ARTICLE

Niche theory for positive plant–soil feedbacks

Athmanathan Senthilnathan 🆔 | Rafael D'Andrea 🆔

Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York, USA

Correspondence
Athmanathan Senthilnathan
Email: athmanathan.senthilnathan@stonybrook.edu

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Abstract

Interactions between plants and the soil are an important ecological process in terrestrial ecosystems as they affect plant community structure: when and where we find different plant species. Those interactions are typically thought of as one-directional: local soil conditions filter through dispersing species to produce a community of locally adapted plants. However, plants can modify local physicochemical soil conditions via their roots and associations with soil microbes. These may in turn affect the local fitness of other plants, making plant–soil interactions bidirectional. In order to understand how they differ from other ecological processes that structure plant communities, we need a theory connecting these individual-level plant–soil feedbacks to community-level patterns. Here, we build this theory with a mathematical model of plant community dynamics in which soil conditioning is explicitly modeled over time and depends on the density of the plants. We analyze this model to describe the long-term composition and spatial distribution of the plant community. Our main result is that positive plant–soil feedbacks will create clustering of species with similar soil preferences. The composition of these clusters is further influenced by niche width and conditioning strength. In contrast with competitive dynamics driven by niche overlap, only species belonging to the same cluster can maintain high relative abundance in the community. Spatial heterogeneity in the form of an environmental gradient generates patches, each representing a single cluster. However, such patchiness is disfavored when species differ in dispersal ability. We show that stronger dispersers cannot take over the habitat as long as an exogenous driver favors soil conditions that benefit the other species. If exogenous drivers supersede soil conditioning by plants, we retrieve classic habitat filtering, where species are selected based on their suitability to the local environment. Overall, we provide a novel mathematical model for positive plant–soil feedback that we use to describe the spatial patterns of plant abundance and traits related to soil preference and conditioning ability.

KEYWORDS
community assembly, mathematical modeling, plant–soil feedback, soil conditioning

INTRODUCTION

The interaction between plants and their environment is a fundamental process in terrestrial ecology. Accordingly, there is a well documented correspondence between plant community composition and phenotypes and their abiotic environment (Bruelheide et al., 2018; Joswig et al., 2021; Keddy et al., 2007; Whittaker, 1970). This correspondence is primarily attributed to habitat filtering; only plants adapted to the local environment will occur in the local community (Cornwell et al., 2006; Grime, 1977; Keddy, 1992; Weiher et al., 1998). However, the narrow focus on how plants respond to the environment misses the other side of this relationship, in which plants modify the abiotic environment.

Plants modify both the aboveground and belowground aspects of their environment. The latter is particularly complex due to the large number of soil microbes and physicochemical components that plants interact with. For example, by exuding polyuronic acid, *Sphagnum* can lower soil pH below 4.5 (Ehrenfeld et al., 2005; van Breemen, 1995). Other plants, particularly invasive species, affect several soil properties. The European buckthorn (*Rhamnus cathartica*) acidifies the soil, reduces nitrogen mineralization, and increases moisture (Cuddington, 2011; Heneghan et al., 2006; van der Putten et al., 2013). In addition, plants selectively associate with complex microbial communities that can modify soil stoichiometry and facilitate nutrient acquisition (Chapin et al., 1994; Kivlin et al., 2022; Northup et al., 1995; Ranelli et al., 2015; Reynolds et al., 2003). This environmental conditioning will have fitness consequences for the plants, thus establishing a feedback. At larger scales of organization, plant–soil feedbacks may have broad consequences for plant species diversity, nutrient cycling, carbon sequestration and other ecosystem services (Carteron et al., 2022; Cornelissen et al., 2001; Wardle et al., 2004). Indeed, the main challenge for plant–soil feedback research is "to show where, when and how plant–soil feedback matters in the real world for explaining and predicting community and ecosystem responses to a changing world" (van der Putten et al., 2016).

To meet this challenge, we need a theory connecting individual-level plant–soil feedbacks to community-level patterns. Competition theory provides a blueprint to address this challenge. For example, competition models suggest that plants competing for light may sort into groups with markedly distinct plant heights (D'Andrea et al., 2019), a pattern that has been observed in tropical forests (D'Andrea et al., 2020). Similarly, we can use mathematical models to obtain expectations for how plant communities are structured when plant–soil feedback is the dominant ecological process. Our mathematical model will complement the empirical effort in linking the strength of plant–soil feedback to relative abundance (Corrales et al., 2016; Klironomos, 2002; Mangan et al., 2010; Reinhart et al., 2021).

The current theory of plant–soil feedbacks is primarily built on phenomenological models of soil conditioning (Bever, 2003; Bever et al., 1997; Eppinga et al., 2018). These models, which can be parameterized by common-garden experiments, have mostly been successful in predicting the community-level consequences of such feedbacks (Bennett et al., 2017; Eppinga et al., 2018; Mangan et al., 2010). However, plant–soil feedback does not always explain community properties. Reinhart et al. (2021) showed this in herbaceous communities where other ecological processes such as herbivory might play a large role in structuring the community. A key result from the plant–soil feedback studies is that stable local coexistence in plant communities requires negative feedbacks—that is, plants conditioning the soil in a way that hampers conspecific performance, for example, via Janzen–Connell effects—in line with the conclusions of modern coexistence theory (Chesson, 2000; Kandlikar et al., 2019; Ke & Wan, 2020). Indeed, negative feedbacks have been the focus of theoretical efforts, although positive feedbacks—when plants are positively affected by increasing conspecific performance relative to heterospecific performance—may allow coexistence in patchy landscapes (Bever et al., 1997).

The connection between classic plant–soil feedback theory and modern coexistence theory is further exemplified by the meta-analysis in Yan et al. (2022). They showed that microbe-mediated plant–soil feedback generally leads to a larger fitness difference than niche difference, which causes competitive exclusion. Coexistence theory was founded on models of competition based on consumer–resource interactions (Barabás et al., 2018; Chesson, 2000; Levine & HilleRisLambers, 2009). When extended to more than two species, such models have successfully explained several trait patterns in consumer communities (D'Andrea et al., 2020; Kraft & Ackerly, 2010; Scheffer & van Nes, 2006; Yan et al., 2012). Conceptually, those models describe strictly competitive interactions, which are then used to explain coexistence as a consequence of negative feedbacks. In contrast, soil conditioning by plants to favor themselves over others can lead to exploitative or facilitative interactions in a community depending on the relationship between the soil preferences of the species in the community and the current soil condition. However, when treated as a pairwise interaction, such soil conditioning by plants will lead to positive plant–soil feedbacks, because plants that are grown in soil conditioned over a long time by a monoculture of conspecific plants will have higher fitness than those grown in other soils (Bever et al., 1997). Positive species interactions have, in general, received less attention in community

ecology due to the overwhelming interest in understanding the role of competition in species coexistence. Recent work such as that by Koffel et al. (2021), which extends classic niche theory to include positive interactions, shows a promising path forward for understanding how positive interactions and feedbacks that emerge from them affect ecological communities.

Here, we expand the theory of plant–soil feedbacks by answering the question: How does positive soil conditioning affect species abundance along an environmental gradient? To achieve this, we examined the impact of positive feedbacks on spatial community patterns in the context of three key factors and processes: historical contingency, exogenous drivers, and dispersal limitation.

1. Historical contingency adds constraints to the trajectory of a freshly assembling community. They result from the conditioning of the soil by previous communities, and as such will depend on the historical composition of the plant community and the broader ecosystem (Cuddington, 2011; van der Putten et al., 2013). Plants are known to leave legacy effects in the soil they condition, and these effects last even after the plants themselves are removed (Grman & Suding, 2010). At a longer timescale, the history of the ecosystem determines geological features such as water flow and the distribution of soil types, which in turn set the initial soil conditions presented to a new plant community. Under positive plant–soil feedbacks, these initial conditions—the *soil origin*—can have a strong influence on community outcomes. However, negative plant–soil feedbacks lead to stable coexistence, and the relative abundance of the plants does not depend on the soil origin.

2. In addition to setting the stage for a new community, geological and climatic features may pull the environment toward a specific abiotic state independently from conditioning by plants, and thus operate as an exogenous driver of local soil conditions. For example, the soil tends to be moister on the windward side of mountains. Such exogenous drivers work to return the environment to a specific state despite conditioning by plants. This may impact coexistence and modulate community composition across space. Previous mathematical models of plant–soil feedback simplify this phenomenon as soil returning to an unconditioned state in which the host-specific soil microbes are absent (Kandlikar et al., 2019; Ke & Levine, 2021).

3. Dispersal limitation is a major driver of plant community composition and coexistence (Ehrlén & Eriksson, 2000; Levine & Murrell, 2003; Muller-Landau et al., 2008; Tilman, 1997). Plants may not be present in habitats where they are expected to thrive due to poor dispersal ability. Alternately, a strong disperser may survive in initially unsuitable habitats, especially if it also strongly conditions the soil (Suding et al., 2013). Interspecific variation in dispersal ability combined with variation in soil conditioning can lead to complex spatial patterns.

We propose a spatial model of plant–soil feedbacks in a plant community in which soil conditions can be spatially heterogeneous and species differ by their soil preference, defined as the soil condition where their carrying capacity is highest. Each plant conditions the soil to match its preference, characterizing positive feedbacks. First, we show that plants differing in their soil preference will form species clusters: that is, groups of species with similar soil preferences that can dominate the community at local scales. Species in the same cluster can maintain high relative abundance, while those in different clusters cannot, in direct opposition to systems with negative feedback. Second, we describe the effects of the soil origin and an exogenous driver on the species clustering pattern. Third, we show that a sufficiently steep gradient in soil origin generates spatial patches where patches differ by which species cluster it represents. Finally, we describe the effect of the exogenous driver and dispersal on the spatial patch size and boundary.

METHODS

Our model describes a community of n plant species that interact with each other by conditioning their shared environment. We assume that each species conditions local soil stoichiometry, either directly or indirectly by associating with a distinct mycorrhizal community, to suit the nutrient needs of the host plant (Ehrenfeld et al., 2005; Northup et al., 1995; van Breemen, 1995; van der Putten et al., 2013). We further assume that different soil stoichiometric states can be arranged on a continuous axis, which we will call the soil condition E. Plant species differ by the soil condition where they do best and can condition the soil toward their own optimum, thus forming a positive plant–soil feedback (Klironomos, 2002; Van Nuland et al., 2019; Wardle et al., 2004). Soil conditioning by a particular plant species can benefit or harm another species, depending on where the two soil preferences are relative to the current soil condition. Finally, we consider our plant community to be distributed along a one-dimensional space, such as along a transect or a mountain slope. While this assumption precludes spatial patterns in higher dimensions, such as labyrinths and gap-and-stripe patterns of vegetation (Rietkerk et al., 2002), our model can be naturally

extended to higher dimensions to explore more complex scenarios. We model the dynamics of the plant population density N_i and the soil condition E at spatial location x (1-dimensional) by the following system of differential equations,

$$\frac{\partial N_i(x,t)}{\partial t} = \gamma_i N_i(x,t) \left(1 - \frac{N_i(x,t)}{K_i \exp\left(- \frac{(\varepsilon_i - E(x,t))^2}{2\omega_i^2} \right)} \right) + \frac{F_i}{\sqrt{2\pi\sigma_i^2}} \int \exp\left(- \frac{(x-y)^2}{2\sigma_i^2} \right) N_i(y,t) dy, \quad (1a)$$

$$\frac{\partial E(x,t)}{\partial t} = \eta_0 (E_0(x) - E(x,t)) + \sum_i \eta_i (\varepsilon_i - E(x,t)) N_i(x,t). \quad (1b)$$

Our model builds upon previous models of population dynamics with dispersal. We assume that plants follow logistic growth independently at each spatial location, and the benefit to the plant from soil conditioning comes as an increase in its local carrying capacity. While strictly positive, the carrying capacity can be arbitrarily low if the soil does not match the species' preference. This assumption enforces the rule that all species will coexist regardless of the soil condition, which in turn signifies that soil conditions in the landscape are fully contained within all species' fundamental niches (Carscadden et al., 2020). While this precludes extinction and competitive exclusion sensu strictu in our model, it serves our purpose of examining how abundance patterns among coexisting species may relate to the process of soil conditioning. Furthermore, our choice to focus on patterns of commonness-rarity among coexisting species, and not on species coexistence per se, circumvents the theoretical challenges involved in finding and interpreting the conditions of stable coexistence in communities with more than two species (Allesina & Levine, 2011; Barabás et al., 2016; Hofbauer & Schreiber, 2010; Saavedra et al., 2017).

We assume that plants disperse following a Gaussian dispersal kernel centered at the parent with a standard deviation σ_i, although any offspring that disperses outside the range perishes. The local soil responds to conditioning by the plants, and may also have a natural tendency toward a specific state driven by exogenous factors such as streams or nutrient deposits.

Equation (1a) represents the change in population density of species i at spatial location x, where γ_i and K_i are the intrinsic growth rate and maximum carrying capacity, respectively. Although plants are discrete entities that occupy finite amounts of space, we use a continuous representation of space for mathematical convenience. This can be done by interpreting $N_i(x)$ as the abundance density of species i at location x, and the abundance of the species in a given area A as the integral of the population density over that area $\int_A N_i(x)dx$. The first term in Equation (1a) represents the balance between local recruitment and mortality, which has a maximum of γ_i: the intrinsic growth rate. The second term accounts for incoming seeds dispersed from elsewhere. Parameter F_i represents per capita seed output: fecundity. The carrying capacity is at its maximum K_i when the local soil is optimal, and drops as a Gaussian function of the difference between the current soil condition E and the soil preference ε_i of species i. This drop in carrying capacity is represented by the species niche width ω_i; that is, the range of soil conditions around its optimum where the species carrying capacity is nonnegligible, $\exp(- (\varepsilon_i - E)^2 / 2\omega_i^2) \lesssim 1$. η_i represents the strength with which a species can condition the soil. We identify species by a unique set of five high-level traits: soil preference ε_i, niche width ω_i, conditioning strength η_i, fecundity F_i, and dispersal range σ_i.

The exogenous driver represents the abiotic forces that maintain the soil condition at $E_0(x)$. The strength of this exogenous driver is denoted by the parameter η_0, which is the exponential rate at which the soil reverts to $E_0(x)$. Because the soil condition will be at $E_0(x)$ in the absence of plants, we use this to also represent the initial soil condition and call it the *soil origin*. Hence, the first term in Equation (1b) represents the tendency of the abiotic environment to return to the soil origin.

RESULTS

We analyze our model in steps starting from the simplest case with two species, no exogenous driver, and no spatial dynamics (*Results: "Two-species community"*). The two-species case lets us establish the concept of species clusters. Next, we add different factors and processes to our model and describe the equilibrium behavior of the community. In *Results: "Three or more species"*, we analyze a three-species community and summarize a numerical method to identify species clusters in larger communities. In *Results: "Effect of an exogenous driver"*, we introduce an exogenous driver in two- and three-species communities. We also describe the broad effects of an exogenous driver in larger communities. The remaining sections contain results on spatial community patterns based on our analysis of two or three species in space. In *Results: "Patchy spatial patterns under environmental gradients"*, we describe the effects of environmental gradients in the absence of exogenous driver and dispersal. *Results: "Effect of dispersal on the patches"* and

"Effect of the exogenous driver on the patches" maintain the environmental gradient and introduce an exogenous driver and dispersal, respectively.

Two-species community

In a two-species plant community with no dispersal and no exogenous driver, the equilibria with at least one species extinct are all unstable, meaning that species will grow away from zero abundance upon any small disturbance. If the species soil preferences ε_1 and ε_2 are sufficiently close, there is a single equilibrium that is always stable. This means that regardless of initial conditions, the soil will always equilibrate at the same value, and so will the abundance of both species. Conversely, if ε_1 and ε_2 are sufficiently different, then there are two alternative stable states. In this case, the system may reach either of

the stable equilibria depending on initial conditions (see Appendix S1: Section S1 and Appendix S2 for details). We classify species into clusters using the stable states in the dynamics. Namely, we associate each cluster with a different stable state, such that the two species belong to the same species cluster if there is only one stable state, and to different clusters if there are two stable states. In all cases, the soil condition at any of the positive equilibria is strictly between the soil preference of the two species. Figure 1a shows the bifurcation diagram with respect to the soil preference of species 2.

Empirically, we can interpret such a bifurcation pattern using a collection of two-species communities. The communities differ in the soil preference (e.g., acidity) of one species while the other species has a fixed soil preference. They are placed along the *x*-axis in increasing order of the difference in their soil preferences in Figure 1a,b. For simplicity, we assume that the species only differ

(a)

(b)

(c)
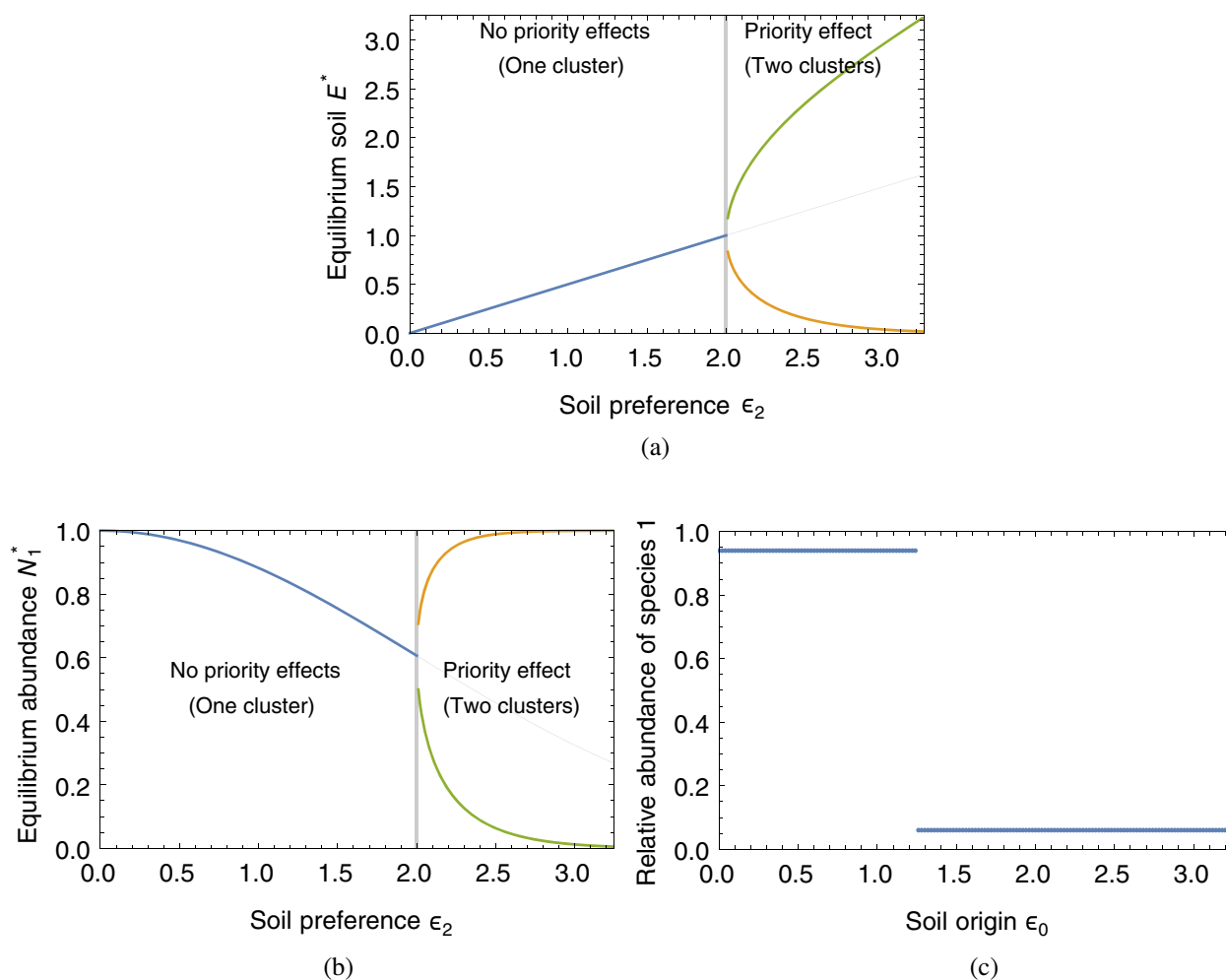
FIGURE 1 Long-term behavior of a two-species community with no spatial dynamics. The blue, orange, and green lines represent stable equilibria, and the gray lines show the unstable equilibrium. The equilibrium soil condition and abundance of species 1 are shown in panels (a) and (b), respectively. Soil preference of species 1 is fixed at $\varepsilon_1 = 0$, and conditioning strengths are $\eta_1 = 1.5$, $\eta_2 = 1$. Intrinsic growth rate (γ_i), carrying capacity (K_i) and niche width (ω_i) of both species were set to 1. In panel (c), we show that the community experiences priority effect (there are two clusters) and the relative abundance depends on the soil origin (ε_0) when $\varepsilon_1 = 0$ and $\varepsilon_2 = 2.5$.

based on their soil preferences (see Appendix S1: Section S2 for the effect of inequality in conditioning strength). These communities can be divided into two types based on the number of clusters. When both species have sufficiently similar soil preferences (left of the gray vertical line in Figure 1a,b), there is a single cluster (i.e., one inevitable outcome), with the equilibrium soil condition midpoint between the soil preference of the two species. Both species have equal relative abundance in this case. When the species have very different soil preferences, there are two clusters. In this case, the equilibrium soil condition and the relative abundance depend on the soil origin (Figure 1c). Particularly, the species with soil preference closer to the soil origin will have significantly higher relative abundance, and we say that species "dominates" the community. Such sensitivity to initial conditions in the two-cluster scenario is often referred to as priority effects (Fukami, 2015). Using the "priority effects" language, we say that the two species belong to the same cluster when the community does not experience priority effects, and to different clusters when the community does.

Figure 2a generalizes those results when the conditioning strength of the species is allowed to differ. The x and y axes show, respectively, different values of the conditioning strength (η_2) and soil preference (ε_2) of species 2 while keeping those of species 1 fixed. The colored region represents the values of species 2's traits leading to

a single cluster, while points in the white region represent values leading to two clusters. Essentially, we get one cluster when both species have similar soil preferences; in that scenario, both species will co-dominate if their strength of conditioning is also similar (teal region in Figure 2a), or the stronger conditioning species will dominate the other when their conditioning strengths are very different (yellow and blue regions). In the white region, species soil preferences are different enough that either species will dominate the other depending on initial conditions but both cannot co-dominate. In extreme cases in which one species has a much stronger conditioning ability than the other, it will dominate regardless of initial conditions (one cluster) even when their soil preferences are very different. Appendix S1: Section S4 shows the effect of niche width on the bifurcation pattern, Appendix S1: Section S5 details the numerical methods used to find these regions.

Three or more species

Now we consider plant communities with more than two species. We only describe the positive equilibria and their stability. Any equilibrium with at least one extinction is unstable because the growth rate of the species is positive when they are rare. In Appendix S1: Section S1, we show
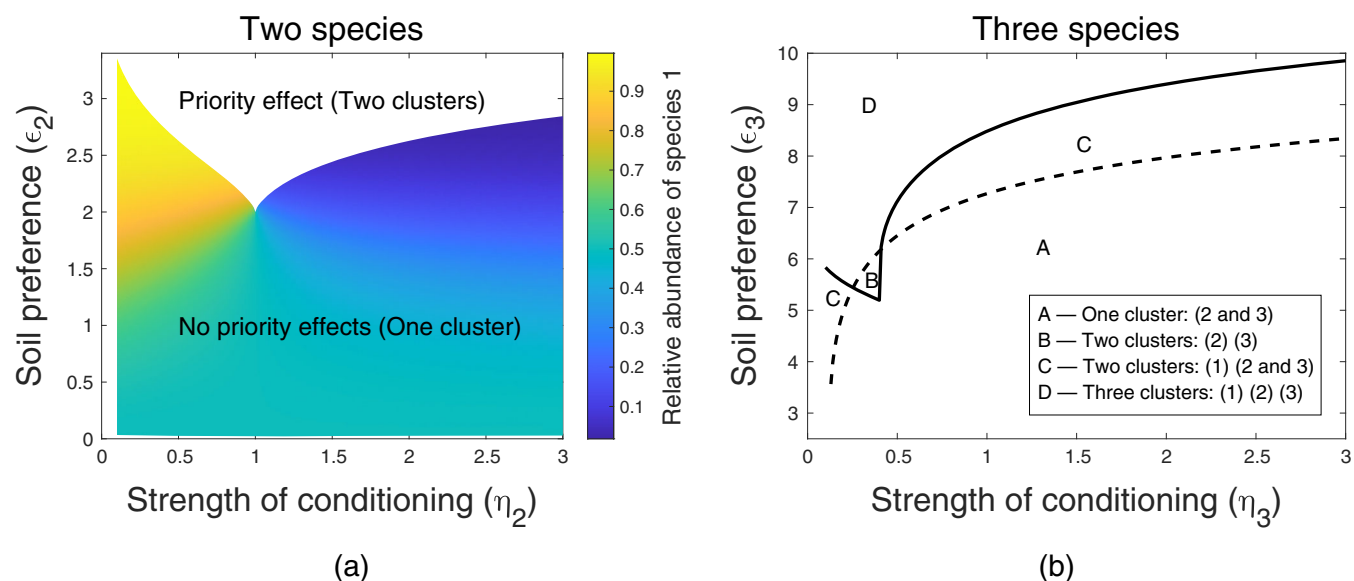
FIGURE 2 Two-parameter bifurcation diagram. The curves divide the $\varepsilon \times \eta$ parameter space into regions of different numbers of species clusters. (a) In a two-species community with $\varepsilon_1 (= 0) < \varepsilon_2$, there are two species clusters when the parameters are above the curves (priority effect), and only one cluster below the curve. (b) In a three-species community with $\varepsilon_1 (= 0) < \varepsilon_2 (= 2.5) < \varepsilon_3$, there are either one-, two-, or three-species clusters. Species 1 will always have very low relative abundance below the dashed curve and forms a single-species cluster above it. Species 2 and 3 belong in the same species cluster below the solid curve and different clusters above the solid curve. Together, the two curves divide the parameter space into four regions that represents different set of possible dynamical outcomes in the community. There are no priority effects only in region A. The strength of soil conditioning (η) for all species not shown on the x-axis is 1. Intrinsic growth rate (γ) and carrying capacity (K) for all species were set to 1. Niche width was set as $\omega_1 = \omega_2 = 1, \omega_3 = 2.5$.

that a community with n species has at most n alternative stable states. These states represent species clusters, as in the two-species case described above. In this section, we provide a recipe to count the clusters and determine their species composition, starting with three species.

When there are more species than clusters, some species must share a cluster. Two species in different clusters will never have high abundance together—that is, they cannot co-dominate regardless of the soil origin—whereas two species in the same cluster will usually both be abundant or both be rare in a local community, depending on the soil origin. The exception to this (hence the "usually" above) is when the strength of conditioning among same-cluster species is highly asymmetric: in that case, when the soil origin favors that cluster, the species with the strongest conditioning ability will dominate the community.

We again use a two-parameter bifurcation diagram to determine the clustering pattern in a three-species community with soil preferences $\varepsilon_1 < \varepsilon_2 < \varepsilon_3$. If species 1 and 2 belong to the same cluster in the absence of species 3, then the clustering structure with species 3 included is qualitatively similar to the two-species case in Figure 2a. All three species belong to a single cluster when ε_3 strategy is sufficiently close to ε_2. Alternatively, there are two clusters, with species 3 being in a cluster by itself.

If species 1 and 2 belong to different clusters in the absence of species 3, and species 3 has a wider niche (i.e., maintains large carrying capacity within a wide range of soil conditions) than species 1 and 2, then there will be four qualitative clustering scenarios (Figure 2b). In region (A), there is a single cluster composed of species 2 and 3. In this scenario, species 3 has high conditioning strength and soil preference close to species 2 but far from species 1. In such a community, species 2 and 3 strongly condition the soil together, which benefits them while suppressing species 1 regardless of the initial conditions. Species 2 and 3 will co-dominate the community, unless they differ in both conditioning ability and soil preference to such a degree that the stronger conditioner dominates the community outright. Region (B) has two clusters: now species 2 and 3 have sufficiently different soil preferences that either of them will dominate, but not both. Species 1 is rare regardless. Region (C) also has two clusters: species 2 and 3 are back to being in the same cluster while species 1 is alone in another cluster. Thus, either species 1 dominates, or species 2 and 3 co-dominate. Finally, region (D) has three clusters: soil preferences of all species are so different that any one of the three species can dominate depending on initial conditions. The situation is qualitatively simpler when species 3 has a comparable niche width to the other species, in which case only regions (C) and (D) are feasible: species 1 can dominate depending on initial conditions. Appendix S1: Section S6 shows bifurcation plots with species clusters of different compositions.

Recall that here the number of clusters is equal to the number of alternative stable equilibria, and not the number of species expected to dominate. The latter will be determined by the initial conditions (the soil origin) and the number of species sharing the prevailing cluster. We also note that when plants do not condition the soil, species abundance will strictly reflect the proximity of their respective soil preferences to the soil origin.

In the general case of a n-species community, we can extend this cluster-counting method to determine the number of species clusters and their composition. We do this using a decision tree where we first determine whether the two species with the lowest values of soil preference would belong to the same cluster if they were the only species in the community (using the equivalent of Figures 1 or 2a). At the second step of the decision tree, we determine whether the species with the third lowest value of soil preference would belong to the same cluster as species 2 in a community with only the three species (using Figure 2b). We continue building the decision tree by including the species with the next lowest value of soil preference, until we reach the species with the highest value of soil preference. This method works because the cluster composition of all the species included in one step of the decision tree does not change in subsequent steps.

Effect of an exogenous driver

We demonstrate the effect of an exogenous driver using a two-parameter bifurcation diagram similar to the multispecies case. Figure 3 shows the species clustering pattern for different strengths of the exogenous driver (η_0) when the soil origin (ε_0) is in between the smallest and largest values of soil preference. First, we consider a two-species community in which the soil preferences are far apart such that there are two species clusters (Figure 3a). In that community, a strong exogenous driver will lead to the loss of a cluster, that is, there is only one cluster containing a single species (colored regions). The species with soil preference closest to the soil origin will dominate. However, the two clusters remain unaffected if the driver is sufficiently weak (white region). The region in $\varepsilon_0 \times \eta_0$ space where the two clusters are unaffected becomes larger as the difference between the soil preferences increase (Appendix S1: Section S7).

Second, we consider a three-species community where the soil preferences are such that there are three single-species clusters. Similar to the two-species community, a strong exogenous driver leads to a loss of species clusters. Clusters are lost one by one as the strength of the exogenous driver increases. When the exogenous driver is weak and the soil origin is close to the species with the
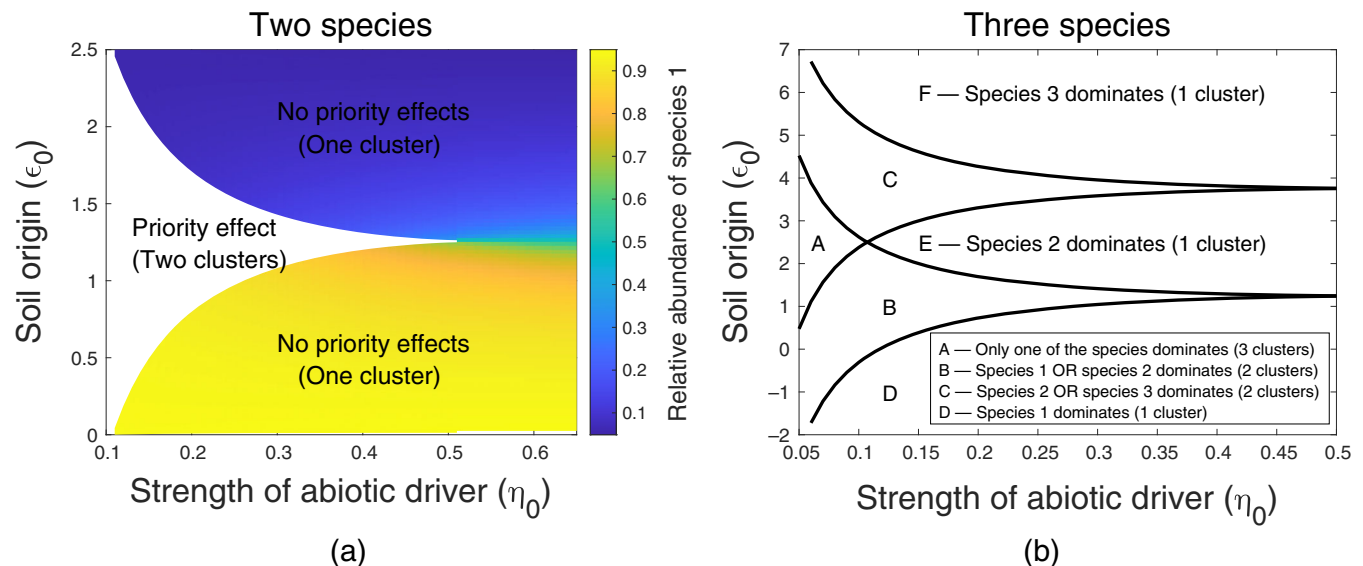
FIGURE 3 Two-parameter bifurcation diagram representing the effect of an exogenous driver. (a) In a two-species community with $\varepsilon_1(=0) < \varepsilon_2(=2.5)$, their initial abundances determine that of them dominates for parameter values in the conical region between the two curves. There are no priority effect outside the conical region. (b) In a three-species community with $\varepsilon_1(=0) < \varepsilon_2(=2.5) < \varepsilon_3(=5)$ either a single species dominates or priority effects determine that species dominates among two or three species. There are no priority effects in regions D, E, and F. The strength of soil conditioning (η) and niche width (ω) are both 1 for all the species. Intrinsic growth rate (γ) and carrying capacity (K) for all species were also set to 1.

intermediate soil preference (region A), all three clusters remain unaffected, as expected in a community with no exogenous driver. In region (B), the soil origin is far from the preference of species 3 ($\varepsilon_3 = 5$) and the exogenous driver is strong enough that species 3 will always be rare, i.e., we lose the cluster with species 3. Similarly, in region (C), species 1 will always be rare. In regions (D), (E), and (F), the exogenous driver is so strong that only one cluster remains (Figure 3b).

In the general case of a *n*-species community, we can infer the exact clustering pattern by first studying the community without the driver and then using the $\varepsilon_0 \times \eta_0$ bifurcation diagram to determine the clusters that are lost for different soil origins and the strengths of the exogenous drivers. In general, we can expect fewer clusters under stronger exogenous drivers but the cluster compositions remain the same. The clusters that are lost will be those that are farthest from the soil origin. Finally, the driver strength at which some clusters are lost decreases as the soil origin gets closer to the extremes of soil preference (see details in Appendix S1: Section S7).
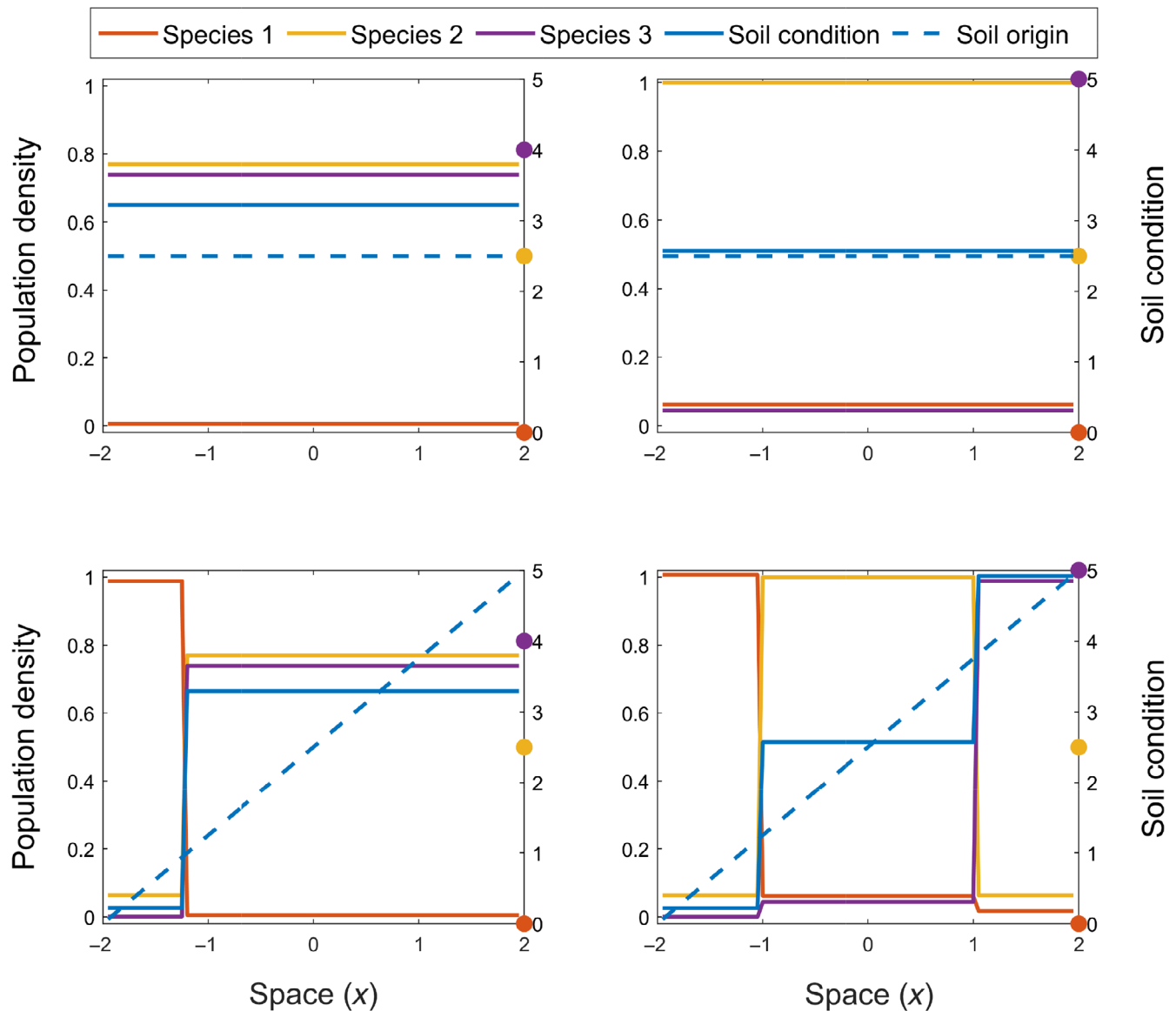
Patchy spatial patterns under environmental gradients

Spatial heterogeneity provides the opportunity for different clusters to be observed simultaneously. When there are multiple clusters in our model, the prevailing cluster at any

location is determined by the initial condition. Therefore, we can expect a spatially heterogeneous soil origin to lead to different species clusters occupying different spatial patches. In Figure 4, we consider three-species communities with two or three clusters (left and right panels). The soil origin, represented by a dashed line, is spatially homogeneous in the top row and forms a linear gradient in the bottom row. At equilibrium, we find patchy dominance of two or three clusters in a nondispersing three-species community due to an environmental gradient (Figure 4, bottom row). Notice that when the soil origin is homogeneous, any number of species can dominate but they all belong to the same cluster (Figure 4, top row).

When the community has more than one cluster, the initial soil conditions and species abundance will determine that cluster will prevail where. We can expect clusters with strong conditioning strength and large initial abundance to form a patch as long as the initial soil condition is close to the cluster's soil preference somewhere. Enumerating the qualitatively different patchy-dominance scenarios is an arduous task because the number of combinations of parameters and initial conditions is vast (a spatially-specific initial soil profile $E(x)$ plus three plant traits ε_i, ω_i, η_i and spatially-specific initial abundance profiles $n_i(x)$ for each species). Regardless, we know that the soil condition and species abundance will be homogeneous within a patch, and the boundaries between patches will be sharp. This is expected of any nondispersing community driven by positive soil conditioning.

FIGURE 4 Patchy spatial pattern in a three-species community due to an environmental gradient. The initial soil condition (soil origin) is uniform in the upper row and forms a gradient in the lower row. The soil preferences (dots on the *y*-axis) of the three species are chosen such that there are 2 and 3 species clusters in the first and second columns respectively. The three species have identical conditioning strength (η) 1 and niche width (ω) 1. Intrinsic growth rate (γ) and carrying capacity (*K*) for all species were set to 1. Simulations were run for 100 time units at steps of 0.0005 and a spatial mesh of size 0.05.
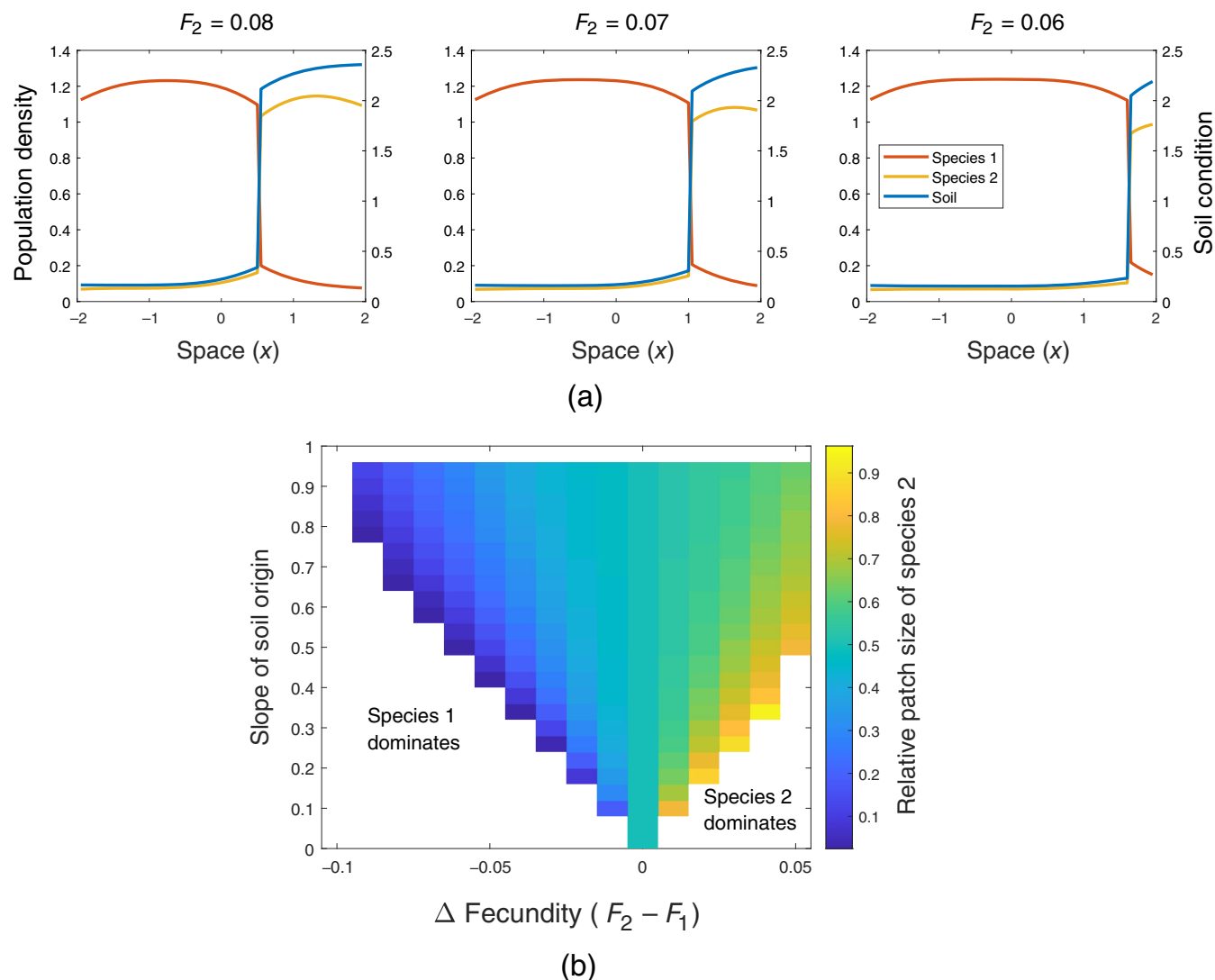
Effect of dispersal on the patches

We consider a two-species community with two clusters to examine the combined effects of plant dispersal and exogenous driver on the patchy spatial pattern. For tractability reasons, we only explore a linear gradient in soil origin. Moreover, we choose the gradient such that the soil origin at the center of the community's spatial range is equal to the average of the two species' soil preferences. We find that, while the number of clusters and their composition obtained in the nonspatial equilibrium analysis remains intact, plant dispersal affects patch size and, when combined with an exogenous driver, the steepness of patch boundaries.

When species disperse, their abundance within patches are not homogeneous (first panel in Figure 5a). Species abundance in the locally prevailing cluster are highest at the center of the patch and decrease symmetrically in either direction from the center. However, the boundary between the patches remains sharp, that is, there is no point between the two patches with intermediate abundance for either species.

While dispersal alone cannot enable patchy spatial patterns, interspecific differences in dispersal ability can

(a)

(b)

FIGURE 5 Effect of dispersal on patchy spatial pattern. (a) Patch size of species 2 (weaker disperser) decreases as dispersal difference increases ($F_1 = 0.1, \sigma_1 = 0.5, \sigma_2 = 0.5$). The soil origin is a linear gradient with slope 0.04 for all three cases and the soil condition at the center of the community is the midpoint of the two optimal soil conditions ($\varepsilon_1 = 0, \varepsilon_2 = 2.5$). (b) Community outcomes under different slopes of environmental gradient and difference in fecundity. Shaded regions show patchy dominance, with the hue indicating the relative patch size of species 2 as a fraction of the entire landscape. Both species have the same dispersal range ($\sigma_1 = \sigma_2 = 0.5$). Fecundity of species 1 is 0.1. Intrinsic growth rate (γ) and carrying capacity (K) for all species were set to 1. Simulations were run for 100 time units at steps of 0.0005 and a spatial mesh of size 0.05.

destroy them. The two species dominate in separate patches only when their fecundity and dispersal range are relatively close to each other. As the difference in dispersal ability increases, patchiness is gradually lost as the patch size of the weaker disperser becomes smaller (Figure 5a). Consider two species with equal dispersal ranges. For a given difference in species fecundity, patchiness will result only under a sufficiently strong gradient in the soil origin. The shaded region in Figure 5b shows values of the slope of the environmental gradient that allow patchy coexistence, with the hue indicating the relative size of each species' patch. Below that region, the

species with higher fecundity dominates the entire landscape. Appendix S1: Section S8 shows analogous results between species with different dispersal ranges.

We can use these results along with the results on species clustering (Figures 1 and 2) to describe the effect of an invader on a plant community. An invader whose soil preference is very different from the resident plants cannot grow to high abundance. However, the invader can modify the patchy spatial structure when it lands in a patch dominated by species with similar soil preferences to its own. When dispersal is limited, we can determine the effect of the invader on the patches it landed in using

the cluster-counting method on the patch community including the invader. The outcome of this analysis will tell us whether the invader can establish and dominate or co-dominate. When the invader is a strong disperser, it will expand the patch and can even lead to the collapse of other patches.

Effect of the exogenous driver on the patches

In the nonspatial case, an exogenous driver pulling the soil toward the soil origin can lead to a loss of clusters, as previously described and shown in Figure 3. This continues to be the case in the spatial scenario. Similarly to our numerical analysis of the effects of dispersal, we

consider a two-species community with two clusters and a linear abiotic gradient spanning the two soil preferences. The exogenous driver creates a smooth boundary between the two patches. Figure 6a shows this effect for increasing the strength of the exogenous driver. As the driver becomes stronger, the patches give way to a smooth gradient of species abundance reflecting the soil origin.

The exogenous driver can also counter the advantages of being the stronger disperser. We demonstrate this numerically with a linear gradient in soil origin as in the previous section. Because we choose the soil origin to be equal to the mean of the two species' soil preference at the center of the range, the exogenous driver does not particularly benefit one species over the other. Figure 6b shows that the patch size of the weaker disperser
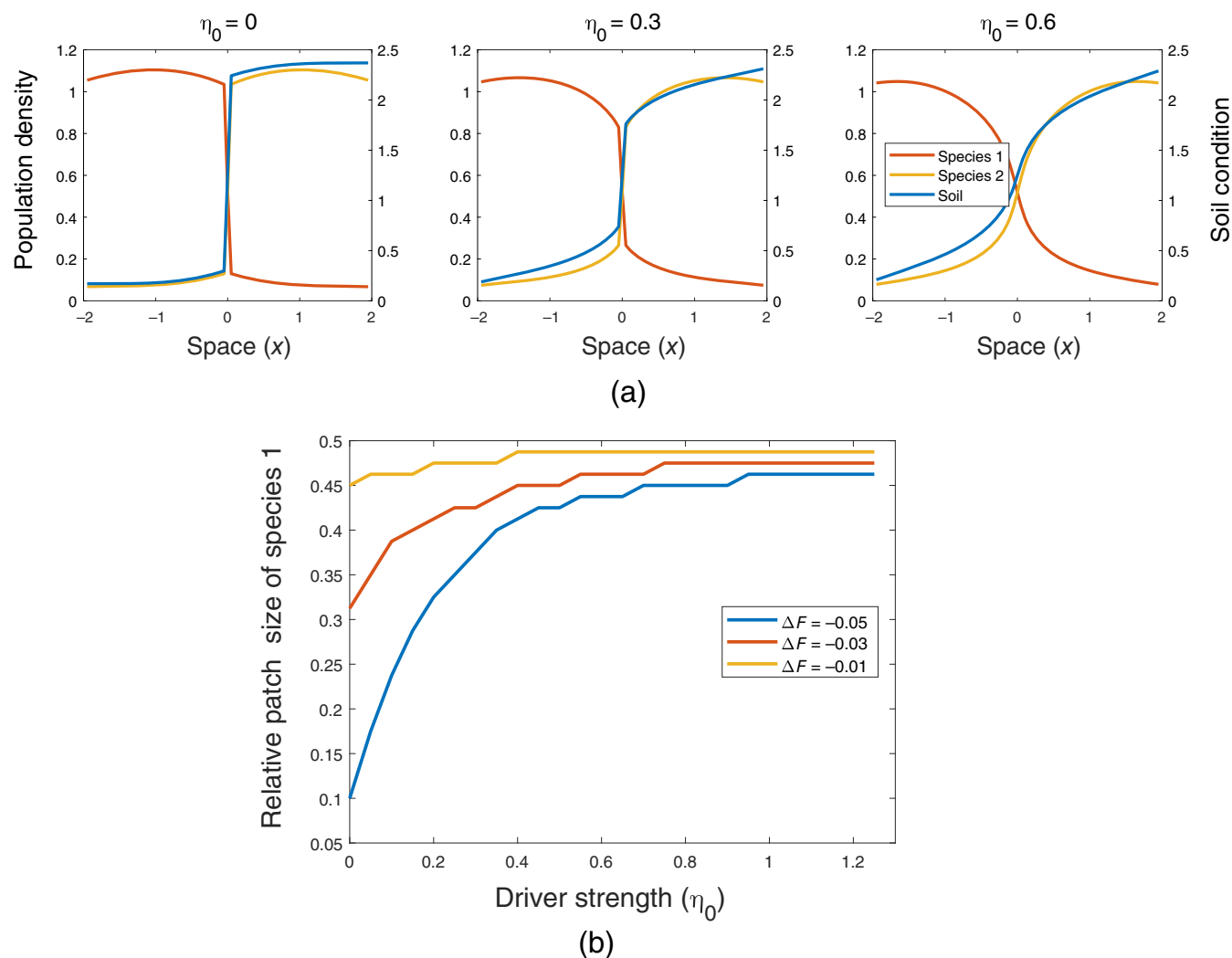
FIGURE 6 Exogenous driver affects the shape and location of patches but does not lead to a loss of any patches. (a) Stronger exogenous drivers lead to smoother patch boundaries. The soil origin is a linear gradient with slope 0.5 and the soil condition at the center of the range is the midpoint of the two species' preferences ($\varepsilon_1 = 0, \varepsilon_2 = 2.5$). (b) The advantage to the stronger disperser, which manifests as a larger patch size, is neutralized by the exogenous driver. Relative patch size of species 1 as a fraction of the entire landscape converges to 0.5 under increasingly stronger exogenous drivers. ΔF is the difference in dispersal fecundity between species 2 and species 1 ($F_2 - F_1$).

increases as the exogenous driver becomes stronger. The patch grows in size until the patch boundary reaches the center of the spatial range, whereupon both species have the same patch size even though one of them is a strong disperser.

To further illustrate this result, consider a scenario where one of the species dominates the other in most of the soil gradient due to being a stronger disperser. Under an increasingly stronger driver, plants can do increasingly little to move the soil condition away from the soil origin, in this case a linear gradient. The patch boundary thus comes gradually closer to the center of the gradient, where the soil origin is the average of the species' preferences. Thus, the advantage of the stronger disperser in parts of the landscape where it is less adapted to the local conditions is increasingly diluted, allowing the weaker disperser to dominate.

DISCUSSION

Several mathematical models explain the effect of plant–soil feedbacks on coexistence and plant community diversity. Bever et al. (1997) characterized the direction and strength of plant–soil feedbacks and suggested empirical tests to measure them. Their model and its successors show that only negative feedbacks permit stable local coexistence among plants that condition the soil. More recently, Eppinga et al. (2018), extended the model to more than two plant species and derived a single metric for the net direction of plant–soil feedback in the community. They found evidence of negative plant–soil feedbacks in northeastern American forests, whose strength correlated with local plant diversity. Here, we complemented and contrasted the models in Bever et al. (1997) and Eppinga et al. (2018), with a focus on how positive plant–soil feedbacks modulate niche structure and plant abundance. Our model predicts abundance and trait patterns in a plant community whose dynamics are driven by plant–soil feedbacks. Species group into clusters based on their soil preference, niche width and conditioning strength. These clusters represent plant species that dominate the community in terms of relative abundance in a locally stable equilibrium. Different clusters may appear as spatial patches when there is a spatial gradient in the environment. Dispersal will affect the location of patch boundaries, but its influence can be weakened by exogenous drivers such as geology and streams that pull soil conditions toward specific states. Exogenous drivers can reverse the fate of species with weaker conditioning ability, which are otherwise expected to be rare, instead have high relative abundance.

Interestingly, we found that these patches have a sharp spatial boundary even when plant species disperse strongly. Stronger dispersal can increase the patch size of a species cluster, but it does not introduce a cline between two patches, which are always sharply separated. Moreover, sufficiently large interspecific differences in dispersal ability can collapse patchy spatial patterns. The presence of a persistent pull toward the soil's origin state—an exogenous driver—loosens the tie between dispersal ability and patch size. The patch boundary becomes smoother as the exogenous driver becomes stronger, a phenomenon that dispersal alone cannot produce. Finally, a strong exogenous driver counteracts the advantages of dispersal and can prevent the loss of patchiness.

Although an exogenous driver of soil conditions can prevent the loss of weak dispersers and thus foster patchiness, it will not allow species belonging to different clusters to have high relative abundance locally. The exogenous driver decreases the number of clusters that can be abundant locally, and will favor the dominance of plants whose soil preferences are close to the soil origin. A sufficiently strong exogenous driver is equivalent to a community purely assembled by habitat filtering.

Our finding of a patchy pattern of species abundance due to self-beneficial soil conditioning by plants is consistent with previous work (Bever et al., 1997; Molofsky & Bever, 2002). The mechanism by which we get patchy patterns is conceptually related to priority effects, a research topic in community ecology (Fukami, 2015) which is recently fast-growing. Priority effect is the phenomenon in which community composition depends on the specific order in which different species arrive in the community. The basic requirement for a community to experience priority effect is positive feedback between species fitness and their abundance. Such positive feedbacks are typically attributed to the increase in the competitive ability of a species due to an increase in its abundance or frequency in the community (Grainger et al., 2019). This is ecologically distinct from the positive density dependence due to soil conditioning in our model. In a majority of the studies on priority effects, the emphasis is on the initial composition and abundance in the community. By contrast, here we draw attention to soil conditioning acting on spatial variation in abiotic conditions and dispersal to produce patchy patterns. Such dependence on the biotic and abiotic history of the ecosystem has been empirically recorded as legacy effects and historical contingency (Cuddington, 2011; Kardol et al., 2007).

Previous plant–soil feedback models have shown that negative soil conditioning can facilitate plant coexistence (Bonanomi et al., 2005) and positive soil conditioning allows plants to persist in infertile habitats (Kylafis & Loreau, 2008). Our model complements the single-species model in Kylafis and Loreau (2008), because we model

positive soil conditioning as well. They study both ecological and evolutionary dynamics with their model and consider severely unsuitable soil conditions where plants will become extinct unless they condition the soil quickly, which requires a large abundance or high conditioning strength. This cannot happen in our model, where species will subsist at low abundance but do not become extinct. The model can be extended in future studies to include this particular effect of positive soil conditioning in infertile soil. For example, one can use the alternative parametrization of the logistic growth model introduced by Verhulst (Mallet, 2012), with a soil-dependent intrinsic growth rate that decreases with soil mismatch and becomes negative under extreme soil conditions.

Jiang and DeAngelis (2013) present a model of ecosystem engineering with a similar approach to ours, where the abiotic environment is a continuous variable with a baseline value (soil origin E_0) and each species has an environmental preference. However, we incorporate density dependence in soil conditioning, and allow for species differences in conditioning strength. More generally applicable ecosystem engineering models have been used to explore scenarios where environmental modification by organisms is an evolvable trait (Krakauer et al., 2009; Scheiner et al., 2021). Follow-up studies will extend our soil-conditioning model to study the evolution of conditioning strength, niche width, and soil preference. This will be crucial for plant species with heritable variation in soil preference or the other two traits. Moreover, we can explore what combination of increasing conditioning or niche width or evolving soil preference is an evolutionarily stable strategy for a plant species under different genetic relationships between these traits.

In the literature, plant–soil feedback is quantified by comparing plant growth in soil conditioned by the same or other species (Bever et al., 1997). If plants grow better in soil conditioned by conspecific individuals than heterospecific individuals, the effect is considered positive. In our framework, the feedback is positive because the plant modifies the soil to its benefit, thus growing better in the soil after conditioning compared with before conditioning. Those interpretations are slightly different: for example, if plants made the soil worse for themselves (thus constituting negative individual feedback) but worse still for other species, the experimenter would conclude the feedback is positive (pairwise feedback). However, this distinction is immaterial here, as plant–soil feedback experiments would detect positive plant–soil feedback in a community driven by our model. Notice that, while a plant always conditions the soil to its benefit, the effect on other species is contextual, as it depends on the current state of the soil. Consider two species with preference $\varepsilon_1 < \varepsilon_2$, and suppose the soil is currently at $E > \varepsilon_2$. In this case, both species will pull the soil in the same direction for their mutual benefit. However, once E crosses to the other side of ε_2 such that $\varepsilon_1 < E < \varepsilon_2$, the mutual interspecific effect becomes negative. This nuanced understanding of plant–soil feedback requires explicitly accounting for soil dynamics.

The tendency of the soil to return to its original state by an exogenous driver emphasizes the temporal aspect of plant–soil feedbacks, which has been shown to be critical to plant coexistence (Ke & Levine, 2021). Specifically, negative plant–soil feedbacks can promote species coexistence as proposed by Bever et al. (1997) only when the microbial effects decay sufficiently slowly to have a cross-generational impact. In our model, the duration of the conditioning effect is modulated by the strength of the exogenous driver. Our finding that the number of species clusters decreases under a stronger exogenous driver is complementary to the result in Ke and Levine (2021) based on a two-species model.

Temporal considerations are particularly important when plant–soil feedback switches between negative and positive from short to long timescales. Corrales et al. (2016) conducted plant–soil feedback experiments with saplings of five neotropical tree species to explain the monodominance of *Oreomunnea* that forms ectomycorrhizal mutualisms. They found that *Oreomunnea mexicana* had the strongest negative feedback, contrary to the expectation that ectomycorrhizal mutualisms lead to positive plant–soil feedback (Bennett et al., 2017). Moreover, they found that the strength of negative plant–soil feedback was negatively correlated with abundance, which is contrary to both theoretical predictions and previous empirical findings (Klironomos, 2002; Mangan et al., 2010). We agree with their conclusion that the negative effects of other soil microbes overwhelm the positive effects of ectomycorrhizal fungi. However, we hypothesize that, at longer timescales, the feedback will turn positive, which can explain the monodominance. The patchiness of the monodominance pattern can also be a consequence of the soil origin as we show in our results (Figure 4). Soil nitrogen was found to be consistently lower in the *Oreomunnea*-dominated patches, which might be indicative of within-patch homogeneity in soil condition, whereas adjacent sites with heterogenous soil nitrogen might be indicative of patchy coexistence among different clusters.

According to traditional environmental filtering models, local conditions will select from a regional pool of dispersing species, resulting in a match between local environments and local plant traits, and regional-scale coexistence in a spatially heterogeneous environment (Cornwell et al., 2006; Keddy, 1992; Weiher et al., 1998). In line with these expectations, our model predicts that local plant traits will form a subset of the regional pool

reflecting local conditions. However, positive conditioning can result in a mismatch between local soil conditions and the environmental preferences of dominant plant species, which is not allowed under pure environmental filtering. Furthermore, while under pure filtering a gradient in environmental conditions will lead to a gradient in community composition, positive feedbacks will create steep transitions between patches. Such drastic turnover of species in space is a general feature of positive feedback. Liautaud et al. (2019) find discontinuous species turnover even in purely competitive communities. In those communities, positive feedback between two competing species emerges indirectly as a consequence of strong negative interaction with a shared competitor.

Our model also contrasts with other biotic–abiotic interactions in which the abiotic factor is consumable, and two species cannot share an ecological niche (MacArthur & Levins, 1967; Tilman, 1985). Those models lead to a community-level pattern in which species form clusters based on their resource preferences. In such communities, only one species persists per cluster, while the other species slowly becomes extinct (Box 1). However, in our model, in which the abiotic factor is conditionable, species clusters represent a collection of species that share an ecological niche and have high relative abundance. For example, if a resident species is invaded by a species with similar abiotic preferences, both the invader and the resident can be dominant if the abiotic factor is conditionable (e.g., soil pH), but not if it is consumable (e.g., nutrients).

While our one-dimensional representation of soil conditions greatly simplifies reality, it can be apt in scenarios in which environmental variables are strongly correlated or when a single environmental index, such as the local soil C:N ratio, pH, or moisture, controls species sorting. Furthermore, recent findings suggesting that plant traits can sufficiently be summarized in terms of size and leaf economic spectrum can be used to find empirical links to our model (Bruelheide et al., 2018; Díaz et al., 2016). The latter is directly related to soil preference in terms of its relative N requirements and conservative versus acquisitive strategy in leaves. Such empirical studies on aboveground and belowground plant traits can be contextualized using the model we developed here and its future iterations.

Our study makes headway toward a more mechanistic theory of plant–soil feedbacks by tying feedbacks to

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BOX 1   Species clusters in niche theory

Soil conditioning, which may lead to interference competition, can be contrasted with consumer–resource interactions, which may lead to exploitative competition. Our understanding of species clustering is founded on studies of consumer–resource interactions. In a community of species competing for a shared continuum of resources (e.g., granivorous birds), we expect coexisting species to differ substantially in their resource preferences (seed size), as this minimizes resource overlap, and subsequently, interspecific competition. MacArthur and Levins (1967) first demonstrated this limit to similarity in a Lotka–Volterra competition model. Later studies observed that species that are not sufficiently differentiated may remain in the community for long transient periods, or indefinitely if their dwindling populations are replenished by immigration (D'Andrea et al., 2019; Scheffer & van Nes, 2006), resulting in a community-level pattern characterized by distinctive clusters of species with similar traits (D'Andrea et al., 2020). In this context, each species cluster represents an ecological niche (e.g., specialization on small seeds) shared by several species (birds with a preference for small seeds). If left alone, each cluster would eventually—possibly after a very long transient—be represented by a single species, as no two species that share a niche can stably coexist.

Here, we show that the species clustering pattern that emerges from plant competition mediated by soil conditioning shares some similarities but also key differences from that of resource consumption. The similarity is that the soil preferences of species in different clusters (i.e., niches) are substantially different from each other, which minimizes competition. However, for soil conditioning, species with similar soil preference can co-occur at high relative abundance. This is possible because positive soil conditioning indirectly benefits species with similar soil preferences and hinders species with dissimilar soil preferences. Furthermore, species in different clusters cannot co-occur at high relative abundance locally, and will do so regionally only if there is sufficient environmental heterogeneity. Both of these are in diametric opposition to the commonness-rarity pattern within and among species clusters under consumption-based competition. Species from different clusters can simultaneously have high relative abundance under conditioning-based competition only if they can niche-differentiate elsewhere.

high-level traits, namely, environmental preference, niche width, and conditioning strength. In Box 2, we propose empirical tests to reject positive plant–soil feedback as the dominant driver of community patterns. While our model captures the phenomenology of plant community dynamics under positive plant–soil feedbacks engendered by plant–mycorrhiza mutualisms, it is generalizable to alternative sources of positive plant–soil feedbacks, such as the release of allelopathic compounds in the soil. However, it cannot

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BOX 2 Empirical tests of soil conditioning

Patterns generated by soil conditioning can be contrasted with those expected from habitat filtering. As the conditioning strength of species increases from zero to very large, the dominant pattern-creating process will range from pure habitat filtering (when plant communities only respond to the abiotic environment) to habitat conditioning (when their impact on the environment supersedes their sensitivity to it).

When we know the soil condition E, which can both affect plant fitness and be conditioned by the plants, we can use our results to directly infer whether soil conditioning is an important process driving community patterns. For example, consider a plant community where species differ in affinity to soil pH. We can determine whether these plants condition the soil by measuring soil pH in sites where different species dominate. If positive plant–soil feedback is an important process in the community, then we can only observe discrete soil pH values in the environment. We can reject soil conditioning as the main driver when we find a continuous gradient of soil pH in a field when we know that there are no geological features that can explain the pH gradient. The reverse is not necessarily true: while a discrete change in pH levels across adjacent sites is consistent with positive conditioning as seen in this study, it can also be caused by historical contingency where the soil origin had a discrete change.

In the more likely scenario in which the soil condition E cannot be easily identified or linked to a single measurable variable, plant–soil feedback experiments in a common-garden or controlled-field setting can determine whether plants condition the soil and the strength of conditioning when they do (Bever et al., 1997; Crawford & Knight, 2017; Van Nuland et al., 2017). In observational studies, one can use species abundances at different local sites to test for the prevalence of soil conditioning. If soil conditioning is the dominant process, our results predict strong constraints on species abundances. For example, consider two species, A and B. If A is common and B is rare in one site, and A is rare and B is common in another site, then one must conclude that the two species belong in different clusters, and therefore cannot be jointly common anywhere. Observing a third site where both are common would then be evidence against soil conditioning. Conversely, if species A and B are jointly common in one site, then one would conclude that both species belong in the same cluster, and therefore neither species should be rare where the other is common. Generally, one expects at most n different combinations of rarity and commonness among n species at different sites.

Ke and Levine (2021) showed that soil conditioning can affect community patterns only when conditioning effects last sufficiently long and affect subsequent generations. Our results reinforce this idea in terms of the exogenous driver. When plants only condition soil temporarily, the soil condition will revert to the soil origin due to the exogenous driver. Such a system may be indistinguishable from a case of pure habitat filtering.

We note two limitations of this abundance-based approach: (1) consistency in abundance correlations among species across sites is necessary but not sufficient to infer positive soil conditioning, as both pure habitat filtering and dispersal limitation could cause similar patterns; (2) while these abundance-based methods can quantify the effects of positive soil conditioning on community structure, they cannot identify the conditioned abiotic features. Tests targeting confounding processes may eliminate alternative explanations, such as using seed traps to estimate dispersal limitation (Nathan & Muller-Landau, 2000).

One potentially important difference between systems with and without soil conditioning is the expected variation in plant abundance over time. When the soil is purely driven by exogenous drivers such as climate, climatic fluctuations will cause changes in environmental filtering, which will then cause changes in plant abundances. However, soil conditioning by plants can act as a buffer against climatic fluctuations. One may thus expect plant abundances in communities with soil conditioning to be less temporally variable than in scenarios of pure habitat filtering.

describe consumer–resource relationships, as those will cause intraspecific negative feedbacks. Similarly, it cannot describe abiotic interactions that do not result in trait-matching beneficial outcomes, such as competition for light, nor conditioning that affects the environment at large rather than a plant's microhabitat, such as rainfall modulation via evapotranspiration.

We did not explicitly model consumable abiotic resources, which have been the primary focus of mathematical models of plant communities and ecosystem ecology (Loreau, 1998; Tilman, 1985). Consumable resources appear indirectly in our model via the carrying capacity, which reflects self-regulation caused by resource depletion. This modeling choice ensures that plants can coexist in the absence of conditioning. The dependence of the carrying capacity on local soil conditions reflects an interaction between consumable and conditionable factors in population dynamics: for example, the plant's nutrient uptake rate is contingent upon local soil pH. However, Ke and Levine (2021) and Krakauer et al. (2009) showed that the outcome of conditioning may depend on whether it affects carrying capacity, fecundity, mortality, or colonization. A more mechanistic understanding of the interplay between consumer–resource dynamics and plant–soil feedbacks will allow the development of trait-based models that can in turn provide further insights into the role of plant–soil feedbacks on plant community dynamics and soil-based niche structure. O'Dwyer (2018) provides useful directions for building such mathematical models. Finally, because microbes mediate many consumptive and conditioning interactions in plant communities, incorporating microbial dynamics into future models will significantly improve our understanding of plant–soil feedback.

Plant–soil feedback is increasingly recognized as a common biological process that is relevant to understanding the consequences of human-induced disturbances to ecosystems. We showed how these feedbacks organize plant communities based on their environmental preferences and ability to condition the soil, and how plant dispersal and exogenous drivers of soil properties further modulate spatial patterns of plant abundance. Our model lays the groundwork for a general niche theory for plant–soil feedback.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Empirical data were not used for this research. The novel codes used for this research (Senthilnathan & D'Andrea, 2023) are provided at: https://doi.org/10.5281/zenodo.7535136.

ORCID

Athmanathan Senthilnathan https://orcid.org/0000-0002-9665-8397
Rafael D'Andrea https://orcid.org/0000-0001-9687-6178

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SUPPORTING INFORMATION

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

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