

Coexistence of competing plants under plant-soil feedback

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Abstract

Plant-soil feedback (PSF), the reciprocal interaction between plants and their soil environment, is a fundamental ecological process that influences coexistence and functional structure in plant communities. Current theory establishes that PSF may enhance diversity or lead to exclusion depending on whether soil conditioning disproportionately benefits heterospecific or conspecific individuals. However, a more complete picture of the impact of PSF requires understanding how PSF synergizes with competition. To that end, here we propose an integrated mathematical model combining trait-based competition and soil-explicit PSF. Contrary to the current paradigm, we find that soil conditioning that disproportionately favors conspecific individuals can promote coexistence. Additionally, we show that priority effects are common when soil-conditioning species differ in their edaphic preferences. These effects can allow species with large differences in competitive ability to coexist under certain soil conditions. Our results provide testable predictions tying community-level functional patterns in plant communities to PSF and competition.

Introduction

Plant communities are the backbone of terrestrial ecosystems. Our understanding of plant communities relies on a robust ecological theory linking processes that affect plants to resulting patterns of abundance and trait diversity. Among such processes, competition for light, nutrients, and water (missing citation) have received most of the attention. However, non-consumptive plant-soil interactions are known to be common and can also affect community patterns (missing citation), very likely in combination with competition (missing citation); (missing citation). Therefore, it is important to not only develop a theory of plant-soil interactions but also one which can be integrated with competition theory.

Soil provides an arena for plant-plant interactions since individual plants modify the biotic and abiotic properties of the soil which feed back to affect the survival, growth, and reproduction of all individuals in the vicinity (missing citation); (missing citation). For example, accumulation of pathogens in the soil harms plants while nitrogen fixers benefit them. The net effect of such conditioning can vary in magnitude and sign between the plant that conditions the soil and the other plants around it. When the benefits of conditioning are higher for conspecifics than heterospecific plants, then the plant-soil feedback (PSF) is positive but can lead to an apparent negative interspecific interaction. On the other hand, negative PSF can lead to an apparent positive interspecific interaction. This leads to the expectation that negative PSF can promote species coexistence while positive PSF causes exclusion. Empirical studies show that this is indeed the case (missing citation); (missing citation); (missing citation); (missing citation); (missing citation). However, understanding the consequences of the interaction between PSF and competition poses some challenges.

Competition models show that dominant species (i.e. species with high abundance) will be evenly distributed on a trait axis (missing citation); (missing citation), thereby maximizing trait differences among them. This

pattern, called limiting similarity, is compounded by another pattern where those dominant species are flanked by other species with similar traits, creating a clumpy distribution of species abundance along the trait axis (missing citation); (missing citation); (missing citation). Those effects of competition can in turn be modulated by local soil conditions—similar species are likely adapted to similar soil conditions—which in turn are affected by plant-soil feedbacks. Therefore, PSF could have synergistic effects with competition in generating unique trait-by-abundance patterns.

While some empirical studies suggest that competition may supersede the effect of PSF in matters of coexistence (missing citation), other studies suggest that both are relevant (missing citation). From a theoretical standpoint, the classic PSF framework (missing citation); (missing citation) ignores fitness differences (missing citation); (missing citation), which are essential to understand the full effect of any community assembly on species coexistence (missing citation); (missing citation). As such, we do not have a clear expectation for the outcome of species interactions where competition and plant-soil feedbacks act in tandem (missing citation).

Theoretical models are essential for scaling up the effects of plant-soil feedbacks to communities, since experimental approaches involving many species face logistical challenges. Models parameterized with pairwise experiments (e.g. (missing citation)) are impractical for predicting coexistence and functional pattern in communities with many species because they require a large number of experiments. Alternatively, trait-based approaches are much less data-intensive as they link competition and PSF processes to species traits; a pairwise approach would require S^2 experiments to parameterize a community with S species, whereas a trait-based approach requires S experiments.

In this study, we fill the theoretical gap by integrating competitive dynamics into a recently proposed trait-based approach to modeling PSF, focusing on positive PSF (missing citation). This approach allows for a wider set of competitive outcomes than current PSF theory, as it explicitly accounts for soil dynamics and the corresponding changes in species fitness. Our model requires a relatively small number of experiments to be parameterized and allows us to predict coexistence patterns in large communities where plants compete and condition the soil.

We ask the following questions: (I) How does positive plant-soil feedback influence the coexistence of two equally competitive species with similar conditioning ability but adapted to distinct soil conditions? (II) What are the coexistence conditions between two soil-conditioning species which differ in competitive ability or conditioning ability? (III) In communities with multiple coexisting species which condition the soil, how do species abundances relate to species similarity in traits linked to competition and soil conditioning? We answer these questions by explicitly modeling the joint dynamics of plant species and the soil. Mathematical analysis of the model shows that positive PSF favors coexistence when species have similar soil preference and hinders coexistence otherwise. Numerical analysis of large communities shows that species group by soil preference into a single cluster but form multiple clusters based on resource preference, the latter matching the predictions of recent competition theory.

Materials and methods

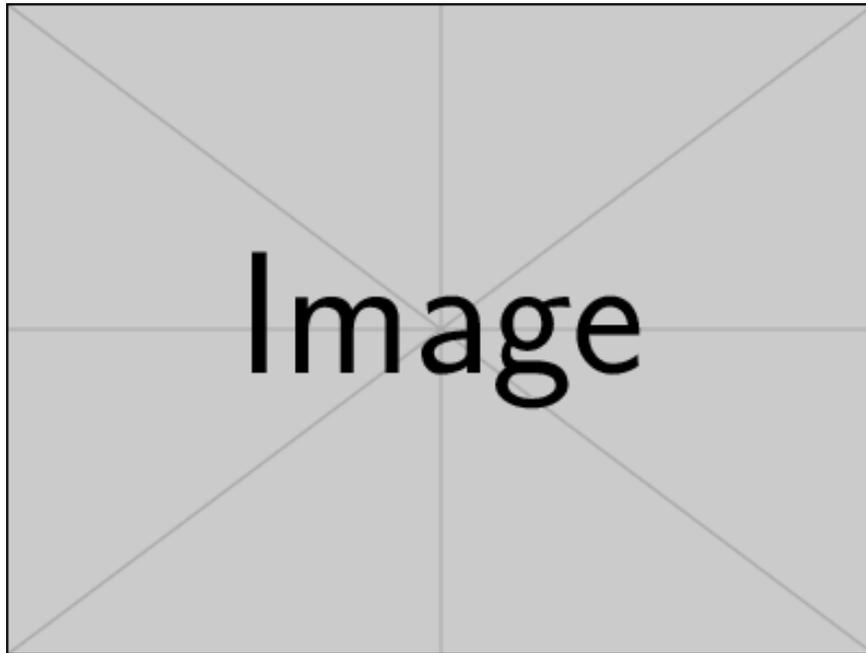
We build our model from an alternate parametrization of the standard logistic growth model in population dynamics (missing citation); (missing citation). In this model, the population of each plant species changes over time in response to the current soil condition as well as the population of competing species. The soil condition E , representing some abiotic property such as soil aridity or acidity and measured in the appropriate units, changes in response to the conditioning ability of the plants (Figure). The dynamics of the population density N_i of species i and the soil condition E follow the equations:

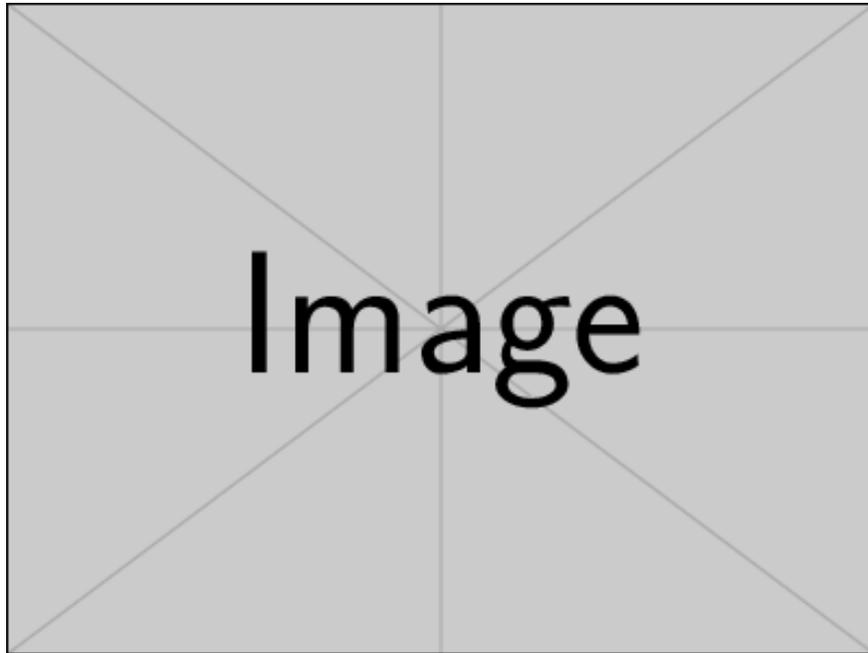
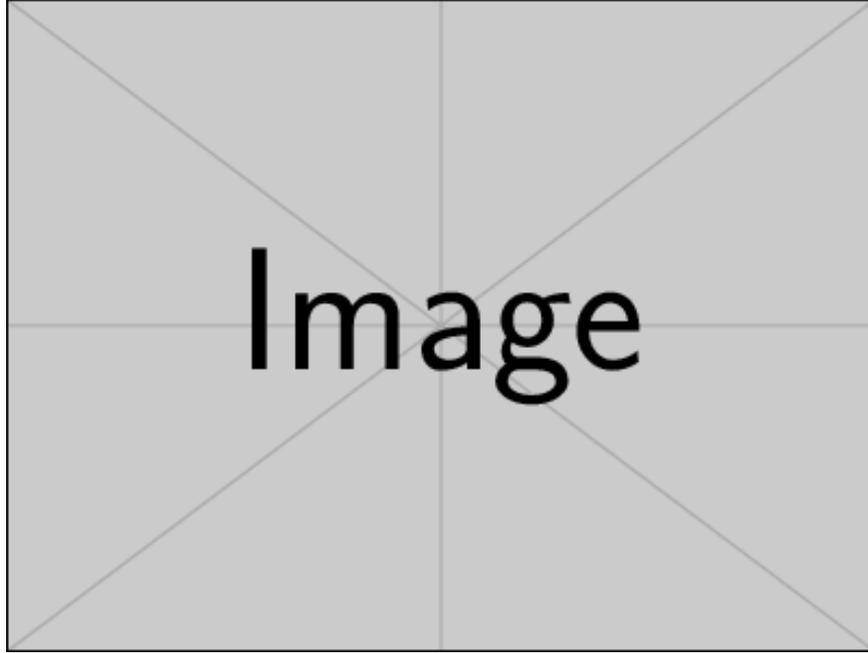
$$\frac{dN_i}{dt} = N_i \left(r_i(E) - \sum_j a_{ij} N_j \right) + \nu, \quad \frac{dE}{dt} = \sum_i \eta_i (\geq_i - E) N_i.$$

The *intrinsic growth rate* $r_i(E)$ of species i in equation () depends on the soil condition E via abiotic filtering as follows:

$$r_i = r_{max} \left(1 - \left(\frac{\geq_i - E}{i} \right)^4 \right).$$

This function is species-specific based on the *soil preference* and *soil niche width* of the species (Figure). A species' soil preference \geq_i is the soil condition at which it has its highest intrinsic growth rate. At extreme soil conditions exceeding the limits of the species' tolerance, the intrinsic growth becomes negative (Figure). The soil niche width i defines the range of soil conditions at which the species has positive intrinsic growth rate. Equivalently, the fundamental niche of species i is the interval $(\geq_i - i, \geq_i + i)$. The parameter r_{max} is the maximum per-capita growth rate attained by any species when the soil condition matches their preference. We set $r_{max} = 1$ for our analysis since it does not affect the coexistence conditions qualitatively. We note that other functional forms for $r_i(E)$ that drop monotonically from its peak and are positive within a finite range produce similar results.





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[] [] Conceptual model of positive plant-soil feedback and competition. (a) The state variables are plant abundance and soil condition. The arrows represent processes that affect the state variables. (b) Filtering is modelled as the effect of soil condition on the intrinsic growth rate. Intrinsic growth rate is maximum (r_{max}) when the soil condition matches the preference of the species \geq and becomes negative when the soil condition is outside the niche $[\geq -, \geq +]$. (c) Competition is modelled as the overlap in resource use of the two species. The solid and dashed curves are the effective resource use of species 1 with resource preference $_1 (U_1(x))$ and the total resource

use of species 2 with resource preference $v_2(V_2(x))$, respectively. The resource niche widths are w_1 and w_2 . Parameter δ (> 1) represents the degree of resource wastage.

The second term within the parenthesis in equation (1) ($\sum_j a_{ij}N_j$) is the mortality due to competitive interactions, where the *pairwise competition coefficient* a_{ij} reflects the competitive impact of species j on species i . Following classical trait-based competition models (missing citation); (missing citation), we assume a continuous spectrum of resources, and species j has a competitive impact on species i to the extent that the *total resource utilization curve* $V_j(x)$ of species j overlaps with the *effective resource utilization curve* $U_i(x)$ of species i (red area in Figure 1, (missing citation); (missing citation); (missing citation)):

$$a_{ij} = \nu_i \frac{\int U_i(x)V_j(x)dx}{\int U_i^2(x)dx},$$

where ν_i is species i 's sensitivity to competition. We assume that both the total and effective resource utilization curves peak at the species' preferred resource x_i and drop off for other resources on the spectrum (Figure 1). Specifically, we set:

$$V_i(x) = \exp\left(-\left(\frac{x-x_i}{w_i}\right)^4\right)U_i(x) = \exp\left(-\left(\frac{x-x_i}{w_i}\right)^2\right)$$

U and V are distinct as only a fraction of consumed resources are assimilated, and species grow more efficiently on resources that resemble their preferred resource—hence the steeper dropoff of U compared to V . The parameter w_i is the *resource niche width*, and δ is a measure of wasted resources. We set $\delta = 3$ for our analysis, ensuring that the V curve is wider than the U curve. This setup ensures that competition is stronger between species with more similar traits—and thus similar resource preferences.

Finally, we assume a steady immigration of individuals in the model to capture the effects of a regional species pool. This is encapsulated in the immigration rate parameter ι in equation (1).

Equation (2) represents the rate of change of the soil condition. Each plant conditions the soil by pulling it closer to its soil preference $\geq x_i$, therefore the conditioning by each species is density-dependent. The parameter η_i represents the per-capita conditioning strength. Lastly, we define the *soil origin* E_0 to be the soil condition of the ancestral state of the community. In terms of the model, the soil origin is simply the initial condition of the dynamics ($E(0) = E_0$). See Table ?? for a full list of parameters, their names, and units.

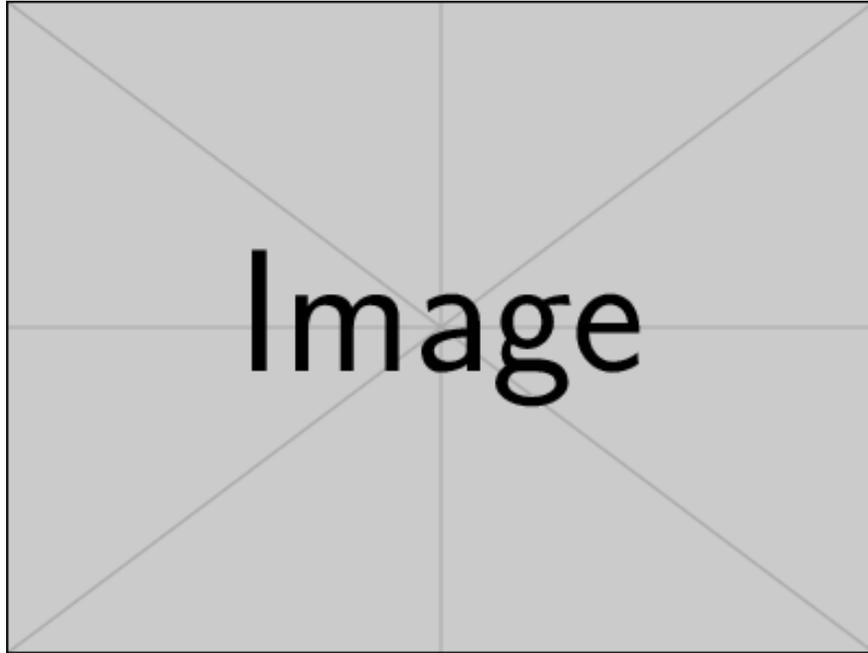
To answer questions (I) and (II), we perform a linear stability analysis of all the feasible equilibria of equations (1) in an immigration-free two-species system using Mathematica (see Appendix A1 and (missing citation)). Briefly, the linear stability analysis entails (i) finding all equilibrium points, (ii) determining parameter conditions at which the equilibrium abundance is positive (i.e., feasibility), and (iii) using the eigenvalues of the Jacobian matrix evaluated at the equilibrium points to determine parameter conditions at which they are stable.

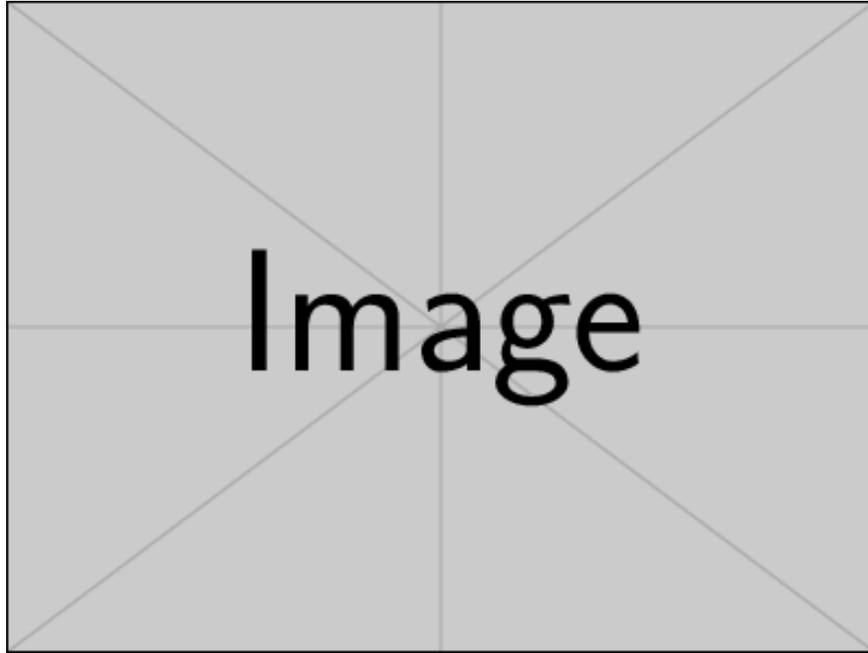
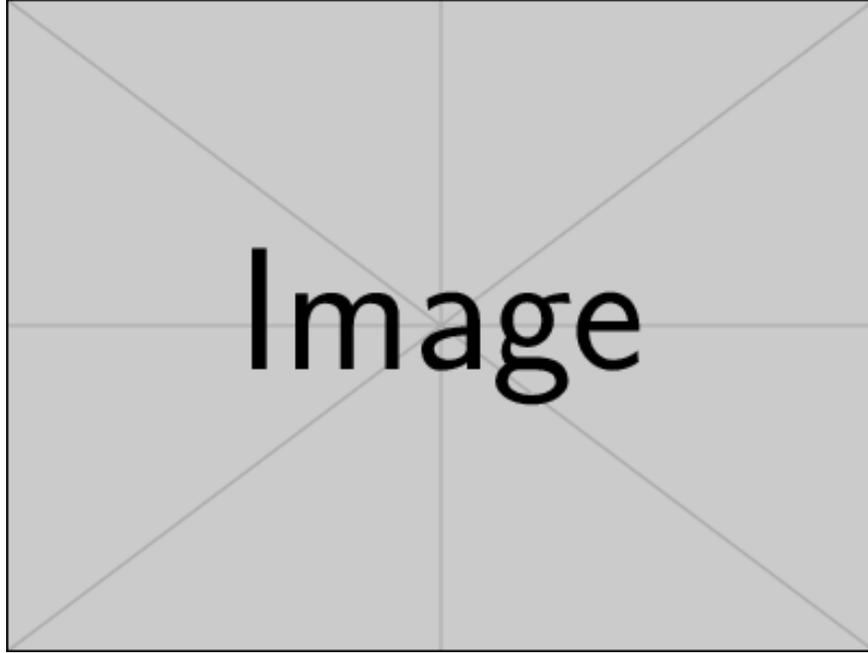
To answer question (III), we solve the equations numerically for a multispecies community with immigration in MATLAB (missing citation). Unlike the two-species case, we assume periodic boundary conditions for the multispecies case to avoid artifactual edge effects (see Appendix A2 for details of the implementation). We perform several parameter sweeps to find general trait patterns that emerge over time and the effect of the different parameters. We analyze the trait pattern using k-means gap cluster analysis developed in ((missing citation), see description in Appendix A3).

Results

I. Effects of positive PSF on coexistence between equal competitors

In a two-species community, there are four possible outcomes depending on the initial soil condition (i.e., the soil origin): (i) both species become extinct, (ii) both species coexist, (iii) only species 1 persists, or (iv) only species 2 persists. Depending on species traits, any combination of these outcomes may be stable. The outcome where both species become extinct is always stable. When multiple outcomes are stable, the soil origin and initial abundances determine whether species coexist. Specifically, when (iii) and (iv) are stable, the species with higher initial abundance will persist, a situation known as priority effects in community ecology (missing citation); (missing citation).





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□ Plant-soil feedback fundamentally alters coexistence conditions. (a) The soil origin and the dissimilarity in soil preference of the two species determines the outcome of interaction when abiotic filtering is the only relevant process. The red line indicates the coexistence region when the species compete with each other. Dashed black line marks the difference in soil preference at which the fundamental niche of the two species stops overlapping. (b) The outcomes of the two species interaction is qualitatively different when plants neither condition the soil nor compete with each other. The three plots on the right illustrate niche overlap between species 1 (blue) and species 2 (red)

for three different values (i) top, $\geq_2 = 2$, (ii) middle, $\geq_2 = 1$, and (iii) bottom, $\geq_2 = 0.5$ (c) Possible outcomes of interaction between two species which differ only in soil and resource preference. The difference in resource preference in (a) and (b), $|\geq_1 - \geq_2| = 2$. Conditioning strength $\eta = 1$ (b) and (c). Other parameters for all panels are $\nu = 0, \mu_1 = \mu_2 = 1, \alpha_1 = \alpha_2 = 1$. (a,c) are analytic based on a stability analysis, while (b) is based on simulations run for 1,000 time steps starting with 0.1 abundance for each species.

To demonstrate the effect of plant-soil feedback on coexistence, we need a baseline expectation of coexistence outcomes for comparison. These are scenarios where (i) only abiotic filtering affects the dynamics, and (ii) abiotic filtering and competition affect the dynamics. In the first scenario ($\nu = 0, \eta = 0$), the outcome of the interaction will depend on how well each species is suited to the soil origin (E_0).

Specifically, if species 1 has soil preference \geq_1 and soil niche width ω_1 and species 2 has soil preference $\geq_2 > \geq_1$ and soil niche width ω_2 , then both species will coexist when the soil origin is in the overlap of their fundamental niches, i.e., $\geq_2 - \omega_2 < E_0 < \geq_1 + \omega_1$. The range of soil condition that causes coexistence decreases as the difference in soil preferences of the two species increases (the green region tapers along the y-axis in Figure). Coexistence range further decreases when the two species compete (red line outlines the modified region in Figure). See Appendix A4 for details of the calculations.

Plant-soil feedback fundamentally alters the outcome of two-species interactions (Figure). As expected, soil conditioning by plants reduces the possibility that both species will be extinct. However, if the soil origin is far outside the fundamental niche of both species, conditioning by the plants cannot move the soil into the fundamental niche of either species. The range of soil condition that causes coexistence is much wider than the scenario without plant-soil feedback only when the two species have a similar soil preference. Moreover, when the soil preferences are similar, single-species outcomes are not possible.

Figure illustrates the contrast between scenarios where plants do not condition the soil ($\eta = 0$) and those where both species have equal conditioning strength ($\eta = 1$). While coexistence outcomes differ when conditioning is present, further increasing the strength of conditioning primarily impacts only the timescale required to reach equilibrium. Notably, species with stronger conditioning ability reach their equilibrium coexistence abundances more quickly. In addition, the region where extinction occurs diminishes with increasing conditioning strength. The effects of asymmetric conditioning strength are further discussed in the following section.

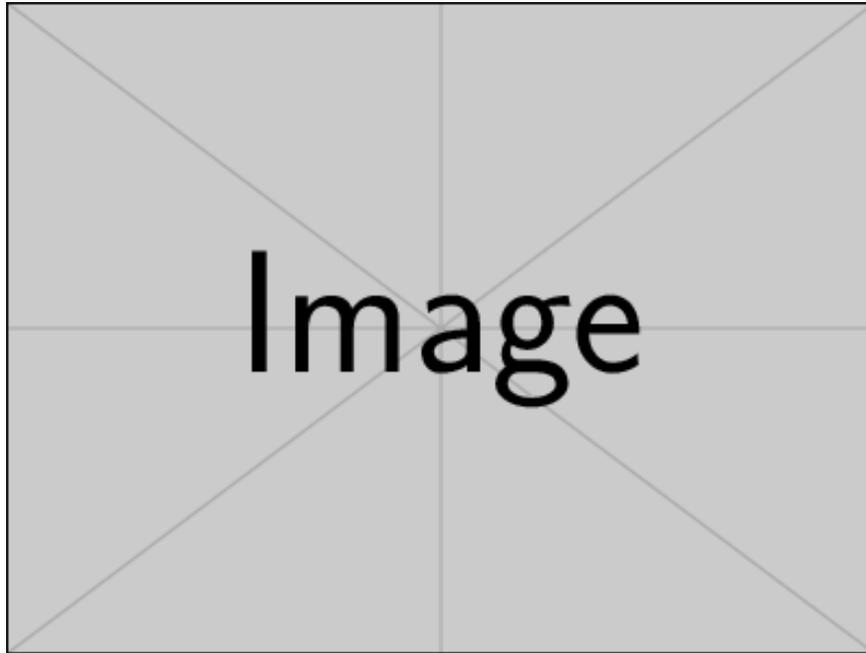
In general, we can classify pairs of species based on the possible outcomes when the two species interact. We will restrict our analysis to soil origins within the window where conditioning can move the soil into the fundamental niche of at least one species. Figure shows the stable outcomes for two species with equal competitive ability and conditioning ability—question (I)—given different combinations of species resource and soil preferences. If multiple outcomes are stable, then the initial abundance and soil origin will determine the exact outcome. We note that those results hold for alternative functional forms of the intrinsic growth rate and the competition coefficients (see Appendix A5).

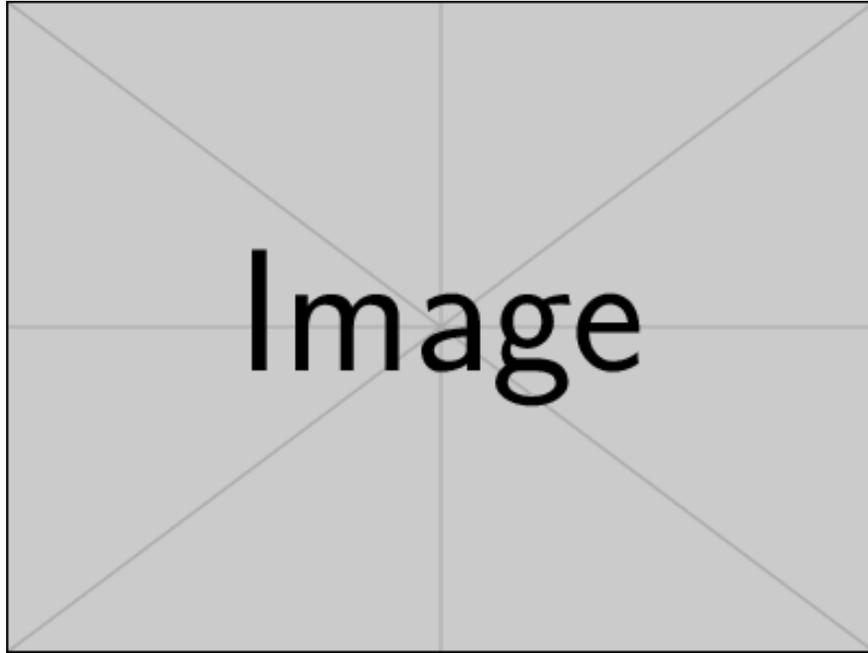
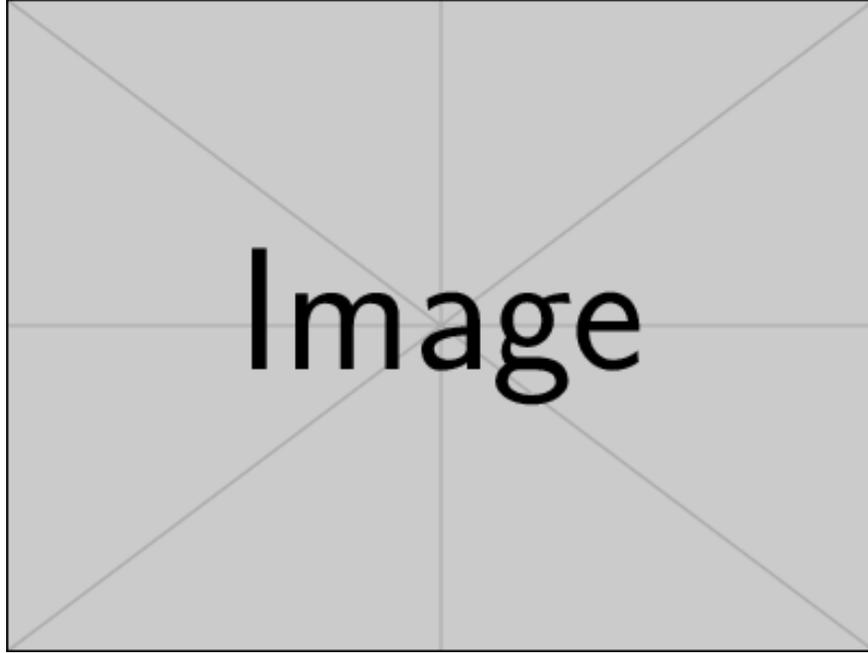
The species pair can coexist only when they have sufficiently different resource preferences and sufficiently similar soil preferences (Figure). The coexistence region increases with differences in resource preference—consistent with classical ideas that coexistence is more likely when species are more dissimilar (missing citation). At increasingly dissimilar resource preferences, the coexistence region initially expands and then saturates. Species with very large differences in resource preference must still be within a limited range of each other’s soil preference to coexist. This limitation is present whether or not plants condition the soil (the dashed line in Figure), but the range is narrower when they do. The coexistence region is subdivided into two subregions: if soil preferences are sufficiently close, coexistence is guaranteed (green region in Figure); for larger gaps in soil preferences (orange region), the possible outcomes are coexistence or exclusion of one species, depending on the soil origin and the initial abundances (see Appendix A6).

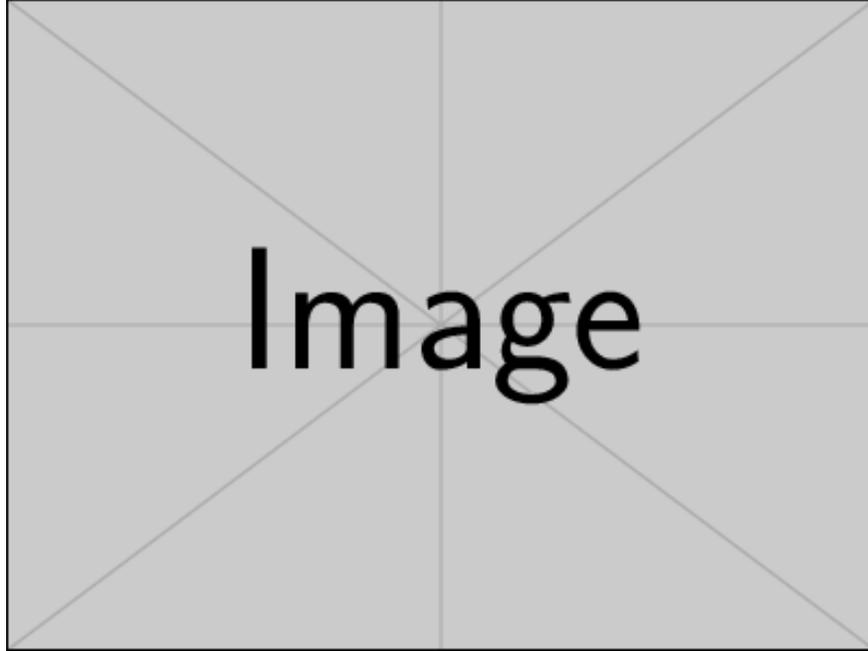
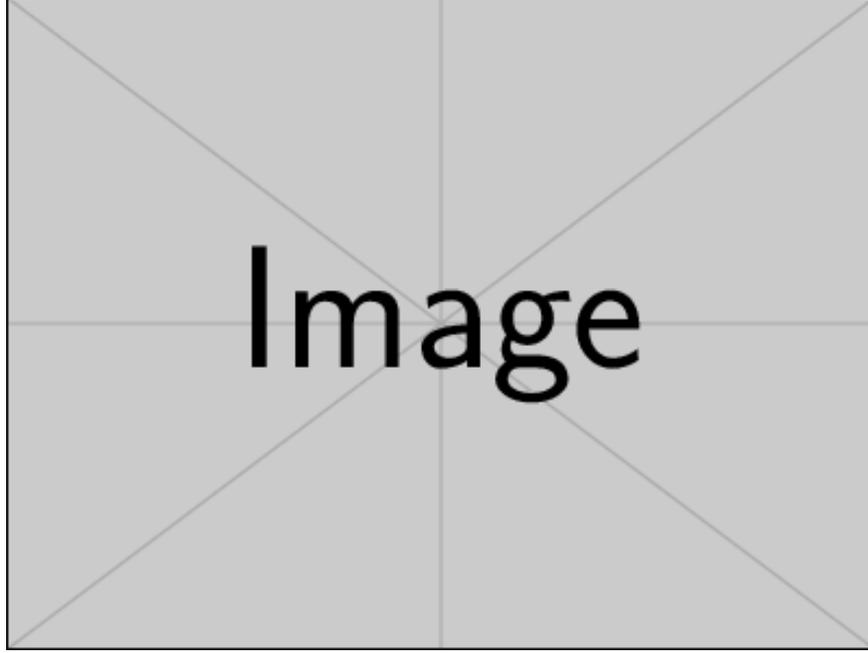
Beyond the boundaries of the coexistence region, one species will be excluded depending on initial conditions.

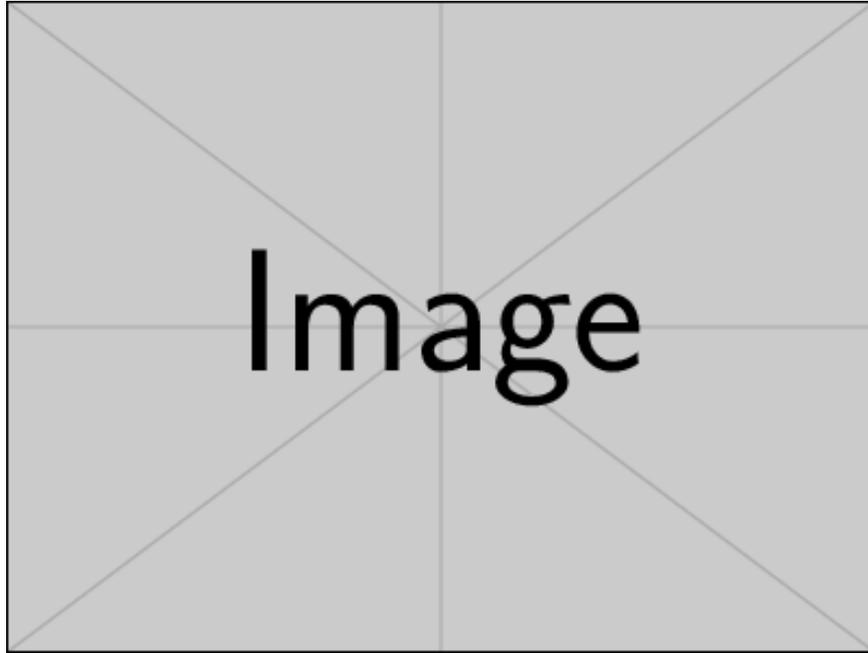
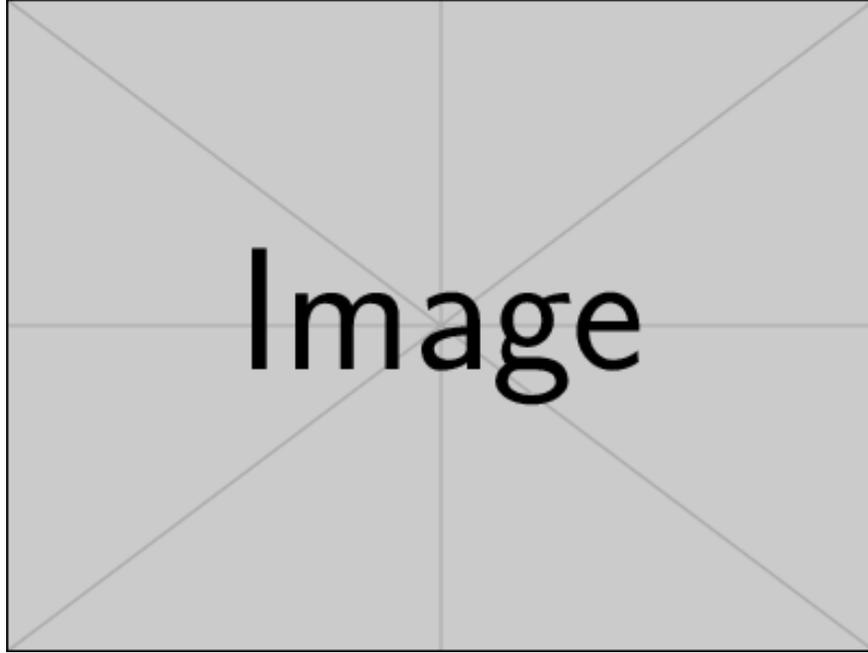
II. Effects of positive PSF on unequal conditioners or competitors

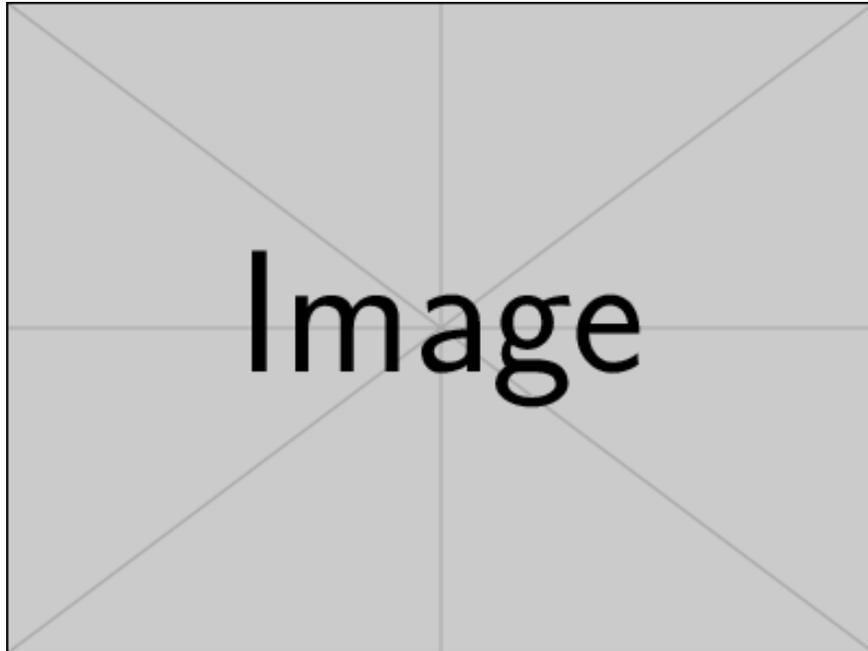
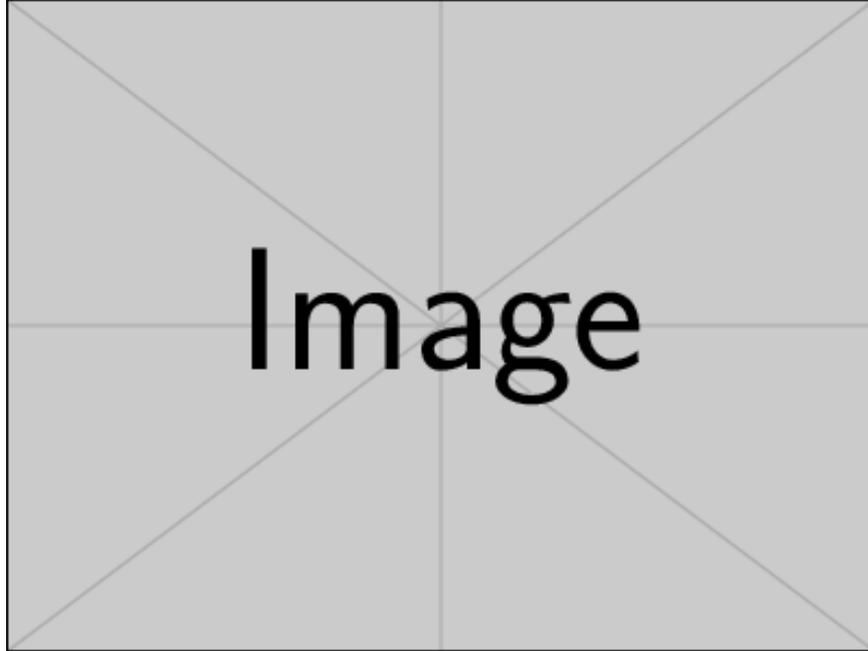
Beyond differences in soil preferences and resource preferences, species are likely to differ in their overall ability to condition the soil and their strength as competitors — question (II). Here, we examine the possible outcomes in these situations by now assuming that species 2 is worse or better at conditioning the soil, or has a wider soil or resource niche. In all of these situations, the range of soil and resource preferences which allows for both priority effects and coexistence as possible outcomes shrinks compared to the symmetric interaction case summarized in Figure (the boundaries of the regions in the symmetric case are shown as dashed lines in Figure).











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□ □ □ Possible outcomes of species interactions with asymmetry in (a-c) soil conditioning strength (η), (d-f) soil niche width (ω), and (g-i) resource niche width (ρ). The dashed lines represent the boundaries between the three regions in Figure . Species 1 has soil preference $\geq_1 = 0$ and resource preference $_1 = 0$ which is indicated by the black dot. All parameters which are not on the title of the plots are set to 1.

Asymmetry in conditioning ability . When the two species differ in conditioning ability, the region of the

parameter space that corresponds to strict priority effects (i.e. where one or the other species wins depending on initial abundances) expands into the region where coexistence and priority effects were alternative stable states (Figures -). This is expected, since the stronger conditioner will tend to maintain the soil closer to its preference, which is to the detriment of the other species. Therefore, the weaker conditioner will either be excluded or exclude the other species when the soil origin favors it, but they cannot coexist. For very large asymmetry in conditioning strength, coexistence and priority effects cannot be alternative stable states (the orange region vanishes).

Asymmetry in soil niche width . When the two species differ in soil niche width, competitive exclusion by the species with the wider niche is a new stable state (Figures -). We demonstrate this by either choosing a narrower or wider niche for species 2. In the former case, competitive exclusion becomes an alternative state along with coexistence (light green in Figure ,). We can expect the coexistence region to shrink when species 2 has a narrow niche since species 2 has a narrower range of soil conditions in which it persists.

When species 2 has a significantly narrower niche, there is yet another region where species 2 always becomes extinct (blue region in Figure). On the other hand, when species 2 has a wider niche, the coexistence region does not shrink. Instead, competitive exclusion of species 1 by species 2 is an alternative stable state with coexistence (orange region in Figure). When species 2 has a significantly wider niche, it always excludes species 1 (yellow region in Figure). This happens since species 2 can now survive in soils where species 1 used to displace it in the symmetric case. As it conditions the soil towards its preference and away from the fundamental niche of the weaker species, species 2 eventually excludes species 1. Note that the size of the coexistence region is limited by whichever species has the narrower niche width.

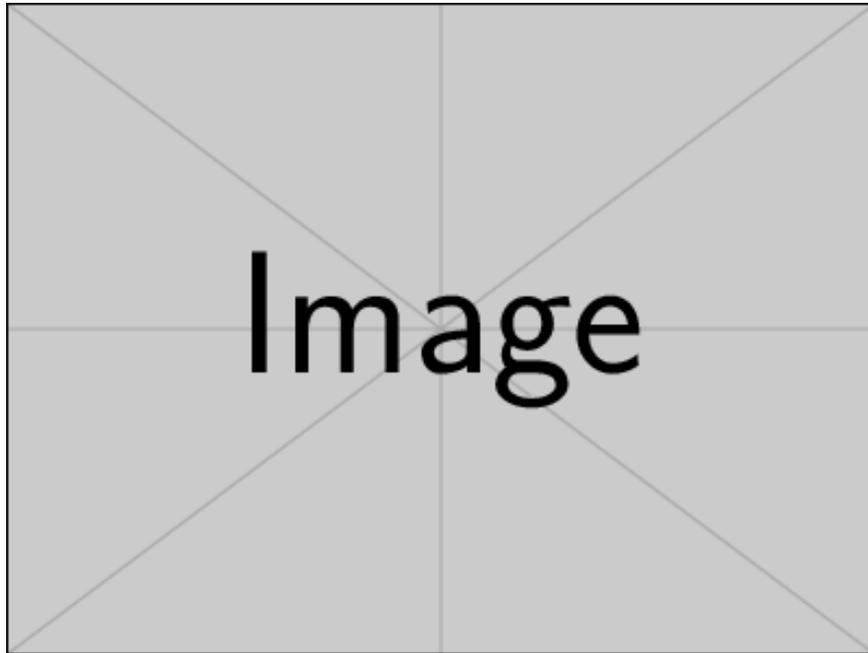
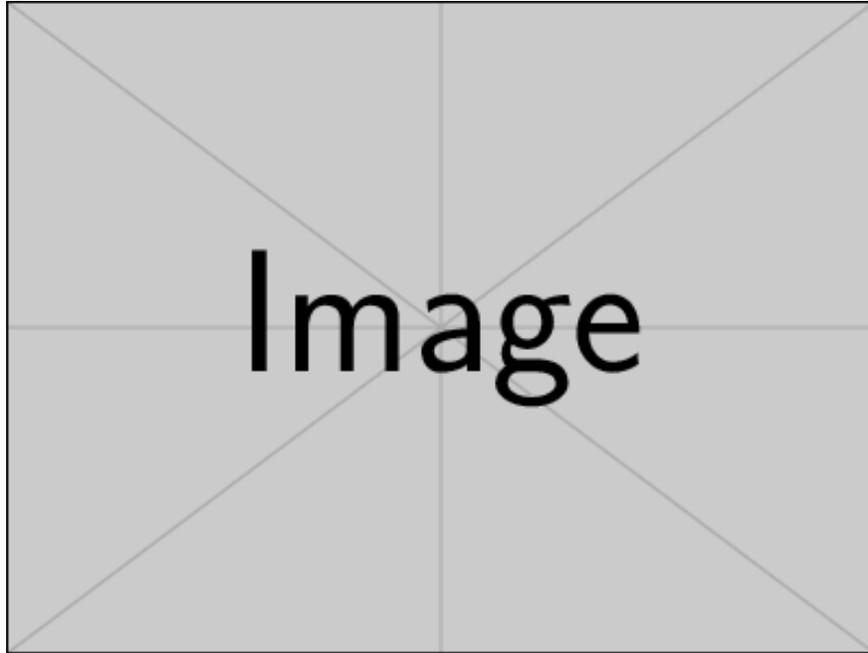
Asymmetry in competitive strength . Similar to asymmetry in soil niche width, competitive exclusion by the species with the wider niche is a new stable state when the two species differ in resource niche (Figures -).

Unlike asymmetry in soil niche width, the coexistence region shrinks whether species 2 has a narrower or wider resource niche. In a small part of the coexistence region, there is an alternate stable state where the stronger competitor excludes the weaker competitor (light green). For a range of similar soil and resource preference for both species, competitive exclusion by the stronger competitor is the only possible outcome (blue region in in Figures , and yellow region in Figure). Asymmetry in sensitivity to competition (ν) has a qualitatively similar effects on coexistence as asymmetry in resource niche width (see Appendix A7)

Figure can be used to infer whether an invader will be able to coexist with the resident or exclude it. For example, a strongly conditioning invader (large η , species 2 in Figure) will be able to coexist as long as its soil and resource preference fall in the region of the parameter space where coexistence is a stable state (green or orange regions in Figure). An invader which can tolerate a wide range of soil conditions (large σ , species 2 in Figure) will be able to coexist with the resident if its resource and soil preferences are sufficiently similar to the resident (green regions in Figure). Note that this region remains the same for an invader which has the same conditioning ability as the resident (Figure). However, there is a specific range of soil and resource preferences where an invader with stronger conditioning ability will exclude the resident (yellow region in Figure). For very large differences in soil preference, the invader will fail to establish (purple region in Figure). Simulation outcomes for these invasion scenarios and other asymmetric interactions are shown in Appendix A8.

III. Effects of positive PSF on trait distribution of coexisting species

We take a different approach to analyze large plant communities. We assume the community is surrounded by a regional pool of species which constantly seeds it with immigrants, preventing extinction of any one species. Thus, instead of focusing on the conditions for coexistence, we describe trait-abundance patterns among co-occurring species — question (III). We also assume that the ecological processes that affect the regional species pool are independent of the processes affecting the distribution of plants in the local community.



[ht!] □ □ Trait-abundance pattern in a multispecies community driven by PSF and competition become more predictable at high conditioning strengths. (a) Each stem represents a species, while the color of the dot at the top indicates the soil preference. These results are the output of simulating the same community of 225 species according to equation for 2000 time steps with initial abundance 0.01. (b) The equilibrium soil condition of a 225-species community with randomly chosen soil and resource preferences matches the soil origin when plants do not condition the soil, and matches the average soil preference of the community (0 here) when plants strongly condition the soil. The points are mean of 100 repetitions while the range around them is the standard deviation.

Other parameters are equal for all species: $\alpha = 0.3$, $\beta = 1.3$, $\nu = 1$ and $\iota = 0.001$.

Overall, we find that species in communities driven by a combination of competition, plant-soil feedback, and immigration tend to have similar soil preferences and fall into distinct groups with mutually similar resource preferences. Figure shows trait-abundance patterns in communities with 225 plant species whose soil preferences are normally distributed and centered at 0 with standard deviation 1.2. Their resource preferences are uniformly distributed from -3 to 3. When plants do not condition the soil (top row in Figure), species whose fundamental soil niche does not contain the soil origin are kept at low abundance and would go extinct without immigration (the soil preference of the dominant species in Figure match the soil origin, as indicated by their color). The resource preferences of the dominant species are contingent on the soil origin, as only those whose soil preference matches the soil origin can thrive (compare community composition in the left and right panels in the top row of Figure). In such low-richness communities, the dominant species are roughly evenly spaced by resource preference (limiting similarity).

Conditioning makes the trait pattern in competitive communities more predictable and leads to higher species richness and community size. When plants condition the soil (bottom row in Figure), the resulting community is similar regardless of the soil origin (compare left and right panels in the bottom row in Figure). Conditioning brings the soil condition towards the center of the distribution of soil preferences across species, allowing more species to maintain sizable abundances. The higher species richness reveals the clustering pattern that typically emerges under competitive dynamics in high-diversity communities (missing citation). The clusters are centered around the peaks in the trait-abundance distribution (Figure), and species' abundances generally decline with the distance between their resource preference and that of the closest peak. As expected from trait-based models of competition, the number of clusters decreases with increasing resource niche width (Appendix A9). Clustering also becomes weak at very low and high immigration rates. Clustering is stronger when the soil niche is wide because in those circumstances there are more viable species for competition to then generate the species clusters. The effect of soil niche width is reversed when immigration is strong, since in this case species filtering is a weaker process. See Appendix A10 for the details of the effect of immigration rate, soil conditioning strength and soil niche width on clustering.

The soil condition shifts over time from the soil origin towards the average of all the soil preferences of the species ($\bar{\mu} = 0$). The magnitude of this shift is proportional to the conditioning strength (Figure). When plants do not condition the soil (blue line), the soil condition does not change over time and exactly matches the soil origin. By contrast, strong conditioning decouples the equilibrium soil condition from the soil origin (yellow line).

Discussion

We found that positive plant-soil feedback, whereby plants favorably condition the soil, often promoted coexistence among competing plants. This is achieved via two mechanisms: (a) it endows all species with the ability to persist in a wider range of environments, (b) it gives weaker competitors the ability to compensate for their competitive disadvantage with a stronger environment-dependent intrinsic growth rate. Positive PSF led to extinctions only when the species had very different optimal soil conditions, in which case the soil origin or competitive asymmetry determined which species was extirpated. In a large plant community, PSF promoted coexistence by bringing the soil towards conditions that favored more species; in doing so, it caused a shift in trait distribution from limiting similarity, whereby dominant species have very different resource preferences, towards clustering, whereby species sort into groups with mutually similar resource preferences.

Our study integrates competitive interactions to a recent trait-based model of PSF (missing citation) and complements other models of plant-soil feedback focused on the soil microbiome (missing citation); (missing citation); (missing citation), yielding novel and sometimes contrasting results to the current

paradigm. Notably, our finding that two species experiencing positive PSF can coexist comes in stark contrast to suggestions that negative PSF is a necessary condition for coexistence (missing citation); (missing citation). In addition, our examination of the influence of the soil origin—associated with unconditioned soil in the PSF literature (missing citation); (missing citation)—yielded a richer set of outcomes (Figures ,) than predicted by previous models of PSF and competition.

Our model revealed the possibility of previously unknown alternative stable states between two-species coexistence and competitive exclusion. The outcome depended on both the soil origin and initial species abundances. Such a dependence on initial conditions is different from priority effects in a Lotka-Volterra competition model and its usual interpretation (missing citation), since coexistence and single-species equilibria cannot be simultaneously stable in Lotka-Volterra competition. For example, a pair of conditioning species pair whose soil and resource preferences are moderately different from each other will coexist only when the soil origin is roughly at the midpoint of their soil preferences (the region between the black lines in Figure). Only one species will survive if the soil origin is near its preferred soil condition, and both species will become extinct if the soil origin is significantly outside the fundamental niche of both species. This dependence on the soil origin is akin to legacy effects in plant communities (missing citation); (missing citation). For example, the biomass of a native California grassland community is significantly lower when they are grown in soil conditioned by exotic plant species compared to a soil conditioned by the native species (missing citation). Conversely, our results suggest that the exotic species, whose biomass were not affected by the soil condition, may have a wider soil niche.

Our reformulation of PSF provides a direct connection to niche theory (missing citation); (missing citation). The fundamental soil niche of a species is the range of soil condition where the intrinsic growth rate is positive, whereas the realized niche is the range of soil conditions in which the species can persist with biotic interactions. Absent interspecific interactions, the realized niche of plants that condition the soil in their favor is wider than their fundamental niche (missing citation); (missing citation). On the other hand, the realized niche of competing species is narrower than their respective fundamental niches if their soil preferences are sufficiently different (see Figure).

Competition theory predicts a limit to how similar two coexisting species can be in their resource preferences (missing citation); (missing citation). We observed limiting similarity in both two-species and multi-species communities in our model (Figure ,). In a two-species community, coexistence occurs only when the difference in the resource preference is sufficiently large. Similarly, the abundant species in a large community are evenly spaced on the resource preference axis, thus maximizing mutual differences (Figure). The observed limit to similarity is proportional to the resource niche width, in agreement with competition theory.

In addition to limiting similarity, we found that species abundances clump along the resource axis. Such a clustering pattern has been shown to be a signature of competition theoretically (missing citation); (missing citation); (missing citation) and was empirically verified in a tropical forest and a semiarid grassland (missing citation); (missing citation). The role of positive PSF in this pattern is similar to that of environmental filtering, since both select for species from the regional pool based on their soil preference.

Using a spatial model of PSF, we previously showed that species under positive PSF will cluster in space (missing citation). Each alternative state in a PSF-only system consists of a set of species with similar soil preference. Only one set can dominate in a given location, leading to a spatially patchy abundance distribution. While the species clusters observed here are of a different nature, we expect similar spatial patterns when PSF interacts with competition, with a few differences. For example, a competitively superior species may exclude a weaker competitor in one patch while coexisting in another patch due to differences in soil origin (e.g., species pairs from the light green regions in Figure).

Empirical studies on the interaction between PSF and competition typically use the classic two-phase PSF experiment and compare plant growth in isolation versus in the presence of other conspecific or heterospecific plants (missing citation); (missing citation). A synthesis of such studies (missing citation)

suggests that i) the synergy between competition and PSF favors coexistence by generating a net-negative density dependence—each species grows better when rare than when abundant, and ii) the density-dependent effects of competition can overwhelm PSF. These were corroborated in a 10-species greenhouse experiment (missing citation) and in a field experiment for *Sorghastrum nutans* (missing citation). Our results suggest that, regardless of the relative strength of PSF and competition, the outcome of species interactions depends not only on the direction and strength of PSF but also on the soil origin.

While this study focused on positive PSF, our model can be easily extended to negative PSF—when plants’ changes to soil inhibit their own growth, e.g. via the accumulation of pathogens. In this case, the intrinsic growth rate curve has a minimum rather than a maximum at the conditioning setpoint (Figure). We expect that such negative PSF will promote coexistence, in alignment with prevalent views, as long as species’ conditioning setpoints are sufficiently different. In large communities, competition and negative PSF should create similar patterns in resource preferences as seen here, but different patterns in soil preferences.

Our soil-explicit formulation of PSF necessitates a map between our “*E*” axis and the relevant soil conditions. In the simplest case, the process effectively entails a single salient soil condition, e.g., soil pH. More commonly, several biotic and abiotic soil properties will need to be measured (missing citation); (missing citation) and a dimensional reduction analysis may be performed (missing citation); (missing citation); (missing citation). These analyses might show that most of the variation occurs along a single linear combination of the soil variables, justifying the use of one-dimensional *E*. In cases where soil condition is irreducibly high-dimensional, extensions of our model to multivariate soil condition will provide a path forward.

In summary, conditioning markedly changes the conditions for coexistence among competing plants without greatly influencing the trait patterns typically arising from competition. Unlike competition, the benefits of conditioning scale with species abundances, which makes the outcomes more sensitive to initial conditions.

Acknowledgements

We thank Po-Ju Ke for providing helpful feedback on a previous version of the manuscript. We acknowledge the Institute for Advanced Computational Science at Stony Brook University for the computational resources.

Appendix

A1: Analytical results for the symmetric two-species community

The equilibria and their stability in ODE system (equations) for two species communities can be found analytically when the intrinsic growth rate is a quadratic function of the soil condition, i.e.

$r_i = r_{max}(1 - (\geq_i - E)^2/\frac{2}{i})$. For any parameter combination, there are a total of either 4 or 6 equilibria; both species extinct, only one species survives, and either 1 or 3 coexistence equilibria (missing citation).

The extinction equilibrium is always locally stable. When there are 3 coexistence equilibrium, two are always unstable and one maybe stable.

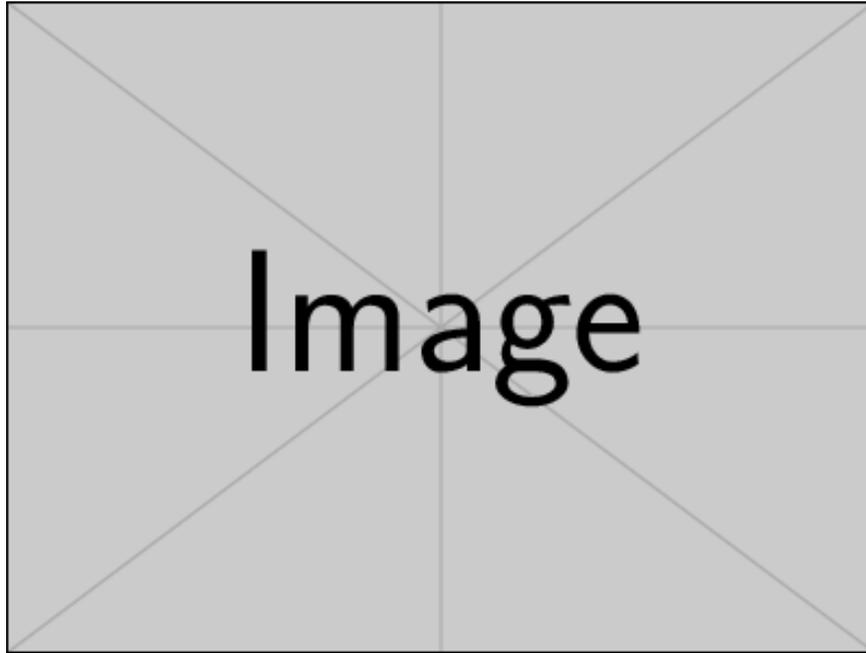
At the stable coexistence equilibrium,

$$N_1 = N_2 = \frac{4^2 - (\geq_2 - \geq_1)^2}{4^2(ii+ij)},$$

$$E = \frac{\geq_1 + \geq_2}{2}.$$

where ν is the competition coefficient which is calculated as $\nu = \int_{-\infty}^{\infty} \exp(-(x-1)^2/2) \exp(-(x-2)^4/(81^4))$.

As expected, the equilibrium abundance of the species decreases with increasing competition coefficient and increasing difference in soil preference. The soil condition at the stable coexistence equilibrium is at the midpoint of the two species' soil preference. The soil and resource preference at which the coexistence equilibrium and the single species equilibrium are stable is qualitatively similar to the situation with quartic intrinsic growth rate function discussed in the main text (Figure and Figure).



[ht!]

Possible outcomes of interaction between two species which differ only in soil and resource preference, and the intrinsic growth rate is a quadratic function of soil condition. Species 1 has fixed preference $\geq_1 = 0$, $\geq_1 = 0$ (shown as black dot). Coexistence equilibrium is only stable when the soil and resource preference of the second species lies

below the orange curve. Single species equilibrium are only stable outside the blue curve. The dashed line marks the condition at which the fundamental niche of the species stop overlapping. All other parameters are fixed at 1.

A2: Calculating competition coefficient under periodic boundary conditions

For any specific total resource utilization curve $V_i(x)$ and effective resource utilization curve $U_i(x)$, we calculate competition coefficient using the equation . The limit of the integrals are over the entire real line.

For the two-species cases (questions (I) and (II)), we compute the integral numerically in Mathematica.

However, for question (III) which pertains to a multispecies community, the competition coefficient will always be smaller for the species with extreme resource preferences. Although this is fair consequence, it leads to edge effects in the trait patterns. Specifically, the species with extreme resource preferences always have high abundance.

We avoid such edge effects by using a periodic boundary condition on the resource preference space. This assumption means that the species with resource preference at the extremes interact with each other such that they face competition from species with preferences not only from one direction of the resource axis but both directions. Mathematically, the integral in equation are now not over the real line but over a closed loop. We can approximate this integral by using a periodic version of the total utilization curve

$$\bar{V}_j(x), (x)=V_j(x-l) + V_j(x) + V_j(x+l), \text{ where } l \text{ is the length of the closed loop.}$$

A3: Trait clustering analysis using k-means and the gap statistic

We quantify clustering patterns by first using the k-means-based gap statistic (missing citation); (missing citation), which can be summarized as follows. We start by performing an abundance-weighted k-means clustering analysis to identify clusters on the resource/niche axis. This analysis finds the optimal grouping of species into a prescribed number of clusters by minimizing within-cluster variation in resource preferences weighted by abundance. Next, we compute the gap statistic (missing citation), which quantifies the strength of the pattern by comparing it to results from randomized data where species abundances are permuted. We then repeat those steps for a range of numbers of clusters, and choose the number that gives the biggest gap. Finally, we assess statistical significance of the result by comparing this maximal gap against a null distribution of maximal gaps obtained from randomized data.

Second, we test the pattern of limiting similarity. This is based on the theoretical prediction that there is a limit to the similarity in resource preference of coexisting species (missing citation); (missing citation). Here, we quantify limiting similarity using the variance in trait differences among dominant species. A low variance indicates that dominant species are maximally separated from their closest neighbors on the trait axis.

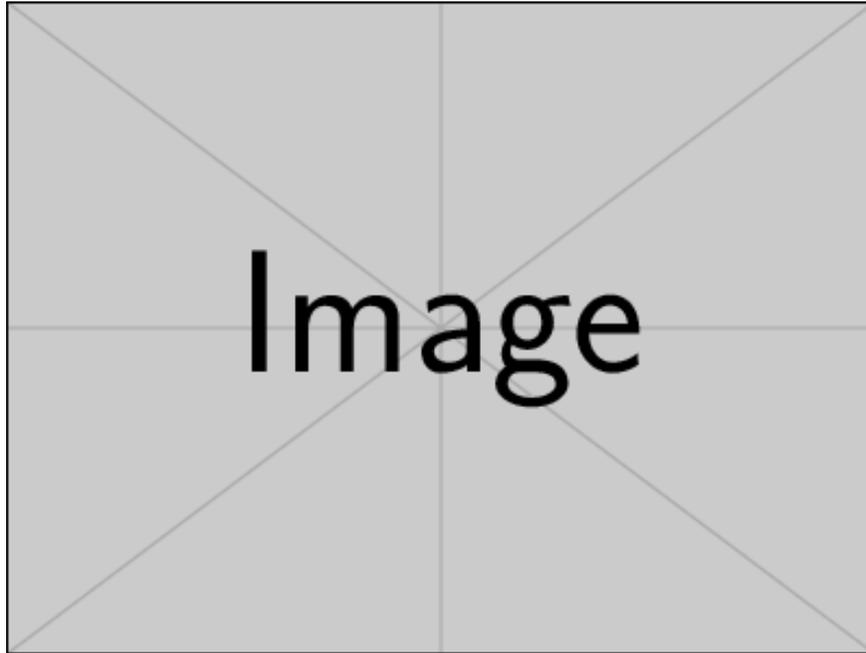
A4: Invasion criteria for determining coexistence in the absence of PSF

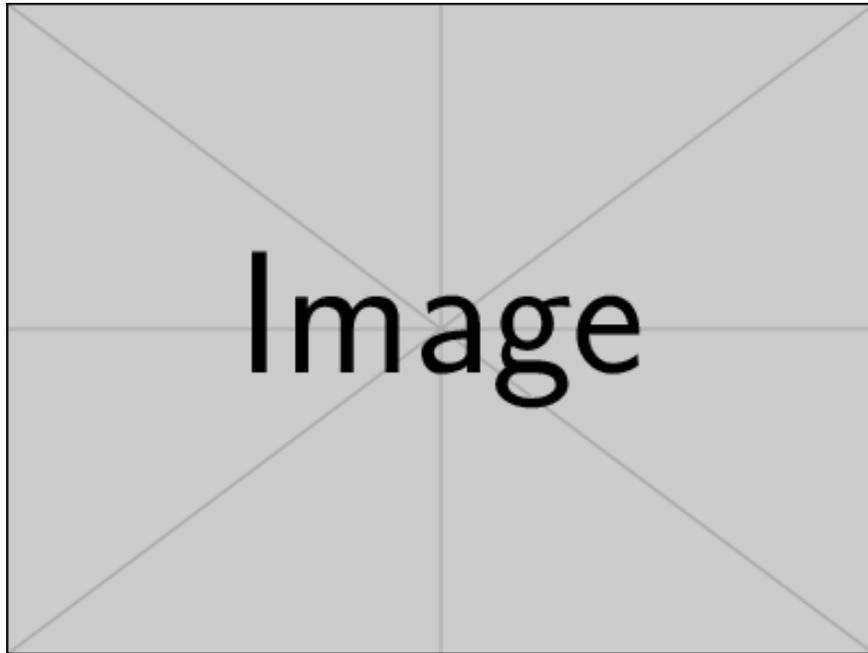
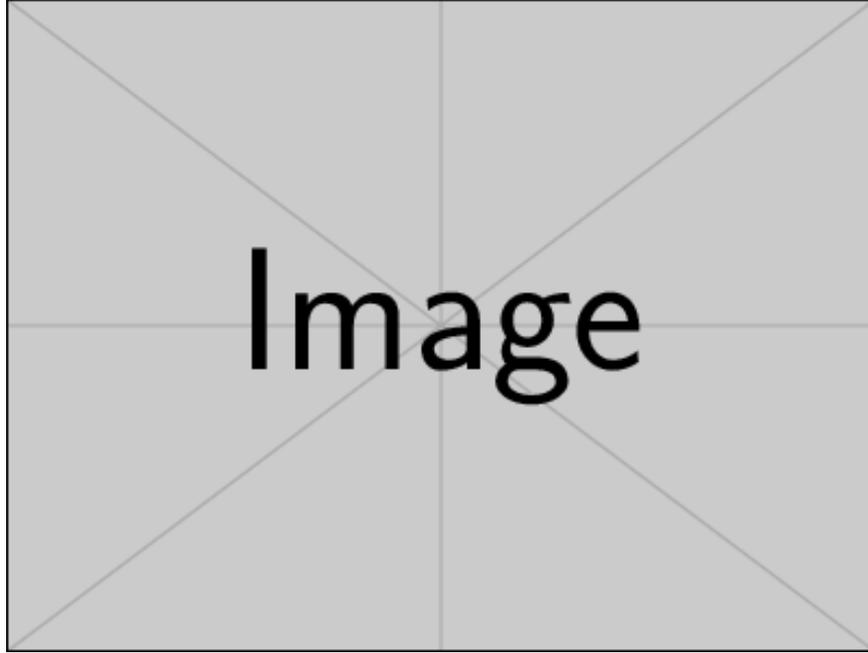
Plants that do not condition the soil and do not compete with each others can coexist when the soil condition belongs to their niche overlap. Following equation , two species with soil preference $\geq_1 < \geq_2$ coexist when $\geq_2 -_2 < E < \geq_1 +_1$.

When plants also compete with each other, we can use the invasion criteria as the necessary condition for coexistence. Invasion criteria tests whether a species can invade a resident population at equilibrium from low abundance. When there is only one species, equation has two equilibrium corresponding to extinction and persistence. The persistence equilibrium is stable when the soil condition lies within the fundamental niche of the species. At this equilibrium, the abundance is $N_i^* = (1 - (E - \geq_i)^4 / \geq_i^4)(r_{max}/ii)$. Therefore, the invasion criteria for species j is $r_{max}(1 - (E - \geq_j / \geq_j^4)) - \geq_j N_i^* > 0$. The two species coexist when invasion criteria is satisfied for both species. If only one species satisfies the invasion criteria, then the other species will be driven to extinction. We use these inequalities to produce Figure .

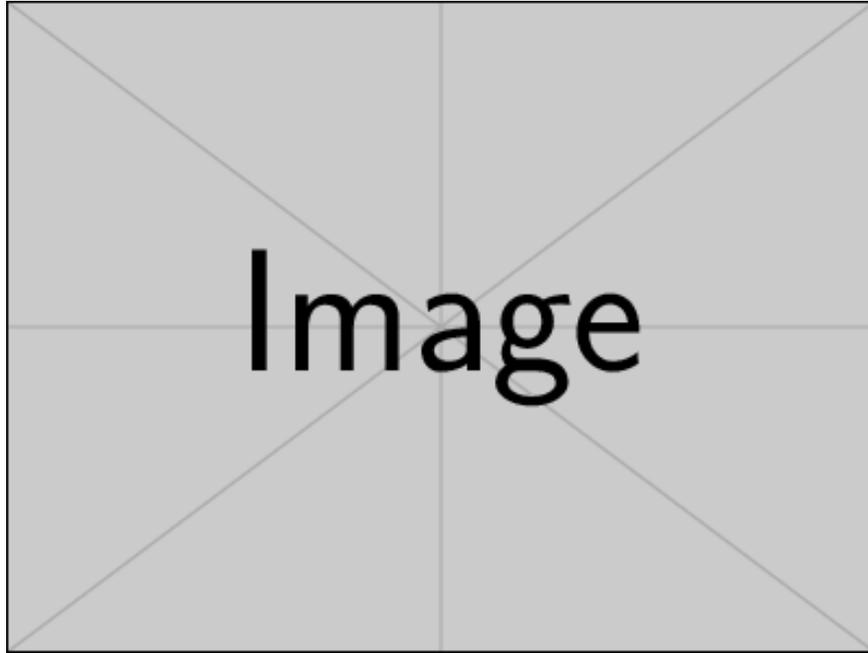
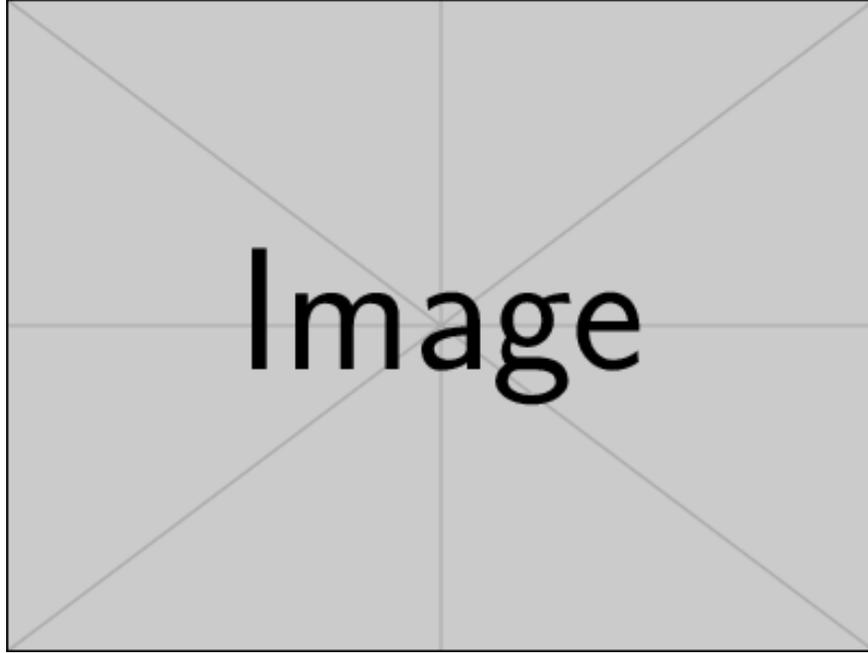
A5: Effects of changing the functional forms of the intrinsic growth rate and competition coefficient calculation

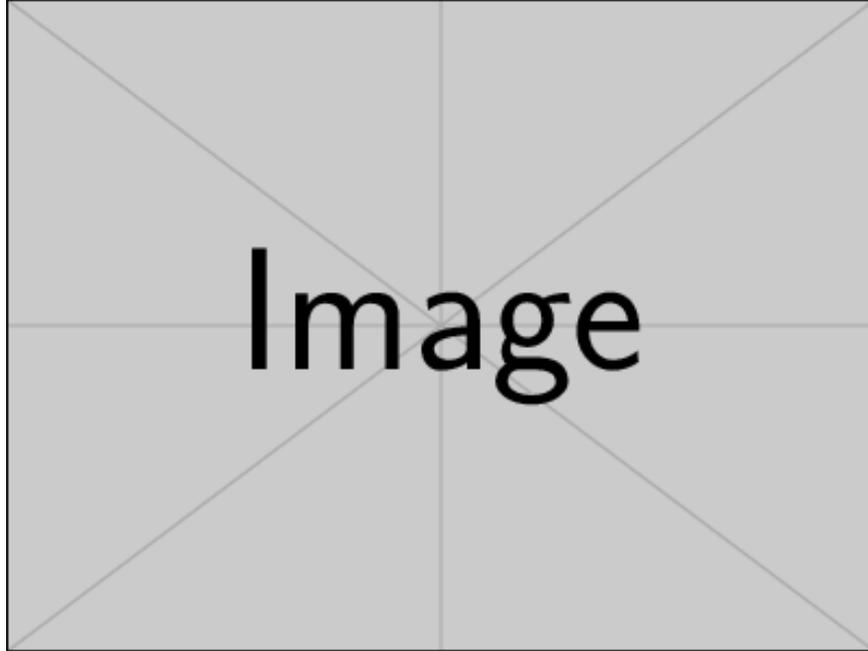
The number of equilibria and the qualitative effect of soil and resource preferences on their stability are robust to changes to the functional form of the intrinsic growth rate function r_i and competition coefficient a_{ij} . Since the competition coefficient vanishes for large differences in resource preference, the range of soil preferences that only permit stable coexistence remains unaffected for any reasonable method of calculating competition coefficient. Interestingly, the intrinsic growth rate function only affects the range of soil preference where coexistence and single species equilibria are simultaneously stable (Figure). This range increases for boxier (large exponent k in $1 - (E - \geq)^k / k$) intrinsic growth curves. The width of the total resource utilization curve (in $\exp(-(x -)^4 / ()^4)$) is directly proportional to the minimum difference in resource preference that permits coexistence (Figure). However, this parameter does not affect the range of soil preference that allows for coexistence to be simultaneously stable with the single species equilibria.





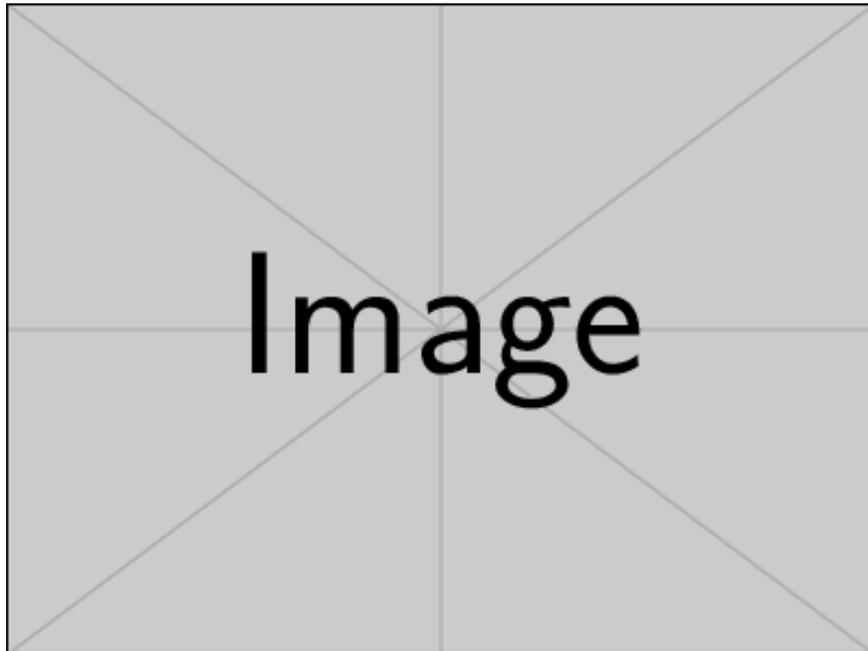
[ht!] Possible outcomes of interaction between two species while varying the intrinsic growth rate function $= 1 - (E - \geq)^k / k$. Parameters: (a) $k=2$, (b) $k=4$, and (c) $k=8$. Other parameters are set to 1.

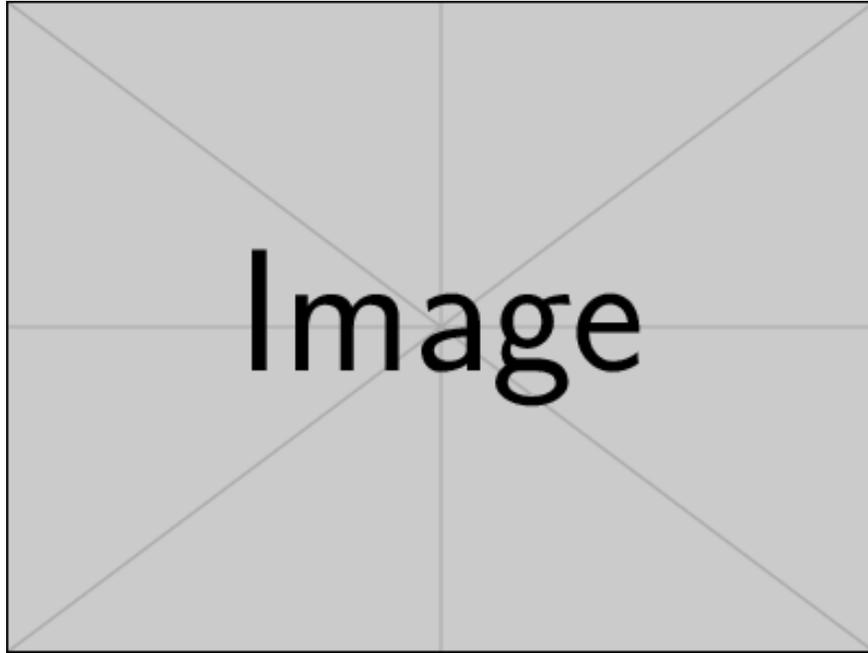
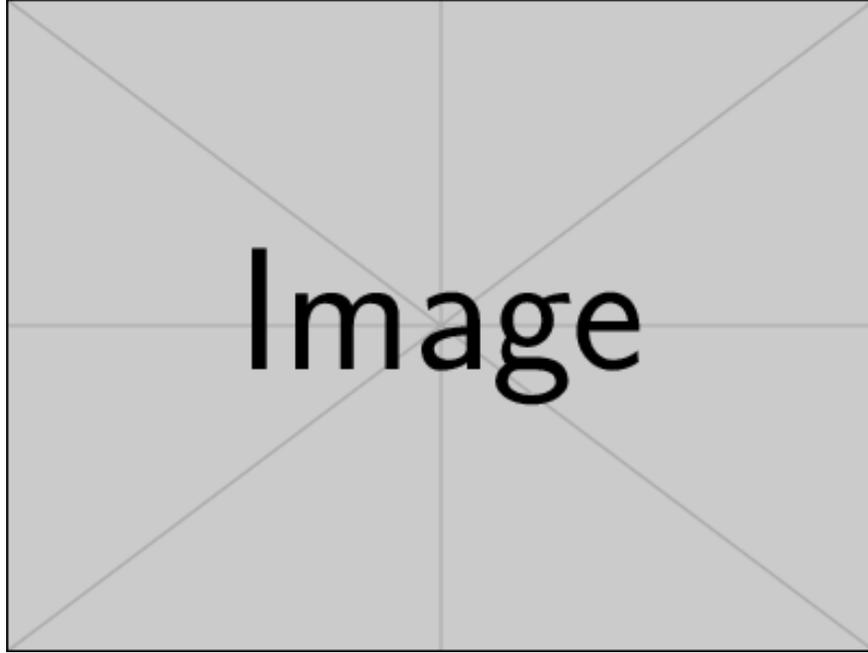




[ht!] □ □ □ Possible outcomes of interaction between two species while changing width of the total utilization curve $V(x) = \exp(-(x-)^4/())^4$. Parameters: (a) = 1, (b)= 2, and (c)= 3. Other parameters are set to 1.

Competition coefficient can also be directly computed based on the difference between resource preferences without an explicit consideration of resource utilization curves. Here, using a trait matching assumption that interaction strength is maximum when trait values match, we can specific competition coefficient by the function $\exp(-|i - j |^k/2^k)$. As this function becomes boxier (large exponent k), the region where coexistence is stable becomes steeper (Figure).

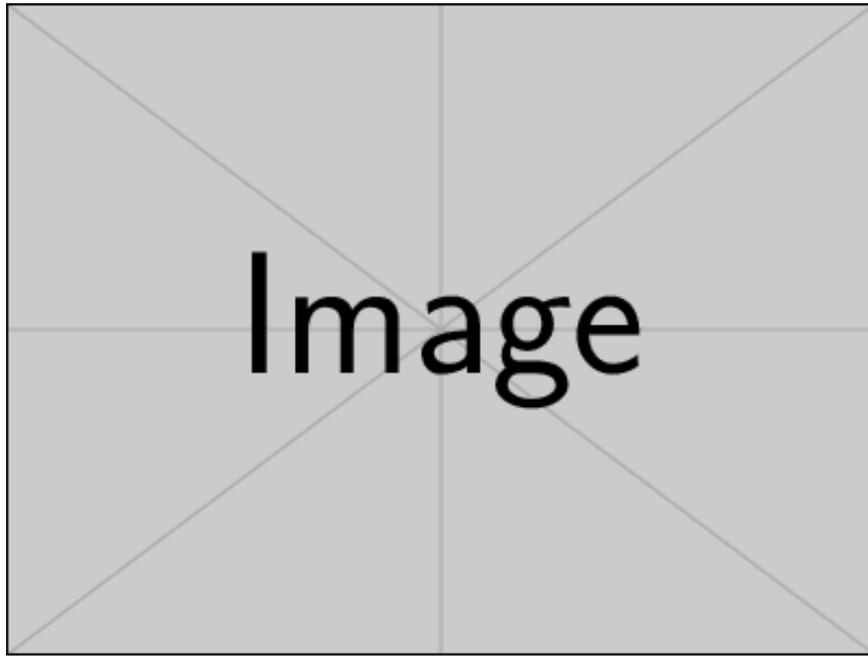


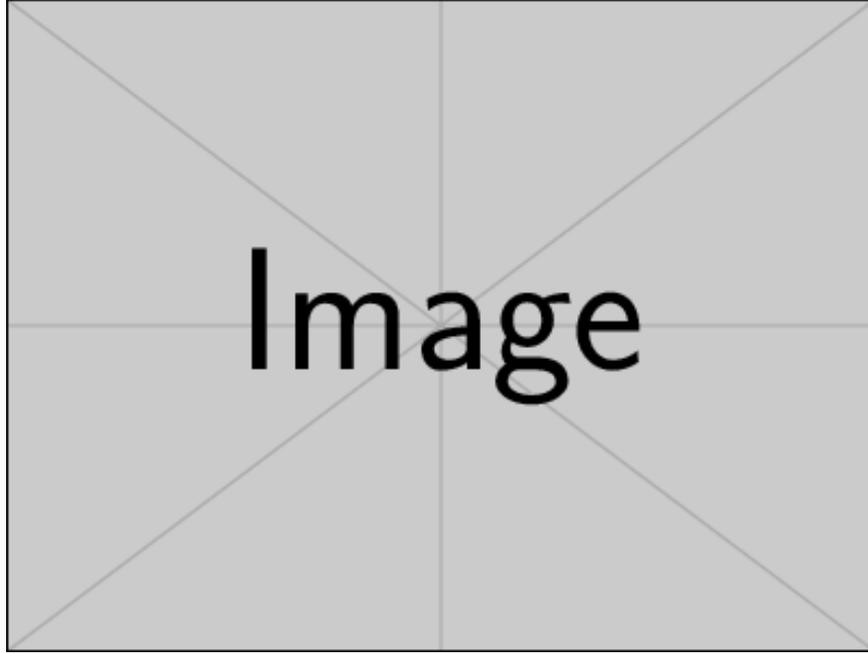


[ht!] Possible outcomes of interaction between two species while directly computing competition coefficients from the difference in resource preferences. Competition coefficient $a = \exp(-|i - j|^k / 2^k)$ with parameter (a) $k = 1$, (b) $k = 2$, and (c) $k = 4$. Other parameters are set to 1.

A6: Allee effect (initial abundance dependence)

The boundaries of the coexistence and extinction regions depend not only on the initial soil (as in Figure but also on the initial abundance. This dependence is particularly interesting in communities where coexistence and priority effects are alternative stable states. We see an Allee effect in such communities. Consider a scenario where species 2 is introduced to a monodominant stand of species 1. Species 2 can coexist with species 1 only when its population is sufficiently high (Figure A). This threshold is the critical population N^c . Figure A shows the effect of the soil preference on the critical population. When the soil preference of the two species are close to each other, the critical population is zero and both species coexist regardless of the initial abundance of species 2. For increasingly wider gaps in soil preferences, the critical population increases, and coexistence and priority effects become alternative stable states. In these scenarios, coexistence is possible even though invasion from low abundance is not. The critical population threshold rises asymptotically up to a critical difference in soil preference, beyond which the two species can never coexist given any initial abundances.

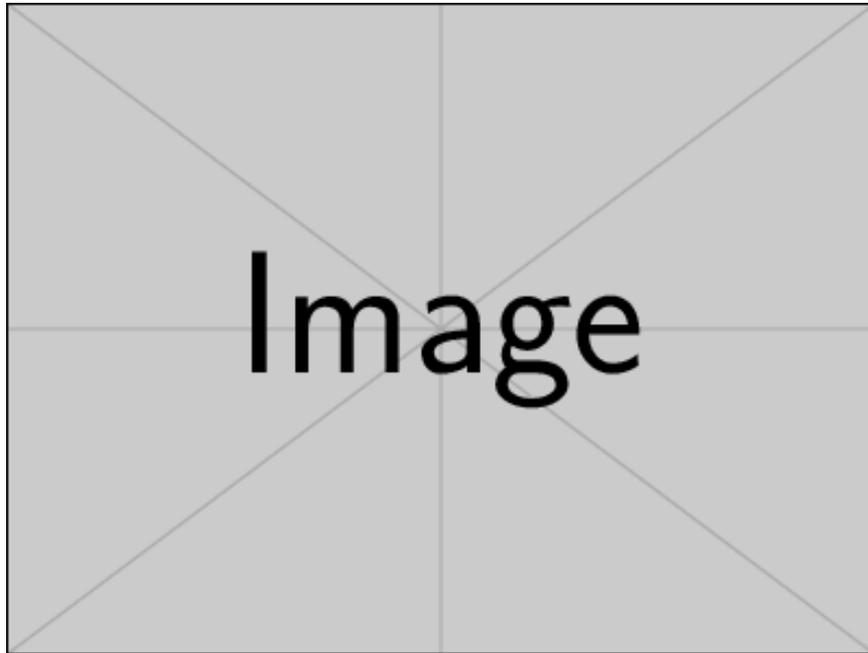
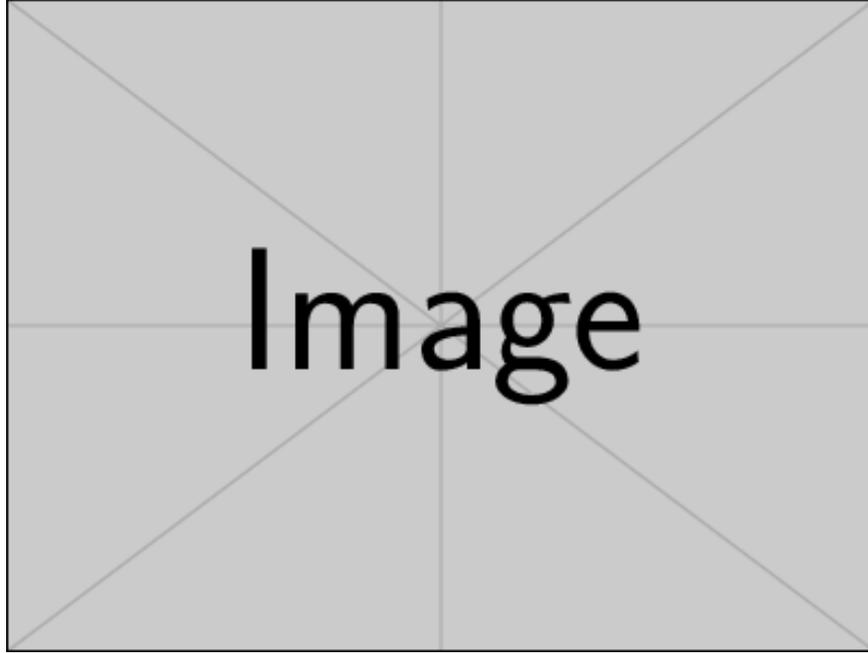




[ht!] □ □ (a) Initial abundance determines whether species 2 ($x_2 = 2, \geq_2 = 0.8$) can coexist when invading a population of species 1 ($x_1 = 0, \geq_1 = 0$). (b) The threshold abundance for invasion increases monotonically in the region where coexistence and exclusion of one species are alternative stable states. All other parameters are fixed for the plots at 1. Simulations for (a-c) was run for 1000 time steps. Ext. = extinction of both species. $N_2^C(0)$ = threshold abundance for invasion by species 2. Extinction of both species is always possible if the soil origin is sufficiently far from the preference of either species. In communities with traits under the blue curve, if one species survives, then the other will necessarily survive as well. Between the blue and orange curves, both species coexist or only one species survives depending on the soil origin. Above the orange curve, the species cannot coexist for any value of soil origin. (b)

A7: Asymmetry in sensitivity to competition

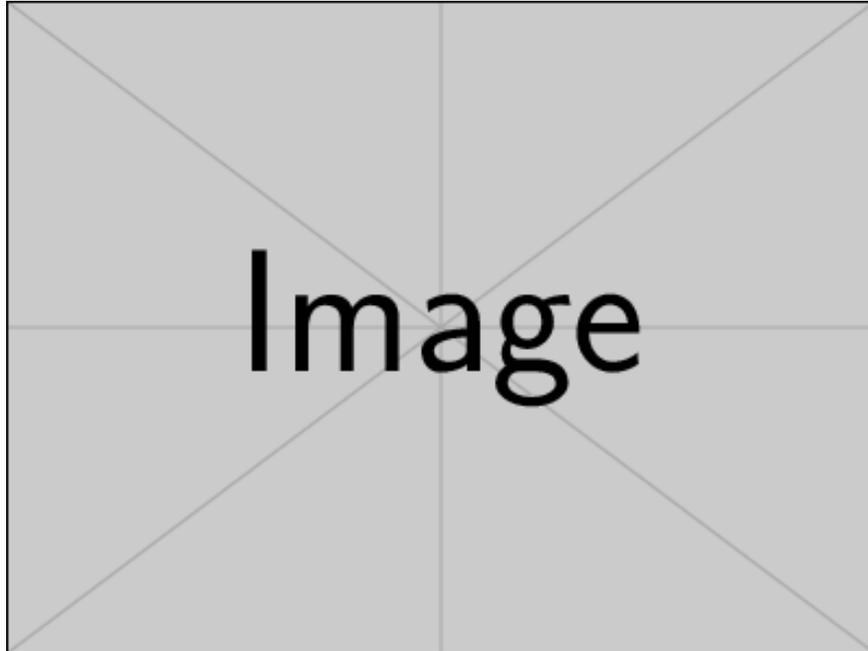
In two-species interactions where both species condition the soil equally but have different sensitivity to competition (ν), the coexistence outcomes are qualitatively similar to when the two species differ in their resource niche width (Figure -). Specifically, the stronger competitor can drive the other species extinct when they have similar resource and soil preferences (Figure).

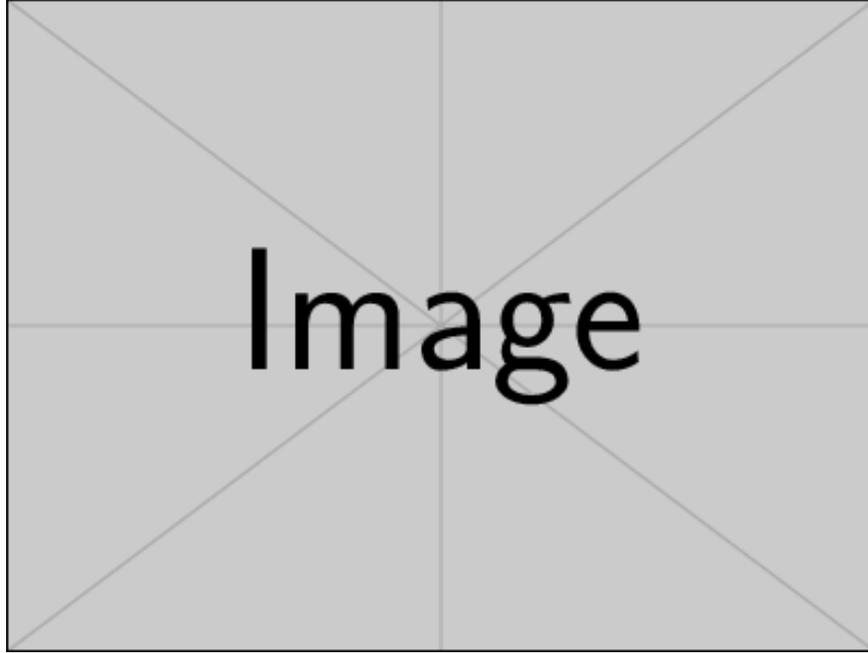


[ht!] □ □ Possible outcomes of species interactions with asymmetry in sensitivity to competition. The dashed lines represent the boundaries between the three regions in Figure . Species 1 has soil preference $\geq_1 = 0$ and resource preference $_1 = 0$ which is indicated by the black dot. All parameters which are not on the title of the plots are set to 1.

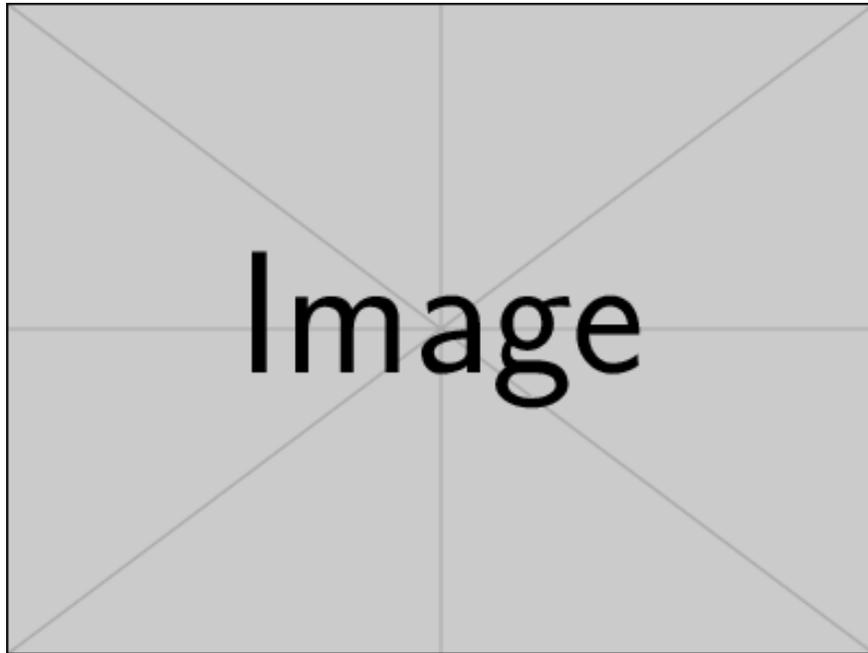
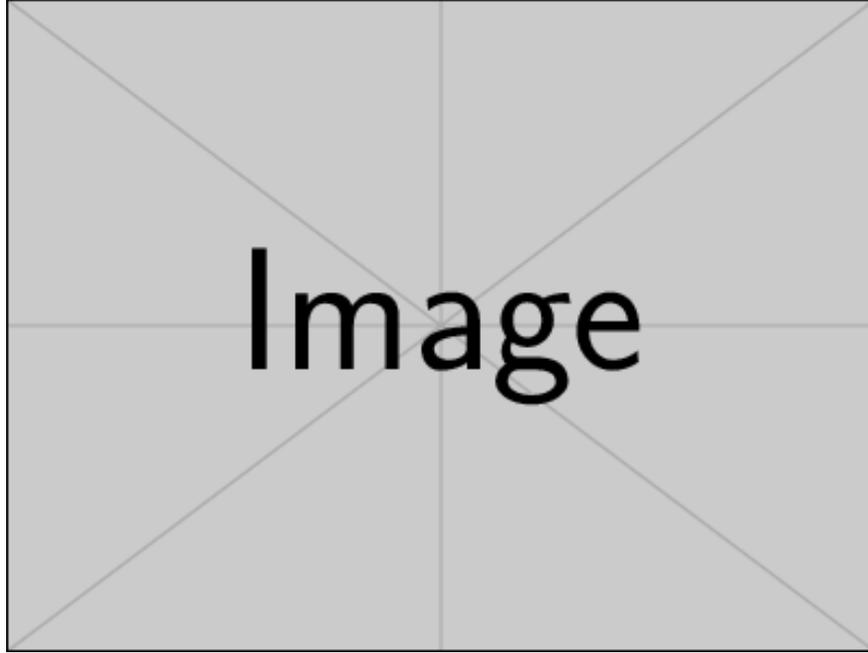
A8: Invasion plots with PSF and competition

Our analysis of the two-species model can be used to predict invasion outcomes. Invasion is guaranteed when the soil and resource preference of the two species fall in the region where coexistence is the only stable equilibrium (Figures -). Since the soil condition when the invader arrives matches the resident's soil preference, invasion is not possible when resident-only equilibrium is stable. When the invader is a stronger competitor either due to wide resource utilization (σ) or less sensitivity to competition (ν), for some invader soil and resource preferences, successful invasion is followed by competitive exclusion of the resident (Figure ,). This is also the case when the invader has a wider soil niche (Figure). The range of such soil and resource preference overlaps with the region where the invader-only equilibrium is the only stable equilibrium.

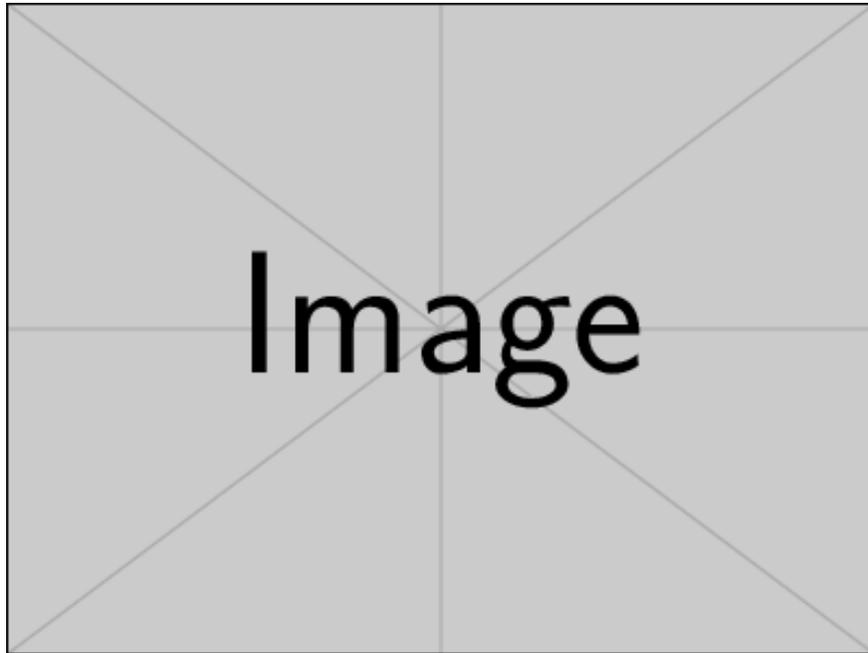
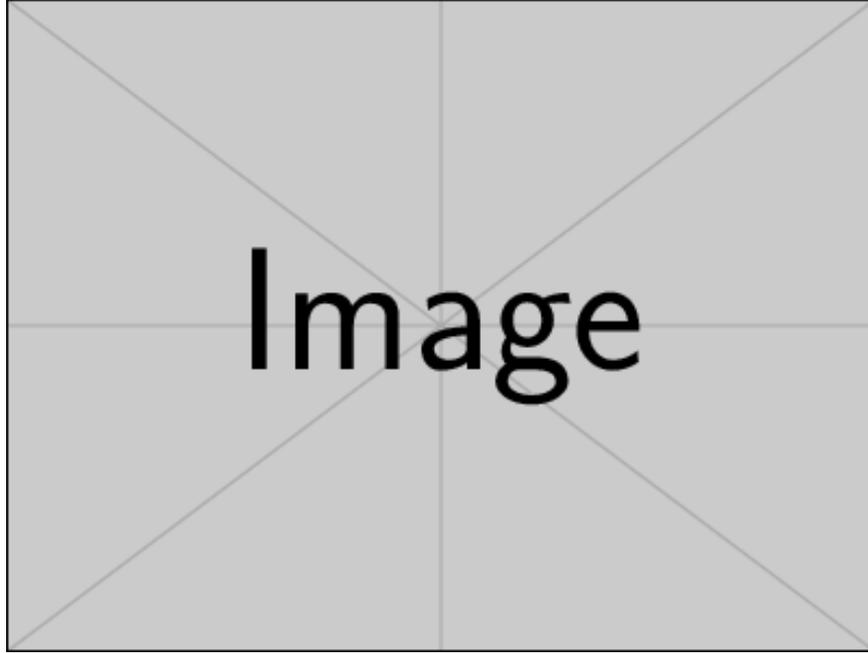




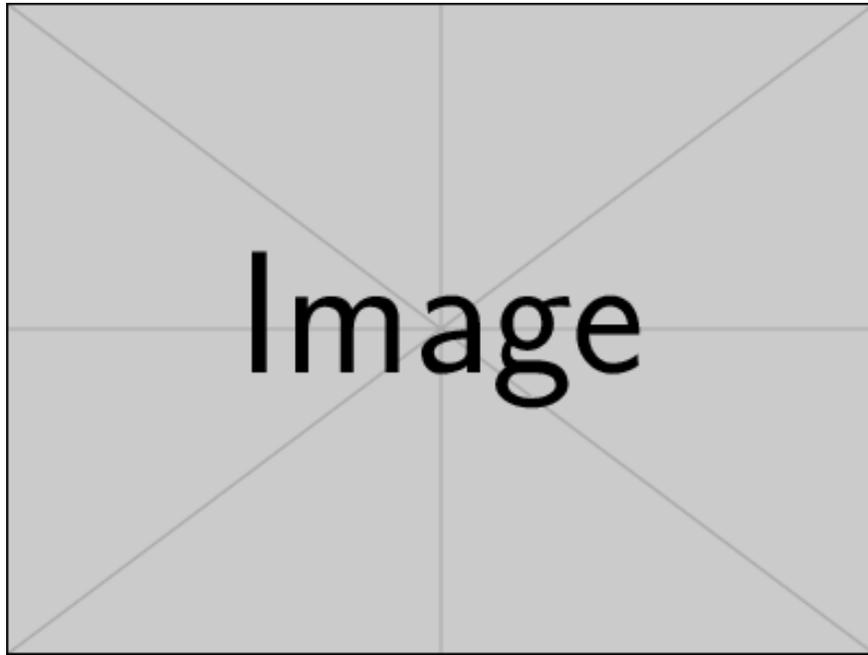
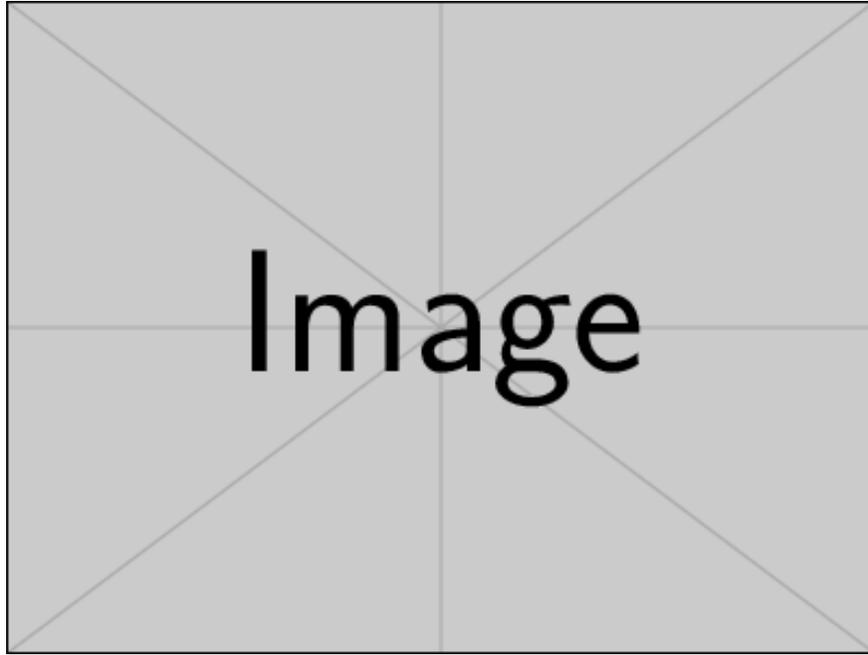
[ht!] □ □ Invasion plots when plants do not condition the soil but only compete with each other. For Figures -, the left and right panels show the abundance of the resident (species 1) and invader (species 2), respectively. The black dot denotes the soil and resource preference of the resident. The curves are boundary between regions where the set of outcomes which are alternative stable states change. All other parameters are set to 1. These are outputs of numerical integration of equations starting at resident-only equilibrium ($N_1 = 1$ and $E = 0$) with initial invader abundance $N_2 = 0.001$ for 10000 time steps.



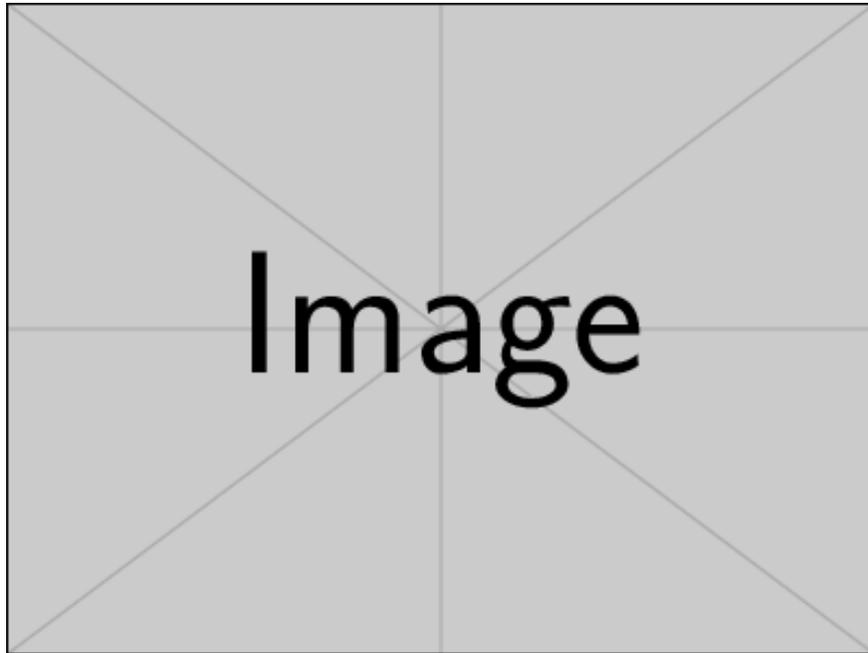
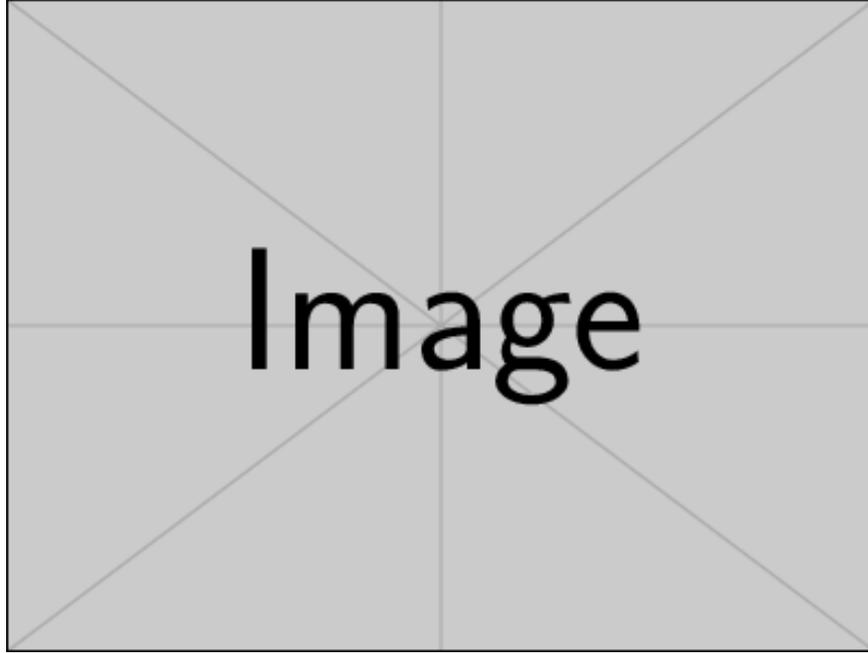
[ht!] □ □ Invasion plots with PSF and competition for symmetric interactions.



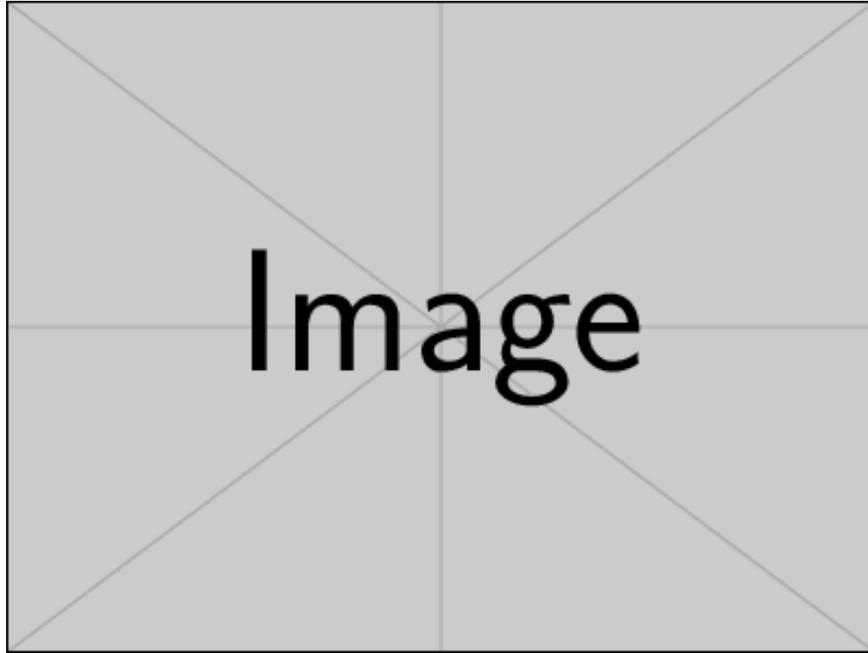
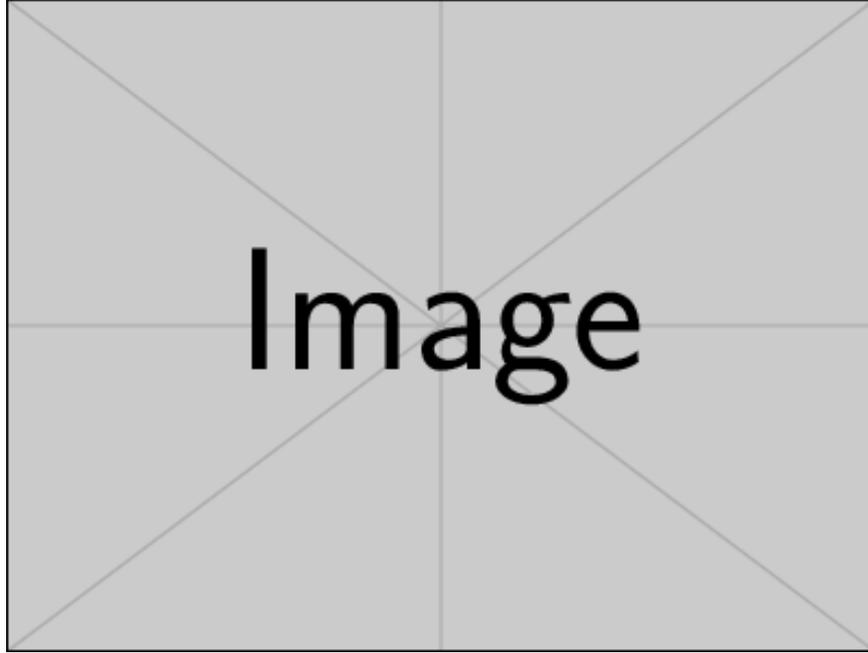
[ht!] □ □ Invasion plots with PSF and competition for a strongly conditioning invader ($\eta_2 = 1.5$).



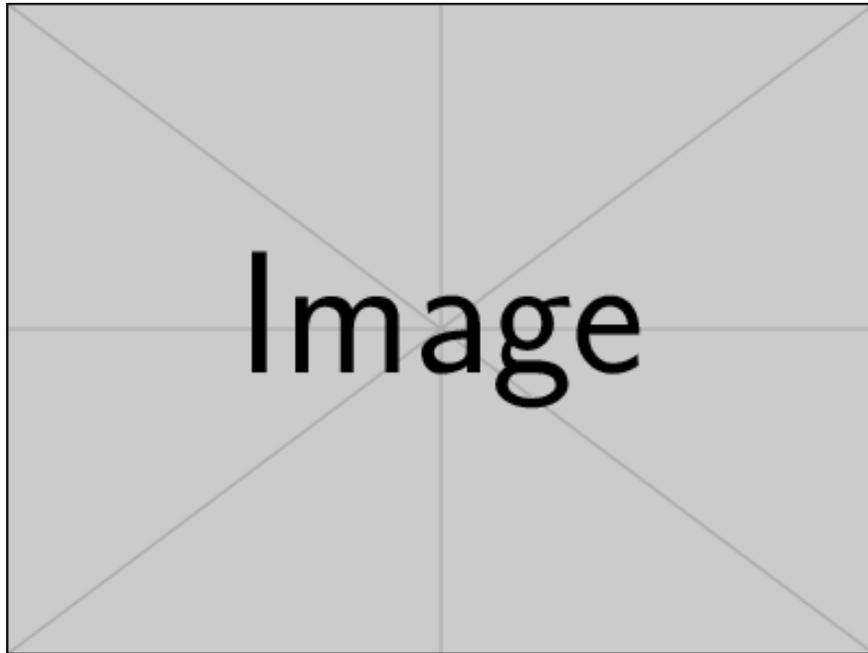
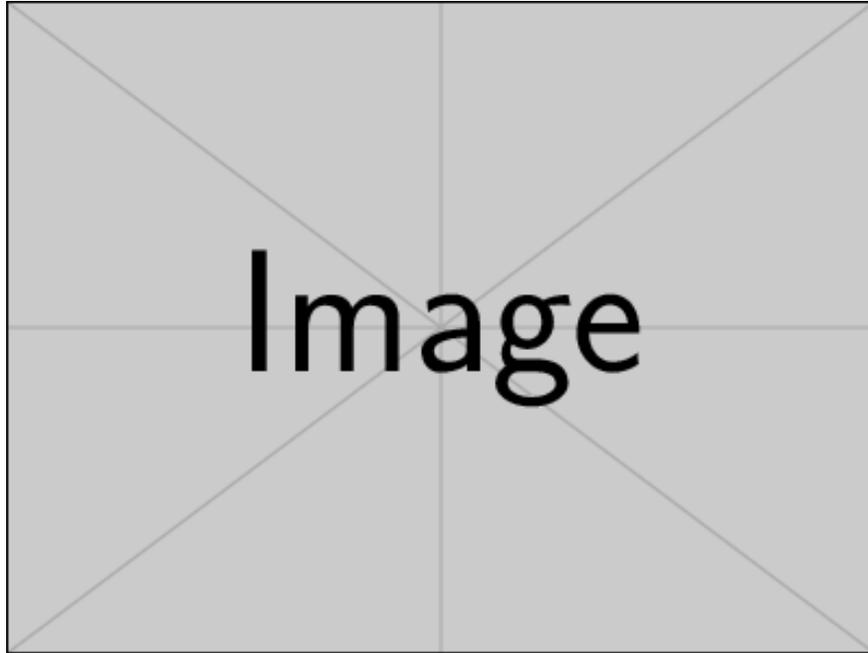
[ht!] □ □ Invasion plots with PSF and competition for a soil tolerant invader (= 1.4).



[ht!] □ □ Invasion plots with PSF and competition for an invader with a wide resource utilization curves (= 1.2).



[ht!] □ □ Invasion plots with PSF and competition for a competitively insensitive invader ($\nu_2 = 0.9$).



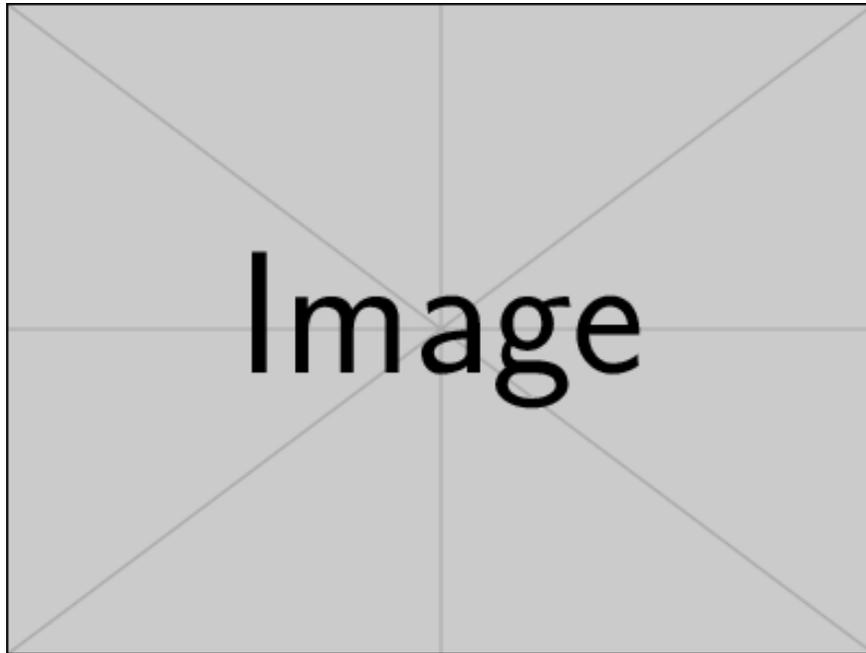
A9: Number of clusters in trait-abundance distribution

When species have a wider resource niche width, the number of clusters decreases (Figure A). This is because the range of competitive influence of each species increases, causing dominant species to be farther apart on the resource axis; since the range of resource preference in the community is fixed, this results in fewer clusters. Both clustering and the limiting similarity pattern remain strong for the entire range of resource niche width. However, when soil niche is narrow and immigration is strong, there are fewer viable

species for competition to choose a winner from. Therefore, clustering tends to weaken at larger resource niche width (Figure A). [ht!] [] Clustering becomes weaker at large resource niche width when soil niche width is narrow and immigration is high. (a) = 1.3, $\iota = 1e - 4$. (b) = 0.7, $\iota = 1e - 3$.

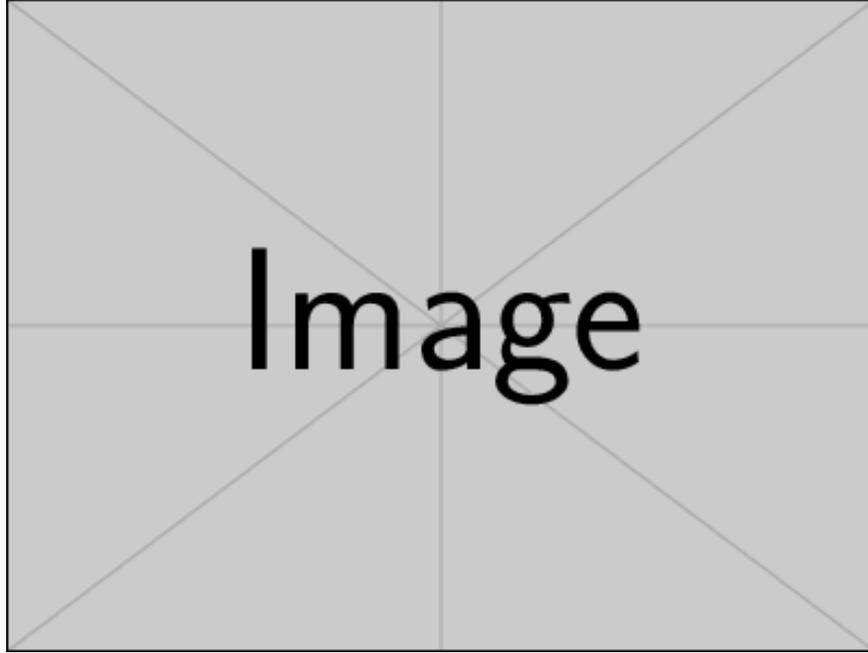
A10: Effect of immigration rates on species clustering

Figure shows the effect of immigration rate, conditioning strength, and soil niche width on the clustering pattern. At low immigration rates, the species near the peaks in the trait-abundance distribution rapidly become extinct without new immigrants, which weakens clustering. At high immigration rates, all species have high abundance due to immigration, and fitness differences due to competition and plant-soil feedback do not translate to differences in abundance. By contrast, conditioning strength does not affect the clustering pattern. Soil primarily plays the role of filtering in large communities. Therefore, clustering is stronger when soil niche is wide because in those circumstances there are more viable species for competition to then generate the species clusters. The effect of soil niche width is reversed when immigration is strong, since in this case species filtering is a weaker process (see Appendix A6).



[ht!] [] Clustering is strongest at intermediate immigration rate and high soil niche width. Letters over the bars indicate significant difference in clustering strength based on pairwise t-tests. Outcomes are based on numerical integration in MATLAB for 10000 time steps, with initial soil at 0 and initial abundance at 0.01 for all species. All species have $\eta = 1$, $\nu = 1.3$ and $\nu = 1$ unless shown otherwise in the plot. (a,b) = 0.3, $\iota = 0.001$, (c) $\iota = 0.0001$, (d) = 0.35, $\iota = 0.0005$.

Clustering pattern is in general stronger for wider soil niche width since there are more viable species for competition to further filter species abundances. However, when immigration is low, narrow soil niche width shows a stronger pattern since species filtering is a weaker process and our assumption of uniform immigration weakens clustering (Figure A).



[ht!] □ Clustering becomes weaker at higher soil niche width when immigration is higher. $\iota = 1e - 3$, $\eta = 1$, $\theta = 0.5$.

References