



The relative influence of habitat density, landscape configuration and spatial sorting on population expansion: a simulation test

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Abstract

Context Population expansion into new areas is a common phenomenon resulting from changes in ecological conditions or human-assisted introduction. In the latter case, populations spread into areas where they did not evolve causing various ecological and socio-economic impacts. Spatial sorting (*i.e.* the enhanced dispersal capacity over time at the periphery of an expanding range) and landscape are two major factors affecting spread dynamics in expanding populations.

Objectives While both factors have been frequently studied independently, their relative influence to

modulate the spread rate of expanding populations has been significantly unexplored. We addressed this issue through a modeling approach.

Methods We simulated the spread of an invasive amphibian, *Xenopus laevis*, in various landscape windows within and around its colonized ranges in western France. Using UNICOR, we ran colonization simulations on 30 km × 30 km windows of an experimentally parameterized resistance layer at three intensities of spatial sorting.

Results Habitat (pond) density and spatial sorting positively affected the rate of population expansion in the windows and interacted: higher spatial sorting and pond density increased the invaded area, number of colonized ponds, and maximal traveled distance per time unit. In contrast, none of the four landscape configuration metrics improved the models, suggesting that they have limited influence on population expansion. Thus, the effect of spatial sorting on population spread was enhanced by pond density but not by landscape configuration.

Conclusions Our results highlight the importance to jointly consider habitat density and spatial sorting in predictive modeling of the spread process in expanding populations, particularly for biological invaders.

Keywords African clawed frog · Alien species · Biological invasion · Connectivity model · Range expansion · *Xenopus laevis*

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Introduction

The expansion of populations may happen for many reasons. It occurs when an ecological barrier like a mountain range or a large body of water is overcome (Paulay 1994), when the distribution of competitors or enemies shifts, as observed in moving hybrid zones (Engler et al. 2013), or when ecosystem changes offer new suitable conditions for the species (Lake 2003). These natural processes are currently exacerbated by global changes, for instance when shifts of climatic zones lead to the colonization of new land or marine areas previously unsuitable for species (Parmesan et al. 1999). Additionally, human-assisted translocations of organisms have led to the surge of introduction of alien invasive populations across the globe. The spread of these populations generates increasing costs for biodiversity and human societies worldwide (Gallardo et al. 2016; Seebens et al. 2018; Diagne et al. 2021). For these reasons, there is a broad interest in investigating the processes underlying population expansion in various contexts and at the demographic, genetic, or ecological level. The identification of factors that promote or hamper the movement at the range front is pivotal to the understanding of range dynamics. From a management perspective, it could help to anticipate and mitigate the spread of alien invasive populations (Phillips et al. 2016).

Spatial sorting and landscape structure can largely influence the dynamics of spread (Phillips et al. 2006; Pachevsky and Levine 2011; Williams et al. 2016b; Ochocki and Miller 2017). Other factors may contribute to expansion dynamics such as the genetic makeup of the expanding population (endogenous factor) (Hargreaves and Eckert 2019) or the presence of other species (exogenous factor) (Svenning et al. 2014). However, we will not address them in this study. Spatial sorting is an endogenous factor that is defined as the increase in dispersal capacity over time occurring at the front of an expanding range. According to the “Olympic village” hypothesis, the best dispersers meet and mate at the range front so that their progeny holds above average dispersal capacity (Phillips et al. 2008). The process is iterative and each new generation of individuals dispersing beyond the current front will produce even better dispersers so that the expansion rate increases over time (Burton et al. 2010). Spatial sorting is generally

viewed as a pull wave driven by increasing dispersal capacity at the range periphery, as opposed to a push wave generated by an outward demographic growth (Chuang and Peterson 2016). It has been observed in groups as diverse as plants, insects or vertebrates (Hughes et al. 2003; Huang et al. 2015) and at a continental scale (Urban et al. 2008) as well as at a local scale (Courant et al. 2019).

Landscape structure is an exogenous factor to organisms and populations. For many continental species, landscape determines the way individuals move across the land. The various components of the landscape, as determined by land use, impose different costs on movement. Some landscape features physically impede displacement or are avoided because of higher risks of meeting enemies, predators in particular, while traveling across other features may be carried out at low physiological expenses or with limited chance of meeting hazardous situations (Bonte et al. 2012; Nowakowski et al. 2015; Vasudev et al. 2015). Resistance cost maps are spatially-explicit quantifications of these costs across entire areas (Zeller et al. 2012). They are used as raw information to model connectivity, *i.e.* the most likely paths individuals will travel across the landscape (Rayfield et al. 2011; Cushman et al. 2013). Eventually, the capacity of individuals to colonize new areas and the population to spread will largely depend on the ability to reach new suitable areas through the landscape and complete their life cycle (Gustafson and Gardner 1996; Berggren et al. 2001; With 2002).

Highly resistant landscape features, by strongly reducing the probability of migrants to reach a suitable habitat, may promote the evolution of reduced dispersal (Schtickzelle et al. 2006; Cheptou et al. 2008). However, these constraints may be overcome if the movement capacity of individuals increases over time, which may occur at the edge of expanding populations due to spatial sorting. We can thus predict that spread dynamics result from the intensity of spatial sorting (the rate of increase of dispersal per generation) and landscape structure. An important piece of information to the understanding of expansion dynamics is to assess the relative contribution of spatial sorting and landscape to population spread. Turning this question into an insightful modeling exercise is not an easy task because of the diversity of landscape structures and

dispersal capacities of biological species. A less ambitious but still informative approach would be to simulate population expansion for a species with known dispersal capacity across a well-defined area. This may allow estimating the relative contribution of spatial sorting and landscape structure, although for a limited set of conditions, and provide information to forecast the expansion of the focal population. Previous studies have investigated the effect of habitat fragmentation on the evolution of dispersal (Schtickzelle et al. 2006; Cheptou et al. 2008; North et al. 2011; Williams et al. 2016a) or range expansion in non-evolving populations (Hodgson et al. 2012; Bocedi et al. 2014; Barros et al. 2016), but less attention has been paid to the interplay between landscape and dispersal evolution in expanding populations (but see Urquhart and Williams 2021). These studies commonly used artificial binary landscapes (habitat vs. matrix) and did not consider the various resistance costs incurred by organisms moving across more realistic landscapes. Hypotheses may not be easily stated unless considering such cases. In binary landscapes, the distances between habitat patches and the fixed resistance cost of the inter-patch matrix mostly matter, whereas in more natural situations the average size and shape of each landscape feature is also important. Further, if for a constant level of fragmentation across an area, spatial sorting is expected to increase connectivity at each increment of the dispersal capacity, predictions are less straightforward when landscape configuration is not constant. This happens when the average size and spatial distribution of each feature, each imposing its own resistance cost on movement, change across the study area, for instance because of different soils or altitudinal variation.

Herein, we carried out such a study by simulating the expansion of the African clawed frog *Xenopus laevis* in one of its main invasive ranges in Europe (Measey et al. 2012). The species is a major model in biological sciences but, unfortunately, it is also recognized as one the three major invasive amphibians in the world (Measey et al. 2016). It has been introduced in several continents because of its use in biomedical research and as a pet (van Sittert and John Measey 2016). Both its global current distribution (including in captivity) and climate changes make it likely that novel populations will be introduced and become invasive in many more parts

of the world (Measey et al. 2012). We used published quantification of dispersal capacities (De Villiers and Measey 2017), experimentally determined resistance costs (Vimercati et al. 2021) for the population investigated here, and resistance cost layers extending beyond the current invasive range (Vimercati et al. 2024). We then simulated population expansion from different starting windows, i.e. square cells of the same area sampled from the resistance cost layer, and let the populations spread across the landscape.

We estimated the dynamics of spread and tested the relative influence of various levels of spatial sorting intensity (SSI), habitat density (i.e. pond density), and landscape structure in the invasive ranges of *X. laevis* and their close surroundings in western France and Bordeaux area. In a metapopulation, isolation, habitat patch size and landscape configuration affect the fraction of occupied patches (Hanski 1994; Gustafson and Gardner 1996). Pond density is correlated to the mean distance to the nearest habitat and is a proxy of isolation. Landscapes with higher ponds densities are expected to be colonized faster. In our system, habitat patches are ponds which are very small (tens to hundreds of square meters for most of them) relative to size of other landscape components. Therefore, we did not consider pond size. We quantified landscape structure through aggregation measures and area and edge metrics. Larger aggregation reflects simpler landscape with larger patches in such an agricultural context. Higher aggregation level of non-habitat is thus expected to increase inter-habitat patches distance, reduce connectivity and slow down expansion. Landscape complexity is also reflected by the length of edges between patch types and the variation in patch size. Agricultural intensification favor larger parcels and more homogeneous landscapes with less edges and increase distances between ponds. The influence of edges on richness, species interaction or dispersal is largely described but remains difficult to predict as opposite effects have been reported (Ries and Sisk 2004; Porensky and Young 2013). However, within the range of landscapes in the study areas, less edges and higher variation between patch sizes are generally expected to decrease expansion rate, although the actual effect may depend on the relative resistance costs of the various patch types to cross and arrangement of patches (Gustafson and Gardner 1996). We also predicted an interaction between

spatial sorting and landscape structure as the slope of the relationship between proxies of expansion and landscape configuration may not depend on SSI in an additive way.

Methods

Model

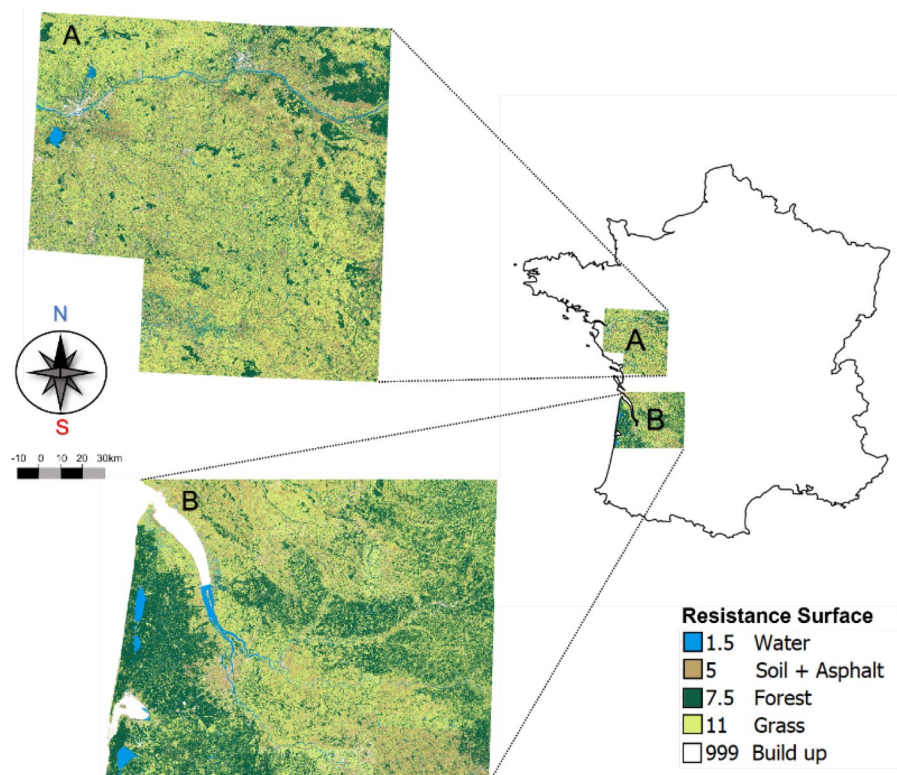
The African clawed frog *Xenopus laevis* is a frog from southern Africa that has been introduced in western France in the early 80's to a single site in Deux-Sèvres. The alien population has been expanding since then (Fouquet and Measey 2006), impacting amphibian (Courant et al. 2018a) and invertebrate communities (Courant et al. 2018b) and is now covering more than 4000 km² (Vimercati et al. 2020). A new population, about 230 km away from the former, has been discovered in 2015 in a single pond near Bordeaux (Fig. 1). Both areas are subjected to an oceanic climate (Joly et al. 2010) and a land use that mostly consists of cropland, grassland, forest, vineyards and urban zones (Meersmans et al. 2012). Both areas also host

a high density of water bodies due to the historical creation of artificial ponds for cattle breeding in Deux-Sèvres and also of larger ponds resulting from material extraction around Bordeaux.

Resistance cost layer

To compute resistance cost layers for each area, we used resistance costs that were experimentally measured for the invasive population of *X. laevis* in Western France (Vimercati et al. 2021). Accordingly, we set resistance to 1.5 for water, 5 for soil and asphalt, 7.5 for forest, 11 for grass, 999 for buildings. Using a classification of SPOT 6/7 satellite images, we mapped these land use types across two areas (dimensions) that expanded beyond each of the two current ranges. The two areas being essentially flat we did not use topography in the computation of the layer. We then built the resistance map by assigning resistance costs of the corresponding land use type to each pixel (Fig. 1). The whole modelling approach has been described elsewhere (Vimercati et al. 2024). We thus had access to a resistance cost layer covering 50,120 km² (24,940 km² for Western France

Fig. 1 Overview of the resistance maps used for this study. Map of France with a projection of the two resistance maps that cover the two study areas: Western France (A), Bordeaux area (B)



and 25,180 km² for Bordeaux area) with a spatial resolution of 5 m (Fig. 1). However, as noted in this study, there is an uncertainty about the resistance cost of lotic habitats, *i.e.* rivers and streams, which was set to 1.5 then. To account for this uncertainty, we built two additional resistance layers, with respectively a higher (3.0) and lower (0.5) resistance cost for rivers, and keeping the same values for all other categories. This assumes that moving across a grass pixel (the most more resistant substrate) is respectively 3.7, 7.3 (original value), and 22.0 times costlier for frogs than moving across a river pixel.

Simulation procedure

To shorten computation time, resistance layers were split into smaller and non-overlapping 30 km × 30 km windows. Incomplete windows located at the edge of the layer were discarded. In total, we retained 25 windows, 14 of which were located in the Western France range and 11 in the Bordeaux range. Each window had a unique landscape pattern and is considered as an independent replicate. Computation for resistance layers were carried out using the R-package *raster*. To simulate window colonization by the frog, we used the software UNICOR (Landguth et al. 2012), which has already been effectively used for connectivity studies on amphibians (Compton et al. 2007). The software is based on “Dijkstra’s shortest path algorithm” (Dijkstra 1959) in combination with a resistant (dispersal) kernel approach so that it integrates the dispersal capacity of the focal species. UNICOR is used as a tool to identify corridors and model population connectivity. Starting points were set at each step of the simulation. The first starting point was the pond most proximal the center of the window from which the population was allowed to expand across the resistance layer. Prior to the next expansion step, 50 percent of potentially accessible uninvaded ponds were extracted at random and defined as new starting points using an automated R-script, wherein the probability of colonization was dependent on the likelihood of accessibility as derived from the dispersal kernels computed with UNICOR. The process was iterated until the twenty first step, or halted earlier if the population had reached the window border. We used QGIS 3.28.0 (QGIS Development Team 2023) to identify the first starting points by hand and the R

packages *dplyr* and *raster* for the R script. We set the maximal cumulative distance per step to 11,032. This is the maximal resistance cost of all cells that can be crossed in one step. This value was estimated from a capture-recapture experiment in the Western France area (Courant 2017). The Gaussian function was used as the Kernel density estimation of the dispersal function to buffer the length of the outcoming paths. Three runs with different intensities of spatial sorting, which categorical variable is hereafter referred to as SSI, and the same starting point were computed. To simulate spatial sorting, we increased the maximal traveled distance by either 2.5% or 5% each step. For comparison, the shift in distance of the invasive range border of the Cane toad in Australia increased by be about 2.5% per year (Phillips et al. 2008). In the control condition, we kept the initial traveled distance unchanged throughout the simulation.

Landscape descriptors

Beyond spatial sorting, range expansion is expected to depend on the characteristics of the landscape individuals move through. We considered two components of landscape which have been described elsewhere (Vimercati et al. 2024). The first is habitat density, quantified here as pond density (number of ponds per km²). Raw data were obtained from BD Topo® provided by the French National Geographic Institute from Géoportail (<https://www.geoportail.gouv.fr>). The second is landscape configuration, *i.e.* the way in which various features are distributed across the landscape. The features are those described in *Resistance cost layer* section. By using the R package *landscapemetrics* (Hesselbarth et al. 2019), we computed four indices: cohesion, contagion, edge density and the coefficient of variation of patch area that quantify different aspects of the landscape. Cohesion (`lsm_c_cohesion`) assesses whether patches of the same class are aggregated or isolated. Contagion (`lsm_l_contag`) gives the probability that two pixels drawn at random in a cell belong to the same class of land use and is another form of aggregation. Edge density (`lsm_l_ed`) represents the total length of edges over a cell area. Area.cv (`lsm_l_area_cv`) provides the coefficient of variation of all patches areas in the cell. We checked the level of correlation between these five predictors in our sample of windows. Pearson correlations were

low ($-0.296 < r < 0.131$) so we considered these descriptors of the window landscape as independent, which was visually confirmed by the representation of a Principal Component Analysis (PCA) on the five predictors described above using R packages *FactomineR* and *factoextra* (SI Figure S1). All predictors were standardized prior to analysis. The first three principal component represented 72.47% of variation.

Statistical analyses and visualization

We estimated the effect of spatial sorting intensity (SSI), habitat density (pond density) and landscape configuration (cohesion, contagion, edge density, area cv) on colonization speed. As expansion proxy we computed for each window the slope of the relationship between time (number of steps) and the colonized area. We also computed two other proxies (maximal travelled distance and cumulative number of colonized ponds) in the same way. However, the correlations between the three proxies were very high within each level of SSIs ($0.705 < r < 0.902$) and river costs ($0.724 < r < 0.951$) (SI Figure S2). For clarity, we present below only the results for colonized area, which is the most informative about the expansion process.

We then computed a single linear mixed model with a Gaussian distribution of errors using the R package *lme4*. The proxy for colonized area was the response variable and SSI (3 levels), river cost (3 levels), pond density and the four landscape descriptors were fixed predictors. Additionally, we included two-way interactions between SSI and all other predictors. Window identity was considered as a random factor since each window was used for simulations at all SSIs (control, +2.5% and +5.0% dispersal) and river costs (0.5, 1.5, 3.0). We then carried out model averaging using the R package *MuMIn*, selecting a subset of models with $\Delta AICc < 4$ to the best model. Model diagnostics to the full model were carried out using the package *DHARMA* and exhibited no significant deviation. We also used R package *performance* to estimate model fit for mixed models (Nakagawa et al. 2017). We computed marginal R^2 (fixed effects), conditional R^2 (fixed effects and random effects), and intra-class correlation ICC (random effects) for the full model.

Graphs representing models were plotted using the R packages *ggplot2*, *ggeffects* and *gridExtra*. In addition to the statistical analysis, we visualized the colonization process in each window. Cumulative resistance layers of UNICOR outputs were created, saved and merged for each window and step, resulting in an image for each step and window, which compares the difference between each SSI. Some examples are provided as supplementary information (SI Figure S3).

Results

We effectively simulated window colonization (SI Figures S3 and S4). The steps at which simulations stopped depended on the window and SSI when the window border was reached. Many simulations ended before reaching the last step. Thus, we needed to optimize the trade-off between a larger sample size of windows and a larger number of time steps during the simulation to compute the regression of expansion proxies against time steps. Figure 1 shows for the resistance layer used in Vimercati et al. (2024) that the relationship is not linear. Thus, we applied a square-root transformation to the response variables (expansion proxies), which appropriately linearized the relationships across the range of step numbers. We then computed the regression on simulation data up to the ninth step to obtain the largest sample size of windows ($n=21$). Four windows (BDcell11, BDcell16, BDcell25, WFcell28; BD and WF stand for Bordeaux area and Western France respectively) were excluded from the final dataset because colonization halted at step one or two for at least one SSI, generating missing values in the dataset and preventing their use in our mixed model. For the first window (WFcell28), colonization did not occur regardless of SSI. For the second window (BDcell16) colonization progressed, but not to the window border, and only at the lowest SSI. For the two remaining windows (BDcell11, BDcell25), colonization was halted at the two lowest SSIs, although it proceeded to the window edge for the simulation at the highest intensity (SI Figure S4).

The predictors explained a large variation of the expansion proxy as $\Delta AICc$ between the best and the null model was substantial (296.55). Model fit for the full model was good (marginal

Table 1 Model selection table for models estimating the relationships between an expansion proxy (slope of the colonized area over time step), and predictors of spatial sorting intensity (SSI), river resistance cost (riv.cost), pond (p.density) and landscape configuration (contagion = contag, cohesion = cohes, edge density = edge, area cv = area. All models with $\Delta AIC < 4$ to the best model have been included in the model subset

Model (AIC _{c null model} = 296.55)	k	logLik	AIC _c	AIC _c	Weight
SSI + riv.cost + density + contag + contag:SSI + density:SSI	13	90.02	- 152.0	0.000	0.306
SSI + riv.cost + density + density:SSI	10	85.66	- 150.1	1.866	0.121
SSI + riv.cost + density + contag + edge + conta:SSI + density:SSI	14	90.22	- 150.0	1.941	0.116
SSI + riv.cost + density + area + conta + conta:SSI + density:SSI	14	90.20	- 150.0	1.974	0.114
SSI + riv.cost + density + cohes + contag + conta:SSI + density:SSI	14	90.04	- 149.7	2.294	0.097
SSI + riv.cost + density + edge + density:SSI	11	86.05	- 148.6	3.349	0.057
SSI + riv.cost + density + contag + density:SSI	11	86.05	- 148.6	3.356	0.057
SSI + riv.cost + density + area + density:SSI	11	85.82	- 148.2	3.806	0.046
SSI + density + contag + contag:SSI + density:SSI	11	85.75	- 148.0	3.948	0.043
SSI + riv.cost + density + area + contag + edge + contag:SSI + density:SSI	15	90.39	- 148.0	3.957	0.042

$R^2=0.841$, conditional $R^2=0.958$, Intra-class coefficient=0.738). Ten models had a ΔAIC_c lower than four and were kept in the final subset to carry out model averaging (Table 1). All predictors remained in the average model but their effects and importance varied greatly (Fig. 2, SI Table S1). SSI, pond density and their interaction were present in all ten models. They all exhibited positive estimates and highly significant p-values ($p < 0.001$). Higher pond density and SSI increased the speed at which cells were colonized. The positive estimates for the interaction between pond density and SSI reflect the acceleration of colonization speed with higher values of these two predictors.

River resistance cost was present in nine models. Logically higher resistance cost would reduce colonization speed. However, only the highest resistance level differed from the others (Fig. 2, SI Table S1). Unlike SSI, we detected no interaction with pond density. Furthermore, the size of main effects was about an order of magnitude lower than for river cost than for SSI. The four landscape predictors were present in fewer models (1–7) as main effects or in interaction with SSI for contagion. The effect sizes were one to two orders of magnitude lower than SSI’s and the estimates did not significantly differ from zero ($0.216 < p < 0.951$), highlighting their limited

contribution to the variation of the expansion proxy (Figs. 2 and 3, SI Table S1).

Another way to highlight the different responses to landscape configuration and habitat density is to analyze the relationships between each of these environmental predictors and the maximum of steps ran by the simulation. Here, we considered the 25 initial windows and the response at intermediate SSI (1.5). Figure 4 illustrates these relationships. The two windows for which the simulation stopped as soon as step 2 are clearly two outliers that cannot be explained by our predictors. Nevertheless, results show a negative relationship with pond density (linear regression; 25 windows: $F_{1,23}=2.802$, $p=0.108$; two outliers excluded: $F_{1,21}=25.56$, $p < 0.001$) but not with the four landscape configuration predictors (linear regression; 25 windows: all, $p > 0.113$; two outliers excluded: all $p > 0.320$). Results for all settings of spatial sorting are presented as supplementary information (SI Figure S5).

Discussion

According to our predictions, we expected SSI and landscape structure to jointly influence the dynamics of colonization. After effectively simulating the colonization of landscape windows by *X. laevis*

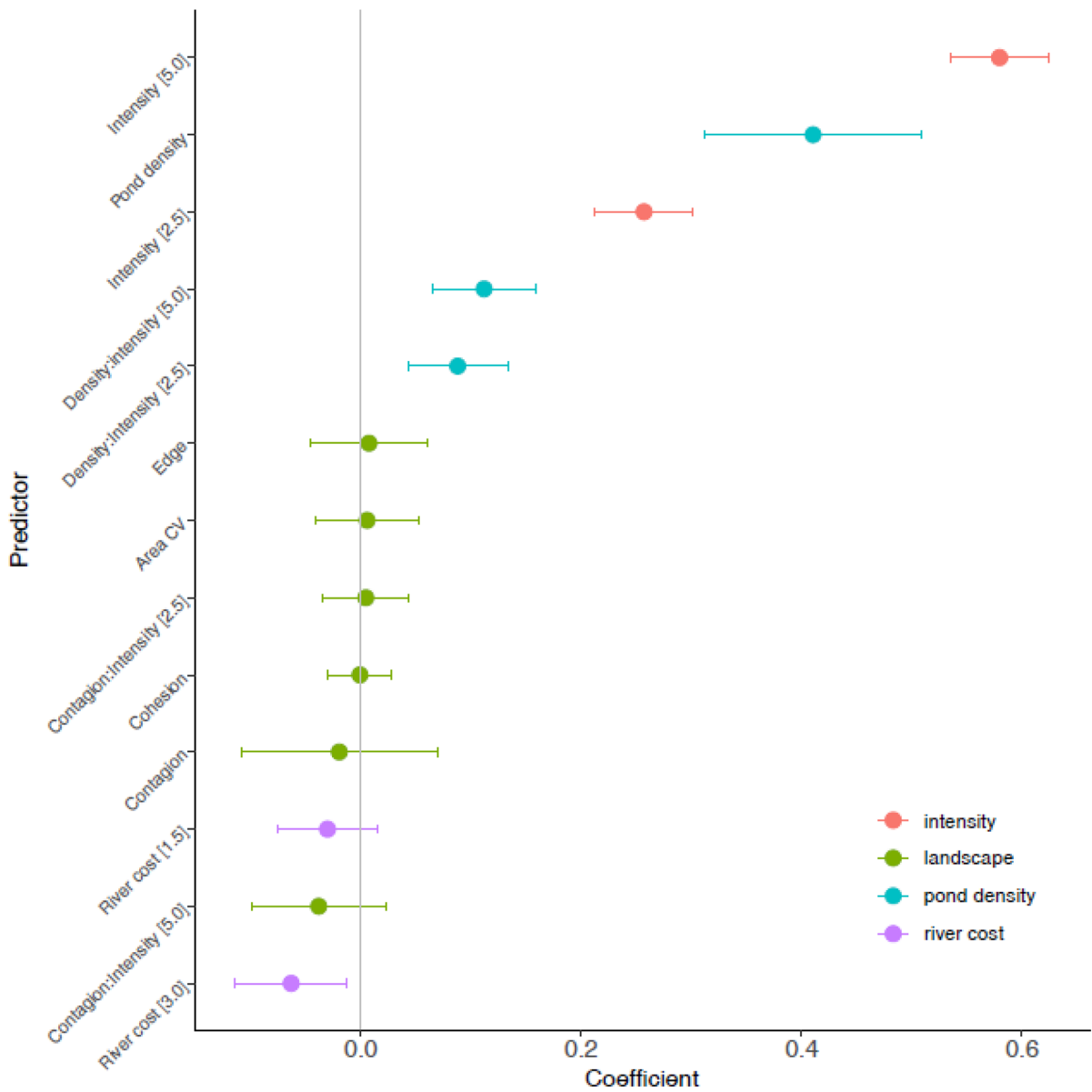


Fig. 2 Effects of spatial sorting intensity, pond density, river resistance cost and four landscape descriptors (cohesion, contagion, edge density, area cv) on colonization speed,

expressed as the slope of the regression of the colonized against time step. Coefficient have been estimated using model averaging

in both areas, we observed a major effect of spatial sorting on population expansion, underlined by the fact that this predictor was included in all best models. Increasing values of spatial sorting led to faster colonization, as shown by change in model estimates between levels for the colonization proxy (colonized area). More surprisingly, we detected no effect of landscape configuration on the colonization

process. None of the four descriptors came close to the explanatory value of SSI. Such a result may be due to the genuine low importance of landscape configuration in the colonization process, which may occur if the scale of movements is large enough so that colonization of novel habitats is not impaired by the landscape grain. An alternative explanation is that the space of landscape parameters was too

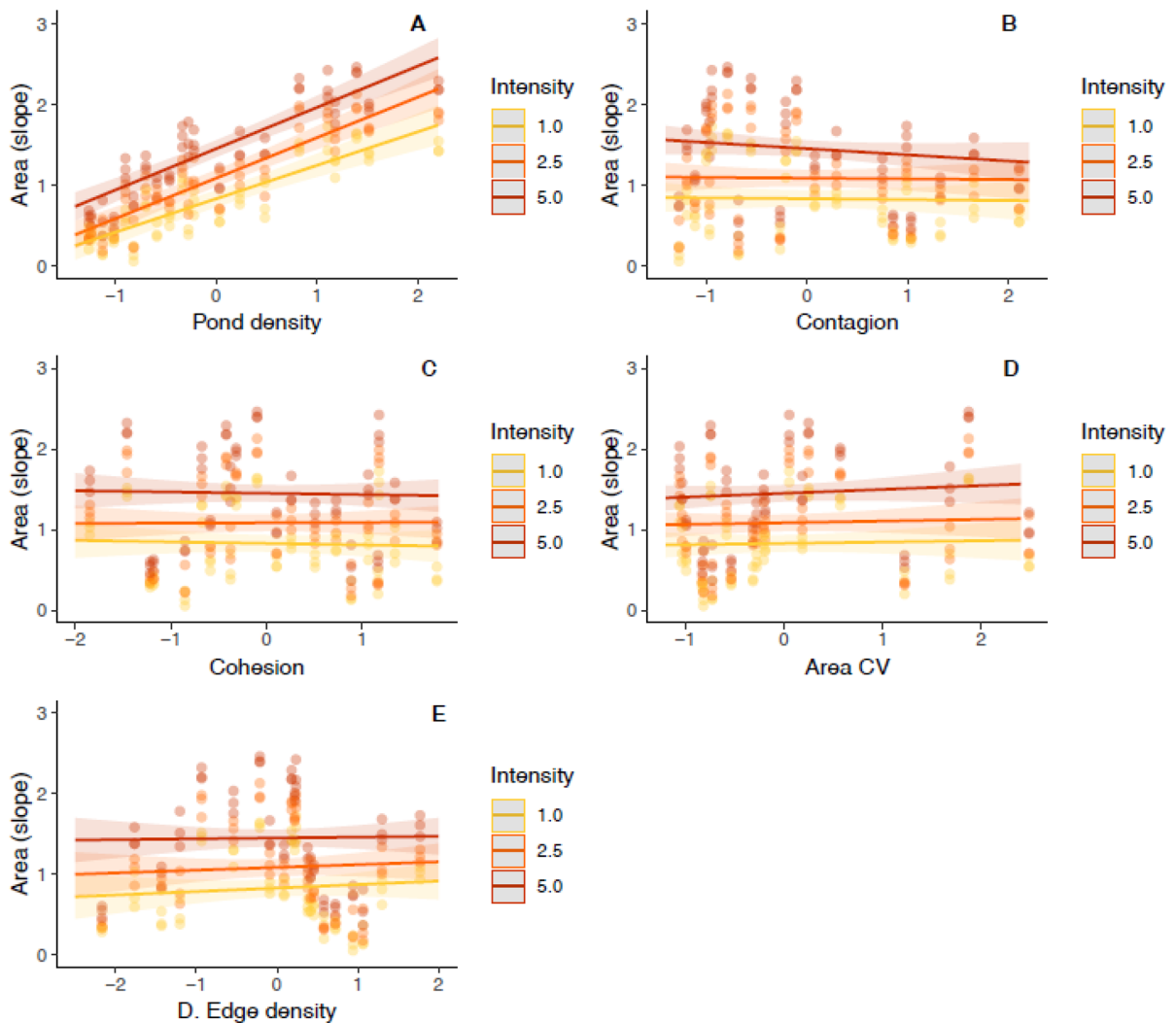


Fig. 3 Effect of spatial sorting intensity and pond density (A), cohesion (B), contagion (C), edge density (D), coefficient of variation of patch area (E) on the area colonized per time step. Three levels of spatial sorting have been selected that represent an increase in 2.5% (2.5), 5% (5.0), or no change

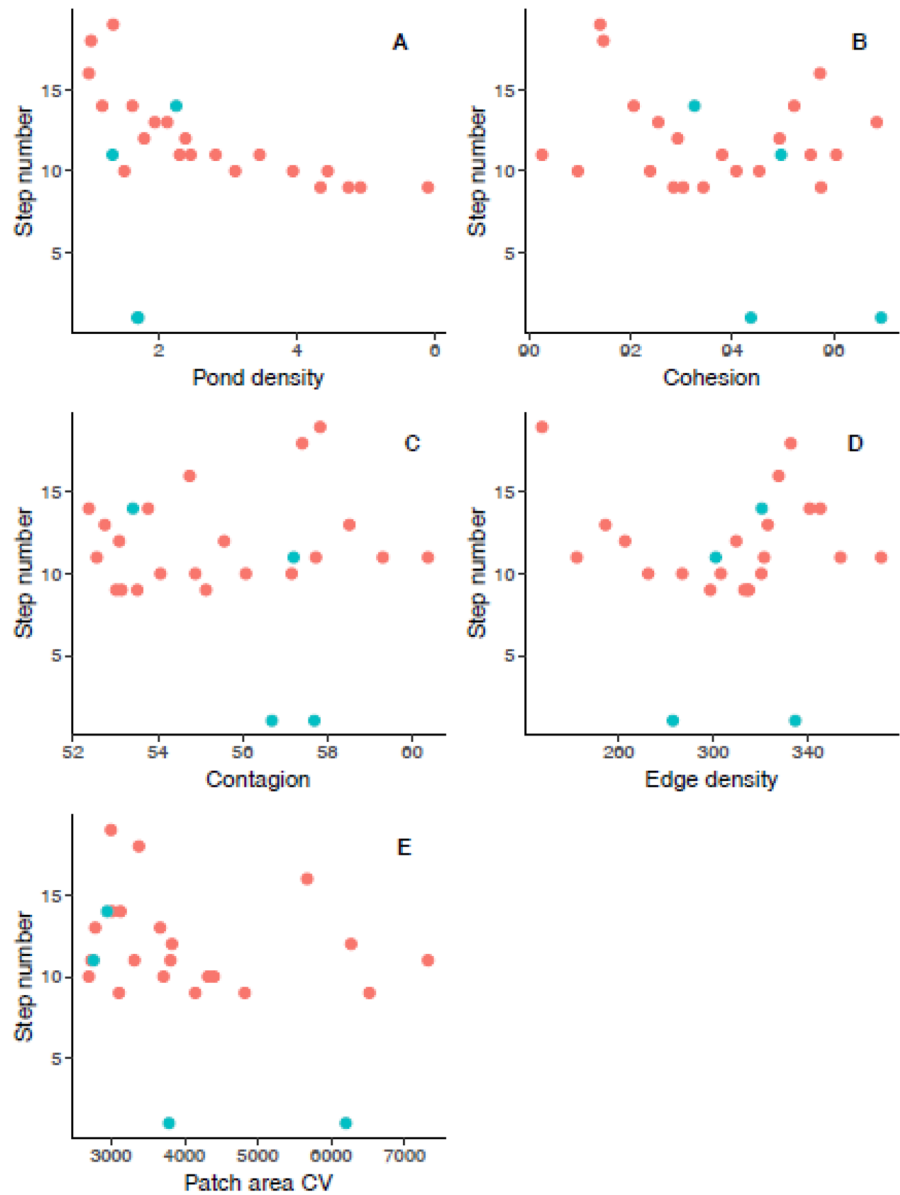
(1.0) in dispersal capacity per time step. Results are shown for the medium river resistance cost (1.5). Note that only for pond density is the relationship statistically supported. The lines represent model outputs for visual comparison, regardless of their statistical significance

narrow. However, this possibility seems improbable. First, we ran simulations across two study zones (Western France and Bordeaux) where landscapes have different historical trajectories and current socio-economic drivers. Second, dominant land use and practices vary locally across each zones, as areas homogeneously covered by the same feature (crop, forest, vineyard) are juxtaposed to areas where features alternate over smaller spatial scale (a bocage landscape where mostly pastures are separated by

hedgerows). Supporting this view, we found that the number of steps to reach the window border was also very variable.

In contrast to landscape configuration, pond density interacted with SSI for the expansion proxy. Slopes modelling the relationship between pond density and the colonized increased with SSI, which corresponds to an accelerating effect of the colonization process due to this interaction. This result might have a straightforward mathematical

Fig. 4 Relationships between the maximum number of steps ran by simulations for habitat density, expressed as pond density (A) and the four predictors of landscape configuration, namely cohesion (B), contagion (C), edge density (D), coefficient of variation of patch area (E). Results are shown for all 25 windows for which simulations were carried out and at the largest intensity of spatial sorting (5.0) and medium river resistance cost (1.5). The 21 windows kept in the analysis are in red. The four windows in blue were discarded because colonization stopped before step 9 at any of the three spatial sorting setting (see text). The graphs for the two other spatial sorting setting are provided as supplementary information (SI Figure S5)



explanation. Considering a binary landscape with a homogeneous density of habitat, the area that can be reached from a starting point, and thus the number of habitat patches, increases with the square of dispersal distance. Given this relationship, we would expect a similar pattern in a more realistic landscape, even if colonization paths are not straight lines. Therefore, habitat density appears, in our situation, a much stronger predictor of range expansion than descriptors of landscape configuration but its effect cannot be estimated without considering the influence

of spatial sorting. To be clear, this result implies that the expected relationship between pond density and expansion proxy in a newly colonized area will depend on the number of dispersing steps away from the introduction site. The older the invasive population the stronger the effect of pond density on expansion rate will be at the range periphery.

We addressed the uncertainty about the cost resistance of rivers by conducting simulations at three levels of resistance. The effect was mild and only the higher cost level differed from the other.

Such a result has an important implication as it shows that selecting lower resistance values would not further enhance the colonization process. Similarly, considering resistance values beyond the highest one selected in this study would be unrealistic as swimming underwater is unlikely to be costlier than moving over a grass substrate on land for this aquatic species. We can therefore be reliably confident that the conclusions about the effect of SSI cannot be invalidated by selecting more extreme resistance cost values for rivers, at least within a realistic range. We may remain cautious about one particular point though. We do not know how much how frogs prefer to stay in a river course once they reached it rather than to leave it and cross the terrestrial environment to find a pond. Although we experimentally quantified the relative preference for the different substrates, we did not measure it for water. For obvious reasons, one is unlikely to recreate conditions encountered in rivers, which includes for instance olfactory cues from predators. Therefore, individuals may have a tendency to stay in water and follow watercourses but it is not known. Selecting lower resistance cost values for rivers partially solve this issue but we should stay aware that this component of resistance cost is currently lacking. Similarly, perceived resistance during daily movements may somewhat differ from perceived resistance during dispersal events which may affect the robustness of connectivity models (Diniz et al. 2020). However, we do not expect a strong bias in our study. First, amphibians move on the ground with a limited perception of their surrounding environments unlike larger flying organisms. The risks (high energetic expenses, dehydration, predation) faced by *X. laevis* are essentially the same when leaving a pond for a short trip or when dispersing, even if individuals could be more risk-taking in the latter case. Second, UNICOR is a resistant kernel modelling approach that integrates a dispersal function.

Even if we did not find evidence of an influence of landscape configuration, the colonization dynamics differed noticeably between all windows. On the one hand, expansion did not occur in four windows at least for some of the setting values. We had to discard these cases from analysis as the slope of the regression of expansion proxies over time steps could not be estimated. We assume that different responses were caused by particular landscape configurations

in these windows that did not allow colonization unless geographical barriers were overcome when dispersal was high enough. According to Fig. 2, these responses were not due to particularly low pond density in the window. The neighboring environment around the starting pond may not allow expansion, for instance if all pixels have high resistance costs and pond density is locally lower. However, if particular landscapes may halt the colonization process in some windows, they do not seem to be common enough to affect the analysis outcome for the whole window sample.

On the other hand, despite using large windows, colonization occurred so rapidly in some windows that window borders were reached as early as step nine, which forced us to discard information from further steps in order to keep a sufficiently large sample size of windows. We thus restricted our analysis to the first nine simulation steps to allow the computation of the regression of expansion proxies against time steps. Examination of the whole dataset shows that the square-root transformation of the expansion proxies properly linearized the relationships so that we obtained reliable estimates of the expansion rate (slope) even when considering only the early steps of the colonization process. Using even larger windows may alleviate this problem, potentially resulting in a lower number of discarded windows, albeit at the expense of computation time.

Habitat density (pond density), which can be viewed as a dimension of landscape, appeared to be a major factor generating variation in colonization success between windows, unlike landscape configuration proxies. The effect of landscape configuration may be stronger in other geographical contexts with different history of landscape formation and current socio-economic uses. For instance, one would expect expansion to be slowed or halted in areas dominated by open field crop areas where very little habitat is available. Exploring a wider range of conditions may help to further explore this issue. Broadening the environmental conditions encountered in windows would require to either consider other colonized regions of the world or to generate artificial landscapes in silico (With 1997), with the risk of simulating unrealistic conditions (Tao et al. 2024). In either case, computation time may be a limit. For the sake of comparison, computing one set of 75 simulations per river resistance cost (25

windows, 3 spatial sorting values) took 127 days with a cluster computer parallelizing the dispersal simulations per window (Intel Xenon CPU E5-2650 v2, 2.6 GHz, two cores, 256 GB Ram). Computation time depends on the total number of ponds in a window, as for each newly colonized pond a single kernel across the landscape of the window needs to be computed by UNICOR.

Our simulations reveal the contrasting influence of two components of the landscape. The density of suitable habitat appears to be the major driver of the colonization rate, while the way other landscape features are spatially arranged in the window was not relevant to the process. Some authors obtained similar results for habitat density (Barros et al. 2016), while others reached opposite conclusions (Bocedi et al. 2014). Both studies used the software Rangeshifter (individual-based model) and considered the proportion of available habitat in artificial binary landscapes. This might be a relevant difference in comparison with our approach, which relies on ponds as small and discrete habitats which total area cannot vary much between windows. Thus, it makes sense that pond density, i.e. the average distance between ponds, rather than the amount of habitat per se matters.

We acknowledge that we did not consider other factors that may affect the expansion process. For instance, studies showed that dispersal distance is enhanced (North et al. 2011; Williams et al. 2016a) or dispersal capacity reduced (Schtickzelle et al. 2006; Cheptou et al. 2008) with higher levels of habitat fragmentation. Likewise, density-dependence effects on dispersal can also influence the expansion process (Pachepsky and Levine 2011; Dahirel et al. 2023). Our modelling approach did not allow to implement such eco-evolutionary feedback or density-dependence effects. Instead, we selected a non-demographic method to avoid making unsupported assumptions on demographic response in our species. This has allowed us to focus on the interaction between landscape features and spatial sorting, while ensuring computation remained tractable. Nonetheless, our study shows that the influence of landscape cannot be considered independently of spatial sorting. Depending on the stage of the colonization process, the dispersal capacity of the colonizing individuals changes because of spatial sorting and this may determine

whether a particular landscape configuration can be colonized or not. In practical terms, some areas may provide efficient buffers to prevent further colonization but their characteristics will necessarily change with the distance to the introduction site and the number of generations since expansion started as dispersal capacity changes over time and space. This outcome has actual consequences for the control of alien invasive populations, whenever practitioners need to anticipate the time before a protected area is reached by an alien invasive population or the speed at which an area will be entirely colonized. The implementation of control measures takes time to engage stakeholders, obtain funding and organize the logistics. Any insight about the time available before an area of particular ecological interest is reached is likely to improve the efficiency of the measures to be deployed. To do so, the effect of spatial sorting on dispersal traits need to be estimated more frequently in control programs not to run the risk of making inappropriate assessments or designing irrelevant solutions.

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Data availability Data are provided as supplementary information.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval Not applicable.

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