



Regional neutrality evolves through local adaptive niche evolution

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Biodiversity in natural systems can be maintained either because niche differentiation among competitors facilitates stable coexistence or because equal fitness among neutral species allows for their long-term cooccurrence despite a slow drift toward extinction. Whereas the relative importance of these two ecological mechanisms has been well-studied in the absence of evolution, the role of local adaptive evolution in maintaining biological diversity through these processes is less clear. Here we study the contribution of local adaptive evolution to coexistence in a landscape of interconnected patches subject to disturbance. Under these conditions, early colonists to empty patches may adapt to local conditions sufficiently fast to prevent successful colonization by other preadapted species. Over the long term, the iteration of these local-scale priority effects results in niche convergence of species at the regional scale even though species tend to monopolize local patches. Thus, the dynamics evolve from stable coexistence through niche differentiation to neutral cooccurrence at the landscape level while still maintaining strong local niche segregation. Our results show that neutrality can emerge at the regional scale from local, niche-based adaptive evolution, potentially resolving why ecologists often observe neutral distribution patterns at the landscape level despite strong niche divergence among local communities.

metacommunity | ecoevolutionary feedback | local adaptation | coexistence | community monopolization

Biologists have long sought to understand what maintains the vast diversity of life on Earth (1). The maintenance of biological diversity among competing species is increasingly understood as a tension between the stabilizing properties of niche segregation in response to environmental variation and the equalizing properties of niche similarity as a result of fitness equality across environments. Niche-based mechanisms assume that competing species differ in their niches such that each species inhibits its own success more than that of other species. This results in stabilizing feedbacks where species can increase when rare. Equalizing mechanisms, where species have similar niches, allow for long-term cooccurrence of species despite the lack of stabilizing ecological feedbacks, even though one species will eventually dominate and the other species will slowly become extinct due to drift (2–4). Is the diversity that we observe in nature determined by niche differentiation or similarity?

Previous work on this question has assumed that stable niche-based coexistence and drift can both operate and that either can predominate depending on landscape features and average species traits (3, 5, 6). However, these approaches have generally ignored the role of local adaptive evolution. While adaptive evolution has often been seen as a slow process relative to ecological dynamics, empirical work increasingly shows that local adaptive evolution can occur rapidly (7–9), and at relatively fine spatial scales (10–12). Thus, evolution may act at the same temporal and spatial scales over which stabilizing and equalizing ecological mechanisms act (9, 13) and can affect ecological patterns in nature (14–16).

Past theoretical work in this area suggests that, depending on assumptions, the effects of local adaptation can either cause competing species to diverge (17) or converge (18–22) in niche traits, facilitating niche partitioning or neutral cooccurrence of species, respectively. This research, however, neglects the regional scale and the process by which communities assemble through repeated colonization, extinction, and competition. Taking this more regional perspective, local adaptive evolution can generate evolution-mediated priority effects wherein early colonizers adapt to local environmental conditions, monopolize local resources, and prevent invasion by, and subsequent local coexistence with, later colonizers (23). This could result in species having narrow, dedicated niches in each local environment (local adaptation and competitive exclusion), but broad overlapping niches at the regional scale (neutrality). This outcome likely depends on the species' relative dispersal rates within a landscape of patches, or metacommunity (24), as dispersal links local ecoevolutionary dynamics with regional processes involving disturbance, and habitat variability (25–27).

Here we study the effects of ecoevolutionary feedbacks on niche versus neutral processes at local and regional scales. We first combine a tractable deterministic patch dynamics model of community assembly with a simple model of adaptive dynamic evolution to highlight several unique features of adaptive evolution in metacommunities. We then study a more realistic

Significance

Coexistence of species depends on two very general mechanisms. In one, species differentiate in their niches and coexist by negative frequency dependence, in the other they have similar niches and cooccur for long periods of time due to (quasi-)equivalence. These explanations ignore the role of local adaptive evolution. We model how local evolution-mediated priority effects (where species that recolonize patches can adapt sufficiently well to resist being displaced by later colonists) affect coexistence in a landscape. We find that evolution often leads to a situation where local patches are strongly dominated by a single species even though all species can be found in any habitat type. This unsuspected result may explain why coexistence of species is often scale dependent.

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Data deposition: The code for the individual-based model has been deposited in Zenodo, <https://doi.org/10.5281/zenodo.2280982>. Data from the individual-based model have also been deposited in Zenodo, <https://doi.org/10.5281/zenodo.2532232>.

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spatially explicit individual-based model where we explore how robust this solution is to dispersal rate, disturbance frequency, and reproductive system (sexual vs. asexual) as well as stochasticity due to demographic and dispersal effects in finite communities.

Patch Occupancy Model of Community Assembly

As a first step toward understanding the role of local adaptation in metacommunity dynamics, we develop a minimalist patch dynamics model that describes community assembly and adaptation as a series of transitions among occupation and adaptive states (28). In this model, species of potential colonizers undergo an iterated process of colonization and extinction depending on disturbance frequency, local environmental conditions, resident species, and colonist traits. The transitions can be described as a set of rules that govern the possible successful colonizations and their consequent effects on extinction of other species in a deterministic way (28–30) as shown in Fig. 1*A* for two strongly competing species in two alternate habitat types [a “harlequin landscape” (31)]. Local adaptation can be included by incorporating additional rules that describe species transitions from maladapted to adapted states and how these states alter further transitions among species (Fig. 1*B*).

Using these rules, we develop a model of two competing metapopulations that tracks the occupancy frequency (not abundance) of each species with each trait value in each patch type. We allow for evolution-mediated priority effects by disallowing local coexistence and assuming that the locally adapted resident (regardless of species identity) cannot be invaded (Fig. 1*B*). To minimize the possibility that regional neutrality is initially important, we start our simulations with two species, each of which is adapted to, and completely dominant in, the two alternate patch types and ask how subsequent evolution alters their niche relations and spatial distributions. We find that in the short term, both species continue to strongly segregate by patch type, similar to results without evolution (Fig. 1*A*), but that little by little, each species is increasingly found in, and adapted to, the alternate patch type (Fig. 1*B*). Eventually, both species are equally distributed in both patch types (Fig. 1*B*) even though (by assumption) they never coexist in any local patch.

This model serves to illustrate some of the key elements of the process that could generate what we define as regional neutrality. These elements include (i) the evolutionary convergence of similar bimodal niche trait distributions at the regional scale, (ii) convergence through time in the habitat distributions of both species toward the frequency of patch types in the landscape, and (iii) erosion of correlations between species distribution and habitat type after the convergence of trait distributions.

Spatially Explicit Individual-Based Model of Community Assembly

To study how regional neutrality could evolve under more realistic assumptions, we used individual-based simulations to model a similar scenario on a spatially explicit 10×10 grid of patches with two patch types and two species (Fig. 2). Evolution was modeled by assuming that competitive dominance was determined by a single multilocus trait with different optimal values for each alternative habitat type. Genetic variance in this trait was modeled by assuming zero initial standing genetic variation and allowing for random mutations at each locus to generate and maintain genetic variation in subsequent time. Initial conditions had each species perfectly adapted to each of the alternate patch types as in the patch occupancy model and all patches filled with the species preadapted to the local environment. Disturbances were imposed randomly on patches, after which the empty patch could be recolonized. After colonization, a locally adapted population could establish from preadapted immigrants and/or evolve from less-adapted ones, dependent on the relative speed of dispersal versus evolution. The speed of evolution in our

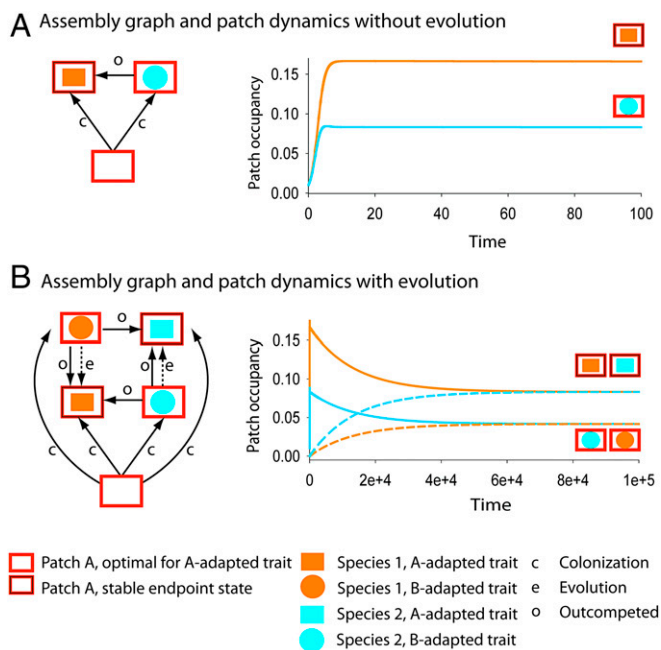


Fig. 1. Evolution alters community assembly by creating neutrality between species at the metacommunity level. We present assembly graphs (*Left*) and results of patch occupancy models (*Right*) for patch type A. The structure and dynamics for patch type B mirror those for patch type A. In *A* we assume no evolution and in *B* we assume that both species can adapt to the other species’ niche. In the assembly graphs on the left, colors indicate species identity (orange for species 1 and blue for species 2). Shapes indicate patch type and trait value. For instance, trait A (orange- or blue-filled rectangle) is optimal in patch type A (orange open rectangle). Arrows indicated by a “c” denote transitions that occur due to colonization, those indicated by an “o” denote transitions that occur when a colonist species outcompetes and excludes a resident one. Not shown are local extinctions due to disturbances that revert any occupied patch back to empty. Without evolution (*A*) only three possible states exist in each patch type (shown for patch type A). In *B*, dotted lines indicated by “e” indicate evolution into a different trait type by a resident species. This expands the number of possible species-trait combinations in each patch type from three to five. (*Right*) Deterministic dynamics of the model for parameters described in *SI Appendix, Table S1* (again just for patch type A; similar mirror patterns occur for patch type B), with both species initially present at low occupancy rate and completely adapted to each alternate patch type. Without evolution (*A*), type-A patches are dominated by preadapted species 1 (full orange line), but maladapted species 2 also occurs in recently disturbed patches (full blue line) as recent colonists from other patches until species 1 arrives. With evolution (*B*), two additional states are observed (dotted orange and blue lines). The initial dynamics are almost identical to what happens without evolution but then slowly change (note the difference in timescale with *A*) so that eventually both species occur in patch A in their adapted states and at equal occupancy frequencies (full orange and dotted blue lines). Maladaptive phenotypes of both species also occur at lower densities through colonization from patch B as shown by the dotted orange and full blue lines.

simulations falls within the range of evolutionary rates observed in the wild (see ref. 27). Code and data for these simulations are available at Zenodo (32, 33).

Confirming the insights from the patch occupancy model, we found that all three of the characteristics we identified in the deterministic model as key elements of regional neutrality could evolve under a range of more realistic conditions (Figs. 3–6) even though the simulations included numerous complications including explicit spatial structure, detailed genetic mechanisms, and stochastic effects of demography, dispersal, and disturbance. Fig. 3*B* and Fig. 4 (*Bottom*) show the evolution of similar bimodal regional niche trait distributions for the two species, and Fig. 4 (*Top*) and Fig. 5 show that both species converge to having

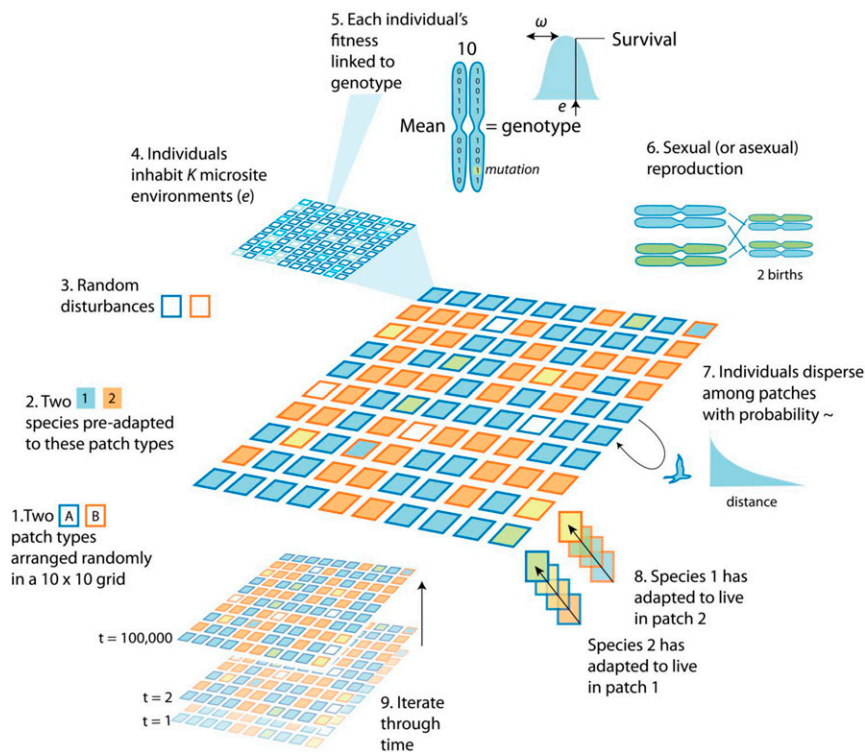


Fig. 2. Schematic illustration of the simulation model. Each simulation starts with species that are optimally adapted to alternate patch types [indicated by the match of the interior color (trait value) to the border color (environmental value)] in patches randomly arrayed in a grid landscape. Each patch has a carrying capacity and populations are maintained through either sexual or asexual reproduction. Random extinctions of the entire population of individuals in patches create empty patches. Mutations on biallelic genes generate quantitative ecotypic variation among individuals that is subject to local selection depending on the local environment (e) and niche tolerance (ω). Dispersal leads to recolonization of empty patches and gene flow among patches with existing populations. This process is iterated through time and allows each species to become more adapted to alternate patch types than it was at the beginning of the simulation [shown by the gradual shift in trait value (interior color) in step 8]. We find that eventually both species can become adapted to both patch types at rates and frequencies that depend on model parameters.

similar patch-type distributions to a degree that varied with key parameters (Fig. 5) which erodes the original species-environment matching (Figs. 3 *A* and *B* and 6). We found that regional neutrality was more prevalent when dispersal was low [in our case when there were fewer than 100 individuals dispersing per patch per generation (Fig. 5)]. It also takes longer to establish neutrality with lower extinction rates and higher dispersal rates. A difference between our simulations and the patch occupancy model is that our simulations could also generate trait convergence within patches that lead to local neutrality (19–22). However, we found that local cooccurrence of species with identical trait values was rare and certainly much less common than evolution-mediated niche priority effects (Fig. 5).

Another important difference between our simulations and the patch occupancy model is that our simulations include stochastic processes that reveal the eventual role of ecological drift at the regional scale on the relative abundances of the two species (Fig. 3C). This occurs in our simulations because of the finite size of the metacommunity (finite number of patches and consequent finite number of individuals) which was absent in the patch occupancy model. Given a finite metacommunity, the relative occupancy (number of sites occupied) and abundances will eventually lead to the extinction of one or the other species even though this can take a very long time. The extent of drift will depend on the size of the metacommunity (patch number), extinction rate, and dispersal (*SI Appendix, Fig. S1*), but is lower than when there is only one environmental type and both species are identical (local neutrality; *SI Appendix, Fig. S2*).

We next used a standard statistical tool [“variation partitioning” (34)] used by ecologists to discern what mechanisms might underlie community patterns in nature. This tool partitions the variance in community composition to that explained by environmental and spatial variation, as well as variation common to the two (confounding of both effects) and an unexplained element largely attributable to stochasticity or unmeasured environmental components (absent in our model where we specify the environment). When environmental variation is randomly

structured in space, variance explained by the environmental component is usually attributed to niche-based processes whereas the spatial and unexplained components are assumed to reflect a combination of dispersal limitation and drift. We applied this technique to our simulation data and found that evolved regional neutrality substantially reduced contributions from niche-based processes and inflated the spatial and residual variation (Fig. 6). However, a similar partitioning of trait variation (rather than community composition) shows that environment explains most of the variation in traits whereas spatial and residual effects are small. These results show that purely neutral (scale-independent) ecological processes and local niche-based evolution of regional neutrality cannot be separated by this method without also looking at trait variation.

Although there are quantitatively different results, we nevertheless find that regional neutrality, linked to local evolution-mediated priority effects as in the two-species case described above, also occurs in simulations with asexual reproduction (*SI Appendix, Fig. S3*), broader dispersal kernels (*SI Appendix, Fig. S4*), weaker selection (*SI Appendix, Fig. S5*), lower reproduction rates (*SI Appendix, Fig. S6*), absence of intrapatch environmental variation (*SI Appendix, Fig. S7*), and more (four) species (*SI Appendix, Fig. S8*). We also find that similar effects occur when patch distributions are uneven (i.e., deviate from the 1:1 ratio we used here), although they increasingly lead to the extinction of one of the species early in the simulations (*SI Appendix, Figs. S9 and S10*).

Discussion

Our results reveal that niche-driven, localized adaptation in a heterogeneous landscape can lead to patterns of regional neutral equivalence of species. If so, the dichotomous tension between neutrality and niche partitioning suggested by purely ecological models (3–5) may be misleading because the two effects can be scale dependent. At the scale of the local patch, the dynamics determining the relative abundances of species in our models are strongly niche-driven while phenotypic variation and fitness

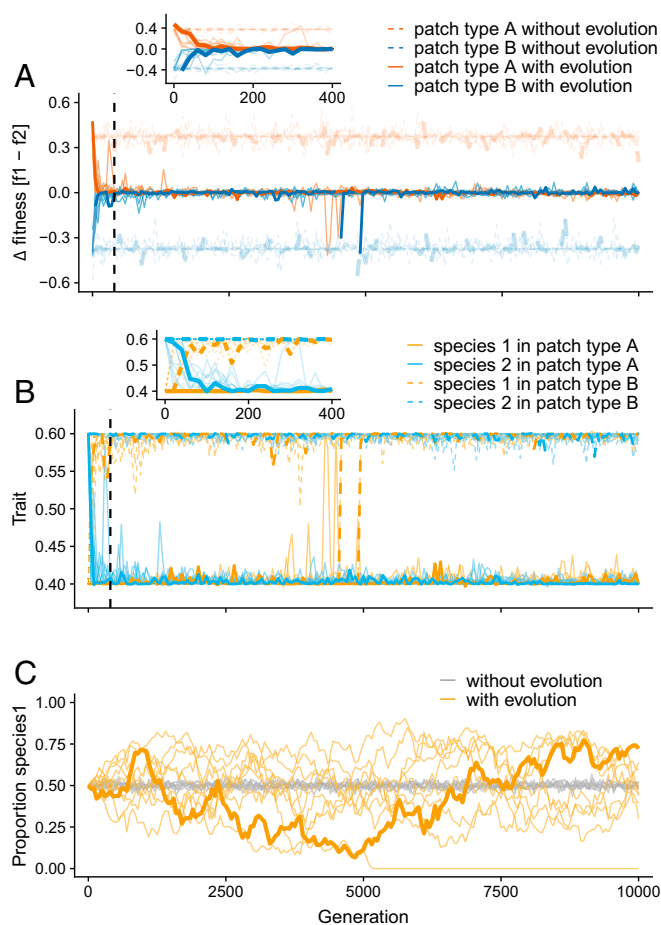


Fig. 3. Temporal dynamics of evolution leading to regional neutrality. Parameter values as given in *Methods* and *SI Appendix, Table S2*. Optimal trait values in each habitat are 0.4 and 0.6 in patch type A (red) and patch type B (blue), respectively. Small panes in *A* and *B* show a detailed view of the first 400 generations (indicated by vertical dashed line). Bold lines show the results of one specific run; thinner lines show the results of the remaining replicate runs. (*A*) Fitness difference (see *SI Appendix* for definition of fitness) between species 1 and species 2. Here evolution has led to mean fitness differences near zero within each patch type within the first 500 generations (*Inset*). Note that there are several points in time in some of the simulations that show strong deviations from the general pattern. This occurs when, due to drift and/or dispersal, only few individuals of a species are present in one of the patch types and these are maladapted to that patch type. Often the species can reestablish itself more broadly in that patch type in subsequent generations after this occasional chance event. (*B*) Mean genotypic value for each species in each patch type through time. Here evolution has led to strong bimodal distributions in both species (shown in Fig. 4 for the same simulation run as the bold lines) that link genotype to patch type within the first 400 generations (*Inset*). (*C*) Proportion of species 1 in the metacommunity through time (gray lines are control simulations without evolution). Evolution results in neutrality between species at the metacommunity level, which enhances drift in relative abundance of species in the metacommunity as a whole.

profiles reveal ecological equivalence among species at the regional level. Thus, patterns that appear neutral at the regional scale might result from ongoing and strongly niche-driven dynamics in different patches mediated by both evolutionary (genetic adaptation to the local habitat type) and ecological (changes in the relative abundance of species) processes.

Regional neutrality makes predictions about the structure and dynamics of ecological communities in heterogeneous landscapes. Under regional neutrality we predict adaptive divergence among populations within species at the local scale and

geographic convergence of fitness-related traits among species with subsequent neutral drift of species toward a single dominant one at the regional scale. With uneven environmental distributions, regional trait and patch occupancy distributions for the two species will reflect environmental distributions and the outcome of drift will be biased toward the species initially adapted to the more prevalent habitat (*SI Appendix, Figs. S9 and S10*). Regional neutrality requires that selection is not so severe as to prevent establishment of maladapted populations, and repeated disturbances that provide the opportunity for these populations to adapt and expand their regional niche.

One of the more important predictions to emerge from the regional neutrality hypothesis is that taxa will show little environmental tracking and potentially show spatial patterning, whereas local variation in trait values (independent of taxa) will show strong environmental tracking and less spatial patterning. This contrasts with more conventional predictions from purely ecological species sorting (no evolution) where both taxa and traits should show environmental tracking, and from conventional predictions based on neutrality involving purely ecological processes where neither species nor traits will show environmental tracking and both show similar spatial patterning. Of course, this will involve measuring traits at the population rather than species level and will depend on there being a close connection between the traits and the fitness response to environment.

Unfortunately we know of no studies that have examined such patterns in sufficient detail to be conclusive. An example that has many features in common with our model involves a pair of amphipod species in the genus *Niphargus* that exist in springs in the Isphrigan peninsula (35). The two species are widespread but they switch habitat niches across the peninsula. While there may be other explanations for this pattern, it is congruent with our model results because both species are regionally equivalent in a qualitative way even though they segregate by habitat niche on smaller scales. We hypothesize that our model may also apply to other systems, especially where local selection is strong, dispersal is moderate to low, and community turnover due to patch dynamics is high. Perhaps the most intriguing such possibility involves internal microbiomes of long-lived hosts.

Our model is not the first to claim that local adaptive evolution can lead to neutrality but it differs in important ways from these previous efforts. Scheffer and van Nes (21) showed that competitive interactions can lead both to niche partitioning as well as to the emergence of subgroups of ecologically similar species at the local scale. In our simulations, the emergence of neutrality at the local scale also occurs in a generally similar way but it is relatively rare. Instead we find that the interaction between local evolution, dispersal, and species sorting leads to a much stronger pattern of ecological equivalence of species at the regional scale and to much more frequent niche specialization at the local scale. The difference is that we incorporate recurrent local disturbances that iterate the process of local adaptive niche evolution and this allows species to eventually colonize alternative habitat types, adapt, and expand the species' overall niche in ways that cannot happen in environmentally fixed landscapes. Hubbell (20) found that spatially autocorrelated environments and random initiation of species can lead to the evolution of habitat generalists with locally distinct niche traits, but his work did not reveal if these conditions are sufficient to obtain regional neutrality in the model. His work also suggests that these results would be most likely in highly diverse communities, while we show that this outcome is possible even for pairwise interactions. Finally, Wittmann and Fukami (36) propose that antagonistic adaptation to intra- vs. interspecific competition between species that show priority effects at the local scale can facilitate regional coexistence of competitors with similar niches. This model shares many features with our approach, including local

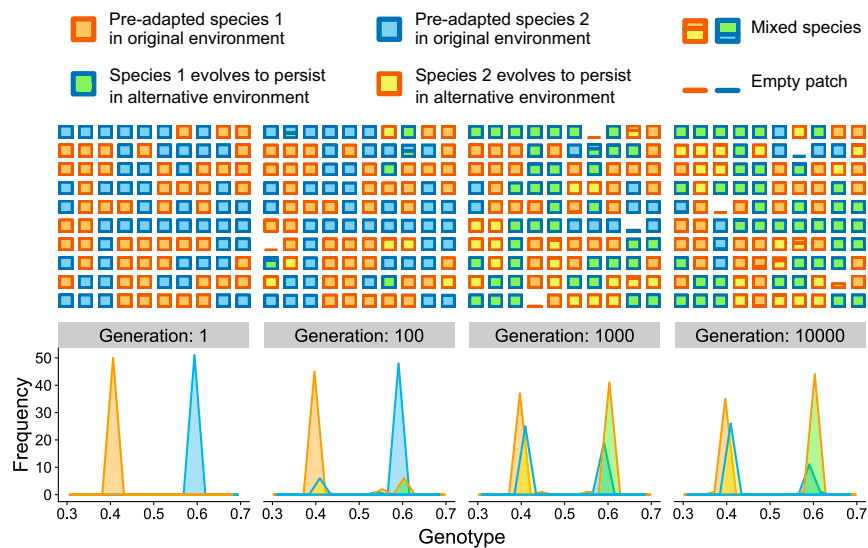


Fig. 4. Patch occupancy and genotype distribution through time. Results for the same simulation run as bold lines in Fig. 3. (*Upper*) Patch occupancy of both species through time for a single run with sexual reproduction. Each square represents a habitat patch in the 10×10 grid. Edge color represents the patch type (red = patch type A, blue = patch type B). Fill color represents species \times niche adaptation. In generation 1 each species dominates in the patch type to which it is preadapted. With time, each species can dominate in either patch type due to evolution into the other niche. (*Lower*) Genotype distribution in the entire metacommunity of both species through time for a single run with sexual reproduction. Edge color represents species identity. Fill color represents species \times niche adaptation. In generation 1 each species is preadapted to one of the patch types (trait values of 0.4 or 0.6). With time, species evolve into each other's niche, resulting in evolutionary convergence of similar bimodal niche trait distributions.

priority effects and regional coexistence, but acts in a different way and does not depend on direct local adaptation to alternate habitat types.

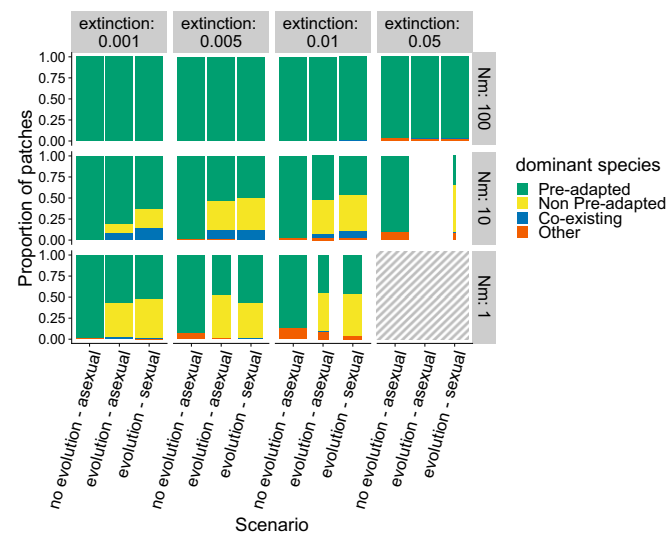


Fig. 5. Patterns of patch dominance at generation 5,000 by preadapted or nonpreadapted species for different levels of patch extinction P_{ext} and dispersal Nm . Results are averaged over 10 replicate runs. Color codes do not represent species or patch type, but indicate whether the dominant species in a patch was preadapted to the patch type at the start of the simulations. Green shows patches occupied either by species 1 with trait values corresponding to A patches in A-type patches or by species 2 with trait values corresponding to B patches in B-type patches. These correspond to patches expected to be dominated by the specialist species for each patch type in the model without evolution. Yellow shows patches occupied by either species 2 with trait values corresponding to A patches in A-type patches or by species 1 with trait values corresponding to B patches in B-type patches. These correspond to patches where species have switched trait values due to evolution so they are dominant in the habitat in which they were initially subordinate. Such patches do not exist in the absence of evolution. Blue shows patches where both species cooccur and are both adapted to the local environment (i.e., local neutral coexistence). Brown shows all other cases including where patches are occupied by populations of either or both species that are not well adapted to local conditions or patches that are empty. Width of the bars indicates the proportion of replicate runs (total of 10) where both species still coexist in the metacommunity (i.e., none of the species has gone extinct due to drift after regional neutrality has established). Hatched area indicates parameter settings where both species go extinct.

Both of our models are highly simplified caricatures of the natural world. A variety of features could decrease the degree to which regional neutrality occurs in natural settings. For example, we assume that both species can evolve the optimal trait and at the same rate. Lower additive genetic variation and other genetic constraints could limit one or both species in this regard or even result in regional exclusion. However, many analyses suggest that ecologically important traits can evolve rapidly, and more closely

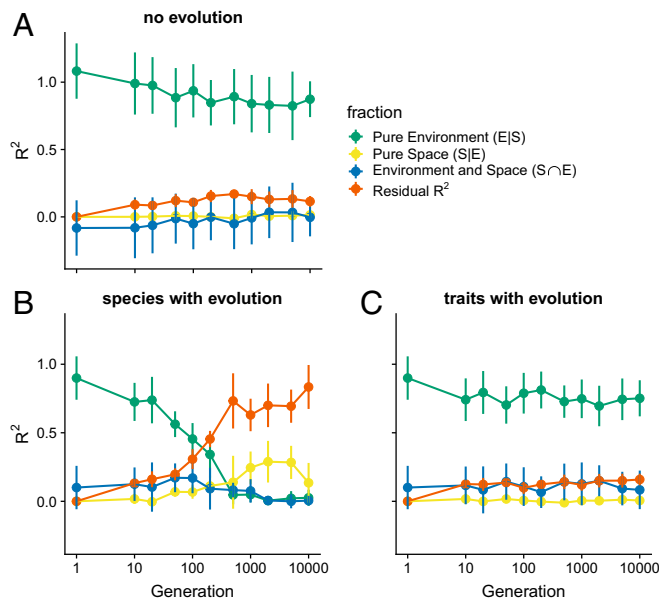


Fig. 6. Variation partitioning of components through time for species and for traits. In each analysis, total variation in species distributions (A and B) or total variation in trait values (C) is partitioned into variation attributed to purely environmental components (i.e., patch type; $E|S$ in green), purely spatial components (i.e., distance between patches; $S|E$ in yellow), components that were attributed to correlated variation between environment and spatial components ($S \cap E$, in blue, due to spatially structured environmental effects), and residual variation (in red). (A) Results in the absence of evolution (controls) for species and for traits. (B) Results for species for dynamics with evolution. (C) Results for traits for dynamics with evolution. In the absence of evolution, species and traits are equivalent. With evolution, the results for traits are very similar to control simulations but the pattern for species shows a very strong decline in effects of environment and a strong increase in residual and spatial effects by generation 1,000.

related species, such as those that are likely to compete for the same resources, might be more likely to have similar evolutionary rates and capacities.

Our models suggest that local adaptive evolution might often contribute to cryptic ecoevolutionary dynamics that alter the regional mechanisms that determine biological diversity and resistance to disturbance. The evolution of regionally neutral species means that drift could reduce diversity over long periods as stochastic events lead one species to dominate and the other to become extinct. However, regionally neutral species would also provide a level of redundancy during perturbations. For instance, if these species contribute to ecosystem function, then losing one species would still maintain this function across all habitat types. Moreover, as habitats change through natural or anthropogenic means, local adaptive evolution could keep pace, allowing each species' regional niche to expand given sufficient additive genetic variation. Fully understanding the contribution of evolution to biodiversity patterns will require a more integrated biology that synthesizes community ecology and evolutionary biology across a range of temporal and spatial scales.

Methods

Patch Occupancy Model. An overview of the model is given in *Patch Occupancy Model of Community Assembly* and legend of Fig. 1. The formal specification of the model is given in *SI Appendix*. Propagule production rate c and extinction rate m of patches are set to 2 and 1, respectively. For further parameterization see *SI Appendix*, Table S1.

Spatially Explicit Individual-Based Model. For a brief verbal description of the model see *Spatially Explicit Individual-Based Model of Community Assembly* and legend of Fig. 2. For a full formal specification of the model and parameterization see *SI Appendix*. Results are based on 10 replicate simulations

for each parameter combination. Unless differently stated, simulations are run with sexually reproducing species, patch extinction rate $P_{ext} = 0.01$, and dispersal rate $Nm = 10$ (individuals per patch per generation). Further parameter settings are given in *SI Appendix*, Table S2. Each simulation is run for 10,000 generations (where one generation equals 10 iterations of mortality, reproduction, and dispersal). At the start of the simulations all patches are filled with the species preadapted to the local environment.

Variation Partitioning. Variation partitioning is used to partition the variance in response (species or trait composition in each patch) between locations (patches) into components ascribed to different sets of explanatory variables (environment and space).

For species composition: For each patch the population size per species is taken and Hellinger transformed (response variables). Environmental data are the type of environment in each patch and spatial data are the principal coordinates of neighborhood matrices (37)-transformed Euclidean distances between patches.

For trait composition: Instead of taking population sizes, the species are pooled within each patch and individuals are counted by phenotype (trait; three categories: $0.35 \leq \text{trait} \leq 0.45$, $0.45 < \text{trait} < 0.55$, $0.55 \leq \text{trait} \leq 0.65$) and Hellinger transformed. Environmental and spatial data are the same as for species composition.

For a given scenario, variation partitioning was performed for each replicate run at given generations. Edge populations on the border of the 10×10 grid were excluded from the analyses. Analyses were done using Package *vegan* (38) in R (39).

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