

Simulating the effects of long-distance dispersal and landscape heterogeneity on the eco-evolutionary outcomes of range expansion in an invasive riverine fish, Tench (*Tinca tinca*)

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Abstract

Predicting how quickly populations expand their range and whether they will retain genetic diversity when they are introduced to new regions or track environmental conditions suited to their survival is an important applied and theoretical challenge. The literature suggests that long-distance dispersal, landscape heterogeneity and the evolution of dispersal influence populations' expansion rates and genetic diversity. We used individual-based spatially explicit simulations to examine these relationships for Tench (*Tinca tinca*), an invasive fish expanding its geographical range in eastern North America since the 1990s. Simulated populations varied greatly in expansion rates (1.1–28.6 patches year⁻¹) and genetic diversity metrics, including changes in observed heterozygosity (–19 to +0.8%) and effective number of alleles (–0.32 to –0.01). Populations with greater dispersal distances expanded faster than those with smaller dispersal distances but exhibited considerable variation in expansion rate among local populations, implying less predictable expansions. However, they tended to retain genetic diversity as they expanded, suggesting more predictable evolutionary trajectories. In contrast, populations with smaller dispersal distances spread predictably more slowly but exhibited more variability among local populations in genetic diversity losses. Consistent with empirical data, populations spreading in a longer, narrower dispersal corridor lost more neutral genetic variation to the stochastic fixation of alleles. Given the unprecedented pace of anthropogenic environmental change and the increasing need to manage range-expanding populations, our results have conservation ramifications as they imply that the evolutionary trajectories of populations characterised by shorter dispersal distances spreading in narrower landscapes are more variable and, therefore, less predictable.

KEYWORDS

fish, individual-based simulation, invasive species, landscape genetics, leptokurtic dispersal kernel, population genetics – theoretical

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1 | INTRODUCTION

Understanding range-expansion dynamics, a long-standing topic of interest in ecology and evolution (Shigesada, 1986; Skellam, 1951), is essential to predict the rate at which introduced species invade new habitats and native species shift in response to changing environments (Hastings et al., 2005; Parmesan & Yohe, 2003). When populations expand geographically, individuals disperse through heterogeneous landscapes and settle in new habitats to reproduce. Variation in range-expansion dynamics shape species' distribution, population density and their genetic composition (Excoffier et al., 2009; Miller et al., 2020). Theoretical studies have highlighted the influence of long-distance dispersal, landscape heterogeneity, biotic interactions and evolution, on shaping populations' rate of spread and genetic diversity (Birzu et al., 2019; Burton et al., 2010; Ibrahim et al., 1996; Phillips, 2015; Phillips & Perkins, 2019; Shigesada et al., 1995; Travis & Dytham, 2002; Williams, Snyder, & Levine, 2016). However, understanding and predicting the outcomes of range expansions remains challenging as empirical investigations are not always consistent with theoretical predictions (Bronnenhuber et al., 2011; Swaegers et al., 2013). Given the increasing incidence of range shifts in response to the unprecedented pace of anthropogenic environmental changes, it is important to improve our understanding – and ability to predict – the eco-evolutionary outcomes of range expansions.

Much of our current understanding of range expansions relies on theoretical models which assume that individuals disperse over short distances in their lifetime (Edmonds et al., 2004; Hallatschek et al., 2007; Klopstein et al., 2006; Skellam, 1951). These models have shown that neutral genetic diversity generally decreases from the core to the front of range expansions owing to sequential bottlenecks and mating between a limited number of genetic lineages (typically good dispersers) on expanding fronts (De Austerlitz et al., 1997; Excoffier et al., 2009; Hallatschek & Nelson, 2008; Klopstein et al., 2006; Phillips et al., 2010). This well-accepted theory is often used to detect the occurrence and the origin of range expansion from neutral genetic data, such as the expansion of humans from East Africa (Peter & Slatkin, 2013; Prugnolle et al., 2007). Yet, occasional movements over large spatial scales (long-distance dispersal, LDD), relative to small-scale dispersal, are widespread in the animal kingdom (Jordano, 2017; Kot et al., 1996).

Numerous studies have reported that LDD increases expansion rates and results in a lack of agreement between theoretically predicted expansion rates and empirical data (Hastings, 1996; Ibrahim et al., 1996). In contrast, the effects of LDD on neutral genetic diversity are not well understood. Specifically, while some studies argue that LDD consistently mitigates genetic diversity losses in expanding populations, others suggest that losses may still occur under certain circumstances, including narrow colonised regions and intermediate levels of LDD (Bialozyt et al., 2006; Fayard et al., 2009; Paulose & Hallatschek, 2020). Furthermore, how LDD interacts with genetic drift to influence variability in genetic diversity among replicates of a single range expansion has not been previously investigated. As LDD tends to homogenise the gene pool by facilitating gene

flow throughout the species' range (Bohrer et al., 2005; Garant et al., 2007), it might limit neutral dynamics (i.e. allele surfing and genetic drift) of allele frequencies (Paulose & Hallatschek, 2020), thereby reducing variability among local gene pools throughout expanding populations. As neutral dynamics can affect the spatial frequency distribution of neutral, beneficial and deleterious alleles (Hallatschek & Nelson, 2009), understanding this variability might be key to forecasting the evolutionary trajectories of range-shifting populations, something increasingly asked of conservation and invasive species researchers (Lässig et al., 2017; Williams et al., 2019).

Empirical investigations of the genetic consequences of range expansion suggest substantial variability in range-expansion dynamics among species, with some species showing decays in genetic diversity along expansions (Demastes et al., 2019; Garroway et al., 2011) while others maintain high levels of genetic diversity (Robalo et al., 2020; Swaegers et al., 2013; Wang et al., 2016). Theoretical predictions related to the eco-evolutionary outcomes of contemporary range expansions have rarely been tested in riverine fishes and received mixed empirical support thus far. For example, Sea Lamprey (*Petromyzon marinus*) populations exhibited a loss of genetic diversity when they expanded into the Laurentian Great Lakes (Bryan et al., 2005); conversely, Round Goby (*Neogobius melanostomus*) maintained high levels of genetic diversity as they spread throughout the same region (Bronnenhuber et al., 2011). Another species, Tench (*Tinca tinca*) exhibited contrasted changes in genetic diversity in different directions from a single point of introduction (Bernos et al., 2023). Variability in the magnitude and significance of genetic diversity losses associated with range expansion may be partially explained by differences in the number of genetic markers used in empirical studies and their statistical power (e.g. Swaegers et al., 2013, 2015). Alternatively, species-specific characteristics might interact with landscape heterogeneity to shape the outcomes of range expansions.

Individual-based simulations are powerful tools to understand variability in range expansion dynamics because they can account for demographic stochasticity (Melbourne & Hastings, 2009). Variation among individuals in their realisation of demographic processes (e.g. birth and dispersal) is known to result in variability among range-expansion outcomes, even in constant environments (Melbourne & Hastings, 2009). Individual-based models aiming to test and contribute to the formulation of range-expansion theories tend to be abstract, with individuals represented as particles spreading in homogeneous landscapes (Bialozyt et al., 2006; Hallatschek et al., 2007; Paulose & Hallatschek, 2020; Phillips, 2015). Comparatively, those aiming to inform pragmatic management focus on detailed representations of individuals, often based on extensive empirical data and expert knowledge in complex landscapes (Dominguez et al., 2020; Fraser et al., 2015). This is important because landscape heterogeneity is pervasive in nature and interacts with other sources of stochasticity to influence range-expansion dynamics (Fraser et al., 2015; Williams, Snyder, & Levine, 2016). Another benefit of individual-based simulation is that, by focusing on lower levels (e.g. individual loci and organisms) to model the emergence of population-level processes, results developed in a specific study system can potentially transfer well to different contexts (Radchuk et al., 2019). Recently developed

modelling frameworks, such as Range Shifter (Bocedi, Palmer, et al., 2014) and Cost-Distance Meta-POPulation (CDMetaPOP: Landguth et al., 2017), provide opportunities to understand and improve predictions related to the consequences of range expansions for wild populations' geographical range and genetic diversity.

Much of the literature examining the eco-evolutionary outcomes of range expansions using simulations has focused on highly abstract systems or specific case studies. Here, we extend these previous research efforts by using an individual-based, spatially explicit demogenetic model to broadly simulate the movement of Tench introduced to a river. Tench provides a good model system because individual attributes influencing population dynamics (e.g. growth and fecundity), within-population structure, recent demographic history and the genetic consequences of range expansion, are well characterised (Avlijas et al., 2018; Bernos et al., 2023; Dumont et al., 2002). As in other riverine fishes, Tench exhibit both short- and long-range dispersal, with the latter hypothesised as being largely responsible for driving range expansions (Morissette et al., 2021; Radinger & Wolter, 2014). We developed 300 model scenarios anchored with empirical data spanning a wide range of dispersal scales in spatially heterogeneous landscapes, leading to a deep understanding of the systems dynamics and testable predictions related to the effects of LDD, landscape heterogeneity, and evolution, on populations' expansion rate and genetic diversity (Grimm, 1999).

Specifically, we used simulations to address the following questions: (1) how are expansion rate and genetic diversity impacted by the shape of the dispersal kernel, landscape heterogeneity and the

degree to which dispersal propensity differs among individuals? and (2) how do expansion rate and genetic diversity changes vary across replicates for an introduced riverine fish exhibiting both short- and long-distance movements? Overall, we seek to advance existing theory on how demographic stochasticity and landscape heterogeneity influence range-expansion dynamics by focusing on predicting variability in their eco-evolutionary outcomes.

2 | MATERIALS AND METHODS

2.1 | Simulated range expansion for riverine fishes

2.1.1 | Study design

Our models were based on the documented introduction of Tench in eastern North America, which involved the escape of farmed individuals into the Upper Richelieu River (Avlijas et al., 2018; Bernos et al., 2023; Dumont et al., 2002). Specifically, simulations were initialised with the introduction of 100 individuals to a single location where range expansion putatively began. From the point of release, individuals could disperse in two directions differing in the spatial arrangement of suitable habitat patches: the southern environment (Lake Champlain) was predominantly lacustrine; and, the northern environments that branched into two expansion fronts (Lower Richelieu River and St. Lawrence River), riverine with several expansions forming lakes (Figure 1). Because our focus was on the

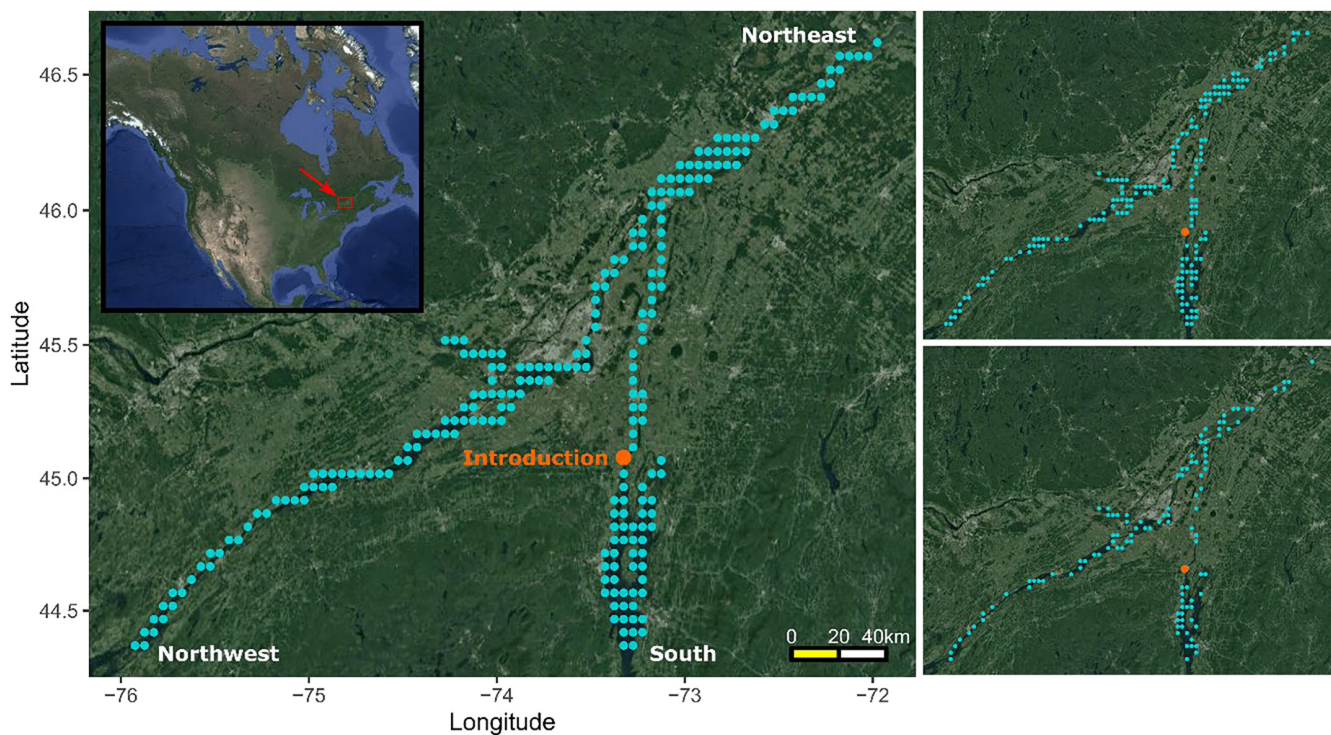


FIGURE 1 Landscapes used in the demogenetic simulation of Tench expansion in the Laurentian Great Lakes-St Lawrence basin: 229 habitat patches (left), 170 habitat patches (top right) and 115 habitat patches (bottom right). The orange patch represents the site of introduction (orange patch). Within each landscape, range expansion can occur southward, northeastward and northwestward.

eco-evolutionary consequences of recent and ongoing range expansions, presumably not at equilibrium, we simulated each scenario over 50 years.

2.1.2 | Model overview

We simulated 300 scenarios of range expansion for an introduced riverine fish using the individual-based spatially explicit model CDMetaPOP (for full model description see Landguth et al., 2017). In the CDMetaPOP framework, a landscape is represented by discrete habitat patches, themselves populated by individuals. Within each habitat patch, length- and age-based class structures are used to simulate stochastic processes, and individuals are assumed to share common environmental conditions (e.g. carrying capacity). At each annual cycle of the simulation and within all patches (including the one where range expansion was initiated), individuals grow, mature, reproduce, disperse and die based on probabilistic distributions. Between patches, individual dispersal is a function of spatially explicit cost–distance matrices. As genes are inherited from parents to offspring in a Mendelian fashion, CDMetaPOP can be used to simulate the genetic processes (e.g. gene drift and gene flow) resulting from inter-individual variability in demographic processes such as dispersal and death.

2.1.3 | Patches

To investigate the effect of habitat availability, we conducted the simulations in three landscapes. The first landscape contained 229 habitat patches (Figure 1), which were defined as the centroid of grid cells ($4 \times 4 \text{ km} = 16 \text{ km}^2$) overlapping with water throughout the invaded region (Figure 1). We then produced two additional landscapes with 170 and 115 habitat patches by randomly subsetting 75% and 50% of the patches respectively. Within each landscape, expansion occurred southward, northeastward and northwestward. Patch quality did not vary throughout the landscape: based on available estimates of catch-per-unit-effort in areas of high Tench density (J. Hill, unpubl. data), we assumed that all patches had a carrying capacity of 600 fish.

2.1.4 | Individual growth, maturity, fecundity and mortality

We initialised the simulation with a random distribution of seven age classes, a number derived from empirical age distributions based on otolith chemistry data (Morissette et al., 2021). At each annual cycle, growth followed the trajectory of the Von Bertalanffy equation (Von Bertalanffy, 1957). Specifically, we used the following equation with parameters derived from length survey data from the eastern North American Tench population (O. Morissette, unpubl. data) (see

Figure S1 for Von Bertalanffy growth curve for Tench and Table 1 for parameters):

$$L = L_{\infty} * (1 - \exp(-R_0 * (i + 1 - t_0))).$$

With L_{∞} the asymptotic size, R_0 the growth coefficient, i the age class, t_0 a modelling artefact said to represent the age when the average length is zero (-0.2 in our model), and L the new size. This equation is particularly well-suited to model fish growth as growth rate is fastest during the early stages of life and declines with age and body length.

The probability of maturation was modelled as a function of size based on a logistic probability curve derived from unpublished maturity data provided by J. Hill (Figure S2, Table 1). Based on these data, individuals had a 50% probability of reaching maturity at $\sim 30 \text{ cm}$ in length (~ 3 years). Although fecundity data were not available for this Tench population, Tench can produce hundreds of thousands of eggs (Ablak Gürbüz, 2011). Due to computational limitations, it was not possible to simulate such high fecundity. We explored a range of values, and modelled fecundity (the number of eggs produced per

TABLE 1 Parameters and associated values used in the simulation model. Parameters in **bold** varied across simulations.

Parameter	Value	Notes
<i>Landscape</i>	229, 117, 115	
Number of patches		
<i>Von Bertalanffy growth equation</i>		Derived empirically (Figure S1)
Asymptotic size (L_{∞})	482	
Growth rate (R_0)	0.52	
<i>Size-dependent logistic maturation curve</i>		Derived empirically (Figure S2)
Intercept (δ)	-7.53006	
Slope (β)	0.02515	
<i>Size-dependent fecundity</i>	0.0002	
Coefficient (a)	2.5989	
Exponent (b)		
<i>Fidimo dispersal kernel</i>		Derived from Radinger and Wolter (2014)
Proportion of sedentary fish (p)	[0.25–0.80]	
Mean dispersal distance for sedentary fish ($\alpha_{\text{sedentary}}$)	[0–4]	
Mean dispersal distance for mobile fish (α_{mobile})	[6–50]	
<i>Genetically controlled dispersal phenotypes</i>	$S = [0–100]$	
Difference between good and poor dispersers (Δ dispersal)		
<i>Neutral genetics</i>		
Number of loci	100	
Number of allele/loci	2	

female) as a power function of size (Ablak Gürbüz, 2011), with a mean of 822 eggs at first reproduction (Figure S3, Table 1). Reproduction was strictly sexual, polygamous, and occurred via random mating between individuals occupying the same habitat patch. Mature individuals were capable of reproducing every year.

Finally, mortality occurred as a function of density-dependent processes to simulate length-based competition and partition of resources within each habitat patch (e.g. Ray et al., 1996). Briefly, size-structured density-dependent mortality was based on the Ricker equation operating within each size class (Ricker, 1954). A generic size distribution was specified to allocate carrying capacity among size classes, and then intraspecific competition occurred at the class level. Carrying capacity is also assumed to be limited from the top down, so that unused space at larger size classes is available to increase survival and abundance of smaller size classes. For more details on the algorithm and default values, see the software's user manual: see the software's user manual: <https://github.com/ComputationalEcologyLab/CDMetaPOP>.

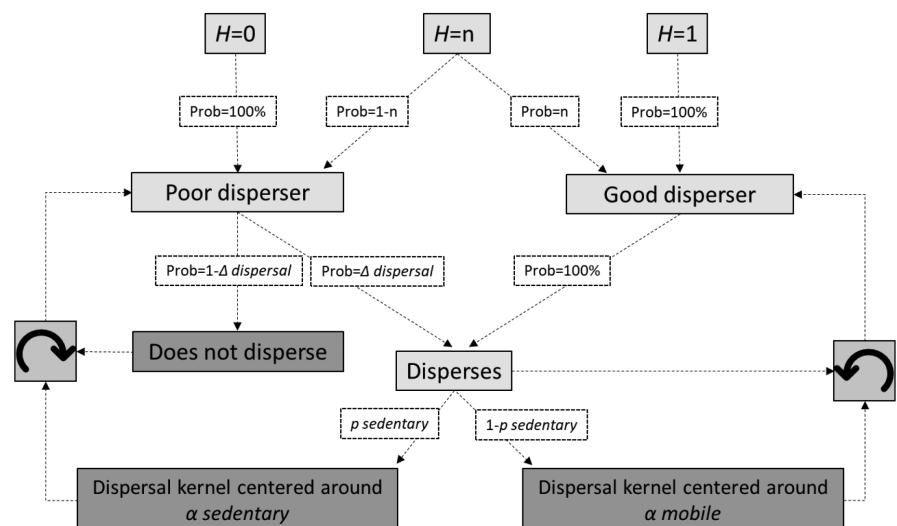
2.1.5 | Dispersal phenotypes and behaviours

In our simulations, dispersal was regulated by two overlapping processes (Figure 2). First, individuals were assigned one of two genetically determined (see 'genetics of dispersal') dispersal phenotypes at birth, with good dispersers being more likely to depart from their habitat patch relative to the poor dispersers. The extent of the difference (Δ dispersal) was determined by reducing departure probability for the poor dispersers relative to the good dispersers by a factor between 0 and 1 (see Table 1 for range of values). Second, each year, the probability for a departing individual – including all good dispersers and the departing proportion of poor dispersers – to move to any given patch relative to and including its current patch followed a leptokurtic dispersal kernel. Specifically, the movement of individuals was governed by resistance surfaces implemented with a cost-distance matrix where each entry represented the shortest in-water

distance (in km) between two patches and rescaled to a probability between 0 and 1. A transformation of the resulting probability vector using the leptokurtic movement function (Fidimo) was then used to determine the probability for a fish to disperse to any patch relative to their current one. The Fidimo function, which includes two superimposed normal distributions (Figure 2), consists of three parameters: the proportion of sedentary fish in the population (p); and, the mean dispersal distances of mobile (α mobile) and sedentary (α sedentary) fish (Radinger and Wolter 2014). As opposed to the good and poor dispersal phenotypes, which referred to individual's ability or decision to depart from their current habitat patch, sedentary and mobile fish differed in the spatial scale of their dispersal: sedentary fish were more likely to disperse close to, or remain within, their initial habitat patch while mobile fish may reach distant locations. Thus, in this study, LDD was two to 50 times larger than the mean dispersal distance of the sedentary fish, effectively characterising the tail of the dispersal function (Figure 2). Species characterised by a tendency to remain in their natal area are characterised by a large share of sedentary fish (p) and migration (seasonal movement between home ranges) was not considered. Contrary to the good- and poor-disperser phenotypes, individuals' affiliations to the sedentary and the mobile components of the dispersal kernel were not genetically determined and changed temporally.

In other words, the probability for good dispersers to move to any given patch (including the one they are in) always followed the Fidimo dispersal kernel, meaning that dispersal distances were heterogeneous as good dispersers included both sedentary and mobile fish. In simulations where the extent of the difference between good and poor dispersers was 1, all individuals with a poor-disperser genotype stayed in their initial habitat patch throughout their lifetime. When it was 0.5, each year, the poor dispersers had a 0.5 probability of staying in their habitat patch, and a 0.5 probability of dispersing to any position relative to their current patch based on the fidimo dispersal kernel. Then, the probability that good dispersers moved to any given patch always followed the fidimo dispersal kernel, with poor dispersers exhibiting sedentary or mobile dispersal distances

FIGURE 2 Flowchart representing the process for assigning dispersal phenotypes and probability to move to any given patch relative to and including its current patch a function of the hybrid index (H), the difference between good and poor dispersers (Δ dispersal), the proportion of stationary fish (p sedentary) and mean dispersal distances (α sedentary and α mobile); n , the average of the parental H indexes, is a number between 0 and 1. The arrow indicate processes occurring through each annual time loop of the model.



based on p sedentary. From (and including) their current patch, individuals could disperse to existing patches in any direction with probability of movement to a given patch varying based exclusively on transformed patch-to-patch riverine distances.

To describe the movement of Tench, we first defined leptokurtic dispersal kernels using the R package fishmove (Radinger and Wolter, 2014). In this package, mean dispersal distance is computed as a function of fish length, aspect ratio of the caudal fin, and stream size, as shown in a recent meta-analysis of dispersal distances for riverine fishes (Radinger & Wolter, 2014). To predict a range of dispersal distances for Tench, we used an average fish size of 36 cm, aspect ratio of 1.82 (as measured from Figure 5 of Avlijas et al., 2018 using imageJ), and a stream order (a proxy for channel size, watershed area, and stream discharge with a positive relationship on mean dispersal distances) of 9 (Strahler, 1957). This predicted a mean dispersal distance of 1 km (0.5–2 km) for the sedentary fish (α sedentary) and 19 km (95% CI=10–35 km) for the mobile fish (α mobile). We then widened this range to include scenarios that were less likely to occur in natural fish populations. As the propensity for individual Tench to remain close to their natal origin is unknown, the range of p [0.25–0.80] (Figure 3) explored those exhibited by riverine fish species (Radinger and Wolter, 2014). The ranges of values for α sedentary [0–4 km] and α mobile [6–50 km] describe the movement of a medium-sized fish with a relatively small caudal fin aspect-size ratio in a large river.

2.1.6 | Genetics of dispersal

As dispersal involves several morphological, behavioural and physiological traits shaped by a myriad of genes and the surrounding environment (Clobert et al., 2009; Saastamoinen et al., 2018), we used a continuously distributed metric bounded between 0 and 1 (the H index, H ; Allendorf et al., 2001; Nathan et al., 2019) to incorporate the polygenic structure underlying the expression of dispersal and assign good and poor disperser phenotypes to individuals at birth. Briefly, at the initiation of the simulation, fish were assigned an H index of 0 or 1

in equal proportions; individuals with an $H=0$ were 'good dispersers' and those with an $H=1$ were 'poor dispersers'. This H index represents the sum of the additive contribution to a phenotype. After initialisation of the simulation, the H index of eggs was computed as the average of parental H indexes. Dispersal phenotype groups were then assigned based on random draws associated with the H index value. For example, eggs with $H=0.9$ had a 90% chance of being 'good dispersers' and a 10% chance of being 'poor dispersers'.

2.1.7 | Neutral genetic diversity

Individuals' neutral genotypes were initialised based on an allele frequency file for diploid individuals assuming maximum genetic diversity (i.e. allelic frequencies were all equal to 0.5), comprised of 100 loci with two alleles per locus. Our models assumed that all genetic diversity was present at the initialisation of the range expansion and that mutation and intrachromosomal recombination did not occur. Offspring received genotypes based on Mendelian inheritance, meaning that they inherited one allele from each one of their diploid parents.

2.2 | Metrics of range expansion and genetic diversity

At the population level, each simulation represented one realisation of a range expansion scenario, where expansion rate was defined as the average number of new colonised patches per year during range expansion, computed as:

$$\frac{\text{Total number of habitat patches}}{\text{Number of years until all patches are colonised by at least two fish}}$$

Genetic diversity losses were quantified as the difference between the founder population and the last generation of the

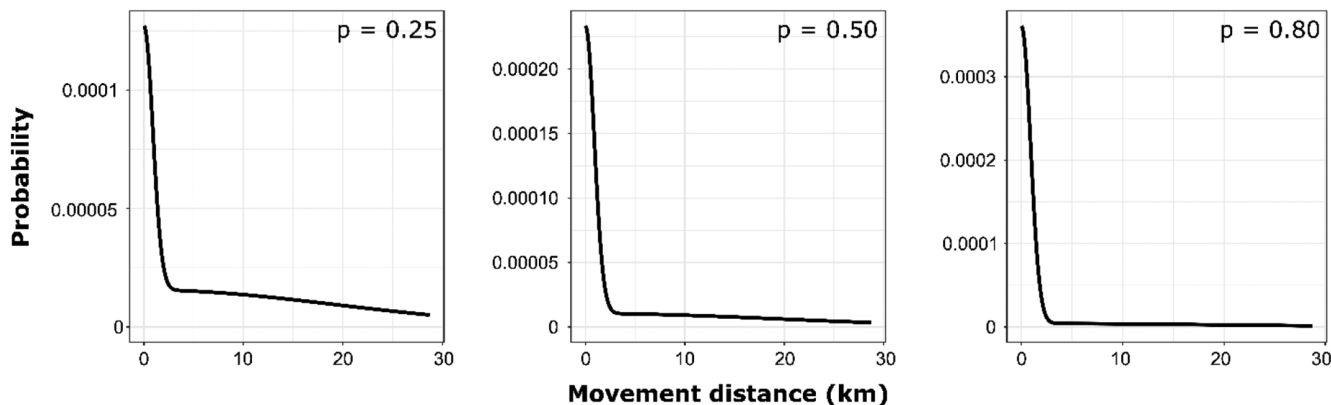


FIGURE 3 Example of the leptokurtic dispersal kernel for Tench (*Tinca tinca*) (aspect ratio=1.82, length=357 mm) in a large river (stream order=9) for a 1-year time interval, with a mean dispersal distance of 1 km and 19 km for, respectively, the sedentary (α sedentary) and mobile (α mobile) fish. Comparisons across a proportion of sedentary fish (p sedentary) of 0.25, 0.50, and 0.80. Long-distance dispersal events represent the tail of the dispersal function.

simulation in observed heterozygosity (H_o) and in the effective number of alleles (A_e) respectively. We computed A_e as defined by Weir (1990), with gene diversity defined as the average probability that two randomly selected alleles are different in a population (Nei, 1973):

$$\frac{1}{1 - \text{gene diversity } (H_e)}$$

To gain further insights into within-population variability, we also computed two metrics of variation among expansion fronts: mean annual variability in expansion rate was computed as the standard deviation in expansion rate (expansion rate was calculated within each of the expanding fronts, effectively accounting for local differences in the number of patches); and, spatial variability in genetic diversity losses as the standard deviation of H_o and A_e losses between the three expansion fronts. Thus, whereas the population-level genetic diversity loss metrics described temporal changes, the variability loss metrics described spatial variation. In this study, we considered the invaded landscape as a closed system (i.e. fish could only disperse to existing patches). To evaluate the effect this might have had on population dynamics, all metrics were computed after completion of 30-year cycles (the average number of years it took for the landscape to be fully invaded; see results) and 50-year cycles. As the results were qualitatively similar, we only report results on 50-year cycles.

2.3 | Baseline scenario

We first ran a scenario to create a baseline against which we compared alternative scenarios. This scenario included no differences in dispersal ability between the poor and the good dispersers group, in conjunction with equal proportion of sedentary and mobile fish ($p=.5$) and the average fitted predicted dispersal distances for Tench ($\alpha_{\text{sedentary}}=2$ km, $\alpha_{\text{mobile}}=19$ km). We ran this scenario in the landscape with the greatest number of habitat patches and computed all output metrics for each of the models. To characterise variability due to stochasticity built into the components of the simulation model, we ran the model ten times and report the average, minimum and maximum values for all metrics. Results did not change qualitatively between 5 and 10 replicates, ensuring that our conclusions were robust to the number of replicates.

2.4 | Alternative scenarios and global sensitivity analysis

Simulation studies examining the eco-evolutionary outcomes of range expansions typically rely on local sensitivity analyses to quantify the effects of input parameters on model outputs and infer their relative influence on range expansions. Compared

to local sensitivity analyses, where researchers vary input parameters one at a time in a factorial design, global sensitivity analyses can be used to vary several parameters simultaneously (Wagner, 1995). This offers two key advantages over local sensitivity analyses. First, global analyses examine sensitivity related to the entire parameter space, while local sensitivity analyses have a limited scope (i.e. researchers typically focus on extreme parameter values or ignore uncertainties around parameters estimated from empirical data) (Wagner, 1995). Second, varying multiple parameters simultaneously enables the detection of nonlinear relationships as well as complex interactions among input variables (Prowse et al., 2016). Recent advances in statistics and computing can be leveraged to analyse and summarise the results of global sensitivity analyses (Elith et al., 2008).

We used global sensitivity analyses to investigate how parameter values related to the dispersal kernel (p , α mobile, α sedentary), the differences in dispersal traits between genetically determined dispersal phenotypes, and landscape patchiness, influenced four metrics of range expansion outcomes in 300 scenarios. The first step of the global sensitivity analysis was to adequately sample the parameter space representing the range of possible parameter values (Table 1). To ensure even coverage, we used the Latin Hypercube Sampling (LHS) approach implemented in the R package lhs (Carnell, 2022). Unlike uniform random sampling, where input parameters are equally likely and drawn independently from one another, LHS first divides the range of possible parameter values into equally sized bins and draws a single value from each bin. Parameter values are then combined with one another without replacement, and in such a way as to maximise orthogonality among parameter sets. Using LHS sampling, we drew 300 samples (see Figure S4) representing unique combinations of parameter values; each parameter set was then used as input in a single simulation. By sampling across the multidimensional parameter space instead of running multiple models per parameter combination, we increased our capacity to capture the true dynamics of the simulation using statistical models (Prowse et al., 2016).

The second step of the global sensitivity analysis used emulators to summarise the model outputs. Specifically, we used boosted regression trees (BRT) to evaluate the relative influence of each parameter and potential interactions on simulation model outputs (average and variability in range expansion rate and genetic diversity losses). BRT is an advanced regression technique that builds multiple regression trees and combines them into accurate aggregated predictions using a boosting algorithm (Elith et al., 2008). BRT do not rely on assumptions regarding distribution of the data (e.g. normality); they can handle complex interactions and fit nonlinear relationships. The optimal number of trees was determined automatically using the `gbm.step` function in the `dismo` R package (Hijmans et al., 2017). As preliminary analyses revealed that results and model fit were consistent across BRT parameter combinations, trees were built with similar parameters to improve comparison across response variables. We specified up to three levels of interactions within tree (tree complexity = 3);

each tree contributed 0.01 to the BRT model (learning rate = 0.01) and was fitted on a random selection of 75% of the data (bag fraction = 0.75). To assess model performance, we evaluated the spearman R^2 and the mean absolute error between predictions and observations for a subset of the data (25%) withheld during model fitting. Large correlation coefficients – we view 0.6–0.79 as strong, >0.79 as very strong – and small absolute errors indicate that the model can make accurate predictions when faced with new data. Finally, we tested the null hypothesis of no interaction among predictor variables using 100 bootstrap samples (Pinsky & Byler, 2015).

To characterise how each predictor variable influenced the metrics (population-level and variation among expansion fronts in expansion rate and genetic diversity losses) in the BRT, we computed the relative influence of predictors and generated partial dependence plots. The metric of relative influence represents the number of times each variable is selected for splitting in individual decision trees weighted based on the square improvement to the model; it is then averaged over all trees and scaled between 0 and 100 (Friedman & Meulman, 2003). We highlighted variables with a relative influence greater than expected due to chance (100 divided by the number of variables; Müller et al., 2013). We then produced partial dependence plots showing the effect of predictors on the response metrics after accounting for the effects of the other predictors. Effects are shown as a function centred around a mean of zero (Friedman & Meulman, 2003), and we generated 1000 bootstrap replicates to produce 95% confidence intervals. Finally, we visualised the most important interactions between predictors using partial interaction plots.

3 | RESULTS

3.1 | Differences and similarities between baseline and alternative scenarios

In the baseline scenario, at the population level, H_o and A_e declined the most rapidly during the period associated with rapid population growth (Figure S5) and concomitant range expansion (Figure 4, Table 2), which occurred for 29.6 years on average (28–32 years) after the introduction. Results from alternative scenarios indicated some variability in mean expansion rate and genetic diversity losses. For example, the simulated population colonised the full extent of the landscape in most (92.3%), but not all, of the 300 alternative scenarios, which averaged an expansion rate of 10.5 patch/year (range = 1.1 to 28.6 patch/year). While H_o declined in most simulations (91.3%), some populations experienced small gains (<0.01%) over the course of the simulation. These populations were typically characterised by large LDD distances (mean = 37.9 km/year). The average change in H_o was a loss of -2.6% (range = -19.0% to 0.8%). The effective number of alleles declined in all simulation by, on average, -0.06 (range = -0.32 to -0.01).

Patterns of variation among expansion fronts in expansion rate, H_o and A_e , were similar in the baseline and alternative scenarios (Figure 4). In the baseline scenario, southward expansion occurred twice faster than both northeastward and northwestward expansions, which did not differ from one another in expansion rate (Figure 4, Table 2). When range expansion began, A_e decreased sharply on the three expansion fronts relative to the founder population; but when population sizes increased on the three expansion fronts, A_e grew rapidly to approach the population-level A_e . For both H_o and A_e , losses were smaller on the southern expansion front compared to the northwestern expansion front and the northeastern front, with losses being greater on the northwestern than the northeastern front. Results from alternative scenarios highlight similar trends: southward expansion occurred faster (Mean (sd) = 13.2 (6.7) patch/year) than northwestward (6.1 (3.4) patch/year) and northeastward (5.8 (3.5) patch/year) expansion. Genetic diversity losses were smaller on the southern expansion front (0.1 (0.06) % for H_o ; <0.01 (0.03) for A_e) compared to the northeastern (0.7 (0.2) % for H_o ; 0.06 (0.10) for A_e) and the northwestern front (3.8 (0.4) % for H_o ; 0.11 (0.15) for A_e).

3.2 | Predicting expansion rate and genetic diversity losses

Overall, the BRT made accurate predictions regarding mean and variation in genetic diversity and expansion rate when tested with the subset of data withheld during model fitting. Correlation coefficients (absolute errors) between new data and values predicted with our fitted models for population-level metrics were 98% (+/- 0.86 patch/year) for mean expansion-rate, 82% (+/- 3.1%) for mean H_o , and 88% (+/- 3.08) for mean A_e . For the variability metrics, we obtained correlation coefficients and absolute errors of 89% (+/- 0.78%) for variation in H_o and 94% (+/- 0.02) for variation in A_e . With a correlation coefficient of 73% (+/- 1.22 patch/year), predictions were comparatively less accurate for the variation in expansion-rate model. Greater discrepancies between predicted values and new data were correlated (probability values <.001) with simulations with greater mean dispersal distances for mobile ($R^2 = 0.60$) and sedentary ($R^2 = 0.38$) fish.

Although the four models highlighted mean dispersal distance of the mobile fish (LDD) as the best predictor, the shape of the relationship varied among models (Figures 5 and 6). Specifically, expansion rate increased linearly with mean dispersal distance of the mobile component of the population (56.9%). The effect of alpha mobile on variation in expansion rate among expansion fronts was non-monotonic (41.4%); it increased with mean dispersal distance up to 30 km/year, then plateaued at 38 km/year after which it began to drop. The shape of the relationship between mean dispersal distance of the mobile components and the genetic diversity metrics, including loss in H_o (68.6% and 83.3% for mean and variation among expansion fronts, respectively) and A_e (70.1%

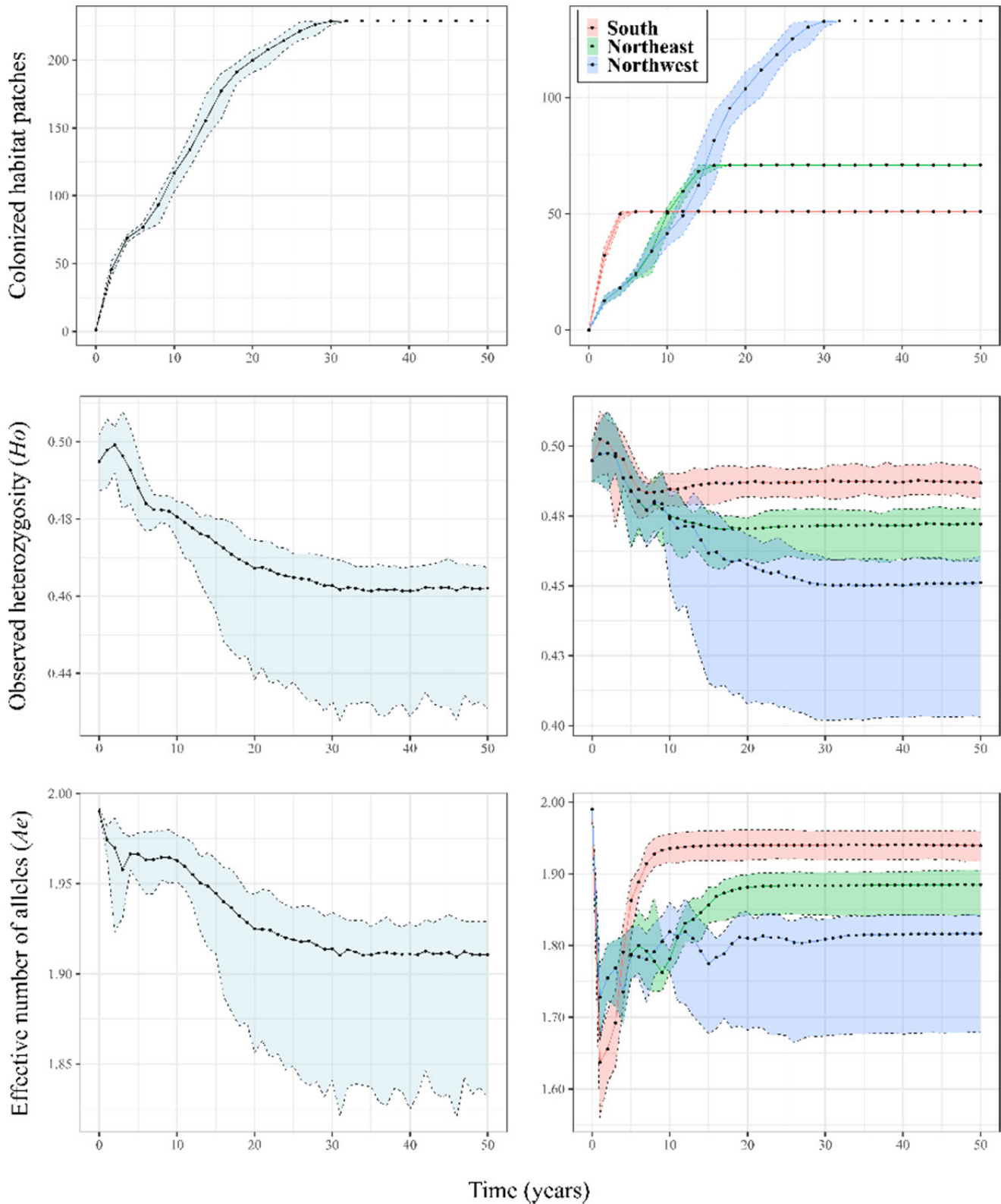


FIGURE 4 Minimum, maximum, and average trends in the number of colonised habitat patches, observed heterozygosity and effective number of alleles over time for 10 independent runs under the baseline scenario. Ran in the continuous landscape (229 habitat patches), this scenario included no differences between poor and good dispersers ($\Delta dispersal=0$), equal proportion of sedentary and mobile fish ($p_{sedentary}=0.5$), and the average predicted dispersal distances for Tench ($\alpha_{sedentary}=2$ km, $\alpha_{mobile}=19$ km). Metrics are shown at the landscape-level (left panel) and within each expansion front (South, Northeast and Northwest).

TABLE 2 Range expansion rate and changes in genetic diversity (observed heterozygosity and effective number of alleles) across 10 replicated runs for the baseline scenario. The table shows the mean and the standard deviation for each metric at the population level and within three expansion fronts (Southern, Northwestern and Northeastern).

	Range expansion rate (patch/year)	Observed heterozygosity (%)	Effective number of alleles
Population level	7.7 (0.1)	-3.3 (0.4)	-0.08 (0.01)
Southern front	10.6 (2.2)	-0.1 (0.1)	-0.05 (<0.01)
Northwestern front	4.5 (0.3)	-4.4 (0.6)	-0.17 (0.02)
Northeastern front	4.5 (0.2)	-2.3 (0.3)	-0.10 (0.01)

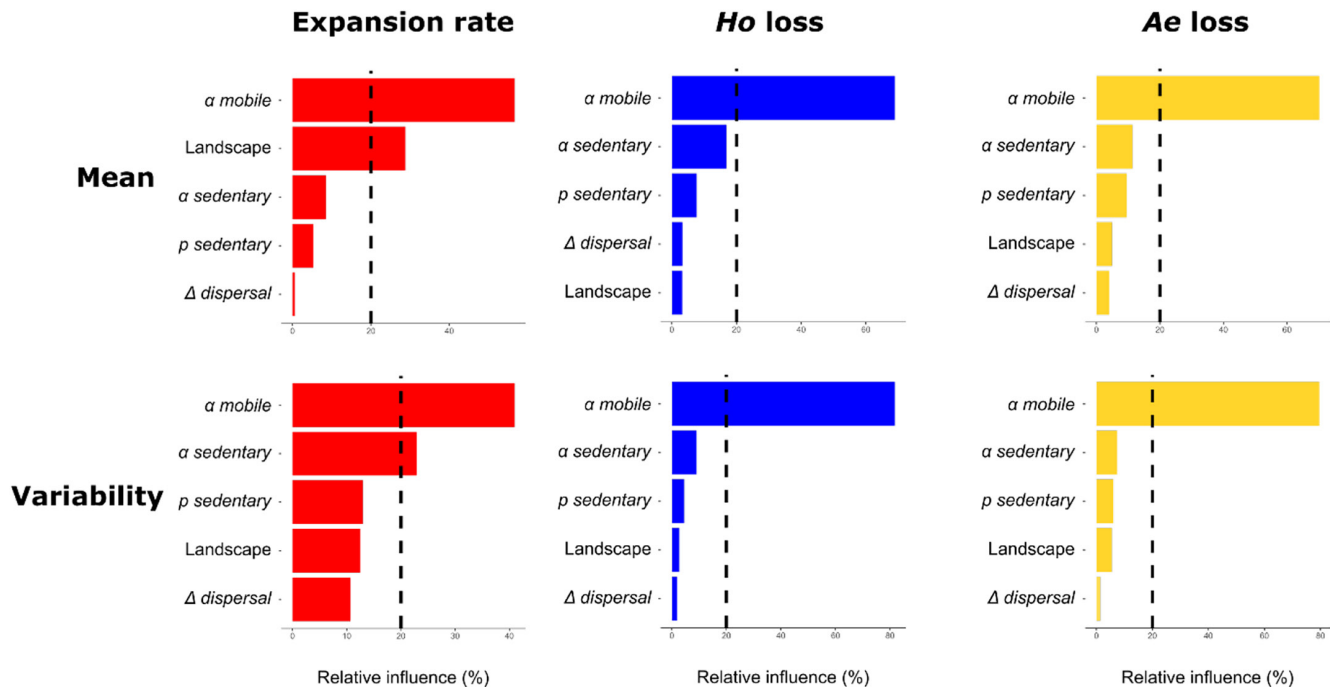


FIGURE 5 Relative influence of predictors on expansion rate, loss of observed heterozygosity (H_o) and loss in allelic richness (A_e) derived from boosted regression trees. Predictors included difference in dispersal probability between mobile and less-mobile fish (Δ dispersal), landscape patchiness (Landscape), mean dispersal distance for sedentary (α sedentary) and mobile fish (α mobile), and proportion of sedentary fish in the population (p sedentary). Metrics of range expansion outcomes include mean at the population level and variability among expansion fronts. Dotted line indicates threshold above which predictors' influence is greater than expected by chance.

and 79.6%), was similar. Specifically, genetic diversity metrics decreased sharply with increasing dispersal distance up to 20 km/year, after which the magnitude of the loss was below average for that metric.

In addition to mean dispersal distance of the mobile fish, landscape patchiness and mean dispersal distance of the sedentary fish were uniquely ranked as more influential than expected by chance in, respectively, the mean and variability in expansion-rate models (Figures 5 and 6). Specifically, the BRT predicted faster mean expansion rates (28.7%) in landscapes with more habitat patches (less patchiness) than in those with fewer habitat patches. In the other models, the relative influence of landscape patchiness was ranked last and second to last. In the variability among expansion fronts model (22.9%), the relationship between variability and mean dispersal distance of the sedentary fish was generally positive, with variability in expansion rate increasing most steeply as mean dispersal distances increased from 0 to 1 km/year. In the other models, the

relative influence of mean dispersal distance of the sedentary fish was ranked second and third.

The proportion of sedentary fish and extent of the difference in dispersal ability between good and poor dispersers were not more influential than expected by chance in any of the models (Figures 5 and 6). The only significant interaction across all four models (Figure 7) was between mean dispersal capacity of the mobile fish and landscape patchiness in the mean expansion-rate model. This interaction involved a two- to three-fold weakening of the positive effect of high dispersal capacity on expansion rates in patchier landscapes.

4 | DISCUSSION

Understanding how range expansions determine species' geographical ranges and the distributions of their genetic diversity

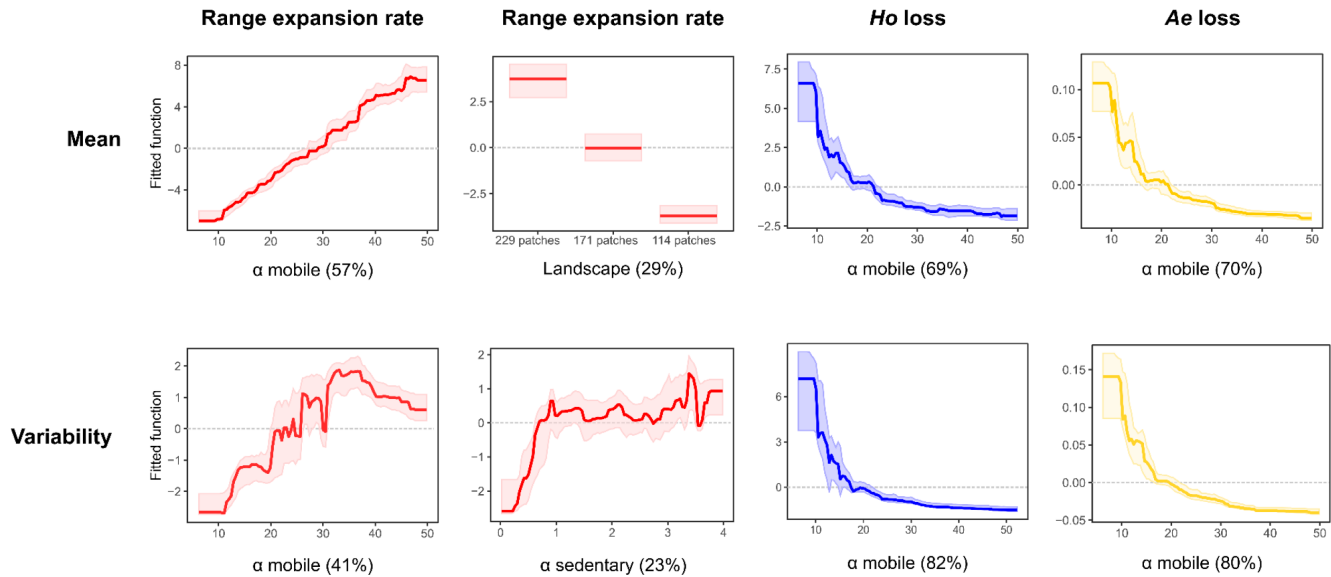


FIGURE 6 Partial dependence plots showing the effect of influential predictors derived from boosted regression trees on expansion rate, loss of observed heterozygosity (H_o) and loss in allelic richness (A_e), while holding other predictors constant. Influential predictors included landscape patchiness (Landscape) and mean dispersal distance for mobile (α mobile) and sedentary (α sedentary) fish. Metrics of range expansion outcomes include mean and variability among expansion fronts in expansion rate and genetic diversity loss (H_o and A_e). Since landscape patchiness is categorical, its partial dependence is displayed as a barplot. Effects are centred around a mean of zero (grey dotted line).

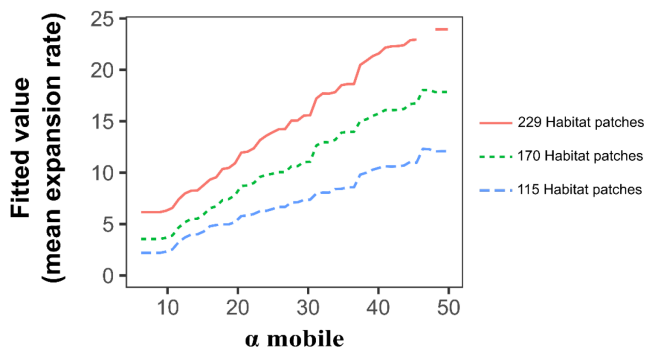


FIGURE 7 Partial dependence plot showing the interaction between the effects of mean dispersal distance for mobile fishes (α mobile) and landscape patchiness on mean expansion rate while holding other predictors constant. Range expansion simulations were conducted in three landscapes: the initial landscape contained 229 habitat patches, and two additional landscapes with 170 and 115 habitat patches were produced by randomly sub-setting 25% and 50% of the patches respectively.

can provide important insights into the ecological success of spreading populations. This study demonstrates that LDD had two main effects on range expansions. First, increasing LDD distance dramatically accelerated the rate of range expansion and favoured the retention of neutral genetic diversity in the entire population during range expansion. Second, there was a trade-off between dispersal and genetic diversity lowering the predictability of range expansions when LDD distance was relatively small (< three-fold larger than short-range dispersal distances). Furthermore, the shape of the dispersal corridor was also

important in differentially shaping expansion rate and genetic diversity losses among local populations. These findings suggest that some of the variability in the eco-evolutionary outcomes of range expansion, which affects how precisely we can predict the trajectories of range expansions, might be predictable based on species and landscape attributes.

4.1 | Predicting range expansion dynamics

Large dispersal distance exerted a powerful influence on expansion rate and neutral genetic diversity. As in several other studies, greater LDD distance boosted expansion rate for the entire population (Kot et al., 1996; Paulose & Hallatschek, 2020; Ray & Excoffier, 2010). In contrast, the effects of LDD on genetic diversity were less linear. Specifically, increasing mean LDD distance was most effective at facilitating the retention of genetic diversity when distances were relatively small ($\ll 20$ km/year). Beyond this distance threshold, most of the genetic variation (i.e. >97% of the H_o and A_e of the originating population) was preserved during range expansion, and a small number of populations even experienced small gains in H_o (<0.001%). This result suggests that LDD can maintain genetic diversity throughout expanding populations, but only when it is above a critical distance threshold, below which the effects of sequential founder effects on neutral genetic diversity are not eliminated (Hallatschek & Fisher, 2014; Paulose & Hallatschek, 2020). In practice, this critical distance threshold may depend on (1) the deviation in dispersal distances around mean LDD distance and (2) the geographical scale of the range expansion.

Although populations with low LDD distances expanded more slowly, they exhibited greater losses in genetic diversity and greater among-replicate variability (i.e. variation among newly established local populations) in neutral genetic diversity losses. This is consistent with the theoretical expectation that LDD mitigates the effects of genetic drift and gene surfing as the flux of individuals dispersing from the core to the expanding front precludes the fixation of other alleles and the erosion of genetic diversity on the expanding front (Klopfstein et al., 2006; Paulose & Hallatschek, 2020). The corollary is that changes in the gene pool due to neutral processes might increase variability in the genetic diversity retained by expanding populations, thereby decreasing the predictability of the evolutionary outcomes of range expansions in populations with limited dispersal ability (Weiss-lehman et al., 2019). However, how allele surfing and genetic drift will affect the adaptive potential of expanding populations remains misunderstood. On the one hand, these neutral processes may reduce the efficacy of selection. On the other hand, they can affect the spatial frequency distribution of beneficial and deleterious mutations (Hallatschek & Nelson, 2009), and intermediate levels of gene flow could promote adaptation by giving more time for selection to operate on expansion fronts (Peischl et al., 2013; Peischl & Excoffier, 2015).

The effects of increasing LDD distance on expansion rate were stronger in continuous landscapes, where populations tended to spread faster than in patchier landscapes (Barros et al., 2016; Cumming, 2002; Shigesada, 1986; Travis & Dytham, 1999; but see Bocedi et al., 2014). For a given mean LDD distance, individuals had more patches to which to disperse in continuous landscapes. However, while patchiness did not influence among-replicate variability in expansion rate (e.g. Williams et al., 2016) nor genetic diversity, the shape of the habitat influenced both population-level and among-replicates variability in expansion rate and genetic diversity. In wider environments, the number of patches within shorter distances increased, thus resulting in higher expansion rates. However, local populations spreading in long, narrow dispersal corridors not only expanded more slowly and lost more genetic variation, on average, than those expanding in wider dispersal corridors (Cumming, 2002; Fayard et al., 2009). They also tended to exhibit more among-replicate variability in expansion rate and genetic diversity losses. This result implies that the degree of divergence between local populations might increase due to reduced connectivity when dispersal corridors are long and narrow, potentially creating opportunities for different alleles to rise in frequency (Crow & Aoki, 1984; Wright, 1951).

Although we expected populations with greater genetically based trait differences between good and poor dispersers to spread faster due to the spatial sorting of good dispersers on newly colonised habitat patches, the parameter did not significantly affect range-expansion dynamics in our study. In contrast, the evolution of dispersal led to faster and more variable range expansion rates in several empirical (Brown et al., 2014; Lombaert et al., 2014) and experimental (Weiss-lehman et al., 2017; Williams, Kendall, & Levine, 2016) studies. For example, there is evidence that the

acceleration of Cane Toad (*Rhinella marina*) spread in Australia is driven by the evolution of dispersal-enhancing traits, including path straightness and daily dispersal rates (Brown et al., 2014; Rollins et al., 2015). One possible mechanism driving our result is that the probability to depart from the native habitat patch, rather than the probability to disperse farther, was genetically determined. However, the lack of influence of the proportion of sedentary fish on range expansion outcomes implies that, in our study, the beneficial effects of large LDD distances were realised independently of their frequency of occurrence. This result implies that, at least for populations able to grow quickly at low abundance, the evolution of traits facilitating dispersal over longer distances (e.g. path straightness and daily dispersal rates) might have a greater effect on range expansion outcomes than that of departure-enhancing traits (e.g. bold and exploratory behaviours).

4.2 | Empirical relevance

Extrapolating our results to natural populations requires care because our simulations assumed that mutation and recombination did not occur, such that all genetic diversity was present when range expansion began. While the trends documented in our study should hold, we anticipate that the magnitude of the genetic diversity losses documented here would be diminished in scenarios where range expansion is accompanied by rapid population growth (Wright, 1931), as is typically the case (Excoffier et al., 2009). Mutations might occur especially frequently in highly fecund species (Williams, 1975), including teleost fish such as Tench, which can produce thousands of eggs per breeding event (Ablak Gürbüz, 2011).

Our simulations helped reconcile some of the discrepancies between theoretical predictions and the eco-evolutionary outcomes of Tench expansion observed empirically in eastern North America. Bernos et al. (2023) found no or small reductions (<0.01%) in two metrics of heterozygosity among 200 Tench genotyped on 2000 single nucleotide polymorphisms and sampled from the origin to the leading edges of the expanding populations of eastern North America. While the distribution of dispersal distances has not been empirically estimated in that system, we predicted that the mean dispersal distance of the mobile component was likely between 10 and 35 km.year⁻¹. For values falling closer to the upper limit of our predictions, our simulation models predict that genetic diversity should be mostly conserved throughout the invaded range.

Our models also demonstrated that the observed variability in range expansion outcomes – faster expansion and slightly greater retention of genetic diversity on the Southern expansion front (Avlijas et al., 2018; Bernos et al., 2023) – can be explained by variability in the spatial arrangement of habitat patches, and was therefore relatively predictable. For invasive species with adverse consequences for native biodiversity, like Tench (Avlijas et al., 2018), timely knowledge of expansion variability could provide an opportunity to identify areas at imminent risk of invasion, initiate mitigation strategies,

and encourage policies to stop the spreading population. From an evolutionary standpoint, we can expect losses in genetic diversity due to neutral dynamics in allelic frequency (i.e. genetic drift and gene surfing) to be limited. However, the impacts on Tench adaptive potential remain difficult to predict as the shuffling of alleles throughout the invaded range might enhance evolutionary potential by maintaining genetic variation, but could also prevent local adaptation and impair local fitness (Garant et al., 2007).

4.3 | Limitations of the modelling results

An important limitation of our study is that we do not include the role of density-dependent mechanisms on population persistence and dispersal rates. When populations experience reduced growth rate at low density (i.e. Allee effects), expansion is pushed from high-density populations behind the expansion front rather than pulled by long-range dispersers establishing new populations ahead of the expansion front (Miller et al., 2020), which may result in greater retention of genetic diversity and variability in expansion rates (Roques et al., 2012; Sullivan et al., 2017). Additionally, in the presence of positive density-dependent dispersal, the magnitude of genetic diversity losses might be reduced, even in populations where LDD distances are small, by the flux of individuals dispersing from the core (Birzu et al., 2019). Given the paucity of empirical data on the strength of density dependence and the processes it operates on (e.g. mortality, growth, dispersal and settlement) for Tench, and more broadly riverine fishes, it was not possible to incorporate density dependence into our model. Nonetheless, the influence of density dependence on range expansion outcomes in riverine fishes warrants further investigation.

Finally, while our models focused on neural dynamics and patterns of genetic diversity derived from unlinked neutral loci, adaptive processes are known to influence neutral genetic diversity during range expansions. For example, neutral alleles located close to beneficially adaptive mutations can increase in frequency as adaptive alleles become fixed in the population (hitchhiking) (Gillespie, 2000; Min et al., 2022; Smith & Haigh, 1974). Alternatively, neutral variants linked to mutations with adverse fitness consequences might decrease in frequency as deleterious alleles are purged from the population (background selection) (Charlesworth et al., 1993). Furthermore, adaptation to local environmental conditions occurring within a few generations can also play a significant role in range expansion outcomes (Andrade-Restrepo et al., 2019; Szucs et al., 2017).

4.4 | Conclusions

As environmental conditions change due to the global intensification of human activities, so do many species' ranges. In this context, understanding how expansion rate, genetic diversity and their variability, are jointly shaped by species' dispersal attributes and landscape

heterogeneity could improve our ability to accurately predict the ecological success of spreading populations (Williams et al., 2019). We showed that varying LDD distances shifted the extent of neutral genetic diversity losses, as well as expansion rate, in a consistent direction. Specifically, populations characterised by mean LDD distances larger than a critical threshold expanded faster and lost minimal amounts of genetic diversity. Importantly, LDD also affected the variability in expansion rate and neutral genetic diversity losses among local populations: expanding populations with LDD distances smaller than the critical threshold exhibited lower variability in expansion rate among local populations, but a wider range of genetic diversity losses. Developing criteria for predicting this critical distance threshold, which likely depends on species-specific dispersal characteristics, landscape attributes, and the scale of the range expansion, is critical. Finally, the possibility that populations characterised by small LDD distances might exhibit more variable, and thus less predictable, genetic diversity losses due to the stochastic forces affecting allelic frequencies (e.g. gene drift and gene surfing) implies that local populations might follow divergent evolutionary trajectories, with different sets of alleles – beneficial, neutral or deleterious – fixed at the leading edges. Possibly mirrored by variation in traits related to dispersal or fitness, this variability in the evolutionary consequences of range expansions could affect our ability to predict range expansion dynamics.

BENEFIT-SHARING STATEMENT

A research collaboration was developed between all collaborators, including scientists in academic and government agencies. Results of the research were shared with the broader scientific community. The research addresses an important topic for conservation, namely the eco-evolutionary consequences of range expansions, using Tench, an invasive species with adverse consequences for native biodiversity and ecosystems, as a model.

AUTHOR CONTRIBUTIONS

J.H., O.M., K.J. and N.M. provided constructive feedback on the manuscript. C.D. provided methodological guidance and constructive feedback on the manuscript; T.B. performed the research, analysed the data and wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data and R code are available on github (https://github.com/Linkr1/Tincatinca_Simulation_RangeExpansion).

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