

RESEARCH ARTICLE

Self-organised pattern formation promotes consumer coexistence by fluctuation-dependent mechanisms

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Abstract

1. In spatially extended ecosystems, habitat heterogeneity facilitates coexistence of species if each competitor experiences environmental conditions in a particular habitat that provide a growth advantage compared to other species, thereby making it locally competitively superior. If the competitive hierarchy among species is the same everywhere, heterogeneity-facilitated coexistence is possible provided that superior competitors disperse maladaptively towards unfavourable habitats or if they hedge insufficiently against fluctuating environmental conditions.
2. We use a generic two-patch metacommunity model to show that the latter mechanisms also operate in metacommunities with homogeneous habitat quality when heterogeneous biomass distributions emerge from self-organised pattern formation. The model consists of an abiotic resource, an autotroph producer and two competing heterotroph consumer species of which one is always competitively inferior to the other, irrespective of resource availability.
3. If the induced biomass patterns are static in time, a lower dispersal rate can allow the inferior competitor to avoid competitive exclusion by retaining most of its biomass in the patch with the higher resource density. However, if the biomass patterns fluctuate spatio-temporally, the inferior competitor must adopt a higher dispersal rate than the superior competitor to persist. This increased movement enables the inferior competitor to effectively distribute its biomass across space, thereby achieving a higher growth rate during periods of recovery from local population minima.
4. Strikingly, we find a novel coexistence mechanism that emerges if the competitors differ in their abilities to induce pattern formation. Similar to relative nonlinearity in resource use (based e.g. on a gleaner–opportunist trade-off), the dominant species modifies the spatial or spatio-temporal variation in the distribution of the resource in a way that favours its competitor. This prevents competitive exclusion due to differently effective dispersal strategies.
5. We conclude that while temporal instabilities that cause, for example, predator–prey oscillations are usually regarded as jeopardising species' persistence,

Christian Guill and Felix Nößler contributed equally to this work.

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spatial instabilities that give rise to self-organised pattern formation should be interpreted more positively, as they provide a generic mechanisms for maintaining diversity in metacommunities without requiring a priori habitat heterogeneity.

KEYWORDS

bet-hedging, coexistence, food chain, maladaptive dispersal, metacommunity, relative nonlinearity, self-organised pattern formation

1 | INTRODUCTION

Understanding the processes that underlie species coexistence in natural ecosystems is central to community ecology (Chesson, 2000; Hutchinson, 1961; Levine et al., 2017). Classical theory distinguishes between mechanisms that operate on the local versus the regional scale of metacommunities, that is, communities of habitat patches that are linked by dispersal of various species (Leibold et al., 2004). Local coexistence mechanisms include relative nonlinearity in resource-dependent growth functions (e.g. the gleaner-opportunist trade-off, Klauschies & Gaedke, 2020; Litchman & Klausmeier, 2001), resource partitioning (Schoener, 1974), specialist predation (Chase et al., 2002) and the temporal storage effect (Chesson & Warner, 1981). In contrast, dispersal between different habitats is a key process for coexistence of species in metacommunities that may not be able to coexist in a non-spatial context (Schlägel et al., 2020).

Several mechanisms have been proposed that can explain species coexistence through dispersal in metacommunities. First, the competitive abilities of species may be strongly influenced by abiotic factors or by biotic interactions with other species, leading to a situation where each competitor has at least one patch where it is dominant. The species thus have different source and sink patches (with positive or negative population growth, respectively) and can persist in all habitat patches due to dispersal from source to sink patches (Amarasekare, 2010; Shmida & Wilson, 1985). Other coexistence mechanisms assume that the competitive rankings are spatially homogeneous, that is, source and sink patches are the same for all species. If patch quality is constant in time, coexistence is possible if the dispersal rate of a superior competitor (specifically, its emigration rate from source into sink patches) is higher than that of an inferior competitor (maladaptive dispersal mechanism, Abrams and Wilson 2004; Namba & Hashimoto, 2004; Nathan et al., 2013). Conversely, if the resource availability on the different patches changes over time, coexistence is facilitated if the inferior competitor has a higher dispersal rate than the superior one (Lin et al., 2013), which allows it to better hedge against fluctuating growth conditions. This mechanism is similar to the classic competition-colonisation trade-off in patch occupancy models (Tilman, 1994).

A prerequisite for coexistence of an inferior competitor with a superior one that is dominant in all patches is that resource densities are not identical everywhere, as otherwise the superior

competitor would always competitively exclude the inferior one (Hardin, 1960). Usually, it is assumed that the patches have different habitat quality due to heterogeneous environmental conditions (Amarasekare, 2010; Lin et al., 2013). However, both static and temporally varying patterns in the quality of the patches can also emerge in a self-organised way, and several studies have demonstrated how this promotes species coexistence and biodiversity (Banerjee & Petrovskii, 2011; Baudena & Rietkerk, 2012; Eigentler, 2021; Guill et al., 2021; Nathan et al., 2013). These patterns are formed by an interplay between the local interactions of the species and their spatial dispersal dynamics (scale-dependent feedback; Rietkerk & Van de Koppel, 2008). This implies that the magnitude and type (static or oscillatory) of the emergent biomass patterns depend on the relative abundance of the coexisting species and on their dispersal rates. However, as shown above, the dispersal rates also have a direct influence on the relative fitness of the competing species, which may lead to a situation where a species, when dominant, induces a type of biomass pattern that is not optimal for itself but rather for a competitor with a different dispersal rate. How such interactions between the capabilities of species to induce different types of biomass patterns, their ability to benefit from them and their competitive strength affect the potential for coexistence in metacommunities has, however, not been explored so far.

In this study, we therefore systematically analyse how different dispersal rates of competing species affect their coexistence through differences in their effect on self-organised formation of heterogeneous biomass patterns and their specific response to them. Most ecological models that describe self-organised pattern formation include as part of the local interactions some form of ecosystem engineering process (such as vegetation in arid systems modifying the infiltration rate of surface water into the ground, or macrophytes changing the flow velocity of streams; Cornacchia et al., 2018; Klausmeier, 1999). Since these processes are very system-specific, transferability of results to different ecological systems is limited. In order to obtain widely applicable results, the system we consider here is therefore deliberately kept very simple. On two adjacent patches with identical environmental conditions, two competing species (heterotrophs) with different competitive strength feed on a shared resource (autotrophs), which in turn relies on nutrients (Figure 1a–c; Figure S1). In addition to movement of all constituents between the patches, the model thus only contains generic trophic and (indirect) competitive interactions. In

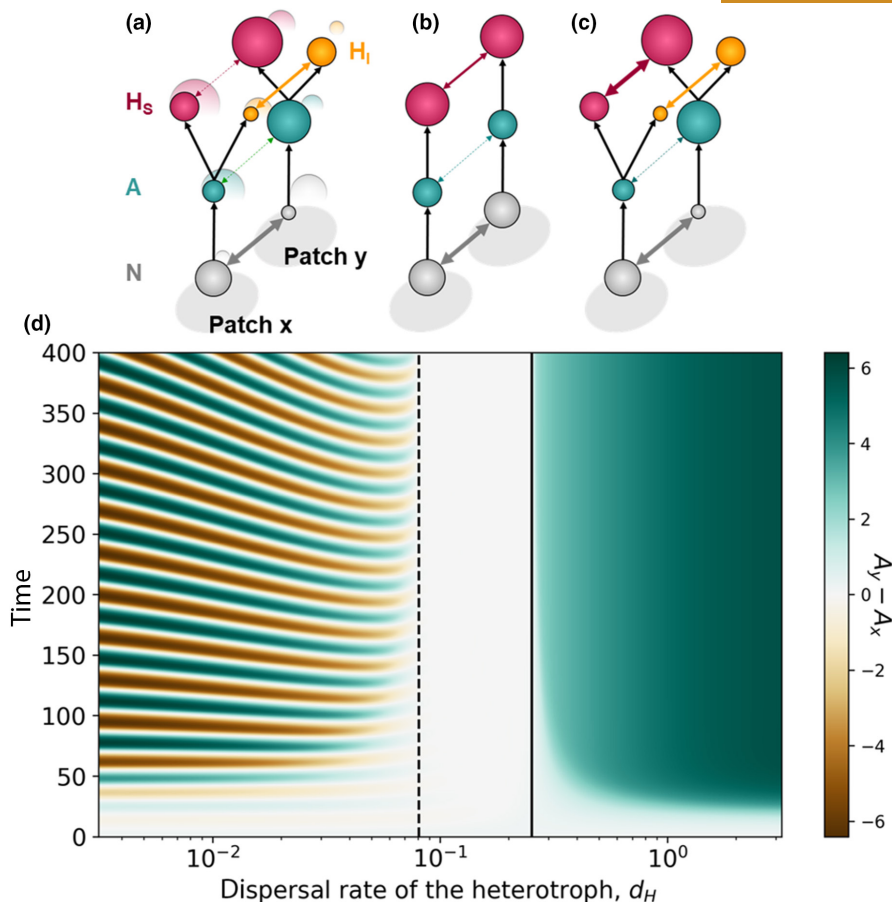


FIGURE 1 Conceptual representation of the model. The system contains nutrients (N, grey), autotrophs (A, green) and two competing heterotrophs (superior competitor H_s in red, inferior competitor H_i in orange) in the two habitat patches x and y. Black arrows denote local trophic interactions; coloured arrows indicate dispersal. The size of the spheres represents the nutrient and population densities in the respective habitat patch. The dispersal rate of the superior competitor determines the basic form of biomass patterns emerging: (a) oscillatory pattern formation at low dispersal rate, (b) no pattern formation (and exclusion of the inferior competitor) at intermediate dispersal rate and (c) static pattern formation at high dispersal rate. In panel (d), time series of the difference in autotroph density between the two patches for different heterotroph dispersal rates is shown (with only one heterotroph in the system). The dashed vertical line indicates an oscillatory Turing instability, the solid vertical line indicates a static Turing instability (i.e. the bifurcation points at which the spatially homogeneous equilibrium is destabilised, cf. Section 2). See Table 1 for parameter values.

such a setting, the dispersal rates of the competitors are important determinants of whether no, static or oscillatory patterns in the species' biomass distributions emerge (Guill et al., 2021). Because the relative dispersal rates also contribute to the fitness of the competitors in heterogeneous metacommunities, we show that a feedback between pattern formation and the relative abundances of the species can emerge that leads to coexistence under conditions where it would not be possible with externally determined environmental heterogeneity.

2 | METHODS

In this study, we analysed the conditions under which two competitors with different dispersal and competitive abilities can coexist in a system of two identical habitat patches. For this, we developed a metacommunity model that describes the local dynamics of a simple

food web comprising nutrients, one autotroph, and two heterotroph species in each patch, and the diffusion of nutrients and dispersal of individuals between the two patches.

2.1 | Model description

For the food web on the first patch (with index x), the differential equations describing the dynamics of the local nutrient concentration N_x , the autotroph biomass density A_x , and the biomass densities of the two heterotroph species, $H_{s,x}$ (superior competitor) and $H_{i,x}$ (inferior competitor) are as follows:

$$\frac{dN_x}{dt} = D(S - N_x) - rN_xA_x + d_N(N_y - N_x), \tag{1}$$

$$\frac{dA_x}{dt} = rN_xA_x - g_{s,x}H_{s,x} - g_{i,x}H_{i,x} - DA_x + d_A(A_y - A_x), \tag{2}$$

Name	Description	Dimension	Value
S	Nutrient supply concentration	mass · area ⁻¹	5.0
D	Turnover rate	time ⁻¹	0.3
r	Growth coefficient of autotroph	area · (mass · time) ⁻¹	0.5
a_i	Attack rates of the heterotrophs	area · (mass · time) ⁻¹	1.3, 1.0
h	Handling time of the heterotrophs	time	0.5
e	Conversion efficiency of the heterotrophs	dimensionless	0.33
d_N	Diffusion rate of nutrients	time ⁻¹	4.0
d_A	Dispersal rate of autotroph	time ⁻¹	0.004
d_i	Dispersal rates of the heterotrophs	time ⁻¹	–

Note: The dispersal rates of the two competing heterotrophs are varied in the analyses; therefore, no values are provided here. The subscript $i \in \{S, I\}$ refers to either the superior or the inferior competitor.

$$\frac{dH_{S,x}}{dt} = eg_{S,x}H_{S,x} - DH_{S,x} + d_S(H_{S,y} - H_{S,x}), \quad (3)$$

$$\frac{dH_{I,x}}{dt} = eg_{I,x}H_{I,x} - DH_{I,x} + d_I(H_{I,y} - H_{I,x}). \quad (4)$$

The equations for the second patch (with index y) are obtained symmetrically by swapping the indices x and y . All model parameters are summarised in Table 1; a flow diagram of the model is provided in Figure S1.

Locally, the model describes flow-through systems like chemostats. Nutrient-rich medium with supply concentration S is constantly replenished with turnover rate D , which also determines the per capita mortality rate of autotrophs and heterotrophs. The nutrient uptake rate of the autotroph increases linearly with nutrient concentration, scaled with autotroph growth coefficient r . The grazing rates of the heterotrophs, $g_{i,x}$ ($i \in \{S, I\}$), are modelled as Holling type II functional responses (Holling, 1959),

$$g_{i,x} = \frac{a_i A_x}{1 + a_i h A_x}, \quad (5)$$

with attack rates a_i (which determine the competitive hierarchy of the heterotrophs, i.e. $a_S > a_I$) and handling time h . Consumed autotroph biomass is converted to heterotroph biomass with conversion efficiency e , accounting for faecal and respiratory energy loss.

Nutrients, autotroph and heterotrophs are assumed to randomly diffuse or disperse between the patches with constant per capita rates d_N , d_A and d_H , respectively. Note that we do not assume a colonisation–competition trade-off in the parametrisation of the model, that is, it is not required that the competitively inferior heterotroph H_I has a higher dispersal rate than the competitively superior heterotroph H_S .

This model set-up represents the minimal complexity needed to demonstrate how different mechanisms based on self-organised pattern formation operate to enable the coexistence of competing consumer species. Sensitivity analyses regarding the effect of varying parameters of the trophic interactions (e.g. the attack rates a_i),

TABLE 1 Description, dimensions and values of the model parameters.

but also of structural changes of the model equations (like linear vs. saturating resource uptake rate or functional responses, or consumer dispersal rates that can be plastically adjusted depending on local food availability) are shown in Appendix S4.

2.2 | Model analysis

First, we determined the conditions for self-organised pattern formation. The onset of this phenomenon is marked by a bifurcation called a Turing instability or diffusion-driven instability (Turing, 1952). At this bifurcation, a stable, spatially homogeneous state becomes unstable under heterogeneous perturbations. Since a spatially homogeneous state does not allow for coexistence of the two heterotrophs (Appendix S2), the analyses are carried out in a system with just a single heterotroph. When the considered metacommunity consists of just two distinct habitat patches, as is the case here, the occurrence of a Turing instability can be determined with a simple linear stability analysis (for the general case of network-organised systems with an arbitrary number of patches and dispersal links, see Appendix S3 and Brechtel et al. (2018)). For this, we construct the matrix

$$\mathcal{T} = \mathcal{J} - 2 \times \mathcal{D} \quad (6)$$

with \mathcal{J} the Jacobian matrix of the local (single-patch) system evaluated at the homogeneous equilibrium $\hat{X}^* = (N^*, A^*, H^*)$, \mathcal{D} the Jacobian matrix of the emigration terms of the system at \hat{X}^* and the factor 2 as the only non-zero eigenvalue of the Laplacian matrix \mathcal{L} that encodes the link structure of the two-patch system (details of \hat{X}^* , \mathcal{J} , \mathcal{D} and \mathcal{L} are provided in Appendix S3). A static Turing instability that leads to the formation of static spatial patterns in nutrient concentrations and biomass densities of autotrophs and heterotrophs is marked by a single, real eigenvalue of \mathcal{T} becoming positive, while an oscillatory Turing instability that leads to the formation of spatio-temporal patterns is marked by a pair of complex-conjugate eigenvalues obtaining a positive real part. The latter case is only possible in systems with at least three interacting agents such as nutrients or biological species

(Turing, 1952). Calculating the zeros of the real part of the dominant eigenvalue(s) of \mathcal{T} for various combinations of the dispersal rates d_N , d_A , and d_H thus reveals the boundaries of the Turing instabilities (note that we use the subscript H instead of i to distinguish the model set-up with just a single heterotroph from the standard case with two competing species).

Provided that self-organised pattern formation can occur, further coexistence conditions were then explored in the full system with both competitors for various combinations of the competitors' dispersal rates d_i . To test for coexistence of the two competitors, the system was simulated first with only the superior competitor, H_S , for 10^4 time steps with the following initial values: $N_x = 7$, $N_y = 2$, $A_x = A_y = 1$, $H_{S,x} = 0.2$, and $H_{S,y} = 0.1$. Then, the inferior competitor, H_I , was added with a low density ($H_{I,x} = 0.001$, $H_{I,y} = 0.0001$). The asymmetry between $H_{I,x}$ and $H_{I,y}$ represents a heterogeneous perturbation that could, in principle, drive the system away from a potentially unstable homogeneous equilibrium. The system was simulated for another 10^5 time steps. If, at the end of a simulation run, both competitors had a density greater than 10^{-10} summed over both patches, coexistence was assumed. For numerical reasons, a variable was set to 0 if its value dropped below 10^{-30} during a simulation run. If the competitors coexisted, we analysed whether the dynamics had reached a stable equilibrium or whether population oscillations occurred by calculating the average coefficient of variation of the competitors over the last 5000 time steps. The threshold for assuming oscillatory dynamics (average coefficient of variation >0.05) was determined manually by checking the type of dynamics in selected time series. We verified that our results are largely independent of the order of invasions (Appendix S4) and that they do not depend on the initial values of the nutrient concentrations and biomass densities.

The simulations were performed in Julia 1.10.4 (Bezanson et al., 2017). The numerical solver Vern9 (Verner, 1978) with an absolute and relative tolerance of 10^{-12} from the DifferentialEquations.jl package (Rackauckas & Nie, 2017) was used. To check that the choice of the solver had no substantial effect on the results, some simulations were repeated with the CVODE solver (Hindmarsh et al., 2005). The figures were produced with Makie.jl (Danisch & Krumbiegel, 2021). We verified the reproducibility of the results using Python simulations. Most of the supporting figures were produced with Python using the packages SciPy (Virtanen et al., 2020), NumPy (Harris et al., 2020) and Matplotlib (Hunter, 2007). The simulation code and detailed information on the required versions of the Julia and Python packages used are available online (see Data Availability Statement).

3 | RESULTS

3.1 | Self-organised pattern formation

In the absence of self-organised pattern formation, the superior competitor always outcompetes the inferior one because the patches have the same a priori habitat quality and the inferior competitor

cannot invade into a homogeneous system with resident superior competitor, while the reverse is always possible (Appendix S2).

The onset of pattern formation is marked by a spatial instability (Turing instability) of a homogeneous single-heterotroph equilibrium. Depending on the parameters of the system (most importantly the dispersal rate of the heterotroph, d_H), either static or oscillatory (spatio-temporal) patterns can occur. At low values of d_H , an oscillatory Turing instability occurs (marking the emergence of spatio-temporal patterns), while at high values of d_H , static patterns emerge (Figures 1d and 2). At intermediate levels of d_H , the homogeneous equilibrium remains stable. Further requirements for pattern formation are that the diffusion rate of the nutrients is sufficiently high ($d_N \gtrsim 0.7$) and the dispersal rate of the autotrophs is comparatively low ($d_A \lesssim 0.08$). These boundaries have been determined with the attack rate of the superior competitor (i.e. $a_H = 1.3$). Calculating them based on the attack rate of the inferior competitor (i.e. $a_H = 1.0$) does not change their general shape but reduces the ranges of diffusion and dispersal rates under which the respective Turing instabilities occur (Figure S4).

3.2 | Coexistence patterns and mechanisms

In Figure 3, coexistence of a superior competitor, H_S , with an inferior one, H_I , is shown as a function of their dispersal rates d_S and d_I . For intermediate values of d_S (between the dashed lines), no Turing instability is induced and coexistence is therefore not possible. At low values of d_S ($\lesssim 0.08$), an oscillatory Turing instability is induced and the autotroph densities on the two patches cycle in anti-phase (see also Figure 4a). Coexistence is possible if H_I has a (moderately) higher dispersal rate than H_S . While the increase of H_S on patch x (between the red triangle markers in Figure 4a) is almost completely driven by autochthonous growth, H_I starts to accumulate biomass on this patch even before the autotroph density is high enough for a positive growth rate (orange upright triangle marker in Figure 4a). Essentially, the higher mobility enables H_I to shift biomass from a patch with momentarily favourable, yet declining growth conditions into a patch with momentarily unfavourable, yet improving growth conditions, suggesting that coexistence is based on bet-hedging behaviour of H_I . Coexistence is not possible if d_I is very high, as this moves too much biomass of H_I from the (temporary) source patch into the (temporary) sink patch. Only if H_I can plastically reduce its effective dispersal rate when growth conditions are favourable, coexistence is possible with arbitrarily high (potential) dispersal rates (Figure S7).

At high values of the dispersal rate of H_S ($d_S \gtrsim 0.25$), a static Turing instability is induced, characterised by constantly large differences in autotroph density A between the patches (Figure 4b). Under these conditions, dispersal of H_S is very maladaptive, as it means exporting lots of biomass from the source (high A) to the sink (low A) patch (red arrow in Figure 4b). Coexistence is possible if H_I has a lower dispersal rate than H_S (or if it can plastically reduce the emigration rate from the source patch, Figure S7), as this balances the competitive

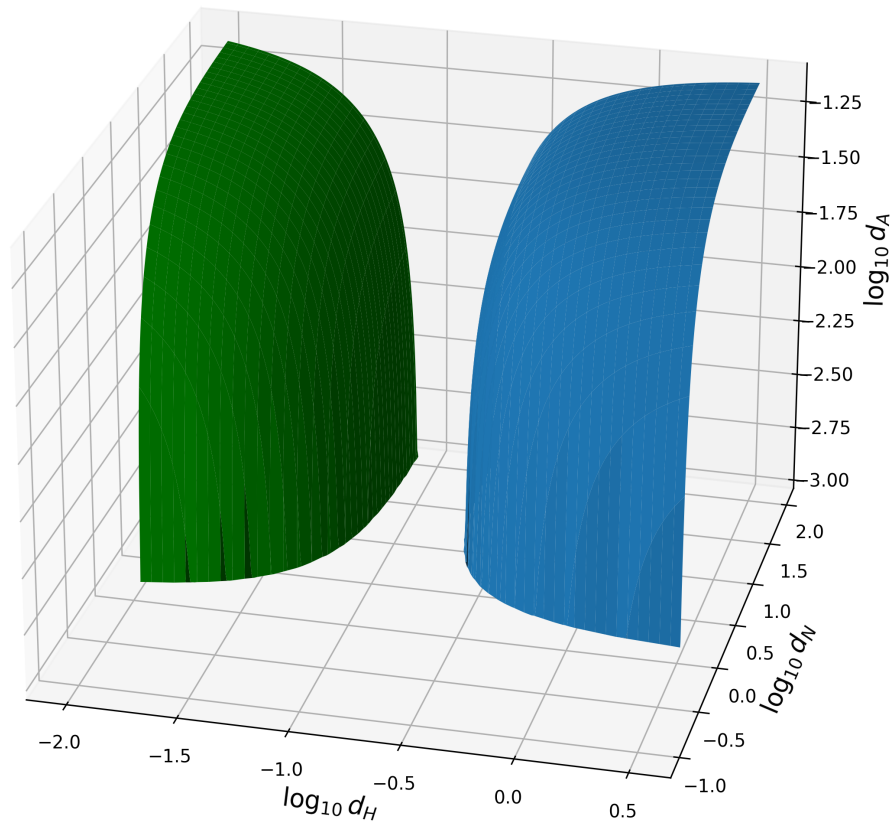


FIGURE 2 Boundaries of Turing instabilities in the $d_N - d_A - d_H$ space in a system with a single heterotroph consumer. Below the green surface, the system exhibits an oscillatory Turing instability leading to antiphase oscillations between the patches. Below the blue surface, the system exhibits a static Turing instability, leading to constantly large differences in autotroph density between the patches. All parameters as in Table 1, $a_H = 1.3$.

disadvantage of H_I by limiting its loss of biomass due to maladaptive dispersal into the sink patch (orange arrow in Figure 4b). Provided a sufficiently low dispersal rate, H_I can even compensate much greater competitive disadvantages (attack rate a_I lower than one-third of that of H_S , Figure S6B) than what we assume in the main analyses.

If pattern formation leads to coexistence of the two heterotroph species, we often observe population oscillations, irrespective of whether H_S initially created a static or an oscillatory spatial instability (Figure 3, darker blue areas, and Figure 4c,d). This is because if H_I persists with a significant density, it also affects the process of pattern formation. For many combinations of the dispersal rates d_S and d_I , the advantage of H_I due to its superior dispersal strategy (given the amount of resource heterogeneity created by H_S) outweighs its competitive inferiority. As H_I becomes more abundant and starts to replace H_S , it suppresses pattern formation or modifies it (from static to oscillatory patterns or vice versa), which causes H_I to lose its advantage again. The time series in Figure 4c,d demonstrate the ensuing permanent or periodic modulation of heterogeneity in the autotroph densities for both coexistence mechanisms discussed above. Dominance of H_S causes the formation of pronounced spatial patterns (large-amplitude anti-phase oscillations before the invasion of H_I , Figure 4c, or repeatedly a large static difference between A_x and A_y , Figure 4d). Under these conditions, a significantly higher or lower dispersal rate, respectively, allows H_I to build up a substantial biomass density and in the case of a static Turing instability induced by H_S even to temporarily outcompete H_S . However, this then suppresses the spatial heterogeneity in autotroph density and allows H_S to persist or even to grow again.

In order to assess the importance of this dynamic modulation of spatial heterogeneity for coexistence, we contrasted the predictions of our model with one that includes the same amount of resource heterogeneity between the patches as H_S creates at a given level of d_S , but as an environmental factor that is not affected by the population dynamics of the species (see Appendix S5 for details). We found that, under these conditions, coexistence of consumers with different dispersal strategies is restricted to much narrower parameter ranges (Figure 3b), as H_I cannot modify the level of resource heterogeneity and consequently often excludes H_S due to its superior dispersal strategy (grey-shaded areas in Figure 3a).

4 | DISCUSSION

Using a generic model, we show that emergent habitat heterogeneity due to self-organised pattern formation enables coexistence of species with different competitive and dispersal abilities in metacommunities. Coexistence relies either on the superior competitor suffering more from maladaptive dispersal between emergent source and sink habitats or on the inferior competitor's more effective bet-hedging in metacommunities with temporally varying resource heterogeneity. Moreover, differences in the species' potential to induce and benefit from spatial pattern formation create a novel mechanism that allows competing species to coexist under conditions where an equivalent amount of environmental, that is, exogenously determined, habitat heterogeneity would not. Underlying this mechanism is a dynamical pattern that strikingly

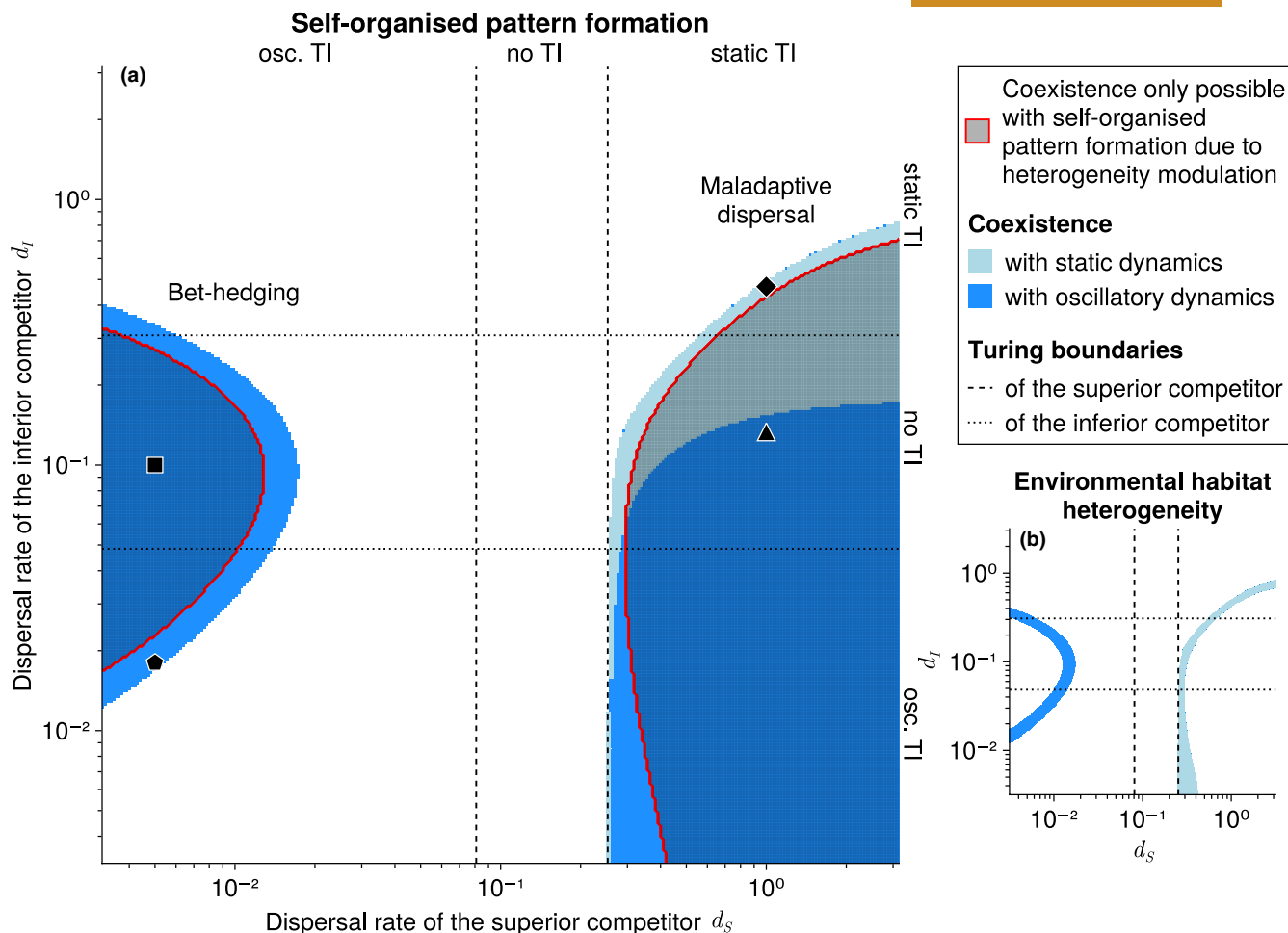


FIGURE 3 Coexistence as a function of the dispersal rates of the competing heterotrophic species H_S and H_I . In panel (a), the coloured regions denote where self-organised pattern formation allows for coexistence with static (light blue) or oscillatory dynamics (blue). In the grey-shaded areas outlined in red coexistence is only possible if the extent of habitat heterogeneity can be modulated dynamically. If habitat heterogeneity is instead determined by the environment, the inferior competitor H_I excludes its competitor H_S in these ranges, leaving only small coexistence areas (b). For reference, the locations of the Turing boundaries in a system with only H_S or only H_I present are included as dashed and dotted lines, respectively. The black geometric symbols indicate the locations of the time series shown in Figure 4 in the $d_S - d_I$ plane.

resembles coexistence due to a gleaner–opportunist trade-off, with each species, when dominant, creating conditions that allow its respective competitor to recover.

4.1 | Consumer coexistence through spatial pattern formation

While superior competitors for shared limiting resources eventually exclude inferior competitors in static, homogeneous environments (Hardin, 1960), species coexistence may be possible in the presence of habitat heterogeneity when different dispersal strategies offset differences in the species' competitive abilities (Abrams and Wilson 2004; Amarasekare, 2010). In contrast to most previous studies, we did, however, not assume that habitat heterogeneity is externally determined, but may intrinsically emerge through the interplay of local trophic interactions and dispersal.

Pattern formation in ecological systems has been studied before, most notably in the context of dryland ecosystems (Kéfi et al., 2010; Klausmeier, 1999; Meron, 2015), but also in other systems such as mussel beds (van de Koppel et al., 2008) or submarine sea grass (Ruiz-Reynés et al., 2017). In these examples, pattern formation is usually linked to an ecosystem engineering process unique to the system under consideration (like the redistribution of ground water by a change in surface water infiltration rate by local vegetation), which limits the generality of findings. In contrast, we study a generic two-patch model which, at its core, only comprises a consumer, a resource and a limiting nutrient. This makes it the simplest ecological model in which both oscillatory and static Turing instabilities (the bifurcations leading to self-organised pattern formation) can occur. While most ecological studies on pattern formation so far have focused on primary producers (Borgogno et al., 2009) and its effect on their (functional) diversity (Guill et al., 2021; Nathan et al., 2013), we show here that the phenomenon is also relevant for higher trophic levels.

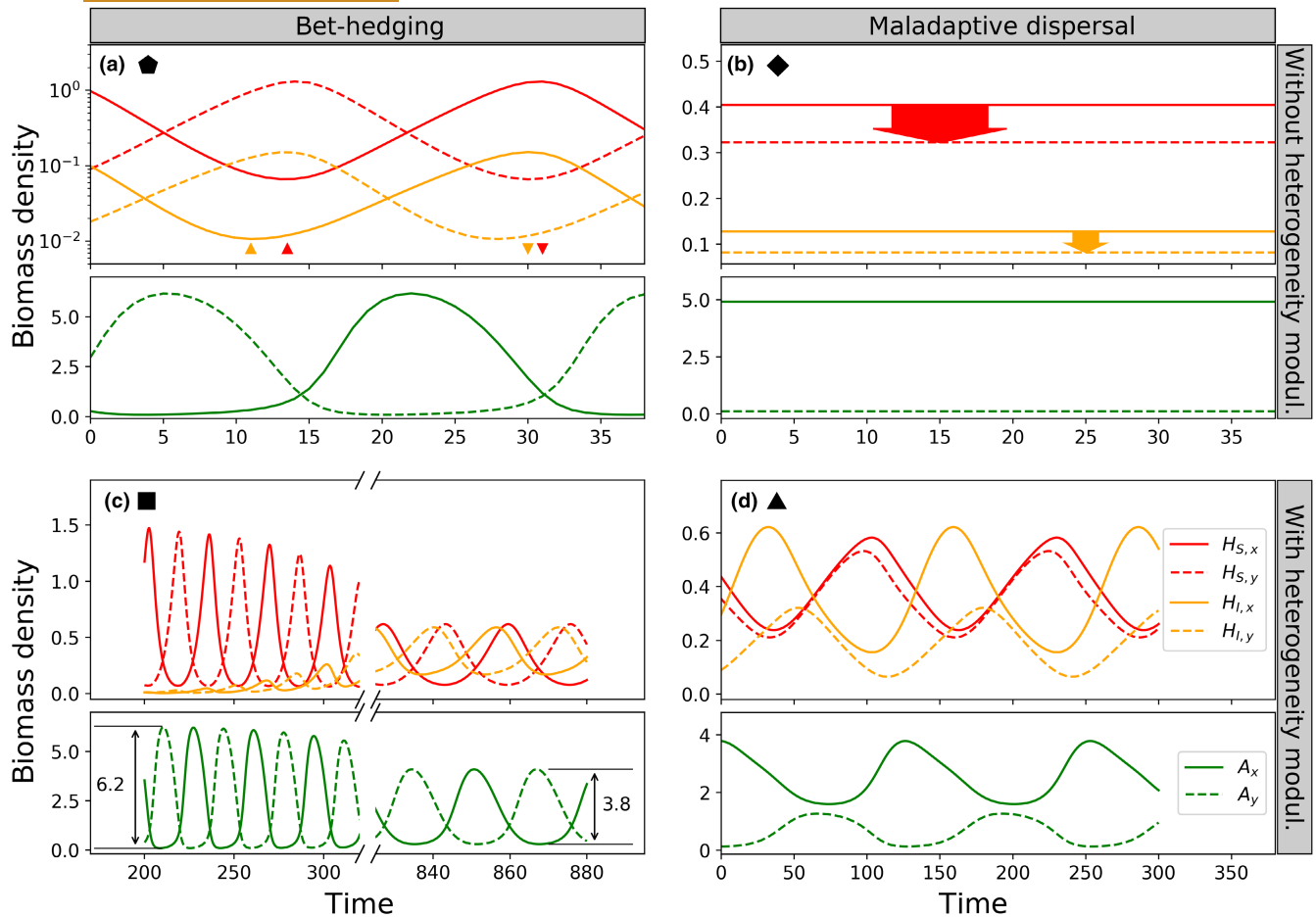


FIGURE 4 Time series of autotroph (green) and heterotroph densities (H_S in red, H_I in orange) illustrating the coexistence mechanisms. Solid lines: Densities on patch x, dashed lines: Densities on patch y. (a) Bet-hedging mechanism, $d_s = 0.005$, $d_l = 0.018$ (pentagon in Figure 3a). The triangle markers indicate where the competitors start (stop) accumulating biomass on patch x. (b) Maladaptive-dispersal mechanism, $d_s = 1$, $d_l = 0.47$ (diamond in Figure 3a). The width of the arrows is proportional to the net flow of biomass from patch x into patch y. (c) Bet-hedging with heterogeneity modulation, $d_s = 0.005$, $d_l = 0.1$ (square in Figure 3a). The numbers indicate the amplitude of the spatio-temporal oscillations of the autotroph biomass density before and after the invasion of H_I . (d) Maladaptive dispersal with heterogeneity modulation, $d_s = 1$, $d_l = 0.13$ (triangle in Figure 3a). Note the different scaling of the axes among panels. All other parameters are as in Table 1.

The basic mechanisms that enable consumer coexistence in this study have been investigated before under the premise of externally provided habitat heterogeneity. In general, coexistence is possible if a trade-off exists between the competitive strength (here expressed as the attack rate on the shared resource) and the dispersal strategy. Whether a low or a high dispersal rate is the superior dispersal strategy, however, is context-dependent. In case of static differences in patch quality, one patch is necessarily a source (enabling positive population growth) while the other is a sink (in which the surplus production of the source dies off) for both species. In this case, a low dispersal rate reduces maladaptive dispersal from source to sink patch and enables coexistence by allowing an otherwise inferior competitor to retain a higher fraction of its total biomass in the source patch (Abrams and Wilson 2004; Amarasekare, 2010; Namba & Hashimoto, 2004). As is shown here for the coexistence of consumers and by Nathan et al. (2013) for coexistence of terrestrial plants that are limited by ground water,

the same mechanism also works when static habitat heterogeneity emerges by self-organisation.

In the contrasting case where the relative quality of the patches changes periodically, an intermediate dispersal rate creates an advantage, which can be best explained through bet-hedging in the spatially and temporally variable landscape. Analogously to bet-hedging strategies that spread reproduction in time via dormant seeds or increased adult survival in temporally variable environments (Childs et al., 2010; Nevoux et al., 2010), dispersal spreads individuals and thus reproductive capacity in space. At intermediate dispersal rates, this increases the total population growth rate during times when the population recovers from low density. However, if the dispersal rate is too high, the phase of positive net immigration into a patch occurs earlier in the population cycle. This implies that a higher fraction of the immigrating individuals faces insufficient resource densities and therefore cannot contribute to population recovery, which ultimately negates the potential of this strategy to balance a

competitive disadvantage. Similar coexistence patterns have been found in a predator–prey model with a priori differences in habitat quality (Lin et al., 2013).

Coexistence through bet-hedging depends on temporal fluctuations in the species densities and can thus be viewed as a generalisation of coexistence due to a competition–colonisation trade-off. The latter focuses on the occupancy of patches by competing species (Levins & Culver, 1971; Tilman, 1994) and considers extreme environmental fluctuations leading to complete extinctions of local populations and necessitating recolonisation of patches. The bet-hedging mechanism, in contrast, explicitly includes the population dynamics of the competitors and their shared resources in the patches. However, in both cases, stability of the environment favours the superior competitor over the species that is dispersing or colonising faster (Pellissier, 2015).

An inferior dispersal strategy of the superior competitor may not only enable persistence of the inferior competitor but can also even lead to the exclusion of the superior competitor. This outcome is especially prevalent if the heterogeneous resource distribution results from environmental differences between the patches (e.g. different supply concentration of nutrients). However, if habitat heterogeneity emerges via self-organisation when the superior competitor is dominant, its exclusion due to a disadvantageous dispersal strategy is much less common. As the inferior competitor gains dominance, it modifies the emergent heterogeneous distribution of the resources in a way that makes its dispersal strategy less advantageous (either by dampening the heterogeneity, or by turning static patterns into spatio-temporal patterns or vice versa) and thus allows the superior competitor to recover. This is similar to coexistence due to a gleaner–opportunist trade-off, where a species that benefits from a fluctuating environment but stabilises it (the opportunist) coexists with a species that benefits from a stable environment but destabilises it (the gleaner, Yamamichi et al., 2022). This mechanism has been considered in a spatial context before (Pacala & Rees, 1998; Wilson & Abrams, 2005), but only under the premise of emergent or forced temporal fluctuations. In contrast, here we show for the first time that this well-established fluctuation-dependent coexistence mechanism (*sensu* Chesson, 2000) can also build upon dynamical creation and dampening of spatial heterogeneity.

Finally, this study focused on random dispersal between the patches, modelled with density-independent per-capita dispersal rates, but species coexistence may also depend on whether the heterotrophs can plastically adjust their dispersal rates in response to fitness-relevant cues. Previous studies found that such dispersal plasticity is essential for coexistence in fluctuating environments, but may make it impossible in static environments if it allows superior competitors to avoid maladaptive dispersal (Amarasekare, 2010; Lin et al., 2013). The last finding aligns with our result that sufficiently plastic dispersal behaviour of the superior competitor prevents the emergence of static spatial heterogeneity (Figure S5F), and thus, the basis for coexistence by the maladaptive dispersal mechanism. On the other side, our

results also show that dispersal plasticity is not necessary for coexistence in fluctuating environments and that the ranges of conditions allowing for coexistence in both oscillatory and static heterogeneous environments expand if only the inferior competitor disperses plastically (Figure S7). This suggests that a trade-off between competitiveness and the ability to plastically adjust dispersal rates can contribute to species coexistence in spatially heterogeneous environments.

4.2 | Relevance of self-organised pattern formation for species coexistence in natural ecosystems

While the structure and parametrisation of our model most closely reflect the properties of plankton organisms in an experimental chemostat set-up, we argue that the findings are relevant for many terrestrial and aquatic ecosystems, given the generic structure and general assumptions of our model and the increasing evidence that self-organised pattern formation may be widespread in natural ecosystems (Medvinsky et al., 2002).

Spatial heterogeneity in the biomass distributions of plankton communities is often observed in aquatic ecosystems (Steele, 1978) and is predominantly attributed to physical processes such as wind-induced mixing or gradients in light, nutrients and temperature (Abraham, 1998; Mackas et al., 1985; Platt, 1972). However, a significant share of the observed variation in the biomass distributions of plankton communities cannot be explained by physical processes alone but may rather result from biological processes (Folt & Burns, 1999; Kornijów et al., 2020; Malone & McQueen, 1983), including self-organised pattern formation (Levin & Segel, 1976). A fundamental requirement for this process is that nutrients, autotrophs and heterotrophs do not all have the same diffusion or dispersal rates (Turing, 1952). In our model, pattern formation occurs for high diffusion rates of nutrients and low dispersal rates of autotrophs. These conditions might be met in very small water bodies or on the microscale within larger water bodies, when molecular diffusion is dominating the movement of nutrients but is irrelevant for macroscopic algal cells (according to the Stokes-Einstein law, Miller, 1924). In contrast, in larger, open water bodies, the movement of nutrients and phytoplankton is likely to be dominated by transport processes of the water (e.g. convection or turbulent diffusion), implying identical diffusion rates. However, other theoretical approaches have shown that, on this scale, self-organised pattern formation in planktonic systems may occur based on the different dispersal rates of phyto- and zooplankton (Levin & Segel, 1976; Malchow, 1993).

A situation that resembles our model system more closely is a number of different, spatially segregated lakes, among which ground water flow may allow for sufficiently fast exchange of nutrients (Hagerthey & Kerfoot, 1998; Robinson, 2015), while dispersal of phytoplankton is limited to passive transport via wind or animals (Incagnone et al., 2014). In our model, the dispersal rate of the zooplankton not only determines whether pattern formation occurs in the first place but also which type of patterns emerges. When water

bodies are directly connected, active swimming and the more directed movement patterns of larger zooplankton organisms (Dodson & Ramcharan, 1991; Pennekamp et al., 2019) may lead to the formation of static biomass patterns, but when zooplankton is restricted to passive dispersal, too, we expect spatio-temporal patterns.

In addition to pattern formation, consumer coexistence in our model further requires that the locally superior competitor has a disadvantage on the regional scale, either by heightened maladaptive switching into resource-poor patches or by insufficient hedging against fluctuating environmental conditions. Evidence exists that especially the second condition is underlying the coexistence of different cladocerans and rotifers. For instance, *Daphnia* species seem to be competitively superior to *Rotifera* species (Gilbert, 1985) while suffering more from dispersal limitation between different segregated ponds (Cáceres & Soluk, 2002). Similarly, the coexistence of several *Daphnia* species with unstable populations that form metacommunities in small rocky pools appears to result from a trade-off between their competitive abilities and dispersal (and colonisation) rates (Hanski & Ranta, 1983).

In terrestrial systems, the autotrophs are sessile plants, that is, they move only once during their lifetime during seed or propagule dispersal. Their dispersal rate is therefore naturally much smaller than the distribution of nutrients (e.g. via groundwater) or even the active movement of herbivores. While considerable variation in maximal dispersal speeds (Hirt et al., 2017) and strategies (Bowler & Benton, 2005) of animals exists, we still expect the comparatively high dispersal rates of terrestrial herbivores to lead to the emergence of static spatial patterns in the species' biomass distributions. Hence, while vegetation patterns in arid ecosystems are often considered to result from water-mediated scale-dependent feedback (Martinez-Garcia et al., 2022), our results suggest that the feeding pressure by mobile herbivores may also play a role.

4.3 | Future perspectives

Self-organised pattern formation in our model requires the transport of nutrients, autotrophs and heterotrophs to occur in both directions along dispersal pathways. This is not always the case in nature as climatic main wind directions or an elevational gradient along freshwater ecosystems can lead to transportation of nutrients and biomass mainly in one direction (Cottenie et al., 2003; Michels et al., 2001). However, theory suggests that spatial pattern formation is still possible under these conditions (Brechtel et al., 2018; Malchow, 2000). The preconditions for pattern formation and its effect on species coexistence may further depend on the complexity of natural food-webs, including additional predators and the potential ability of the consumers to plastically increase their emigration rate in response to high predation pressure (Fronhofer et al., 2018). Finally, the size and topology of the patch network can also affect coexistence possibilities. While we deliberately used the simplest possible patch network, consisting

of only two patches, Zhang et al. (2021) showed that in large, heterogeneous patch networks, multiple species with a strict competitive hierarchy can coexist if they perceive different dispersal networks.

5 | CONCLUSIONS

We show that two different dispersal strategies known to be able to offset competitive disadvantages, namely avoidance of maladaptive dispersal in static environments and bet-hedging in fluctuating environments, do not require external factors to set the stage for consumer coexistence, but also work if the required spatial heterogeneity emerges due to self-organisation. Compared to externally determined heterogeneity, this process adds dynamic flexibility to metacommunities and creates a novel mechanism for coexistence of consumers based on their different abilities to induce spatial patterns and to benefit from them. At the core of this mechanism, a competitive cycle is generated in which each species affects the environment in a way that allows the other species to recover and to become temporarily dominant. Considering that our metacommunity model is very simple and generic, we conclude that spatial instabilities that underlie the demonstrated coexistence mechanisms can be as commonplace as instabilities giving rise to temporal oscillations (e.g. predator–prey oscillations). However, while the latter are often considered as jeopardising species' persistence, we argue that the former should be interpreted more positively, as they support persistence and enable coexistence.

AUTHOR CONTRIBUTIONS

Christian Guill and Toni Klauschies conceived the study design. Felix Nöbler wrote the computer code and performed the numerical simulations (with contributions of Christian Guill); Christian Guill and Felix Nöbler evaluated the data. All authors interpreted and discussed the results. Felix Nöbler wrote the first draft of the manuscript (with contributions of Christian Guill); Christian Guill led the editing. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

No empirical input data were used to conduct the study. The code and data required to reproduce the results are available at Zenodo: <https://doi.org/10.5281/zenodo.10641791> (Nöbler & Guill, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Flow diagram of the model.

Appendix S2: Dynamics in single-patch and spatially homogeneous systems.

Appendix S3: Mathematical criteria and ecological mechanisms for Turing instabilities.

Appendix S4: Sensitivity analyses.

Appendix S5: Model with environmental habitat heterogeneity.

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