

Community assembly is a race between immigration and adaptation: eco-evolutionary interactions across spatial scales

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Both ecological and evolutionary mechanisms have been proposed to describe how natural communities become assembled at both regional and biogeographical scales. Yet, these theories have largely been developed in isolation. Here, we unite these separate views and develop an integrated eco-evolutionary framework of community assembly. We use a simulation approach to explore the factors determining the interplay between ecological and evolutionary mechanisms systematically across spatial scales. Our results suggest that the same set of ecological and evolutionary processes can determine community assembly at both regional and biogeographical scales. We find that the importance of evolution and community monopolization effects, defined as the eco-evolutionary dynamics that occur when local adaptation of early established immigrants is fast enough to prevent the later immigration of better pre-adapted species, are not restricted to adaptive radiations on remote islands. They occur at dispersal rates of up to ten individuals per generation, typical for many species at the scale of regional metacommunities. Dispersal capacity largely determines whether ecological species sorting or evolutionary monopolization structure metacommunity diversity and distribution patterns. However, other factors related to the spatial scale at which community assembly processes are acting, such as metacommunity size and the proportion of empty patches, also affect the relative importance of ecology versus evolution. We show that evolution often determines community assembly, and this conclusion is robust to a wide range of assumptions about spatial scale, mode of reproduction, and environmental structure. Moreover, we found that community monopolization effects occur even though species fully pre-adapted to each habitat are abundant in the metacommunity, a scenario expected a priori to prevent any meaningful effect of evolution. Our results strongly support the idea that the same eco-evolutionary processes underlie community assembly at regional and biogeographical scales.

Species colonize and assemble new communities on patches at scales ranging from local tree fall gaps to oceanic volcanic islands. Ecological community assembly theories at both regional (metacommunity) and biogeographical scales have variously focused on species sorting (local colonization–extinction dynamics) among niches (Mouquet and Loreau 2002, Leibold et al. 2004), tradeoffs among species' colonization and competitive abilities (Levins and Culver 1971, Tilman 1994, Urban and De Meester 2009), priority effects or incumbency advantage (Shulman et al. 1983, Jablonski and Sepkoski 1996, Law and Morton 1996, Tilman 2004, Law and Leibold 2005), and a balance between colonization and extinction dynamics as a function of island size and isolation (MacArthur and Wilson 1967, Kadmon and Allouche 2007). However, these ecological assembly mechanisms might also interact with evolutionary mechanisms to determine community assembly at both regional (Vellend 2006, Urban et al. 2008) and biogeographical (Wilson 1961, Ricklefs and Bermingham 2002, Gillespie 2004, Emerson and Gillespie 2008) scales. Hence, we require theories of

community assembly that incorporate both evolutionary and ecological mechanisms and that span from local patches and regional metacommunities to distantly connected islands.

Depending on the spatial scale of interest, existing theories of community assembly differ in the degree to which they incorporate joint evolutionary and ecological dynamics. Island biogeography theory generally emphasizes random colonization–extinction dynamics across large spatial scales, often assumes a mainland source of colonists (MacArthur and Wilson 1967), and has long recognized the potential importance of evolution in community assembly on isolated islands (Wilson 1959). Evolutionary biologists have stressed the importance of adaptive radiations and secondary species sorting across these biogeographical scales (Gillespie 2004, Gillespie and Baldwin 2009). New colonists to an island are predicted to evolve a changed or expanded niche via ecological release (Wilson 1961, Roughgarden 1972, Case and Taper 2000), which might also be followed by differentiation into locally adapted populations or separate species (Ricklefs and Bermingham 2002). In contrast, at regional metacom-

munity scales, ecologists have generally stressed niche-based species sorting among heterogeneous environments (Leibold et al. 2004) and have often overlooked evolutionary dynamics. Evolutionary effects on community assembly at finer metacommunity scales likely have been less explored because of the perception that higher dispersal rates will distribute pre-adapted species across environments and spread maladaptive genes that swamp local adaptation (Lenormand 2002, de Mazancourt et al. 2008). However, adaptation might often occur at finer spatial scales than previously appreciated (Richardson et al. 2014), and this adaptation might interact with local community and colonization dynamics in ways that alter community assembly (Urban et al. 2008).

The community monopolization hypothesis offers one way to unite the eco-evolutionary dynamics of community assembly across metacommunity and biogeographical scales. The community monopolization effect describes the eco-evolutionary dynamic that characterizes when a species arrives early and evolves to monopolize resources in a way that decreases the establishment success of future competitors (De Meester et al. 2002, Loeuille and Leibold 2008, Urban and De Meester 2009). In biogeographical terms, we explore a part of the proposed taxon cycle (Wilson 1959, 1961, Ricklefs and Bermingham 2002), whereby a colonist expands its niche to include new habitats. However, we characterize how well the newly adapted species can resist invasion from pre-adapted species (Gillespie 2004), which is not generally included in standard descriptions of the taxon cycle. The first species that arrives in an empty patch might not only experience a demographic release from resource limitation, but also an evolutionary release from ecological constraints on niche expansion caused by the absence of competitors (Losos et al. 1998, Gavrillets and Losos 2009, Yoder et al. 2010). Strong natural selection in the new environment can then elicit local niche evolution or adaptive radiations (Lack 1947, Bush 1969, Reznick et al. 1990, Losos et al. 1998, Schluter 2000, Turner et al. 2001). However, depending on the time of arrival, a species better adapted to the new environment could establish and outcompete the first species before this first species adapts to the new conditions (Emerson and Gillespie 2008, Urban et al. 2008, Urban and De Meester 2009). The basic process is similar whether one considers speciation on islands (Roughgarden 1972, Gillespie 2004) or the adaptive divergence of populations among habitat patches (Urban et al. 2008, Urban and De Meester 2009). In each case, ecological and evolutionary processes interact to varying degrees to determine community assembly. Previous work suggests that community monopolization is important under the conditions most conducive to an evolutionary priority effect – when potential colonists are equally maladapted to the new patch and the second species disperses poorly, which allows the first species to adapt before its competitor arrives (Urban and De Meester 2009). Monopolization effects are expected to be less common when better adapted species exist in the region to colonize and outcompete poorly adapted residents and dispersal is equivalent among species (de Mazancourt et al. 2008, Loeuille and Leibold 2008). Moreover, compared to the dynamics at biogeographical scales, regional metacommunities are likely to be characterized by less restricted dispersal rates and a greater proportion

of initially occupied patches that might prevent community monopolization effects. For example, a disturbance creates a single empty patch. In contrast, more open patches are available in an island archipelago that is colonized from a single mainland source.

Here, we explore the relative importance of ecological versus evolutionary processes during community assembly. Because our key objective is to study the interplay between colonization, dispersal, stochastic demographic processes, ecological interactions within and among species in environmentally divergent habitats and evolution through the action of standing genetic variation and recurrent mutation, we rely on a complex individual based model approach to incorporate and investigate the importance of all these key features. Our modeling approach spans regional and biogeographical scales and incorporates within-patch environmental variation as an important structuring element as highlighted by its role in community assembly (Williams 1964, Chesson 2000, Tilman 2004), population differentiation (e.g. color morphs in lakes, Hargeby et al. 2005), and speciation (Emerson and Gillespie 2008, Gavrillets and Losos 2009, Kisel and Barraclough 2010). In particular, we vary dispersal, patch number and initial occupancy, three factors encapsulating major aspects of biogeographic and metacommunity structure across varying spatial scales. We make three major advances compared to earlier work on eco-evolutionary interactions and community assembly (de Mazancourt et al. 2008, Loeuille and Leibold 2008, Urban and De Meester 2009). First, we assume a worst case scenario for monopolization effects whereby pre-adapted species are available to colonize each habitat on heterogeneous patches, and all species disperse at equal rates. Second, by evaluating results along a gradient in dispersal both within and among patches, we can evaluate the relative importance of ecology versus evolution along a continuum from movement among nearby habitat patches in a regional metacommunity (De Meester et al. 2002, Leibold et al. 2004, Urban and De Meester 2009) to colonization and adaptive radiation on isolated islands (Roughgarden 1972, Gillespie 2004, Emerson and Gillespie 2008). Third, we compare results for a range of metacommunity sizes (number of patches) and for different scenarios of initial patch occupancy (the proportion of empty patches at the start of the simulations). Both metacommunity size and initial patch occupancy relate to the degree to which initial conditions determine the opportunity for community monopolization effects. We expect that a larger number of patches will allow for a higher occurrence of monopolization effects, as more habitats are present that can be colonized and monopolized. We also expect that monopolization effects will occur more commonly when a lower proportion of patches are initially occupied because the number of immigrants (which is dependent on the proportion of occupied patches) is lower and therefore there is more time for a maladapted colonizer to adapt before a pre-adapted species arrives. By altering dispersal rates within and among patches along with the number and proportion of occupied patches, we thus unite microevolutionary and macroevolutionary mechanisms of community assembly and species range expansion within the unifying rubric of community monopolization effects.

Methods

The model

We developed an individual-based simulation model in which we assume a hierarchically structured metacommunity of environmentally different habitats nested within a set of larger patches (Fig. 1). We assume the same set of four environmentally divergent habitats in each patch. The patches are akin to islands with different habitats like those found in the example of *Tetragnatha* spider colonization of Hawaiian islands (Gillespie 2004) or regional patches containing different (sub)habitats such as stream pools that vary in predation risk (Reznick et al. 1990). We assume varying degrees of parapatric separation among different habitats within a patch as would occur, for example, if habitats are separated spatially. This tunable level of spatial segregation generates dynamics that simulate different degrees of reproductive isolation because individuals only mate within a habitat. A community occupies one habitat, and a metacommunity constitutes all patches. Our metacommunity consists of $s = 4$ species, each adapted to one of $habs = 4$ habitat types. We chose to focus on the results of four species and four habitat types to represent one of the better empirical examples of eco-evolutionary dynamics in community assembly, the *Tetragnatha* spiders of Hawaii (Gillespie 2004). However, assuming different numbers of species and habitats did not affect our results substantially. In preliminary work, we found that a larger number of habitats enhanced the relative importance of evolution. Therefore, by presenting results with four habitat types, we concentrate on a slightly more conservative

scenario that moreover indicates the environmental structure found in an empirical example.

Species are labeled by a unique identifier which is set at the start of the simulations and is passed to the offspring. All species have discrete reproduction, overlapping generations and newborn dispersal (Fig. 1). Within each habitat, individuals compete via a lottery for one of n microsites that each can host one individual. If a local microsite is already occupied, newborns cannot establish in that microsite. Newborns can only establish in a microsite when the resident individual dies and the microsite becomes empty. Therefore, we assume pre-emptive competition for space. Within each habitat, microsite environments e_m equal the mean habitat environment e plus stochastic Gaussian variation ($\sigma_e = 0.025$) across space. Each individual has a phenotype z that determines its survival probability in the microsite where it resides and that consists of a genetic component and some random non-genetic contribution according to a Gaussian distribution (mean = 0, standard deviation $\sigma_z = 0.025$) determined at birth. The genotypic value ranges from zero to one and is calculated as the mean of $L = 20$ bi-allelic additive genes (value 0 or 1). Mutation (change of value from 0 to 1 or vice versa) occurs with probability $\mu = 10^{-4}$ (except in scenarios in the absence of evolutionary potential where $\mu = 0$ (see below)) at each gene and reproductive event. This mutation rate, together with standing genetic variation (see below), results in rates of microevolution between 0.5 and 0.01 haldanes per generation, which falls well within the range of estimated rates of microevolution in the wild (Hendry and Kinnison 1999) (Supplementary material Appendix 2). Probability

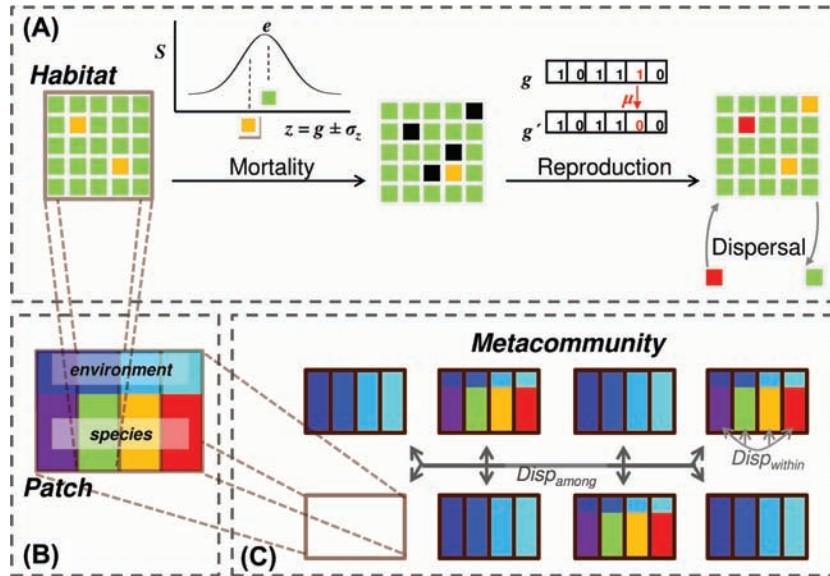


Figure 1. The model is hierarchically structured with microsites within habitats (A) within patches (B) within a metacommunity (C). Each habitat consists of a number of microsites that can each host one individual. Survival S is determined by the match between phenotype z and environment e . Empty microsites are filled with juveniles after reproduction. During reproduction, mutations occur with probability μ for each of the additive genes. A patch consists of four distinct habitats (blue shades) with one of four species (purple–green–yellow–red) pre-adapted to each habitat type. At the start of the simulations, metacommunities have a number of patches occupied by their respective pre-adapted species, and a number of initially empty patches. There is no explicit spatial structure and all patches and habitats are connected by bidirectional juvenile dispersal. We distinguish between within patch dispersal (light grey arrows in (C)) and among patch dispersal (dark grey arrows in (C)). The initially occupied patches continue to undergo dynamic changes over the course of the simulations but we only record changes in the initially unoccupied patches.

of survival S_i of an individual at each time step is calculated according to

$$S_i = (1 - d) \exp - \left(\frac{z_i - e_m}{\omega} \right)^2 \quad (1)$$

where $d=0.1$ is the baseline mortality and $\omega=0.5$ is the width of stabilizing selection. At each time step, a random uniform number u between 0 and 1 is drawn for each individual. If $u > S_i$, the individual dies.

Following survival, the number of offspring individuals I produced in each habitat is

$$I_{ph} = bN_{f,ph} \quad (2)$$

where b is the per capita birth rate, and $N_{f,ph}$ is the number of female individuals in habitat h in patch p . The number of empty microsites available in a habitat sets a maximum to the number of offspring that will successfully establish in that habitat (lottery competition). We consider both asexual and sexual reproduction. For asexual reproduction, all individuals are female and N_f equals N . Offspring inherit the genome from their mother without recombination. For sexual reproduction, only individuals with the same species identifier can mate, and selfing is not allowed. A 1:1 sex ratio is assumed, and at each time step, individuals within each habitat and species are randomly divided into fixed pairs for that time step, such that N_f equals $N/2$. If N is odd, the one unpaired adult does not reproduce. Offspring inherit from each parent one randomly selected allele for each of the 10 diploid loci.

There is no explicit spatial structure in the model; all patches are equidistant from each other and the same assumption holds for all habitats within a patch. We assume different dispersal levels among patches and among habitats within patches, controlled by dispersal rates m_{among} and m_{within} , respectively. We express absolute dispersal $Disp$ as the expected number of emigrant offspring leaving a habitat per generation

$$Disp_{ph,q} = I_{ph} m_q \quad (3)$$

where q denotes within or among patch dispersal and m_q is the fixed dispersal proportion per generation and one generation consists of 10 simulated time steps of mortality and reproduction (see Supplementary material Appendix 1 for details on the calculation of generation time). Individuals dispersing into a habitat compete with the locally produced offspring for establishment in the empty microsites. We independently manipulate dispersal levels among patches $Disp_{among}$ and among habitats within patches $Disp_{within}$. See Supplementary material Appendix 1 for more technical details on the specifications of reproduction and dispersal. Because the number of females N_f is only half the population size N for sexual reproduction (sex ratio = 1:1), we double the birth rate b per sexual female compared to asexual reproduction to standardize the number of dispersing offspring Im_q ($b=0.5$ and 1 for asexual and sexual reproduction, respectively). We evaluate results in the context of Im_q because the absolute number of dispersers determines the time given to an early colonizer to grow to carrying capacity and prioritize available

resources (Tilman 2004). Preliminary simulations demonstrated that the absolute number of dispersing juveniles is more important than dispersal rate m in determining community dynamics. The number of emigrants Im_q from each habitat is nearly constant and at its maximum except for a brief time during the colonization of an empty patch before the carrying capacity is reached. The number of immigrants to each habitat is dependent on the proportion of occupied patches.

At the beginning of the simulations, s species dominate their optimal habitat in the initially occupied patches (*occ*; Fig. 1), and communities in each habitat are at carrying capacity. All other patches (*col*= patches that need to be colonized) are initially empty. Individuals of the dominant species within an occupied habitat have genotypic values distributed around the optimal genotypic value for that habitat (equal to e for that habitat) with standard deviation σ_g . We assumed a moderate initial amount of standing genetic variation ($\sigma_g = 0.045$) except in scenarios without evolutionary potential where $\sigma_g = 0$ (see below). For further details on the generation of the initial species composition and genetic composition in each occupied patch, see Supplementary material Appendix 1.

Explored scenarios

Parameters b (per capita birth rate) and μ (mutation rate) are changed according to assumptions about mode of reproduction and evolutionary capacity, respectively. Parameter n is set according to scenarios on number of patches or initial patch occupancy. Parameters *occ* (number of initially occupied patches) and *col* (number of initially empty patches that need to be colonized) are changed according to a set of focal scenarios of metacommunity size and initial patch occupancy (see below). All other parameters except for dispersal are fixed (Table 1). Depending on the scenario, we explore patterns of community assembly for values of within patch dispersal $Disp_{within}$ and among patch dispersal $Disp_{among}$ ranging between 1 and 1000 and between 0.1 and 100, respectively. We did not consider cases where $Disp_{among}$ exceeds $Disp_{within}$ because we assume that habitats within a patch are always more accessible than other patches. For each scenario and combination of dispersal rates $Disp_{within}$ and $Disp_{among}$, we performed $r=10$ (scenarios for initial patch occupancy) or $r=20$ (scenarios for number of patches) replicate runs with 5000–20 000 time steps T per run (= 500 to 2000 generations) in order to reach quasi-equilibrium. The number of time steps needed to reach quasi-equilibrium was determined during preliminary simulations and is dependent on $Disp_{among}$. In all cases, we compared between reproductive modes (sexual versus asexual reproduction).

We primarily focus on outcomes based on different numbers and proportions of initially occupied patches that characterize different aspects of regional and biogeographical scales.

a) Number of patches: we compare results for simulations ranging from 4 to 32 patches. For these simulations, we assume that half of the patches are occupied with fully pre-adapted species dominating each habitat type regardless of the number of patches. Hence, we control for the

Table 1. Parameters and values used in simulations.

Parameter	Description	Value(s)
Environment		
<i>habs</i>	Number of different habitat types	4
<i>s</i>	Number of species	4
<i>n</i>	Number of microsites per habitat	a) 250 b) 1000
<i>e</i>	Environment type	0.2 to 0.8 in steps of 0.2
σ_e	Microsite environmental variation	0.025
(<i>occ</i> – <i>col</i>)	(Number of initially occupied patches – number of initially empty patches)	a) (2–2), (4–4), (8–8), (16–16) b) (1–8), (8–1)
Demography		
<i>d</i>	Baseline mortality	0.1 individual ⁻¹ timestep ⁻¹
<i>b</i>	Per female birth rate	Asexual: 0.5 individuals timestep ⁻¹ Sexual: 1 individuals timestep ⁻¹
ω	Width of the fitness function	0.5
σ_z	Non genetic phenotypic variation	0.025
σ_g	Genetic trait variation within each habitat at the start of the simulations	0.045
<i>Disp_{within}</i>	Dispersal rate within patches	1 to 1000 individuals generation ⁻¹ (1 generation = 10 timesteps)
<i>Disp_{among}</i>	Dispersal rate among patches	0.1 to 100 individuals generation ⁻¹ (1 generation = 10 timesteps)
Genetics		
<i>L</i>	Number of genes	20
μ	Mutation rate	0, 10 ⁻⁴ gene ⁻¹ timestep ⁻¹
Simulations		
<i>T</i>	Total time steps	5000 to 20 000
<i>r</i>	Replicate runs	a) 10 b) 20

a) parameter values for scenarios with different size of the metacommunity.

b) parameter values for scenarios with different initial patch occupancy.

proportion of empty patches, while varying the absolute number of empty patches. For each number of patches, we ran simulations in the presence and absence of evolutionary potential to compare purely ecological community assembly with assembly driven by eco-evolutionary interactions. In the absence of evolutionary potential, $\mu = 0$ and $\sigma_g = 0$. Note that there is still non-heritable phenotypic variance within each genotype determined by σ_z .

b) Initial patch occupancy: for a fixed number of nine patches, we alter the proportion of initially empty patches. In the first scenario, one initially occupied patch (e.g. a mainland) occurs together with eight initially empty patches at the start of the simulations. This ‘island biogeography’ scenario is consistent with a newly formed set of islands equidistant from a single source of colonists. This scenario captures the basic processes that repeatedly have produced separate radiations of spider and lizard ecomorphs on remote islands (Losos et al. 1998, Gillespie 2004). In a second scenario, eight initially occupied patches (e.g. a regional metacommunity) exist together with one initially empty patch at the start of the simulations. This scenario is consistent with a metacommunity in which a new patch has formed (e.g. a new pond or lake) or a natural disturbance has eradicated the community in one patch.

We evaluate all values of within- and among-patch dispersal in each scenario to capture orthogonal effects of two aspects associated with differences in spatial scale, i.e. dispersal and the number of unoccupied patches. Thus, we develop theory that spans from regional metacommunities to the biogeographical scale of species radiations on distant islands.

Analysis of results

In all of the analyses and results, the initially occupied patches are excluded, and we focus on the species composition in the initially empty patches. We plot results based on *Disp_{within}* and *Disp_{among}* when populations are at carrying capacity. Based on the abundance of each species in each habitat, each patch and across all patches at the end of the simulations (excluding those filled at the outset), we calculated species diversity based on the Simpson concentration in each colonized habitat, patch and global metacommunity, and used these measures to compare alpha diversity within habitats, beta diversity between habitats within patches and gamma diversities of the entire metacommunity (Jost 2007) between dispersal rates and scenarios. To assess the importance of ecological versus evolutionary processes throughout our investigated parameter space, we link observed patterns of diversity to different mechanisms of community assembly, i.e. species sorting, mass effects and monopolization effects. Species sorting will result in patterns with high beta diversity in each patch (\approx number of pre-adapted species) and low alpha diversity in habitats within patches (one species dominates each habitat). Mass effects can be distinguished by the occurrence of more than one species within one habitat (alpha diversity > 1) and a reduction of beta diversity within patches below the number of pre-adapted species. With increasing monopolization effects, beta diversity within patches will decrease below the number of pre-adapted species as one species colonizes and adapts to additional habitats within a patch, but alpha diversity will stay close

to one as each habitat is still dominated by a single species. For the scenarios that differ in initial patch occupancy, we further distinguished between habitat monopolization, patch monopolization and global monopolization based on a decision table (see Supplementary material Appendix 1 for details). Monopolization occurs in general when a species dominates in > 1 habitat within a patch. Habitat monopolization occurs when a species dominates > 1 habitat but not all habitats in a patch, patch monopolization occurs when a species dominates all habitats in a patch, and global monopolization occurs when one species dominates all initially empty patches (Loeuille and Leibold 2008; only possible in the island scenarios). In total, the following mechanisms of assembly are recognized: species sorting, mass effects, habitat monopolization, patch monopolization and global monopolization. Based on this classification, we calculated for each simulation run the proportion of patches in the metacommunity (excluding those occupied at the start) characterized by each community assembly mechanism, and determined for each combination of parameter settings which is the dominant mechanism.

For the set of simulations that vary patch number, we also compared genetic trait variance within species to genetic trait variance among species within the metacommunity. To calculate genetic trait variation, we pooled all individuals within the entire metacommunity (i.e. all patches that were empty at the start of the simulations), either within or over all species present. We subsequently estimated average genetic trait variance within species and total genetic trait variance within the metacommunity. A higher proportion of genetic trait variance within species indicates increasing effects of monopolization.

An example movie of a simulation showing the community assembly dynamics through time is given in Supplementary material Appendix 5, Movie A1.

Results

Effects of dispersal rates on community assembly

Without evolution, alpha diversity within habitats is one and beta diversity within patches is close to its maximum (= number of pre-adapted species) at low to intermediate within-patch dispersal rates ($Disp_{within} < 1000$; Fig. 2A, B, blue symbols) indicating the occurrence of species sorting. For high within-patch dispersal ($Disp_{within} = 1000$), alpha diversity within habitats is similar to gamma diversity, and beta diversity within patches is reduced to one (Fig. 2, blue symbols) indicating the occurrence of mass effects. Total species diversity (gamma diversity) in the newly colonized metacommunity remains close to the maximum except for within patch dispersal levels of 1000 (Fig. 2C, blue symbols). With evolution, when the number of migrants per generation among patches ($Disp_{among}$) is less than or equal to one (asexual reproduction) or ten (sexual reproduction), beta diversity within patches is often reduced below the number of pre-adapted species while alpha diversity remains at one, indicating the occurrence of monopolization effects (Fig. 2, red and green symbols; Fig. 3A, B, blue and green cells and lines). The probability and degree of monopolization increase as among-patch dispersal decreases. Mixtures of evolutionary monopolization effects and ecological processes occur at moderate dispersal levels ($Disp_{among} = 0.5-10$; Fig. 3A, green

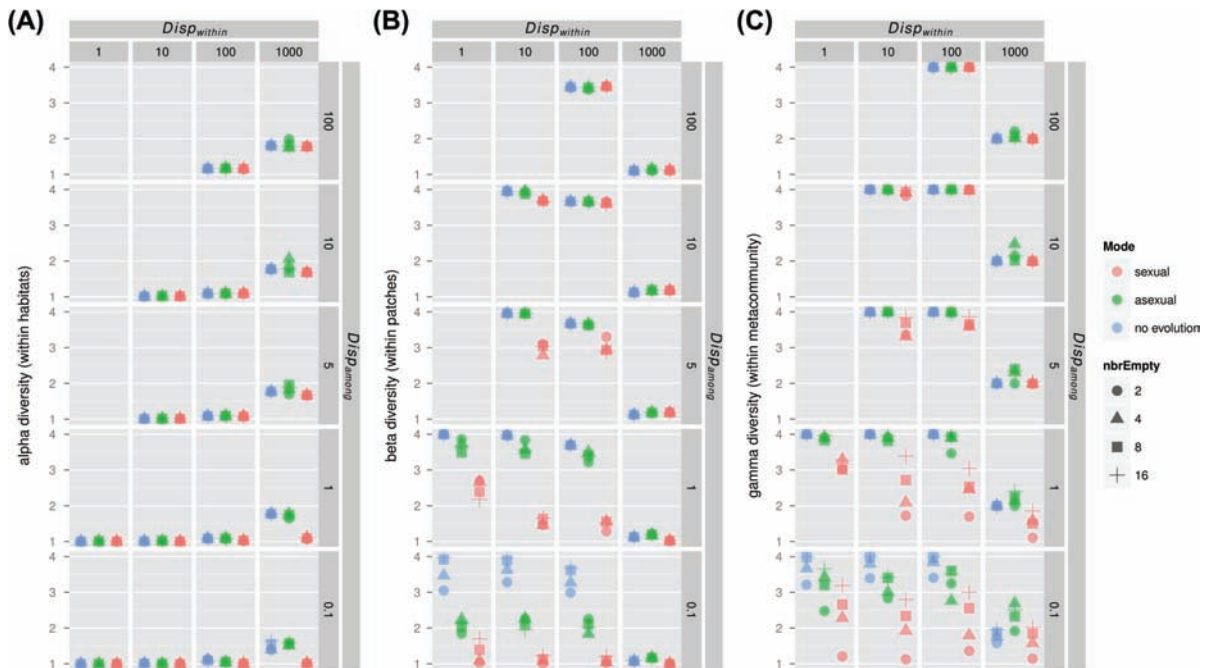


Figure 2. Patterns of species diversity in relation to dispersal rates and metacommunity size. Blue symbols represent the absence of evolutionary potential (results averaged over asexual and sexual reproduction), green and red symbols represent community assembly in the presence of evolutionary potential for asexual and sexual reproduction, respectively. nbrEmpty = number of initially empty patches at the start of the simulations. (A) Alpha diversity within habitats; (B) beta diversity within patches; (C) gamma diversity within the total metacommunity (species abundances pooled over habitats and patches). Results are averaged over patches and replicate runs.

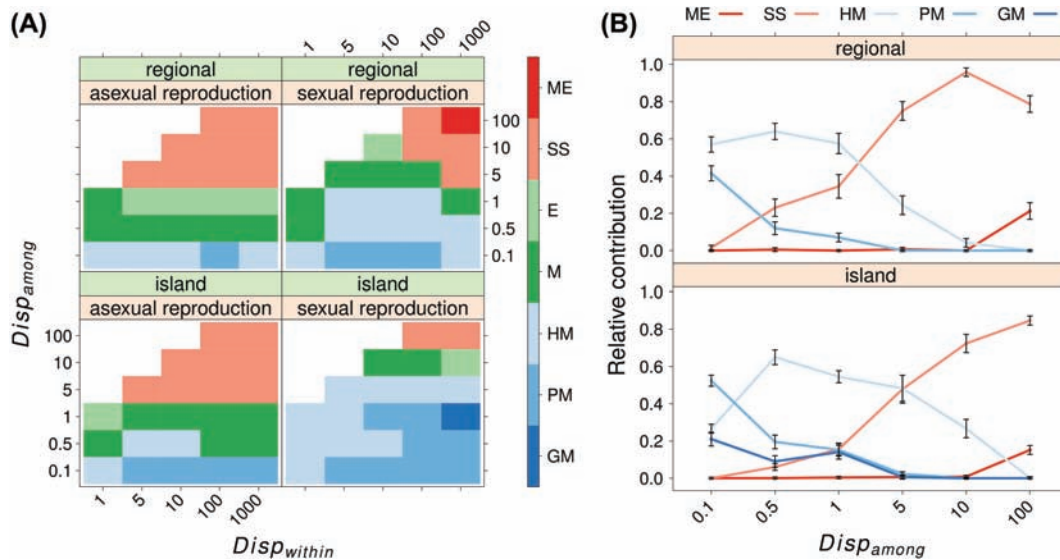


Figure 3. Mechanisms of community assembly in relation to dispersal rates, initial patch occupancy and mode of reproduction. regional = scenario of initial patch occupancy with 8 initially occupied patches and one initially empty patch; island = 1 initially occupied patch and 8 initially empty patches. The legend represents all five possible mechanisms of community assembly as described in the methods. ME: mass effects; SS: species sorting; HM: habitat monopolization; PM: patch monopolization; GM: global monopolization. (A) Each cell indicates the dominant (highest frequency) process in determining community composition for the given levels of within (x-axis) and among (y-axis) patch dispersal. Red cells: community composition in more than 90% of the patches is determined purely by ecological processes; green cells: community composition in more than 10% of the patches involves evolutionary processes (E: ecology (ME + SS) most frequent; M: monopolization (HM + PM + GM) most frequent); blue cells: community composition in more than 90% of the patches involves evolutionary processes. (B) Relative contribution of ecological and evolutionary processes in relation to between patch dispersal ($Disp_{among}$); values represent the average over mode of reproduction and over explored levels of $Disp_{within}$.

cells; Fig. 3B), and monopolization dominates at intermediate to low among-patch dispersal levels depending on the scenario and mode of reproduction ($Disp_{among} \leq 0.5-5$; Fig. 3A, blue cells; Fig. 3B). As a result, gamma diversity decreases with decreasing among-patch dispersal because species can adapt to multiple habitats and reduce the abundance of other species pre-adapted to those habitats in the metacommunity (Fig. 2C). In its most extreme form, the entire metacommunity becomes monopolized by a single species (Fig. 3B, dark blue lines). With decreasing levels of among patch dispersal, the relative contribution of within species genetic trait variance tends to increase at the expense of between species genetic trait variance (Fig. 4A).

Effects of different scenarios on incidence of monopolization effects

Dispersal among patches is the main driver of the incidence of evolutionary monopolization effects. However, monopolization effects also depend on number of patches (Fig. 2), initial patch occupancy (Fig. 3) and mode of reproduction (Fig. 2, 3). Patch number did not affect the dispersal threshold at which monopolization effects occur (Fig. 2A, B). Yet, assuming more patches preserved greater gamma diversity in the metacommunity by allowing for a refuge for pre-adapted species that would normally have become extinct (Fig. 2C). We observed that monopolization effects were also stronger with a greater proportion of initially empty patches (Fig. 3). As for patch number, the proportion of initially empty patches did not affect the dispersal threshold at which

monopolization effects occur, but for the same dispersal levels, the proportion and degree of monopolization effects were higher.

Mode of reproduction clearly affected our results. Sexual reproducers underwent monopolization effects more than asexual reproducers: monopolization occurred at higher among-patch dispersal for sexual species ($Disp_{among} \leq 10$) than for asexual species ($Disp_{among} \leq 1$), and monopolization effects were more pronounced in sexual than in asexual species. For the same levels of dispersal, sexual species showed lower beta and gamma diversity (Fig. 2B, C), a higher proportion of monopolization effects (Fig. 3A), and a higher relative contribution of within species genetic trait variance (Fig. 4A).

Discussion

Multiple theories make predictions about community assembly in heterogeneous environments (MacArthur and Wilson 1967, Schluter 2000, Gillespie 2004, Leibold et al. 2004). Each theory focuses on a particular spatial scale and emphasizes either ecological or evolutionary processes. Here, we span a gradient from a set of local patches in a regional metacommunity to a set of distant islands and demonstrate that the same ecological and evolutionary processes and their interactions can span the predictions of each of these separate theories from metacommunity ecology, island biogeography, and adaptive radiations simply by varying a few key parameters. In particular, we are able to reproduce the community assembly dynamics predicted by disparate fields by varying dispersal within and among patches.

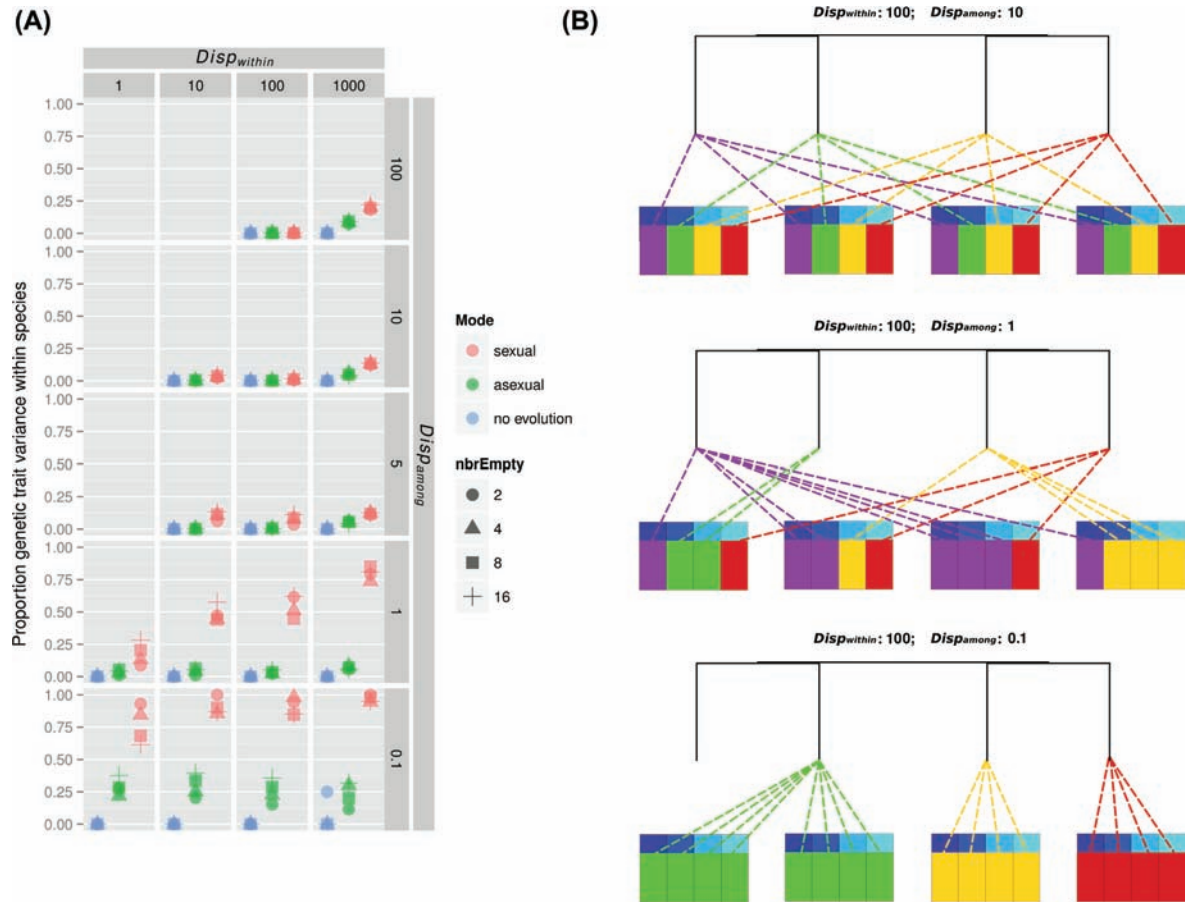


Figure 4. (A) Patterns of genotypic trait variance. Blue symbols represent the absence of evolutionary potential (results averaged over asexual and sexual reproduction), green and red symbols represent community assembly in the presence of evolutionary potential for asexual and sexual reproduction, respectively. $nbrEmpty$ = number of initially empty patches at the start of the simulations. Results are averaged over patches and replicate runs. (B) Diagram depicting the dominant species within each habitat. Examples for a sexual species, with 4 empty patches at the start and $Disp_{within} = 100$. The top part of each subplot (black lines) represents the ‘pseudo’ phylogenetic relatedness between the 4 species (all species are equally related to each other). Below the phylogenetic tree, the 4 patches and habitats within patches are represented with the respective dominant species within each habitat (purple–green–yellow–red). The band with shades of blue above the species colors indicates the type of environment within each habitat. At high between patch dispersal, a given species will dominate the same environment on different patches due to habitat filtering. At low between patch dispersal, a given species will dominate different environments on the same patch due to historical contingency and monopolization effects.

We find that regardless of our assumptions, evolution frequently interacts with ecological processes to determine the assembly of communities. In particular we find broad support for community monopolization, whereby early colonizers rapidly adapt to monopolize resources and prevent late-arriving competitors from establishing (De Meester et al. 2002, Loeuille and Leibold 2008, Urban and De Meester 2009). Monopolization effects occurred commonly even when 1–10 migrants move between patches per generation. These monopolization effects happen regardless of the number of patches, whether we modeled a single empty patch surrounded by multiple communities (e.g. a regional metacommunity) or a single source that colonizes multiple empty patches (e.g. a biogeographical island archipelago), or whether species reproduce sexually or asexually. Compared to previous studies (de Mazancourt et al. 2008, Loeuille and Leibold 2008, Urban and De Meester 2009), we show that the relative importance of evolution can be considerable even

under conditions expected to minimize its contributions: community monopolization occurred even when dispersal rates are relatively high, landscapes are made up of repeated habitats, and pre-adapted species are available to outcompete a maladapted species for every habitat. Monopolization effects occurred less often in two models that investigated the interaction between evolution and species sorting under varying degrees of temporal variation in selection (de Mazancourt et al. 2008, Loeuille and Leibold 2008). These models use much stronger selection ($\omega \leq 0.1$) without compensating with increased generation of genetic variance such that little standing genetic variation existed and genotypes that only slightly diverted from the optimum had very low fitness.

Community monopolization occurs in three steps. First, an initially maladapted species colonizes a new habitat type. Next, the colonist population adapts to the new environment. Lastly, the adapted population dominates the habitat patch despite the immigration of species that were

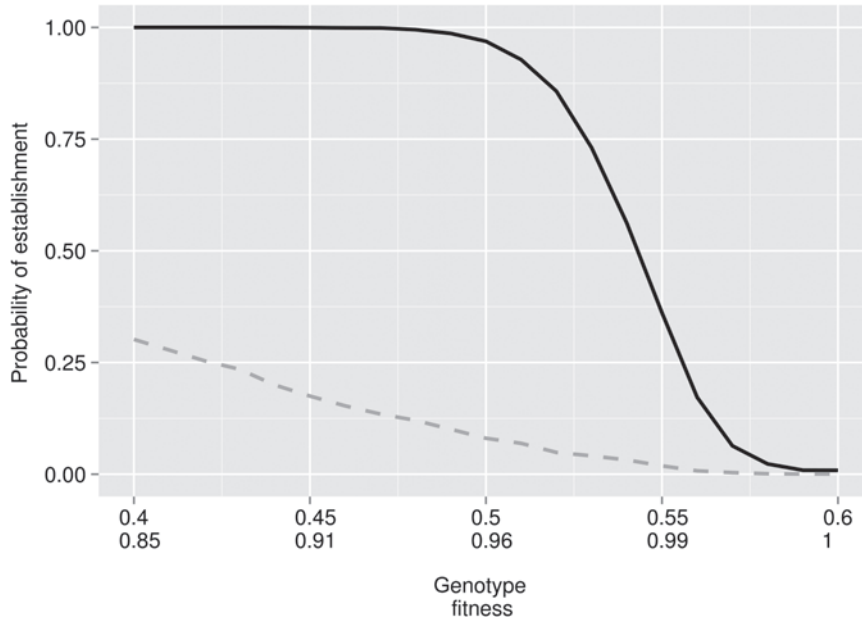


Figure 5. Probability of establishment of a fully pre-adapted asexual immigrant species when arriving in a habitat in which the local population is at carrying capacity. The x-axis represents the genotype/fitness of the resident population (the genotype of the resident population is fixed (no evolution)). Grey line: probability that a pre-adapted immigrant individual reaches a relative contribution in the habitat of 13% or more (i.e. the threshold for dominance of the resident species, equivalent to a habitat diversity of 1.3; Supplementary material Appendix 1) after 50 generations (500 time steps). This line depicts the advantage of an established population over a single pre-adapted immigrant individual on arrival. The result is a function of the numerical advantage of the local population during juvenile establishment (lottery competition between juveniles for space), demographic stochasticity following establishment and the difference in fitness between residents and immigrant (x-axis). Black line: probability that a pre-adapted immigrant species reaches a relative contribution in the habitat of 13% or more after 50 generations (500 time steps) when immigrant dispersal is 1 individual per generation. This line depicts the advantage of an established population over a pre-adapted species, accounting for recurrent immigration.

pre-adapted to the habitat. Monopolization effects thus require that a species has a sufficient colonization rate, evolutionary rate, and competitive ability against immigrants. Even a small dispersal rate is sufficient in our model for colonization to occur. Adaptation depends on standing genetic variation, mutation rates and gene flow. Hence, the second stage of monopolization that requires rapid local adaptation suggests a link to classic theory on migration-selection balance (Haldane 1930, Wright 1931) and the evolution of ranges (Kirkpatrick and Barton 1997). Selection must be sufficient to overcome gene flow from more abundant source populations that would otherwise swamp local adaptation in marginal habitats. To some degree, monopolization is controlled by the capacity for local adaptation in the face of gene flow. However, the monopolization effect is also strongly enhanced by the third ecological step, which relates to the degree to which a resident can resist invasion by competing species. An important mechanism underlying the resident's ability to dominate a patch is the ability to monopolize resources. In our model, we assume lottery competition for limited space, which strongly reduces the probability that a pre-adapted immigrant can establish as the local resident becomes better adapted (Fig. 5). When an immigrant arrives, it must compete with the locally produced offspring for the available (empty) microsites. If the resident population is near carrying capacity, the immigrant has a strong numerical disadvantage. As a result, if the local population is fully adapted to the habitat, the probability of successful establishment of a pre-adapted species becomes

almost zero even at relatively high dispersal rates (Fig. 5). In our model, we use overlapping generations, resulting in pre-emptive competition for available space. Whereas pre-emptive competition (Amarasekare 2003, Calcagno et al. 2006) will reduce the establishment success of immigrants, it is not a prerequisite for successful monopolization. We compare our results for populations with overlapping generations to results for annual populations for which there is no pre-emptive competition (Supplementary material Appendix 3). In doing so, we standardize for the number of dispersing individuals per generation and for per capita establishment success of juveniles. Absolute dispersal ($Disp$) and per capita establishment success determine the head start of early colonists over later immigrants and their numerical advantage, respectively. In annual populations, strong numerical effects still occur, resulting in similar patterns of monopolization (Supplementary material Appendix 3, Fig. A2). Hence, monopolization effects might be widespread in nature wherever competition or numerical effects reduce immigrant establishment success and populations can rapidly adapt to new environments.

The most important factor determining the degree to which ecological or evolutionary processes dominate in our model is dispersal among patches. The absolute number of dispersers per generation (Im_q) determines the rate of exchange of individuals between habitats and thus the time given to an early colonizer, once established, to grow to carrying capacity and adapt to the local conditions before a pre-adapted immigrant arrives. As dispersal decreases among

patches, the probability of monopolization increases. Low among-patch dispersal increases the average time available for the first species to adapt before a pre-adapted species arrives. This result leads to the prediction that monopolization will increase as either spatial scales increase or dispersal capacities decrease (Gillespie et al. 2012). At large spatial scales, the incidence of species sorting versus evolution is likely to differ among taxonomic groups that differ in dispersal capacities. For instance, evolution dominates the assembly of poorly dispersing lizards on the Caribbean islands. In this case, a single ancestor colonized each island and then radiated predictably into multiple ecomorphs to fill vacant niches (Losos et al. 1998), with little evidence for species sorting. For better dispersing, wind-carried Hawaiian island spiders, communities are comprised of both ecomorphs originating from the adaptive radiation of a common ancestor and the colonization of other pre-adapted species (Gillespie 2004), suggesting the possible operation of both monopolization effects and species sorting. At the other end of the spectrum, Coyne and Price (2000) showed that the community assembly of birds with high dispersal on island archipelagos occurs mostly via species sorting. These three biogeographical examples illustrate different outcomes in the race between immigration and adaptation that can be related to differences in dispersal capacities between taxonomic groups.

Monopolization effects in our model can occur for dispersal rates as high as 10 migrants per generation. Rates of microevolution in our simulations are between 0.5 and 0.01 haldanes per generation, which falls well within the range of estimated rates of microevolution in the wild (Hendry and Kinnison 1999) (Supplementary material Appendix 2). In addition, Morjan and Rieseberg (2004) estimated that the median gene flow at the scale of the regional landscape was 0.7 and 1.9 migrants per generation for plants and animals, respectively. Considering that gene flow can be 10 times lower than actual dispersal after accounting for establishment and lasting genetic contributions to the new population (Whitlock and McCauley 1999), the resulting regional dispersal is in the range of 5 to 20 migrants per generation, which is in the same order of magnitude in which we observe monopolization effects. Therefore, our results suggest that monopolization effects are not limited to remote islands or biogeographic scales but that community assembly also can depend on local adaptation over much smaller temporal and spatial scales.

Unfortunately, we know of no field study that has documented community monopolization effects at finer metacommunity scales. Such data would be more difficult to collect than for community monopolization on remote islands: whereas phylogenetic analysis can sometimes reveal the history of colonization in adaptive radiations, the genetic signal that would be associated with monopolization in a regional metacommunity would be far more subtle. Monopolization implies the evolution of improved performance or local niche expansion, which requires common garden experiments to detect. And even if detected, it would be difficult to demonstrate that local adaptation caused failure of establishment of the initially better adapted species. However, while detection in the field may be problematic, the phenomenon has been shown in experiments where manipulating the timing of introduction of bacterial

ecomorphs altered the colonization success of subsequent morphs (Fukami et al. 2007). An advantage of only a few generations allowed for rapid evolution of new ecomorphs, which subsequently changed lineage assembly. Although the pattern was called an example of adaptive radiation, the time between colonization events was short enough to apply equally well to adaptation within a metacommunity. Additional experiments have shown that locally adapted genotypes of *Daphnia* from neighboring ponds can affect the establishment success of other species (De Meester et al. 2007), and that the genetic composition of focal plant species can alter the establishment success of competing species (Weltzin et al. 2003, Crutsinger et al. 2008).

Our model considers discrete or ‘patchy’ communities (ponds, islands) with clear boundaries. This is a realistic setting for many habitats, such as ponds and lakes, forest fragments, parks, and nature reserves in an urbanized landscape or a landscape dominated by agriculture or plantations. At a smaller scale, it mimics habitats such as dung, rotten fruit and host individuals for parasite communities. Environmental variation in natural landscapes often will be structured as a number of repeated habitat types at both regional (pelagic/littoral zones (Schluter and McPhail 1992); high- and low-predation stream segments (Reznick et al. 1990)) and biogeographical (e.g. island habitat types, (Losos et al. 1998, Gillespie 2004)) scales. Our model incorporates this natural within-patch heterogeneity in habitat types and uncouples dispersal among four habitats in a patch from dispersal among patches. Natural environments will often be more variable than the four that we assume in our model. Therefore, no single colonizing species will be perfectly adapted to the local conditions, which will further promote monopolization effects in nature. We analyzed a scenario with seven species and habitats types (unpubl.) and found that monopolization effects became more prevalent. Hence, monopolization should become more prevalent in regions with higher environmental heterogeneity.

Our results indicate that for comparable dispersal rates, the number of patches and the number of initially empty patches affect patterns of community assembly and the relative importance of monopolization effects. We observe stronger monopolization effects for more patches and when more of these patches are empty. In both cases, more monopolization effects are associated with more opportunities to colonize new patches. Gamma diversity is higher in larger than in smaller metacommunities, indicating that a larger metacommunity is better buffered against extinction of competing species. Under the biogeographic island scenario (1 occupied patch and 8 empty patches), the monopolization effects were also stronger than under the regional metacommunity scenario (8 occupied patches and 1 empty patch). Yet, even for a low number of patches or low proportion of empty patches, monopolization effects were observed up to levels of 1–10 individuals per generation.

Also mode of reproduction clearly affected the relative importance of evolution. Through recombination of genetic variation, sexual reproduction facilitated rapid evolution in our model. Rates of microevolution early after exposure to a new environment (first 30–40 generations) are indeed higher in sexuals than in asexuals (Supplementary material Appendix 2, Fig. A1B), and sexuals evolve to the optimal

genotype more quickly than asexuals (Supplementary material Appendix 2, Fig. A1A). Although colonization success may be lower in sexuals compared to asexuals because two individuals need to colonize the same habitat simultaneously (an Allee effect), once established, sexually reproducing species can rapidly evolve to levels of adaptation sufficient to prevent pre-adapted species to invade.

Our patterns of community composition also reveal a link to community (Webb et al. 2002, Cavender-Bares et al. 2009, Vamossi et al. 2009) and metacommunity (Leibold et al. 2010) phylogenetics, where relatedness between species is compared to similarity in ecological niche occupancy. Habitat filtering (species sorting) is predicted to result in patterns of phylogenetic clustering whereas adaptive radiation and evolutionary convergence will result in patterns of phylogenetic overdispersion or evenness (Vamossi et al. 2009). Our results suggest that this framework should be extended to the within species level, taking into account trait variance both within and among species in the comparison of ecological traits between populations and communities (Violle et al. 2012). We find that most trait variance can be attributed to species differences when ecological processes dominate community assembly but that an increasing contribution of within species genetic trait variance is associated with increasing importance of evolution and monopolization effects (Fig. 4A). We thus observe a decreasing importance of ecological filtering and increasing importance of historical contingency and adaptive radiation within species with decreasing colonization rates. This shows how monopolization increases the importance of historical colonization in determining phylogenetic overdispersion. This is also exemplified in Fig. 4B, where grouping of habitats occupied by each species is mainly among similar environments on different patches (habitat filtering and phylogenetic clustering) at the highest among patch dispersal but mainly among different environments on the same patches (historical contingency, phylogenetic overdispersion caused by monopolization) at lower among patch dispersal. Monopolization effects thus tend to make species more similar to each other as they expand their niches to match available environments leading to a niche-based process that can eventually lead to a community dominated by more neutral processes (Hubbell 2006). We assume, however, that all species can become equally adapted to each habitat. In real systems, genetic constraints are likely to prevent adaptation to the full range of available niches and thus may still allow for better adapted species to colonize specific niches as has been repeated numerous times on isolated islands (Sax and Gaines 2008). Awareness of the potential effects of microevolution and within species trait variance will be particularly important at scales that allow for direct interactions among species and individuals (the ‘Darwin–Hutchinson zone’, Vamossi et al. 2009). The fact that patterns of phylogenetic evenness become more prominent with smaller taxonomic scales, where competitive interactions among more closely related species are more likely (Vamossi et al. 2009), might indeed reflect that community monopolization effects are not restricted to biogeographical scales but also relevant for regional metacommunities.

In our original model, we did not provide a mechanism of speciation. However, we performed additional simulations allowing for the evolution of reproductive isolation,

independent from the evolution of the ecological trait (a ‘non-magic’ trait (Servedio et al. 2011) modeled by 20 additional bi-allelic loci that determine mating preference; Supplementary material Appendix 4). Even though reproductive isolation did evolve and create new species, we found that it had only minor effects on the relative importance of ecology versus evolution in community assembly (Supplementary material Appendix 4, Fig. A3). In our model we explored how a particular mechanism, competition for limited resources, determines monopolization effects. However, monopolization effects can occur via additional mechanisms. For instance, the evolution of reproductive incompatibilities between resident and colonist species that can hybridize combined with an Allee effect for colonists can result in evolutionary priority effects due to interspecific reproductive interference (Gorman et al. 1971, Case et al. 2005).

Conclusions

We unify disparate views from ecology and evolution developed at both the regional metacommunity and biogeographical scales under the general framework of community monopolization. We find clear monopolization effects at dispersal rates of 10 migrants per generation or less, a level that corresponds to the median dispersal values found in nature (Morjan and Rieseberg 2004). Overall, we find a strong role for eco-evolutionary feedbacks between local adaptive divergence among different environments and community assembly across a wide range of spatial scales. In many cases, the community patterns that we observe in nature might result from an ongoing race between the immigration of pre-adapted migrants and the adaptive evolution of initially less well-adapted colonists. We thus advocate the need to understand the role of genetic variance within species and evolution during community assembly at both regional and biogeographical scales.

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Supplementary material (Appendix ECOG-01394 at <www.ecography.org/readers/appendix>). Appendix 1–5.