



Classical metapopulation dynamics and eco-evolutionary feedbacks in dendritic networks

Emanuel A. Fronhofer and Florian Altermatt

E. A. Fronhofer (<http://orcid.org/0000-0002-2219-784X>)(emanuel.fronhofer@eawag.ch) and *F. Altermatt*, *Eawag: Swiss Federal Inst. of Aquatic Science and Technology, Dept of Aquatic Ecology, Dübendorf, Switzerland, and: Dept of Evolutionary Biology and Environmental Studies, Univ. of Zurich, Zürich, Switzerland.*

Eco-evolutionary dynamics are now recognized to be highly relevant for population and community dynamics. However, the impact of evolutionary dynamics on spatial patterns, such as the occurrence of classical metapopulation dynamics, is less well appreciated. Here, we analyse the evolutionary consequences of spatial network connectivity and topology for dispersal strategies and quantify the eco-evolutionary feedback in terms of altered classical metapopulation dynamics. We find that network properties, such as topology and connectivity, lead to predictable spatio-temporal correlations in fitness expectations. These spatio-temporally stable fitness patterns heavily impact evolutionarily stable dispersal strategies and lead to eco-evolutionary feedbacks on landscape level metrics, such as the number of occupied patches, the number of extinctions and recolonizations as well as metapopulation extinction risk and genetic structure. Our model predicts that classical metapopulation dynamics are more likely to occur in dendritic networks, and especially in riverine systems, compared to other types of landscape configurations. As it remains debated whether classical metapopulation dynamics are likely to occur in nature at all, our work provides an important conceptual advance for understanding the occurrence of classical metapopulation dynamics which has implications for conservation and management of spatially structured populations.

Evolution is recognized to be rapid enough to affect ecological dynamics, which may lead to eco-evolutionary feedbacks (Yoshida et al. 2003, Hairston et al. 2005, Fussmann et al. 2007, Hanski 2012, Ellner 2013, DeLong et al. 2016). Although a majority of species on earth live in fragmented habitats and therefore form spatially structured populations, most of eco-evolutionary research (reviewed by Koch et al. 2014) has focused on single, isolated populations and communities in a non-spatial context (but see Legrand et al. 2017 for a summary of eco-evolutionary dynamics in fragmented landscapes). It remains therefore less well appreciated that evolutionary dynamics affect classical spatial patterns, such as the dynamics of populations living in networks of interconnected local patches, that is, metapopulations and metacommunities.

The classical metapopulation concept (Levins 1969, Hanski and Gaggiotti 2004), and the notion that most natural populations are spatially structured, has extensively influenced decades of research in spatial ecology and conservation (Driscoll et al. 2014). More recently, spatial structure has found its way into community (Leibold et al. 2004) and ecosystem research (Loreau et al. 2003). While the metapopulation, -community and -ecosystem concepts are at the heart of spatial ecology, a large fraction of theoretical and conceptual work on these spatial systems has still not

included an explicit description of space. Space, and more specifically spatial network configuration and inter-patch connectivity, is often included only implicitly, for example, by assuming global dispersal abilities (Poethke et al. 2011, Weigang and Kisdi 2015) or only considering two patches (McPeck and Holt 1992, Amarasekare 2004). Even when space is considered explicitly, often simplistic connectivity patterns are assumed, such as grid-based, nearest-neighbour dispersal (Travis and Dytham 1998, Altermatt et al. 2011, Kubisch et al. 2016). However, these assumptions are most likely erroneous in any natural spatially structured population, community or ecosystem.

Existing research on consequences of alternative network connectivities and topologies suggests that these properties are of pivotal importance for ecological and evolutionary dynamics. For example, Bascompte and Solé (1996), Fagan (2002), Vuilleumier and Possingham (2006), Labonne et al. (2008), Gilarranz and Bascompte (2012) and Shtilerman and Stone (2015) have studied the effects of network topology, respectively symmetry, on metapopulation viability and persistence. They found that network structure impacts demography and leads to higher extinction probabilities than otherwise expected. In a multi-species context, Carrara et al. (2012) and Seymour et al. (2015) have demonstrated that spatial and temporal patterns of biodiversity are

impacted by the specific connectivity pattern of a landscape (see also Holland and Hastings 2008, Salomon et al. 2010). Generally, these findings suggest that branching networks may support higher levels of biodiversity in comparison to more simply structured landscapes. Similarly, Nuismer et al. (2003) and Gibert et al. (2013), to name but two, show that the explicit spatial arrangement of coevolving populations (co-evolutionary hot- and coldspots) impacts coevolutionary dynamics and the maintenance of polymorphisms in antagonistic systems (for a detailed treatment of the geographic mosaic of coevolution see Thompson 2005). In analogy, Morrissey and de Kerckhove (2009) and Paz-Vinas and Blanchet (2015) have shown that network topology heavily impacts genetic diversity. Recently, Muneeppeerakul et al. (2011) and Henriques-Silva et al. (2015) have reported that network topology may even impact the evolution of dispersal kernels respectively density-dependent dispersal strategies in metapopulations.

Other examples of spatially explicit models that explore metapopulation dynamics or dispersal evolution include developments of classical metapopulation models (Hanski 2001, Hanski et al. 2004, Baguette et al. 2013), the inclusion of fractal landscapes (Hovestadt et al. 2001, Gamarra 2005, Bonte et al. 2010) and other forms of spatially correlated landscapes (Kallimanis et al. 2005, North et al. 2011, Fronhofer et al. 2014). Furthermore, space is explicitly modelled for the study of long-distance dispersal and dispersal kernels (Johst et al. 2002, Bohrer et al. 2005, Fronhofer et al. 2015) and of course in models of range expansions and biological invasions (Dytham 2009, Dewhurst and Lutscher 2009, Oborny et al. 2009, Kubisch et al. 2014), to name but a few examples.

While all of these studies have addressed important aspects of spatial ecology and evolution, no study to date has integrated the individual elements of explicit space and evolutionary change in order to understand how spatial network structure interacts with evolution to impact the occurrence of classical metapopulation dynamics. Therefore, we investigate theoretically how evolutionary and ecological dynamics interact in networks of populations with different connectivity and topology. We focus on the evolution of dispersal, as this trait has been shown to be evolving in a wide range of taxa (Phillips et al. 2006, Saastamoinen 2008, Fronhofer et al. 2014, Fronhofer and Altermatt 2015), and to centrally influence the dynamics of spatially structured populations. Specifically, we ask how the evolution of dispersal in networks of varying connectivity and topology impacts the occurrence of classical metapopulation dynamics.

Our interest in exploring the occurrence of classical metapopulation dynamics stems from the current debate on whether these dynamics occur at all in natural systems (Baguette 2004, Driscoll 2007, 2008, Driscoll et al. 2010). A range of alternative scenarios, including mainland–island, source–sink or panmictic spatially structured systems seem to be possible (Harrison 1991), but would all lead to altered system properties such as extinction probabilities, number of occupied patches (occupancy), number of extinctions and recolonizations (turnover), and genetic structure (the fixation index, F_{ST}). Clearly, appropriate conservation and management strategies must take these differences into account.

While our theoretical considerations are, in principle, valid for any type of terrestrial or aquatic network of patches, we apply our findings to a classical example of habitat networks: dendritic, riverine systems. Rivers are not only very diverse and of high significance with respect to ecosystem services (Vörösmarty et al. 2010), but they also have an inherent dendritic network structure which drives dispersal and diversity patterns (Grant et al. 2007, Muneeppeerakul et al. 2008, Altermatt 2013, Mari et al. 2014). Furthermore, riverine ecosystems are an especially interesting testbed for theoretical predictions regarding the consequences of network properties, as they are currently experiencing large changes in network configuration and connectivity by ongoing fragmentation, dam and channel building (Grant et al. 2012, Grill et al. 2015).

We find that network topology and connectivity lead to predictable, spatio-temporally correlated, patterns of fitness expectations, which alter evolutionarily stable (ES) dispersal strategies and lead to eco-evolutionary feedbacks on landscape level metrics. Dendritic networks, and especially riverine connectivity patterns, thereby favour the emergence of classical metapopulation dynamics. In comparison to such dendritic spatial structures, classical metapopulation dynamics are less likely found in symmetric networks, which are often assumed in metapopulation models. In the context of the ongoing debate regarding the occurrence of classical metapopulation dynamics in natural systems (Baguette 2004, Driscoll 2007, 2008, Driscoll et al. 2010), our findings highlight the significance of network connectivity and topology for spatial ecological and evolutionary dynamics.

Model description

General overview

We use a general, stochastic simulation model of a spatially structured population of individuals living in distinct habitat patches with local competition for resources and non-overlapping generations (Fronhofer et al. 2013, 2014). Local populations are connected by dispersal, which is defined by every individual's dispersal rate and by the landscape's topology, that is, the spatial arrangement of habitat patches (connectivity matrix, Seymour et al. 2015). Dispersal is natal. Importantly, the dispersal trait is heritable and subject to evolution.

Using network topologies that either only differ in connectivity (i.e. number of links from one patch to other patches) or in topology (regular, grid-like networks versus branching, dendritic networks), we explore the eco-evolutionary consequences of network structure on dispersal evolution and metapopulation dynamics, measured as occupancy (O , the relative number of occupied patches), turnover (T , the relative number of extinctions and recolonizations) and genetic structure (F_{ST} , which captures variation in allele frequencies among populations). Following Hanski et al. (1995) and Fronhofer et al. (2012), we define classical metapopulations as any spatially structured population that shows less than 90% occupancy, more than 5% turnover and a global $F_{ST} \geq 0.1$. To relate our results to real-world systems,

we supplement our general analysis with the example of riverine networks, which typically exhibit dendritic network structure, also including characteristic variation in habitat size (carrying capacity; Rodriguez-Iturbe and Rinaldo 1997) and downstream water flow.

Individuals, inheritance and evolutionary dynamics

Local patches are inhabited by diploid male and female individuals. All individuals are characterized by a diploid locus coding for dispersal rate and by 10 diploid neutral marker loci with 100 alleles. The latter neutral loci are used to track population genetic summary statistics such as F_{ST} . Females mate randomly in their local patch and produce diploid offspring that inherit half of their dispersal and neutral alleles randomly from their mother and the other half randomly from their father. During inheritance, all traits inherited from the mother and the father may change due to mutations. For the dispersal rate locus this is captured by altering the respective parental allele value by a random number drawn from a normal distribution with mean zero and standard deviation 0.2, in case of a mutation (mutation rate: $m_{dispersal} = 0.0001$; no boundary conditions). For the neutral loci, the mutation rate is $m_{neutral} = 0.00001$ and, in case of a mutation, any of the 100 alleles can be drawn. Mutation rates and widths of these magnitudes are routinely used in similar simulation models (Bonte et al. 2010, Kubisch and Poethke 2011).

Individuals inherit their attributes with only small mutations from their parents setting the basis for evolutionary dynamics to occur during the simulations. The 10 loci we track for measuring F_{ST} follow neutral dynamics in our model, because they are not linked to any fitness relevant phenotypic attributes. By contrast, the dispersal loci define the dispersal phenotype which is subject to selection. Therefore, what we describe for the dispersal trait is a genetic algorithm (Fraser 1957), an approach that has been widely used in ecological modelling (for an overview see DeAngelis and Mooij 2005). More specifically, an individual's dispersal phenotype is determined as the mean of the individual's two dispersal alleles. As these alleles may mutate and we do not assume any boundary conditions, values may be below 0 or above 1. Dispersal phenotypes < 0 and > 1 are rounded to 0 and 1, respectively. This procedure avoids assuming boundary conditions for mutations and the associated biases. Selection on dispersal is an emergent phenomenon in our individual-based model, as fitness gains and losses are related to the landscape structure (Henriques-Silva et al. 2015), kin competition (Hamilton and May 1977, Poethke et al. 2007, Kubisch et al. 2013) or dispersal costs (Bonte et al. 2012), to name but three relevant selective agents.

Reproduction and local patch dynamics

We assume local density regulation in all patches, that is, competition acts at the local population level. As our model assumes discrete, non-overlapping generations, we use the logistic growth model provided by Beverton and Holt (1957):

$$N_{i,t} = N_{i,t-1} \lambda_i \frac{1}{1 + aN_{i,t-1}} \quad (1)$$

with i as the patch number, t as the time step and $a = \frac{\lambda_0 - 1}{K}$.

K is the local carrying capacity and λ_0 represents the growth rate. Consequently, every female produces a mean of

$$2\lambda_i \frac{1}{1 + aN_{i,t-1}}$$

offspring (the multiplication with 2 allows

to interpret λ_i as a per capita rate even though males do not reproduce). The offspring's sex is randomly chosen to yield an average sex ratio of 0.5. The realized number of offspring is drawn from a Poisson distribution in order to capture demographic stochasticity. Our model includes spatio-temporally uncorrelated environmental stochasticity caused by variation in offspring number: for every patch and generation λ_i is drawn from a log-normal distribution with mean λ_0 and standard deviation σ .

Finally, we assume that every patch may go extinct at a certain rate (ϵ) due to external, density-independent factors, such as catastrophic floods or geologic events. Using non-overlapping generations, all adults die after reproduction and the juveniles start a new generation in the next time step.

Landscape

Patches are linked together to form landscapes. We assume a lattice-type spatial network, in which nodes are habitat patches and links are uninhabited 'matrix', reflecting a spatially structured population in a network. Dispersal can therefore only occur between patches connected by links. For an overview of continuous space networks see Grant et al. (2007). We analyse the eco-evolutionary consequences of three types of landscapes, that all have 36 nodes (patches) for comparability:

1) Lattice landscapes with varying connectivity, that is, links per node (see Fig. 1 top row for a graphical representation). Our choice covers the two extreme possibilities, namely a fully connected network (often termed 'global dispersal') where every node connects to every other node (maximal number of links), and a circular network where every node has only two links. We additionally explore two intermediate cases: a network allowing for nearest neighbour dispersal to the eight nearest neighbours (NN8, Moore neighbourhood) and one allowing for dispersal to the four nearest neighbours (NN4, von Neumann neighbourhood) on a regular grid. We assume periodic (i.e. wrapped) boundaries in order to avoid edge effects.

2) We further analyse the effect of topology by comparing the dynamics in the lattice landscapes with a number of bifurcating networks (see Fig. 4 top row, two networks on the left, for a graphical representation): we use one landscape which is dendritically bifurcating in analogy to Morrissey and de Kerckhove (2009) and complement our analysis with five realizations of fractal dendritic landscapes (OCNs; optimal channel networks; we here use the same OCNs as Carrara et al. 2014). Dispersal in all bifurcating networks follows exactly the connectivities represented in Fig. 4.

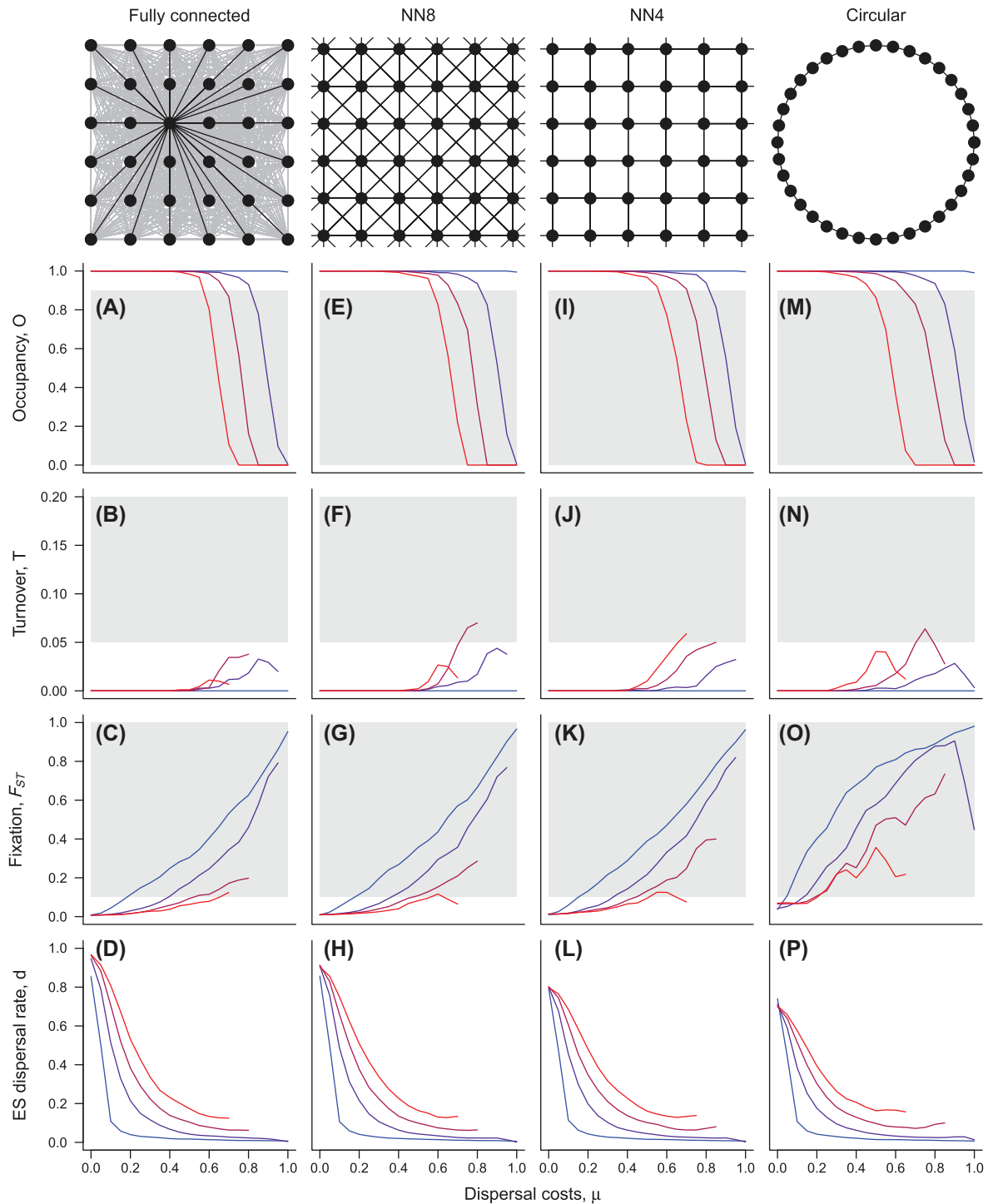


Figure 1. Ecological and evolutionary dynamics of spatially structured populations with different degrees of connectivity. Environmental stochasticity (σ) increases from blue to red ($\sigma \in \{0, 1, 1.5, 2\}$). Grey areas indicate values of occupancy (O), turnover (T) and genetic fixation (F_{ST}) typically assumed to be characteristic of classical metapopulations (Fronhofer et al. 2012), that is, $O \leq 0.9$, $T \geq 0.05$ and a global $F_{ST} \geq 0.1$. Note that, as the curves are relatively steep, the exact choice of values does not critically alter the qualitative results. Fixed parameters: $K = 100$, $\sigma \in \{0, 1, 1.5, 2\}$, $\varepsilon = 0$, $\lambda_0 = 2$. The lines were smoothed with a running mean window of 2. See Supplementary material Appendix 1 Fig. A1–A4 for non-smoothed median and quartile values of the statistics. Note that the left network representation in the top row ('Fully connected') only highlights the connection from one patch to all others; all other connections are analogous.

3) We finally use an OCN in combination with the characteristic riverine distribution of carrying capacities found in nature (i.e. carrying capacities increasing from up- to downstream patches; Rodriguez-Iturbe and Rinaldo

1997, Carrara et al. 2014) and two strengths of downstream flow (probability of up-/downstream dispersal: 0.5/0.5 and 0.1/0.9; for a more formal treatment linking flow and ecological dynamics see Jin et al. 2014) in order to explore

the robustness of our findings in more realistic settings and for the most characteristic example of dendritic networks, namely rivers (see Fig. 4 top row, two networks on the right, for a graphical representation). The typically riverine distribution of carrying capacities in nature results from the drainage area of the respective patches as described by Carrara et al. (2014). Based on their drainage area, patches were assigned to four relative size categories (1, 1.75, 3 and 6). In order to keep the simulations comparable, we kept the landscape-level carrying capacity (sum of all local carrying capacities) for all landscapes constant, while assigning local carrying capacities according to their relative sizes. For a more detailed description refer to Carrara et al. (2014).

Dispersal

Dispersal occurs along the links of the above described landscapes. We assume dispersal to be natal, that is, to occur before reproduction. Dispersal is defined by the individual dispersal rate (mean of an individual's two dispersal alleles) and by the landscape's topology (connectivity matrix). Emigration must not necessarily lead to successful immigration, as we assume dispersal costs (μ) in form of dispersal mortality. This mortality term summarizes all possible costs related to dispersal, such as time, opportunity, risk or energetic costs (Bonte et al. 2012).

In the case of riverine networks including downstream flow, we assume that emigrants have a reduced probability of dispersing upstream. In the 'slow flow' scenario, we assume a 0.5 probability of up- and downstream dispersal. This is less upstream dispersal than in the 'no flow' scenarios, as, in dendritic networks, nodes have more links to up- than to downstream nodes. The 'fast flow' scenario assumes a probability of 0.1 for up- and a probability of 0.9 for downstream dispersal. We therefore do not assume differential costs of up- versus downstream dispersal. Note that additional simulations indicate that adding such differential costs only make the patterns we report stronger. Our assumption is therefore conservative.

Numerical analyses

All simulations, with 25 replicates each, were run for 5000 generations, which allowed the system to reach quasi-equilibrium. The simulations were initialized with fully occupied patches and a sex ratio of 0.5. At initialization, dispersal alleles were randomly drawn between 0 and 1, and neutral alleles were randomly assigned one of 100 possible alleles (integer numbers).

Turnover (T) was quantified as the relative number of extinctions and recolonizations after dispersal between two subsequent generations. Turnover thus takes into account rescue effects, i.e. patches that went extinct due to demography or environmental stochasticity in the previous time step and have now been recolonized do not increase the turnover rate as the census happens after dispersal. Occupancy (O) is the relative number of occupied patches. Population genetics analyses were performed on the individuals of the last generation ($t = 5000$) with the statistical software package R

(ver. 3.2.0 <www.r-project.org>; package "hierfstat" ver. 0.04-14).

To investigate spatial relatedness patterns as a possible driver of dispersal evolution, we used pairwise F_{ST} -values between patches of origin and potential target patches, which are inversely proportional to relatedness. The distribution of these pairwise F_{ST} -values was subtracted from the distribution of all pairwise F_{ST} -values (including non-target patches). This difference indicates deviations in pairwise F_{ST} -values between origin and possible target patches relative to a global average, thereby capturing possible spatial patterns in relatedness.

The reported values of turnover, occupancy, F_{ST} and dispersal rates were always measured in the last generation of the simulations and are means over the 25 replicates. We report only mean values in the main text as the inter-replicate variation is relatively small and does not impact our interpretations. Information on median values and quartiles is reported in the Supplementary material Appendix 1 Fig. A1–A8. See Table 1 for the explored parameter space and the Supplementary material Appendix 1 Fig. A9–A18 for a sensitivity analysis.

Data deposition

The simulation code is available on GitHub: <https://github.com/efronhofer/dendritic_metapopulations> (doi: 10.5281/zenodo.168572).

Results

Consequences of the degree of connectivity

We found substantial evolutionary effects of network connectivity on the evolutionarily stable (ES) dispersal rate (d , Fig. 1D, H, L and P). Landscapes with less connectivity, for example the circular landscape, lead to the evolution of lower dispersal rates. The evolutionary effect of network connectivity on dispersal is explained by an altered spatial kin structure (Fig. 2). We find that dispersers in less connected networks are confronted with lower pairwise F_{ST} -values

Table 1. Important model parameters, their meaning and tested values. Standard values are underlined. Note that we assume only very few parameters to be fixed. Carrying capacities are well within typical values observed in the field (Hanski et al. 1995) and we test the effect of both higher and lower values in the Supplementary material Appendix 1 Fig. A9–A18. The same is true for fecundities (Hassell et al. 1976). While we test different levels of local patch extinction probabilities in the Supplementary material Appendix 1 Fig. A9–A18, we focus on the case $\epsilon = 0$ in the main text, as we are interested in the emergence of metapopulation dynamics (e.g. turnover) and do not want to bias our results by assuming that patch extinctions are not intrinsically linked to population dynamics.

Parameter	Values	Meaning
K	50, <u>100</u> , 200	carrying capacity
σ	0, 0.25, 0.5, ..., 4	environmental stochasticity
ϵ	<u>0</u> , 0.05, 0.1	local patch extinction probability
λ_0	1.5, <u>2</u> , 4	fecundity
μ	0, 0.05, 0.1, ..., 1	dispersal costs

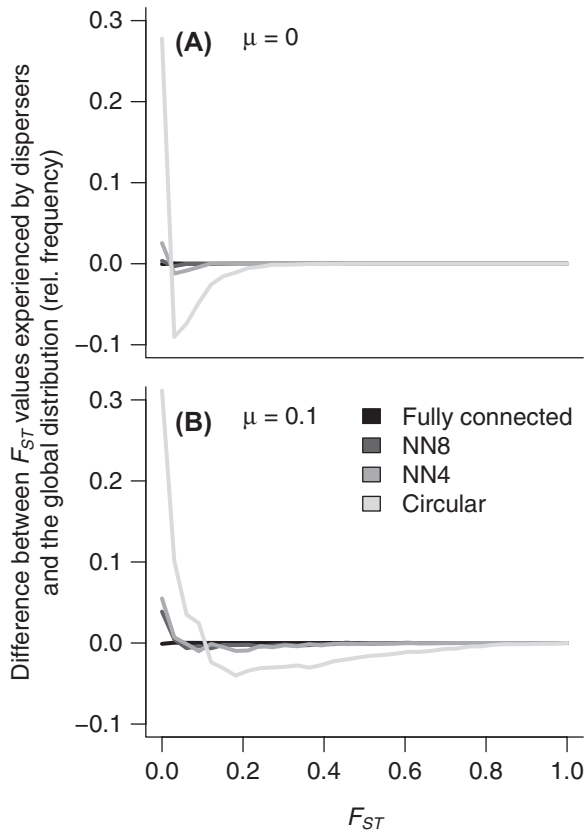


Figure 2. Difference between the distribution of F_{ST} -values experienced by dispersers and the global distribution of pairwise F_{ST} -values. To visualize how network connectivity impacts spatial kin structure, we use the difference between the distribution of pairwise F_{ST} -values between all possible origin and target patches (genetic differentiation) and the global distribution of pairwise F_{ST} -value. Note that genetic differentiation is inversely proportional to relatedness. In a fully connected network the two distributions are identical and the difference is zero, implying that there is no spatial kin structure. By contrast, in a circular network dispersers experience relatively more often low F_{ST} -values, that is, higher kin structure. The two nearest-neighbour networks lie in between these two extremes. This holds regardless of dispersal mortality (A; $\mu = 0$; B; $\mu = 0.1$). Fixed parameters: $K = 100$, $\sigma = 0$, $\varepsilon = 0$, $\lambda_0 = 2$.

compared to the respective global distribution of pairwise F_{ST} -values. Consequently, relatedness between natal and target patches is, on average, increased in less connected networks which leads to the evolution of lower dispersal rates (Fig. 1D, H, L and P).

These evolutionary dynamics change ecological patterns, implying a decrease in occupancy (Fig. 1A, E, I and M), and an increase in turnover (Fig. 1B, F, J and N). When looking at global F_{ST} -values, we also find consequences for population genetic patterns where the functional relationship between F_{ST} and dispersal costs (μ) changes from convex to concave (Fig. 1C, G, K and O).

The evolutionary effect of network connectivity on dispersal, and the feedback on occupancy, turnover and genetic structure (Fig. 1), has important consequences for the occurrence of classical metapopulation dynamics (Fig. 3). We typically find that increasing dispersal costs (μ) and decreasing connectivity (Fig. 3A–D) leads to a higher

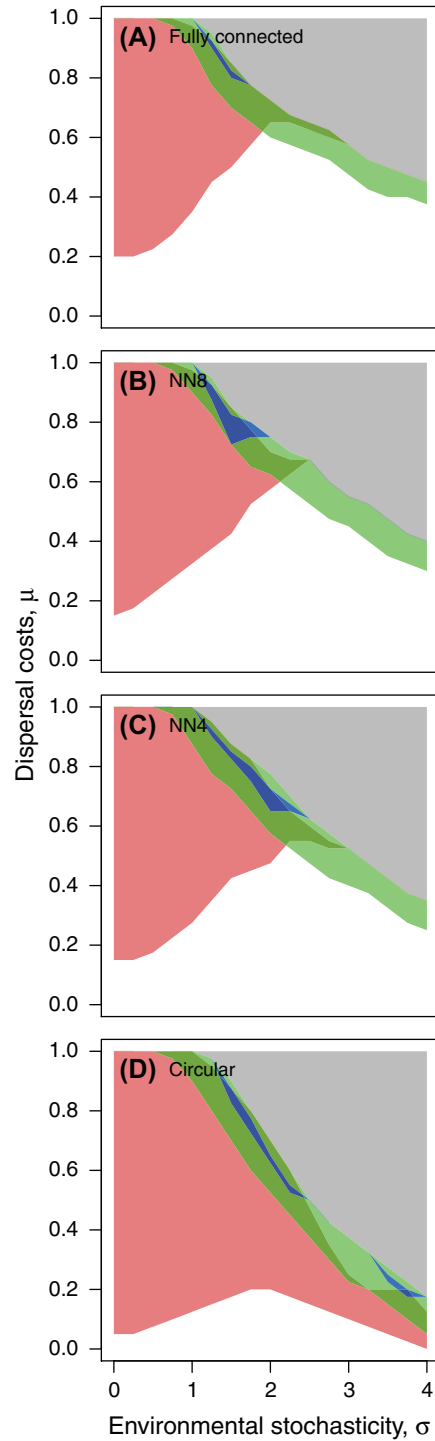


Figure 3. Classical metapopulation dynamics in systems with different degrees of connectivity (for visualisations of the networks, see Fig. 1). Grey: extinction; red: $F_{ST} \geq 0.1$; blue: $T \geq 0.05$; green: $O \leq 0.9$. Fixed parameters: $K = 100$, $\varepsilon = 0$, $\lambda_0 = 2$. The polygon lines were smoothed with a running mean window of 2. The original simulation results are reported in the Supplementary material Appendix 1 Fig. A9–A12.

probability of metapopulation extinction due to reduced rescue effects and recolonizations. Metapopulation extinction also increases with increasing environmental stochasticity (σ) due to increased local extinctions. Occupancy typically

decreases abruptly from 1 (fully occupied) to zero (extinct; see also Fig. 1A, E, I and M). Therefore, we consistently find a narrow band of intermediate occupancies, which are characteristic for classical metapopulation dynamics, right before the extinction region.

Genetic structure (F_{ST}) typically increases with decreasing ES dispersal rates (Fig. 1C, G, K and O), that is, with increasing dispersal costs (μ) and decreasing environmental stochasticity (σ). As decreasing connectivity leads to the evolution of lower dispersal rates, F_{ST} also increases with decreasing connectivity; more specifically, the shape of the relationship between F_{ST} and dispersal costs (μ) changes from convex to concave (Fig. 1C, G, K and O). Only in networks with very low connectivities (here: circular; Fig. 3D) very high values of environmental stochasticity lead to an additional increase in F_{ST} . This increase in F_{ST} is due to an increase in local extinctions, leading to founder effects and locally increased drift due to small population sizes. As a result, populations become genetically more differentiated at a global scale.

In general, significant turnover only occurs within the band of intermediate occupancy. However, high environmental stochasticity decreases turnover because such stochasticity selects for increased dispersal which leads to rescue effects. This changes for circular networks (Fig. 3D): an additional region with increased turnover appears due to the same reasons as F_{ST} increases.

Consequences of dendritic topology

Changing network topology from equally connected to bifurcating and dendritic has a similar effect as reducing network connectivity (Fig. 4). However, dendritic networks select even stronger against dispersal than reduced connectivity (Fig. 4D, H), which, as outlined above, reduces occupancy (Fig. 4A, E), and increases turnover rates (Fig. 4B, F) and F_{ST} (Fig. 4C, G).

While selection for reduced dispersal emerges in systems with low connectivity due to a strong local kin structure (Fig. 2), dendritic networks select for even less dispersal due to an emergent spatial heterogeneity in population densities (Fig. 5). Patches that are less connected typically show lower densities in comparison to well-connected patches. This is a result of altered dispersal patterns: patches with only one link usually connect to patches with two or more links. As dispersal is active, that is, the number of emigrants is determined per patch by the ES dispersal rate and not by the number of links, patches with one link lose all emigrants to their neighbouring patch via this link. However, they only receive a fraction of the emigrants of the neighbouring patch, as the latter patch, on average, has more than one link and the emigrants are distributed randomly among those links. As a consequence, patches with less links lose more emigrants than they receive immigrants, which leads to lower densities. The opposite is true for the receiving patch. Taken together, the reduced connectivity and the topology of dendritic networks allows for the occurrence of classical metapopulation dynamics in a broader portion of parameter space (Fig. 6A–B).

Consequences of riverine characteristics

Riverine dendritic networks, characterized by unidirectional flow and a hierarchical distribution of carrying capacities, select even more for low dispersal rates, which generally strengthens all patterns discussed above (Fig. 4I–P). Especially the pattern of variation in local densities is increased, as dispersal is now biased from low density headwaters to high density confluences. Consequently, classical metapopulation dynamics emerge across a larger part of parameter space (Fig. 6C–D).

Discussion

Our results corroborate that the specific network structure has strong eco-evolutionary consequences for the populations occurring therein. Connectivity and topology impact large-scale spatial dynamics and the genetic structure of metapopulations by affecting the evolution of dispersal strategies. Importantly, we show that network structure influences spatial dynamics in predictable ways, leading to an eco-evolutionary feedback loop in the broad sense: decreasing connectivity and increasingly dendritic topologies select against dispersal (i.e. an ecological pattern impacts evolution), while in turn the evolution of decreased dispersal decreases occupancy, increases turnover and increases the risk of metapopulation extinction (i.e. evolution impacts ecological patterns; for a recent summary of eco-evolutionary dynamics in fragmented landscapes see Legrand et al. 2017).

We find that network topologies with realistic natural analogues, such as rivers, are more likely to exhibit classical metapopulation dynamics than the commonly assumed lattice-like networks (see also Fronhofer et al. 2012). Our findings have direct conservation relevant implications: we suggest that conservation strategies need to better, and system-specifically, incorporate effects of habitat network topology and connectivity, and changes thereof, for the long-term protection of populations and communities. As species in riverine networks exhibit an increased occurrence of classical metapopulation dynamics, they may also be more sensitive to changes in patch availability and connectivity, possibly making riverine ecosystems even more vulnerable to environmental changes than already known (Vörösmarty et al. 2010, Altermatt 2013, Grill et al. 2015).

Connectivity impacts spatial kin structure and dispersal evolution

The transition from spatially implicit connectivity patterns (fully connected, i.e. following classical Levin's type dynamics) to spatially explicit connectivity patterns (nearest-neighbour, circular; no variation in connectivity) has clear consequences for the cost-benefit balance underlying dispersal evolution (Fig. 1). While the costs of dispersal do not change, the benefits of dispersal do. More specifically, the probability of encountering related individuals (kin) after dispersal is altered (Fig. 2): trivially, a disperser's chance of encountering related individuals from its patch of origin increases with

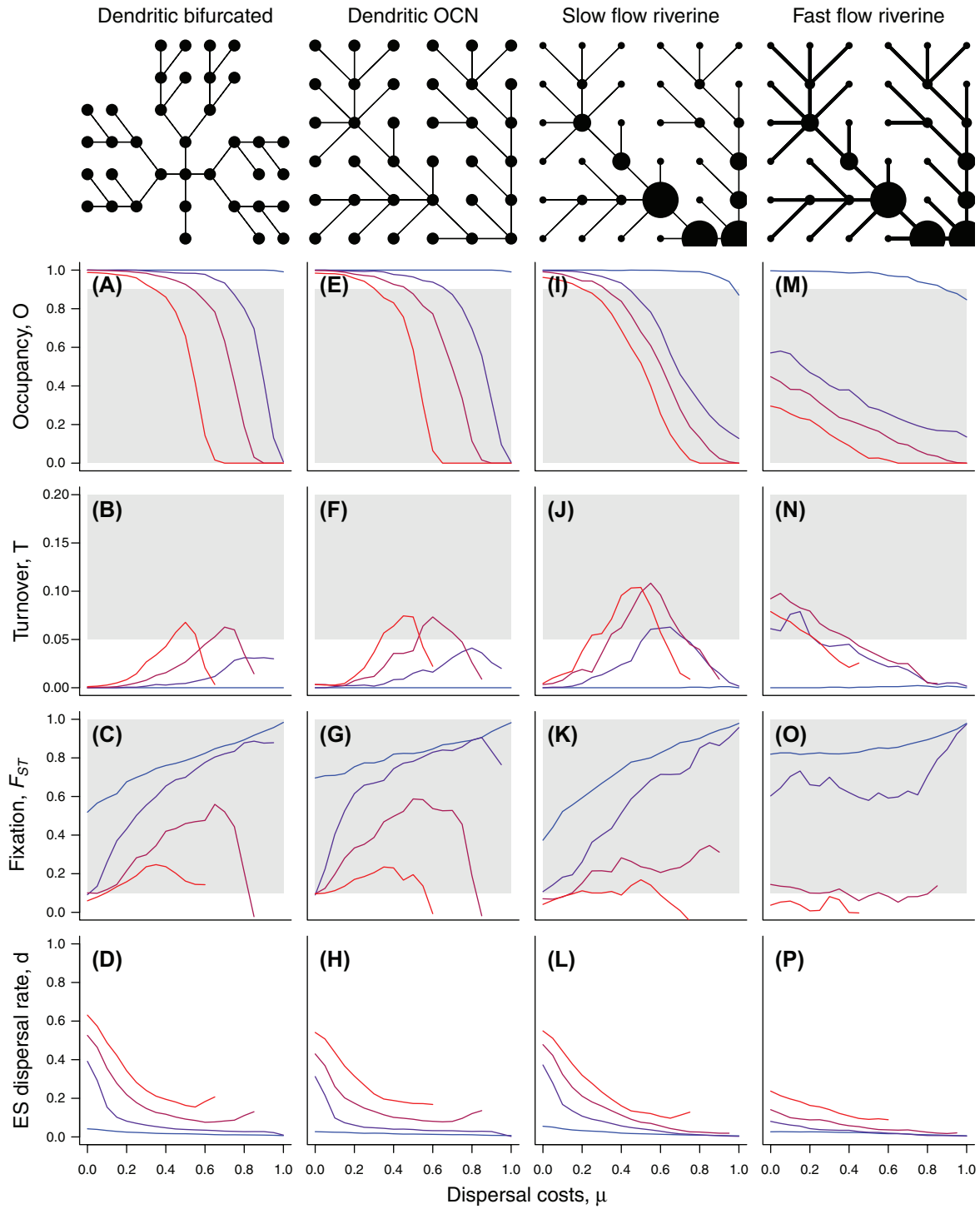


Figure 4. Ecological and evolutionary dynamics of spatially structured populations with different network topologies, including typical riverine networks with different degrees of flow (slow: 0.5 probability of up- or downstream dispersal; fast: 0.1 and 0.9 probability of up- respectively downstream dispersal). Environmental stochasticity (σ) increases from blue to red ($\sigma \in \{0, 1, 1.5, 2\}$). Grey areas indicate values of occupancy (O), turnover (T) and genetic fixation (F_{ST}) typically assumed to be characteristic of classical metapopulations. Fixed parameters: $K = 100$ (riverine: ($K \in \{57, 99, 170, 340\}$)), $\sigma \in \{0, 1, 1.5, 2\}$, $\epsilon = 0$, $\lambda_0 = 2$. The lines were smoothed with a running mean window of 2. See Supplementary material Appendix 1 Fig. A5–A8 for non-smoothed median and quartile values of the statistics.

decreasing connectivity, since the dispersers from a given patch of origin are dispersed to fewer target patches. The important effect of kin competition for the evolution of dispersal is well known since the seminal work of Hamilton and May (1977). Note that even without dispersal mortality the ES dispersal rate does not reach 1 (Fig. 1). This is due to our

assumption of dispersers not being able to return to their natal patch once they have dispersed.

As the selective effect of connectivity on dispersal is due to the spatial correlation of kin structure, a possible adaptation to escape from such a situation would be long-distance dispersal. In our model, dispersal distance or the shape of the

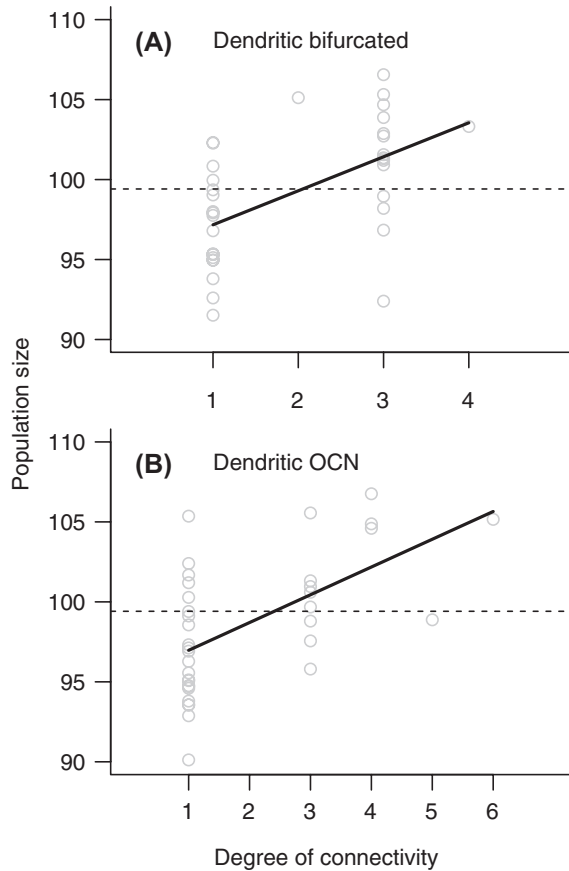


Figure 5. Spatial distribution of population sizes in dendritic networks as a function of patch connectivity. The solid line is a mean-squared regression. The dashed line shows mean population size in a fully connected network. Fixed parameters: $K = 100$, $\sigma = 0$, $\varepsilon = 0$, $\lambda_0 = 2$, $\mu = 0$.

dispersal kernel cannot evolve (but see Fronhofer et al. 2014, 2015). Critically, this would reduce genetic structure (F_{ST}), increase rescue effects and recolonizations and, therefore, occupancy, which would reduce the occurrence of classical metapopulation dynamics.

Dendritic topology selects against dispersal

The selective effect of network topology has recently been demonstrated by Henriques-Silva et al. (2015) for density-dependent dispersal. As expected, this also holds for density-independent dispersal strategies (Fig. 4). The mechanism behind the evolution of reduced dispersal in dendritic networks is linked to emerging and predictable heterogeneities in population densities, and, therefore, fitness (Fig. 5). Less connected patches characteristically have lower population densities and are typically connected to patches with higher population densities due to asymmetries in the number of dispersers linked to variation in connectivity as described in the results. Importantly, these density patterns and the resulting distribution of fitness in a network are spatio-temporally invariable which selects against dispersal. Note that these conclusions hold true for actively dispersing organisms. If dispersal rates are mainly driven by the

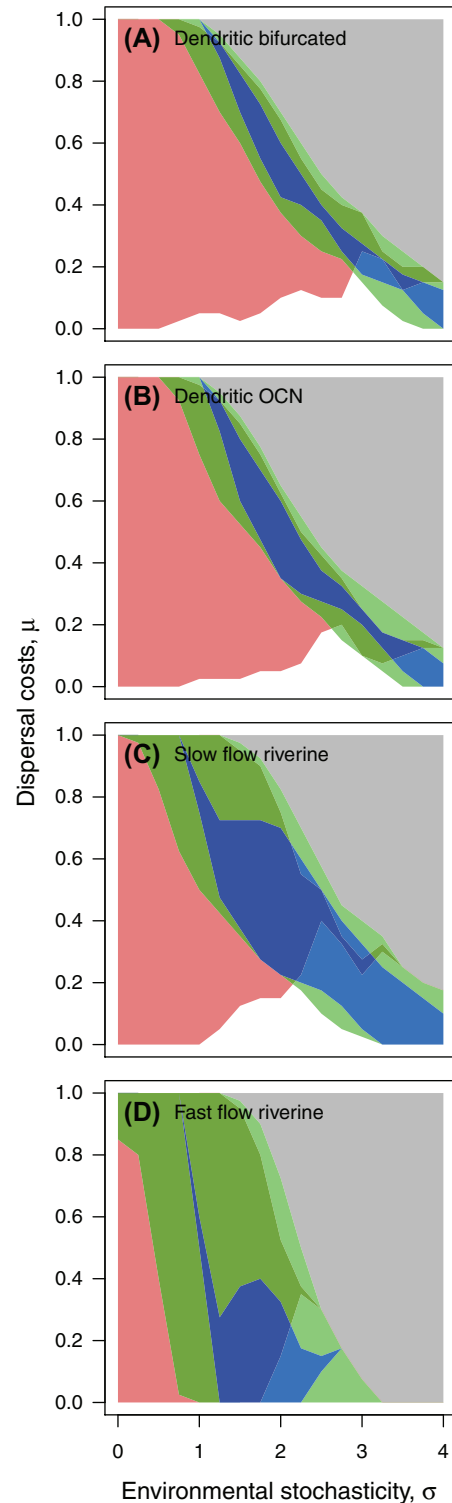


Figure 6. Classical metapopulation dynamics in systems with different network topologies (for visualisations of the networks, see Fig. 4). Grey: extinction; red: $F_{ST} \geq 0.1$; blue: $T \geq 0.05$; green: $O \leq 0.9$. Fixed parameters: $K = 100$ (riverine: $K \in \{57, 99, 170, 340\}$), $\varepsilon = 0$, $\lambda_0 = 2$. The polygon lines were smoothed with a running mean window of 2. The original simulation results are reported in the Supplementary material Appendix 1 Fig. A13–A14.

landscape, for instance if dispersal rates are a function of the number of connections a patch exhibits, the heterogeneity in

patch densities does not emerge. However, the first mechanism we discuss, spatial kin structure, is generally valid.

Low dispersal abilities and behavioral mechanisms preventing dispersal are well-known empirically for many riverine organisms that typically live in dendritic, spatially structured populations. For example, there is a strong tendency of aquatic macroinvertebrates to escape passive drift (Elliott 2003), and many aquatic macroinvertebrates have flight strategies in their adult stage to compensate larval downstream drift and thus reduce effective dispersal. The relatively low dispersal ability of riverine organisms is also reflected in commonly high genetic differentiation among local populations (Westram et al. 2013).

Classical metapopulation dynamics emerge in dendritic networks

Both, reduced connectivity and dendritic topology lead to spatio-temporally correlated variation in fitness expectations, which strongly selects against dispersal. Lower ES dispersal rates lead to reduced rescue effects and recolonization rates, which, together with some environmental stochasticity, leads to the emergence of patch extinctions. As a consequence, occupancies and turnover are intermediate, and genetic differentiation (F_{ST}) is increased. Additionally, metapopulation persistence decreases as predicted by Vuilleumier and Possingham (2006) and discussed in detail by Gilarranz and Bascompte (2012).

Altogether, dendritic networks lead to an increased probability of observing classical metapopulation dynamics (Levins 1969, Hanski and Gaggiotti 2004) which are thought to be characterized by intermediate occupancies, some turnover and a more or less clear genetic differentiation between local populations (Fronhofer et al. 2012). In a theoretical study, following the often made general assumption of global or nearest-neighbour dispersal, Fronhofer et al. (2012) showed that such classical metapopulation dynamics only rarely occur in parameter space, which is in good accordance with the empirical scarcity of such classical metapopulations (Baguette 2004, Driscoll 2007, 2008, Driscoll et al. 2010). Of course, examples of classical metapopulation dynamics exist in nature (Harrison 1991, Hanski and Gaggiotti 2004, Altermatt and Ebert 2010), however, these may often be extrinsically driven, for instance, by ephemeral habitats or other forms of extrinsic extinctions. We here report that the occurrence of classical metapopulation dynamics may be tightly linked to the underlying landscape topology, with dendritic spatially structured populations being more likely to exhibit classical metapopulation dynamics. Importantly, the exact values assumed for occupancy, turnover and genetic structure are not relevant for these conclusions as the transitions are very steep as depicted in Fig. 1.

Classical metapopulations can likely be found in riverine systems

Among dendritic systems, riverine systems are also characterized by directional flow of water and a typical

hierarchical distribution of carrying capacities (Rodríguez-Iturbe and Rinaldo 1997, Carrara et al. 2014). Our results (Fig. 4, 6) clearly show that adding these two features reinforces the patterns described above. Therefore, our model predicts that species living in rivers are especially likely to show classical metapopulation dynamics (Fig. 6). As for connectivity and topology, the effect of variation in carrying capacities and directional flow can be explained by an eco-evolutionary feedback linked to the evolution of dispersal: variation in carrying capacities typically selects against dispersal (Poethke et al. 2011) and the directionality of water flow leads to an increased probability of dispersal towards more connected and denser patches, which should also lead to lower ES dispersal rates.

Our theoretical prediction is in good agreement with recently reported empirical results suggesting the occurrence of metapopulation dynamics in riverine ecosystems, in a wide range of taxa, from plants, to invertebrates and vertebrates (Göthe et al. 2012, Perkin and Gido 2012, Kuglerová et al. 2015). Evidently, dendritic connectivity is not limited to rivers. Montane terrestrial systems characterized by valleys or other habitats that are typically dendritic, like hedgerows, caves or transportation networks (Grant et al. 2007), can exhibit similar dynamics.

Conclusions

We analysed the evolutionary dynamics of dispersal in dendritic and other types of networks, and related these effects to the emergence of classical metapopulation dynamics. Our results illustrate eco-evolutionary feedbacks, in which landscape topology changes the evolutionarily stable dispersal strategy, which in turn feeds back on landscape level metrics like occupancy, turnover and genetic structure. Characteristically, dendritic connectivities are predestined for the emergence of classical metapopulation dynamics.

More generally, we highlight the relevance of taking the spatial structure of populations explicitly into account in order to understand and predict ecological and evolutionary dynamics. In this sense, our results are in good accordance with evidence from population genetics (Morrissey and de Kerckhove 2009, Paz-Vinas and Blanchet 2015), metapopulation (Bascompte and Solé 1996, Fagan 2002, Vuilleumier and Possingham 2006, Labonne et al. 2008, Gilarranz and Bascompte 2012, Shilerman and Stone 2015) and meta-community ecology (Holland and Hastings 2008, Salomon et al. 2010, Carrara et al. 2012, Seymour et al. 2015) as well as the geographic mosaic of coevolution (Nuismer 2006, Nuismer et al. 1999, 2000, 2003, Gibert et al. 2013), for example.

Our work has potentially important consequences for conservation: First, classical metapopulation dynamics are likely to occur in dendritic landscapes. Second, these specific dynamics are typically linked to an increased probability of extinction. This implies that populations living in dendritic landscapes, such as rivers, may be in specific need of intense and adequate conservation measures. Such measures should especially take into account anthropogenic interventions affecting connectivity (especially heterogeneity in connections between patches) and fragmentation, such as dam- and

channel building (Grant et al. 2012, Grill et al. 2015). Our work indicates that riverine ecosystems, and populations in branching networks in general, may not only be threatened by changes in local conditions (Vörösmarty et al. 2010), such as habitat modifications, but also, and maybe especially, by altered large-scale landscape attributes and the resulting eco-evolutionary feedbacks.

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References

- Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. – *Aquat. Ecol.* 47: 365–377.
- Altermatt, F. and Ebert, D. 2010. Populations in small, ephemeral habitat patches may drive dynamics in a *Daphnia magna* metapopulation. – *Ecology* 91: 2975–2982.
- Altermatt, F. et al. 2011. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. – *Ecology* 92: 859–870.
- Amarasekare, P. 2004. The role of density-dependent dispersal in source–sink dynamics. – *J. Theor. Biol.* 226: 159–168.
- Baguette, M. 2004. The classical metapopulation theory and the real, natural world: a critical appraisal. – *Basic Appl. Ecol.* 5: 213–224.
- Baguette, M. et al. 2013. Individual dispersal, landscape connectivity and ecological networks. – *Biol. Rev.* 88: 310–326.
- Bascompte, J. and Solé, R. V. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. – *J. Anim. Ecol.* 65: 465–473.
- Beverton, R. J. H. and Holt, S. J. 1957. On the dynamics of exploited fish populations. – Chapman and Hall.
- Bohrer, G. et al. 2005. Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales. – *J. Ecol.* 93: 1029–1040.
- Bonte, D. et al. 2010. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. – *Oikos* 119: 560–566.
- Bonte, D. et al. 2012. Costs of dispersal. – *Biol. Rev.* 87: 290–312.
- Carrara, F. et al. 2012. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. – *Proc. Natl Acad. Sci. USA* 109: 5761–5766.
- Carrara, F. et al. 2014. Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. – *Am. Nat.* 183: 13–25.
- DeAngelis, D. L. and Mooij, W. M. 2005. Individual-based modeling of ecological and evolutionary processes. – *Annu. Rev. Ecol. Evol. Syst.* 36: 147–168.
- DeLong, J. P. et al. 2016. How fast is fast? Eco-evolutionary dynamics and rates of change in populations and phenotypes. – *Ecol. Evol.* 6: 573–581.
- Dewhurst, S. and Lutscher, F. 2009. Dispersal in heterogeneous habitats: thresholds, spatial scales, and approximate rates of spread. – *Ecology* 90: 1338–1345.
- Driscoll, D. 2007. How to find a metapopulation. – *Can. J. Zool.* 85: 1031–1048.
- Driscoll, D. A. 2008. The frequency of metapopulations, metacommunities and nestedness in a fragmented landscape. – *Oikos* 117: 297–309.
- Driscoll, D. A. et al. 2010. Classic metapopulations are rare among common beetle species from a naturally fragmented landscape. – *J. Anim. Ecol.* 79: 294–303.
- Driscoll, D. A. et al. 2014. The trajectory of dispersal research in conservation biology. Systematic review. – *PLoS ONE* 9: e95053.
- Dytham, C. 2009. Evolved dispersal strategies at range margins. – *Proc. R. Soc. B* 276: 1407–1413.
- Elliott, J. M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. – *Freshwater Biol.* 48: 1652–1668.
- Ellner, S. P. 2013. Rapid evolution: from genes to communities, and back again? – *Funct. Ecol.* 27: 1087–1099.
- Fagan, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. – *Ecology* 83: 3243–3249.
- Fraser, A. S. 1957. Simulation of genetic systems by automatic digital computers. – *Aust. J. Biol. Sci.* 10: 484–491.
- Fronhofer, E. A. and Altermatt, F. 2015. Eco-evolutionary feedbacks during experimental range expansions. – *Nat. Commun.* 6: 6844.
- Fronhofer, E. A. et al. 2012. Why are metapopulations so rare? – *Ecology* 93: 1967–1978.
- Fronhofer, E. A. et al. 2013. Picky hitch-hikers: vector choice leads to directed dispersal and fat-tailed kernels in a passively dispersing mite. – *Oikos* 122: 1254–1264.
- Fronhofer, E. A. et al. 2014. Spatially correlated extinctions select for less emigration but larger dispersal distances in the spider mite *Tetranychus urticae*. – *Evolution* 68: 1838–1844.
- Fronhofer, E. A. et al. 2015. Evolution of dispersal distance: maternal investment leads to bimodal dispersal kernels. – *J. Theor. Biol.* 365: 270–279.
- Fussmann, G. F. et al. 2007. Eco-evolutionary dynamics of communities and ecosystems. – *Funct. Ecol.* 21: 465–477.
- Gamarra, J. G. P. 2005. Metapopulations in multifractal landscapes: on the role of spatial aggregation. – *Proc. R. Soc. B* 272: 1815–1822.
- Gibert, J. P. et al. 2013. The spatial structure of antagonistic species affects coevolution in predictable ways. – *Am. Nat.* 182: 578–591.
- Gilarranz, L. J. and Bascompte, J. 2012. Spatial network structure and metapopulation persistence. – *J. Theor. Biol.* 297: 11–16.
- Göthe, E. et al. 2012. Metacommunity structure in a small boreal stream network. – *J. Anim. Ecol.* 82: 449–458.
- Grant, E. H. C. et al. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. – *Ecol. Lett.* 10: 165–175.
- Grant, E. H. C. et al. 2012. Interbasin water transfer, riverine connectivity, and spatial controls on fish biodiversity. – *PLoS ONE* 7: e34170.
- Grill, G. et al. 2015. An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. – *Environ. Res. Lett.* 10: 015001.
- Hairston, N. G. et al. 2005. Rapid evolution and the convergence of ecological and evolutionary time. – *Ecol. Lett.* 8: 1114–1127.
- Hamilton, W. D. and May, R. M. 1977. Dispersal in stable habitats. – *Nature* 269: 578–581.
- Hanski, I. 2001. Spatially realistic theory of metapopulation ecology. – *Naturwissenschaften* 88: 372–381.
- Hanski, I. 2012. Eco-evolutionary dynamics in a changing world. – *Ann. N. Y. Acad. Sci.* 1249: 1–17.
- Hanski, I. A. and Gaggiotti, O. E. 2004. Ecology, genetics and evolution of metapopulations. – Academic Press.
- Hanski, I. et al. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. – *Oikos* 72: 21–28.
- Hanski, I. et al. 2004. Variation in migration propensity among individuals maintained by landscape structure. – *Ecol. Lett.* 7: 958–966.

- Harrison, S. 1991. Local extinction in a metapopulation context – an empirical evaluation. – *Biol. J. Linn. Soc.* 42: 73–88.
- Hassell, M. P. et al. 1976. Patterns of dynamical behavior in single-species populations. – *J. Anim. Ecol.* 45: 471–486.
- Henriques-Silva, R. et al. 2015. On the evolution of dispersal via heterogeneity in spatial connectivity. – *Proc. R. Soc. B* 282: 20142879.
- Holland, M. D. and Hastings, A. 2008. Strong effect of dispersal network structure on ecological dynamics. – *Nature* 456: 792–794.
- Hovestadt, T. et al. 2001. Evolution of reduced dispersal mortality and ‘fat-tailed’ dispersal kernels in autocorrelated landscapes. – *Proc. R. Soc. B* 268: 385–391.
- Jin, Y. et al. 2014. Seasonal invasion dynamics in a spatially heterogeneous river with fluctuating flows. – *Bull. Math. Biol.* 76: 1522–1565.
- Johst, K. et al. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. – *Oikos* 98: 263–270.
- Kallimanis, A. S. et al. 2005. Metapopulation extinction risk under spatially autocorrelated disturbance. – *Conserv. Biol.* 19: 534–546.
- Koch, H. et al. 2014. Why rapid, adaptive evolution matters for community dynamics. – *Front. Ecol. Evol.* 2: 17.
- Kubisch, A. and Poethke, H. J. 2011. Range border formation in a world with increasing climatic variance. – *Evol. Ecol. Res.* 13: 159–169.
- Kubisch, A. et al. 2013. Kin competition as a major driving force for invasions. – *Am. Nat.* 181: 700–706.
- Kubisch, A. et al. 2014. Where am I and why? Synthesising range biology and the eco-evolutionary dynamics of dispersal. – *Oikos* 123: 5–22.
- Kubisch, A. et al. 2016. The downward spiral: eco-evolutionary feedback loops lead to the emergence of ‘elastic’ ranges. – *Ecography* 39: 261–269.
- Kuglerová, L. et al. 2015. Local and regional processes determine plant species richness in a river-network metacommunity. – *Ecology* 96: 381–391.
- Labonne, J. et al. 2008. Linking dendritic network structures to population demogenetics: the downside of connectivity. – *Oikos* 117: 1479–1490.
- Legrand, D. et al. 2017. Eco-evolutionary dynamics in fragmented landscapes. – *Ecography* 40: 9–25.
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – *Bull. Entomol. Soc. Am.* 15: 237–240.
- Loreau, M. et al. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. – *Ecol. Lett.* 6: 673–679.
- Mari, L. et al. 2014. Metapopulation persistence and species spread in river networks. – *Ecol. Lett.* 14: 426–434.
- McPeck, M. A. and Holt, R. D. 1992. The evolution of dispersal in spatially and temporally varying environments. – *Am. Nat.* 140: 1010–1027.
- Morrissey, M. B. and de Kerckhove, D. T. 2009. The maintenance of genetic variation due to asymmetric gene flow in dendritic metapopulations. – *Am. Nat.* 174: 875–889.
- Muneepeerakul, R. et al. 2008. Neutral metacommunity models predict fish diversity patterns in Mississippi-Missouri basin. – *Nature* 453: 220–222.
- Muneepeerakul, R. et al. 2011. Evolution of dispersal in explicitly spatial metacommunities. – *J. Theor. Biol.* 269: 256–265.
- North, A. et al. 2011. Evolutionary responses of dispersal distance to landscape structure and habitat loss. – *Evolution* 65: 1739–1751.
- Nuismer, S. L. 2006. Parasite local adaptation in a geographic mosaic. – *Evolution* 60: 24–30.
- Nuismer, S. L. et al. 1999. Gene flow and geographically structured coevolution. – *Proc. R. Soc. B* 266: 605–609.
- Nuismer, S. L. et al. 2000. Coevolutionary clines across selection mosaics. – *Evolution* 54: 1102–1115.
- Nuismer, S. L. et al. 2003. Coevolution between hosts and parasites with partially overlapping geographic ranges. – *J. Evol. Biol.* 16: 1337–1345.
- Oborny, B. et al. 2009. Metapopulation dynamics across gradients – the relation between colonization and extinction in shaping the range edge. – *Oikos* 118: 1453–1460.
- Paz-Vinas, I. and Blanchet, S. 2015. Dendritic connectivity shapes spatial patterns of genetic diversity: a simulation-based study. – *J. Evol. Biol.* 28: 986–994.
- Perkin, J. S. and Gido, K. B. 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. – *Ecol. Appl.* 22: 2176–2187.
- Phillips, B. L. et al. 2006. Invasion and the evolution of speed in toads. – *Nature* 439: 803–803.
- Poethke, H. J. et al. 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. – *Evol. Ecol. Res.* 9: 41–50.
- Poethke, H. J. et al. 2011. A metapopulation paradox: partial improvement of habitat may reduce metapopulation persistence. – *Am. Nat.* 177: 792–799.
- Rodriguez-Iturbe, I. and Rinaldo, A. 1997. Fractal river networks: chance and self-organization. – Cambridge Univ. Press.
- Saastamoinen, M. 2008. Heritability of dispersal rate and other life history traits in the Glanville fritillary butterfly. – *Heredity* 100: 39–46.
- Salomon, Y. et al. 2010. Effects of asymmetric dispersal on the coexistence of competing species. – *Ecol. Lett.* 13: 432–441.
- Seymour, M. et al. 2015. Dendritic network structure and dispersal affect temporal dynamics of diversity and species persistence. – *Oikos* 124: 908–916.
- Shtilerman, E. and Stone, L. 2015. The effects of connectivity on metapopulation persistence: network symmetry and degree correlations. – *Proc. R. Soc. B* 282: 20150203.
- Thompson, J. N. 2005. The geographic mosaic of coevolution. – Univ. of Chicago Press.
- Travis, J. M. J. and Dytham, C. 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. – *Proc. R. Soc. B* 265: 17–23.
- Vörösmarty, C. J. et al. 2010. Global threats to human water security and river biodiversity. – *Nature* 467: 555–561.
- Vuilleumier, S. and Possingham, H. P. 2006. Does colonization asymmetry matter in metapopulations? – *Proc. R. Soc. B* 273: 1637–1642.
- Weigang, H. C. and Kisdi, E. 2015. Evolution of dispersal under a fecundity–dispersal tradeoff. – *J. Theor. Biol.* 371: 145–153.
- Westram, A. M. et al. 2013. Hidden biodiversity in an ecologically important freshwater amphipod: differences in genetic structure between two cryptic species. – *PLoS ONE* 8: e69576.
- Yoshida, T. et al. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. – *Nature* 424: 303–306.

Supplementary material (Appendix ecog-02761 at <www.ecography.org/appendix/ecog-02761>). Appendix 1.