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▶ To cite this version:

Amaïa Lamarins, Etienne Prévost, Stephanie M Carlson, Mathieu Buoro. The importance of network spatial structure as a driver of eco-evolutionary dynamics. Ecography, In press, pp.e06933. 10.1111/ecog.06933 . hal-04235812

HAL Id: hal-04235812
https://hal.inrae.fr/hal-04235812

Submitted on 11 Oct 2023

ECOGRAPHY

Research article

The importance of network spatial structure as a driver of eco-evolutionary dynamics

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Ecography
2023: e06933
doi: 10.1111/ecog.06933
Subject Editor: Kyle Haynes
Editor-in-Chief: Miguel Araújo
Accepted 30 August 2023

Investigating eco-evolutionary responses of populations to environmental changes requires a solid understanding of the spatial context in which they evolve. While the interplay between local adaptation and dispersal in guiding evolutionary outcomes has been studied extensively, it is often in a context of divergent selection and simplified spatial structure. Alternatively, we used a spatially-explicit demo-genetic agent-based model to simulate a complex network of interconnected populations of Atlantic salmon facing a perturbation shifting their genetic composition to create diversity among populations. Our model allowed us to track emerging demographic, phenotypic, and evolutionary changes from the individual to the metapopulation in a single, spatially realistic framework. We analyzed the influence of the spatial structure of genetic diversity and populations on the evolutionary dynamics under convergent selection (toward a common optimum). Our simulations showed adaptation and demographic recovery of local populations was enhanced by dispersal between initially diverse populations, providing general support for the adaptation network theory. This was particularly true for increased dispersal rates and a random spatial genetic structure. Importantly, our spatially realistic model emphasized that the evolutionary and demographic trajectories of local populations are context-dependent and can be heavily influenced by the spatial configuration of populations linked by dispersal. Overall, the adaptive capacity of the network depended on the 'opportunity for adaptation' provided by immigration patterns that emerged from the connectivity structures of the scenarios tested. We highlight the importance of spatial diversity and population structure for the ability of species to respond to environmental change, with implications for management and conservation of spatially structured populations.

Keywords: demo-genetic agent-based model, dispersal, diversity, evolution, metapopulation, spatial structure

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Introduction

Dispersal and genetic adaptation are ecological and evolutionary processes that can promote species persistence to environmental changes. However, gene flow (a consequence of dispersal) can alter recipient populations trajectories and limit local adaptation. The extensive literature on the balance between gene flow and selection emphasizes that divergent selection across populations favors adaptive divergence, while gene flow can homogenize populations (Ronce and Kirkpatrick 2001, Lenormand 2002). Many studies from diverse taxa provide evidence of this tension by documenting negative correlations between genetic (or phenotypic) variation and degree of gene flow (e.g. in fish, Hendry et al. 2002; in insects, Nosil and Crespi 2004; in plants, Sambatti and Rice 2006).

While gene flow can lead to homogenization and maladaptation, it can also benefit adaptation to changing conditions (Garant et al. 2007, Blanquart and Gandon 2011). Maladaptation of populations may arise from many eco-evolutionary origins (Brady et al. 2019), but perturbations constitute an important factor. Natural or anthropogenic perturbations may alter the phenotypic and genetic compositions of populations (i.e. diversity within populations), deviating them from their optimum and becoming maladapted (e.g. extreme climate events, Vincenzi et al. 2017, stocking, Stringwell et al. 2014, selective harvest, Anderson et al. 2008). But perturbations can have different effects on a population network, influencing the diversity among populations (Shama et al. 2011). Recovery and evolutionary dynamics of populations after perturbations have been extensively studied (Vincenzi et al. 2014, García-Ulloa et al. 2020), albeit primarily at local scales and on isolated population (Bell and Gonzalez 2011, Uecker et al. 2014). Yet, dispersal and gene flow between spatially structured populations can provide demographic, genetic (i.e. increase of within population genetic diversity), and evolutionary rescue effects (Carlson et al. 2014, Fitzpatrick et al. 2020) favoring resilience and adaptation of populations.

Importantly, gene flow cannot occur without dispersal but dispersal does not always result in gene flow, which might explain observed local adaptation patterns despite high rates of dispersal (Moore et al. 2013). Indeed, the reproductive success of immigrants can be lower than philopatric individuals (Mobley et al. 2019, Barbraud and Delord 2021). Understanding the factors contributing to gene flow necessitates a consideration of the factors contributing to dispersal, including the spatial structure of populations. Many theoretical studies assumed simple spatial structures like a linear environment (Andrade-Restrepo et al. 2019), two demes (Pontarp et al. 2015), or populations structured as grid cells, with equal size and distance among them (Schiffers et al. 2013). However, other experimental and theoretical studies with more complex spatial structure of populations have revealed that spatial structure has a major influence on demography, including potential consequences for metapopulation persistence (Vuilleumier et al. 2007, Gilarranz and Bascompte 2012, De Roissart et al. 2015), synchrony (Yeakel et al. 2014, Larsen et al. 2021), or metacommunity biodiversity (Carrara et al. 2014).

Similarly, the spatial structure of a network of surrounding populations is expected to play an important role in the evolutionary dynamics of the local populations. Indeed, heterogeneous spatial structure can induce asymmetry in dispersal with potential consequences on eco-evolutionary dynamics (e.g. via density-dependent effects). For example, De Roissart et al. (2016) experimentally showed divergence in life history traits of spider mites with variation in patch size, while theoretical studies have revealed the influence of spatial distribution of habitats on specialization (Débarre and Gandon 2010, Papaïx et al. 2013) and adaptation to environmental change (McManus et al. 2021). Another line of work has explored how the configuration of dendritic riverine networks influences patterns of genetic diversity (Labonne et al. 2008, Thomaz et al. 2016). We build on these findings to investigate the impact of spatial structure on the evolutionary dynamics of local populations, specifically 1) the spatial genetic structure (i.e. spatial distribution of diversity among populations) and 2) the spatial configuration of the network (i.e. distance between populations and their respective carrying capacities).

But investigating the interplay between dispersal and genetic diversity by considering eco-evolutionary feedbacks and the spatial structure of a network is challenging. It requires precise monitoring of populations at various spatio-temporal scales and levels of organization (from genes to metapopulation, Baguette et al. 2017) as well as knowledge of the eco-evolutionary processes at work. Analytical and adaptive dynamics modeling approaches have been developed to provide parsimonious frameworks (Papaïx et al. 2013, McManus et al. 2021) but they may not be adequate to comprehend the complex eco-evolutionary feedbacks occurring in nature (Bonte and Bafort 2019, Govaert et al. 2019). In silico modeling approaches such as demo-genetic agent-based models (DG-ABMs, or individual-based) including evolutionary processes and genetic mechanisms, offer an alternative. Importantly, DG-ABMs do not assume an a priori fitness function. Instead, variation in fitness emerges from eco-evolutionary processes, individual decisions, interactions and feedbacks, resulting in the evolution of patterns structuring genetic diversity and population dynamics (Lamarins et al. 2022a). By also allowing the explicit representation of the spatial structure of populations, these models facilitate the emergence of unanticipated eco-evolutionary feedbacks (Travis and Dytham 1998). However, implementing such complex biological systems into a generic model can be challenging. Models based on well-known case studies with established parameters based on empirical knowledge, on the other hand, preserve the complexity of the real world while investigating unobserved but realistic scenarios (e.g. dispersal patterns).

In this study, we investigated the eco-evolutionary dynamics resulting from the interplay between dispersal, genetic diversity among populations, and their spatial configuration using a spatially-explicit demo-genetic agent-based model simulating a network of Atlantic salmon *Salmo salar* populations. Our model allowed to track demographic, phenotypic, and evolutionary changes from the individual to the metapopulation in a single, spatially realistic framework. Several adaptive traits could evolve, and their optimal value emerged dynamically from the interactions between eco-evolutionary processes. At initialization, populations genetic compositions were altered, simulating a sudden and temporary perturbation, moving them away from their optimum. We designed diversity across populations while exposing them to diverse spatial genetic structures (none, gradient and random) and dispersal rates. The spatial configuration was then gradually adjusted, starting with a basic configuration (equal distances and carrying capacities among populations) and progressing to the complexity of an observed Atlantic salmon metapopulation in Brittany (France). We evaluated for these scenarios the dynamics of return to local optimum for each populations on an ecological time scale (out-of-equilibrium dynamics). While the combination of dispersal and genetic variation among populations is predicted to promote patterns of adaptation, we predicted that the spatial configuration of local populations has a strong influence on their evolutionary dynamics within the network, particularly through the number and characteristics of immigrants.

Material and methods

Model overview

We used a spatially explicit demo-genetic agent-based model, called MetaIBASAM (metapopulation individual-based Atlantic salmon model), simulating the eco-evolutionary dynamics of interconnected populations of Atlantic salmon (Lamarins et al. 2022b). MetaIBASAM simulates the salmon's life cycle and combines all of the species' current knowledge. Atlantic salmon is an anadromous species that divides its life cycle into two phases: the freshwater phase, where reproduction and development of juveniles take place, and the marine phase, where growth and maturation occur. Although this species remains emblematic of philopatry, some adults disperse to non-natal rivers during their breeding migration, though this is often overlooked (Birnie-Gauvin et al. 2019).

Two prior studies have outlined the model employed here: Piou and Prévost (2012) focused on a single population (IBASAM) and Lamarins et al. (2022b) extended the model to consider multiple populations connected by dispersal (MetaIBASAM). We present an overview of the model's primary aspects here and refer the reader to the preceding works for further details.

First, the model explicitly simulates each individual's entire life cycle, from birth to death, with growth, life history tactics and reproduction, tracking individual life history traits in each population. Second, it includes eco-evolutionary processes such as environmental effects (e.g. temperature and density dependent effects on growth and survival) and the genetic basis of traits (growth potential and maturation thresholds), allowing their transmission to succeeding generations through a quantitative genetics approach combined with a Mendelian inheritance system (Piou and Prévost 2012). The optimal genetic trait values evolve dynamically as a result of interactions between the model's eco-evolutionary processes and the resulting fitness. For example, the optimal value of growth potential (i.e. intrinsic growth rate of individuals), an heritable and fitness-related trait, results from a tradeoff between growth and survival in river and at sea (Lamarins et al. 2022b, Supporting information). Finally, during the spawning migration of adults from the sea to the rivers, a parsimonious dispersal process allows individuals to disperse between populations (i.e. between patches), with a constant emigration rate over time and space, regardless of the individual's features. The recipient population is chosen based on its distance from the natal population, moderated by its carrying capacity via a dispersal kernel (Lamarins et al. 2022b). We did not impose any direct costs of dispersal (e.g. no additional mortality), and the reproductive success of dispersing individuals was subject to the same factors as philopatric individuals (i.e. sexual selection and offspring survival). Each population in the network has its own eco-evolutionary dynamics, which are influenced by dispersal (i.e. demographic changes) and gene flow.

Scenarios, simulations, and model parameterization

Our goal was to investigate the eco-evolutionary dynamics of maladapted populations caused by the interplay between dispersal, genetic diversity among populations, and their spatial configuration (Fig. 1). As in Lamarins et al. (2022b), we simulated a network of fifteen populations inspired by the spatial configuration of the salmon metapopulation of Brittany (France, Perrier et al. 2011), i.e. adjacent rivers along a coastline (Fig. 2). Our general approach is explained below. First, we reshaped the genetic composition of populations to varied degrees, resulting in diverse spatial genetic structures (i.e. spatial distribution of populations genetic composition). Then, we modified the spatial configuration of populations (i.e. distance and carrying capacity of populations). Finally, we tested these spatial scenarios for a gradient of dispersal rates ranging from 0 to 30%, i.e. around the theoretical optimal rates (10–20%) that maximize metapopulation demographic stability in this model (Lamarins et al. 2022b). All other parameters were kept identical for all populations in all scenarios (e.g. environmental conditions regimes, exploitation rates, stage-survival rates, heritabilities, etc.; Lamarins et al. 2022b). Below we detail each of these three steps.

First, we tested the effects of the spatial genetic structure of maladapted populations in a simple spatial configuration, i.e. equal carrying capacity and distance between populations (Fig. 2A–C), which maintained similar emigration and immigration rates between neighboring populations (i.e. symmetrical dispersal, Supporting information). We compared scenarios with (A) no spatial genetic structure, (B) a gradual spatial genetic structure and (C) a random

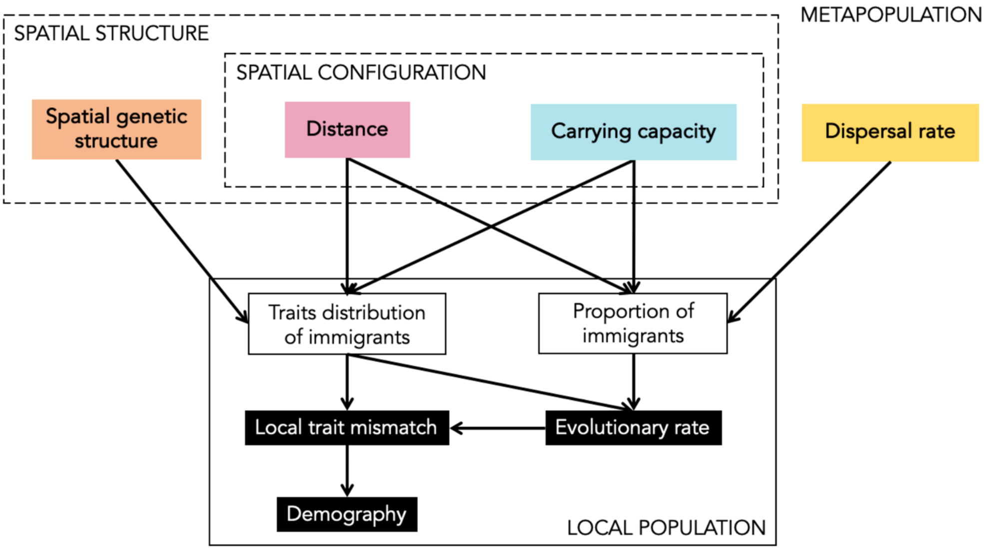

Figure 1. Schematic representation of the interplay between dispersal and both components of spatial structure, i.e. the spatial genetic structure of populations, and their spatial configuration, on the eco-evolutionary trajectories of local populations. Dispersal intensity, when combined to diversity among populations, is expected to influence the proportion of immigrants and the evolutionary rates (Eq. 2) of local populations. Spatial genetic structure, when combined with dispersal, can modify the genetic traits distribution of immigrants, and ultimately the local trait mismatch and evolutionary rates of local populations. The spatial configuration of populations (distance or carrying capacity) can modulate both the composition and quantity of immigrants, and ultimately the evolutionary trajectories of local populations. Finally, the evolutionary trajectories of local populations can influence their demography and dynamically feedback on the metapopulation spatial genetic structure and dispersal patterns.

distribution of diversity across the network (Fig. 2). To set both populations maladaptation (as induced by a perturbation) and spatial genetic structure, populations were initialized with genetic traits distributions (maturation thresholds and growth potential) shifted away from their emerging optimum. More precisely, in scenario A, all populations genetic distributions were shifted by + 15% of the mean compared to Lamarins et al. (2022b). In scenario B and C, however, each population had its own distribution of genetic traits at initialization, with a mean shift across populations of + 15% and a range from 0 to + 30% between populations (Fig. 2B–C). The initial genetic diversity within populations (i.e. variance of genetic traits) was set equal among populations. But in the scenario A, it was set with higher values compared to the scenario B and C in order to simulate equal standard genetic variation over the whole metapopulation between scenarios. Thus, for genetic growth potential, the mean value over the metapopulation was 0.15 while the total standard deviation was 0.22 for all scenarios. According to the optimal fitness value of growth potential emerging from the model simulations presented by Lamarins et al. (2022b), most populations were maladapted at the start of the simulations in all scenarios (optimum around zero at log scale, Fig. 2, Supporting information). This allows us to assess the adaptation capacity of populations following a disturbance in various network configurations.

Second, we investigated how different network spatial configurations, such as unequal carrying capacity and population distance, impacted asymmetrical dispersal and eco-evolutionary dynamics but only in the context of random spatial genetic structure (Fig. 2D–F, Supporting information). The simulated spatial configuration, i.e. adjacent rivers along a coastline (Fig. 2), contrasts with most studies of riverine systems, which have focused on the configuration of dendritic networks within basins (Paz-Vinas and Blanchet 2015, Fronhofer and Altermatt 2017), but is particularly relevant to dispersal among basins and across gradients of diversity. We sequentially modified the distance between populations (Fig. 2D), carrying capacities (Fig. 2E), and both (Fig. 2F), based on the distance between populations and the area of juvenile production of each population as measured in the Brittany Atlantic salmon metapopulation by Lamarins et al. (2022b). Variation of carrying capacities of populations (scenarios E–F) slightly changed the overall mean (0.14 for growth potential) and standard deviation (0.224 for growth potential) of genetic traits at the metapopulation scale.

We ran 50 replicates over 50 years for each of the 24 scenarios (four dispersal rates × six network genetic and spatial structures). With a generation time of approximately 2.5 years, our simulation time was sufficient to detect the evolution of life-history traits but short enough to remain in a non-equilibrium state to be able to contrast our scenarios. For each population, simulations began with a random draw of individuals from the population distribution parameters based on the scenarios. To limit computational time, simulations were performed for only 25% of the estimated carrying capacities for the set of rivers. We ran the simulations using R ver. 3.6.3 (www.r-project.org) and the package ‘MetaIBASAM’ ver. 0.0.6 (https://github.com/Ibasam/

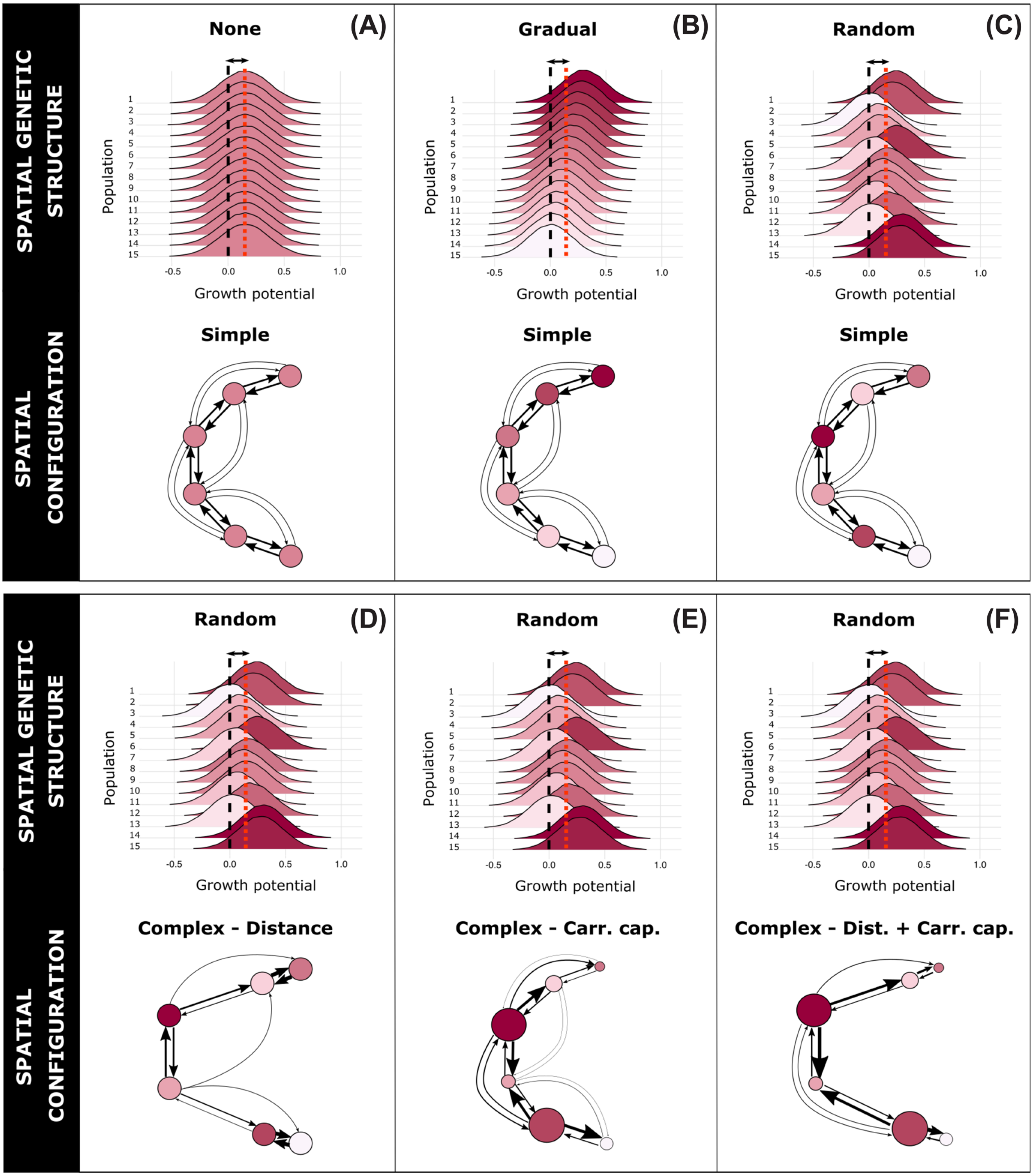

Figure 2. Schematic representation of the spatial genetic structure and the spatial configuration of the network for each scenario (A–F). At the top of each scenario box are represented the distributions of genotypic growth potential (log scale, optimum represented by the black dashed line) at initialization of simulations for the 15 populations (average over populations represented by the red dashed line). At the bottom of each scenario box, the circles represent populations (distance between them, size relative to their respective carrying capacities, color indicating the mean of the genetic distribution of growth potential at initialization), the arrows represent the dispersal of individuals (thickness of the line indicating the intensity resulting from the dispersal kernel and spatial configuration). The full simulated network is shown in the Supporting information.

MetaIBASAM). Code and R scripts are freely available at https://github.com/Ibasam/SpatialStructure.

Simulation outcomes analysis: local adaptation/maladaptation

The evolution of genetic features was monitored by measuring the average value of philopatric adult traits across time, averaged over simulation replicates. Hereafter, we only show evolution patterns of the genotypic growth potential because it was the trait under the strongest selection compared to maturation thresholds (Supporting information). To compare patterns of local adaptation versus maladaptation in populations, we adapted the 'mismatch metrics' proposed by McManus et al. (2021). For each scenario, we calculated the local population's trait mismatch (hereafter, LTM) as the difference between the median trait value of philopatric individuals of a year *t* of all simulation replicates and the optimal value of the trait (0 for growth potential, Eq. 1).

$$\text{LocalTraitMismatch}_{i,t} = \left|\delta_i - X_{i,t}\right| \qquad (1)$$

Where δ_i is the optimal genetic trait value of the population *i* and $X_{i,t}$ is the median of the genetic trait of the philopatric individuals from the population *i* at a year *t* over all simulation replicates of a given scenario.

We also calculated the rate of evolution for each population by comparing absolute LTM values at the start of simulations (averaged over years 1–5, $\text{LTM}_{i,1:5}$) to the end of simulations (averaged over years 45–50, $\text{LTM}_{\text{i},45:50}$), divided by the time required to reach the final LTM value ($T(\text{LTM}_{i,45:50})$, Eq. 2). For example, over the 50 years of simulation, the more reduced LTM, and/or the shorter time of stabilization of the LTM, the higher the evolutionary rate.

$$\text{EvolutionaryRate}_i = \frac{\left|\text{LTM}_{i,1:5} - \text{LTM}_{i,45:50}\right|}{T\left(\text{LTM}_{i,45:50}\right)} \qquad (2)$$

We tracked the distribution of genetic traits of immigrants in each of the local populations over time, as well as the proportion of immigrants, to reveal the impact of immigrants on the local dynamics of recipient populations. Finally, the number of returning adults (philopatric and immigrants) averaged over simulation replicates for each population, year, and scenario was used to assess the demographic repercussions of evolutionary trajectories and population adaptation.

Results

Dispersal and diversity among populations with a simple spatial configuration

At the network scale, the three scenarios of spatial genetic structure showed contrasted pattern of traits evolution. Without dispersal, while maturation thresholds didn't change over time (Supporting information), growth potential evolved toward the optimum ($\text{LTM}_{\text{optimal}} = 0$), illustrated by a lower trait mismatch at the end of simulations compared to initialization. But evolution was stronger for the scenario without diversity among populations due to higher initial within-population diversity (black color; –50% on average compared to $\text{LTM}_{\text{initial}} = 0.15$ without dispersal; Fig. 3A). However, with dispersal, the final LTM of populations in this scenario remained high (–49% on average compared to initialization) regardless of the dispersal rate, while the evolutionary rates remained low (Fig. 3A–B). In contrast, the final LTM of populations decreased with increasing dispersal when combined with genetic diversity among populations, and this pattern was stronger when genetic diversity was distributed randomly compared to gradually (respectively, orange and green color; –79 and –56% on average compared to initialization with 10% dispersal; Fig. 3A). The evolutionary rates of populations increased with dispersal for a gradual genetic structure, and even more when genetic diversity was randomly distributed among populations (Fig. 3B). Finally, population recovery following perturbation was enabled by the evolution of growth potential within the population network, which was facilitated by dispersal and diversity among populations. Indeed, adaptation alone (without dispersal) did not allow the metapopulation to recover within the time frame we observed (Fig. 3C). For example, in the scenario with a random distribution of diversity and no dispersal (orange color), the metapopulation abundance remained at its lowest level 50 years after the perturbation despite a reduced LTM by 44%. But when combined with dispersal, it had the highest recovery and stability (respectively, + 65% of abundance and lower CV by 36% on average for 10% dispersal compared to the scenario without diversity) in the metapopulation's demography (Fig. 3C–D). These results suggest that resilience of metapopulation is enhanced within a diversified and connected network of populations.

At the local population scale, the overall differences of local trait mismatch, evolutionary rates and demography between scenarios of dispersal rates and spatial genetic structures can be explained by the resulting immigration patterns (Fig. 4). First, changes with increasing dispersal rates can be explained by the increase in the proportion of immigrants (Fig. 4A, Supporting information). Indeed, increasing dispersal rates had small influence on the average value of growth potential of the immigrants; it rather increased their quantitative contribution to local populations.

Second, changes with spatial genetic structures can be explained by the trait distributions of immigrants, which were more or less diverse and close to the optimum on average (Fig. 4A, Supporting information). Without initial diversity among populations (shades of grey), immigrants from neighboring populations showed the same average value of growth potential that the recipient population (Fig. 4A1). Populations thus evolved at a slow rate and didn't show demographic recovery from perturbation whatever the dispersal rate within 50 years (Fig. 4B2). In the scenario of gradual genetic structure (shades of green), populations were

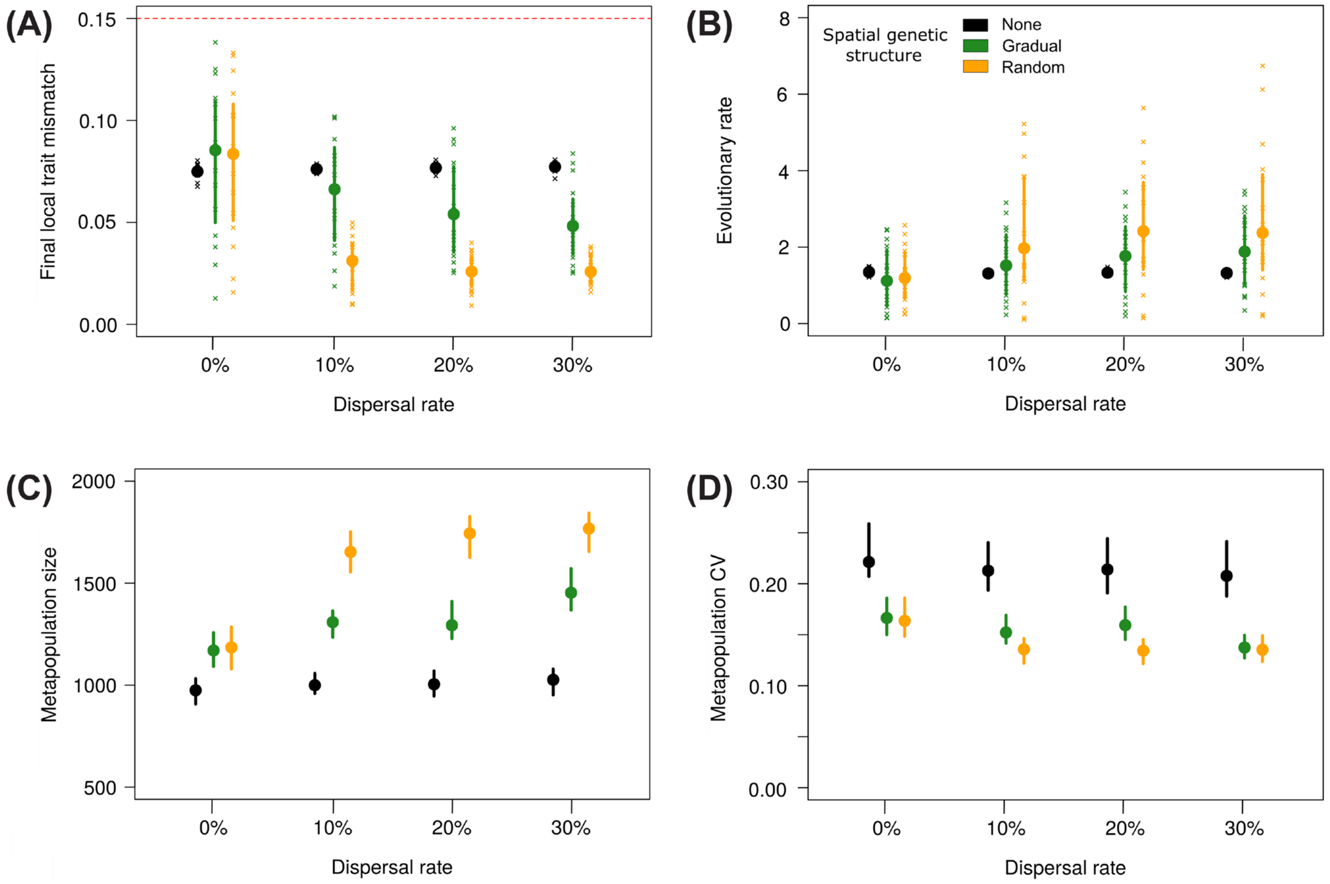

Figure 3. (A–B) Distributions (median, quantiles 50%) of (A) the final local trait mismatch (averaged over the last five years) and (B) the evolutionary rates of the 15 local populations (represented by the crosses). (C–D) Distributions (median, quantiles 50%) over simulation replicates of (C) the metapopulation size (number of returning adults averaged over the last five years) and (D) the coefficient of variation of metapopulation abundance (calculated over the 50 years). Distributions are represented for each scenario of dispersal rate and spatial genetic structure under a simple spatial configuration of populations. The dashed red line represents the initial local trait mismatch averaged over populations, simulation replicates and scenarios.

surrounded by populations with close genetic distributions. However, these small differences among populations and the diversity of growth potential among immigrants (Supporting information) were beneficial to populations adaptation and demographic recovery once there was dispersal, particularly for the most maladapted populations and high dispersal rates (Fig. 4A2–4, B1–3). Finally, in the scenario with random genetic structure (shades of orange), where the genetic composition of immigrants was more diverse (Supporting information) and more distinct on average from that of the recipient populations, populations with high initial LTM benefited quickly and strongly, both in terms of adaptation and demographic recovery, from immigration (Fig. 4A5, B1). But the opposite also occurred, to a lesser extent though, for populations already adapted, where immigration from maladapted populations limited their adaptation (Fig. 4A7, B3). For populations with intermediate LTM, random structure was still beneficial if immigrants were better adapted. Even though the patterns of evolution were contrasted among populations in this later scenario, the overall effect was an improvement in terms of adaptation of the metapopulation and of its demography (Fig. 3). This suggests the importance of the spatial genetic structure in determining evolutionary and demographic trajectories of local populations interconnected by dispersal.

Dispersal and diversity among populations with a complex spatial configuration

On average, no significant differences in local trait mismatch and evolutionary rates were observed at the population network scale between scenarios of population spatial configuration (distance and/or carrying capacity; Supporting information). However, variable patterns were noticeable at the local population scale (Fig. 5), showing contrasted evolutionary trajectories of populations induced by the variable spatial configurations tested. For example, variations in distances within the network (red color; scenario D in Fig. 2) reduced adaptation of some populations (i.e. higher local trait mismatch and/or lower evolutionary rate, such as for the populations 10 and 14), increased adaptation of others (such as for the populations 1 and 2), or did not change

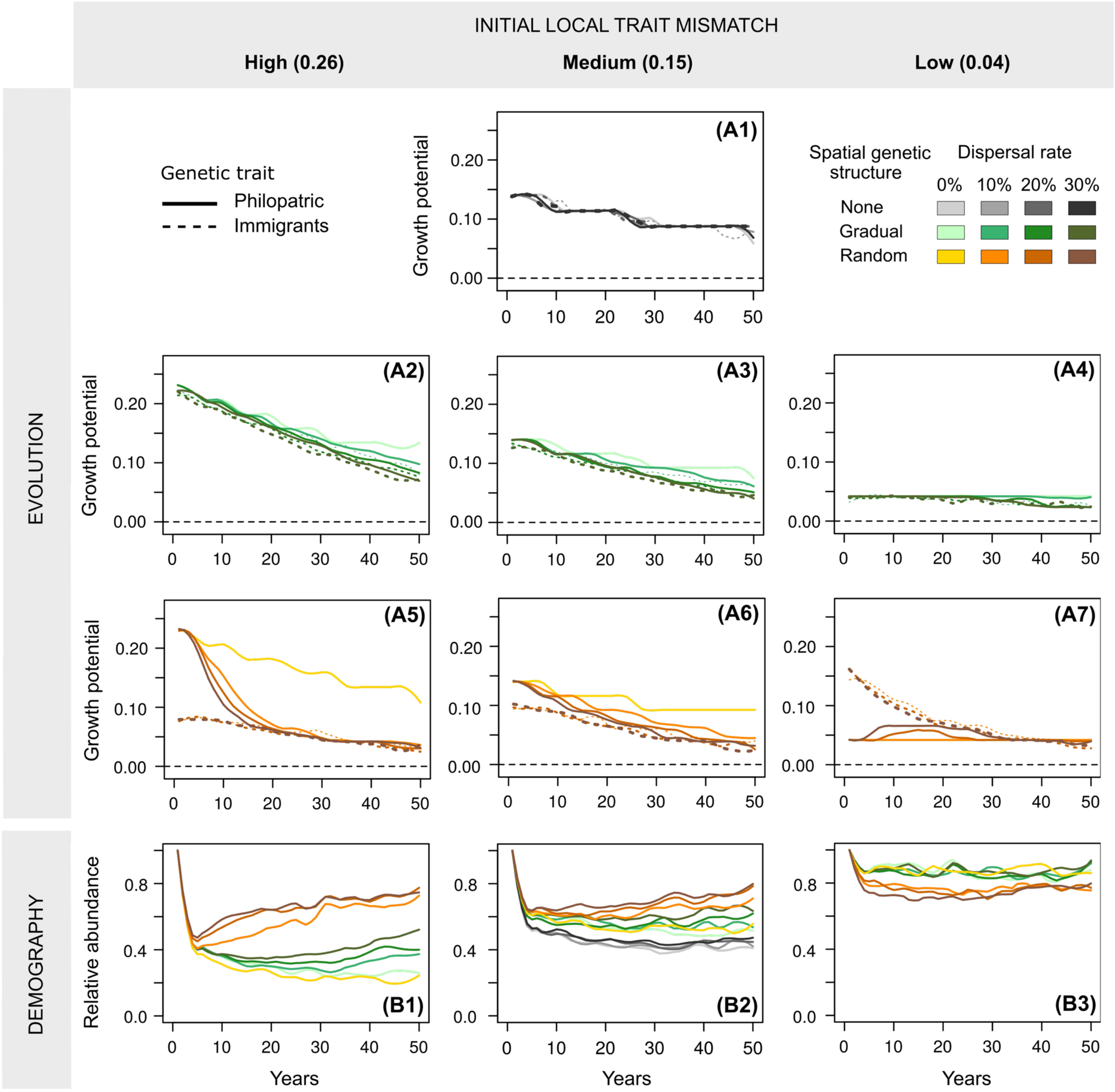

Figure 4. Temporal dynamics of (A) the genetic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line) and (B) of the relative abundance of returning adults, averaged over simulation replicates, for each scenario of dispersal rate and spatial genetic structure under a simple spatial configuration of populations, in examples of populations of the network starting simulations at different local trait mismatch (high-medium-low). In (A), the horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates. See the Supporting information for all populations.

populations trajectories (e.g. population 13) compared to the scenario of simple spatial configuration (orange color, Fig. 5). The different patterns associated to distance variation within the network can be explained by changes of the trait distribution of immigrants relative to the optimum. For instance, the increased adaptation of population 1 was fostered by a trait distribution of immigrants which was closer to the optimum, mainly resulting from a reduced distance with population 3 which started simulation close to the optimum (Fig. 5). Conversely, the reduced adaptation of the population 10 can be explained by the isolation of this population from others that were more adapted.

Variations in carrying capacities within the network (blue color; scenario E in Fig. 2) also limited (e.g. populations 1–3), fostered (e.g. population 10 and 14), or did not change (e.g. population 13) their adaptation (Fig. 5), both through changes

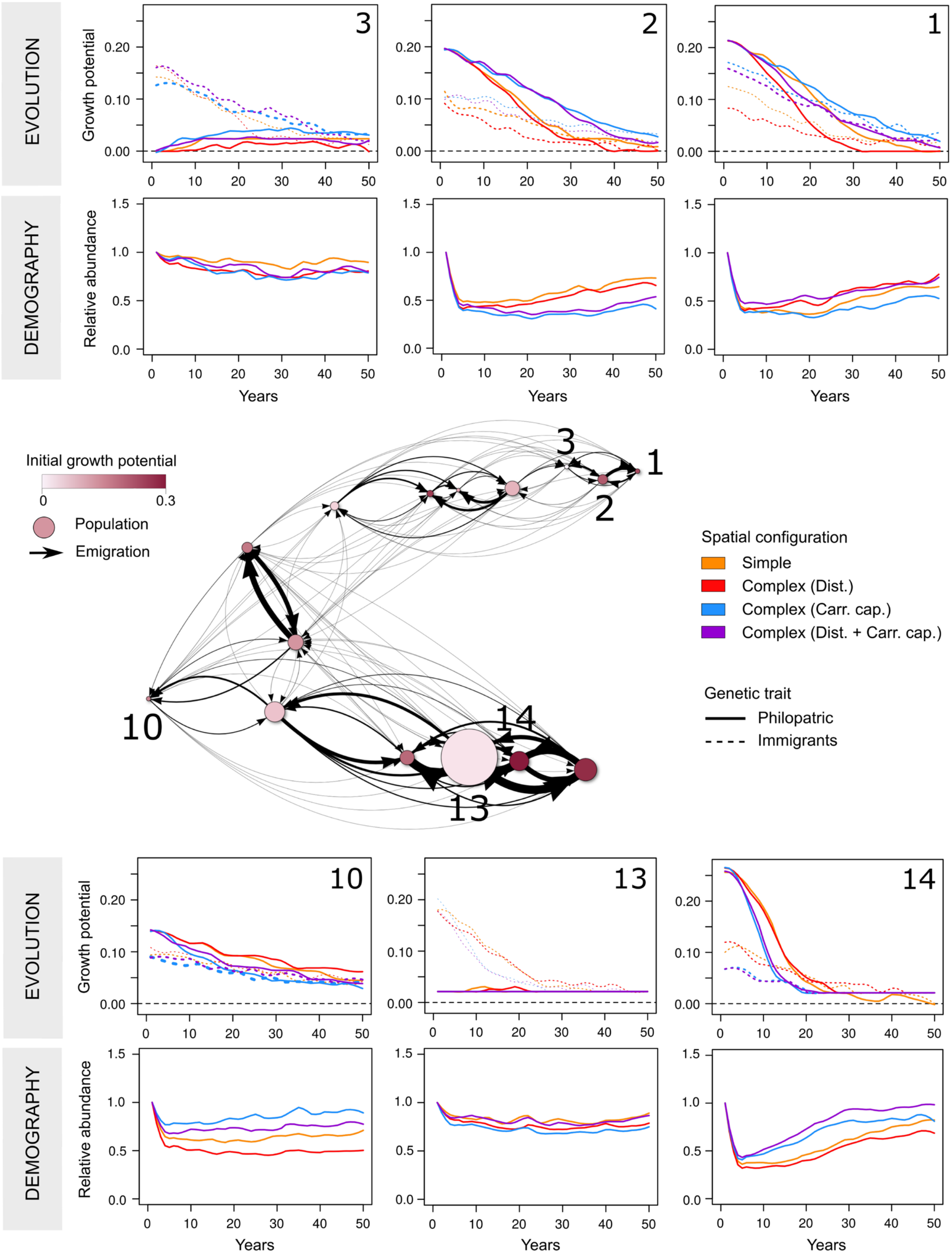

Figure 5. Temporal dynamics of the genetic value of growth potential (log scale) of philopatric adults (full line) and immigrants (dotted line), and of the relative abundance of returning adults, averaged over simulation replicates, for each scenario of spatial configuration under a random genetic structure and dispersal rate of 10%. Only six populations of the network (each box is a single population identified by its number from 1 to 15) are represented (Supporting information for all populations). The horizontal dashed black line represents the optimum value of growth potential. The thickness of the immigrants lines (color dotted lines) represents the averaged proportion of immigrants over time and simulation replicates. The spatial network illustrates the spatial structure (distances, carrying capacities, spatial genetic structure) of the last scenario F.

of the trait distribution of immigrants (e.g. farther from/closer to the optimum) and the proportion of immigrants (e.g. higher/lower immigration). For instance, the smaller and the larger carrying capacity of the population 3 and 2, respectively, modulated their contribution to the population 1, which pushed away the immigrant's distribution from the optimum and reduced adaptation of population 1 compared to the scenario of simple spatial configuration (orange color, Fig. 5). Conversely, the increased contribution of population 13, a large population starting simulations close to the optimum, to both population 10 and 14, increased their adaptation via the distribution of immigrants (e.g. in population 14) but also via their proportion in the recipient population (e.g. increased proportion in population 10, Fig. 5).

The simultaneous variation of distance and carrying capacities between populations (purple color; scenario F in Fig. 2) resulted in combined effects of the scenarios with distance or carrying capacity variation only on adaptation patterns (Fig. 5). Ultimately, these contrasted effects of variation in spatial configuration on local populations explain why we did not observe difference of adaptation metrics at the network scale. However, these local changes of evolutionary trajectories also had an impact on the demography of local populations, and strongly determined their dynamics of return to equilibrium (Fig. 5).

Discussion

Interplay between dispersal and diversity among populations

Our successive scenarios allowed us to disentangle the effects of multiple components of a network on evolutionary dynamics, such as spatial genetic structure, population distance and demography. Our simulations revealed stronger adaptation when diversity among populations was paired with dispersal, especially at higher dispersal rates and when genetic diversity was randomly structured. Indeed, dispersal rates increased the contribution of immigrants, and the spatial genetic structure determined the distribution of immigrants traits, which both determined the 'opportunity for adaptation' via immigration into the recipient populations. This higher evolutionary potential of interconnected and diversified populations supports the concept of adaptation networks (Webster et al. 2017), where diversity among populations, additionally to the widely recognized within-population diversity (Jump et al. 2009), contributes to evolutionary options favoring adaptation. We also demonstrated that the spatial structure of genetic diversity across the network (e.g. random versus gradual) strongly influences the outcomes of the adaptive network.

McManus et al. (2021) also investigated the influence of environmental heterogeneity on evolutionary responses in the context of coral reefs experiencing rapid environmental change. They found that populations in a network with regular dispersal had a stronger adaptive response to local temperature compared to populations with random dispersal, because the latter resulted in gene swamping and trait mismatch. The differences between our studies might be explained because populations were confronted with different trait optimums in their scenarios (i.e. divergent selection) and adaptation was favored overall if populations remained diversified (the similar results of Papaïx et al. 2013, where aggregation and specialization lead to a better adaptation). We chose the opposite scenario, a convergent selection, as we would predict on a regional scale due to climate change's synchronizing influence (Hansen et al. 2020). Our findings show that spatial genetic structure has an impact on population trajectories, but only in the situation of maladapted populations in the absence of divergent selection. Taking advantage of the demo-genetic modelling approach, our study also showed demographic recovery of maladapted populations was not observed without dispersal despite adaptation within 50 years, but only when dispersal occurred, providing evidence for the evolutionary rescue effect of dispersal. We thus showcased the strong positive demographic consequences arising from the rescue effects provided by dispersal and the random genetic structure of populations, at both local and metapopulation scales (Fig. 3–4).

Spatial configuration influences local populations evolutionary trajectories

Our work also shed light on the interaction between the genetic diversity among populations and the network spatial configuration. Even though no discernible difference in trait mismatch and evolutionary rate was observed on average at the network scale between simple and complex spatial configurations, the model revealed contrasted patterns at the scale of local populations. Our findings showed that variation in populations' distance and carrying capacity can modulate dispersal patterns and contributions of populations to neighboring populations via asymmetrical flow of individuals for a given spatial genetic structure (Supporting information). These variable dispersal patterns, characterized by the intensity and genetic distribution of migrants, changed the 'opportunity for adaptation' of immigration to recipient populations, fostering their adaptation in some cases (e.g. increased contribution of a large or nearby adapted population), while hindering adaptation in others (e.g. decreased contribution of a small or far population). Although not explored here, we suggest this opportunity for adaptation provided by dispersal may interact with within-population diversity, which can also be influenced by populations size. Ultimately, these variable evolutionary trajectories observed depending on the spatial configuration further impacted local and metapopulation demography (Fig. 5, Supporting information). These results emphasize the spatial context-dependence of evolutionary trajectories of diversified populations connected by dispersal, and the importance of considering their spatial configuration (distance, carrying capacity), combined with spatial genetic structure, to fully understand evolutionary and demographic dynamics of a network of populations.

Our results build on earlier work highlighting the influence of spatial configuration on demographic trajectories of populations. The increasing recognition of the importance of considering the influence of demography in dispersal dynamics and their consequences on population dynamics was recently reviewed by Drake et al. (2022b) who further emphasize the value of considering the 'demographically-weighted connectivity' (which they define as 'an extended conceptual representation of landscape connectivity that considers, explicitly, the population dynamics and demographics'). It has also been empirically demonstrated that considering connectivity patterns as coming from the spatial structure of a landscape is critical to better understand demographic dynamics of populations (Drake et al. 2022a). In addition to demography, we emphasize the relevance of studying the spatial structure of genetic traits of interconnected populations in order to understand the evolutionary and demographic trajectories of local populations. Similarly, Ranke et al. (2021) described asymmetrical dispersal that was linked to the spatial structure of a metapopulation of sparrows *Passer domesticus* and expected consequences for evolutionary dynamics of populations.

Perspectives and management implications

Spatially explicit demo-genetic individual based models are powerful tools to explore eco-evolutionary dynamics of spatially structured populations. One of the most interesting properties of this type of approach is the ability to generate eco-evolutionary patterns without specifying the fitness function. For example, Fronhofer and Altermatt (2017) showed that dispersal strategies evolve in response to the spatial structure of genetic relatedness (to avoid kin competition) and network properties (topology and connectivity) influence spatio-temporal correlations in fitness expectations. More realistic design of spatial and temporal heterogeneity between populations in modeling approaches such as MetaIBASAM hold promise for providing insight into dynamics of diversified networks (Travis and Dytham 1998).

Having said that, there is much room for improvement of our model, including a consideration of additional mechanisms that could strongly influence eco-evolutionary dynamics. Given the complexity of the model, we adopted a parsimonious approach focusing on the evolution of growth potential, an important trait in life history theory. The dispersal trait was kept as simple as possible, only influenced by distance between populations and attractivity (carrying capacity). But other important dispersal mechanisms could be explored, such as density-dependence (both for emigration and immigration, e.g. reviewed by Harman et al. 2020, in salmonids, Berdahl et al. 2016), habitat choice (e.g. based on environmental similarity, Mortier et al. 2019), as well as the genetic basis of dispersal itself (Saastamoinen et al. 2018). Including these mechanisms might change the dispersal patterns in space and time, influencing the eco-evolutionary dynamics of local populations (Peniston et al. 2019).

While we did not explore the evolution of dispersal, this is a potential fruitful direction for future research building on our approach. Prior work has revealed that dispersal can be selected against in heterogeneous environments because of local adaptation, but dispersal can also be selected for as a spreading strategy when environments vary in space and time, to reduce kin competition, or because it favors the propagation of advantageous genes (Lenormand 2002). Thus, we hypothesize that in our model dispersal should evolve in response to 1) the spatial structure of adaptive traits, 2) characteristics of populations within a network (e.g. small versus large populations to avoid kin competition) and 3) environmental changes (e.g. increasing spatial synchrony), modifying the local trait mismatch and evolutionary rates. Regardless of the dispersal rate, gene flow could be lower than the dispersal rate because of reduced reproductive success of immigrants (i.e. pre/post zygotic lower fitness) or higher if immigrants have higher reproductive success (due to sexual selection favoring immigrants and/or higher survival of their offspring). This pattern emerged from our model simulations, in which immigrants had higher reproductive success than philopatric adults in most maladapted populations, but lower in adapted populations (for females only, Supporting information); dispersal propensity could thus evolve as function of local adaptation patterns. It is then crucial to consider both dispersal (i.e. demographic consequences) and gene flow (i.e. evolutionary consequences) and their variation in space and time (Peniston et al. 2019, Drake et al. 2022a).

Many studies advocate for the conservation of adaptation networks with population diversity and connectivity (Webster et al. 2017, Walsworth et al. 2019). However, our findings highlight the importance of population spatial structure, i.e. spatial genetic structure and population spatial configuration, as key drivers of local evolutionary and demographic dynamics that must be considered when managing populations. Ideally, identifying key populations based on their influence on eco-evolutionary dynamics of the metapopulation (e.g. adaptive value, higher genetic diversity) could enhance adaptation and conservation success. Importantly, exploitation and climate change are expected to affect the spatial structure of diversity via the synchronization of environmental conditions and/or selective effects (Parmesan and Yohe 2003, Bellmore et al. 2022). A future avenue of research building on our approach is to investigate how a network of diverse populations cope with selective exploitation and climate change, and to determine if there are preferable management strategies considering the spatial structure of populations. More generally, we argue that management strategies should consider not only diversity within populations but also among interconnected populations to foster rescue effects and adaptation network (Webster et al. 2017, Moore and Schindler 2022).

Acknowledgements – We want to thank the Bretagne Grands Migrateurs association and angling clubs for allowing us access to Atlantic salmon datasets from Brittany. This work was conducted within the International Associated Laboratory MacLife. We thank Sylvie Oddou-Muratorio for reviewing an earlier version of this manuscript.
Funding – We gratefully acknowledge funding from the Region Nouvelle Aquitaine, E2S-UPPA and OFB Pôle Migrateur.

Author contributions

Stephanie M. Carlson and **Mathieu Buoro** contributed equally to this publication. **Amaïa Lamarins**: Conceptualization (equal); Formal analysis (lead); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Etienne Prévost**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (equal). **Stephanie M. Carlson**: Conceptualization (equal); Methodology (supporting); Supervision (equal); Writing – review and editing (equal). **Mathieu Buoro**: Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Software (equal); Supervision (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.06933.

Data availability statement

Code and R scripts are freely available at Github, https://github.com/Ibasam/SpatialStructure (Lamarins et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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