



Emergent encoding of dispersal network topologies in spatial metapopulation models

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We address a generalization of the concept of metapopulation capacity for trees and networks acting as the template for ecological interactions. The original measure had been derived from an insightful phenomenological model and is based on the leading eigenvalue of a suitable landscape matrix. It yields a versatile predictor of metapopulation persistence through a threshold value of the eigenvalue determined by ecological features of the focal species. Here, we present an analytical solution to a fundamental microscopic model that incorporates key ingredients of metapopulation dynamics and explicitly distinguishes between individuals comprising the “settled population” and “explorers” seeking colonization. Our approach accounts for general network characteristics (in particular graph-driven directional dispersal which is known to significantly constrain many ecological estimates) and yields a generalized version of the original model, to which it reduces for particular cases. Through examples, including real landscapes used as the template, we compare the predictions from our approach with those of the standard model. Results suggest that in several cases of practical interest, differences are significant. We also examine, with both models, how changes in habitat fragmentation, including removal, addition, or alteration in size, affect metapopulation persistence. The current approach demonstrates a high level of flexibility, enabling the incorporation of diverse “microscopic” elements and their impact on the resulting biodiversity landscape pattern.

ecological corridors | metapopulation capacity | habitat fragmentation | landscape structure | microscopic models

Understanding spatial ecology and unraveling the intricate dynamics of ecological interactions in relation to biodiversity and population dynamics has been a longstanding pursuit in ecological research (1–6). Models of metapopulations (7, 8) proved central to the description of extinction and colonization events, especially in connection with population persistence and dynamics (9, 10). Habitat patches arise from, and are decisively influenced by, the spatiotemporal changes of landscapes and play a crucial role in the persistence and extinction of metapopulation (9, 11, 12).

One significant aspect of this pursuit has been the recognition of the vital role of river networks acting as ecological corridors, facilitating the movement of species, populations, and pathogens, as well as constraining the related ecological processes (11). The strong influence of dendritic connectivity on biodiversity patterns has been observed across diverse models and is supported by massive empirical and experimental evidence (13–19). Such evidence underscores the crucial role of spatially constrained connectivity in the river basin, with its universal self-organized critical scaling features (20), in shaping dendritic metapopulations (13), fluvial community composition (14, 21), and species persistence (22, 23). Complex life cycles of specific focal species have also been studied in this context (24).

The application of network theory to ecological problems, particularly in the field of spatial ecology, has emerged as a valuable approach (3, 25, 26), but it often overlooks exact results derived in the context of river networks (27–29). Graph theory, which allows the representation of space as a network comprising of interconnected habitats and fragmented dispersal pathways (30), enables a shift in focus from spatially continuous characteristics to the relationships between patches (31–33). Networks, *sensu* Southwood (34), act as templates for ecological strategies. This network-based perspective has yielded valuable insights into how networks of habitat patches can support metapopulations and how connectivity affects a multitude of properties including persistence and invasibility, in both experimental and field studies (12, 35–38). Such studies underscore the profound influence of network structure on ecological dynamics (4, 39, 40).

In this context, the pioneering work of Hanski and Ovaskainen (HO) holds particular significance (7, 8, 32, 41). It introduced a novel measure known as metapopulation

Significance

Recent theoretical, field, and laboratory evidence has greatly improved our understanding of the role of networks acting as templates for key ecological processes, such as the maintenance of biodiversity in river basins, biological invasions, and disease spread. Major progress in this field came through the definition of a measure, termed metapopulation capacity of the ecological templates, quantifying the survival probability of focal species within a given landscape. However, new fundamental approaches are needed to incorporate into metapopulation capacities the detailed features of the landscape and the differences arising in the composition of the metapopulation. These integrations could solidify our insight into how changes in habitat arrangements affect the ability of the ecological substrate to support metapopulations.

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capacity, derived from a phenomenological metapopulation model, to assess survivability in fragmented landscapes (41). This measure can be readily applied to both randomly fragmented landscapes (42) and real-world networks of habitat fragments where the areas and connectivities of the patches are known (32, 43). Technically, metapopulation capacity is quantified as the leading eigenvalue of a carefully defined landscape matrix (41). By comparing the metapopulation capacity of a landscape to a threshold value determined by species-specific properties, predictions can be made regarding species persistence in that landscape (41). This measure offers a convenient ranking system for assessing the ability of different landscapes to support viable metapopulations (32, 41, 44). Furthermore, similar results have been independently derived outside of ecology and metacommunities, most notably in the context of epidemic spreading (45, 46) where the influence of networks and stochasticity has been extensively investigated (47–49).

Motivated by the need for a deeper understanding of metapopulation dynamics, our study introduces a fundamental approach that aims at capturing the essential ingredients of spatial ecology in arbitrarily connected patches. Our framework explicitly distinguishes between two groups of individuals within the metapopulation: the “settled population” comprising individuals that remain in a specific habitat patch, and the “explorers” who venture out to colonize new regions. By incorporating this distinction, we construct a stochastic individual-based model that accounts for the specific landscape characteristics and fundamental processes driving metapopulation dynamics. We propose a general exact solution to our model, which allows us to derive an explicit metapopulation kernel that naturally reflects both the microscopic dynamical features and the underlying dispersal network. We then study how this mechanism interacts with the ecological template on various structures, including real topographic landscapes, whose features are ultimately encoded in the global metapopulation dynamics.

Results

Microscopic Dynamics. Fig. 1 illustrates the core ideas of our microscopic model. We describe the dynamics of a focal species

in a dispersal network consisting of N different patches, each of them with a finite number of colonizable sites. We make the distinction between individuals who remain in a given patch, the “settled population”, and those who instead move between patches and attempt to colonize them, the “explorers.”

Individuals of the settled population die at a rate e_i , and with a rate C_{ij} give birth to explorers in a neighboring patch j . Once an explorer is born, it diffuses between patches connected by the dispersal network with a rate $D_{ij} = D_{i \rightarrow j}$. An explorer then may attempt to colonize one of the sites of its current patch with a rate λ . If the site is empty, it settles and stops moving. If it chooses an already occupied site, it dies in the process. Remarkably, the explorer dynamics corresponds to that of diffusion with random stopping times, which has been long argued to be at the core of the HO metapopulation model (32). Further, an intrinsic mortality rate for explorers may be immediately added to the model, but without qualitatively changing our results.

We write the diffusion rate as $D_{ij} = DA_{ij}$, where D is a baseline rate and A_{ij} are the elements of the adjacency matrix, \hat{A} , describing the dispersal network. Similarly, given that explorers are created locally in neighboring patches, we set $C_{ij} = c_i h(D, \lambda) A_{ij}$, where c_i is the colonization rate and the function h encodes the feasibility of exploration. Since C_{ij} and c_i are both rates, h must be dimensionless. Thus, we must have that $h = h(D/\lambda)$. We note that $f = D/\lambda$ is a species parameter that characterizes how many patches explorers visit before attempting to settle and thus quantifies the exploration efficiency. If $D \ll \lambda$, explorers will remain close to the originating patch. In the other limit, $D \gg \lambda$, they will explore large parts of the dispersal network before settling. Let us note that, in all the processes above, \hat{A} does not need to be symmetric nor binary—that is, the dispersal network may be directed and weighted. Therefore, our microscopic model also admits the possibility of biased diffusion and directed dispersal, which is particularly relevant for nonstandard topographies such as river networks and insurmountable barriers (11). Further, these choices ensure that $D_{ij} = 0$ if the two patches are not connected, as well as $D_{ii} = 0$, and $C_{ii} = 0$. Hence, the explorers’ dynamics is local—they cannot move directly among distant patches, but only along the dispersal network.

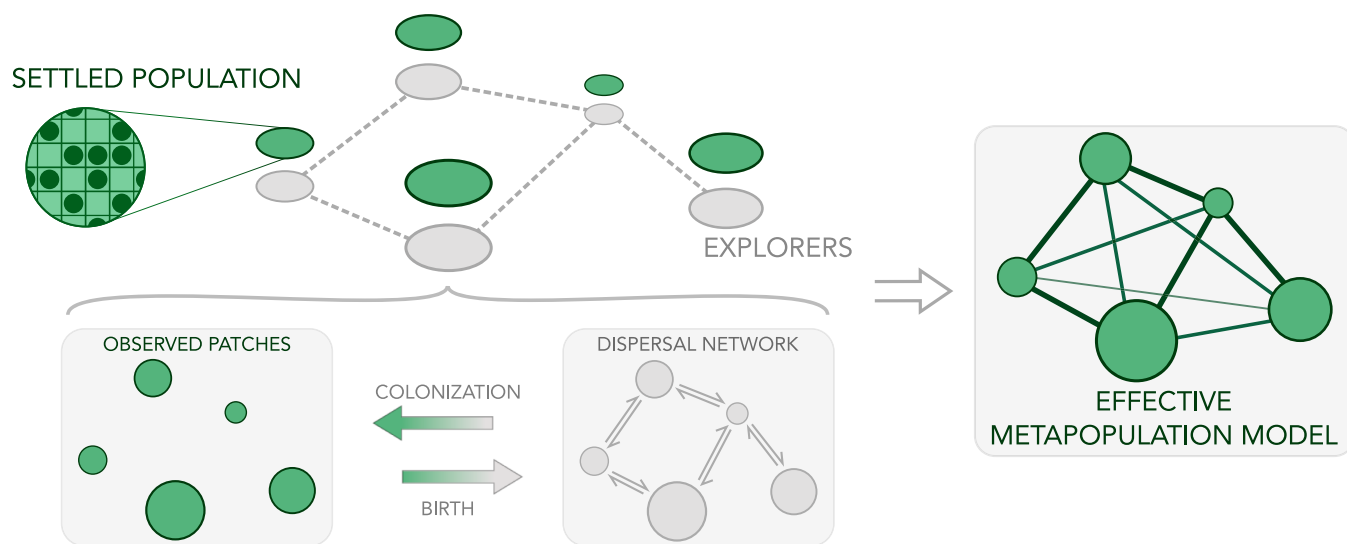


Fig. 1. Sketch of the microscopic derivation of the metapopulation model. We explicitly consider a dispersal network and describe, in each of its patches with a finite number of inhabitable sites, the local population of a given species. These settled individuals may give birth to explorers, whose role is to diffuse along the dispersal network. At any time, an explorer can attempt colonization by settling on a new patch. By assuming that only the settled population can be observed, we derive an effective metapopulation model with an all-to-all dispersal kernel that explicitly includes the effects of the underlying dispersal topology.

Effective Metapopulation Model. From the microscopic model, we derive the equations for the evolution of the density of the settled population in patch i (ρ_i) and the number of explorers per empty site (x_i) (*Materials and Methods*). Crucially, these equations give rise to a generalized version of the HO model in the limit in which the dynamics of the explorers is much faster than the dynamics of the settled population. This quasistationary approximation amounts to setting $\dot{x}_i = 0$ (*Materials and Methods*) and leads to the effective equation for ρ_i

$$\dot{\rho}_i = -e_i \rho_i + (1 - \rho_i) \sum_{j=1}^N c_j K_{ji} \rho_j, \quad [1]$$

where e_i is the extinction rate at patch i and K_{ji} are the elements of a matrix kernel \hat{K} that describes the effective dispersal strength from patch j to patch i . Eq. 1 is indeed the HO metapopulation model, yet with a major difference: the kernel K_{ji} is not given a priori but rather determined by the microscopic dynamics and the morphology of the habitat. Moreover, as we will show below, the kernel not only depends on the distance between patches i and j but also incorporates other aspects of the dispersal network. Importantly, even if a patch i is not a direct neighbor of patch j , it will still be influenced by the latter through the effective coupling described by K_{ji} , which in general is nonzero. Thus, in this sense, the global couplings in the metapopulation model emerge from purely local processes.

We derive an exact expression for \hat{K} , finding that the kernel between two patches depends manifestly on the topological features of the dispersal network even if it describes an effective fully connected model. We obtain

$$K_{ji} = b(f) \sum_{l=1}^N A_{jl} \sum_{k=1}^N \frac{V_{ik}(V^{-1})_{kl}}{1 + f\omega_k}, \quad [2]$$

where ω_k the k -th eigenvalue of the transpose out-degree Laplacian of the dispersal network, and $V_{ij} = v_i^{(j)}$ with $\mathbf{v}^{(k)}$ the corresponding right eigenvector (*SI Appendix*). Eq. 2 tells us that the kernel depends on the spectral properties of the dispersal network (50, 51). Furthermore, we can explicitly show that the spectral part of K_{ji} can be rewritten as a sum over all possible paths between patches i and j . The weight associated with each path $j \rightarrow i$ depends on f and on the path length, so shorter paths are more likely and longer paths are not, which remarkably leads to a finite effective kernel despite summing over all possible paths (*Materials and Methods*).

The results of Hanski and Ovaskainen (7, 8, 32, 41) can be directly applied to Eq. 1. In particular, we may assume $c_i = cA_i$ and $e_i = e/A_i$, where A_i is the area of patch i . Note that in dendritic metapopulations, the area of the patch may be derived from the total contributing area at the site (11, 52), which holds universal distributions for fluvial networks in runoff-producing areas (20). The survival of a species is determined by the maximum eigenvalue of the landscape matrix $M_{ij} = K_{ij}A_iA_j$, i.e., the metapopulation capacity λ_M —if $\lambda_M > e/c$, the species survives; otherwise, it goes extinct. In our case, λ_M will depend on the form of the function $b(f)$, which models the feasibility of exploration, i.e., the explorability of the focal species. We take a Monod function $b(f) = \xi/(1 + 1/f)$, where the saturating value ξ represents the maximal explorability at large efficiency f (*Materials and Methods*).

Although we cannot find a general analytical expression for λ_M , we can compute it in certain limits in undirected dispersal

networks. Not surprisingly, $f \rightarrow 0$ gives $\lambda_M \rightarrow 0$, implying that in the absence of exploration, survival is not possible. On the other hand, in the opposite limit of large exploration efficiency $f \rightarrow \infty$, the metapopulation capacity is proportional to the average out-degree of the network (*Materials and Methods*). This clearly shows that the topological features of the dispersal network affect a species' persistence. In particular, we expect more densely connected networks to have larger metapopulation capacity, whereas species in highly fragmented landscapes are more prone to extinction (*SI Appendix*). This result had been pinpointed earlier for patchy landscapes (10, 43, 44) and for dendritic metapopulations (53, 54) using the original kernel, and it is reinforced by the present results employing a more general framework.

Effects of Network Topology. In Fig. 2, we study how the topological features of the dispersal network affect both species survival and dynamics. We first focus on the simple case of a ring network, which represents a one-dimensional model with periodic boundary conditions. We find that the kernel elements K_{ij} decay exponentially with the network distance d_{ij} , in striking similarity with the HO effective kernel where this decay was phenomenologically assumed (Fig. 2A). Notably, the characteristic decay length increases with f , leading to a stronger effective coupling between patches at large distances. This suggests a direct relation between the exploration efficiency f and the average dispersal distance, α , appearing in the HO model (*Materials and Methods* and *SI Appendix*, Fig. S2).

Crucially, we are now able to study how changes in the underlying dispersal network topology are reflected in the metapopulation model. In particular, small-world networks (55) introduce long-range connections between patches that may be otherwise very far apart. In Fig. 2B, we show that such connections have a deep impact on the kernel elements K_{ij} , which are not solely a function of the network distance d_{ij} , i.e., of the minimum number of edges that connect the two patches. Rather, at fixed d_{ij} , we have a distribution of values of K_{ij} . This effect becomes especially relevant at higher f , and it is a direct consequence of the fact that K_{ij} encodes contributions from all possible paths between patch j and patch i . Thus, it will depend on the entire network structure rather than on distance alone. Although on average the kernel $\langle K_{ij} \rangle$ still displays an exponential behavior with the network distance, heterogeneity in the network structure induces heterogeneity in the elements of the kernel matrix at fixed d_{ij} . In other words, for a given pair of patches i and j , there are two contributions to the kernel K_{ij} : an approximately exponential decay like in the original HO model and an entropic contribution associated with the multiplicity of paths connecting i and j . Such a contribution emerges naturally and was not present in previous approaches.

In the case of Barabási–Albert dispersal networks (56), few patches behave as hubs, connecting to a large number of other nodes and resulting in a scale-free degree distribution. This highly heterogeneous structure translates into very diverse kernel elements at equal distances, as we show in Fig. 2C. This is not surprising, since being closer or farther from a hub introduces significant differences in the number of steps an explorer needs to take before reaching farther parts of the network.

Furthermore, topological features also affect the survival of a species. In particular, the metapopulation capacity increases with the heterogeneity of the network (Fig. 2D). This effect is particularly significant at intermediate values of exploration efficiency f , where the fine structure of the dispersal network is

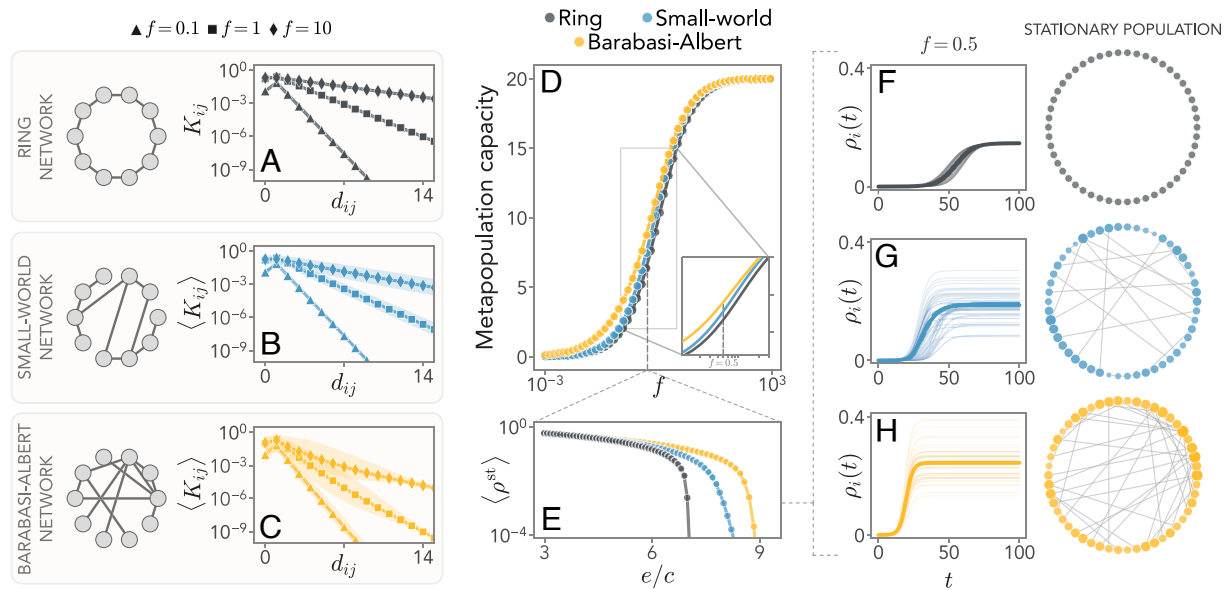


Fig. 2. Effects of network topology on the effective dispersal kernel. (A) Behavior of the kernel elements K_{ij} as a function of the network distance d_{ij} (in log-linear scale) in ring networks (sketched on the left). The kernel decays exponentially with d_{ij} regardless of the patches' identities, and larger values of f imply a larger characteristic length of such decay. (B and C) Behavior in small-world and Barabasi-Albert networks. At the same distance d_{ij} , there are, in general, multiple values of K_{ij} , which depend on all possible paths between patch i and j . Scatter points represent their average $\langle K_{ij} \rangle$, and the shaded area is the area between their maximum and minimum value. (D and E) The metapopulation capacity as a function of f (at fixed $\xi = 10$) and the average stationary population (ρ^{st}) as a function of e/c (at $f = 0.5$) show that, in general, survival is favored by more heterogeneous topologies. (F–H) Dynamical evolution of the population density in different patches ρ_i (shaded lines) and its average (solid line) at $e/c = 6$. The stationary population shows localization in heterogeneous topologies, e.g., with a larger population in the hubs of Barabasi-Albert networks.

most relevant. Conversely, in the limit $f \rightarrow \infty$, explorers can reach all patches before attempting colonization (*SI Appendix*). The relevance of dispersal network structure at intermediate values of f consequently affects the average stationary population as well (Fig. 2E). Such differences across diverse dispersal topologies result not only in distinct extinction thresholds but also in different approaches to extinction. For instance, in small-world networks, a species' decay to extinction is slower than in a ring, which could have a significant impact when demographic stochasticity is considered.

Finally, we observe marked differences in both the total population and the population in each patch. In Fig. 2F–H, we show that settlement is more favored in nodes with a higher degree, and hubs in particular. Overall, heterogeneity and long-range connections drive faster colonization dynamics and strongly boost the total population. These results imply that the same species may colonize and survive in, for example, a small-world dispersal network, but go extinct in a ring topology at the same value of extinction threshold, e/c . Such beneficial effects on survivability are not unexpected. However, our results arise in a global metapopulation model derived from purely local microscopic dynamics, demonstrating its fundamental improvements over previous approaches (see *SI Appendix* for a comparison with the HO model).

Effects of Modularity and Fragmentation. A crucial aspect of dispersal networks that has important ecological implications is the presence of multiple weakly interconnected communities, with each community consisting of strongly connected patches. This modular structure (Fig. 3A) reflects that of ecological corridors, with few corridors between ecosystems for species to move across. Understanding dynamics in such structures is a key ingredient in habitat conservation efforts (58).

In Fig. 3B, we show that a modular dispersal network is associated with a block-like metapopulation kernel, where patches belonging to the same community are more strongly coupled. Notably, the metapopulation capacity increases with the probability of connection between different communities (Fig. 3C). Thus, more connections between ecosystems allow for easier dispersal, thereby increasing survivability. It is a natural consequence of the entropic effect alluded to above, which is associated with the multiplicity of corridors connecting ecosystems. Hence, sparsity is detrimental to a species, whereas more dense networks are less prone to extinction (*SI Appendix*).

The modular structure of the network is also reflected in the dynamics. This point represents a crucial difference between our microscopic model and the HO model (see *Material and Methods* for details on the comparison). Fig. 3D and E show that the dynamics in the microscopic model immediately reflects the different communities, with patches of a given community being colonized together. On the contrary, this is completely absent in the dynamical evolution predicted by the HO model, since only the patch distances are considered. As a consequence, pair of patches at the same distance are equivalent in the HO model regardless of the communities they belong to, whereas such topological information is naturally encoded in our approach.

This fundamental difference is especially relevant to understand the resilience of the metapopulation model in events of landscape fragmentation (59). In particular, the presence of ecological corridors favors a larger total population, both in HO and our microscopic model (Fig. 3F and G). However, since the HO effective kernel does not distinguish between communities, the total population in the absence of intercommunity connections drastically decreases. On the contrary, in our microscopic model, the settled population in each community does not solely depend on the presence of corridors among them. We can also study in detail the effect of landscape fragmentation

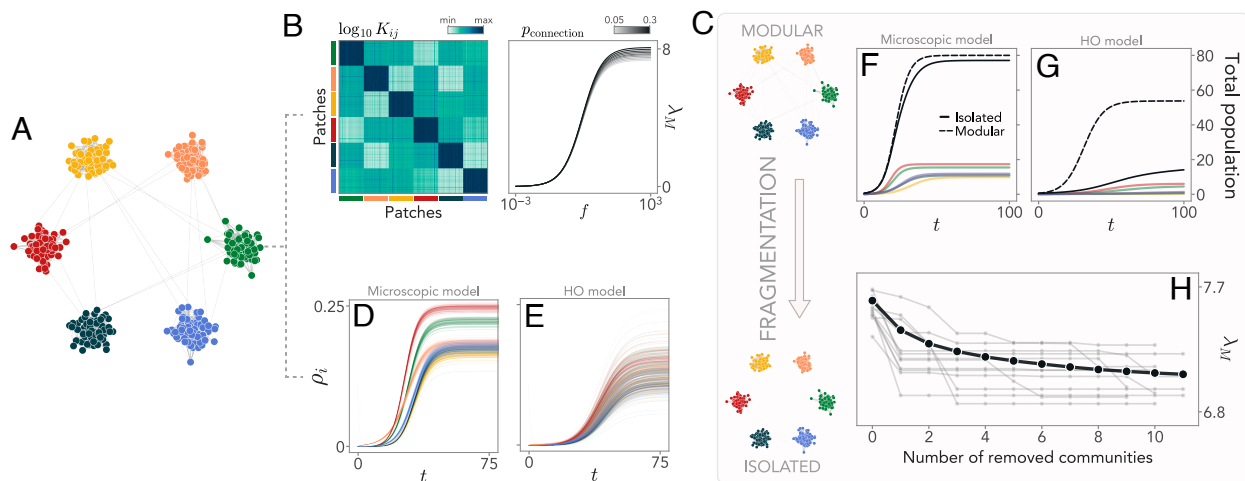


Fig. 3. Effects of modularity and fragmentation on the metapopulation model. (A) A modular network composed of six realizations of Erdős–Rényi networks (50, 57) with the same wiring probability $P_{\text{intra}} = 0.05$, i.e., with the same average intracommunity degree. Patches belonging to different communities are connected with a low probability $P_{\text{connection}} = 0.2$. (B) The matrix kernel displays a block structure, with larger elements between patches belonging to the same community. (C) The metapopulation capacity increases with the connection probability between communities, suggesting that persistence is higher in more dense networks. (D and E) Evolution of the settled population ρ_i in each patch and comparison with the HO model. Each color represents patches in different communities. In our model, a clear separation between different communities is maintained, whereas the HO kernel fails to distinguish among them. (F and G) Comparison of the total population in the modular network (dashed black line) and the isolated network (solid black line), where all links across communities have been removed, in our and in the HO model. Notably, the HO model overestimates the effects of fragmentation, predicting a much lower total population. (H) Effect of fragmentation on the metapopulation capacity on a modular network with 11 communities. As we randomly isolate communities from the network, the metapopulation capacity decreases, showing that a fragmented landscape hinders species survival. The gray lines represent a single realization of the stochastic disconnection process, showing significant drops when the network fragments.

by randomly disconnecting communities from the rest of the network. Fig. 3H shows the decreasing metapopulation capacity of the whole network with increasing fragmentation. Hence, isolation is detrimental to survivability, and the metapopulation capacity eventually saturates to that of the weakest isolated community. Remarkably, this shows that although the overall change to the total population may not appear significant (Fig. 3F), fragmentation—and sparsity in general—drastically reduces a species' persistence.

Effects of Landscape Topography. Topography plays a vital role in shaping the ecological features of real landscapes (60), from hindering the movement of species in mountain regions to impacting the behavior of fishes inhabiting lakes located far apart in terms of water flow. The presence or absence of such topographic features could significantly alter the effective distance between two areas. We now exploit our microscopic approach to study how elevation gradients affect metapopulation models.

HydroSHEDS Digital Elevation Models (DEM) (61) provide elevation data at 15 arc-second resolution obtained from the NASA Shuttle Radar Topography Mission. We select two mountainous areas of interest (Fig. 4 A and B): a part of Ene River in Peru, in the Andes region, and the Kauriala River in Nepal, in the Himalayas. These areas show geographic features that could potentially have ecological effects—the Ene region displays a fractal-like flow channel structure, and the Kauriala region includes a bottleneck-like passage between two zones of high elevation. In each region, we construct a grid of points at the latitudes and longitudes where elevation data exist. From this grid, we construct the exponential HO kernel using an elevation-dependent distance matrix with a characteristic migration distance α (Materials and Methods). Our model, however, allows for biased exploration. Thus, in our case, we consider exploration along the elevation gradient, with a downhill diffusion rate much larger than the uphill one (Materials and Methods).

Fig. 4 C and D show the stationary population density at each grid point for increasing dispersal parameter— α and f —for the chosen regions (see SI Appendix for the dynamical evolution). At low dispersal parameters, the resulting metapopulation capacity is low, and in both models, the only surviving population is in low-lying areas. With increasing dispersal, it becomes easier and easier to move against the elevation difference. Hence, perhaps unsurprisingly, species with different dispersal parameters experience the topography differently. While both models predict similar qualitative behaviors, there are stark differences in the stationary populations. In the HO model, species immediately occupy low-lying areas at significantly high population densities with respect to higher-elevation zones. Conversely, in the microscopic model, the densities increase smoothly along the elevation gradient.

This difference is a direct consequence of the fact that, in the HO kernel, the dispersal between two points at different elevations is the same regardless of whether the species is trying to colonize uphill or downhill. This naturally leads to a preference for connected regions at similar elevation levels but does not take into account the fine topographic structure that arises from changes in the elevation gradients. Hence, only the overall topography is qualitatively reflected in the stationary population densities, which is strongly biased toward colonizing uniformly regions at the same elevation. This is in clear contrast with our model, where downhill exploration is intrinsically favored and thus allows for elevation gradients to be encoded into the dynamics through the entropic contribution due to the multiplicity of paths between two points. As a result, species are able to settle along the fractal-like flow channel structure in the Ene region and are forced to move across the bottleneck of the Kauriala region. The reflection of the topographic structure is not only limited to the DEM, as it does follow the dendritic river network constructed from elevation data. Therefore, the influence of topography is clearly reflected in the species dynamics.

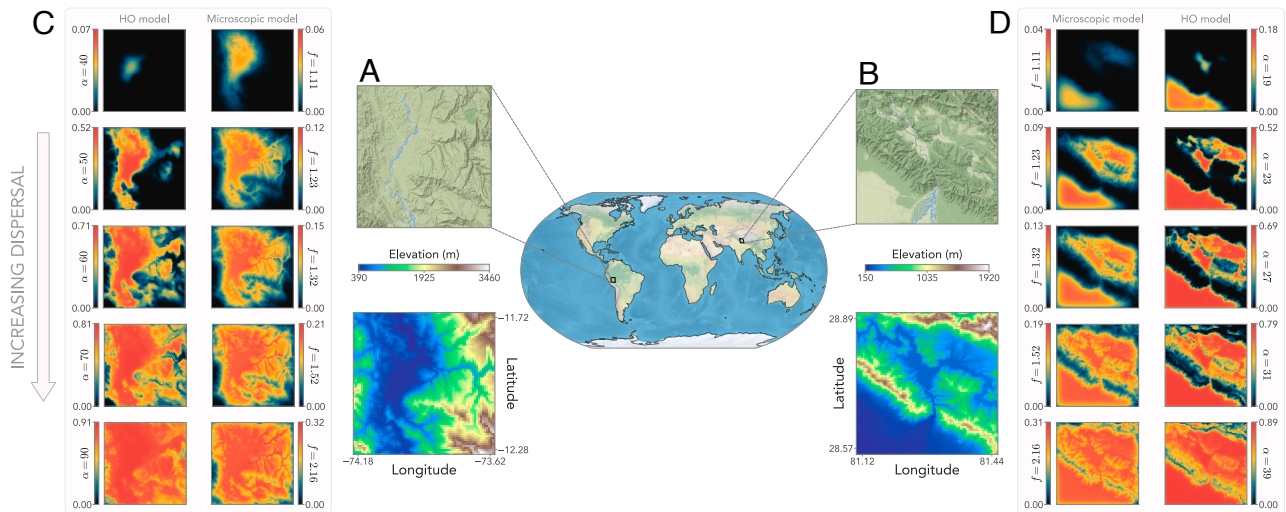


Fig. 4. Stationary populations in Digital Elevation Models (DEMs). In the microscopic model, we consider a directed dispersal network, where moving against the altitude gradient is less favored. The HO kernel, instead, is intrinsically unbiased and only takes into account the absolute altitude differences. (A and B) Topography and DEM of a region of the Ene River in Peru, South America, and of the Kauriala River in Nepal. (C) Comparison between the stationary population at different values of f and α for the first DEM. The microscopic model is able to take into account the altitude gradient, and thus better reflects the features of landscape topography. Remarkably, the stationary population consistently reflects the fractal-like structure of the underlying river network, even at different values of f . Conversely, the HO model is only able to capture rough topographic features, and the population density is extremely high in low-lying areas even for small dispersal parameters. (D) Same, but the Kauriala River. Notice that the bottleneck created by mountains is captured by the stationary population. Importantly, while we can keep the same value of f in our model, the value of α needs to be tuned to each DEM for the HO model to give meaningful predictions.

In principle, this allows for a deeper understanding of how changes to the landscape topography directly affect metapopulation models, e.g., changes in river flow due to natural or anthropogenic causes, landslides changing the elevation of a region, urbanization creating more flat areas, etc. When topography is involved, the basic assumption of unbiased colonization would become invalid, further highlighting the need for a consistent microscopic description.

Discussion. In this work, we have derived a general metapopulation model that incorporates key features of dispersal networks and a detailed microscopic dynamics of settlers and explorers. We have found that the metapopulation capacity, which determines whether a species survives or goes extinct, is manifestly dependent on the template for ecological interactions. In particular, dense and heterogeneous networks with hubs and long-range connections favor survival, whereas sparse and fragmented templates are detrimental. Crucially, our approach encompasses asymmetric dispersal, allowing for the study of real landscapes and biased colonization. With respect to the original metapopulation model proposed by Hanski and Ovaskainen (41), our model explicitly displays settlement along dendritic corridors and better captures the topographic features of the underlying landscape.

In future works, it will be critical to explore the interplay between the topology of complex dispersal networks and both dynamical and stationary metapopulation patterns. We expect this to be particularly relevant in the presence of regions that are suboptimal for survival due to natural or anthropogenic causes. Most notably, the reflection of the dendritic connectivity of river networks in DEMs ultimately stems from downhill colonization being favored, thereby highlighting how our model presents a tractable approach to characterize how metapopulations are affected by physical constraints, trade-offs and universality in river and optimal channel networks (62, 63). It will also be of particular interest to understand whether and how the exact microscopic kernel can be well approximated by some suitable

phenomenological kernel that depends solely on the distance, as in the HO model (42).

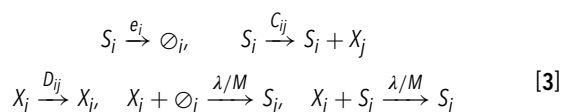
Additionally, our current study does not factor in the cost associated with the explorers' birth. We believe that this aspect may be essential to understanding the trade-offs between exploration and colonization. Expanding the model further could involve incorporating informed exploration, where explorers take into account which parts of the network are more favorable to settlement. This could be achieved by including either information about patches in the colonization step or by considering previously taken diffusion paths. Such scenarios will lead to vastly different results, suitable to model diverse ecological processes. Incorporating different dispersal strategies in the microscopic processes would also allow us to study competition between different strains or species as well, potentially including evolutionary effects (64). In all these cases, stochastic effects may be readily included by considering higher orders of the Kramers–Moyal expansion of the master equation governing our model, or a van Kampen system-size expansion (65). It would be of particular interest to compare these results against the recent open-systems approach to ecology, where the environment plays a significant role in determining the type of noise in the dynamics (66, 67). The timescales at play—e.g., the one of the dispersal mechanism—would then play a central role in shaping the modeling approach. Finally, we note that our approach has strong parallels with spatially explicit epidemiological models (45–48, 68, 69). Its notable advantage is that asymmetric spreading emerges naturally from the microscopic dynamics, a desirable feature in models of several diseases, e.g., sexually transmitted diseases or pathogens whose spread is influenced by mobility patterns (49). The very concept of metapopulation capacity (41) finds a direct parallel in the maximum eigenvalue of suitable Jacobians pinpointing the stability of disease-free equilibrium in spatially explicit models of disease spread, see for example, ref. 11.

Overall, deriving the metapopulation dynamics from explicit microscopic reactions allows for a deeper and quantitative investigation of the relevant processes underlying colonization

and spreading, a facet that was not straightforward to achieve in previous models. Further, current metapopulation models typically require the choice of a specific colonization kernel, tailored to suit the problem at hand and often distance-dependent (70). While such choices may yield good results, they inherently remain phenomenological in nature and miss the entropic effect associated with the multiplicity of paths connecting different regions. In contrast, here we derive a spectrum of interesting and ecologically relevant phenomena by explicitly modeling the microscopic dynamics of dispersal. This enables the incorporation of more complex dispersal mechanisms and unravels the direct relation between the underlying ecological template and the emergence of effective metapopulation kernels. While the simplicity of our approach yields itself to a range of theoretical studies, the diverse range of predictions presents excellent grounds to test against decades of observational studies in this field.

Materials and Methods

Microscopic equations. We denote a settled individual in patch i with S_i and an explorer with X_i . The microscopic model is defined by the microscopic reactions



where the first line specifies the dynamics for an individual of the settled population of the i -th patch, S_i , and the second line that of explorer individuals, X_i . We assume that, at the microscopic level, colonization is a local process, so that $C_{ij} \propto A_{ij}$, and that each patch has a finite number of colonizable sites M . We are interested in the number of individual of the settled population, which we denote by $[S_i]$, and of explorers, $[X_i]$, whose dynamics is described by a master equation for the probability $p([S], [X], t)$, where $[S] = ([S_1], \dots, [S_N])$ and $[X] = ([X_1], \dots, [X_N])$ (65). In particular, we are interested in the averages

$$\langle S_i \rangle(t) = \sum_{[S_i]=0}^{\infty} [S_i] p([S_i], t), \quad \langle X_i \rangle(t) = \sum_{[X_i]=0}^{+\infty} [X_i] p([X_i], t).$$

We define $\rho_i = \langle S_i \rangle / M$ and $x_i = \langle X_i \rangle / M$, i.e., the density of settled population and explorers, respectively. The leading order of the Kramers-Moyal expansion of the master equation (SI Appendix) leads to the following deterministic evolution equations of ρ and x :

$$\begin{aligned} \dot{\rho}_i &= -e_i \rho_i + \lambda(1 - \rho_i)x_i \\ \dot{x}_i &= -\left(\lambda x_i - \sum_{j=1}^N C_{ji} \rho_j\right) + \sum_{j=1}^N (D_{ji} x_j - D_{ij} x_i), \end{aligned} \quad [4]$$

where $D_{ij} = DA_{ij}$, $C_{ij} = c_i h(D/\lambda)A_{ij}$ and A_{ij} are the elements of the adjacency matrix describing the dispersal network.

Quasistationary Approximation. We assume that the dynamics of the explorers is faster than that of the settled population. This separation of timescales allows us to perform a quasistationary approximation, which amounts to set $\dot{x} = 0$. This is equivalent to setting the value of the explorers' densities equal to their instantaneous stationary state, as determined by the current values of the settled population's densities. Crucially, this approximation is exact in the stationary limit—i.e., the effective dynamics obtained from the quasistationary approximation has the same stationary state as the complete one for the entire ecosystem (explorers and settled population).

To get the effective dynamics for ρ , we rewrite the previous equation for the explorers at quasistationary as

$$\sum_{j=1}^N C_{ji} \rho_j(t) = \lambda \sum_{j=1}^N [\delta_{ij} + fL_{ji}] x_j(t), \quad [5]$$

from which we can get the density of explorers x_i as a function of ρ (SI Appendix). Notice that this expression is still local in the dispersal network, that is, the two sums in Eq. 5 receive nonzero contributions if and only if j is connected to i . The matrix kernel appearing in Eq. 1 then is given by

$$\hat{K}^T = h(f) (\mathbb{I} + f\hat{L}^T)^{-1} \hat{A}^T, \quad [6]$$

where $f = D/\lambda$, \mathbb{I} is the identity matrix, and $\hat{L} = \hat{A} - \hat{q}$ is the out-degree Laplacian matrix of the dispersal network, with $q_{ij} = \delta_{ij} \sum_k A_{ik}$.

Effective Kernels as Sums Over Paths. The effective kernel derived from the dispersal network can be written in terms of $\hat{F} = (\mathbb{I} + f\hat{L}^T)$, which represents the dispersal part of the kernel. Its inverse can be computed exactly in a range of different ways (SI Appendix). One possibility, which generalizes to more complex models, is to employ the Woodbury matrix identity (71). It allows us to formally write the kernel as

$$\hat{K}^T := h(f) \hat{F}^{-1} \hat{A}^T = h(f) \sum_{n=0}^{\infty} (-1)^n f^n (\hat{L}^T)^n \hat{A}^T, \quad [7]$$

provided that the inverse of \hat{F} exists. We can interpret the sum in Eq. 7 in terms of its analytic continuation (SI Appendix), leading to the same result as in Eq. 2. Remarkably, this infinite sum has a deep physical meaning. We can grasp its significance if we consider regular networks where every patch is connected to exactly q other patches—e.g., a two-dimensional grid. In this case, we have

$$(\hat{F}^{-1})_{ij} = \sum_{n=0}^{\infty} \frac{f^n}{(1 + fq)^{n+1}} (\hat{A}^n)_{ji} = \sum_{n=0}^{\infty} p^{\text{path}}(n) N_{ij}^{\text{path}}(n), \quad [8]$$

where $p^{\text{path}}(n)$ is the probability associated to a path of length n , and $N_{ij}^{\text{path}}(n) = (\hat{A}^n)_{ji}$ is the number of paths of length n connecting j and i . Hence, the effective coupling between two patches quantified by the metapopulation kernel represents the total contribution of all possible paths taken by the unobserved explorers. For general networks, a similar argument holds since the n -th power of the Laplacian depends on the powers of the adjacency matrix as well.

Metapopulation Capacity. We write the birth rate of explorers from patch i to patch j as $C_{ij} = c_j h(f) A_{ij}$, where $h(f)$ encodes the feasibility of exploration. Indeed, explorers' birth occurs in neighboring patches and thus implicitly includes a step of diffusion. Hence, in the limit $f \rightarrow 0$, exploration should not be possible and h must vanish. Similarly, as $f \rightarrow \infty$, we require that h converges to a finite parameter ξ which corresponds to the maximal dispersal capacity of the species. A simple parametric form for h is a Monod function of the form

$$h(f) = \frac{\xi}{1 + 1/f}, \quad [9]$$

although our results are qualitatively unchanged provided that h satisfies the limiting behaviors outlined above. As stated in the main text, ξ thus quantifies the feasibility of exploration at large f . If ξ is small, exploration is hindered even when $f \rightarrow \infty$.

If we take $e_i = c_i/\mathcal{A}$ and $c_i = c\mathcal{A}$ for all $i = 1, \dots, N$, we find that the metapopulation capacity in the $f \rightarrow \infty$ limit converges to

$$\lambda_M \xrightarrow{f \rightarrow \infty} \mathcal{A}^2 \frac{\xi}{N} \sum_{i=1}^N q_i, \quad [10]$$

where $q_i = \sum_j A_{ij}$ is the weighted out-degree of patch i (SI Appendix). Eq. 10 shows that the metapopulation capacity depends manifestly on the topology of the dispersal network.

Comparison with Hanski's Model. Hanski's effective metapopulation kernel appearing in the HO model (41) is defined as

$$K_{ij}^H = \exp\left[-\frac{d_{ij}}{\alpha}\right], \quad [11]$$

where α is the average migration distance of the species, d_{ij} is the distance between patch i and j , and $K_{ii}^H = 0$. In order to compare our model with the HO one, thus, we need to set an appropriate value for α . We do so by taking

$$\alpha = -\frac{\langle \hat{d} \rangle}{\langle \log \hat{K} \rangle}, \quad [12]$$

where

$$\langle \hat{d} \rangle = \frac{1}{N(N-1)} \sum_{i=1}^N \sum_{j \neq i}^N d_{ij}$$

is the average distance and

$$\langle \hat{K} \rangle = \frac{1}{N(N-1)} \sum_{i=1}^N \sum_{j \neq i}^N K_{ij}$$

is the average matrix kernel in our model. The resulting α is a nonlinear function of both f and ξ and is exact in the case where \hat{K} decays exponentially with the distance, e.g., in ring networks (SI Appendix).

Biased Exploration in DEMs. DEMs assign to each pixel i at a given latitude and longitude an elevation z_i . We consider that each pixel is directly connected to its nearest and next-nearest neighbors, and the corresponding diffusion coefficient is

$$D_{ij} = Dg(z_j - z_i), \quad [13]$$

where g is a generic function of the elevation difference. It is reasonable to expect that downhill diffusion should be favored, and uphill diffusion should be suppressed. To this end, we take

$$g(z_j - z_i; \beta) = a + b \exp\left[-\beta(z_i - z_j)\right],$$

where the parameters a and b are set in such a way that $g \in [0, 1]$, and β sets the stiffness of the exponential suppression of uphill diffusion. With this choice, the dispersal network is both weighted and directed. Other functional forms for g with different properties may lead to different behaviors of the model, and one can assume that g itself may be a species-dependent strategy.

In the HO model, we consider that d_{ij} is the three-dimensional Euclidean distance between pixels, taking into account their elevation. For simplicity and to take into account the topographic features of the DEM, we assume that the grid of pixels is equally spaced with a spacing $\Delta x = \Delta y$ equal to the median elevation. In this way, the planar distance in the grid space and the elevation distance along the vertical direction are of the same order of magnitude, and the resulting distance matrix can be used to build the HO kernel.

Data, Materials, and Software Availability. Code, scripts and DEM data have been deposited in Microscopic Metapopulation Model (<https://doi.org/10.5281/zenodo.8143931>) (72).

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