

Supplementary material

**Emergent properties of urban landscapes
shape urban eco-evolutionary dynamics -
Proof of concept**

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1 Model and Methods

The purpose of this model is to provide insights into how landscape connectivity and heterogeneity affect eco-evolutionary dynamics, and vice versa, in mutualistic metacommunities. To this end, we used the non-spatial, eco-evolutionary plant-pollinator model by Weinbach et al., 2022 as a starting point. Using this specific model offered at least three key advantages: (1) all model assumptions are very general and might hence apply to a broad range of different systems, (2) the original, non-spatial model is relatively simple, meaning that the additional effect of spatial complexity is relatively easy to disentangle from eco-evolutionary effects and (3) the eco-evolutionary feedback in the original model is not only well understood from a conceptual point of view, but also quantifiable, e.g. by comparing extinction time points with or without evolution (as done by Weyerer et al., 2023). We extended this non-spatial model version to form eco-evolutionary metacommunities, where pollinators can migrate between patches, following the migration rules introduced by Ryser, Häussler, et al., 2019. Using our metacommunity model, we demonstrate that emergent properties of urban landscapes (such as specific patterns in connectivity and heterogeneity) can modulate local eco-evolutionary dynamics, and vice versa.

1.1 Model description

An overview of the model variables and parameters is given in Tab. S1. Model implementation and analysis were carried out in Python (version 3.8.8). All relevant scripts, notebooks and data are available on GitHub (<https://github.com/palmer-ma/Spatial-eco-evo>).

Table S1: Overview of model variables (top) and ecological parameters (bottom).

Variable / Parameter	Meaning	Unit	Standard value / Range
P_i	plant population density on habitat i	$\frac{\text{plants}}{\text{area}}$ or $\frac{\text{plants}}{\text{volume}}$	-
A_i	pollinator population density on habitat i	$\frac{\text{pollin.}}{\text{area}}$ or $\frac{\text{pollin.}}{\text{volume}}$	-
f	overall migration success	-	-
C	landscape connectance	-	-
r_P	intrinsic plant growth rate coefficient	1/t	-
r_A	net pollinator growth rate coefficient	1/t	-
c_P	intraspecific competition strength of plant	$\frac{1}{i\text{-plant density}}$	1
c_A	intraspecific competition strength of pollinator	$\frac{1}{i\text{-pollinator density}}$	1
α	plant attractiveness	-	-
γ_A	interaction benefit provided to the plant by the pollinator	$\frac{1}{i\text{-pollinator density}}$	0.2
γ_P	interaction benefit provided to the pollinator by the plant	$\frac{1}{i\text{-plant density}}$	1
s	form factor of the trade-off function	-	2.5
δ_{ij}	distance between habitat i and habitat j	length unit	-
δ_{max}	maximum dispersal distance the pollinators can move	length unit	[0,1]
d	dispersal rate	1/t	0.2
K_i	plant carrying capacity of habitat i	$\frac{\text{plants}}{\text{area}}$ or $\frac{\text{plants}}{\text{volume}}$	-
h	degree of heterogeneity	-	[0,2]
$\Delta_{max}\alpha$	maximum mutation step size	-	0.02
$r_{A,change}$	change of r_A per time step	1/t	$-8 \cdot 10^{-6}$

1.1.1 Local population dynamics

The local population dynamics were adopted from the model by Weinbach et al., 2022. Their dynamical system describes the dynamics of two mutualistically interacting populations. The populations are considered to be a plant population with biomass density P and a pollinator population with biomass density A , but the model could also represent other types of mutualism:

$$\begin{aligned}\frac{dP}{dt} &= r_P \cdot P - c_P \cdot P^2 + \alpha \cdot \gamma_A \cdot A \cdot P \\ \frac{dA}{dt} &= r_A \cdot A - c_A \cdot A^2 + \alpha \cdot \gamma_P \cdot A \cdot P\end{aligned}\tag{1}$$

Both populations grow logistically, with growth rate coefficients r_P and r_A , and are limited through intraspecific competition with the competition strengths c_P and c_A , respectively. r_P is defined to be an intrinsic, positive growth rate coefficient, representing for example vegetative reproduction. r_A is defined as a net pollinator growth rate coefficient including intrinsic growth (e.g. using other food sources) but also a mortality rate. Therefore, this parameter can take positive or negative values. Note that negative pollinator growth rates ($r_A < 0$) do not automatically lead to pollinator extinction but simply describe a scenario where pollinators depend on the plant population for their survival. Finally, the last term in equation 1.1.1 describes the mutualistic interaction, with α representing the plants' investment into the interaction. It can be interpreted as the attractiveness of the plants for pollinators and determines the strength of the interaction. γ_A represents the benefit the pollinators provide for the plants, i.e. the pollination service, and γ_P the benefit the plants provide for the pollinators, i.e. the energetic gain from nectar and pollen.

1.1.2 Landscapes

Spatial landscapes were set up as random geometric graphs, following the approach of Ryser, Häussler, et al., 2019: N habitat patches were placed by randomly drawing their x- and y-coordinates from uniform distributions between 0 and 1. In this way, we generated spatially explicit landscapes with fragmented structure, consisting of discrete habitat patches (e.g. gardens in a city) located in a hostile matrix (e.g. of impervious surfaces). From the x- and y-coordinates of the habitat patches, we calculated for each landscape a $N \times N$ landscape matrix containing the distances between the habitat patches:

$$\delta = \begin{pmatrix} 0 & \delta_{12} & \delta_{13} & \dots \\ \delta_{21} & 0 & \delta_{23} & \dots \\ \delta_{31} & \delta_{32} & 0 & \dots \\ \vdots & \vdots & \vdots & \ddots \delta_{NN} \end{pmatrix}\tag{2}$$

Each matrix element δ_{ij} represents the distance between two habitat patches i and j .

1.1.3 Dispersal dynamics

On each habitat i a local plant - pollinator community is represented via the dynamical system given in eq. 1.1.1 (see Fig. 3 in the main manuscript). In order to create a metacommunity,

the local communities are connected through dynamic pollinator dispersal. Again following the approach of Ryser, Häussler, et al., 2019, we added an emigration term E_i and an immigration term I_i to the pollinator equation. Thus, the overall population dynamics on a focal habitat patch i are given by:

$$\begin{aligned}\frac{dP_i}{dt} &= r_P \cdot P_i - c_P \cdot P_i^2 + \alpha \cdot \gamma_A \cdot A_i \cdot P_i \\ \frac{dA_i}{dt} &= r_A \cdot A_i - c_A \cdot A_i^2 + \alpha \cdot \gamma_P \cdot A_i \cdot P_i - E_i + I_i\end{aligned}\quad (3)$$

The emigration E_i from habitat i is defined as

$$E_i = dA_i \quad (4)$$

with d representing the dispersal rate that describes which fraction of the pollinator population leaves a patch. For the sake of simplicity, we set d as a fixed value for all habitats. The immigration I_i to habitat i is defined as

$$I_i = \sum_{j \in N_j} dA_j \cdot \max(1 - \delta_{max,ij}; 0) \cdot \frac{\max(1 - \delta_{max,ij}; 0)}{\sum_{k \in N_k} \max(1 - \delta_{max,jk}; 0)} \quad (5)$$

N_j and N_k are the sets of habitat patches directly connected through dispersal links to habitat i or habitat j , respectively. The immigration is determined by the amount of pollinators emigrating from the source habitats j ($dA_j = E_j$), as well as by the relation between habitat distances δ_{ij} and the maximum dispersal distance δ_{max} pollinators can move, written as:

$$\delta_{max,ij} = \frac{\delta_{ij}}{\delta_{max}}$$

The term $\max(1 - \delta_{max,ij}; 0)$ describes the migration success through the respective link, i.e. which fraction of pollinators moving from source patch j towards target patch i survives the migration process. The migration success decreases linearly with the distance from the source patch, which reflects the assumption that biomass flow is highest between patches with small distances. Note that if $\delta_{ij} \geq \delta_{max}$ the migration success becomes zero, meaning that two habitats i and j are only considered connected if $\delta_{ij} < \delta_{max}$. Additional references concerning the maximum dispersal distance δ_{max} (and how it scales with body mass) can be found in the supplementary material of Ryser, Häussler, et al., 2019. Finally, the last term $\frac{\max(1 - \delta_{max,ij}; 0)}{\sum_{k \in N_k} \max(1 - \delta_{max,jk}; 0)}$ gives the fraction of pollinators leaving patch j that migrate towards patch i . To which neighbor habitats the pollinators preferably move depends on the relative distance of the potential target habitats $k \in N_k$ from the source habitat j . In short, pollinators tend to migrate to nearby patches rather than distant ones.

1.1.4 Connectivity

The first spatial property varied in our study is the connectivity of the landscape (see Fig. 3 in the main manuscript). In the following, we use "connectance" as a proxy for connectivity, which is defined as the fraction of possible links that is realized. Connectance has been widely used

in network theory, e.g. for ecological network analysis (e.g. Dunne et al., 2002) but also for describing spatial connectivity (e.g. Bierwagen, 2007; Spanowicz and Jaeger, 2019; Turner and Gardner, 2015; Lookingbill and Minor, 2017). For spatial networks the connectance is given by:

$$C = \frac{L}{\frac{1}{2}N(N-1)} \quad (6)$$

with L giving the number of realized links.

Note that the connectivity of a landscape can also be considered to be higher if the overall migration success is higher and thus the dispersal loss is lower. In this case, the existing links are strengthened, without necessarily changing the number of links. As this change in connectivity may not always be captured by C alone, we additionally calculated the relative migration success for the whole landscape, i.e. the fraction f of all dispersing pollinators that are able to reach a new habitat:

$$f = \frac{\sum_{i \in N} I_i}{\sum_{i \in N} E_i} \quad (7)$$

We modeled different degrees of landscape connectivity by varying the maximum dispersal distance δ_{max} of the pollinators (see Fig. 3 in the main manuscript). The resulting values for the used connectivity metrics vary between 0 and 1, as shown in Fig. S1. If $\delta_{max} = 0$, each patch is isolated, resulting in connectance $C = 0$ and relative migration success $f = 0$, as all dispersing pollinators will inevitably get lost. On the other hand, if $\delta_{max} > \max(\delta_{ij})$, all patches are connected to all other patches, resulting in connectance $C = 1$. However, the relative migration success would still be smaller than 1, reflecting the fact that some dispersal loss is inevitable. Intermediate values of δ_{max} result in patches being coupled to patches in their close neighborhood, resulting in connectance values $0 < C < 1$ and $0 < f < 1$.

1.1.5 Heterogeneity

To create heterogeneity in the landscapes, different values of plant carrying capacities were assigned to the habitat patches, representing different habitat qualities (see Fig. 3 in the main manuscript). The plant carrying capacity is hidden in the plant competition strength c_P , which can be written alternatively as $\frac{r_P}{K}$. The values of K for the N habitat patches of the landscape were drawn from a uniform distribution and different degrees of heterogeneity were generated by varying the range of this uniform distribution. More precisely, for heterogeneous landscapes with $0 < h \leq 2$, we considered carrying capacities $K_i \in (1 - h/2, 1 + h/2)$ and for completely homogeneous landscapes with $h = 0$ we assigned $K_i = 1$ for all habitats i . Local plant competition strengths $c_{P,i}$ were then defined as $c_{P,i} = \frac{c_P}{K_i}$.

Please note that due to the fact that the K_i -values are drawn randomly within the respective range, the average carrying capacity $\bar{K}$ of the landscape is not fixed at 1 but can, in principle, vary. However, this effect is generally rather small (except for systems with very few patches and very high heterogeneity) and vanishes when averaging over several replicate simulations, as done in the data shown in the main manuscript.

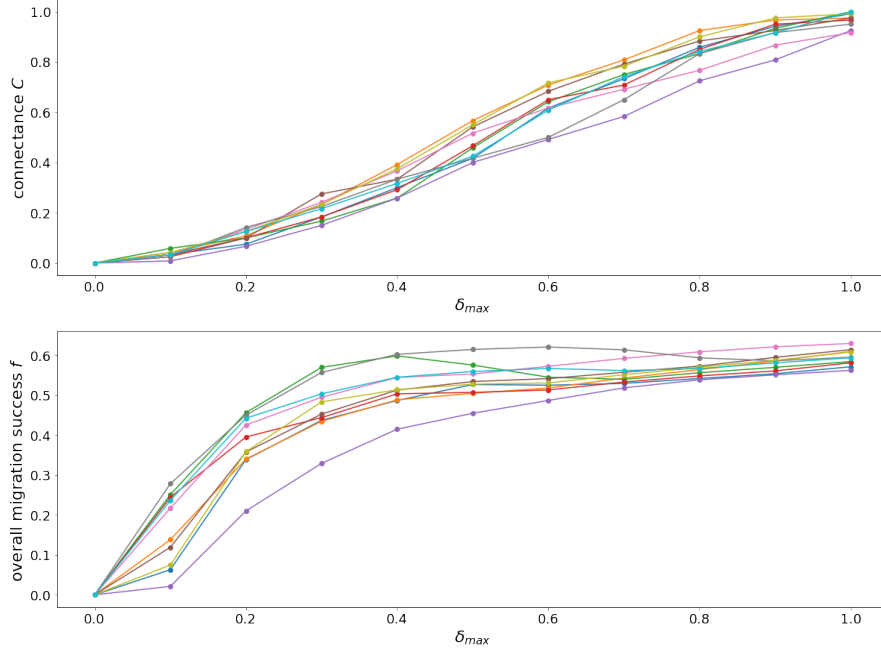


Figure S1: Connectance C and overall migration success f across maximum dispersal distances. For 10 random geometric graphs with $N = 16$. Each color shows one landscape. Values were measured immediately after system initialisation.

1.1.6 Modelling eco-evolutionary dynamics

Exactly as in Weinbach et al., 2022, the plants evolve their attractiveness trait α , following the framework of Adaptive Dynamics (Geritz et al., 1998; Metz et al., 1996). The ecological dynamics are determined by the plant's phenotype and by its ecological conditions, which affect how successful a given phenotype is. The plant attractiveness α is assumed to be in a trade-off with the plants' intrinsic growth rate coefficient r_P :

$$r_P(\alpha) = \left(1 - \left(\frac{\alpha}{\alpha_{max}}\right)^s\right)^{1/s} \quad (8)$$

with α_{max} giving the maximum attractiveness the plants are allowed to have. It is necessary to define such a limit to avoid unrealistic exponential population growth, as explained in more detail in Weinbach et al., 2022 and in section 2.1. If $\alpha = \alpha_{max}$ and hence the attractiveness ratio $\frac{\alpha}{\alpha_{max}} = 1$, the plants' intrinsic growth rate coefficient is $r_P = 0$, i.e. they are completely dependent on the interaction with the pollinator. At the other extreme, when $\alpha = 0$ and $r_P = 1$, the interaction is lost, meaning that plant and pollinator are independent from one another. Finally, the parameter s defines the shape of the trade-off function, with a linear relationship for $s = 1$, a concave one for $s > 1$ and a convex curve for $s < 1$ (see Fig. S2).

Evolution takes place through a repeated addition of mutant plant populations into the resident population, as explained in more detail in the next subsection. The mutant strategy α_m differs

just slightly from the resident strategy α_r and the mutant density P_m is very low compared to the resident density P_r . We assume that each local population on its patch evolves independently from the populations of the other patches. All local populations $P_{r,i}$ and $P_{m,i}$ consequently had their own values for $\alpha_{r,i}$ and $\alpha_{m,i}$. However, in the following we omit the index i , which indicates the patch number, for the sake of readability.

Whether or not a given plant mutant can invade the system depends on its fitness. For very low densities of the mutant population P_m it can be assumed that the resident population is not influenced by the mutant population. The populations are thus considered to have the same densities as if there was no mutant. The relative fitness of the mutant is then given by its per capita growth rate, calculated with the fixed point densities P_r^* and A^* :

$$\begin{aligned}\omega(\alpha_m, \alpha) &= \frac{dP_m}{dt} \frac{1}{P_m} = r_{P_m} - c_P \cdot P_m - c_P \cdot P_r^* + \alpha_m \cdot \gamma_A \cdot A^* \\ &= \left(1 - \left(\frac{\alpha_m}{\alpha_{max}}\right)^s\right)^{1/s} - c_P \cdot P_m - c_P \cdot P_r^* + \alpha_m \cdot \gamma_A \cdot A^*\end{aligned}\quad (9)$$

When $\omega(\alpha_m, \alpha) > 0$, the mutant can invade the system and potentially replace the resident. The system reaches at an evolutionary equilibrium if the selection gradient (defined as the derivative of the fitness function) becomes zero:

$$\frac{\partial \omega(\alpha_m, \alpha)}{\partial \alpha_m} = -\frac{\left(\frac{\hat{\alpha}}{\alpha_{max}}\right)^s \left(1 - \left(\frac{\hat{\alpha}}{\alpha_{max}}\right)^s\right)^{1/s}}{\hat{\alpha} \left(1 - \left(\frac{\hat{\alpha}}{\alpha_{max}}\right)^s\right)} + \gamma_A \cdot A^*(\hat{\alpha}) = 0 \quad (10)$$

Such an evolutionary equilibrium is called an evolutionarily singular strategy (ESS). An ESS is considered convergent stable if it is gradually approached in its neighborhood. Furthermore, it is considered evolutionarily stable if a population at the ESS is not invasible for mutants with a strategy close to the ESS. An ESS that is both convergent stable and evolutionarily stable represents a so-called continuously stable strategy (CSS) (Brännström et al., 2013) and describes a potential evolutionary endpoint. At this point, $\hat{\alpha}$ can be considered the optimum attractiveness strategy. Note that Weinbach et al., 2022 showed that for the given system a CSS exists only for concave trade-offs. Therefore, we chose $s > 1$.

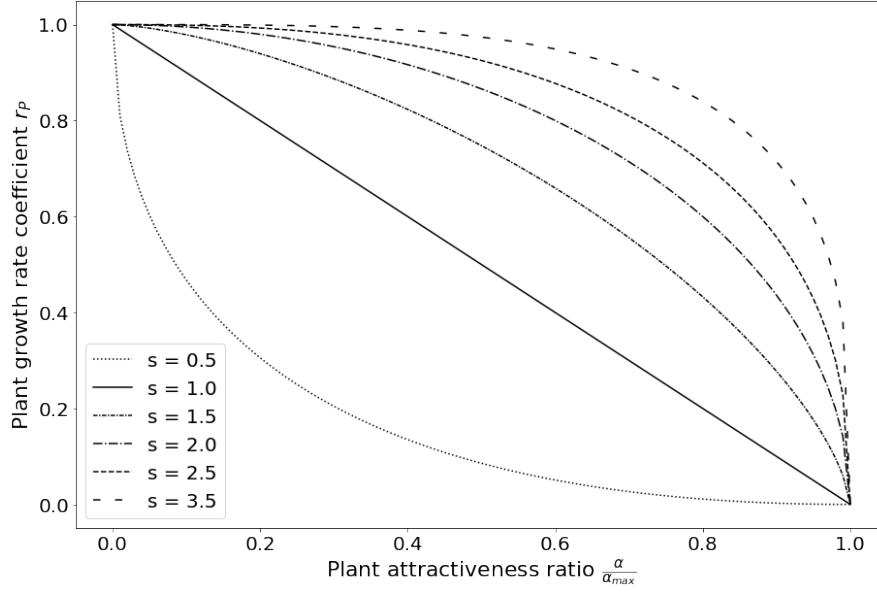


Figure S2: Trade-off shapes. Illustrated is the plant growth rate coefficient r_P depending on the plant attractiveness ratio $\frac{\alpha}{\alpha_{max}}$ for different shape parameters s . For $s > 1$ the trade-off is concave, i.e. a combination of high attractiveness and still relatively high growth rate coefficient is possible, allowing for a best combination somewhere between the extremes.

1.2 Simulating eco-evolutionary dynamics

As our system is too complex to be solved analytically, we analysed the model with the help of numerical simulations. At simulations start, the system is supposed to be at an eco-evolutionary equilibrium with $A_i = A_i^*$, $P_i = P_i^*$ and $\alpha_{r,i} = \hat{\alpha}_i$ for all habitat patches i (the details on the initialisation process are outlined below). During the simulations the net pollinator growth rate coefficient r_A slowly decreased linearly with a rate of $r_{A,change} = -8 \cdot 10^{-6}$ for all pollinator populations, mimicking increasing mortality rate, e.g. due to environmental degradation. At regular time intervals (all $t_{mut} = 20$ time steps), new local plant mutants were introduced with very low density ($P_m = 10^{-6}$). The mutant strategy α_m was set close to the respective local resident strategy α_r , by drawing a random value in the range $\alpha_r \pm \Delta_{max}\alpha$ (with a maximum mutation step size $\Delta_{max}\alpha = 0.02$). The mutants were introduced simultaneously for all habitats i , i.e. one mutant per habitat. As the mutant strategies were drawn separately for the local populations, each local population evolved independently.

To be able to run simulations within a reasonable time span, we accelerated the process by skipping the dynamical replacement of the resident by the mutant. If the mutant's fitness $\omega(\alpha_m, \alpha)$ was positive, the resident strategy α_r was immediately replaced by the mutant strategy α_m . Note that in case of isolated systems, our simulation results are perfectly in line with the analytical results by Weinbach et al., 2022. For more details on the opportunities and constraints of this method see Weyerer et al., 2023, who provide a detailed comparison between the algorithm used

here and a more realistic (but slower) simulation algorithm and demonstrate that results obtained with both versions were generally consistent. For the fitness calculation, we used equation 9, which needs equilibrium densities A^* and P_r^* as input. Given that we do not have analytical expressions for these equilibrium densities (as explained in section 2.1), we instead used the densities resulting from our numerical simulation, as observed at the time point of mutation, as estimates for the equilibrium densities. Simulations were run until all local pollinator populations fell below a defined extinction threshold ($A_{ext} = 0.0001$), i.e. until time t_{ext} of global pollinator extinction.

Note that some authors see an overlap of evolutionary and ecological time scales as a compulsory requirement for the emergence of eco-evolutionary feedback (e.g. Post and Palkovacs, 2009). However, our algorithm is based on the separation of the time scales, in line with classical adaptive dynamics (see Metz et al., 1996; Geritz et al., 1998; Brännström et al., 2013; Govaert et al., 2018). Even if evolution is very fast using the described algorithm, ecology is still much faster than evolution, as the community is assumed to have reached an ecological equilibrium when the next mutant appears. According to Govaert et al., 2018, overlapping time scales are by no means a necessary requirement for eco-evolutionary feedback to occur in the adaptive dynamics framework, which is in line with what several other models using this framework have successfully demonstrated (see for example Weinbach et al., 2022 or Ferriere and Legendre, 2013 and references therein). Eco-evolutionary feedback can still be observed in these models, because the mutant's fitness depends on the ecological conditions in the respective system. The approach used here is thus sufficient for demonstrating that landscape properties can alter eco-evolutionary dynamics.

1.2.1 Initialisation process for simulations

The initialization procedure depends on the results of some analytical investigations, as described in more detail in section 2.1. After setting up the landscape with the respective connectivity and heterogeneity, we first determined α_{max} for all habitat patches, depending on the respective $c_{P,i}$ (see Eq. 16). Given these values, we approximated the optimum value of attractiveness $\hat{\alpha}$ with help of the selection gradient (Eq. 10 with approximated A_i^* , Eq. 14) and set it as resident strategy α_r . This was done by looping through all α -values between 0 and α_{max} (in steps of 0.001), calculating the respective selection gradient, and searching for the α for which the selection gradient was closest to zero. This whole procedure was conducted because Eq. 10 is not analytically solvable for non-linear trade-off shapes. With the approximated $\hat{\alpha}$, we then initialized the populations following Eq. 14 and 15.

Since both $\hat{\alpha}$ and the population densities were just approximately set, we gave the system some time to develop with constant pollinator growth rates, before the actual simulation experiment with decreasing values of pollinator growth rates started, until the true equilibrium was reached. Preliminary results (not shown) suggested that a few hundred time steps are generally sufficient, even when spatial heterogeneity is high, but we nevertheless allowed for 2000 time steps to make sure the system is sufficiently close to the eco-evolutionary equilibrium. As initial pollinator growth rate we chose $r_{A,0} = 0.8$. In completely isolated systems, where immigration is zero, the intrinsic growth term and the emigration loss term in eq. 3 hence add

up to $r_A \cdot A - d \cdot A = (0.8 - 0.2) \cdot A = 0.6 \cdot A$, which corresponds to the starting point of the scenario shown in Fig 4 in Weinbach et al., 2022.

1.2.2 Simulation experiments

We conducted several simulation experiments, which differed in the number N of patches in the landscapes (4, 9, 16 or 25). For each simulation experiment, the following steps were executed:

- We first ran simulations without evolution (no mutation events) for all combinations of connectivity and heterogeneity across defined gradients of both. The heterogeneity was varied in the range $h = [0, 2]$ in steps of 0.2, i.e. across 11 levels. Connectivity was also varied across 11 levels within $\delta_{max} = [0, 1]$, resulting in 121 combinations in total.
- These simulations were then repeated, but now with plant evolution, using the exact same landscapes, i.e. with the same habitat positions and qualities.
- Finally, for each simulation the time of global pollinator extinction t_{ext} was measured and averaged over 10 replicas. The results were visualized as heatmaps (see Fig 4 in the main text) with connectivity on one axis and heterogeneity on the other axis. The color code indicates the extinction time difference against a defined reference scenario $\Delta t = t_{ext} - t_{ext,ref}$, given via isolated ($\delta_{max} = 0$), homogeneous ($h = 0$) systems.

2 Supplementary results

2.1 Coexistence fixed point analysis

Here, we derive the population densities A_i^* and P_i^* at the coexistence fixed point of the dynamical system. For a more concise presentation, the distance dependent terms in the immigration part I_i are written as a function f depending on the maximum dispersal distance δ_{max} and the landscape matrix δ :

$$f(\delta_{max}, \delta) = \max(1 - \delta_{max,ij}; 0) \cdot \frac{\max(1 - \delta_{max,ij}; 0)}{\sum_{k \in N_k} \max(1 - \delta_{max,jk}; 0)}$$

At equilibrium, all differential equations are equal to zero (for all habitats i):

$$\frac{dP_i}{dt} = 0 \quad \text{and} \quad \frac{dA_i}{dt} = 0$$

First, both differential equations are solved for P_i (with $P_i > 0$ and $A_i > 0$):

$$\begin{aligned} \frac{dP_i}{dt} &= r_P \cdot P_i - c_P \cdot P_i^2 + \alpha \cdot \gamma_A \cdot A_i \cdot P_i = 0 \\ P_i(r_P - c_P \cdot P_i + \alpha \cdot \gamma_A \cdot A_i) &= 0 \\ \rightarrow P_i &= \frac{r_P + \alpha \gamma_A A_i}{c_P} \end{aligned} \tag{11}$$

$$\begin{aligned} \frac{dA_i}{dt} &= r_A \cdot A_i - c_A \cdot A_i^2 + \alpha \cdot \gamma_P \cdot A_i \cdot P_i - dA_i + \sum_{j \in N_j} dA_j \cdot f(\delta_{max}, \delta) = 0 \\ A_i(r_A - c_A \cdot A_i + \alpha \cdot \gamma_P \cdot P_i - d + \sum_{j \in N_j} d \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta)) &= 0 \\ \rightarrow P_i &= \frac{-r_A + c_A A_i + d(1 - \sum_{j \in N_j} \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta))}{\alpha \gamma_P} \end{aligned} \tag{12}$$

Set 11 = 12 and solve for A_i :

$$\begin{aligned} \frac{r_P + \alpha\gamma_A A_i}{c_P} &= \frac{-r_A + c_A A_i + d(1 - \sum_{j \in N_j} \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta))}{\alpha\gamma_P} \\ r_P + \alpha\gamma_A A_i &= \frac{-c_P r_A + c_A c_P A_i + d c_P (1 - \sum_{j \in N_j} \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta))}{\alpha\gamma_P} \\ \alpha\gamma_P r_P + \alpha^2 \gamma_A \gamma_P A_i &= -c_P r_A + c_A c_P A_i + d c_P (1 - \sum_{j \in N_j} \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta)) \\ c_A c_P A_i - \alpha^2 \gamma_A \gamma_P A_i &= \alpha\gamma_P r_P + c_P r_A - d c_P (1 - \sum_{j \in N_j} \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta)) \\ A_i (c_A c_P - \alpha^2 \gamma_A \gamma_P) &= \alpha\gamma_P r_P + c_P r_A - d c_P (1 - \sum_{j \in N_j} \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta)) \end{aligned}$$

2.1.1 First solution

Without any assumption about the local pollinator densities:

$$\begin{aligned} A_i (c_A c_P - \alpha^2 \gamma_A \gamma_P) &= \alpha\gamma_P r_P + c_P r_A - d c_P (1 - \sum_{j \in N_j} \frac{A_j}{A_i} \cdot f(\delta_{max}, \delta)) \\ A_i^2 (c_A c_P - \alpha^2 \gamma_A \gamma_P) &= A_i (\alpha\gamma_P r_P + c_P r_A - d c_P) + d c_P \sum_{j \in N_j} A_j \cdot f(\delta_{max}, \delta) \\ 0 &= A_i^2 (c_A c_P - \alpha^2 \gamma_A \gamma_P) - A_i (\alpha\gamma_P r_P + c_P r_A - d c_P) + d c_P \sum_{j \in N_j} A_j \cdot f(\delta_{max}, \delta) \end{aligned}$$

We use the well known formula $x_{1,2} = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$ to solve this quadratic equation, with:

$$a = c_A c_P - \alpha^2 \gamma_A \gamma_P \quad ; \quad b = -(\alpha\gamma_P r_P + c_P r_A - d c_P) \quad ; \quad c = d c_P \sum_{j \in N_j} A_j \cdot f(\delta_{max}, \delta)$$

This results in the fixed point densities:

$$\begin{aligned} A_i^* &= \frac{\alpha\gamma_P r_P + c_P r_A - d c_P + \sqrt{(-\alpha\gamma_P r_P - c_P r_A + d c_P)^2 - 4(c_A c_P - \alpha^2 \gamma_A \gamma_P)(d c_P \sum_{j \in N_j} A_j f(\delta_{max}, \delta))}}{2 \cdot (c_A c_P - \alpha^2 \gamma_A \gamma_P)} \\ P_i^* &= \frac{r_P + \alpha\gamma_A A_i^*}{c_P} \end{aligned} \tag{13}$$

These equations are not very useful to actually calculate the fixed point density, as the densities of all populations depend on each other whenever the habitats are connected.

2.1.2 Second solution

Under the assumption that all local pollinator populations have the same density ($A_j = A_i$), the equations can be simplified to:

$$A_i^* = \frac{\alpha\gamma_P r_P + c_P r_A - d c_P (1 - \sum_{j \in N_j} f(\delta_{max}, \delta))}{c_A c_P - \alpha^2 \gamma_A \gamma_P} \quad (14)$$

Set 14 into 11 and solve for P_i :

$$\begin{aligned} P_i &= \frac{r_P + \alpha\gamma_A A_i^*}{c_P} \\ &= \frac{r_P}{c_P} + \frac{\alpha^2 \gamma_A \gamma_P r_P + \alpha\gamma_A c_P r_A - d\alpha\gamma_A c_P (1 - \sum_{j \in N_j} f(\delta_{max}, \delta))}{c_P (c_A c_P - \alpha^2 \gamma_A \gamma_P)} \\ &= \frac{r_P (c_A c_P - \alpha^2 \gamma_A \gamma_P) + \alpha^2 \gamma_A \gamma_P r_P + \alpha\gamma_A c_P r_A - d\alpha\gamma_A c_P (1 - \sum_{j \in N_j} f(\delta_{max}, \delta))}{c_P (c_A c_P - \alpha^2 \gamma_A \gamma_P)} \\ &= \frac{\alpha\gamma_A c_P r_A + c_A c_P r_P - d\alpha\gamma_A c_P (1 - \sum_{j \in N_j} f(\delta_{max}, \delta))}{c_P (c_A c_P - \alpha^2 \gamma_A \gamma_P)} \\ &= \frac{\alpha\gamma_A r_A + c_A r_P - d\alpha\gamma_A (1 - \sum_{j \in N_j} f(\delta_{max}, \delta))}{c_A c_P - \alpha^2 \gamma_A \gamma_P} \\ &= \frac{\alpha\gamma_A r_A + c_A r_P - d\alpha\gamma_A (1 - \sum_{j \in N_j} f(\delta_{max}, \delta))}{c_A c_P - \alpha^2 \gamma_A \gamma_P} \quad (15) \end{aligned}$$

Note that this assumption is only fulfilled if the following two conditions apply:

1. The landscape is homogeneous, i.e. all habitats i have the same carrying capacity K_i .
2. The habitat patches are distributed in the landscape in a way that all habitats have the same distance to their neighbors and the same number of links.

These conditions may be met for homogeneous, regular rings or grids, completely isolated or 2-patch systems. However, in landscapes generated as random geometric graphs, with connectance $C > 0$, the second condition is never fulfilled. As the distances to the neighbors and the number of links vary between habitats, the dispersal losses are unique for each single habitat, resulting in unique population densities.

Note that without migration ($d = 0$) both expressions, 13 and 14+15, simplify into the equilibrium densities derived for the non-spatial model by Weinbach et al., 2022. As in the non-spatial case, we find that the given coexistence fixed point is only feasible when the denominator is positive, that is if $c_A c_P > \alpha^2 \gamma_A \gamma_P$. Otherwise the benefit from the mutualistic interaction would outweigh the limiting effect of competition and the populations would grow infinitely, as their

growth is not limited by other factors in this model. Hence, the critical level of attractiveness below which the coexistence fixed point is feasible (and stable) is given by:

$$\alpha_{cl} = \sqrt{\frac{c_A c_P}{\gamma_A \gamma_P}} \quad (16)$$

This critical level is exactly the same as for the non-spatial system by Weinbach et al., 2022. As in Weinbach et al., 2022, we limited the plant attractiveness to a maximum of $\alpha_{max} = 0.8 \cdot \alpha_{cl}$. Following the relation $c_P = \frac{r_P}{K}$ and equation 16, the maximum attractiveness α_{max} increases with decreasing habitat quality K_i .

2.2 The underlying mechanisms: Source-sink dynamics and quality-dependent disinvestment speed

2.2.1 Plant response to declining pollinator abundances counteracts positive effect of heterogeneity

To clearly reveal the mechanisms underlying the observed patterns reported in the main text, and especially the reason for the strong reduction of the heterogeneity effect when plant evolution was taken into account, we reduced system complexity and analyzed time series for landscapes with just two patches. For this, we compared perfectly homogeneous with very heterogeneous landscapes, as well as isolated with closely coupled habitats. All four scenarios were simulated once without (Fig. S3) and once with evolution (Fig. S4). In the heterogeneous case one patch had a very high quality ($K = 1.8$) while the other had a very low quality ($K = 0.2$). The patches had a distance of $\delta_{ij} = 0.2$.

We first consider scenarios without evolution, i.e. with constant plant attractiveness values (see Fig. S3). The landscape with isolated and homogeneous patches is the reference scenario (in orange, see Fig. S3, top). The pollinators declined due to increasing mortality until extinction at time $t_{ext,ref}$. For the populations in the heterogeneous landscape the same decline occurred (in blue), but faster on the low-quality patch ($t_{ext} < t_{ext,ref}$), due to lower plant densities, and slower on the high-quality patch ($t_{ext} > t_{ext,ref}$), due to higher plant densities. When the same patches were coupled (red and purple, see Fig. S3, bottom) extinction was delayed compared to the isolated case. This can be explained by an overall increase in migration success f , given that emigration losses within each patch were now partly compensated by immigration gains. In addition, in case of heterogeneous habitat qualities, source-sink dynamics occurred: the pollinator population on the low-quality patch strongly benefited from the migration input it received from the larger population on the high-quality neighbor patch, which allowed much longer survival on this patch. Simultaneously, the pollinators on the high-quality patch experienced a negative effect of the source-sink dynamics due to emigration. Because of that, the positive effect of coupling was weaker than in the homogeneous system (compare vertical lines in Fig. S3). Nevertheless, extinction time was delayed compared to the reference time $t_{ext,ref}$ and also compared to the coupled homogeneous system. Hence, spatial heterogeneity was beneficial, as it increased the pollinator survival chances.

Note that the biomass flow from high to low quality patches can, in principle, lead to rescue. To illustrate this point, let us consider a scenario where pollinator growth rates stop declining at approximately $t = 200000$, mimicking a scenario where environmental conditions stabilize at a new level after a period of deterioration. In the isolated case, we see that the pollinator population on the high quality patch would be able to survive in this scenario (but with drastically reduced population density) while the population on the low-quality patch would go extinct. By contrast, in the coupled case, we find that both populations are still present at $t = 200000$, because the population on the high quality patch (the source) produces a surplus of individuals that immigrate to the low quality patch (the sink).

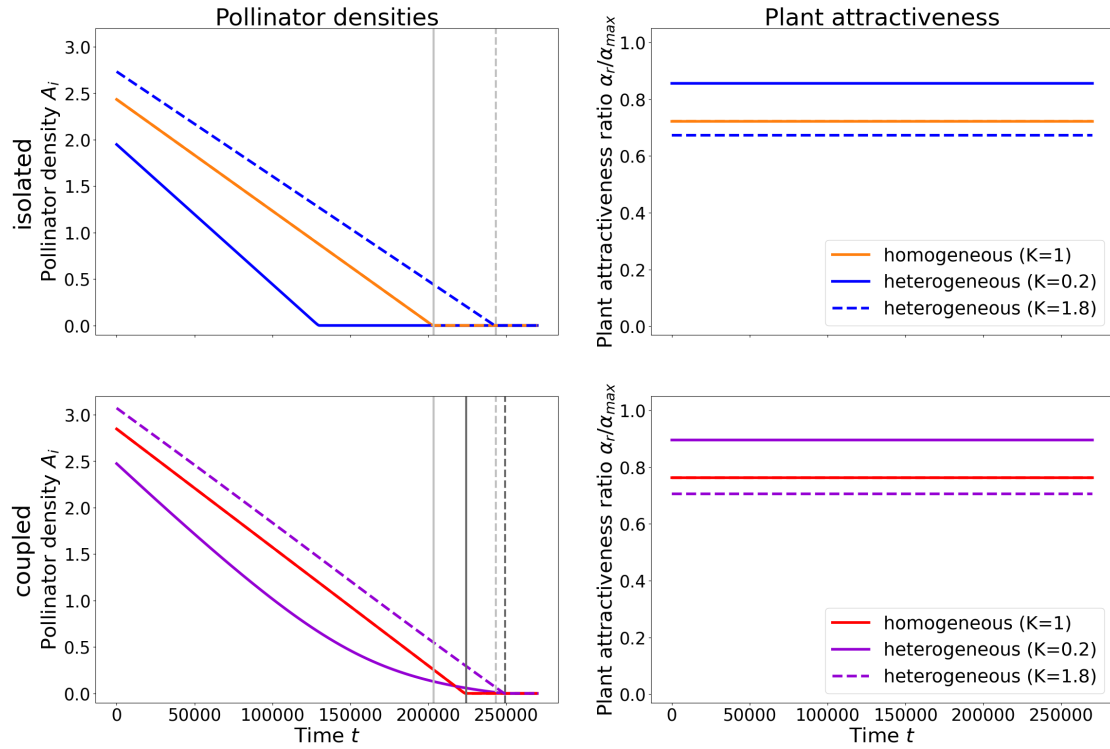


Figure S3: Simulations without evolution in landscapes with $N = 2$ habitat patches. Development of pollinator densities A_i (left) and plant attractiveness ratios $\frac{\alpha_i}{\alpha_{max}}$ (right) over time. r_A decreases with a rate of $r_{A,change} = -8 \cdot 10^{-6}$. The landscapes are homogeneous or heterogeneous (see color legend), isolated ($\delta_{max} = 0$, top) or coupled ($\delta_{max} = 1$, bottom). The vertical lines mark the pollinator extinction times t_{ext} for the respective landscape. Light grey lines show t_{ext} for the landscape with isolated patches, dark grey for the connected ones. All simulations were run with standard parameter values (see Tab. S1).

When evolution was switched on, the plants' attractiveness decreased with accelerating pace in response to pollinator decline (see Fig. S4). In consequence, the pollinators declined even faster, as the beneficial interaction was weakened, resulting in earlier extinction, i.e. $t_{ext,evo} < t_{ext,ref}$ (compare Fig. S4 and Fig. S3). However, the speed of evolution and the exact timing of the extinction depended on the spatial context, and in particular on habitat quality and hence plant density.

Considering isolated patches (see Fig. S4 top), if plant density is low ($K = 0.2$), then the additional benefit from the interaction with an abundant pollinator population is very high. At the same time, the cost of investment into this interaction is also relative high and quickly exceeds its benefits when pollinator abundance declines. By contrast, if plant density is high ($K = 1.8$), both the additional benefit from the interaction and the cost of investing into this interaction are relatively small. This explains why the attractiveness on the low quality patch is initially higher than on the high quality patch, but declines faster (Fig. S4 top right).

As on lower-quality patches the initial attractiveness was higher, the plant strategy was also closer to the upper end of the concave allocation trade-off. There, a tiny shift in the attractiveness ratio comes along with a comparably large one in r_P (see Fig. S2). Consequently, the plants on low-quality habitats benefited stronger from little disinvestment than those on high-quality habitats, which could partially mitigate the negative effect of disinvestment on pollinators. In contrast, for high-quality patches the initial attractiveness ratio was relatively low, such that a decrease in attractiveness led to a much smaller increase in r_P (compared to the low-quality habitats) due to the trade-off shape. The resulting small increase in plant density cannot compensate for the loss in attractiveness. For the pollinator this meant that all patches became increasingly unattractive, but this process was more severe on previously high-quality patches. Thus, the evolutionary response of the plants counteracted the positive effect that arises from heterogeneity, which explain the qualitative differences between scenarios with and without evolution shown in Fig. 4 in the main text.

In the coupled landscapes (see Fig. S4 bottom), we again found delayed extinction compared to the isolated systems, explained by the higher overall migration success f . Heterogeneity, however, did not provide an additional benefit, meaning that the pollinators in the heterogeneous scenario did not survive longer compared to the homogeneous scenario (see Fig. S4, bottom left). The source-sink dynamics, as already explained for the non-evolutionary system, accelerated the local pollinator loss in the high-quality habitat and decelerated it in the low-quality neighbor. This consequentially changed the speed of evolution in the plants (accelerating the disinvestment on the source and decelerating it on the sink), such that the patch first reaching zero attractiveness was no longer the low-quality sink but the high-quality source habitat, which is also visible in the bottom right panel of Fig. S4. Thus, for the pollinator the coupling of habitats with different quality further amplified the development towards unattractive conditions in the high-quality habitats.

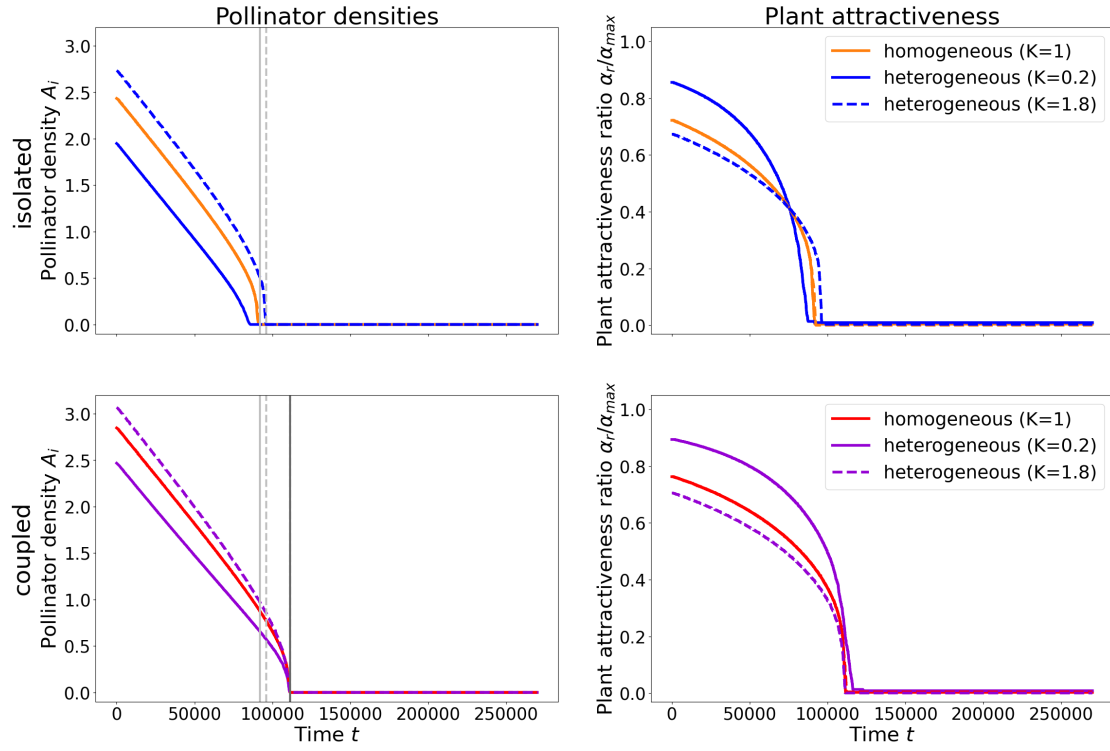


Figure S4: Simulations with evolution in landscapes with $N = 2$ habitat patches. Development of pollinator densities A_i (left) and plant attractiveness ratios $\frac{\alpha_r}{\alpha_{max}}$ (right) over time. r_A decreases with a rate of $r_{A,change} = -8 \cdot 10^{-6}$. The landscapes are homogeneous or heterogeneous (see color legend), isolated ($\delta_{max} = 0$, top) or coupled ($\delta_{max} = 1$, bottom). The vertical lines mark the pollinator extinction times t_{ext} for the respective landscape. Light grey lines show t_{ext} for the landscape with isolated patches, dark grey for the connected ones. All simulations were run with standard parameter values (see Tab. S1).

2.2.2 The survival optimum for intermediate connectivity is an artifact of the model assumptions

The results shown in Fig 4 of the main text suggest a survival optimum for intermediate dispersal distances, i.e. at intermediate connectivity, visible as a darker blue vertical stripe in the respective heatmaps. Such an optimum occurred for several but not all landscapes. Furthermore, the exact position of the optimum varied between landscapes and sometimes also across levels of heterogeneity within one landscape. The latter was particularly the case for scenarios without evolution (see Fig. S5). The optimum was especially pronounced in large systems ($N = 16$ and $N = 25$) (see Fig. S7).

To understand these patterns, we compared time series and landscape structures for landscapes with and without an intermediate optimum. We found that intermediate optima occurred in landscapes, where pairs or small groups of habitats were very close to each other, while they were relatively distant from the other habitat patches, as visualized in Fig. S6. For low values of δ_{max} , when such pairs of habitats were still isolated from the rest of the landscape (as in Fig. S6, left), they supported each other via a strong link with high migration success. As they became connected to further, more distant habitats (as in Fig. S6, right), the dispersal loss abruptly increased for these patches. This was caused by the assumptions used to determine the direction in which pollinators migrate: The pollinators emigrating from a patch are distributed across the available links depending on the relative distances (see Sect. 1.1.3). Hence, if a habitat is connected to only one neighbor patch, all pollinators emigrating from that habitat will migrate via the single link that is available (see Eq. 5). In the landscape visualized in Fig. S6, this was the case for the two marked patches when $\delta_{max} = 0.3$ (left panel). As the link is short, the migration success was high. When the dispersal distance increased to $\delta_{max} = 0.4$ (right panel), additional links appeared for these two patches (see Fig. S6, right). The fraction of pollinators moving through the shortest link then dropped, as some pollinators emigrated via the new links, with much lower migration success.

Consequently, the occurrence of intermediate optima depends on strong differences in the distance between habitats and thus on the additional spatial heterogeneity intrinsic to random geometric graphs. In a regular grid (with periodic boundary conditions), where all habitats have the same number of links and the same distances to their neighbors, such intermediate optima would not occur. In line with this we found that the strength of optima predominantly depends on the distance between the relevant patches and that in landscapes without survival optimum the habitats were relatively evenly distributed. We furthermore found that the magnitude and the position of the optimum could be shifted in heterogeneous landscapes when evolution was switched off, as the pollinators did not always survive longest on these closest coupled patches. For instance, when the quality is very low for the respective patches, the positive effect of the high migration success might be exceeded by the positive effect of another, very high-quality patch. As habitat quality became less important when plant evolution was active (see previous subsection) the position of the optimum did not vary in the scenarios with evolution.

In summary, we acknowledge that the survival optimum for intermediate connectivity is an artifact of our model assumptions and that it is unlikely to occur when alternative assumptions about the migration rules (as for example discussed by Plitzko and Drossel, 2015) are implemented.

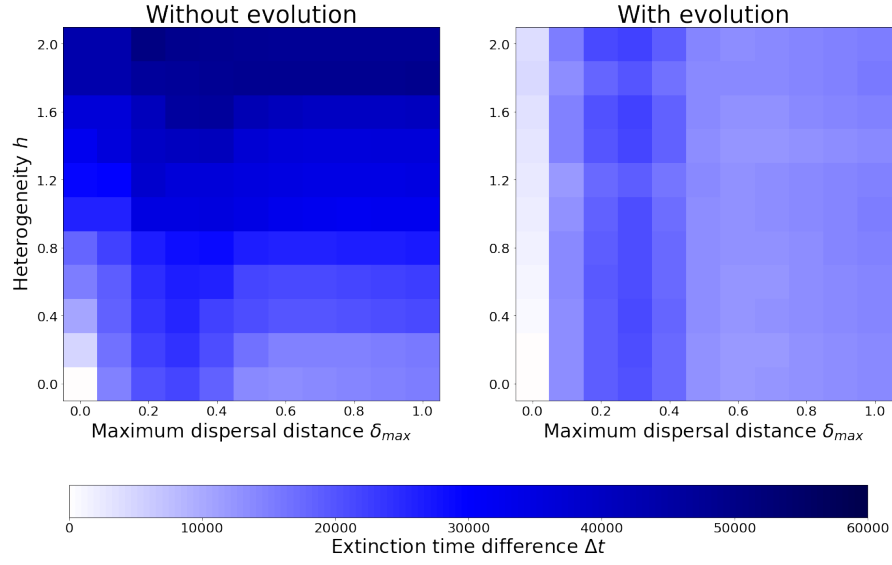


Figure S5: Intermediate optimum in a landscape with $N = 16$ habitats, without (left) and with (right) evolution. The color shows the absolute time difference Δt in pollinator extinction times, relative to the isolated ($\delta_{max} = 0$) and homogeneous ($h = 0$) landscape. All simulations were run with standard parameter values (see Tab. S1). The corresponding landscape is shown in Fig. S6.

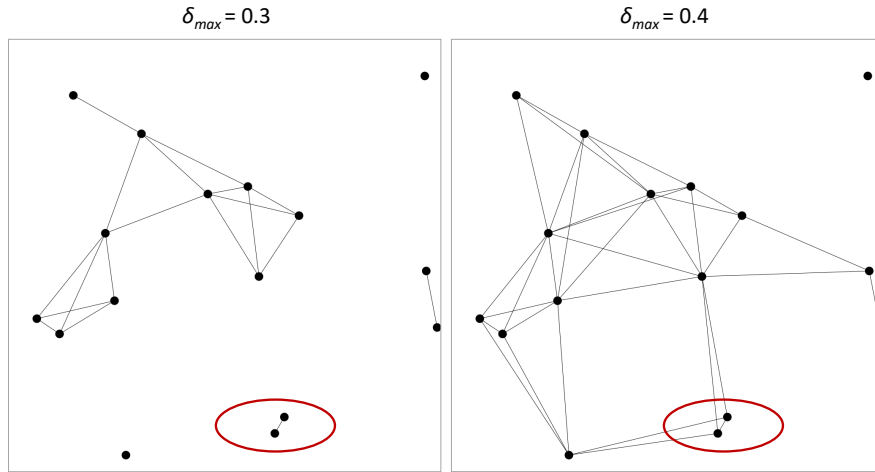


Figure S6: Landscape with $N = 16$ habitats. This is the landscape used for the simulations presented in the heatmaps Fig. S5. Two levels of connectivity: On the left $\delta_{max} = 0.3$, which refers to the optimum connectivity (see Fig. S5), and on the right $\delta_{max} = 0.4$. The pair of habitats with the shortest distance and therefore strongest link is marked with red ellipses.

2.3 Effect of patch number

In general, we found that the results reported above and in the main text remain robust to variation in patch number (and hence patch density), see Fig. S7. However, some minor differences are still observable when comparing landscapes with a lower or higher number of patches. First, in systems with fewer patches the effect of randomness is higher, as could be expected. For some landscapes, single levels of heterogeneity show earlier extinction than expected for this level, caused by the fact that the local carrying capacities K_i are drawn randomly. This can shift the mean carrying capacity of the landscape to lower values by chance, which is more likely with just few patches. Therefore, the positive effect of heterogeneity is on average weaker in landscapes that contain only a few habitats. Second, in landscapes with more patches, the pollinator survival chances start to increase at a smaller δ_{max} , as the probability of having other habitats in close proximity is higher there. Finally, the intermediate optimum is more pronounced for landscapes containing more patches, because its position is relatively stable, while it is quite variable for smaller systems, as explained above in section 2.2.2). Moreover, in landscapes with more patches the chance is higher to have two patches very close together, which are not extremely far from other habitats. This explains why the respective intermediate optima are located at relatively low δ_{max} -values and more pronounced than in landscapes with fewer patches.

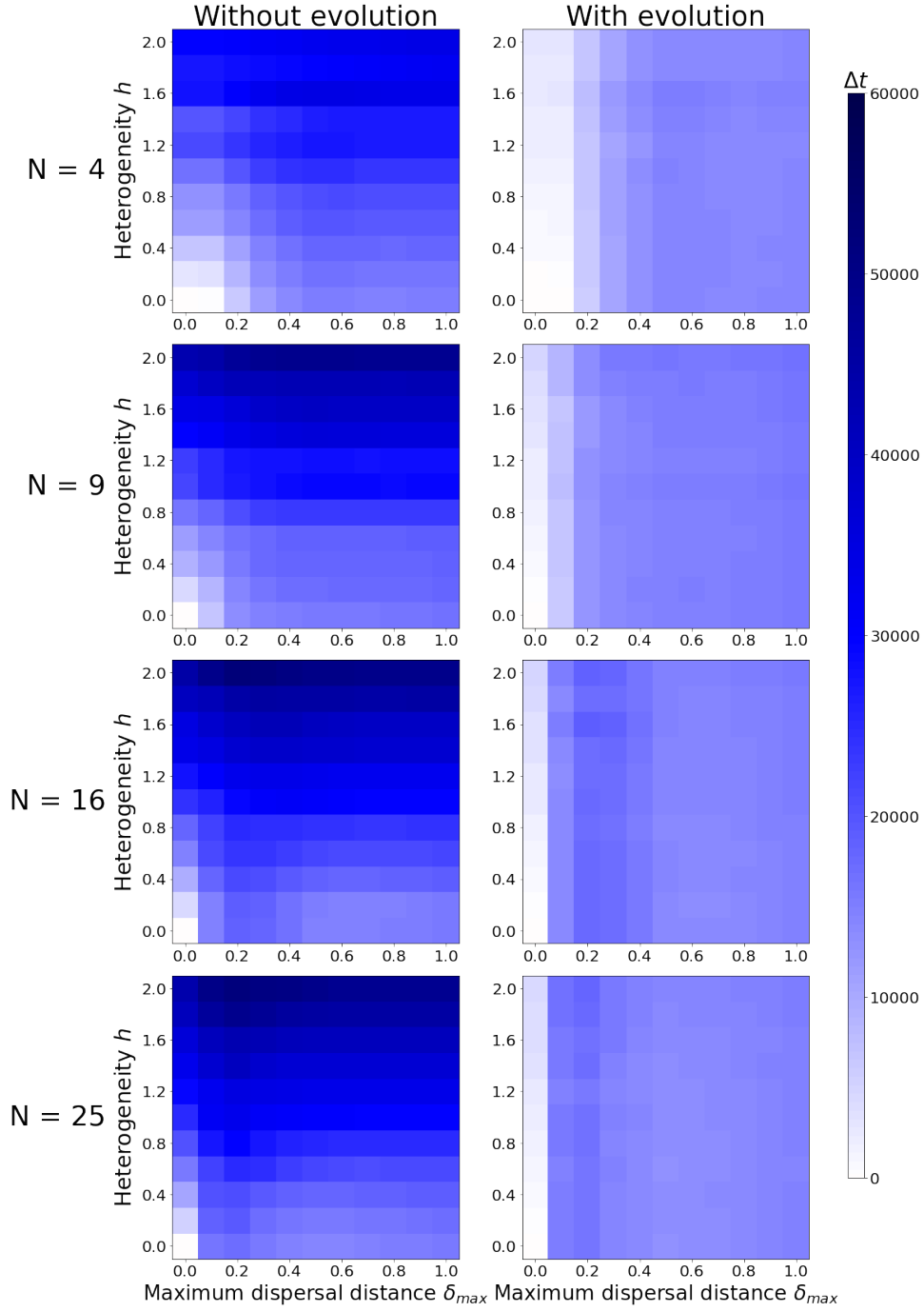


Figure S7: Heatmaps for random systems, representing the mean effect of connectivity and heterogeneity without (left) and with (right) evolution. Mean across 10 landscapes with patch numbers $N = [4, 9, 25]$ (rows). The color shows the absolute time difference in extinction time relative to isolated ($\delta_{max} = 0$) and homogeneous ($h = 0$) landscapes. All simulations were run with standard parameter values (see Tab. S1).

2.4 Parameter choice and effect sizes

The results presented here and in the main text indicate that the negative effect of plant evolution on pollinator survival outweighs the positive effect of spatial coupling. More precisely, we find that the differences in extinction time points between scenarios with or without evolution were typically larger than the differences in extinction time points between scenarios with or without spatial coupling. A thorough analysis of the forces that modulate these effect sizes would go far beyond the scope of this study, but a few selected simulation runs with alternative parameter values are discussed here.

In particular, we show that the effect of evolution is weaker when considering a more concave trade-off between plant attractiveness and growth (see Fig. S8) and/or for smaller mutation step sizes (see Fig. S9). The first case describes a scenario where the speed of plant evolution is initially very slow (and increases later) due to the considered trade-off between α and r_P , see Fig. S2, whereas the second case corresponds to a scenario where evolution of plant attractiveness is simply slowed down completely. In both cases, we find that relatively high levels of attractiveness are maintained longer compared to the case discussed in Fig. S4, which explains why also pollinator abundance is maintained longer. Note that a smaller effect of plant evolution can also be observed when choosing a lower mutation frequency (which also slows down the speed of evolution, similar to the case with smaller mutation step sizes, not shown) and/or a faster environmental decline rate (which essentially translates into slow evolution relative to the environmental decline, also not shown).

Furthermore, we demonstrate that the effect of spatial coupling is stronger for higher migration rates (compare Fig. S10 with Fig. S3 and Fig. S4). Note that in Fig. S10 we chose a higher initial value for r_P to partly compensate for the emigration losses so that the initial equilibrium densities at simulation start are identical with the cases discussed above. The larger effect size of spatial coupling is hence due to an increase in immigration rates, as the migration rate d appears as a scaling factor in eq. 5. Also note that an even stronger effect of spatial coupling can be observed in even more heterogeneous landscapes, e.g. by choosing K -values from a bimodal distribution or by increasing the mean and the range of the uniform distribution used here (not shown).

In summary, these additional results suggest that the relative effect sizes of plant evolution and spatial coupling strongly depend on specific parameter choices, indicating that these effect sizes are system specific. In systems with relatively slow evolution, relatively strong spatial coupling and/or relatively high heterogeneity, we might observe that the positive effect of spatial coupling outweighs the negative effect of plant evolution. However, we would like to emphasize that with this study we do not aim at realistic predictions for specific systems, but for a general proof-of-concept. While the parameter variations discussed above indeed affect relative effect sizes, they do not affect the direction of effects. In all scenarios studied, evolution of plant attractiveness was detrimental, while spatial coupling was beneficial, and the effect of spatial heterogeneity was considerably smaller when evolution was taken into account compared to scenarios without evolution.

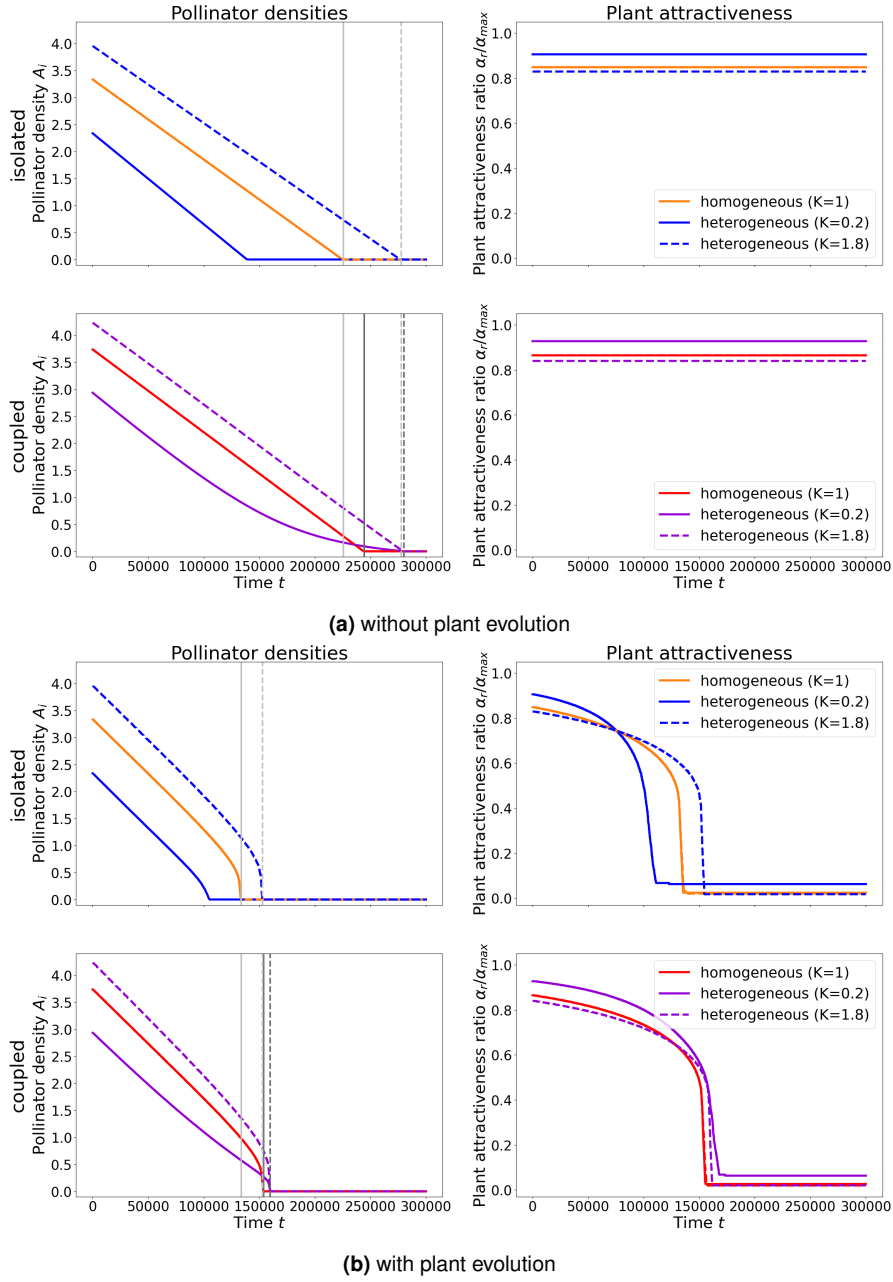


Figure S8: Effect of trade-off shape parameter s : Here, $s = 3.5$ (standard value $s = 2.5$). Simulations (a) without and (b) with evolution, $N = 2$. Development of pollinator densities A_i (left) and plant attractiveness ratios $\frac{\alpha_r}{\alpha_{max}}$ (right) over time. r_A decreases with a rate of $r_{A,change} = -8 \cdot 10^{-6}$. The landscapes are homogeneous or heterogeneous (see color legend), isolated ($\delta_{max} = 0$, top) or coupled ($\delta_{max} = 1$, bottom). The vertical lines mark the pollinator extinction times t_{ext} for the respective landscape. Light grey lines show t_{ext} for the landscape with isolated patches, dark grey for the connected ones. A more concave trade-off shape reduces the negative effect of evolution. Except for s , the standard parameter values were used (see Tab. S1).

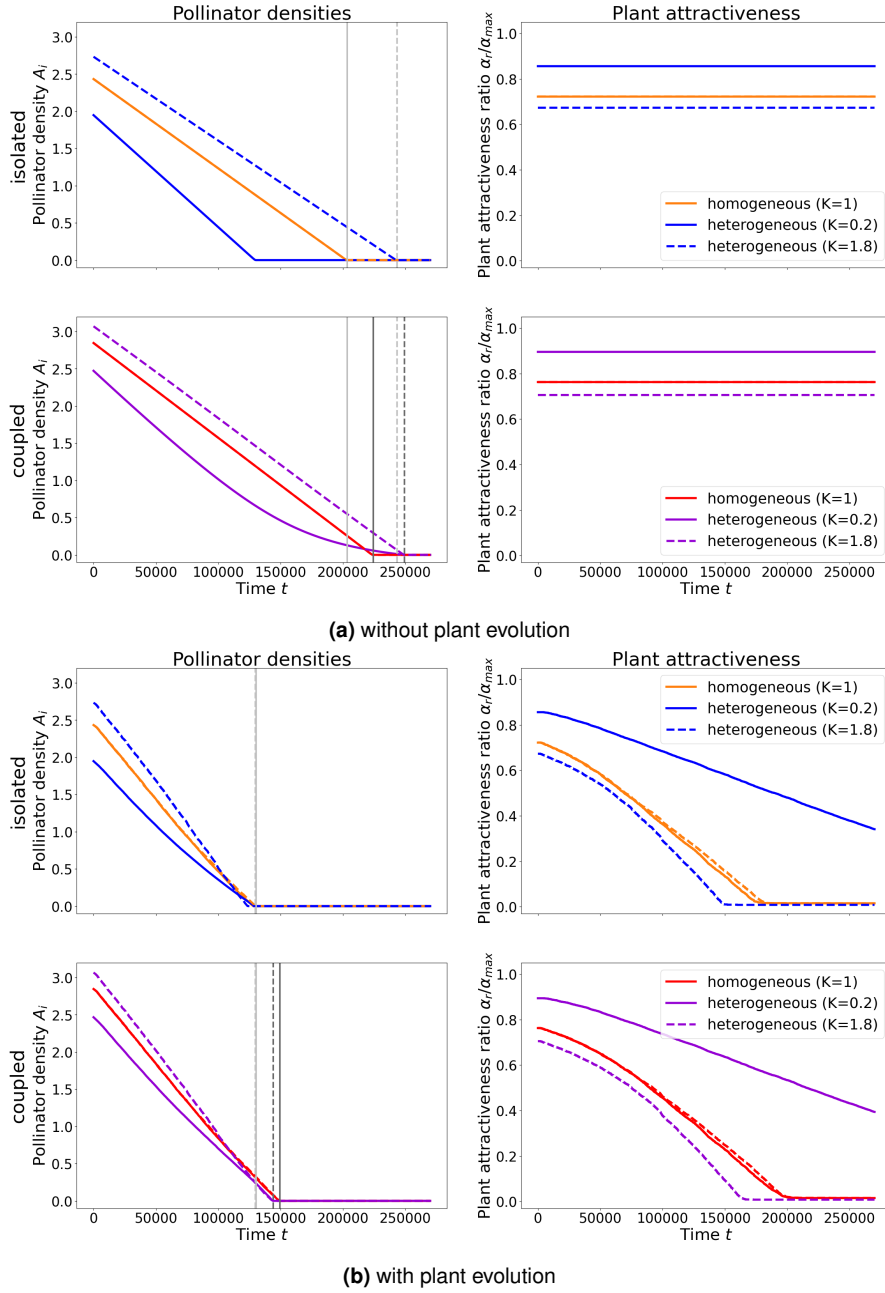


Figure S9: Effect of max. mutation step size $\Delta_{max}\alpha$: Here, $\Delta_{max}\alpha = 0.001$ (standard value $\Delta_{max}\alpha = 0.02$). Simulations (a) without and (b) with evolution, $N = 2$. Development of pollinator densities A_i (left) and plant attractiveness ratios $\frac{\alpha_r}{\alpha_{max}}$ (right) over time. r_A decreases with a rate of $r_{A,change} = -8 \cdot 10^{-6}$. The landscapes are homogeneous or heterogeneous (see color legend), isolated ($\delta_{max} = 0$, top) or coupled ($\delta_{max} = 1$, bottom). The vertical lines mark the pollinator extinction times t_{ext} for the respective landscape. Light grey lines show t_{ext} for the landscape with isolated patches, dark grey for the connected ones. A smaller mutation step size reduces the negative effect of evolution. Except for $\Delta_{max}\alpha$, the standard parameter values were used (see Tab. S1).

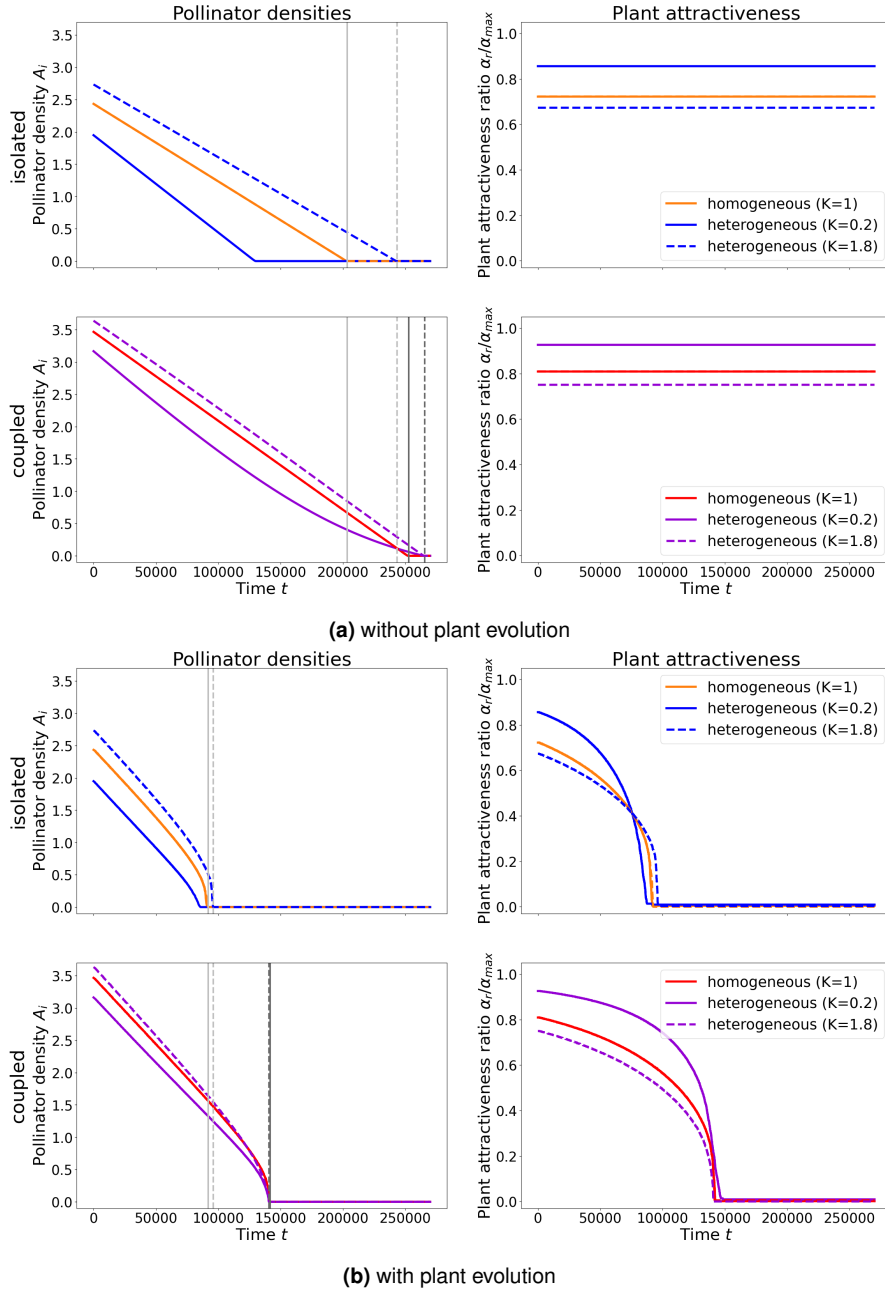


Figure S10: Effect of dispersal rate d : Here, $d = 0.5$ (standard value $d = 0.2$). Simulations (a) without and (b) with evolution, $N = 2$. Development of pollinator densities A_i (left) and plant attractiveness ratios $\frac{\alpha_r}{\alpha_{max}}$ (right) over time. r_A decreases with a rate of $r_{A,change} = -8 \cdot 10^{-6}$, starting at a value of 1.1. The landscapes are homogeneous or heterogeneous (see color legend), isolated ($\delta_{max} = 0$, top) or coupled ($\delta_{max} = 1$, bottom). The vertical lines mark the pollinator extinction times t_{ext} for the respective landscape. Light grey lines show t_{ext} for the landscape with isolated patches, dark grey for the connected ones. A higher dispersal rate increases the effect of space. Except for d and the initial value of r_a , the standard parameter values were used (see Tab. S1).

3 Discussion

We studied the effects of landscape connectivity and heterogeneity on local eco-evolutionary dynamics and species survival in a mutualistic system. To this end, we combined the eco-evolutionary plant-pollinator model by Weinbach et al., 2022 with elements of the metacommunity model by Ryser, Hirt, et al., 2021. Our model revealed three key results: (1) plant evolution systematically accelerated pollinator extinction, independent of the spatial scenario under consideration, (2) without plant evolution, both heterogeneity and connectivity delayed pollinator extinction and (3) plant evolution changed the relative importance of landscape connectivity and heterogeneity for pollinator survival. In the following, we discuss these findings in the context of urban ecology, where both connectivity and heterogeneity have been highlighted as important drivers of eco-evolutionary dynamics (see Alberti et al., 2020).

3.1 Plant evolution accelerates pollinator extinction

In our model, plant evolution had a strongly negative effect on pollinator survival chances, which is perfectly consistent with the original, non-spatial model version by Weinbach et al., 2022 and also with a follow-up study that considered pollinator evolution in addition to plant evolution Weyerer et al., 2023. Both studies reported that plants tend to disinvest from the interaction, which accelerates the decline of the pollinator population, resulting in a self-reinforcing feedback loop that potentially leads to eco-evolutionary murder. Notably, we found that this general pattern of self-reinforcing eco-evolutionary feedback was found for all spatial systems, independent of the number of patches, the type of landscape (grid versus random geometric graph), as well as spatial characteristics (level of connectivity and heterogeneity). This is easily explained by the fact that evolution of the plants is driven by the change in pollinator densities and the pollinators experienced the same environmental degradation in all habitat patches without any exception.

Our results are furthermore also consistent with insights from empirical work, as already discussed in the original publication by Weyerer et al., 2023. For example, experimental studies showed that a loss of efficient pollinators can trigger plant evolution, which reduces the investment in costly pollinator attracting floral signals, like e.g. volatile compounds, while on the other hand increasing independent reproduction via self-fertilisation (Roels and Kelly, 2011; Gervasi and Schiestl, 2017). Note, however, that our model specifically assumes positive plant growth rates even in the absence of pollinators, in order to account for some degree of independence from the interaction partner, e.g. via selfing or vegetative reproduction. In consequence, it can not capture the dynamics of plant populations that exclusively rely on pollination service for reproduction.

3.2 Without plant evolution both connectivity and heterogeneity have a positive effect on pollinator survival

The positive effect of connectivity on species persistence found in our model is generally consistent with findings from previous studies. For instance, a recent review of trophic metacommunities showed that an increase in dispersal (or connectivity) is typically associated with higher system stability (Gross et al., 2020). Along similar lines, it has been shown that landscape modifications

that result in a reduction of connectivity, such as fragmentation and isolation of habitats, result in increased dispersal costs (Bonte et al., 2012), which can destabilise communities (Ryser, Häussler, et al., 2019).

The positive effect of heterogeneity on species persistence found in our model is also well known in the literature, at least as long as the respective area per habitat type remains sufficiently large (Kadmon and Allouche, 2007), and typically explained via a higher variety of environmental conditions where more niches can be occupied by various species and via the provision of refuges, where species can overcome difficult periods, which in turn enables source-sink dynamics, rescue effects and spatial insurance in face of disturbances (Stein et al., 2014; Ryser, Hirt, et al., 2021; Bolchoun et al., 2017; Leibold et al., 2004; Pulliam, 1988; Runge et al., 2006). These findings are consistent with our own simulation results, where the positive effect of heterogeneity on pollinator survival is tightly linked to the occurrence of high-quality habitats, which promote local pollinator abundances and hence support smaller population on low-quality patches.

3.3 Plant evolution changes the relative importance of landscape connectivity and heterogeneity for pollinator survival

Several authors have highlighted the need to consider spatial dynamics in complex landscapes, evolutionary processes and species interactions in combination and predicted that evolution can change the effect of landscape properties in unexpected ways (see for example Urban et al., 2012 or Alberti et al., 2020). Our work corroborates this prediction, by demonstrating that all three components - spatial dynamics, evolutionary processes and biotic interactions - indeed affect each other. More precisely, we find that while the negative effect of plant evolution on pollinators via disinvestment in the mutual interaction was observed in all scenarios and on all patches, it was particularly strong on high quality habitats and considerably weaker on the lower quality ones, which in turn weakened the positive effect of source-sink dynamics on low-quality patches, since high quality patches quickly lost their ability to sustain low quality patches. Thus, with this model we could clearly demonstrate that spatial properties influence eco-evolutionary dynamics by shaping species' adaptive responses, and vice versa, that these adaptive responses in turn also modulate the effect of spatial coupling.

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