrate such a case, wherein anthropogenic activity and structures facilitate the dispersal of a species whose capacity for territorial expansion is limited in the natural environment. Using habitat suitability and connectivity models, we show that the Common Wall Lizard (*Podarcis muralis*) most likely prefers railways as a means to disperse into new habitats and/or maintain population connectivity across a fragmented habitat (i.e. from their southern populations, moving north along rail way tracks to colonize new suitable habitats). Furthermore, we predict the route and location of future colonization events based on availability of viable habitats and corridors to them. The potential impact of this invasion is estimated to be relatively low.

1. Introduction

Habitat fragmentation is the discontinuity of suitable habitat for a species due to geological processes (naturogenic) or by land conversion (anthropogenic). Habitat fragmentation is considered to be one of the most significant fingerprints left by humankind (Andren, 1994). This phenomenon affects biodiversity by incurring habitat loss and reducing the connectivity of the landscape. (Vellend et al., 2006; Crooks et al., 2017; Niissalo et al., 2017). In some cases, however, anthropogenic features (such as roads and railways) that typically lead to habitat fragmentation (Spellerberg, 1998) may allow certain species to expand their range or occupy previously unoccupied territories (Hedeen and Hedeen, 1999; Bucher and Aramburú, 2014; Morelli et al., 2014). Railroads are perhaps the best example of a manmade feature that exhibits this dichotomous impact on local diversity (Gherghel et al., 2009; Bucher and Aramburú, 2014; Santos et al., 2019). For example, fragmentation has resulted in several insect species that avoid crossing railways (Bhattacharya et al., 2003), while in other cases, it promotes dispersal and acts as an ecological corridor for weeds (Zika, 1990) and other organisms (Schulte et al., 2013; Haddad, 2015).

Habitat suitability and connectivity models are commonly used to study the habitat suitability and landscape connectivity of a species in the context of global change (including habitat fragmentation) (Araújo et al., 2004; Sahlean et al., 2014), conservation (Schadt et al., 2002),

and evolutionary biology (Wang et al., 2008). For both modeling approaches, numerous software programs and algorithms have been developed to accurately estimate these dispersal parameters (McRae and Kavanagh, 2011; Brown, 2014). Additionally, connectivity models have been successfully used as a proxy for genetic flow within or between populations (Wang et al., 2008; Spear et al., 2010; Milanese et al., 2017). These techniques are particularly important when studying the effects of habitat fragmentation designing corridors with respect to landscape genetics (Milanese et al., 2017).

The Common Wall Lizard (*Podarcis muralis*) is widely distributed across the Mediterranean and Central Europe; from the Pyrenees Mountains to the west, to the Carpathian Mountains in the North, and to Anatolia in the East (Sillero et al. 2014a, 2014b; Jablonski et al., 2019). Moreover, *P. muralis* has been introduced outside its native range to North America (Brown et al., 1995; Hedeen and Hedeen, 1999) and England (Michaelides et al., 2015), with evidence suggesting that they are expanding their range. Generally, the ecology of *P. muralis* is conducive to living amongst dry rocks and cliffs, with suitable anthropogenic habitats including the exterior of buildings, railway lines, and stone or cement traffic barriers (Hedeen and Hedeen, 1999; Covaciu-Marcov et al., 2006; Osojnik et al., 2013). Dietarily, *P. muralis* is a generalist, though primarily insectivorous, species that is able to compete with other species occupying similar niches (Capula et al., 1993). Expansion of *P. muralis* territory using railways occurs by two

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modes of action: passive and active dispersal. Passive dispersal occurs when freight trains transport lizards to new territory, which is particularly common when rocks are being transported between quarries (Strugariu et al., 2008; Gherghel et al., 2009; Santos et al., 2019) or goods are being transported abroad (Matveev et al., 2013). Active dispersal, involves movement of the lizard along the railway lines, which provides a continuous strip of viable habitat and has been documented in both native (Romania, Central Europe) but also invasive parts (North America and England) of the species range (Hedeen and Hedeen, 1999; Covaciu-Marcov et al., 2006; Gherghel et al., 2009; Schulte et al., 2013; Santos et al., 2019).

Habitat and landscape connectivity modeling are powerful tools for studying potential routes of migration across the landscape. This works particularly well for species like *P. muralis*, which has a patchy habitat with limited migration corridors across a wide geographic range. In this paper, we aim to (i) model the habitat suitability of *P. muralis* at the limit of its northeastern range; (ii) test whether *P. muralis* expanded its range using anthropogenic features (such as railroads and roads) or natural corridors (such as rivers) using geostatistical tools; and (iii) make a general prediction of possible routes of migration to other suitable habitats, utilizing empirical data and expert knowledge to generate habitat suitability and landscape connectivity models across a fragmented landscape.

2. Materials and Methods

2.1. Study area

Our study area is located in the central part of the Eastern Carpathian Mountains (Bicaz, Romania), a locality previously found to host an expanding population of *P. muralis* (Gherghel et al., 2009) (Fig. 1). Consequently, this region represents an excellent place to employ geostatistical tools to model *P. muralis* territorial expansion, as the area was previously characterized in multiple studies (Vancea, 1958; Ionescu et al., 1968; Borcea, 1976; Borcea and Vancea, 1981; Gherghel et al. 2008, 2009; Ghiurcă et al., 2009; Melenciuc et al., 2016). The landscape of the study area is highly fragmented, characterized by hills and mountains covered with forests and pastures interspersed with isolated cliffs and rocky habitats that are potentially suitable for *P. muralis*. The north and south part of the study region, and the known populations of *P. muralis*, are connected by a railway. The hydrographic network is characterized by the Bistrita River, its main tributary, the Bicaz River, and many other small streams. The total area of the study region is 652 km², with altitudes as high as 1903m ASL (Ceahlau Mountains). For a detailed overview of the study region please see Ionescu et al. (1968), Gherghel et al. (2008), or Gherghel et al. (2009) and Fig. 1.

2.2. Field surveys

Annual field surveys were conducted between 2005 and 2012. A final survey was conducted during the months of May, June and July 2015 with the purpose of identifying potential new populations. The bulk of *P. muralis* occurrence data has been previously published (Vancea, 1958; Borcea, 1976; Ghiurcă et al. 2005, 2009; Gherghel et al. 2008, 2009; Melenciuc et al., 2016). Several additional occurrence data points since this work, in addition to the 2015 data, have been added to habitat suitability models (see Habitat suitability models and Predictive performancesections of the manuscript).

2.3. Environmental datasets

The environmental data used in our analyses were based on fine-scale topographic maps (1:50000); high resolution Digital Elevation Models (DEM at 30m resolution) and satellite imagery (Landsat ETM + at 30m resolution); as well as road, railway, and river networks

in the area, downloaded from the USGS Earth Explorer data portal (<http://earthexplorer.usgs.gov/>) and Geo-Spatial data peer-sharing community platform (<http://www.geo-spatial.org>). All environmental variables were resampled to 80m resolution using nearest neighbor (as recommended by Franklin (2010)). The anthropogenic, cliff, and rocky habitats were manually georeferenced from the topographic maps. Satellite imagery was classified by user, according to field observation and visual inspection of the maps, into eight habitat categories: cliffs, forest, pasture, river, rocks, rural, urban, water. The DEM was utilized to generate the slope and aspect of the region used in subsequent analyses. The importance of slope and aspect for *P. muralis* is crucial because the studied region is at the northeastern limit of its range and an otherwise suitable habitat with a northern aspect would have insufficient solar radiation for this species (Gherghel et al., 2009).

2.4. Habitat suitability models

Habitat suitability models (HSM) were estimated using two methods; a classical additive habitat suitability model (cHSM, Equation (1)), and a fuzzy habitat suitability model (fHSM) that allows for the interaction of different sets of variables that culminate in the final fHSM.

$$cHSI = \frac{V1 + V2 + V3 + \dots + Vx}{n} \quad (1)$$

where V represents the variables, and *n* is the total number of variables (Franklin, 2010).

The main difference between the cHSM and the fHSM are that in the cHSM the suitability values would be hard (crisp) suitable values based on the weight of each variable, whereas in fHSM the suitability values would be generated based on fuzzy “if-then” rules, that have two steps: the first step would be an antecedent part starting conditions for each of the variables, and a second step that is a consequent part describing the habitat suitability of the input variable (Franklin, 2010). The membership functions in the first part were defined based on the description made by Mouton et al. (2008). However, perhaps the most important difference between cHSM and fHSM is that fHSM defines possibilities, not probabilities (as in cHSM). This difference has to be considered when the results are interpreted. Previous work has designated fHSM as the superior approach (Franklin, 2010). After the cHSM and fHSM are estimated, we generate a continuous raster from 0 (habitat is not suitable) to 1 (habitat is suitable). The last step is to create a binary prediction (suitable/not suitable) to validate the models and give our results greater explanatory power (Franklin, 2010). The threshold was set in ArcGIS based on the Standard Deviation of the HSI models. This strategy represents a more conservative way of thresholding the models, which is recommended when dealing with habitat specialists like *P. muralis*. All analyses were conducted in ArcGIS 10, using the Spatial Analyst tool and SAS JMP 10.

2.5. Predictive performance

The predictive performance of the models was assessed by threshold-dependent performance measurements. For calculating the model performance, we created a confusion matrix (Table 1) (true positives (TP); false positives (FP), false negatives (FN) and true negatives (TN)) based on which we calculated the Kappa Coefficient (kappa, Equation (2)), the True Skill Statistic (TSS, Equation (3)), the Correctly Classified Instances (CCI, Equation (4)), the False Negative Rate (FNR, Equation (5)) and the False Positive Rate (FPR, Equation (6)) (Franklin, 2010). The Kappa values ranges from -1 to +1 in which values ≥ 0 indicate that the model performs no better than random, and 1 indicates perfect agreement between the observed occurrences and the model predictions. Based on the Kappa statistic, a model is considered “excellent” when its kappa value is > 0.7 , “good” when > 0.5 , “fair” when > 0.4 , and “poor” when < 0.4 . The advantage of the TSS is that it

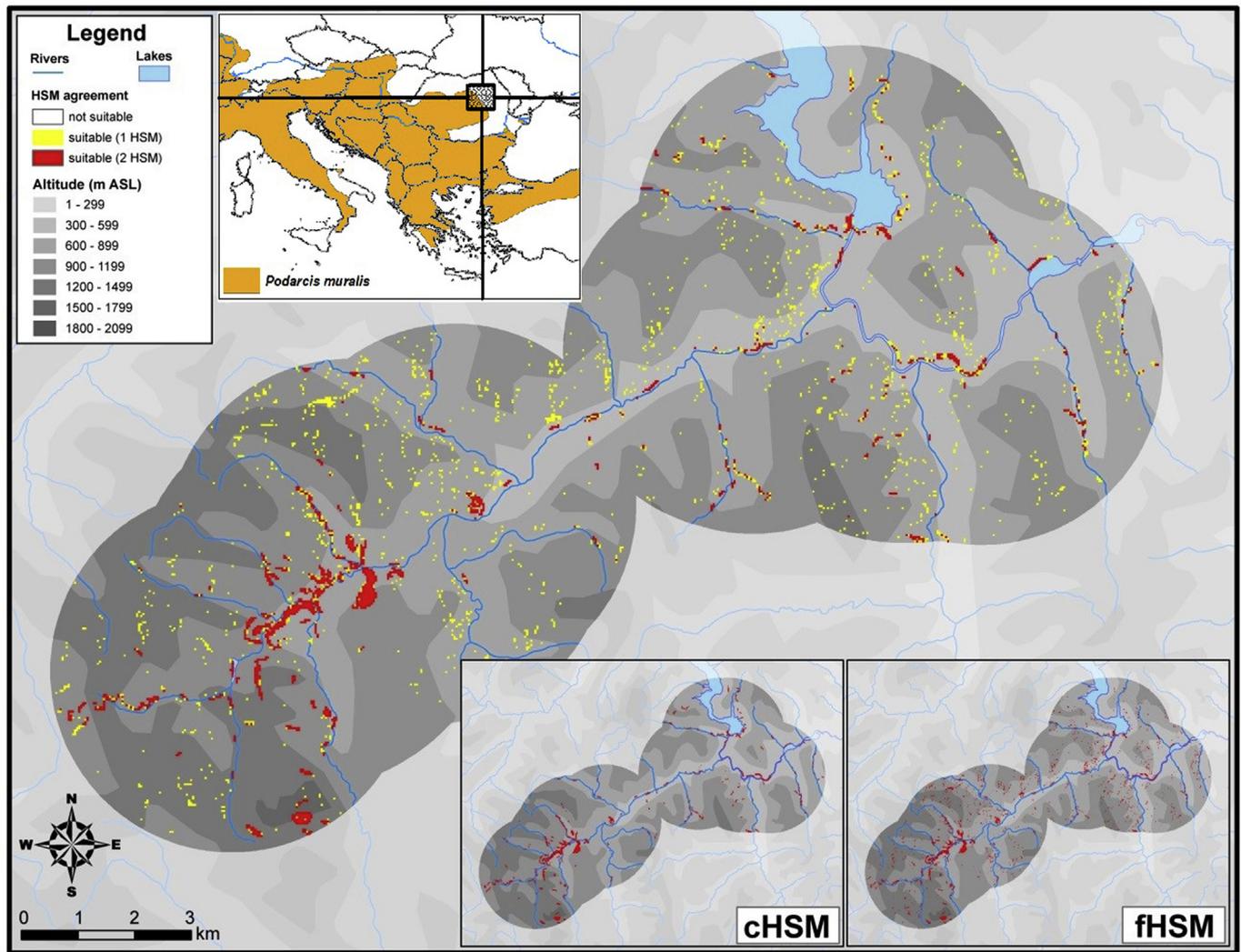


Fig. 1. *Podarcis muralis* habitat suitability agreement model as predicted by the cHSM and fHSM.

Table 1
Confusion matrix used to calculate the threshold-dependent performance of the estimated HSM's (from Franklin, 2010).

		OBSERVED		
		Present	Absent	Sum
PREDICTED	Present	True positive (TP)	False positive (FP)	Total occurrences predicted present
	Absent	False negative (FN)	True negative (TN)	Total occurrences predicted absent
	Sum	Total observed presences	Total observed absences	Total number of occurrences

is independent of prevalence, whereas Kappa can have problems when comparing between models or regions (see Allouche et al., 2006 for details). Therefore, models are evaluated with the results of the TSS, and the remaining accuracy metrics are reported in supplementary tables.

$$\begin{aligned}
 \text{Kappa} &= \frac{(\text{TP} + \text{TN}) - [((\text{TP} + \text{FN})(\text{TP} + \text{FP}) + (\text{FN} + \text{TN})(\text{FP} + \text{TN}))/n]}{n - [((\text{TP} + \text{FN})(\text{TP} + \text{FP}) + (\text{FN} + \text{TN})(\text{FP} + \text{TN}))/n]} \\
 &= \frac{(\text{TP} + \text{TN}) - [((\text{TP} + \text{FN})(\text{TP} + \text{FP}) + (\text{FN} + \text{TN})(\text{FP} + \text{TN}))/n]}{n - [((\text{TP} + \text{FN})(\text{TP} + \text{FP}) + (\text{FN} + \text{TN})(\text{FP} + \text{TN}))/n]} \quad (2)
 \end{aligned}$$

$$\text{TSS} = \text{Sensitivity} + \text{Specificity} - 1 \quad (3)$$

$$\text{CCI} = \frac{\text{TP} + \text{TN}}{n} \quad (4)$$

$$\text{FNR} = 1 - \text{Sensitivity} \quad (5)$$

$$\text{FPR} = 1 - \text{Specificity} \quad (6)$$

where sensitivity is the true positive rate (TP/(TP + FN)), specificity is the true negative rate (TN/(TN + FP)), and *n* is the total number of points.

2.6. Landscape connectivity models

Modeling the landscape connectivity for *P. muralis* was completed in two steps: the first step was creating the cost surface that represents the resistance to movement of the study area; and the second step was to estimate the cost distance values of the landscape, as well as identify the potential corridors and paths that *P. muralis* could use to expand its range and possibly conquer new suitable habitats.

The cost surface was generated using the same environmental variables of the habitat suitability models, but instead of weighting variables for persistence of the species in the habitat, they were weighted for the mobility of the species in that variable. For example, *P. muralis* is likely to have a higher dispersal ability in a pasture, but is very unlikely to establish a population in this type of habitat. After all variables have been weighted for species mobility, we used a geographical overlay to obtain the final cost surface. The final cost surface comprises values from 1 (representing areas that have low resistance to movement for *P. muralis*) to 6 (areas that have high resistance to movement for *P. muralis*). The values in-between represent a gradient of resistance to movement.

The cost distance estimates were calculated using the cost surface and the available occurrence data. The cost distance estimates the shortest weighted distance from each pixel to the nearest occurrence point (nearest source location). Next, we calculated the direction of movement in order to estimate the direction in which *P. muralis* is likely to expand its territory. Finally, we used the Cost Path tool to locate corridors and least-cost paths for *P. muralis* dispersal. This tool ran 35 analyses, each analysis representing a population of *P. muralis* known in the area. The dispersal corridor model was generated as a tool to find the least-cost corridor between the *P. muralis* source populations from the southern part of the study area to the newly conquered area in the north (see Gherghel et al., 2009 for details on this hypothesis). Finally, we ran linear regressions to test which linear landscape feature (river, road, or railway network) best explains the proposed ecological corridor and least-cost paths. All analyses were completed in ArcGIS 10 and SAS JMP 11.

3. Results

3.1. Habitat suitability model evaluation

Because the methods used to estimate the habitat suitability are methodologically different (see the Habitat suitability models section from Materials and Methods), the intent behind model evaluation is not to compare which method is better to estimate the habitat suitability of *P. muralis*; but rather to evaluate the robustness of the HSM's and their ability to predict the empirical data. Furthermore, because the absence of *P. muralis* in a habitat can be due to imperfect detection or because the lizard has not yet colonized that region, we recommend interpreting the model accuracy metrics with caution. Both HSM's performed well at predicting the observed presence of *P. muralis* across all model accuracy metrics (Table 2). We found that generally, cHSM outperformed the fHSM in both Kappa index (0.775 in cHSM vs 0.723 in fHSM) and TSS (0.755 in cHSM vs 0.684 in fHSM). However, because the two models show different patterns, and because the fHSM has a very high predictive power (Table 2) we will discuss the results from both HSM's.

Table 2
Model accuracy metrics for *Podarcis muralis* habitat suitability models.

	cHSM	fHSM
TSS	0.755	0.684
FPR	0.045	0.030
FNR	0.200	0.286
CCI	0.901	0.881
Kappa	0.775	0.723

3.2. Habitat suitability models

We found significant differences in the size and location of predicted suitable habitat for *P. muralis* between the two HSM's. cHSM predicted 2% of the total study area (representing 1301 ha) as suitable (Fig. 1), whereas fHSM predicted 3.1% (presenting 1999 ha) as suitable habitat (Fig. 1). cHSM is the more conservative model, restricting suitable habitat to cliffs and anthropogenic habitats (stone walls along the roads and railways), compared with fHSM which also includes small rocky habitats on steep slopes. Although the fHSM predicted more suitable habitat overall (Fig. 1), areas corresponding to the anthropogenic habitats in the northern part of the study region were predicted to be unsuitable. Both HSM's predicted that in the southern part of the study area, the amount of suitable habitat for *P. muralis* is more abundant than in the northern region (Fig. 1). The model agreement between the two HSM's (Fig. 1) revealed that the available suitable habitat for *P. muralis* is highly fragmented, with only 1.55% of the study area (representing 1000 ha) characterized as suitable. The HSM's were also in agreement on several areas not yet colonized by *P. muralis*, including the areas north and northwest of the Bicaz Dam and along numerous rivers and forest roads (Fig. 1), suggesting potential future routes for habitat expansion.

3.3. Landscape connectivity models

Our models show that there is a relatively high connectivity between the southern and northern populations of *P. muralis* from the study area. The least cost paths for range expansion were found along the valley of the Bicaz River (from north to south) and the Bistrita River (from west to east). This region hosts three main linear features that could be used by *P. muralis* to expand its range: along the river, the road, and the railway. Due to the inability of the least cost path analysis to distinguish which feature is the most likely to be utilized by *P. muralis*, we have included a migration corridor model. The corridor model was best explained by distance from the railway ($r^2 = 0.726$, $P > 0.0001$) (Fig. 1) and the distance from the roads ($r^2 = 0.24$, $P > 0.0001$) (Fig. 2), suggesting that *P. muralis* primarily relies on railways, followed by roads, to expand its territory. On the other hand, distance from rivers ($r^2 = 0.039$, $P > 0.0001$) (Fig. 2) reveals that this is the least likely linear feature *P. muralis* would use to move to new territory; suggesting that the absence of anthropogenic structures would leave *P. muralis* with high resistance to movement in its environment. This might explain the absence of *P. muralis* from the areas north and northwest of the Bicaz Dam (Fig. 1), a predicted suitable habitat that is not connected to the railway system. However, this area is connected by roads and the shore of the Bicaz Lake, which may eventually serve as sufficient corridors for *P. muralis* to colonize these habitats.

4. Discussion

4.1. Habitat suitability modeling

The accuracy statistics from our HSM models reveal high performance in predicting the habitat suitability of our study species, especially across a small area. Although fHSM is often considered the superior modelling approach (Franklin, 2010), our cHSM performed slightly better. That said, both produced excellent accuracy metrics, and the fHSM detected potential habitat that was overlooked by the cHSM. Consequently, we recommend that the researcher consider more than accuracy metrics alone. The researcher's knowledge and experience with the biology of the study organism and the study region can and should play an integral role in model choice and interpretation.

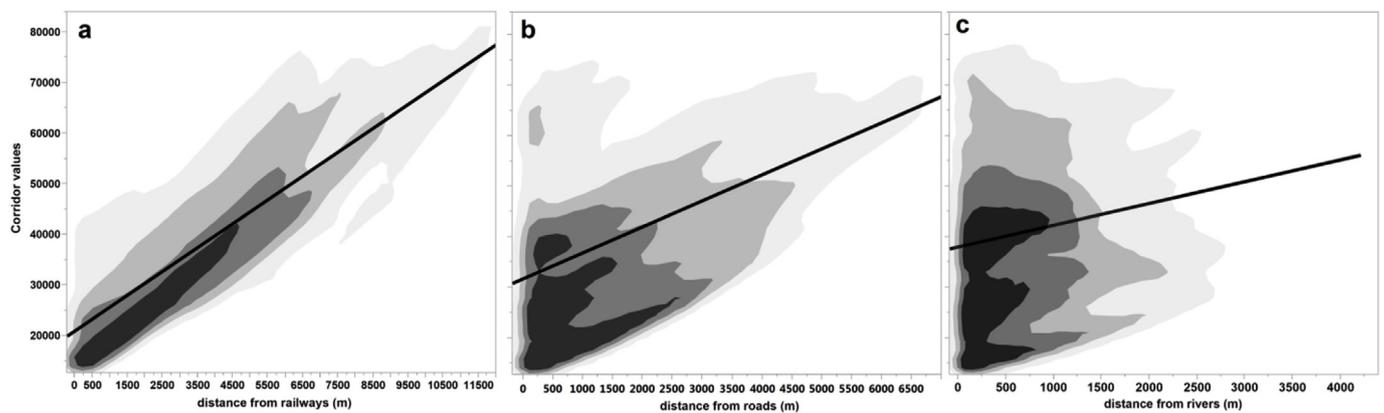


Fig. 2. Regression models showing the patterns of migration across the corridor using the selected linear features: distance from railways (a), distance from roads (b), and distance from rivers (c). The different grey shaded area represents the sampling points used to generate the regression models (light grey is low number of sampling points, whereas dark grey represents greater density of sampling points).

4.2. Species distribution and habitat fragmentation

Species distributions are generally determined by factors such as environment (e.g. climate tolerance), biotic interactions (e.g. competition, predation), and historical factors that influence the availability of corridors (Gherghel et al., 2019; Araújo et al., 2004; Araújo and Luoto, 2007). As the human population grows, so too does anthropogenic activity that changes and fragments the natural environment. For *P. muralis*, a significant chunk of suitable climatic space remains unoccupied. The primary limiting factor for expansion into this territory is likely the lack of migration corridors due to this species' preference for rocky habitat. Anthropogenic transportation networks provide artificial corridors that closely resemble the preferred habitat of *P. muralis*, providing an interesting case study of a lizard benefiting (at least temporarily) from an increase in human-built infrastructure (Figs. 1 and 2). Previous work has established the presence of *P. muralis* on railways and road fences (Covaciu-Marcov et al., 2006; Gherghel et al., 2009; Michaelides et al., 2015; Schulte et al., 2012), but this is the first attempt to characterize the significance of these structures as ecological corridors to mediate dispersal across the landscape. Our results demonstrate that suitable habitat for *P. muralis* is highly fragmented across the landscape, and in the absence of manmade corridors, connectivity between these habitats is severely limited.

4.3. Habitat availability vs. occupancy

The amount of habitat available in the study region is estimated to be between 1301 ha and 1999 ha, with a refined estimation based on the model agreement to 1000 ha (Fig. 1). However, our data shows that only a third of these available habitats are currently inhabited by these lizards (Table 2). Moreover, most of the occupied habitats are along at least one potential migration corridor (e.g. railway, road, or river). These data agree with previously published distribution maps (Gherghel et al. 2008, 2009) for *P. muralis* in the region, but demonstrate that the amount of available habitat is much greater than the habitat these lizards occupy. It should be recognized, however, that the lack of corridors is not the only potential factor limiting dispersal. There is no evidence that the lizards dispersed (yet) to areas outside of significant dispersal corridors along railways (Figs. 1 and 2), which might occur as climate change, rivers, and lakeshores open new opportunities for dispersal. Other interspecific interactions (such as competition, predation, and food availability) may limit the capacity for *P. muralis* to colonize these areas. Further, despite the best efforts of the field surveys, we may fail to detect this species in areas where they do in fact exist.

4.4. Landscape connectivity and ecological corridors

Previously, Gherghel et al. (2009) proposed that *P. muralis* may have utilized railways to disperse from the southern to the northern regions of the study area. However, Gherghel et al. (2009) did not estimate the suitable habitat available to *P. muralis*, nor did it consider other possible routes of migration for this species. Our analyses clearly demonstrate the existence of suitable habitat beyond the current range of *P. muralis*, and we can expect new incidences of colonization to occur. Due to the degree of fragmentation, we would expect these colonization events to occur in a series of steps dictated by the availability of dispersal corridors. Our study suggests that the scenario proposed by Gherghel et al. (2009) is highly plausible, but not complete. Specifically, we show that the availability of railway corridors is the primary driver for *P. muralis* expansion across this lizard's fragmented habitat. It is not the only corridor, however, with roads and rivers acting as a viable, though not optimal, means of dispersal. Tools that estimate the landscape connectivity, least-cost paths, and habitat corridors help us to predict the destination and mechanism of future colonization events. In this scenario, we expect colonization to occur in the northwestern unoccupied suitable habitats due to the short distance from existing populations combined with the availability of anthropogenic and natural corridors.

A number of reptilian species have been documented on railways, including *Natrix tessellata* (particularly near water) (Strugariu and Gherghel, 2008; Strugariu et al., 2016), *Coronella austriaca*, and *Vipera nikolskii* (Strugariu et al., 2008b). Whether these railways play a role in dispersal for these species is unknown. Consequently, future studies will seek to establish the potential utility of these manmade structures for dispersal across a fragmented landscape in additional species. Nevertheless, we cannot neglect the potential negative impact of these railways and roads, which themselves may fragment viable habitat, kill numerous individuals stricken by moving vehicles, and add significant pollution and waste to the surrounding environment, and facilitate the dispersal of potentially invasive species. Recent records also confirm that other reptile species (i.e. *Podarcis sicula*, *Podarcis muralis maculiventris* and *Mediodactylus danilewskii*, in Bucharest, Romania - Ciofleac V. 2019, personal communication) have recently been found outside of their range, north of Danube, in business and economic centers (i.e. Bucharest, Romania), and their presence poses questions regarding their origins. Considering our results, we can certainly hypothesize that these new findings of *Podarcis sicula*, *Podarcis muralis maculiventris* and *Mediodactylus danilewskii*, in Bucharest, Romania can be explained either by passive (intentional or nonintentional) or active means (such as *Mediodactylus danilewskii*, which could disperse (although, unlikely) along transportation routes or passively (intentional or

nonintentional)). However, these hypotheses need to be validated by future studies, when more information is available.

4.5. What is the potential impact of this “invasion”?

Podarcis muralis has previously been characterized as a species with high invasiveness potential (Schulte et al., 2013). This is an accurate representation of this species in Mediterranean Europe, where it will compete with endemic or range-restricted wall lizards (Schulte et al., 2012). Its impact in the Carpathian Mountains, however, will be limited by niche segregation and differences in habitat preferences with locally abundant species like *Zootoca vivipara* (Common Lizard), *Lacerta agilis* (Sand Lizard), and *Lacerta viridis* (Green Lizard) (Gherghel et al., 2008). These lizards have very broad ranges (*Z. vivipara*, for example, inhabits most of northern Eurasia, and extends as far east as Japan) and primarily inhabits pastures and wet meadows. *Lacerta viridis* will overlap with *P. muralis* in rocky habitats, but due to a significant size difference is more likely to become prey than a competitor. Therefore, much like the “invasion” of the Mediterranean Gecko in North America, we suspect the “invasion” of *P. muralis* will fill an unoccupied niche.

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