Multispecies coexistence in fragmented landscapes

Mingyu Luo (罗明宇)[a] [ID], Shaopeng Wang (王少鹏)[a,1] [ID], Serguei Saavedra[b] [ID], Dieter Ebert[c,d] [ID], and Florian Altermatt[e,f] [ID]

Spatial dynamics have long been recognized as an important driver of biodiversity. However, our understanding of species' coexistence under realistic landscape configurations has been limited by lack of adequate analytical tools. To fill this gap, we develop a spatially explicit metacommunity model of multiple competing species and derive analytical criteria for their coexistence in fragmented heterogeneous landscapes. Specifically, we propose measures of niche and fitness differences for metacommunities, which clarify how spatial dynamics and habitat configuration interact with local competition to determine coexistence of species. We parameterize our model with a Bayesian approach using a 36-y time-series dataset of three *Daphnia* species in a rockpool metacommunity covering >500 patches. Our results illustrate the emergence of interspecific variation in extinction and recolonization processes, including their dependencies on habitat size and environmental temperature. We find that such interspecific variation contributes to the coexistence of *Daphnia* species by reducing fitness differences and increasing niche differences. Additionally, our parameterized model allows separating the effects of habitat destruction and temperature change on species extinction. By integrating coexistence theory and metacommunity theory, our study provides platforms to increase our understanding of species' coexistence in fragmented heterogeneous landscapes and the response of biodiversity to environmental changes.

coexistence criterion | *Daphnia* species | habitat destruction | metacommunity | temperature

The coexistence of species is among the most central questions in ecology and has evoked long-standing interest among experimental and theoretical ecologists (1–3). While previous studies have advocated different hypotheses to explain species coexistence (3–7), coexistence theory provides an integrated framework to reconcile different perspectives (2, 8–11). Specifically, coexistence theory clarifies that the outcome of interspecific competition is determined by the balance of two key ecological processes: the niche difference that facilitates coexistence and the fitness difference that begets exclusion (2). This theory has been widely adopted to study species coexistence in experimental and natural communities under constant and changing environmental conditions (12–15). Yet, coexistence theory, as well as its empirical testing, has so far mainly focused on local communities, despite the fact that most species live in fragmented landscapes (16, 17). Because habitat loss and fragmentation have been identified as dominating drivers of species extinction (18, 19), this focus on local communities not only limits the understanding of species' coexistence to a hypothetical single-site perspective but also largely restricts the practical application of coexistence theory.

Indeed, spatial processes have long been recognized as important drivers of species coexistence (20–23). By modeling the interplay of spatial dynamics and local species interactions, metacommunity theory allows the explicit incorporation of spatial characteristics, such as habitat configurations and local environmental conditions, and translates the problem of species coexistence from local communities to fragmented landscapes (20, 21, 24). However, coexistence theory and metacommunity theory have been largely disconnected in the literature. One difficulty in integrating these two theories is the complexity of realistic landscape configurations, which prevents analytical investigations on the effects of spatial processes on species coexistence. Previous metacommunity models have thus often relied on numeric approaches (25–27) or simplified assumptions ignoring habitat heterogeneity (28, 29), which lag behind spatially explicit models of metapopulations that characterize the heterogeneity and spatial configurations of habitat patches for single-species persistence (30). Hence, a tractable metacommunity theory is needed for an analytical description of species' coexistence in the context of natural and anthropogenic fragmentation, as well as predicting biodiversity responses to habitat and environmental changes (17–19).

In this study, we develop a spatially explicit metacommunity model of multiple competing species to understand species coexistence in fragmented heterogeneous landscapes, that is, spatially separated habitats with varying conditions (e.g., patch size) and connected via species migration. Our model builds on the spatially explicit patch

Significance

The maintenance of biodiversity is a central theme in ecology and conservation biology. Although spatial dynamics have long been documented to influence biodiversity, coexistence theory has so far mainly focused on local communities. This not only limits the understanding of species coexistence to a single-site perspective but also largely restricts our ability to predict the impacts of habitat destruction. Here, we develop a spatially explicit competition model and derive analytical criteria for multispecies coexistence under realistic landscape configurations. By parameterizing our model using a long-term dataset of three *Daphnia* species in a rockpool metacommunity, we predict its possible responses to habitat destruction and temperature change. Our study provides theoretical and empirical platforms to understand multispecies coexistence in fragmented landscapes.

occupancy model of metapopulations (30), which predicts that species' persistence in a fragmented landscape is determined by metapopulation capacity—a single metric that characterizes the impacts of habitat area and spatial arrangement on metapopulation dynamics. Despite the elegancy and tractability of the metapopulation capacity theory, it has been solely focusing on single species, a significant shortcoming in the context of the current biodiversity crisis and the understanding of species' coexistence in general. Only very recently its possible application to multispecies communities has been recognized (e.g., in food chains; refs. 31 and 32).

Here, by integrating coexistence theory with a spatially explicit metacommunity model, we derive analytical criteria for multispecies coexistence in fragmented heterogeneous landscapes. These criteria—built upon the concept of metapopulation capacity (30)—clarify how spatial dynamics and landscape configurations affect niche and fitness differences. We then parameterize our model using long-term metacommunity data, where the dynamics of three *Daphnia* species have been monitored in 546 clearly delimited habitat patches (rock pools) for >35 y (33, 34). In light of our coexistence criteria, we show that interspecific trade-offs between the three *Daphnia* species contribute to a higher niche difference than fitness difference, and thereby facilitate coexistence. Moreover, our proposed model allows predicting the consequences of habitat destruction and temperature change on the coexistence of the *Daphnia* metacommunity by examining their effects on niche and fitness differences, respectively. Our theoretical results and the large-scale and long-term empirical example provide platforms for understanding multispecies coexistence in fragmented heterogeneous landscapes in particular and can be used as a quantitative tool to predict biodiversity responses to habitat changes in general.

Results

A Spatially Explicit Metacommunity Model of Competitors.
To develop a spatially explicit metacommunity model of multiple competitors, we assume that species live in a patchy landscape and that their patch dynamics are governed by local extinction and recolonization processes, which are in turn determined by species' dynamical parameters and landscape configurations (*SI Appendix,* Fig. S1; ref. 28). Moreover, we also consider that species compete with each other when they cooccur locally, which alters species' local extinction rates. Our model thus reads as

$$\frac{d}{dt}p_{i,k}(t) = C_{i,k}(t)\left(1 - p_{i,k}(t)\right) - E_{i,k}(t)p_{i,k}(t),\qquad [1]$$

where $p_{i,k}(t)$ is the occupancy probability of species k in patch i. $C_{i,k}(t)$ and $E_{i,k}(t)$ represent the colonization and extinction rates of species k in patch i, respectively, which are modeled as follows:

$$C_{i,k}(t) = c_k A_i^{z_{im,k}} \sum_{j\neq i} e^{-\frac{d_{ij}}{\xi_k}} A_j^{z_{em,k}} p_{j,k}(t) \qquad [2]$$

$$E_{i,k}(t) = \left(1 + \sum_{l\neq k} Q_{kl} p_{i,l}(t)\right)\frac{e_k}{A_i^{z_{ex,k}}}, \qquad [3]$$

where A_i is the size of patch i and d_{ij} is the distance between patch i and j. c_k and e_k are the species-specific colonization and extinction parameters of species k, respectively. $z_{im,k}$, $z_{em,k}$, and $z_{ex,k}$ are, respectively, the scaling exponents of immigration, emigration and extinction rates with patch size for species k (35). A positive (resp. negative) exponent indicates that the respective

rate increases (resp. decreases) with increasing patch size. ξ_k is the characteristic dispersal distance of species k, with a higher ξ_k indicating a slower decay rate of dispersal with increasing distance. Q_{kl} characterizes the effect of competition of species l on the extinction rate of species k. In sum, our model involves three types of parameters: species dynamical parameters (c_k, e_k), landscape-related parameters ($z_{im,k}$, $z_{em,k}$, $z_{ex,k}$, ξ_k), and competition-related parameters (Q_{kl}) (*SI Appendix,* Fig. S1).

Criteria for Species Coexistence in Fragmented Landscapes.
Although our model (Eq. **1**) cannot be solved analytically in general settings, we can derive criteria for multispecies coexistence when habitat patches have constant size and pairwise distance (referred to as the homogeneity assumption; see also ref. 32). Under the homogeneity assumption, we first derive the criterion of coexistence for two competing species (see *Methods* and *SI Appendix, Appendix 1*):

$$\rho_{12} < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho_{12}}, \qquad [4]$$

where $\rho_{12} = \sqrt{\frac{Q_{12}e_1}{c_1\lambda_1}\cdot\frac{Q_{21}e_2}{c_2\lambda_2}}$ and $\frac{\kappa_1}{\kappa_2} = \frac{c_1\lambda_1 - e_1}{c_2\lambda_2 - e_2}\sqrt{\frac{Q_{21}e_2}{Q_{12}e_1}\cdot\frac{c_2\lambda_2}{c_1\lambda_1}}$ characterize the niche overlap (the lower the niche overlap, the higher the niche differences) and fitness ratio (no fitness differences are attained at a ratio of 1), respectively. Here, λ_k denotes the metapopulation capacity of species k, which is calculated as the leading eigenvalue of the corresponding landscape matrix:

$$\mathbf{M}_{ij}(k) = \begin{cases} A_i^{z_{im,k}+z_{ex,k}} A_j^{z_{em,k}} e^{-\frac{d_{ij}}{\xi_k}}, & i \neq j \\ 0, & i = j \end{cases} \text{ (ref. 33; see } \textit{Methods}).$$

For multiple competing species, recent work (9) has introduced a structural (geometric) approach to define analogs of niche (Ω) and fitness (θ) differences in local communities. In our metacommunity models, these two metrics can again be structurally derived from the metapopulation capacity (λ_k) and parameters governing species dynamics and competition (i.e., e_k, c_k, Q_{kl}; see *Methods*). Specifically, the "structural niche difference" is expressed as $\Omega = \frac{2^n|\det\mathbf{A}|}{(\pi)^{n/2}}\int_0^{+\infty}e^{-\mathbf{x}^T\mathbf{A}^T\mathbf{A}\mathbf{x}}d\mathbf{x}$, where $\mathbf{A}$ is an $n\times n$ matrix with $A_{kk} = c_k\lambda_k$ and $A_{kl} = Q_{kl}e_k$ for $k\neq l$, and n is the number of species. In turn, the "structural fitness difference" reads $\theta = \arccos\left(\frac{\mathbf{r}\cdot\mathbf{r}_c}{\|\mathbf{r}\|\cdot\|\mathbf{r}_c\|}\right)$, where $\mathbf{r} = (c_1\lambda_1 - e_1,\ldots,c_n\lambda_n - e_n)^T$ and $\mathbf{r}_c = \frac{1}{n}\left(\frac{\mathbf{v}_1}{\|\mathbf{v}_1\|} + \ldots + \frac{\mathbf{v}_n}{\|\mathbf{v}_n\|}\right)$ are both vectors, with $\mathbf{v}_i$ denoting the i-th column of $\mathbf{A}$ and $\|\mathbf{v}_i\|$ denoting its Euclidean norm. Put simply, the structural niche difference (Ω) corresponds to the probability that a randomly chosen set of intrinsic-growth-rate parameters (i.e., $\mathbf{r}$) rends the community feasible, whereas the structural fitness difference (θ) indicates how much the set of intrinsic-growth-rate parameters deviates from having all species with the same positive abundance. To make these structural measures comparable, we propose to normalize them as $\Omega_1 = \Omega^{\frac{1}{n-1}}$ and $\theta_1 = \sqrt{n}\theta$. This provides a criterion of coexistence for multiple competing species in fragmented landscapes (see *Methods* and *SI Appendix, Appendix 2*):

$$\theta_1 < \Omega_1 \qquad [5]$$

Note that this criterion (Eq. **5**) is a conservative approximation and likely to underestimate the possibility of species coexistence (see *SI Appendix, Appendix 2*). In two-species cases, it is equivalent to Eq. **4**.

To investigate whether the above approximate criteria (Eqs. **4** and **5**, derived under a homogenization assumption) can be used to predict species coexistence in heterogeneous landscapes,
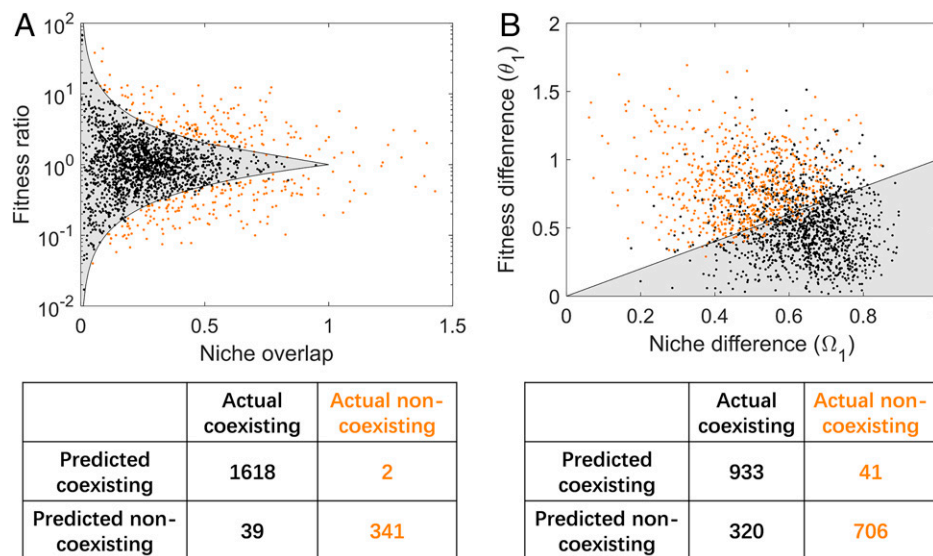
Fig. 1. Simulation outcomes of two (*A*) and three (*B*) competing species in fragmented heterogeneous landscapes. Each point indicates one of 2,000 simulated metacommunities, where all species coexist (black) or at least one species goes extinct (orange). The gray area represents the coexistence region predicted by our criteria (i.e., Eqs. **4** and **5**). The tables below each figure show the number of simulated metacommunities (in total 2,000) that are predicted to coexist (first row) or not (second row) and that show coexistence (first column) or exclusion (second column), respectively. Detailed parameters are given in *Methods*.

we performed numerical simulations of Eq. **1**. We did so by simulating metacommunities consisting of habitat patches with size variation mimicking empirical systems (e.g., *SI Appendix, Fig. S2*) and randomly distributed in the landscape. We found that our coexistence criteria predicted well the outcome of competition between two or more species (Fig. 1). For two-species cases, among the 1,620 simulated communities for which our criteria (Eq. **4**) predicted coexistence, 1,618 (99.9%) could indeed coexist, and among the 380 communities for which our criteria predicted exclusion 341 (89%) indeed displayed exclusion, while the other 11% could coexist. For three-species cases, 96% of communities for which our criteria (Eq. **5**) predicted coexistence can indeed coexist, and 69% of communities for which our criteria predicted exclusion indeed displayed exclusion. Thus, as expected, our criteria tended to underestimate the probability of coexistence, especially in more diverse communities (see *SI Appendix, Fig. S3* for four-species cases), working as a conservative condition for coexistence.

It is worth mentioning that as the variation in patch size increased the prediction precision of our coexistence criteria on exclusion decreased but that on coexistence remained almost unchanged (*SI Appendix, Fig. S4*). In addition, we found that the precision of our criteria was robust to different distributions of patches (e.g., random or clustering; *SI Appendix, Fig. S5*). Because our deterministic metacommunity model (Eq. **1**) represents a mean-field approximation of stochastic patch occupancy models, we additionally corroborated that our criteria captured well the coexistence of species with stochastic patch dynamics (*SI Appendix, Fig. S6* and *Appendix 3*).

Application to a *Daphnia* Metacommunity. To illustrate the applicability of our theoretical framework, we apply our model to characterize the dynamics of a *Daphnia* metacommunity, which consists of three species (*Daphnia longispina*, *Daphnia magna*, and *Daphnia pulex*) inhabiting rock pools along the coast of Skerry islands of the Baltic Sea (*SI Appendix, Fig. S2*). The patch occupancies of the three species have been monitored twice every year during 1982 to 2017 in 546 rock pools (33, 34). Early experiments using the same study system had

shown that interspecific competition could increase local extinction rates of species (36). However, competition may not alter the rate of recolonization, because these species disperse passively as mediated by wind and animals (37). Such characteristics of extinction and recolonization processes make this system ideal to apply our model.

Previous studies have shown that fluctuations in summer temperature could influence the rate of recolonization (34, 38). We thus assumed that parameters governing species patch dynamics (c_k, e_k) and competition (Q_{kl}) are temperature-dependent, whereas landscape-relevant parameters are assumed to be independent of temperature (see *Methods*). We used Bayesian methods to fit all model parameters of the discrete-time counterpart of Eq. **1** (i.e., Eq. **11**; see *Methods*), and their posterior distributions are summarized in *SI Appendix, Table S1*. Overall, our model captured well the general patch occupancy at the metacommunity level ($R^2 > 0.67$) and predicted reasonably well the extinction and colonization processes at the patch level (*SI Appendix, Appendix 4*).

We found that *D. pulex* displayed a larger colonization parameter than *D. longispina* and *D. magna* (Fig. 2*A*). While the colonization parameter of *D. pulex* decreased with temperature, those of *D. longispina* and *D. magna* both increased with temperature (see Fig. 2*A*). For all three species, we found that their extinction rates decreased with increasing temperature (Fig. 2*B*) and patch size (i.e., positive z_{ex}; Fig. 2*C*). The immigration rates of all three species increased with the size of the recipient patch (i.e., positive z_{im}; Fig. 2*C*). The emigration rates of *D. longispina* and *D. magna* increased with the size of the source patch (positive z_{em}), whereas that of *D. pulex* decreased with patch size (negative z_{em}; Fig. 2*C*). These results are in line with a recent study that revealed both positive and negative area dependencies of emigration rates across a broad range of taxa (39). Besides, *D. magna* displayed a much larger characteristic dispersal distance (ξ), compared with those of *D. longispina* and *D. pulex* (Fig. 2*C*).

Based on the above parameters, we derived the posterior distributions of metapopulation capacities for the three species (Fig. 2*D*). Overall, *D. magna* had the largest metapopulation
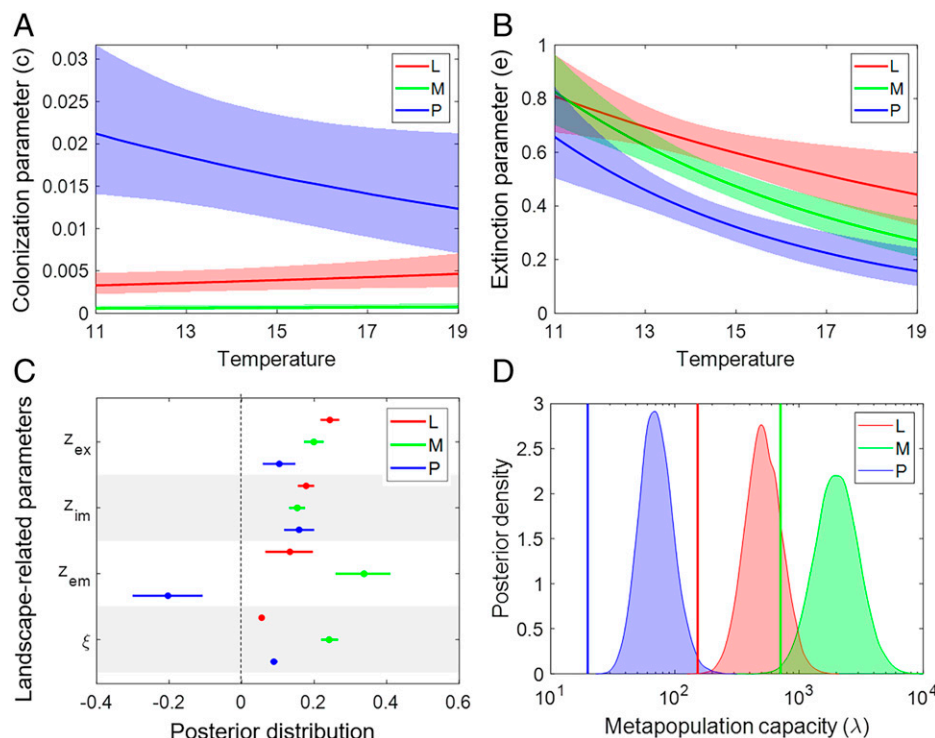
Fig. 2. Posterior distributions of species parameters for *D. longispina* (L), *D. magna* (M), and *D. pulex* (P). (*A* and *B*) Posterior medians and 80% credible intervals (i.e., 10% and 90% posterior quantiles) of colonization parameter *c* and extinction parameter *e*, along the gradient of temperature. (*C*) Posterior medians and 80% credible intervals of landscape-related parameters, i.e., scaling exponents of extinction rate (z_{ex}), immigration rate (z_{im}), and emigration rate (z_{em}) with area, and the characteristic dispersal distance (ξ). Note that the error bars are sometimes too small to be visible (e.g., ξ for *D. longispina* and *D. pulex*). (*D*) Posterior density of metapopulation capacities λ_k (curves and shades) and posterior medians of extinction threshold (e_k/c_k) (vertical lines) for each species under temperature $T = 15°C$.

capacity due to its high emigration parameter (z_{em}) and characteristic dispersal distance (ξ), whereas *D. pulex* had the lowest metapopulation capacity due to its negative patch size dependency of emigration rate (i.e., $z_{em} < 0$). For all species, their metapopulation capacities were generally higher than the respective persistence thresholds predicted by classic metapopulation theory (i.e., $\lambda_k > e_k/c_k$; ref. 30) (Fig. 2*D*), suggesting that each species is able to persist on its own (i.e., in the absence of its competitors) irrespective of the temperature fluctuations.

In the presence of competitors, we found that competition could increase local extinction rates and the magnitude of such influences might change with temperature (Fig. 3*A*). Under lower temperatures (e.g., average summer temperature at 13 °C), competition between *D. longispina* and *D. pulex* increased the extinction rates of both species, and the competition with *D. magna* increased the extinction rate of *D. longispina*. Under higher temperatures (e.g., average summer temperature 15 °C), the extinction rate of *D. magna* was increased by competition with *D. pulex* or *D. longispina*, and that of *D. pulex* was increased by competition with *D. longispina* (with a higher magnitude compared with that under low temperature). We note, however, that the inclusion of competition only improved model fit slightly compared with metapopulation models without competition (*SI Appendix, Appendix 4*).

Using the inferred posterior distributions of all parameters (i.e., species dynamical, landscape- and competition-related parameters; *SI Appendix,* Fig. S1), we calculated our normalized structural metrics to evaluate species coexistence (Eq. **5**). We found that for the three-species community or any two-species pair of *Daphnia* species niche differences were always greater than fitness differences, indicating that species were located in an area of coexistence across the wide range of temperature conditions

experienced by this system (Fig. 3*B*). Compared to the whole community, the subcommunity of *D. longispina* and *D. magna* exhibited lower fitness difference because of their similarity in species dynamical and landscape-related parameters, and the subcommunity of *D. magna* and *D. pulex* exhibited higher niche difference due to their weak competition (Fig. 3*B*).

Next, we projected how temperature change and habitat destruction might modulate species coexistence in the three-species community, using the current landscape configuration at a temperature 15 °C—the average summer temperature after 2005—as the baseline. Our results showed that niche difference changed slightly as temperature changed, whereas fitness difference tended to increase and approach niche difference at very low and high temperature conditions (Fig. 4 *A* and *E*). However, because the fitness difference was generally lower than niche difference, the three species were predicted to coexist over a broad range of temperature changes (Fig. 4*I*). In comparison, we found that habitat deterioration (i.e., reducing the size of all patches proportionally) increased fitness differences while moderately decreasing niche differences (Fig. 4 *B* and *F*). This caused the extinction of *D. magna* when the size of all patches was reduced by 68%, followed by the extinction of *D. longispina* when the size of patches was reduced by 85% (Fig. 4*J*). Habitat loss (i.e., removal of patches) simultaneously decreased niche differences and increased fitness differences (Fig. 4 *C, D, G,* and *H*). The loss of small patches (i.e., slight decrease of total habitat area) caused the extinction of *D. pulex* when 65% of smaller patches were lost, but it had weak effect on the persistence of *D. longispina* and *D. magna* (Fig. 4*K*). Due to the different responses of species to decreases of patch area and number, a random loss of habitats (i.e., decrease in both number and total area of patches) led to the extinction of all three species when 60 to 70% patches were lost (Fig. 4*L*).
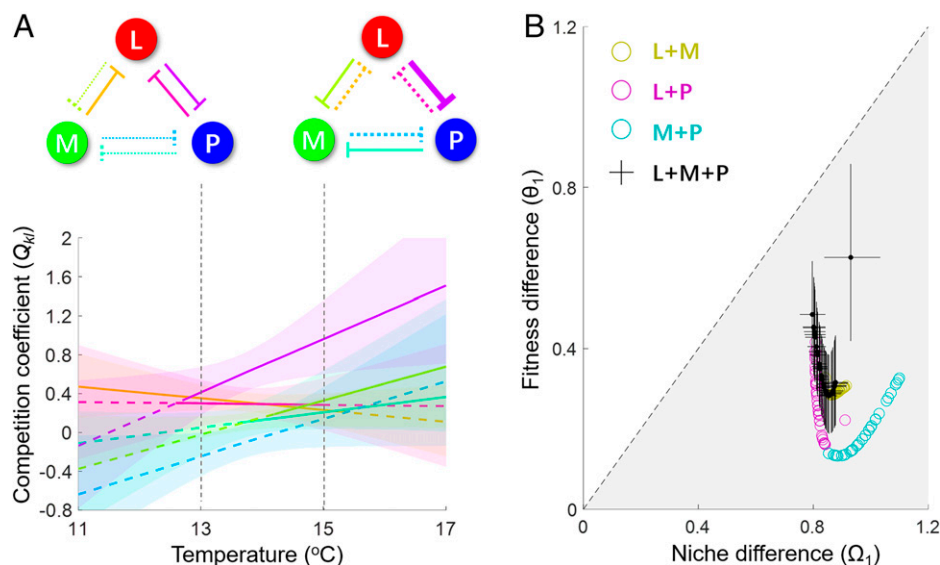
Fig. 3. (A) Posterior medians and 80% credible intervals of pairwise competition strengths Q_{kl} between the three species *D. longispina* (L), *D. magna* (M), and *D. pulex* (P) under different temperature conditions. The posterior median lines are solid when Q_{kl} is significantly positive, i.e., the 10% posterior quantile is positive, and are dashed when Q_{kl} is nonsignificant. The competition patterns under temperature $T = 13°C$ and $T = 15°C$ are illustrated above. (B) Niche and fitness differences of the three-species *Daphnia* community or its two-species subcommunities. Black crosses show the posterior medians and 80% credible intervals of the structural niche differences Ω_1 and fitness differences θ_1 under different temperatures conditions over the study period (1982 to 2017). The blue, red, and green circles are the niche and fitness differences, respectively, between two species. The gray area indicates the predicted region for coexistence (i.e., $\Omega_1 > \theta_1$).

Discussion

Over the last two decades, major progress has been made in disentangling two ecological processes modulating species coexistence in communities of competing species: niche and fitness differences (2, 8–12). However, these advancements in coexistence theory have not been fully integrated with metacommunity theory (21, 24), limiting our understanding of how local ecological processes investigated under coexistence theory can drive multispecies dynamics in fragmented landscapes. Here, we have worked toward unifying coexistence theory and metacommunity theory. Our analytical criteria of multispecies coexistence capture the effects of spatial dynamics on analogs of niche and fitness differences via metapopulation capacity. The metapopulation capacity characterizes information of not only the physical conditions of the landscape (e.g., A_i and d_{ij}) but also how such conditions are perceived by the resident species (e.g., ξ_k, $z_{im,k}$, $z_{em,k}$, $z_{ex,k}$) (30). Using metapopulation capacity, these criteria clarify how spatial processes interact with local competition to determine coexistence of species under realistic landscape configurations. This gives a new, and hitherto largely overlooked, relevance of spatial dynamics for the maintenance of multiple competing species in fragmented heterogeneous landscapes.

In particular, on the basis of recently developed structural (geometric) approaches (9), we proposed analog and normalized metrics of niche and fitness differences, such that they are directly comparable (see Eq. **5**) and useful to estimate the possibility for coexistence of two or more competitors within fragmented landscapes. We have shown one normalization approach that gives conservative criteria for coexistence (Eq. **5**), but alternative normalization approaches may also be applied (see *SI Appendix, Appendix 2* for details). These criteria provide tools to approximate multispecies coexistence in fragmented landscapes in both simulated and empirical metacommunities. Indeed, our normalization approach based on structural measures of niche and fitness differences may similarly be used to assess coexistence of multiple species in communities with positive and negative species interactions (40).

We applied our model to a well-studied natural metacommunity of three *Daphnia* species (33, 34, 41, 42) and illustrated how trade-offs between the three species facilitate their coexistence in a fragmented habitat. We found significant interspecific variation in species parameters, which contribute to reducing fitness differences and increasing niche differences (41, 43). For instance, *D. pulex* displayed higher colonization between nearby patches (i.e., a higher c), whereas *D. longispina* and *D. magna* showed lower colonization between nearby patches (Fig. 2A). However, *D. magna* exhibited a large characteristic dispersal distance (ξ; Fig. 2C) and thus a higher colonization between far-away patches. Moreover, the emigration rate of *D. magna* increased dramatically with patch size ($z_{em} > 0$), whereas that of *D. pulex* decreased with patch size ($z_{em} < 0$). Such interspecific variations in spatial dynamical parameters lead to previously unrecognized trade-offs among species, which reduces differences in colonization probabilities and hence decreases fitness differences (Fig. 3B). Trade-offs also exist between spatial dynamics and competition. For instance, while *D. longispina* had a lower colonization parameter than *D. pulex*, the former exerted a strong competition and increased the local extinction rate of the latter, indicating a competition–colonization trade-off (41, 44). It is worth noting that the overall weak effect of competition on species extinction rates (Fig. 4 and *SI Appendix, Appendix 4*) indicates a high niche difference, possibly attributed to trade-offs in their biology, such as differences in resource use strategies of the three species (37) or differential effects of parasites and negative frequency-dependent selection (38).

By establishing the dependency of species dynamics on habitat area and temperature, our parameterized model predicted that habitat destruction imposes a severe challenge to the *Daphnia* community, compared with the effect of temperature change (Fig. 4). In particular, our model predicted that the three *Daphnia* species responded differentially to different types of habitat destruction: Whereas *D. pulex* was more threatened by habitat loss (e.g., decrease in the number of patches), *D. longispina* and *D. magna* were more threatened by habitat deterioration (e.g., decrease in patch size or quality) (Fig. 4). Such differential
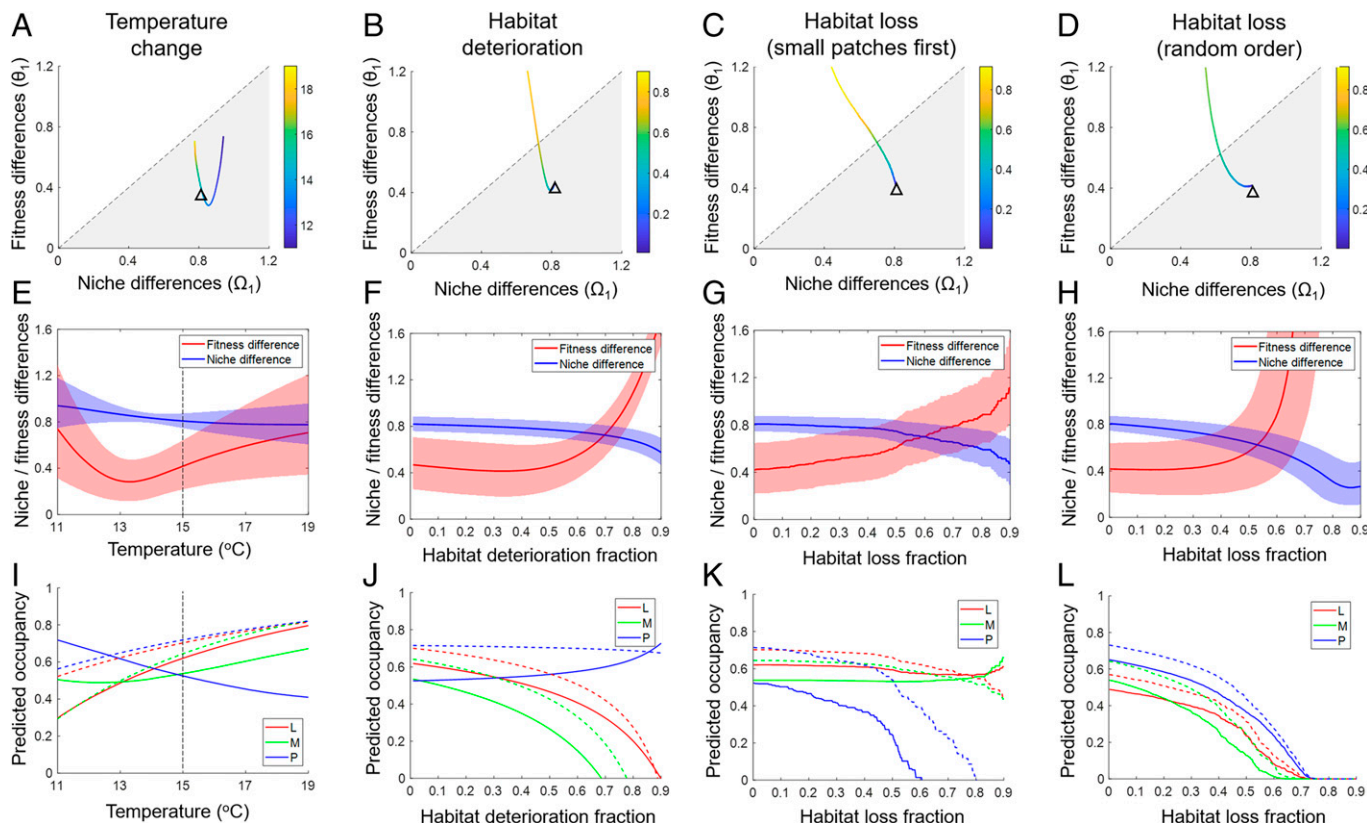
Fig. 4. Changes of niche and fitness differences (*A–H*) and equilibrium average occupancy (*I–L*) of our metacommunity model parameterized by the *Daphnia* dataset under four scenarios of environmental changes: (*A*, *E*, and *I*) temperature change, (*B*, *F*, and *J*) habitat deterioration (i.e., sizes of all patches decrease by a same fraction), (*C*, *G*, and *K*) habitat loss of small patches (i.e., the habitat patches are removed one by one from the smallest), and (*D*, *H*, and *L*) habitat loss in a random order. In *A–D*, the colored lines show the responses of niche and fitness differences (their posterior medians) to environmental changes, with the black triangles indicating the current state (i.e., current habitat and temperature $T = 15°C$). In *E–H*, the posterior medians and 80% credible intervals of niche differences (blue) and fitness differences (red) are exhibited under different environmental conditions. In *I–L*, the solid lines represent the equilibrium species occupancy obtained by simulating Eq. **1**, and the dashed lines represent similar equilibria but without interspecific competition (i.e., setting $Q_{kl} \equiv 0$ in Eq. **3**). In scenarios of habitat changes, temperature is set as $T = 15°C$.

responses are in line with metapopulation theory, which predicts that species with negative size dependency of emigration rate (e.g., *D. pulex* in our study; Fig. 2*C*) are more sensitive to changes in the number of habitat patches, and those with positive size dependency (e.g., *D. magna* and *D. longispina*; Fig. 2*C*) are more sensitive to changes in the total area of habitat patches (39). Our model also predicted that competition could accelerate extinction risk in the face of habitat destruction by lowering the thresholds of habitat destruction causing extinction (Fig. 4). While individual species' persistence in metapopulation networks has repeatedly been associated with patch size, patch connectivity, and global environmental change in previous studies (e.g., refs. 30 and 45), our work expands this for the realistic scenario of multiple interacting species that are subject to species-specific extinction–colonization dynamics and are competing for the same resources.

Conclusion

Our study provides a theoretical framework for increasing our understanding of the coexistence of multiple competing species in fragmented heterogeneous landscapes. By integrating coexistence theory and metacommunity theory, we studied the interplay among interspecific competition, landscape configuration, and species extinction and colonization processes in determining multispecies coexistence in a spatial context. We illustrated the implications of our theory using an empirical system and demonstrated its potential to predict the response of species' coexistence to environmental changes. Our formalism can serve as a

benchmark for future development. For instance, recent studies have suggested that competition may alter the colonization process by decreasing local population sizes (46) or imposing selection on local populations to increase dispersal propensity (47). Thus, in addition to the effect of competition on extinction processes considered in our model, future studies may incorporate the effect of competition on colonization processes. While we have focused on the coexistence of a small number of species at the metacommunity scale, future extensions to more diverse systems at broader scales (e.g., beyond the scale of dispersal) may shed new light on how coexistence mechanisms influence the spatial scaling of species diversity and species range size distributions (22, 48). Such theoretical developments will contribute to further transforming coexistence theory into a practical framework to explain species diversity in natural landscapes and predict their responses to environmental changes.

Methods

Analytical Investigations of Coexistence Criterion. First, as in the spatially explicit patch occupancy model of single-species metapopulations (28, 33), we define the landscape matrix $\mathbf{M}(k)$ of species k as

$$\mathbf{M}_{ij}(k) = \begin{cases} A_i^{z_{im,k} + z_{ex,k}} A_j^{z_{em,k}} e^{-\frac{d_{ij}}{\xi_k}}, & i \neq j \\ 0, & i = j \end{cases}. \qquad [6]$$

Note that $\mathbf{M}(k)$ is a nonnegative matrix, which has a positive leading eigenvalue λ_k. This leading eigenvalue represents the metapopulation capacity of species k (30). In single-species system, the metapopulation capacity

determines the persistence of a metapopulation and its equilibrium patch occupancy: $p_k^* = 1 - \frac{e_k}{c_k \lambda_k}$.

To derive the criterion of species coexistence for Eq. **1**, we first consider a homogeneous condition where all patches have same area and pairwise distance. Under such a homogeneity assumption, the model reduces to a spatially implicit model (*SI Appendix, Appendix 1*):

$$\frac{d}{dt}p_k(t) = \frac{1}{A^{z_{ex,k}}}\left[c_k\lambda_k p_k(t)\Big(1 - p_k(t)\Big) - \Big(1 + \sum_{l \neq k} Q_{kl}p_l(t)\Big)e_k p_k(t)\right], \quad [7]$$

where p_k denotes the occupancy probability of species k in any patch. We can then provide the coexistence criterion based on the coexistence theory (2), because Eq. **7** could be rewritten in the form of generalized Lotka–Volterra competition models:

$$\frac{1}{p_k(t)}\frac{dp_k(t)}{dt} = \frac{1}{A^{z_{ex,k}}}\left(r_k - \sum_{l=1}^{n} \alpha_{kl}p_l(t)\right), \quad [8]$$

where $r_k = c_k\lambda_k - e_k$, $\alpha_{kk} = c_k\lambda_k$ and $\alpha_{kl} = Q_{kl}e_k$ for $l \neq k$. In two-species systems, we define the niche overlap between species 1 and 2 as $\rho_{12} = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} = \sqrt{\frac{Q_{12}e_1}{c_1\lambda_1}\cdot\frac{Q_{21}e_2}{c_2\lambda_2}}$ and the fitness ratio between species 1 and 2 as $\frac{\kappa_1}{\kappa_2} = \frac{r_1}{r_2}\sqrt{\frac{\alpha_{21}\alpha_{22}}{\alpha_{12}\alpha_{11}}} = \frac{c_1\lambda_1 - e_1}{c_2\lambda_2 - e_2}\sqrt{\frac{Q_{21}e_2}{Q_{12}e_1}\cdot\frac{c_2\lambda_2}{c_1\lambda_1}}$. The criterion for the coexistence of two competing species is thus: $\rho_{12} < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho_{12}}$ (2).

In multispecies systems, we can solve the feasible equilibrium of Eq. **8** as $\mathbf{p}^* = \mathbf{A}^{-1}\mathbf{r}$, where $\mathbf{A} = (\alpha_{kl})$ is a matrix and $\mathbf{r} = (r_1,\ldots,r_n)^T$ is a column vector. Let $\mathbf{J}$ be the Jacobian matrix at $\mathbf{p}^*$, and thus the condition that $\mathbf{p}^*$ is feasible and locally stable is $\mathbf{p}^* > 0$ and $\lambda_{max}(\mathbf{J}) < 0$, where $\lambda_{max}(\mathbf{J})$ is the real part of the leading eigenvalue of $\mathbf{J}$. For competitive communities, we follow the structural approach developed by Saavedra et al. (9) to define niche difference and fitness difference. Specifically, the structural niche difference is defined as

$$\Omega = \frac{2^n|\det \mathbf{A}|}{(\pi)^{n/2}}\int_0^{+\infty} e^{-\mathbf{x}^T\mathbf{A}^T\mathbf{A}\mathbf{x}}d\mathbf{x}, \quad [9]$$

which can be interpreted as the product of 2^n and the probability that $\mathbf{x} = (x_1,\ldots,x_n)^T$ satisfies $x_i > 0$ for all i conditioned that $\mathbf{x}$ follows a multivariate normal distribution with mean zeros and covariance matrix $\Sigma = (\mathbf{A}^T\mathbf{A})^{-1}$. Let $\mathbf{v}_i = (\alpha_{1i},\ldots,\alpha_{ni})^T$ be the i-th column of $\mathbf{A}$ and $\mathbf{r}_c = \frac{1}{n}\left(\frac{\mathbf{v}_1}{\|\mathbf{v}_1\|} + \ldots + \frac{\mathbf{v}_n}{\|\mathbf{v}_n\|}\right)$, where $\|\mathbf{v}_i\|$ is the Euclidean norm of $\mathbf{v}_i$. The structural fitness difference is then defined as

$$\theta = \arccos\left(\frac{\mathbf{r}\cdot\mathbf{r}_c}{\|\mathbf{r}\|\cdot\|\mathbf{r}_c\|}\right), \quad [10]$$

which quantifies the radian between vectors $\mathbf{r}$ and $\mathbf{r}_c$. To make structural niche and fitness differences comparable, we normalize them as $\Omega_1 = \Omega^{\frac{1}{n-1}}$ and $\theta_1 = \sqrt{n}\theta$, such that an approximate coexistence criterion can be given: $\theta_1 < \Omega_1$ (see *SI Appendix, Appendix 2* for details). We note that the normalization can be done with alternative approaches, and the one we use here tends to provide a conservative criterion (*SI Appendix, Appendix 2*).

Numerical Simulation. We performed simulations of Eq. **1** to evaluate our criteria for species coexistence (Eqs. **4** and **5**). In each simulated metacommunity, the number of species was fixed as $n = 2, 3$, or 4, and the number of patches was drawn with equal probability from $\{100, 101, \ldots, 200\}$. We simulated 2,000 replicates for each number of species ($n = 2, 3$, or 4). The two-dimensional coordinates of patches were drawn from uniform distributions over $[0, 10] \times [0, 10]$. The sizes of patches (A_i) were drawn independently from log-normal distributions, i.e., $\log_{10}A_i \sim N(1, 0.5^2)$, mimicking empirical systems (e.g., *SI Appendix, Fig. S2*). The colonization rate (c_k), extinction rate (e_k), and characteristic dispersal distances (ξ_k) were also drawn from log-normal distributions: $\log_2 c_k \sim U[-2, 0]$, $\log_2 e_k \sim U[-1, 1]$, and $\log_2 \xi_k \sim U[0, 1]$. The patch-size scaling exponents and competition strengths (Q_{kl}) were drawn from uniform distributions: $z_{im,k} \sim U[0, 1]$, $z_{em,k} \sim U[-1, 1]$, $z_{ex,k} \sim U[-1, 1]$, and $Q_{kl} \sim U[0, 3]$.

With above parameters, we first calculated the single-species equilibrium of patch occupancy for each species k (without competition with others): $K_k = 1 - (e_k/\lambda_k c_k)$. The simulated metacommunity was accepted if all species

had their equilibrium (K_k) within (0.2, 0.9); otherwise, we repeated the parameter generation procedure. Once a set of valid parameters was generated, we simulated the metacommunity model (Eq. **1**) for 5,000 steps using MATLAB, with 20 sets of randomly generated initial values of $p_{ik} \sim U[0, 1]$. We consider that species coexist in the metacommunity if all species persist in at least one patch (i.e., $p_{i,k}(T) > 0.01$) across all 20 sets of initial values.

Because Eq. **1** describes patch occupancy dynamics in a deterministic manner that represents mean-field approximations of stochastic patch dynamics, we also simulated the discrete-time, stochastic counterpart of Eq. **1** where local extinction and recolonization processes occur with probabilities during discrete time steps (see *SI Appendix, Appendix 3* for details).

The *Daphnia* Metacommunity Data. We use a long-term dataset of a *Daphnia* metacommunity, which consists of three species, *D. longispina* (L as the subscript to indicate this species), *D. magna* (subscript M), and *D. pulex* (subscript P), inhabiting 546 rock pools located on 17 rocky islands in the Tvärminne Archipelago in the Baltic Sea (33, 34). The occupancies of these rockpools for the three species have been recorded twice annually during 1982 to 2017. For each patch, two samples were collected during each year, once in spring and once in midsummer. To apply our model, we converted the two samples per year into annual presence/absence occupancy data and used $X_{i,k}(t)$ to represent the occupancy of species k ($k = L, M, P$) in patch i ($i = 1, 2, \ldots, 546$) at the year t ($t = 1982, \ldots, 2017$). $X_{i,k}(t)$ equals 1 if species k is observed at least once in patch i at year t, and it equals 0 otherwise. The dataset includes a small fraction of missing data after 2008, which were treated as zeros. For each patch (i.e., rock pool), patch size is represented by the product of surface area and depth.

Based on climatic data from WorldClim (https://www.worldclim.org/), mean summer temperature (T) in that region was calculated by taking the average temperature from May to September during 1982 to 2017. Summer temperature is strongly positively correlated with droughts or days without rain, which is then highly correlated with the probability of *Daphnia* populations to go locally extinct and to trigger dispersal (34).

Bayesian Data Analysis. We used the discrete-time, stochastic counterpart of Eq. **1** to model the occupancy dynamics of the *Daphnia* metacommunity and performed Bayesian statistical inference procedures to infer model parameters (49, 50). Denote $C_{i,k}(t)$ as the colonization probability of species k in patch i at time t and $E_{i,k}(t)$ the extinction probability. Thus, the transient probability of occupancy during one step is

$$\begin{cases} \Pr\Big(X_{i,k}(t+1) = 1|X_{i,k}(t) = 0\Big) = C_{i,k}(t) \\ \Pr\Big(X_{i,k}(t+1) = 0|X_{i,k}(t) = 0\Big) = 1 - C_{i,k}(t) \\ \Pr\Big(X_{i,k}(t+1) = 0|X_{i,k}(t) = 1\Big) = E_{i,k}(t) \\ \Pr\Big(X_{i,k}(t+1) = 1|X_{i,k}(t) = 1\Big) = 1 - E_{i,k}(t) \end{cases}. \quad [11]$$

Based on early findings from this system (34, 38, 51), we assumed that parameters of competition, colonization, and extinction all depend on summer temperature. For species k, we assumed $Q_{kl}(T) = \beta_{0,Q_{kl}} + \beta_{1,Q_{kl}}T$, $e_k(T) = \exp(\beta_{0,e_k} + \beta_{1,e_k}T)$, and $c_k(T) = \exp(\beta_{0,c_k} + \beta_{1,c_k}T)$, where T is the average summer temperature. The parameters in the Bayesian model were fitted using Stan (52). Four chains were run for 10,000 iterations with a warm-up period of 5,000 iterations. The prior distributions of positive parameters (z_{ex}, z_{im}, and ξ) are exponential with mean 1, and those of unconstrained parameters (z_{em} and all βs) are standard normal distributions. The Markov chain Monte Carlo trace plots of the parameters are shown in *SI Appendix, Fig. S7* and all $\hat{R}$ values are 1, indicating that the chains have well converged (50). We evaluated the model fit in terms of average patch occupancy and processes of colonization and extinction (*SI Appendix, Appendix 4*).

Data, Materials, and Software Availability. Data and codes used in this paper have been deposited in Figshare (https://figshare.com/articles/software/code_SpatialCoex_zip/20329245/1) (53).

Author affiliations: [a]Institute of Ecology, Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, 100871 Beijing, China; [b]Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA 02139; [c]Department of Environmental Sciences, Zoology, University of Basel, CH-4051 Basel, Switzerland; [d]Tvärminne Zoological Station, University of Helsinki, 10900 Hanko, Finland; [e]Department of Evolutionary Biology and Environmental Studies, University of Zurich, CH-8057 Zürich, Switzerland; and [f]Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology, CH-8600 Dübendorf, Switzerland

1. G. E. Hutchinson, Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159 (1959).
2. P. Chesson, Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
3. J. M. Levine, J. Bascompte, P. B. Adler, S. Allesina, Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* **546**, 56–64 (2017).
4. D. Tilman, *Resource Competition and Community Structure* (Princeton University Press, Princeton, NJ, 1982).
5. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton University Press, Princeton, NJ, 2001).
6. J. M. Chase, M. A. Leibold, *Ecological Niches Linking Classical and Contemporary Approaches* (University of Chicago Press, 2003).
7. M. Vellend, Conceptual synthesis in community ecology. *Q. Rev. Biol.* **85**, 183–206 (2010).
8. A. D. Letten, P. Ke, T. Fukami, Linking modern coexistence theory and contemporary niche theory. *Ecol. Monogr.* **87**, 161–177 (2017).
9. S. Saavedra et al., A structural approach for understanding multispecies coexistence. *Ecol. Monogr.* **87**, 470–486 (2017).
10. G. Barabás, R. D'Andrea, S. M. Stump, Chesson's coexistence theory. *Ecol. Monogr.* **88**, 277–303 (2018).
11. J. W. Spaak, F. De Laender, Intuitive and broadly applicable definitions of niche and fitness differences. *Ecol. Lett.* **23**, 1117–1128 (2020).
12. J. HilleRisLambers, P. B. Adler, W. S. Harpole, J. M. Levine, M. M. Mayfield, Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.* **43**, 227–248 (2012).
13. S. P. Ellner, R. E. Snyder, P. B. Adler, G. Hooker, An expanded modern coexistence theory for empirical applications. *Ecol. Lett.* **22**, 3–18 (2019).
14. S. P. Hart, M. M. Turcotte, J. M. Levine, Effects of rapid evolution on species coexistence. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 2112–2117 (2019).
15. A. D. Letten, A. R. Hall, J. M. Levine, Using ecological coexistence theory to understand antibiotic resistance and microbial competition. *Nat. Ecol. Evol.* **5**, 431–441 (2021).
16. N. M. Haddad et al., Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
17. J. M. Chase, S. A. Blowes, T. M. Knight, K. Gerstner, F. May, Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature* **584**, 238–243 (2020).
18. T. Newbold et al., Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).
19. D. Tilman et al., Future threats to biodiversity and pathways to their prevention. *Nature* **546**, 73–81 (2017).
20. D. Tilman, P. M. Kareiva, *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (Princeton University Press, Princeton, NJ, 1997).
21. M. A. Leibold et al., The metacommunity concept: A framework for multi-scale community ecology. *Ecol. Lett.* **7**, 601–613 (2004).
22. S. P. Hart, J. Usinowicz, J. M. Levine, The spatial scales of species coexistence. *Nat. Ecol. Evol.* **1**, 1066–1073 (2017).
23. T. Wiegand et al., Consequences of spatial patterns for coexistence in species-rich plant communities. *Nat. Ecol. Evol.* **5**, 965–973 (2021).
24. M. A. Leibold, J. M. Chase, *Metacommunity Ecology* (Princeton University Press, Princeton, NJ, 2017).
25. L. G. Shoemaker, B. A. Melbourne, Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology* **97**, 2436–2446 (2016).
26. B. Zhang et al., Directed movement changes coexistence outcomes in heterogeneous environments. *Ecol. Lett.* **25**, 366–377 (2022).
27. S. P. Ellner, R. E. Snyder, P. B. Adler, G. Hooker, Toward a "Modern Coexistence Theory" for the discrete and spatial. *Ecol. Monogr.*, 10.1002/ecm.1548 (2022).
28. P. Pillai, A. Gonzalez, M. Loreau, Metacommunity theory explains the emergence of food web complexity. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 19293–19298 (2011).
29. S. Wang, M. Loreau, Biodiversity and ecosystem stability across scales in metacommunities. *Ecol. Lett.* **19**, 510–518 (2016).
30. I. Hanski, O. Ovaskainen, The metapopulation capacity of a fragmented landscape. *Nature* **404**, 755–758 (2000).
31. J. Häussler, G. Barabás, A. Eklöf, A Bayesian network approach to trophic metacommunities shows that habitat loss accelerates top species extinctions. *Ecol. Lett.* **23**, 1849–1861 (2020).
32. S. Wang, U. Brose, S. van Nouhuys, R. D. Holt, M. Loreau, Metapopulation capacity determines food chain length in fragmented landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2102733118 (2021).
33. V. I. Pajunen, Distributional dynamics of *Daphnia* species in a rock-pool environment. *Ann. Zool. Fenn.* **23**, 131–140 (1986).
34. F. Altermatt, V. I. Pajunen, D. Ebert, Climate change affects colonization dynamics in a metacommunity of three *Daphnia* species. *Glob. Change Biol.* **14**, 1209–1220 (2008).
35. O. Ovaskainen, Habitat destruction, habitat restoration and eigenvector-eigenvalue relations. *Math. Biosci.* **181**, 165–176 (2003).
36. J. Bengtsson, Interspecific competition increases local extinction rate in a metapopulation system. *Nature* **340**, 713–715 (1989).
37. E. Ranta, Niche of *Daphnia* species in rock pools. *Arch. Hydrobiol.* **87**, 205–223 (1979).
38. F. Altermatt, V. I. Pajunen, D. Ebert, Desiccation of rock pool habitats and its influence on population persistence in a *Daphnia* metacommunity. *PLoS One* **4**, e4703 (2009).
39. S. Wang, F. Altermatt, Metapopulations revisited: The area-dependence of dispersal matters. *Ecology* **100**, e02792 (2019).
40. S. Saavedra, L. P. Medeiros, M. AlAdwani, Structural forecasting of species persistence under changing environments. *Ecol. Lett.* **23**, 1511–1521 (2020).
41. I. Hanski, E. Ranta, Coexistence in a patchy environment: Three species of Daphnia in rock pools. *J. Anim. Ecol.* **52**, 263–279 (1983).
42. D. Ebert, J. W. Hottinger, V. I. Pajunen, Unsuitable habitat patches lead to severe underestimation of dynamics and gene flow in a zooplankton metapopulation. *J. Anim. Ecol.* **82**, 759–769 (2013).
43. J. M. Kneitel, J. M. Chase, Trade-offs in community ecology: Linking spatial scales and species coexistence. *Ecol. Lett.* **7**, 69–80 (2004).
44. D. Tilman, Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2–16 (1994).
45. I. A. Hanski, O. E. Gaggiotti, *Ecology, Genetics and Evolution of Metapopulations* (Academic Press, 2004).
46. I. Hanski, Spatial patterns of coexistence of competing species in patchy habitat. *Theor. Ecol.* **1**, 29–43 (2008).
47. E. A. Fronhofer, J. Klecka, C. J. Melián, F. Altermatt, Condition-dependent movement and dispersal in experimental metacommunities. *Ecol. Lett.* **18**, 954–963 (2015).
48. R. A. Chisholm et al., Species-area relationships and biodiversity loss in fragmented landscapes. *Ecol. Lett.* **21**, 804–813 (2018).
49. R. B. O'Hara, E. Arjas, H. Toivonen, I. Hanski, Bayesian analysis of metapopulation data. *Ecology* **83**, 2408–2415 (2002).
50. R. S. Etienne, C. J. ter Braak, C. C. Vos, "Application of stochastic patch occupancy models to real metapopulations" in *Ecology, Genetics and Evolution of Metapopulations*, I. Hanski, O. E. Gaggiotti, Eds. (Elsevier, 2004), pp. 105–132.
51. F. Altermatt, D. Ebert, The influence of pool volume and summer desiccation on the production of the resting and dispersal stage in a *Daphnia* metapopulation. *Oecologia* **157**, 441–452 (2008).
52. B. Carpenter et al., Stan: A probabilistic programming language. *J. Stat. Softw.* **76**, 1–32 (2017).
53. M. Luo et al., Multi-species coexistence in fragmented landscapes. Figshare. https://figshare.com/articles/software/code_SpatialCoex_zip/20329245/1. Deposited July 19 2022.