

Habitat Heterogeneity, Environmental Feedbacks, and Species Coexistence across Timescales

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ABSTRACT: Classic ecological theory explains species coexistence in variable environments. While spatial variation is often treated as an intrinsic feature of a landscape, it may be shaped and even generated by the resident community. All species modify their local environment to some extent, driving changes that can feed back to affect the composition and coexistence of the community, potentially over timescales very different from population dynamics. We introduce a simple nested modeling framework for community dynamics in heterogeneous environments, including the possible evolution of heterogeneity over time due to community-environment feedbacks. We use this model to derive analytical conditions for species coexistence in environments where heterogeneity is either fixed or shaped by feedbacks. Among other results, our approach reveals how dispersal and environmental specialization interact to shape realized patterns of habitat association and demonstrates that environmental feedbacks can tune landscape conditions to allow the stable coexistence of any number of species. Our flexible modeling framework helps explain feedback dynamics that arise in a wide range of ecosystems and offers a generic platform for exploring the interplay between species and landscape diversity.

Keywords: environmental heterogeneity, ecosystem engineering, habitat modification, metapopulations, coexistence theory, legacy effects.

Introduction

Environmental heterogeneity provides the raw material for niche partitioning in ecological communities. When the environment varies from place to place, differences in how species respond to local conditions can facilitate their coexistence at the landscape scale, even when local coexistence is impossible (Chesson 2000; Amarasekare 2003). This connection between environmental heterogeneity and the maintenance

of species diversity has deep roots in ecology (Andrewartha and Birch 1954; MacArthur et al. 1966; Whittaker 1967) and has been well studied both theoretically (Horn and MacArthur 1972; Chesson 1985, 2000; Iwasa and Roughgarden 1986) and empirically (Schoener 1974; Silvertown et al. 1999; Codeco and Grover 2001; Oliver et al. 2010).

However, this picture becomes more complex when species themselves shape their environment. Feedbacks between the biotic community and landscape conditions across space can enhance or reduce environmental heterogeneity over time (Crooks 2002; Wright et al. 2002; Pastor 2005). Prominent examples include plant-soil feedbacks (Bever et al. 1997; Mangan et al. 2010; Van der Putten et al. 2013) and related Janzen-Connell effects (Janzen 1970; Connell 1971), wherein plants directly or indirectly shape the local densities of soil microbes or natural enemies such as seed predators, generating a dynamic landscape of legacy effects. These processes are thought to play an important role in maintaining the diversity of many natural plant communities, but they may also lead to positive feedbacks that drive monodominance (Wolfe and Klironomos 2005; Van der Putten et al. 2013).

Here, we introduce a flexible modeling framework for community dynamics in heterogeneous landscapes with and without feedbacks that change environmental conditions through time (fig. 1). We build on the classical metapopulation paradigm (Levins 1969) and related patch models, which provide a minimalist approach to studying ecosystems with distinct local and global scales (Chesson 1985; Iwasa and Roughgarden 1986; Amarasekare 2003). The simplicity of this framework allows us to capture and analyze essential features of complex environmental feedbacks. While a range of conceptual and quantitative models (Roughgarden 1978; Gurney and Lawton 1996; Bever et al. 1997; Hui et al. 2004; Raynaud et al. 2013; Liataud

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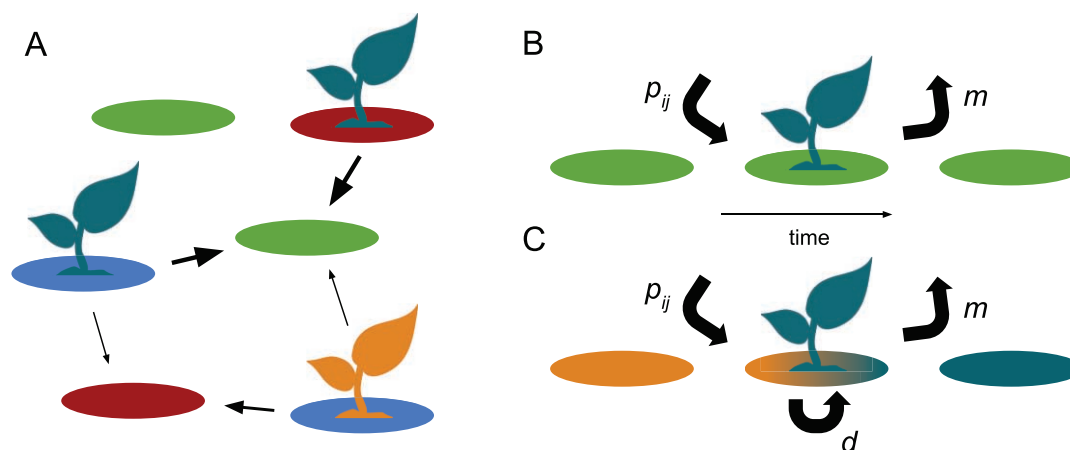


Figure 1: Metapopulation models with exogenous and endogenous patch heterogeneity. We model ecosystems where species disperse between patches with varying local conditions (A). The environmental conditions within a patch, summarized by the patch type or state, influence the rates at which different species can colonize and establish. We consider models where variation in patch conditions is a fixed property of the landscape (B; eq. [2]) or shaped by the biotic community over time (C; eq. [5]). Here, colors indicate patch types/states and species identities. When heterogeneity is endogenous (C), each patch state is identified with a species in the community, reflecting environmental modifications (occurring at a rate d) due to that species.

et al. 2020; Monk and Schmitz 2021) have shed light on such processes—and particularly on when they might help or hinder coexistence—they remain challenging to incorporate in tractable mathematical frameworks. One central obstacle is the high species diversity in many natural systems, although accounting for this diversity is crucial to understanding real-world coexistence (Miller et al. 2021). Additionally, many studies—and even subfields of ecology—focus on a single source of heterogeneity, making it hard to draw general conclusions that cut across system specifics. In particular, fixed (or “exogenous”) heterogeneity and biotically generated (or “endogenous”) heterogeneity have often been approached from very different perspectives (Bolker 2003; Smith 2022). Our models and analysis help overcome these challenges by providing coexistence criteria that extend naturally to communities of arbitrary size and by building endogenous environmental feedbacks directly into a core model for landscapes with exogenous heterogeneity.

We develop a general approach that is agnostic to the specific sources of environmental heterogeneity and allows us to consider feedbacks on a wide range of timescales. We show that our framework includes a recent model for rapid habitat modification (Miller and Allesina 2021) as a limiting case. To delineate the full spectrum of possible dynamics, we focus here especially on the opposite extreme of feedbacks that shape the landscape over very long times. In this limit, we can fully characterize community coexistence. Using a combination of analytical theory and simulations, we show that the same mathematical conditions delineate coexistence more generally. By comparing our

models, we identify essential features of coexistence maintained by exogenous and endogenous heterogeneity. We show that over long times, ecosystems with feedbacks—whether fast or slow—behave similarly to one another and qualitatively differently from systems with exogenous heterogeneity, even though slow feedbacks are difficult to distinguish from exogenous heterogeneity on short timescales. Our results help explain how environmental feedbacks emerge and play out over different timescales, and the modeling framework we introduce offers a platform for comparing exogenous and endogenous heterogeneity on equal footing. Finally, we briefly discuss how our models might be parameterized from observational data and examine other implications for community dynamics in natural communities.

Model

Exogenous Heterogeneity

We consider a landscape composed of many local patches, which can be classified into ℓ discrete types. The type of a patch summarizes its internal conditions, as they are relevant to a focal community of n species inhabiting the landscape. For example, in the context of a plant community, patches might be classified by soil type or topography. The rate at which each species can establish in a patch depends on the patch type and may differ between species, reflecting interspecific differences in niche requirements. For simplicity, we follow conventional models and assume that there is global dispersal between all patches and that

each patch can be occupied by at most one species at any time. Denoting the proportion of all patches that are of type j and occupied by species i at time t by $X_{ij}(t)$ and the proportion of all patches that are of type j and vacant by $y_j(t)$, we can model the dynamics of these proportions across a sufficiently large landscape by

$$\begin{aligned} \frac{dX_{ij}(t)}{dt} &= -m_{ij}X_{ij}(t) + p_{ij}y_j(t) \sum_{k=1}^{\ell} X_{ik}(t), \\ \frac{dy_j(t)}{dt} &= \sum_{i=1}^n m_{ij}X_{ij}(t) - y_j(t) \sum_{i=1}^n p_{ij} \sum_{k=1}^{\ell} X_{ik}(t). \end{aligned} \quad (1)$$

The parameters $p_{ij} \geq 0$ and $m_{ij} > 0$ specify the rates at which species i establishes or becomes locally extinct in patches of type j , respectively. As in classic metapopulation models, the dynamics represent the net action of these two processes: colonization of empty patches by propagules or dispersers from occupied patches and local extinctions at a constant rate per patch. Summations over patch type (index k) reflect the fact that empty patches of type j may be colonized by propagules of species i dispersed from patches of any type. Summations over species identity (index i) reflect the fact that the type is a fixed property of each patch, so a patch of type j always returns to the y_j class when vacated. This also implies that the total proportion of patches of type j , which we denote by $w_j = y_j(t) + \sum_i X_{ij}(t)$, is constant through time for every j .

In principle, local extinction rates may depend on both species identity and patch type; however, in this study we focus primarily on the simplest case where $m_{ij} = m$. Thus, the effects of landscape heterogeneity are realized through rates of establishment, not local persistence. The suitability of this assumption will depend on the community of interest, but environmental heterogeneity is thought to act more strongly on establishment than persistence in many systems, typically because smaller populations or immature individuals are more sensitive to patch conditions (Grubb 1977; Kryazhimskiy et al. 2007; Mächler and Altermatt 2012; Baldeck et al. 2013). We are also assuming that there are no significant differences in local extinction rates between species, reflecting a community of demographically similar species, or a system where local extinctions are primarily driven by external disturbance.

Under this equal m assumption, we can greatly simplify the dynamics by tracking only the proportion of patches—regardless of type—occupied by species i at time t . We denote these proportions by $x_i(t) = \sum_j X_{ij}(t)$. Instead of $\ell \times (n + 1)$ equations, there are now $n + \ell$, given by

$$\begin{aligned} \frac{dx_i(t)}{dt} &= -mx_i(t) + x_i(t) \sum_{j=1}^{\ell} p_{ij}y_j(t), \\ \frac{dy_j(t)}{dt} &= m(w_j - y_j(t)) - y_j(t) \sum_{i=1}^n p_{ij}x_i(t). \end{aligned} \quad (2)$$

The w_j , which must sum to 1, are now seen as parameters that describe the composition of the landscape.

These dynamics take precisely the same mathematical form as a consumer-resource model with external inflow of abiotic resources (Tilman 1980; Butler and O’Dwyer 2018; Cui et al. 2020; Marsland et al. 2020). In this parallel, each species plays the role of a consumer, and each patch type is interpreted as a resource with inflow proportional to w_j . Both “consumers” and “resources” experience density-independent mortality at a rate m , and the p_{ij} are analogous to consumption rates.

Consumer-resource systems of the form in equation (2) have been studied extensively, allowing us to immediately draw conclusions about multispecies dynamics in heterogeneous metapopulations simply by translating results from the consumer-resource setting. For example, it is well known that the number of coexisting consumers is at most equal to the number of resources, a classic result known as the competitive exclusion principle (Levin 1970). Our model equivalence provides a formal demonstration that this intuitive principle carries over to the context of environmental heterogeneity. Given this upper limit, we study coexistence assuming $\ell = n$, representing a fully “packed” consumer community. In this case, equation (2) has at most a single coexistence equilibrium, which is easily expressed in matrix form:

$$\begin{aligned} \mathbf{y}^* &= mP^{-1}\mathbf{1}, \\ \mathbf{x}^* &= m(P^T)^{-1}(D(\mathbf{y}^*)^{-1}\mathbf{w} - \mathbf{1}). \end{aligned} \quad (3)$$

Here, we use the notation \mathbf{y}^* for the vector of equilibrium proportions (and similarly for \mathbf{x}^* and \mathbf{w}), and we collect the coefficients p_{ij} in the matrix P . We also use $D(\mathbf{y}^*)$ for the diagonal matrix with nonzero elements given by \mathbf{y}^* and $\mathbf{1}$ for a vector of n 1s.

Many properties of this equilibrium are known. Coexistence of all n species requires that the equilibrium is biologically feasible, meaning that the components of \mathbf{y}^* and \mathbf{x}^* are all positive. In fact, it can be proven that this equilibrium is globally stable whenever it is feasible, and therefore coexistence is entirely controlled by feasibility (see, e.g., Marsland et al. 2020; for completeness, we provide a novel proof in the supplemental PDF, sec. S1.3).

In accordance with the fact that \mathbf{x} and \mathbf{y} are proportions in our original framing of the model, feasibility of \mathbf{x}^* requires $\sum_j y_j^* < 1$. This means that there is an upper limit on m imposed by the matrix of establishment rates: $m < \mathbf{1}^T(P^{-1})\mathbf{1}$. Remarkably, the vacant patch equilibrium values, \mathbf{y}^* , are completely insensitive to the underlying distribution of patch types in the environment, \mathbf{w} . As in consumer-resource models, this “shielded” behavior arises because the species in the system drive the supply of vacant patches to a point determined only by their own demographic rates (Tikhonov and Monasson 2017). Feasibility of these values

requires that every element of $P^{-1}\mathbf{1}$ is positive, ensuring that there is an attainable mix of vacant patches at which all species have zero net growth. Loosely, in ecological terms this requires that species are sufficiently similar in overall colonization ability (i.e., p_{ij} averaged across patch types) or sufficiently specialized on distinct habitat types (see the supplemental PDF, sec. S1.2, for a detailed interpretation of this condition).

The equilibrium frequencies for species themselves are very sensitive to the landscape parameters, \mathbf{w} . The effect of changing \mathbf{w} on \mathbf{x}^* can be difficult to predict a priori (Tikhonov and Monasson 2017). For example, in figure 2A we show that for many choices of \mathbf{w} , coexistence of all species is precluded, even though all species would persist in all patch types in isolation (i.e., $p_{ij} > m$ for all i and j). Somewhat counterintuitively, species diversity does not peak when the underlying landscape is most diverse (even), which means that increasing the diversity of habitat types will often decrease species diversity (fig. 2B), even leading to extinctions. This kind of unimodal relationship between habitat heterogeneity and biodiversity is often observed in natural ecosystems (Ben-Hur and Kadmon 2020), and our model illustrates a simple generic mechanism for this phenomenon.

Species coexistence is constrained by competitive interference, which arises because the joint distribution of species and patch types reflects not just habitat preference but also source-sink dynamics between patches. The potential for such dynamics in heterogeneous landscapes has long been noted (Horn and MacArthur 1972; Holt 1997; Shurin et al. 2004). In our model, we can examine this joint distribution more closely by returning to the full dynamics in equation (1). The hierarchical structure of equations (1) and (2) implies that each X_{ij} reaches a stable equilibrium value:

$$X_{ij}^* = \frac{1}{m} p_{ij} x_i^* y_j^*. \quad (4)$$

From this expression and visually in figure 3, we see clearly that the net pattern of patch occupancy in an equilibrium landscape is shaped by both the particular rates at which a focal species i can colonize and establish in patches of type j (p_{ij}) and the overall abundance of i and availability of j in the system ($x_i^* y_j^*$). These two factors can be identified with species-sorting and mass effects processes, respectively, which are usually viewed as two ends of a continuum for metacommunity dynamics (Leibold et al. 2004; Shoemaker and Melbourne 2016).

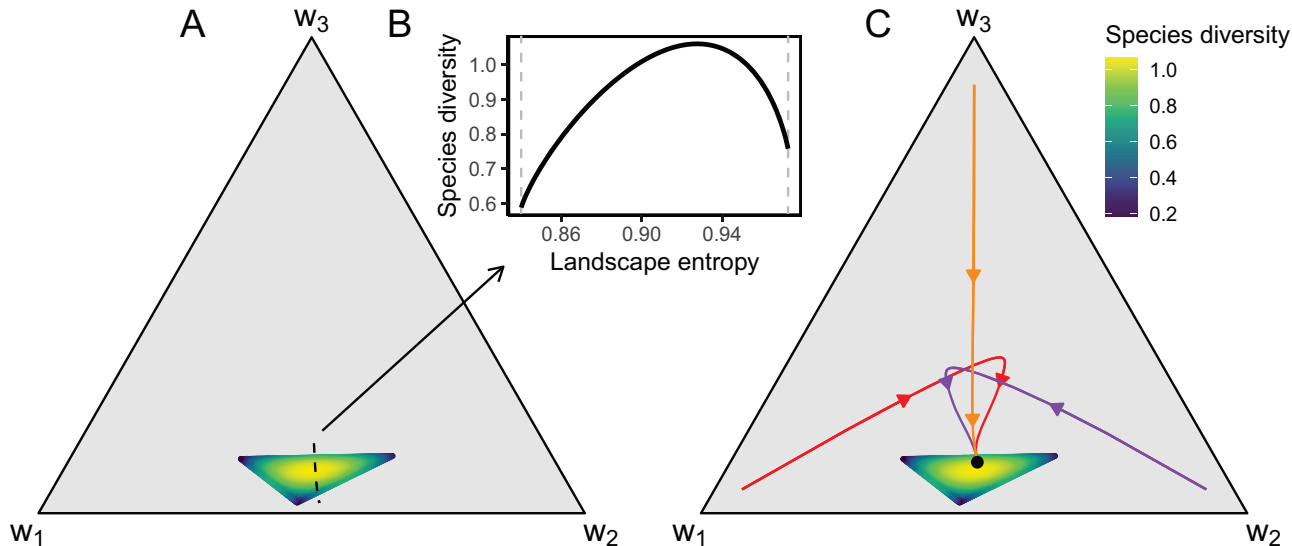


Figure 2: Relationship between landscape parameters (\mathbf{w}) and coexistence for a three-species community without (A) and with (C) feedbacks. When heterogeneity is exogenous (A), coexistence of all three species is possible only for a small subset of \mathbf{w} parameters (colored region; gray points indicate at least one extinction). Diversity of the equilibrium community (measured as Shannon entropy of \mathbf{x}^*) is indicated by colors. The indirect relationship between species frequencies and patch type frequencies (eq. [3]) typically leads to a hump-shaped relationship between species diversity and landscape diversity along a gradient of \mathbf{w} parameters, as illustrated in B. When heterogeneity is instead endogenous (C), the frequencies of patch types change through time. Here, we show trajectories corresponding to $\mathbf{w}(t)$ for three different (infeasible) initial conditions. The P matrix used here satisfies the stability condition discussed in the main text; consequently, these trajectories converge on the equilibrium \mathbf{w}^* (black point), in the feasible region. Here, $d = 1$, illustrating that our results apply for intermediate values of d . Parameters are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.08kpr564>; Miller and Allesina 2023).

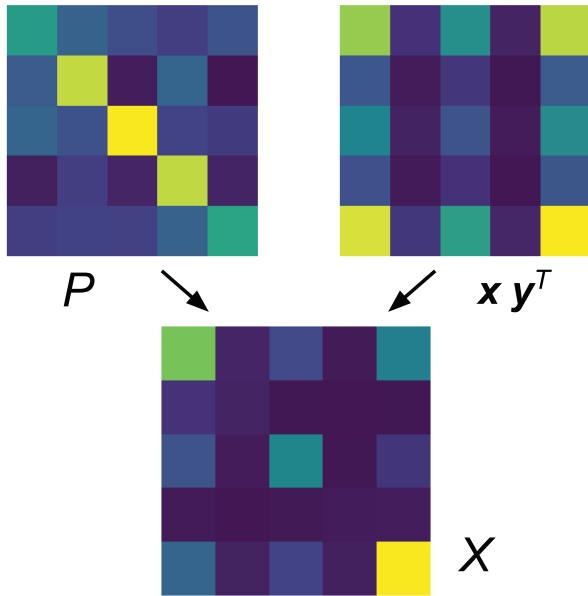


Figure 3: Pattern of habitat association reflects a combination of species sorting and mass effects. The joint distribution of species and patch types at equilibrium, X_{ij}^* (eq. [4]), shown at bottom, is shaped by the matrix of colonization and establishment rates P (left) and the overall abundance of species and vacant patch types in the ecosystem, given by $\mathbf{x}\mathbf{y}^T$ (right). The left pattern sets an expectation based on species' habitat preferences (in this example, strong specialization on distinct patch types), while the right pattern shows the expected distribution if patches were homogeneous. The actual pattern of habitat association is the element-wise product of the two. For visualization, matrices are normalized to have the same mean value. Higher values are indicated by light colors (yellow), and low values are indicated by dark colors (blue).

While many studies of metacommunities focus on determining the importance of one or the other process in a particular community, our model quantitatively predicts how the two act together to shape observed patterns of habitat association.

Endogenous Heterogeneity

Next, we consider how community dynamics change when patch heterogeneity is no longer a static feature of the environment but an outcome of biotic feedbacks. For simplicity and for compatibility with the framework developed for exogenous heterogeneity, we maintain the assumption that patches can be classified into distinct types, although now we refer to patch “states,” since these attributes change through time. Each patch state is associated with a distinct species, reflecting its net impact on local environmental conditions. For example, we might consider distinct soil microbial communities associated with particular host plants (Bever 2002; Schweitzer et al. 2008; Philippot et al. 2013),

immune statuses corresponding to recent infection history in vertebrate hosts (Kucharski et al. 2016), substrate morphologies shaped by benthic “ecosystem engineers” (Levinton 1995; Gutiérrez et al. 2003), or chemical concentrations maintained by different bacterial strains (Ratzke and Gore 2018; Amor et al. 2020). Thus, the number of species and patch states are both n , and we assume these are labeled so that state i corresponds to legacy effects of species i . As before, patch states affect the dynamics of the community by governing the rate of colonization and establishment by each species. We focus on feedbacks mediated by establishment rates, rather than mortality effects, both because establishment may generally be more sensitive to local environmental conditions (as discussed above) and because recent theory suggests that differences in establishment are more likely to have qualitative effects on community dynamics (Ke and Levine 2021).

We approximate changes in local environmental conditions as discrete shifts between patch states. In a patch occupied for some time by species i , we assume that the local population of species i can drive a transition from the current patch state j to state i at some rate d_{ij} . In the main text, we focus on the case where $d_{ij} = d$ is constant across species and patch types for simplicity. However, in the supplemental PDF (secs. S2.2, S2.5), we show that our results also apply to the more general case.

With biotic feedbacks operating, the distribution of patch states in the landscape is now a dynamic variable. But given a particular distribution of patch states $\mathbf{w}(t)$ at time t , we assume that the instantaneous dynamics of colonization and extinction are exactly the same as in equation (1). This leads to the following model for a community with endogenous heterogeneity:

$$\begin{aligned} \frac{dx_i(t)}{dt} &= -mx_i(t) + x_i(t) \sum_{j=1}^n p_{ij}y_j(t), \\ \frac{dy_j(t)}{dt} &= m(w_j(t) - y_j(t)) - y_j(t) \sum_{i=1}^n p_{ij}x_i(t), \\ \frac{dw_k(t)}{dt} &= d(x_k(t) + y_k(t) - w_k(t)). \end{aligned} \quad (5)$$

Intuitively, the total proportion of patches in state k increases when the number of patches occupied by species k , regardless of state, exceeds the total number of occupied patches in state k , regardless of occupant (given by $w_k(t) - y_k(t)$). A detailed derivation of equation (5) is given in the supplemental PDF (sec. S2.1).

As $\mathbf{w}(t)$ evolves over time, it is possible for feedbacks to drive the landscape from a configuration where coexistence would not be feasible to one where all species coexist. For example, in figure 2B, we illustrate a scenario where feedbacks robustly lead to coexistence, as species collectively engineer a landscape (i.e., \mathbf{w}) where all $\mathbf{x}^* > 0$. In fact,

provided that $\mathbf{y}^* = mP^{-1}\mathbf{1}$ is feasible—indicating, as before, that there is some distribution of available patches at which all species have zero net growth—equation (5) always possesses an equilibrium where $\mathbf{x}^* > 0$. In the supplemental PDF (sec. S2.2), we show how this equilibrium can be found by solving an eigenvalue problem and prove that it is always feasible.

Having established that a feasible coexistence equilibrium exists, we now ask when environmental feedbacks will drive the system to it. Unlike equation (2), the dynamics of equation (5) are more complex, and the coexistence equilibrium is not always attracting. Other outcomes may be possible—potentially including nonequilibrium coexistence or multistability—making it difficult to fully characterize the behavior of this model. To better understand when feedbacks will lead to coexistence or other long-term outcomes, we first analyze two limiting cases where patch dynamics and underlying landscape dynamics operate on very different timescales (Liautaud et al. 2020). This permits a natural simplification of the model via fast-slow decomposition (Tikhonov 1952; O’Dwyer 2018; fig. 4).

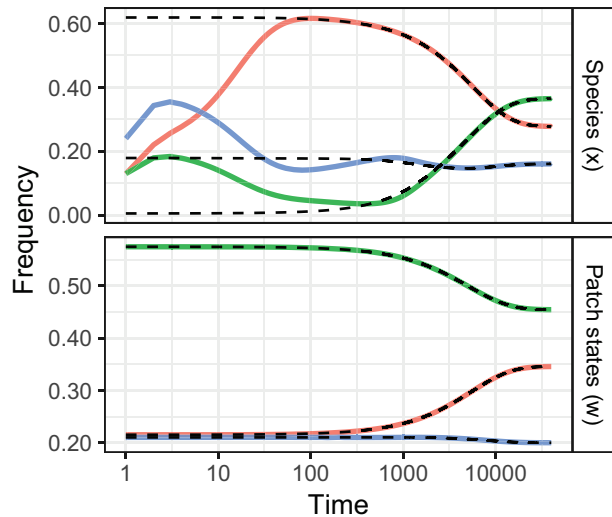


Figure 4: Stable feedback dynamics converge to fast-slow limit. We show the evolution of species frequencies (*top*) and the distribution of patch states (*bottom*) over time when feedbacks are slow. Colored lines indicate the solution obtained by numerically integrating equation (5) with $d = 10^{-5}$. Dashed lines show the predicted dynamics using the fast-slow decomposition. Predictions for patch states were obtained by solving the slow system (eq. [7]), and species’ frequencies were calculated from the predicted $\mathbf{w}(t)$ using equation (3) at each time point. The dynamics rapidly collapse to the slow manifold derived analytically. In these simulations, $m = 0.1$ and the elements of P were sampled symmetrically (independently and identically distributed) from the standard uniform distribution (parameters are available in the Dryad Digital Repository [<https://doi.org/10.5061/dryad.08kpr564>; Miller and Allesina 2023]). Note that time is shown on a log scale to highlight dynamics on short and long timescales.

In the first case, all species modify their local environment very rapidly. Consequently, the state of a vacant patch will invariably reflect the identity of the most recent resident species. Formally, this scenario represents the limit where $d \rightarrow \infty$, and we can apply a fast-slow decomposition. Treating $\mathbf{x}(t)$ and $\mathbf{y}(t)$ as fixed, because these variables change slowly compared with patch states, $\mathbf{w}(t)$, the dynamics of $\mathbf{w}(t)$ become a set of n decoupled differential equations, each with a stable equilibrium where $w_k(x_k(t), y_k(t)) = x_k(t) + y_k(t)$. We take \mathbf{w} to be at this equilibrium at all times (i.e., we fix $d\mathbf{w}(t)/dt = 0$) and substitute in the dynamics for $\mathbf{y}(t)$ to obtain the slow system:

$$\begin{aligned} \frac{dx_i(t)}{dt} &= -mx_i(t) + x_i(t) \sum_{j=1}^n p_{ij}y_j(t), \\ \frac{dy_j(t)}{dt} &= mx_j(t) - y_j(t) \sum_{i=1}^n p_{ij}x_i(t). \end{aligned} \quad (6)$$

In fact, this system is precisely the habitat modification model we have studied previously (Miller and Allesina 2021).

At the opposite extreme, patches change state very slowly (i.e., rarely). This limit corresponds to a system where patches resist modification—for example, where patch states are alternative stable states (Petraitis and Latham 1999; Amor et al. 2020)—but species occasionally drive patches from one state to another. Again, we consider a fast-slow decomposition, now with $d \rightarrow 0$. Taking $\mathbf{w}(t)$ as fixed over short timescales, we obtain a fast system that is identical to equation (2). Provided the equilibrium for this system (given by eq. [3]) is feasible, we have seen that it is globally stable, so we take $\mathbf{x}(t)$ and $\mathbf{y}(t)$ to be at this equilibrium at all times. Then we find the slow system for the gradual evolution of patch states:

$$\frac{1}{d} \frac{d\mathbf{w}(t)}{dt} = ((D(P^{-1}\mathbf{1})P^T)^{-1} - I)\mathbf{w}(t) + m(P^{-1})_A\mathbf{1}. \quad (7)$$

Here, I is the identity matrix of size n , and S_A denotes the antisymmetric part of a matrix, $S_A = S - S^T$. This system is a matrix differential equation, which is very amenable to analysis. In the supplemental PDF (sec. S2.3), we derive a simple graphical condition that characterizes the stability of the coexistence equilibrium, \mathbf{w}^* , in terms of the eigenvalues of the matrix $PD(P^{-1}\mathbf{1})$ (see fig. S1). This matrix is a weighted version of P , which accounts for differences in overall quality between different habitat types. If P satisfies this eigenvalue condition, equation (7) approaches the unique equilibrium solution \mathbf{w}^* , and the corresponding \mathbf{x}^* is feasible.

In the special case where P is symmetric (i.e., $p_{ij} = p_{ji}$), the analysis and interpretation of the model become even simpler. This kind of symmetry may arise naturally (at

least approximately) in systems where the effect of one species' habitat modifications on another species' establishment rate depends on some measure of similarity between them. For example, the degree of spillover of Janzen-Connell effects between two tropical tree species is a function of their phylogenetic relatedness (Gilbert and Webb 2007). In this symmetric case, \mathbf{x}^* , \mathbf{y}^* , and \mathbf{w}^* all become proportional to $P^{-1}\mathbf{1}$. This equilibrium is stable if and only if P has exactly one positive eigenvalue (see the supplemental PDF, sec. S2.3, for a proof). This characterization of stability extends somewhat beyond the context of strict symmetry: for arbitrary P , if exactly one eigenvalue of $PD(P^{-1}\mathbf{1})$ lies in the right half of the complex plane, then the coexistence equilibrium will be stable (although this condition is only necessary for stability if P is symmetric).

Precisely the same stability condition characterizes the dynamics of equation (6) when P is symmetric (Miller and Allesina 2021). The appearance of this stability criterion at both limiting extremes of equation (5) suggests that it might apply more broadly to feedbacks on any timescale. Indeed, this condition characterizes local stability of the coexistence equilibrium when P is symmetric for any value of d (see the supplemental PDF, sec. S2.4). This stability condition offers a quantitative generalization of the notion that each species must modify the environment in a way that disadvantages itself in order to generate negative frequency-dependent feedbacks that maintain diversity. This interpretation is grounded in two mathematical facts. First, for a nonnegative symmetric matrix P to have exactly one positive eigenvalue, it is necessary that $p_{ij} \geq \min(p_{ii}, p_{jj})$ for all i and j . Second, if $p_{ij} > \sum_{k=1}^n p_{ik}/n$ for all $i \neq j$, then the condition is guaranteed to hold. These necessary and sufficient characterizations both effectively limit the rate at which species can colonize patches modified by conspecifics, in agreement with classic conceptual arguments (Janzen 1970; Connell 1971; Bever et al. 1997).

Inspired by the generality of this result, we used numerical simulations to investigate whether the stability condition we derived for nonsymmetric P in the limit $d \rightarrow 0$ also applies more broadly. We find that when P is not symmetric, the local stability of the coexistence equilibrium can vary depending on m . Typically, as m increases, there may be a transition from a stable equilibrium to an unstable one (corresponding to limit cycles or extinction of some species). Miller and Allesina (2021) found this behavior for the fast-feedback model, and we show that these transitions can happen for many values of d (supplemental PDF, sec. S2.5). However, our stability criterion is highly predictive of the model dynamics when m is sufficiently small (see figs. S2, S3). Additionally, when this stability criterion is violated, we find that coexistence

is nearly always precluded, suggesting that this condition is necessary for stability, regardless of the relative timescales of feedbacks and population dynamics. This condition is similarly predictive for the more complex model where there is a distinct d_{ij} for each combination of species and patch state (fig. S4).

These results show that our stability theory, although derived in the extremes of very fast and very slow feedbacks, can explain coexistence much more generally. This consistency highlights the broad features that determine coexistence in the model with endogenous heterogeneity and set these dynamics apart from the model with exogenous heterogeneity. In both cases, we find the same feasibility condition for \mathbf{y}^* , which must always be satisfied for coexistence. With endogenous feedbacks, this is sufficient to ensure the existence of a coexistence equilibrium—coexistence then depends on whether feedbacks are organized in such a way that the system evolves toward it. In contrast, when heterogeneity is exogenous, coexistence depends strongly on \mathbf{w} , because there is no mechanism to engineer landscape conditions favorable to coexistence.

The dynamics of fast and slow feedbacks are not entirely identical, however. The fast-feedback dynamics (eq. [6]) can exhibit stable limit cycles when P is not symmetric (Miller and Allesina 2021). Because equation (7) is a linear system, this behavior is impossible when feedbacks occur on very long timescales. But as $d \rightarrow 0$, the model can still exhibit complex dynamics in the form of long transients (Hastings et al. 2018). In figure 5, we illustrate two interesting and ecologically relevant behaviors that can arise. First, if P meets the stability condition for the slow system (eq. [7]), then the dynamics will eventually reach a stable, feasible equilibrium. However, $\mathbf{w}(t)$ may transiently take on values that are incompatible with the feasibility of some species (i.e., some $x_i(\mathbf{w}(t)) < 0$ for a range of t). In this case (fig. 5A), the dynamics will “jump” between feasible subsystems where some species reach extremely low frequencies. In natural systems with finite size, this might lead to the extinction of these species before the coexistence equilibrium is reached. Alternatively, in very large systems or where there is a source of immigration that can rescue populations from rarity, the dynamics will be highly episodic as the system abruptly switches between feasible states, potentially over long times.

If instead P is not compatible with stability, some species will eventually be excluded from the system because of long-term feedbacks between the community and the landscape. On short timescales, however, the distribution of patch states is approximately constant, and the dynamics of equation (5) will closely resemble those of equation (2). In particular, species frequencies will be stable to perturbations. Thus, we find surprising scenarios where a species rapidly recovers from reduction to low abundance in the

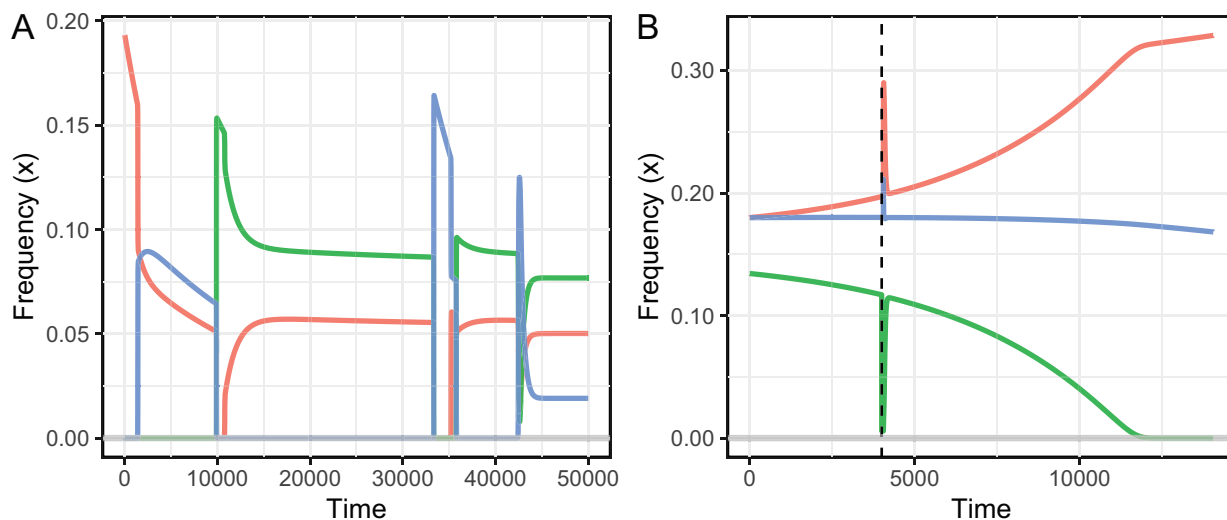


Figure 5: Complex transient dynamics when environmental feedbacks are much slower than community dynamics. We show species' frequencies, $x(t)$, for the two scenarios described in the main text. *A*, When the slow system (eq. [7]) is stable, the ecosystem will eventually evolve toward a distribution of patch states such that species coexistence is feasible. However, if w is transiently incompatible with feasibility of the full community, the system will jump between (transiently) feasible subcommunities, producing highly episodic dynamics. Each species reaches very low abundances during the transient dynamics, which would lead to extinctions in the absence of immigration or storage mechanisms (e.g., seed banks). *B*, When the slow system is unstable, one or more species will eventually be excluded. During the transient period, however, all species are robust to perturbations. Here, the green species, which is driven to extinction by the long-term feedback dynamics, rapidly recovers from reduction to near extinction (dashed line) early in the dynamics. Here, $m = 0.5$, $d = 10^{-5}$, and the elements of P were sampled (independently and identically distributed) from the standard uniform distribution (parameters are available in the Dryad Digital Repository [<https://doi.org/10.5061/dryad.08kpr564>; Miller and Allesina 2023]).

short term, even though it is ultimately doomed to a gradual extinction (fig. 5*B*).

These two scenarios illustrate that species' ability to invade when rare can change at different points in the dynamics, as the community modifies conditions across the landscape.

Discussion

Environmental heterogeneity is commonly understood to beget species diversity, but the converse can also be true. To better understand the relationships between the two, we introduced a simple, tractable modeling framework for species coexistence in an ecosystem where habitat heterogeneity is either a fixed feature of the landscape or dynamically generated through biotic feedbacks. Our models, which are grounded in the metapopulation formalism, add to the rich literature on species coexistence in spatially varying environments and advance ecologists' growing understanding of feedbacks between multispecies communities and environmental variation. For fixed, or exogenous, heterogeneity, our work extends classic models (Horn and MacArthur 1972; Holt 1997; Shurin et al. 2004), recapitulates foundational theory in a new setting (Chesson 1985, 2000; Iwasa and Roughgarden 1986), and formalizes a

connection between habitat partitioning and consumer-resource dynamics. In the context of endogenous heterogeneity, our model demonstrates how environmental modification by different species can lead to the stable maintenance of landscape and species diversity over long timescales and clarifies the conditions under which these processes will occur. The minimal nature of our model makes it a promising tool to understand generic aspects of such feedbacks, which have been studied in many system-specific contexts (Bever et al. 1997; Kucharski et al. 2016; Ratzke and Gore 2018; Ke and Levine 2021).

Crucially, our approach also allows us to study exogenous and endogenous heterogeneity in a shared framework, revealing similarities and differences between coexistence mediated by both kinds of environmental variation. We showed that coexistence under exogenous heterogeneity is sensitive to the distribution of patch types in a landscape but that the stability of a coexistence equilibrium is insensitive to the structure of species' colonization and establishment rates. When heterogeneity is endogenously generated, in contrast, the ecosystem has the capacity to self-tune the distribution of patch states to ensure feasibility. However, the landscape will evolve toward this coexistence equilibrium only if species' patch modifications generate negative frequency-dependent feedbacks.

We derived quantitative criteria for such feedbacks to maintain coexistence and showed that these criteria apply very broadly, beyond the limiting cases we use to derive them.

The connection between our models and well-studied consumer-resource dynamics offers immediate insight and suggests an interesting consequence of environmental feedbacks. Recent studies of consumer-resource models identical to our equation (2) demonstrate that when there are many species and resources, it is exceedingly unlikely to find n species coexisting on n resources; typically, $n < \ell/2$ (Cui et al. 2020). However, in our feedback model (eq. [5]), the resource supply w can be tuned by the community dynamics to allow the coexistence of all species. This self-organization arises naturally from very minimal model assumptions. Additionally, even when some species become extinct in this model, their associated patch states will disappear from the system, leaving an equal number of species and patch types at steady state. Thus, our model predicts that ecosystems with endogenous heterogeneity will always be packed, poised at a shielded equilibrium where the availability of vacant patches is decoupled from their underlying frequency.

Although our models are quite abstract, they may nonetheless lay a foundation for inference in natural systems. Equation (4) expresses a relationship between the joint distribution of patch types and resident species at equilibrium (X_{ij}^*) and the model parameters p_{ij} . A similar relationship holds for equation (5) once the distribution of patch states has equilibrated (see the supplemental PDF, sec. S2.2). We have discussed how this relationship expresses a net pattern of habitat association emerging from the combined effects of species sorting and mass effects. By inverting this relationship, one can also obtain an estimator for each p_{ij} parameter (up to a constant factor, m) in terms of X_{ij}^* and the marginal frequencies x_i^* and y_j^* . In principle, these frequencies could be computed in systems where well-resolved census and environmental data are available. Such data have been collected in plant communities, for example (Harms et al. 2001; Phillips et al. 2003). This method may make it possible to estimate dynamical model parameters from static, observational data, which is highly desirable for systems such as tropical forests, where the slow pace of dynamics complicates experimental or time-series analysis. However, an important challenge to putting this approach into practice is defining operational patch types in context.

Our results suggest other practical considerations for inference and management in natural landscapes. For example, we found that manipulating the distribution of patch types in a landscape (with exogenous heterogeneity) can produce unexpected changes in species frequencies. In particular, we illustrated a case where increasing

habitat diversity quantitatively decreases species diversity qualitatively (causing extinctions), even though all species can persist in all patches (Horn and MacArthur 1972; Shurin et al. 2004). Without a very accurate knowledge of P , it is difficult to predict the effects of a perturbation to the landscape, and without considering the entire community context, it is impossible to determine important practical thresholds, such as the minimum abundance of a habitat type needed to sustain a certain species that relies on it. As another example, we showed that biotic feedbacks can produce situations where all species are transiently resilient to perturbations, despite long-term dynamics that drive some of them to extinction. In such systems, efforts to characterize stability using experimental perturbations or analysis of population fluctuations over short timescales may be misleading over longer timescales (Hastings et al. 2018).

Of course, the abstract formulation of our model means that significant caveats may apply. We sought to explore the relationships between habitat heterogeneity, environmental feedbacks, and species coexistence in a minimal framework for these processes; therefore, our model necessarily neglects other important processes present in real ecosystems. Following other patch models, our framework assumes no local co-occurrence of species and therefore no direct species interactions. This allows us to isolate dynamics mediated by landscape heterogeneity, but direct, local interactions are certainly crucial in many systems and might interact with regional dynamics in nontrivial ways. By focusing strictly on dynamics at the regional scale, we address systems where diversity is maintained by a steady-state mosaic of local patch turnover (Chambers et al. 2013). We also treat space implicitly in our model, but the spatial structure of ecological landscapes could shape how patch modification and dispersal interact. For example, a recent theoretical analysis incorporating both habitat partitioning and Janzen-Connell effects (endogenous heterogeneity) showed that these processes can combine to promote coexistence in a strongly synergistic manner when the spatial autocorrelation of patches is accounted for (Smith 2022). Even when only one source of heterogeneity is present, the spatial arrangement of patches could modulate our understanding of coexistence, for instance by reducing source-sink effects that limit the coexistence of imperfect habitat specialists (Snyder and Chesson 2003).

Our approach also relies on a highly idealized implementation of environmental modification and legacy effects. We assume that patches can be classified into discrete types, and when heterogeneity is generated by the community we assume that each species' effects on the environment can be summarized by a single patch state. This discreteness will only approximate the variation of environmental conditions in some natural systems, although

in others it may be apt. For instance, plant-associated microbial communities can differentiate into discrete types (Bever 2002; Schweitzer et al. 2008; Philippot et al. 2013). We also assume that when environmental conditions change, they do so by shifting abruptly between these discrete states. In reality, local conditions may change gradually, potentially reflecting the legacy effects of multiple past resident species at a single time, especially when change is slow (e.g., in the $d \rightarrow 0$ limit).

Intriguingly, one case where these simplifying assumptions might apply, even for $d \rightarrow 0$, comes from multi-strain pathogen systems (Kucharski et al. 2016). It has long been known that a host's first infection by a pathogen can induce a lifelong imprinting effect, specific to the strain of first infection, that shapes future immune response (Oidtman et al. 2021). This phenomenon, known as original antigenic sin, can have consequences at the level of population and strain dynamics. Recasting individual hosts as patches and imprinting effects that modulate susceptibility as patch states, our model maps naturally onto these dynamics. Here, changes in the "landscape" occur not through shifts between states but through demographic turnover that replaces imprinted hosts (lost to mortality) with naive, newborn hosts on timescales much longer than infection dynamics. In the supplemental PDF (sec. S2.6), we show that an alternative model incorporating these processes behaves qualitatively identically to the model studied above. Our modeling approach could help explain how imprinting effects impact the maintenance of strain diversity. Interestingly, Miller and Allesina (2021) showed that our stability criterion for symmetric feedbacks would imply a "burden of diversity" in such systems—greater strain diversity would raise the threshold for interventions aimed at eradicating the pathogen, a phenomenon that has been investigated in some endemic pathogen systems (He et al. 2021).

This example aside, our mathematical description of environmental modification is likely to be a coarse approximation in many systems. Still, our approach provides a tractable way to link environmental conditions and community composition across varied timescales, offering a first step toward a more complete picture of landscape feedbacks in a multispecies context. Unlike most existing approaches, our model can provide analytical guidance for such dynamics and is even fully solvable in special cases. It has become increasingly clear that environmental feedbacks play a ubiquitous role in mediating interspecific interactions, whether maintaining species coexistence (Bever et al. 1997; Wright et al. 2002), shaping patterns of abundance and productivity (Roughgarden 1978; Mangan et al. 2010; Monk and Schmitz 2021), or driving species invasions (Wolfe and Klironomos 2005; Van der Putten et al. 2013; Amor et al. 2020). Ecosystems

are rarely a one-way street from landscape variation—set by abiotic features or bottom-up biotic process—to species diversity. As such, understanding the dynamic interplay between environmental heterogeneity and top-down habitat modification is an important goal for ecology (Crooks 2002; Pastor 2005; Monk and Schmitz 2021). Simple models for these processes can illuminate essential features of each source of heterogeneity and help unravel how they act and interact to structure natural communities.

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Statement of Authorship

Z.R.M. and S.A. conceived the research. Z.R.M. analyzed the model, implemented simulations, and wrote the manuscript. Both authors contributed to editing and revision.

Data and Code Availability

Code to generate all figures and simulation results, including all parameters used in the text, is available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.08kpr8564>; Miller and Allesina (2023)).

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