

Ecography

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Supplementary material

Appendix 1: Additional information on methods

Detailed specification of reproduction and dispersal dynamics in the model

We create a set of habitats that are inhabited by species competing for available space. Habitats are organized into larger patches, with each patch containing a set of habitats that differ in environment. Our landscape consists of multiple patches each with the same distinct set of habitats. Our metacommunity consists of $s = 4$ species, each adapted to one of $habs = 4$ mean habitat types. Habitats are linked by dispersal of individuals from all species present. All species have discrete reproduction, overlapping generations and newborn dispersal. Within each habitat, individuals compete via a lottery for one of n microsites that each can host one individual. Newborns can only establish in a microsite when the resident individual dies and the microsite becomes empty (pre-emptive competition). Survival of resident individuals is determined by the match between their phenotype z and the microsite environment e_m (see main document).

Following survival, individuals in each habitat will reproduce and a proportion m of the newborns will disperse. The number of offspring individuals I produced in each habitat is

$$I_{ph} = bN_{f,ph} \quad (1)$$

where b is the per capita birth rate, and $N_{f,ph}$ is the number of female individuals in habitat h in patch p . We assume different dispersal levels among patches and among habitats within patches, controlled by dispersal rates m_{among} and m_{within} , respectively. The expected number of emigrants (offspring leaving a habitat) per generation is given by

$$Disp_{ph,q} = I_{ph}m_q \quad (2)$$

Where q denotes within or among patch dispersal and m_q is the fixed dispersal rate per generation and one generation consists of 10 simulated time steps of mortality and reproduction.

More precisely, combining reproduction and dispersal, the number of offspring O_{ph} to be assigned to each habitat h in each patch p of the metacommunity is calculated as

$$O_{ph} = \sum_{1..i} \sum_{1..j} I_{ij} \cdot P_{(ij \rightarrow ph)} \quad (3)$$

where I_{ij} is the number offspring individuals produced in habitat j in patch i and $P_{(ij \rightarrow ph)}$ is the probability for individuals in habitat ij of parenting offspring in habitat ph . If habitat ij and ph are different habitats on the same patch, $P_{(ij \rightarrow ph)}$ is a function of m_{within} and if habitat ij and ph are on different patches, $P_{(ij \rightarrow ph)}$ is a function of m_{among} . Each time step, we draw the actual values of $P_{(ij \rightarrow ph)}$ from a random **Beta distribution** with mean $e_{P(ij \rightarrow ph)}$ and standard deviation $\sigma_P = 10^{-8}$. If habitat ij is in a different patch than habitat ph , the expected parental contribution from habitat ij , $e_{P(ij \rightarrow ph)}$, equals $m_{among}/(habs * (total\ number\ of\ patches - 1))$. If habitat ij and ph are different habitats in the same patch, $e_{P(ij \rightarrow ph)}$ equals $m_{within}/(habs - 1)$, if habitat ij and ph are the same $e_{P(ij \rightarrow ph)}$ equals $(1 - m_{among} - m_{within})$. The use of actual dispersal rates drawn from a random Beta distribution allows for clustered dispersal. This assumption facilitates joint dispersal of individuals and reduces the incidence of Allee effects in the case of sexual reproduction, where at least two individuals must colonize a new habitat simultaneously to be successful. The parameter σ_P is chosen such that the effects of clustered dispersal are mainly expressed at the lowest levels of dispersal and are negligible at higher levels of dispersal.

If the number of offspring O_{ph} is larger than the number of empty microsites in habitat ph , the number of offspring that effectively establish is truncated to the number of empty microsites (lottery competition). For each offspring that successfully establishes in habitat ph , the parents (parent pairs for sexual reproduction) are randomly drawn from the entire metapopulation (all individuals of the same species in the entire metacommunity) with replacement, based on the probabilities:

$$\frac{I_{ij} \cdot P(ij \rightarrow ph)}{\sum_{1..k} \sum_{1..l} I_{kl} \cdot P(kl \rightarrow ph)} \quad (4)$$

for each habitat j in patch i .

As mentioned in the main document, we evaluate results in the context of the absolute number of dispersing juveniles. Levels of m_{within} and m_{among} are thus set depending on the carrying capacity (= number of microsites n in a habitat), to standardize levels of $Disp_q$ across simulations.

Generation of the initial species and genetic composition in the initially occupied patches

At $t = 0$, s species occupy their optimal habitat in the initially occupied patches (*occ*; see Fig. 1) at carrying capacity. Genotypes of all individuals in an occupied habitat are created such that in each environment e both alleles are set to 1 in $e \cdot 10$ diploid loci and both alleles are set to 0 in $(1 - e) \cdot 10$ diploid loci. In all individuals, the same loci are set to 1, except for two loci. For these two loci, half of the population has one locus (= two alleles) set to 1 and the other half has the other locus set to one. The same set of loci is used in all initially occupied habitats with identical environment e . During the first 25 time steps of each simulation, no dispersal is allowed between habitats or patches. During this period sexual reproduction will generate the initial standing genetic variation by recombining the alleles at the two loci that are not initially fixed in the population. During the next 25 time steps ($t = 26$ to 50), dispersal is allowed between habitats within patches, but not among patches. This process sets the initial species distribution within the occupied patches prior to the colonization of the initially empty patches. During this initial phase without dispersal among patches ($t = 0$ to 50), asexual species are set to reproduce as sexual species, to create identical initial standing genetic variance and species distribution as in

scenarios with sexual reproduction. From $t = 51$, when colonization of initially empty patches is allowed, all species become asexual in scenarios with asexual reproduction.

Note that because there is no mechanism to actively maintain standing genetic variation in the populations (except for mutation), this genetic variation is transient and erodes during the course of the simulations. Given that standing genetic variation is mainly important, however, at high dispersal rates where a rapid evolutionary response is necessary before a better pre-adapted competitor arrives, the slow erosion of standing genetic variation does not affect our results significantly, as all habitats and patches are colonized before standing genetic variation is eroded (see Supplementary material Appendix 5, Movie A1).

Calculation of generation time

Generation time is calculated as (Gotelli 2008):

$$Generation\ time = \frac{\sum l_x b_x x}{\sum l_x b_x}$$

with l_x indicating the survival probability until time step x from birth and b_x indicating the realized per capita birth rate at time step x from birth. We calculated generation time under assumption of a stable population at carrying capacity (no population growth or decline) where $l_x = S^x$ (with S being the survival probability during each time step for an individual) and $\sum l_x b_x = 1$. For a fully adapted population, $b_x = 0.11$ and $S = 0.9$ and the generation time equals 10 time steps. Given that populations will be close to their genetic optimum at equilibrium, this is the generation time we used for expressing dispersal (*Disp*). For individuals that are one mutational step away from the optimum genotype, $b_x = 0.17$ and $S = 0.86$ and the generation time equals 7

time steps. This is the generation time we used for calculating evolutionary rates (Supplementary material, Appendix 2).

Analysis of results

In all of the analyses, the initially occupied patches are excluded, and we focus on the species composition in the initially empty patches. Based on the abundances 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 in each habitat, patch and global metacommunity as the inverse of the Simpson index of species concentration. Using the diversity indices at these three levels (averaged over habitats within each patch for habitat diversity) we classified simulations in categories associated with different mechanisms of community assembly (Table A2). We made a distinction between the following mechanisms of assembly: Species Sorting, Mass Effects, Habitat Monopolization, Patch Monopolization and Global Monopolization.

To decide which of the five community assembly mechanisms characterizes each colonized patch, we used a decision table based on habitat diversity, patch diversity and global diversity for each patch and for each run (Table A1). The decision table relies on two critical values $c_1 = 1.3$ and $c_2 = 1$. c_1 is used to determine whether a habitat, patch or metacommunity is dominated by one species ($\text{diversity} \leq c_1$), and is used, for example, to make the distinction between mass effects ($\text{habitat diversity} > c_1$) and other mechanisms ($\text{habitat diversity} \leq c_1$); c_2 is used to assess whether diversity in colonized patches (col) is reduced compared to initially occupied patches (occ) and to determine whether habitat monopolization occurs ($\text{diversity occupied} - \text{diversity colonized} \geq c_2$). The value of c_1 is chosen such that a dominant species has at least a proportion of 0.9 in 95% of the cases. The value of c_2 is set to one unit of diversity

(measured as inverse of the Simpson index of species concentration). Based on this decision table, we calculated for each simulation run the proportion of patches characterized by each community assembly mechanism, and determined for each combination of parameter settings which is the dominant mechanism. Any reductions in species diversity in the initially occupied populations are taken into account in our assessment of mechanisms of community composition as the species diversity in the colonized populations is always compared to the diversity in the initially occupied populations at the end of the simulations.

Literature Cited

- Gotelli, N. 2008. *A primer of ecology* (4th éd.). — Sunderland, MA: Sinauer Associates
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. — *Ecol. Lett.* 7: 601-613.
- Loeuille, N. and Leibold, M. A. 2008. Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. — *Am. Nat.* 171: 788-799.

Table A1: Decision scheme for the levels of habitat, patch and global species diversity associated with each of the six mechanisms of community assembly.

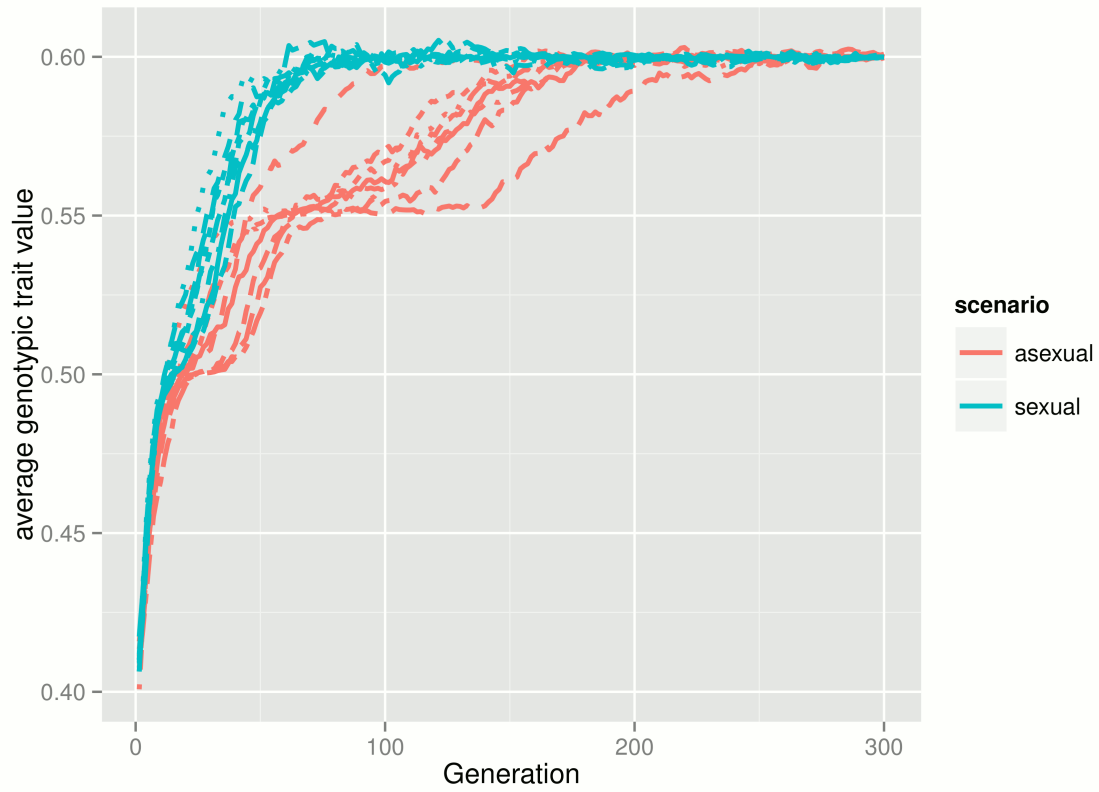
Mass effects (= source-sink dynamics) and species sorting (= dominance of a pre-adapted species) are defined according to Leibold et al. (2004). Monopolization effects refer to evolution-mediated priority effects. See main text for definitions of Habitat, Patch and Global monopolization. Global monopolization (Loeuille and Leibold 2008) is only relevant in the island scenario. D_{col} : diversity in habitats or patches that were empty at the start of the simulation run and have been colonized; D_{occ} : average diversity in the initially occupied habitats or patch(es) at the end of the simulation run; $c_1 = 1.3$; $c_2 = 1$.

	Mass effects	Species sorting	Habitat monopolization	Patch monopolization	Global monopolization
Habitat diversity	$D_{\text{col}} > c_1$	$D_{\text{col}} \leq c_1$	$D_{\text{col}} \leq c_1$	$D_{\text{col}} \leq c_1$	$D_{\text{col}} \leq c_1$
Patch diversity	$D_{\text{occ}} - D_{\text{col}} < c_2$	$D_{\text{occ}} - D_{\text{col}} < c_2$	$D_{\text{col}} > c_1$ & $D_{\text{occ}} - D_{\text{col}} \geq c_2$	$D_{\text{col}} \leq c_1$	$D_{\text{col}} \leq c_1$
Global diversity			$D_{\text{col}} > c_1$	$D_{\text{col}} > c_1$	$D_{\text{col}} \leq c_1$

Appendix 2: Evolutionary rates

Evolutionary rates were calculated in steps of 10 generations, taking a generation time of 7 time steps of mortality and reproduction (see Supplementary material Appendix 1). Given an initially non-adapted population, we compare evolutionary rates for an asexual species and a sexual species. To exclude variability associated with gene flow, low population sizes or source-sink dynamics, we simulated populations in isolation and at carrying capacity ($n = 1000$) and started with a difference of 0.2 between mean genotypic trait value ($g = 0.4$) and mean environment e ($e = 0.6$). For each setting we ran 8 replicate runs. We express evolutionary rates as haldanes according to Hendry and Kinnison (1999).

A



B

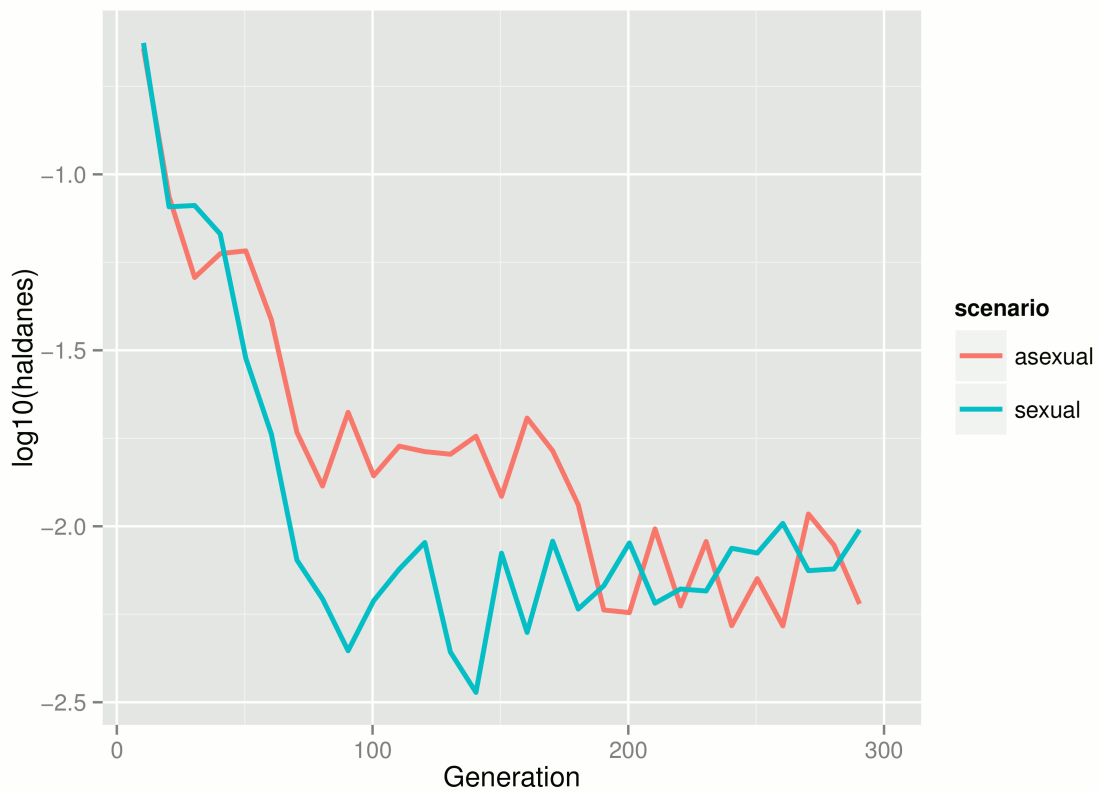


Figure A1

Rates of evolution in an asexual population (red lines) and a sexual population (blue lines). **(A)** Mean genotypic trait value over generations in each replicate population. **(B)** Evolutionary rates (haldanes) over generations, averaged over replicate populations.

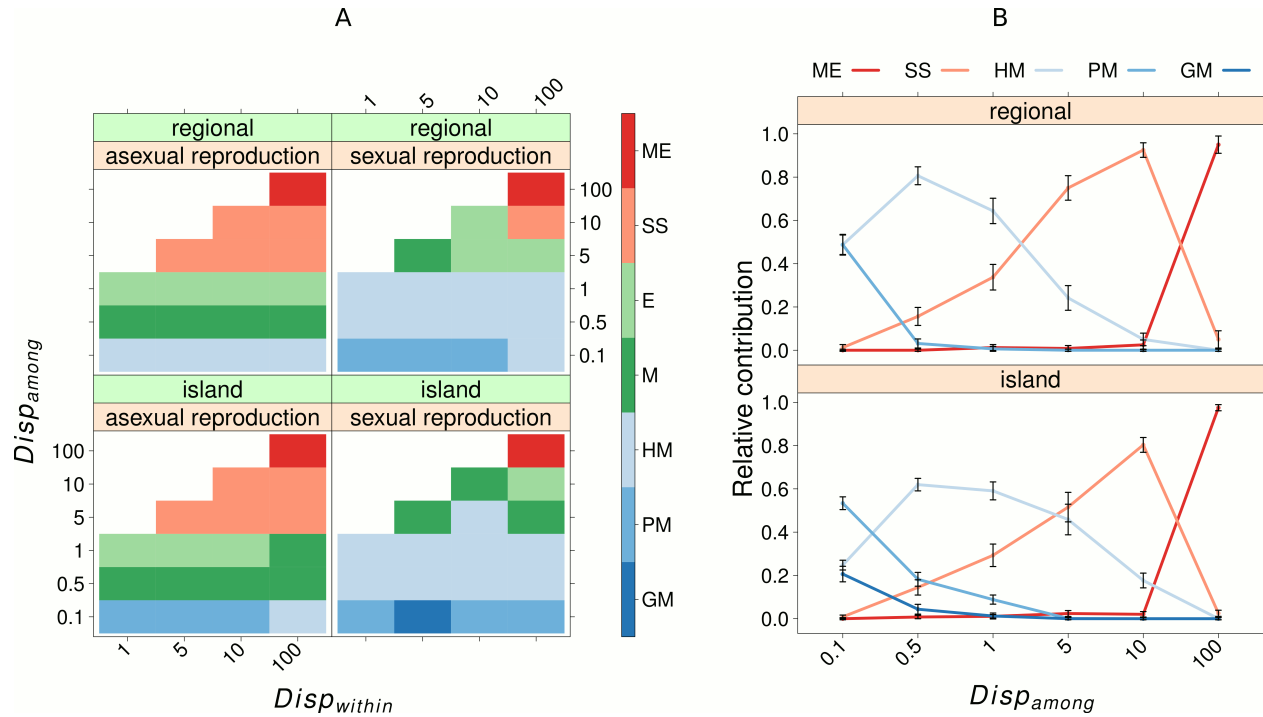
Appendix 3: Annual populations

We ran simulations for annual populations for the scenarios of varying initial patch occupancy to understand the degree to which pre-emptive competition in the baseline model with overlapping generations affected our results. In the setup for annual populations, species have no overlapping generations. Selection acts on juvenile survival to adulthood (S , see equation (1) in main document), prior to reproduction. In contrast to the setup with overlapping generations, all surviving individuals die after reproduction, and all n microsites in a habitat are available for establishment of the juveniles. Otherwise, the specifications of the model are the same as for populations with overlapping generations.

Because all individuals die after reproduction, generation time is one time step compared to 10 time steps for populations with overlapping generations. We set up our simulations such that the actual number of dispersers per generation $Disp_q$ is the same as for populations with overlapping generations (which means that dispersal per time step is ten times higher). In addition, to make the ratio of the number of available (empty) microsites for juvenile establishment over the local offspring pool I_{ph} comparable between annual populations and populations with overlapping generations, we increased the per female birth rate ($b = 5$ for asexuals and 10 for sexuals in annual populations). This ratio determines the establishment success of individual offspring in the habitat. Absolute dispersal rate ($Disp$) and per capita establishment success of juveniles determine the head start of early colonists over later immigrants and their numerical advantage, respectively. By standardizing the parameter settings in relation to absolute dispersal and establishment success, we make sure that the results for annual populations are comparable with the results for populations with overlapping generations.

Fig. A2 shows that the relative importance of ecology versus evolution in annual populations is comparable to populations with overlapping generations (Fig. 3) with respect to

levels of dispersal, scenario initial patch occupancy and mode of reproduction. Only at the highest level of dispersal within patches ($Disp_{within} = 100$) and dispersal among patches ($Disp_{among} = 100$), we observe a higher importance of mass effects compared to populations with overlapping generations.

**Figure A2**

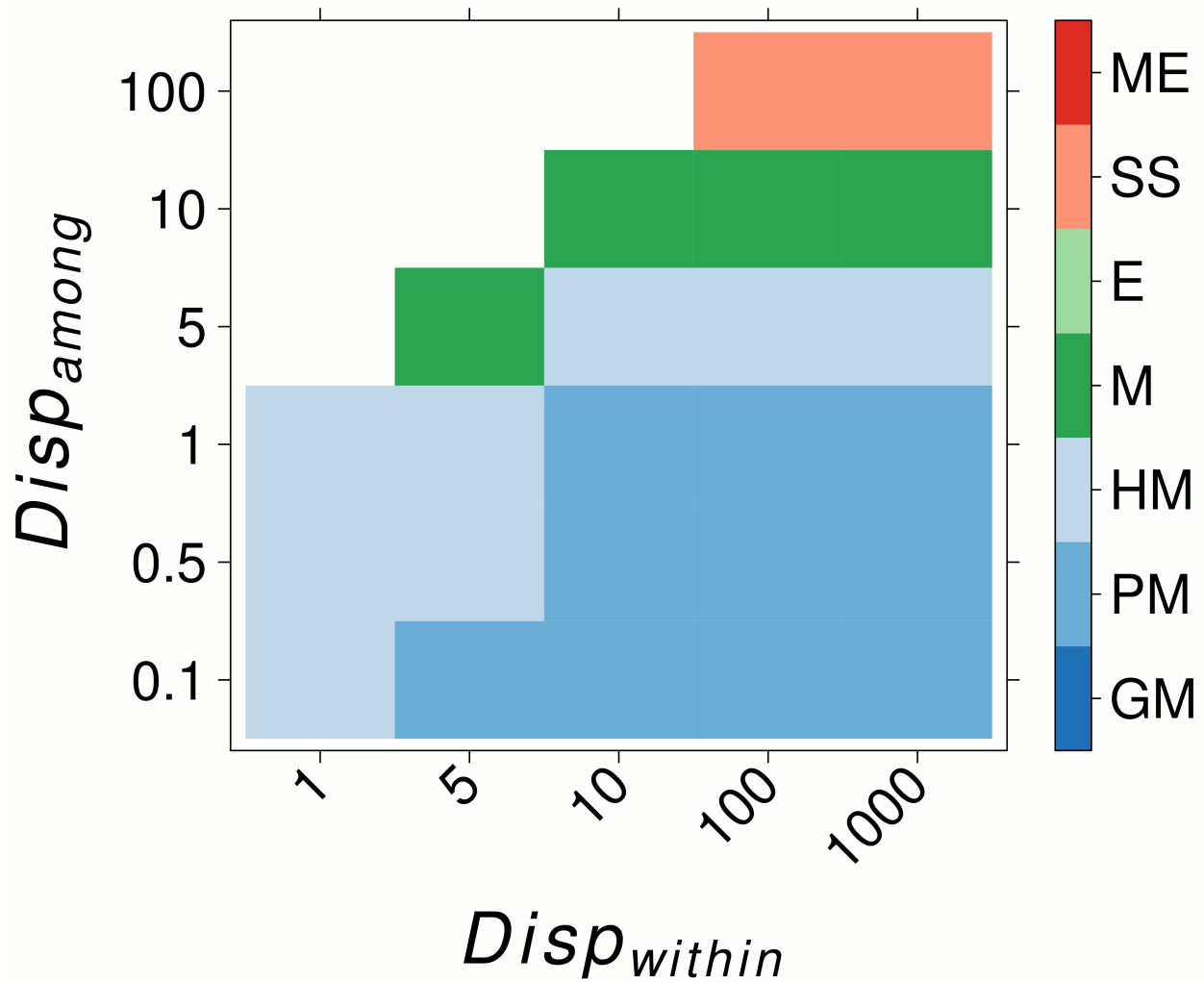
Mechanisms of community assembly in annual populations in relation to dispersal rates, initial patch occupancy and mode of reproduction. regional = scenario of initial patch occupancy with 8 initially occupied patches and one initially empty patch; island = 1 initially occupied patch and 8 initially 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 $Disp_{within}$.

Note that $Disp_{within} = 1000$ is not included as this level of dispersal is not applicable for annual population with number of microsites $n = 1000$.

Appendix 4: Reproductive isolation

To allow for the potential evolution of reproductive isolation within a species, we included an additional 20 bi-allelic additive genes that code for mating preference (ranging from 0 to 1) independent of the fitness of the individuals (non-magic trait). An individual thus has a mating preference phenotype z_{mp} that consists of the genetic component and random non-genetic contribution according to a Gaussian distribution (mean = 0, standard deviation σ_z ; i.e. same distribution as for the fitness related phenotype). During sexual reproduction, individuals are randomly paired within (original) species and habitats while taking into account similarity in mating preference phenotype. More specifically, within each species and habitat individuals are sorted according to z_{mp} and adjacent individuals in the sorted list are paired. To allow for some degree of mismatch in mating preference between each round of sexual reproduction, a small amount of random variation is each time added to z_{mp} before sorting. This variation is drawn from a random uniform distribution with range $[0, u]$ where u is set to 0.1. Mutation rate for mating preference genes is set the same as for fitness genes ($\mu = 10^{-4}$). At the start of the simulations, all individuals within a species are characterized by the same mating preference genotype ($g_{mp} = 0.5$). Reproductive isolation within a species will arise when subpopulations appear that evolve different mating preferences.

**Figure A3**

Mechanisms of community assembly in a sexual species when including evolution of reproductive isolation in the biogeographical island configuration (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. 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.

Appendix 5: Example movie of a simulation showing community assembly dynamics through time

The configuration in the movie consists of 9 patches (grid of 3 by 3 patches) with 4 distinct environments within each patch. Each patch is represented by a graph consisting of 3 parts. The upper part (shades of blue) represents the niche in each environment (see also Fig. 1 in main article). Within patches, each environment has a different niche along a niche gradient, but the niche gradients are replicated among patches. The middle part represents the individuals occupying microsites within each environment (1000 horizontal lines). The colors (green-yellow-orange-red) represent the species to which an individual belongs. If the microsite is empty it is colored blue. The lower part represents a histogram of the genotype frequency distribution for each species within the patch (axis scale ranging from zero to one).

Movie Caption**Movie A1: Example of community assembly dynamics through time**

The simulation represents the ‘biogeographical island’ scenario with one initially occupied patch and 8 initially empty patches. The squares represent the different patches with four distinct habitats (shades of blue) and four distinct species (green-yellow-orange-red). The histogram represents the genotype frequency distribution for each species within the patch (axis scale ranging from zero to one). Dispersal levels are set at $Disp_{within} = 10$ and $Disp_{among} = 1$ and mode of reproduction is asexual. Total duration of the simulation equals 1500 timesteps = 150 generations. The first 50 timesteps, no dispersal among patches (and thus no colonization) is allowed to stabilize initial dynamics within the occupied patch.