

No robust coexistence in a canonical model of plant-soil feedbacks

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Abstract

Plant-soil feedbacks (PSFs) are thought to represent a crucial mechanism generating frequency dependent dynamics in plant communities. Negative feedbacks, in particular,

are routinely invoked to explain coexistence and the maintenance of diversity in species-rich communities. However, the primary modeling framework used to study PSFs considers only two plant species, and we lack clear theoretical expectations for how these complex interactions play out in communities with natural levels of diversity. Here, we demonstrate that this canonical model for PSFs is equivalent to a well-studied model from evolutionary game theory, and using this equivalence, we are able to characterize the dynamics with an arbitrary number of plant species. Surprisingly, we find that coexistence of more than two species is virtually impossible in this model, suggesting that alternative theoretical frameworks are needed to describe feedbacks observed in diverse natural communities.

1 Introduction

It has become well understood that reciprocal interactions between plants and the soil biota, known as plant-soil feedbacks (PSFs), play an important role in structuring the composition and dynamics of plant communities. PSFs operate alongside other factors, including abiotic drivers (Bennett & Klironomos 2019) and above-ground trophic interactions (Van der Putten *et al.* 2009), but are thought to be a key mechanism generating negative frequency-dependent feedbacks that promote coexistence and maintain plant diversity (Kulmatiski *et al.* 2008; Van der Putten *et al.* 2013; Bever *et al.* 2015). The existence of PSFs has long been known (Van der Putten *et al.* 1993; Bever 1994), but our understanding of their importance – particularly in relation to patterns of coexistence – has developed rapidly in recent years (Klironomos 2002; Petermann *et al.* 2008; Mangan *et al.* 2010). Broad interest in PSFs was ignited by the development of simple mathematical models, which illustrated the potential of PSFs to mediate plant coexistence (Bever *et al.* 1997; Bever 2003; Ke & Miki 2015). These models have played a guiding role for a wide range of empirical studies, as well (Kulmatiski *et al.* 2008, 2011; Pernilla Brinkman *et al.* 2010).

The first, and still most widely known and used, model for PSFs was introduced by Bever and colleagues in the 1990s (Bever 1992; Bever *et al.* 1997; Bever 1999, 2003). In this framework, often referred to simply as the Bever model, each plant species is assumed to promote the growth of a specific soil component (i.e. associated bacteria, fungi, invertebrates, considered collectively) in the vicinity of individual plants. In turn, the fitness of each plant

species is impacted by the relative frequency of different soil components. Starting from minimal assumptions, Bever *et al.* (1997) derived a set of differential equations to capture these dynamics. PSFs can be either positive (fitness of a plant species is increased by its corresponding soil component) or negative (a plant species experiences lower relative fitness in its own soil). Bever *et al.* introduced a single quantity to summarize whether community-wide PSFs are positive or negative, and showed that this value characterizes the dynamical behavior of the model. In the original Bever model of two plant species, positive PSFs lead to exclusion of one species, while negative PSFs result in neutral oscillations. It is thus widely suggested that negative PSFs help sustain coexistence in real-world plant communities (Kulmatiski *et al.* 2008; Van der Putten *et al.* 2013), perhaps with spatial asynchrony playing a role in stabilizing the cyclic dynamics (Revilla *et al.* 2013; Bever 2003).

Subsequent studies have generalized this model to include, for example, more realistic functional forms (Umbanhowar & McCann 2005; Eppinga *et al.* 2006), more explicit representations of the soil community (Bever *et al.* 2010), spatial structure (Eppinga *et al.* 2006; Molofsky *et al.* 2002; Suding *et al.* 2013), or additional processes such as direct competitive interactions between plants (Bever 2003). However, the original Bever model remains an important touchstone for the theory of PSFs (Ke & Miki 2015; Ke & Wan 2020), and informs empirical research through the interaction coefficient, I_s , derived by Bever *et al.*, which is commonly measured and used to draw conclusions about coexistence in experimental studies. Despite the ubiquity of this model, and the fruitful interplay of theory and experiment in the PSF literature, extensions to communities with more than two or three species have appeared only rarely and recently (but see Eppinga *et al.* 2018; Mack *et al.* 2019). While PSF models motivate hypotheses and conclusions about species-rich natural communities, there is much still unknown about the behavior of these models with natural levels of diversity (Van der Putten *et al.* 2013).

Here, we extend the Bever model to include any number of plant species, and show that the model is equivalent to a special form of the replicator equation studied in evolutionary game theory (Hofbauer & Sigmund 1998). In particular, this model corresponds to the class of bimatrix games, where there are two players (here, plants and soil components) which interact with asymmetric strategies and payoffs. The replicator dynamics of bimatrix games are well-studied, allowing us to characterize many properties of the Bever model with n plant species.

65 Surprisingly, using this equivalence, we show that coexistence of more than two species in this
 66 model is never robust.

67 2 Results

68 2.1 Generalizing a classic PSF model

69 Inspired by emerging empirical evidence for the important role of PSFs in plant community
 70 dynamics and coexistence (Van der Putten *et al.* 1993; Bever 1994), Bever *et al.* (1997)
 71 introduced a simple mathematical model to investigate their behavior. In this model, two
 72 plant species, 1 and 2, grow exponentially with growth rates determined by the state of the
 73 soil biota in the system. These effects of soil on plants are specified by parameters α_{ij} , the
 74 growth rate of plant species i in soil type j . There is a soil component corresponding to each
 75 plant species, which grows exponentially in the presence of its associated plant at a rate β_i .
 76 Bever *et al.* set an important precedent by considering dynamics of *relative* abundances in
 77 such a system; starting from dynamics of the form

$$\begin{cases} \frac{dx_i}{dt} &= x_i \left(\frac{\alpha_{ii} y_i + \alpha_{ij} y_j}{y_i + y_j} \right), \quad i, j = 1, 2 \\ \frac{dy_i}{dt} &= y_i \left(\frac{\beta_i x_i}{x_i + x_j} \right) \end{cases} \quad (1)$$

78 for the *absolute* abundances of plants (x_i) and soil components (y_i), one considers the rela-
 79 tive abundances (frequencies), $p_i = x_i / \sum_j x_j$ and $q_i = y_i / \sum_j y_j$. The dynamics for these
 80 frequencies are easily derived from Eq. 1, and using the facts $p_i = 1 - p_j$ and $q_i = 1 - q_j$, can
 81 be written as:

$$\begin{cases} \frac{dp_i}{dt} &= p_i p_j ((\alpha_{ii} - \alpha_{ji}) q_i + (\alpha_{ij} - \alpha_{jj}) q_j), \quad i, j = 1, 2 \\ \frac{dq_i}{dt} &= q_i q_j (\beta_i p_i - \beta_j p_j). \end{cases} \quad (2)$$

82 This model may admit a coexistence equilibrium where

$$\begin{cases} p_i^* &= \frac{\beta_j}{\beta_i + \beta_j}, \quad i, j = 1, 2 \\ q_i^* &= \frac{\alpha_{jj} - \alpha_{ji}}{\alpha_{ii} - \alpha_{ij} + \alpha_{jj} - \alpha_{ji}}. \end{cases} \quad (3)$$

83 A central finding of the analysis by Bever *et al.* was that the denominator of q_i^* , which they
 84 termed the “interaction coefficient”, $I_s (= \alpha_{ii} - \alpha_{ij} + \alpha_{jj} - \alpha_{ji})$, controls the model dynamics:
 85 When $I_s > 0$, which represents a community with positive feedbacks, the equilibrium in
 86 Eq. 3 is unstable, and the two species cannot coexist. On the other hand, when $I_s < 0$,
 87 the equilibrium is neutrally stable, and the dynamics cycle around it, providing a form of
 88 non-equilibrium coexistence. In fact, these conclusions depend on the existence of a feasible
 89 equilibrium (i.e. positive equilibrium values), which further requires that $\alpha_{ii} < \alpha_{ji}$, for both
 90 $i, j = 1, 2$, in order for the model to exhibit coexistence (Bever *et al.* 1997; Ke & Miki 2015).

91 This coexistence is fragile. Species frequencies oscillate neutrally, similar to the textbook
 92 example of Lotka-Volterra predator-prey dynamics. Any stochasticity, external forcing, or
 93 time variation in the model parameters can destroy these finely balanced oscillations and
 94 cause one species to go extinct (Revilla *et al.* 2013). However, coupled with mechanisms
 95 that buffer the system from extinctions, such as migration between desynchronized patches
 96 or the presence of a seed bank, the negative feedbacks in this model might produce sustained
 97 coexistence (Revilla *et al.* 2013; Bever 2003).

98 Of course, most natural plant communities feature more than two coexisting species, and
 99 it is precisely in the most diverse communities where mechanisms of coexistence hold the
 100 greatest interest (Van der Putten *et al.* 2013). While it is not immediately clear how to
 101 generalize Eq. 2 to more than two species, Eq. 1 is naturally extended by maintaining the
 102 assumption that the overall growth rate for any plant is a weighted average of its growth rate
 103 in each soil type:

$$\begin{cases} \frac{dx_i}{dt} &= x_i \left(\sum_j \alpha_{ij} q_j \right), \quad i = 1, \dots, n \\ \frac{dy_i}{dt} &= y_i (\beta_i p_i). \end{cases} \quad (4)$$

104 From Eq. 4, one can derive the n -species analogue of Eq. 2 (Fig. 1),

$$\begin{cases} \frac{dp_i}{dt} &= p_i \left(\sum_j \alpha_{ij} q_j - \sum_{j,k} \alpha_{jk} p_j q_k \right), \quad i = 1, \dots, n \\ \frac{dq_i}{dt} &= q_i \left(\beta_i p_i - \sum_j \beta_j p_j q_j \right) \end{cases} \quad (5)$$

105 giving the dynamics for species and soil component frequencies. Eq. 5 is conveniently expressed
106 in matrix form as

$$\begin{cases} \frac{d\mathbf{p}}{dt} &= D(\mathbf{p}) (A\mathbf{q} - (\mathbf{p}^T A\mathbf{q})\mathbf{1}) \\ \frac{d\mathbf{q}}{dt} &= D(\mathbf{q}) (B\mathbf{p} - (\mathbf{q}^T B\mathbf{p})\mathbf{1}) \end{cases} \quad (6)$$

107 where vectors are indicated in boldface (e.g. \mathbf{p} is the vector of species frequencies $(p_1, p_2, \dots, p_n)^T$
108 and $\mathbf{1}$ is a vector of n ones) and $D(\mathbf{z})$ is the diagonal matrix with vector \mathbf{z} on the diagonal.
109 We have introduced the matrices $A = (\alpha_{ij})$ and $B = D(\beta_1, \beta_2, \dots, \beta_n)$, specifying soil effects
110 on plants and plant effects on soil, respectively. Because \mathbf{p} and \mathbf{q} are vectors of frequencies,
111 they must sum to one: $\mathbf{1}^T \mathbf{p} = \mathbf{1}^T \mathbf{q} = 1$. Using these constraints, one can easily show that the
112 Bever model (Eq. 2) is a special case of Eqs. 5 and 6 when $n = 2$.

113 2.2 Equivalence to bimatrix game dynamics

114 Systems that take the form of Eq. 6 are well-known and well-studied in evolutionary game
115 theory. Our generalization of the Bever model is a special case of the *replicator equation*,
116 corresponding to the class of *bimatrix games* (Taylor 1979; Hofbauer 1996; Hofbauer & Sig-
117 mund 1998; Cressman & Tao 2014). Bimatrix games arise in diverse contexts, such as animal
118 behavior (Taylor 1979; Selten 1988), evolutionary theory (Hofbauer & Sigmund 1998; Cress-
119 man & Tao 2014), and economics (Friedman 1991), where they model games with asymmetric
120 players. In a bimatrix game, each player (here, the plant community and the soil) has a dis-
121 tinct set of strategies (plants species and soil components, respectively) and payoffs (realized
122 growth rates).

123 Much is known about bimatrix game dynamics, and we can draw on this body of knowledge
124 to characterize the behavior of the Bever model with n species. Essential mathematical

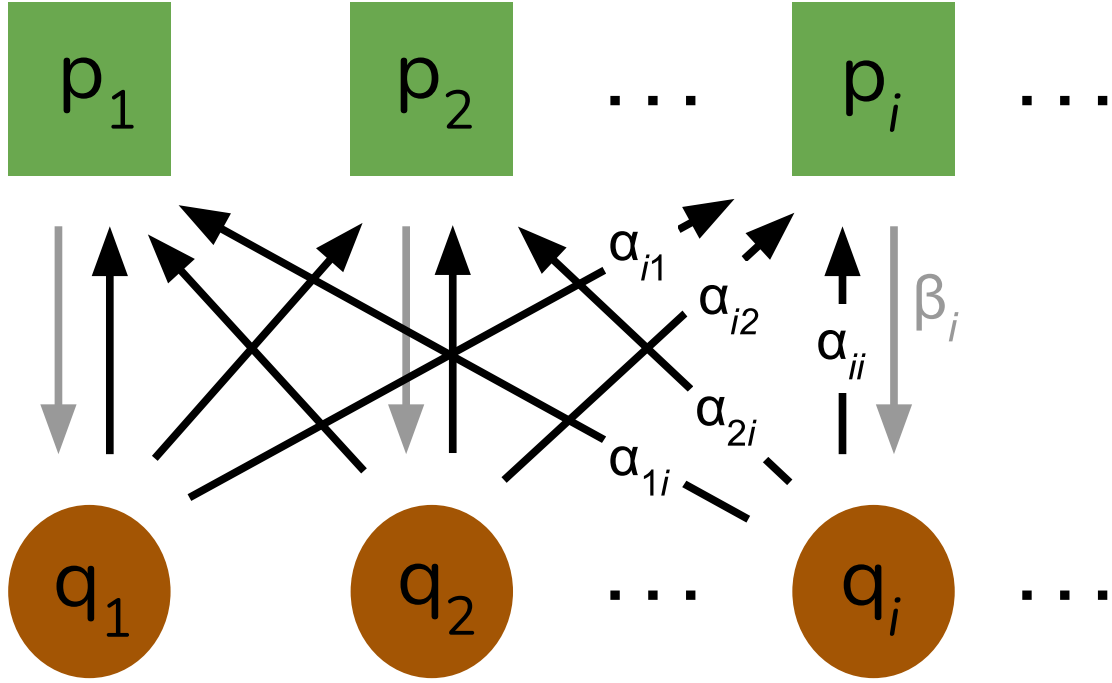


Figure 1: The model described by Eqs. 5-6 is shown here graphically. Plant species (green squares) promote the growth of their respective soil components (brown circles) at a rate β_i (gray arrows). In turn, growth of each plant is governed by the mix of soil components present in the system, with the effect of soil component j on species i quantified by the parameter α_{ij} (black arrows). This model is a straightforward extension of the model proposed by Bever *et al.* (1997) to an arbitrary number of species. Note only selected parameter labels are shown for clarity.

background and details are presented in the Supplemental Methods; for a detailed introduction to bimatrix games, see Hofbauer & Sigmund (1998).

Under the mild condition that matrix A is invertible, Eq. 6 admits a unique coexistence equilibrium given by $\mathbf{p}^* = k_p B^{-1} \mathbf{1}$ and $\mathbf{q}^* = k_q A^{-1} \mathbf{1}$, where $k_p = 1/(\mathbf{1}^T B^{-1} \mathbf{1})$ and $k_q = 1/(\mathbf{1}^T A^{-1} \mathbf{1})$ are constants of proportionality that ensure the equilibrium frequencies sum to one for both plants and soil. Because B is a diagonal matrix, and all β_i are assumed positive, the equilibrium plant frequencies, \mathbf{p}^* , are always positive, as well. Thus, feasibility of the equilibrium hinges on the soil frequencies, \mathbf{q}^* , which are all positive if the elements of $A^{-1} \mathbf{1}$ all share the same sign.

As we have seen, when the community consists of two species, the coexistence equilibrium, if feasible, can be either unstable or neutrally stable. In fact, the same is true for the n -species extension (and, more generally, for any bimatrix game dynamics, Eshel *et al.* 1983; Selten 1988; Hofbauer & Sigmund 1998). This can be established using straightforward local stability analysis, after accounting for the relative abundance constraints, which imply $p_n = 1 - \sum_{i=1}^{n-1} p_i$ and $q_n = 1 - \sum_{i=1}^{n-1} q_i$. Using these substitutions, Eq. 5 can be written as a system of $2n - 2$ (rather than $2n$) equations, and the community matrix for this reduced model has a very simple form (see Supplemental Methods). In particular, due to the bipartite structure of the model, the community matrix has all zero diagonal elements, which implies that the eigenvalues of this matrix sum to zero. These eigenvalues govern the stability of the coexistence equilibrium, and this property leaves two qualitatively distinct possibilities: either the eigenvalues have a mix of positive and negative real parts (in which case the equilibrium is unstable), or the eigenvalues all have zero real part (in which case the equilibrium is neutrally stable). Already, we can see that the model never exhibits equilibrium coexistence, regardless of the number of species.

Another notable property of bimatrix game dynamics is that the vector field defined by the model equations is divergence-free or incompressible (see Hofbauer & Sigmund 1998, for a proof). The divergence theorem from vector calculus (Arfken 1985) then tells us that Eq. 6 cannot have any attractors – that is, regions of the phase space that “pull in” trajectories – with multiple species. This rules out coexistence in a stable limit cycle or other non-equilibrium attractors (e.g. chaotic attractors). Thus, only the relatively fragile coexistence afforded by neutral oscillations is possible, as in the two-species model.

Based on the local stability properties of the coexistence equilibrium, Bever *et al.* concluded that such neutral cycles arise for two species when $\alpha_{11} < \alpha_{21}$ and $\alpha_{22} < \alpha_{12}$. The equivalence between their model and a bimatrix game with two strategies allows us to give a fuller picture of these cycles. Namely, we can identify a constant of motion for the two-species dynamics:

$$H = (\alpha_{12} - \alpha_{22}) \log q_1 + (\alpha_{21} - \alpha_{11}) \log q_2 + \beta_2 \log p_1 + \beta_1 \log p_2. \quad (7)$$

Using the chain rule and time derivatives in Eq. 2, it is easy to show that $\frac{dH}{dt} = 0$ for any plant and soil frequencies (see Supplemental Methods). The level curves of H form closed orbits around the equilibrium when the equilibrium is neutrally stable. Thus, H implicitly defines the trajectories of the model, and can be used to determine characteristics such as the amplitude of oscillations arising from particular initial frequencies.

Because neutral cycles provide the only possible form of coexistence in this model, a key question becomes whether and when neutral cycles with n species can arise. Do the “negative feedback” conditions identified by Bever *et al.* generalize in richer communities? Indeed, they do; however, for more than two species, these conditions are very severe. The model in Eq. 6 supports oscillations with n species – for any n – if matrices A and B satisfy a precise relationship (Fig. 3; see Supplemental Methods for details). In particular, the model parameters must satisfy the conditions $\alpha_{ij} = \gamma_i + \delta_j$ for some constants γ_i, δ_i in $i = 1, \dots, n$ (when $i \neq j$), and $\alpha_{ii} = \gamma_i + \delta_i - c\beta_i$ (where c is a positive constant independent of i). In the language of bimatrix games, such systems are called *rescaled zero-sum games* (Hofbauer 1996; Hofbauer & Sigmund 1998). It is a long-standing conjecture in evolutionary game theory that these parameterizations are the *only* cases where n -species coexistence can occur (Hofbauer 1996, 2011).

Ecologically, these conditions mean there is a fixed effect of each soil type and plant species identity, and the growth rate of plant i in soil type j is the additive combination of these two, with no interaction effects. The only exception is for plants growing in their own soil type, which must experience a fitness cost $(\gamma_i + \delta_i - \alpha_{ii})$ exactly proportional to the rate at which they promote growth of the soil type (β_i) . These conditions clearly extend the intuitive notion that each plant must have a disadvantage in its corresponding soil type to allow coexistence.

184 But the parameters of the model are constrained so strongly that we never expect to observe
185 cycles with more than two species in practice. When $n > 2$, a great deal of fine-tuning is
186 necessary to satisfy the conditions yielding a rescaled zero-sum game; the probability that
187 random parameters will be suitable is infinitesimally small. We confirm this numerically with
188 simulations shown in Fig. 2. Although n -species cycles are clearly possible (as in Fig. 3), for
189 parameters drawn independently at random, communities always collapse to zero, one, or two
190 species, regardless of the initial richness.

191 Not only are parameter combinations permitting many-species oscillations rare, they are
192 also extremely sensitive to small changes to the parameter values. The rescaled zero-sum
193 condition imposes many exact equality constraints on the matrix A (e.g. $\alpha_{ij} - \alpha_{ik} = \alpha_{lj} - \alpha_{lk}$
194 for all i, j, k , and l). Even if mechanisms exist to generate the requisite qualitative patterns,
195 inevitable quantitative variation in real-world communities will disrupt coexistence (Fig. 3).
196 Coexistence of $n > 2$ species – even in the weak sense of neutral cycles – is not robust to
197 small changes in the model parameters.

198 Interestingly, the two-species model is not subject to the same fragility. It can be shown
199 (see Supplemental Methods) that all 2×2 bimatrix games take the same general form as a
200 rescaled zero-sum game, although the constant c may be positive or negative, depending on
201 the parameters. When I_s , the interaction coefficient identified by Bever *et al.*, is negative, c
202 is positive, ensuring (neutral) stability. This condition amounts to an inequality constraint,
203 rather than an equality constraint, and so it *is* generally robust to small variations in model
204 parameters (Fig. 3). As we can now see, the case $n = 2$ is unique in this regard.

205 **3 Discussion**

206 The Bever model has played a central role in motivating PSF research, and continues to guide
207 both theory and experiment in this fast-growing field (Bever *et al.* 2015; Kandlikar *et al.* 2019;
208 Ke & Wan 2020). Here, we extend the Bever model to any number of species, and highlight
209 its equivalence to bimatrix game dynamics. Taking advantage of the well-developed theory
210 for these dynamics, we are able to characterize the behavior of the generalized Bever model
211 in detail.

212 Our central finding is that there can be no robust coexistence of plant species in this model.

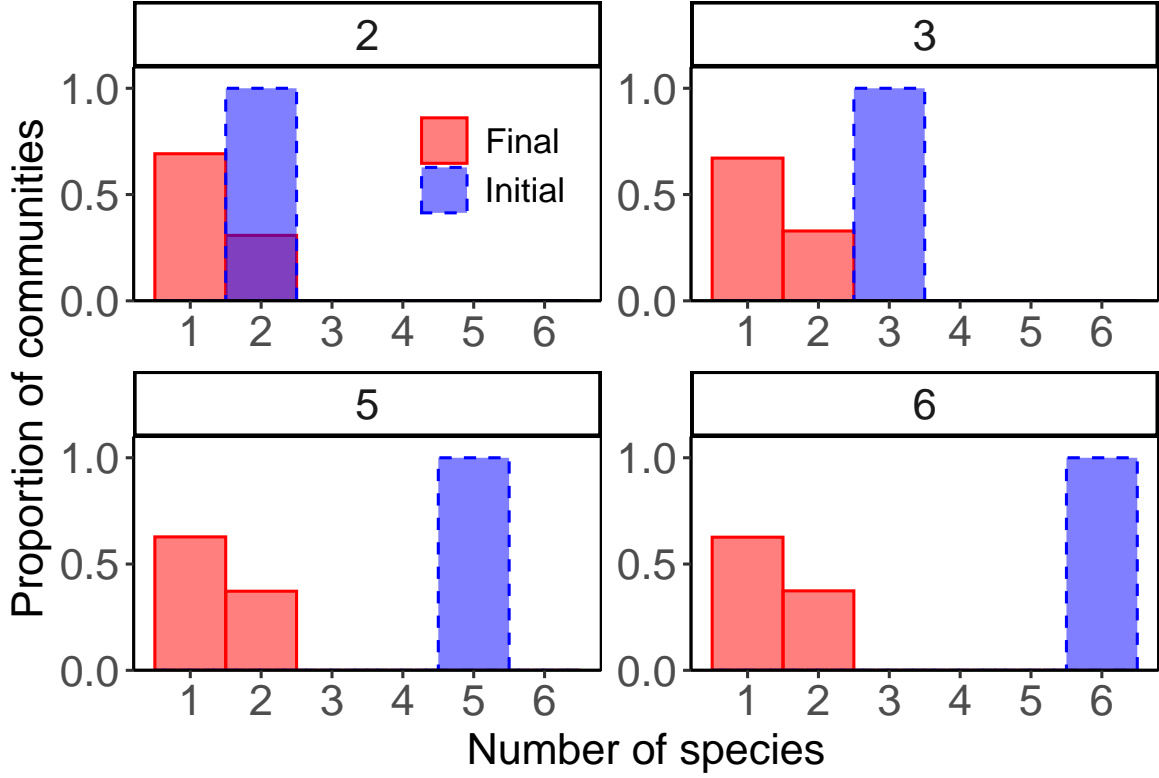


Figure 2: Final community sizes with varying initial richness. We show the distribution of final richness (number of species, in red) for 500 (???) communities governed by the n -species Bever model, initialized with 2, 3, 5, or 6 plant species. Parameters α_{ij} and β_i were sampled independently from a standard uniform distribution, $U[0, 1]$. For each random parameterization at each level of initial richness, we integrated the dynamics of Eq. 6 until the system reached a periodic orbit or until only one species remained. In agreement with the conjecture that coexistence of more than two species is vanishingly unlikely, we found that, regardless of the number of species initially present, every community collapsed to a subset of one or two surviving species.

Figure 3: LABEL FOR FIG 3

213 Regardless of the number of species, n , the model never exhibits equilibrium coexistence or
 214 other attractors. Coexistence can be attained through neutral oscillations, but these dynamics
 215 lack any restoring force and are easily destabilized by stochasticity or exogenous forcing. In
 216 this respect, the generalized model behaves similarly to the now-classic two-species system.
 217 However, unlike the two-species model, oscillations with $n > 2$ species can only result under
 218 very restricted parameter combinations. These parameterizations are vanishingly unlikely to
 219 arise by chance, and highly sensitive to small deviations. Thus, coexistence of more than two
 220 species is neither dynamically nor structurally stable.

221 This result may be surprising, because a significant body of experimental evidence indi-
 222 cates that PSFs can play an important role in mediating the coexistence of more than two
 223 species in natural communities (Kulmatiski *et al.* 2008; Petermann *et al.* 2008; Mangan *et al.*
 224 2010; Bever *et al.* 2015). Apparently, the picture suggested by the two-species Bever model
 225 generalizes in nature, but not in the model framework itself. We note that this framework was
 226 introduced as an intentional simplification to illustrate the potential role of PSFs in mediating
 227 coexistence, not to accurately model the biological details of PSFs. Indeed, the model has
 228 been wildly successful in spurring research into PSFs. Alongside empirical study of these
 229 processes, other modeling approaches have emerged, accounting for more biological realism
 230 (e.g., Umbanhowar & McCann 2005; Eppstein & Molofsky 2007; Bever *et al.* 2010), or with
 231 the demonstrated capacity to produce multispecies coexistence (e.g., Bonanomi *et al.* 2005;
 232 Miller & Allesina 2021). Some of these are minor modifications of the Bever model framework;
 233 others build on distinct foundations (Ke & Miki 2015; Ke & Wan 2020). Our results suggest
 234 that these various avenues are worth pursuing further.

235 Alternative modeling approaches are particularly important for better integration of the-
 236 ory and data. The predictions of the Bever model are commonly used to guide the design
 237 and analysis of PSF experiments, especially in drawing conclusions about coexistence. Our
 238 analysis cautions that applications of this model in multispecies communities might lead to
 239 incorrect inference. For example, attempts to parameterize the Bever model for three species
 240 using empirical data have produced predictions of non-coexistence in plant communities that
 241 coexist experimentally (Kulmatiski *et al.* 2011). In many other studies, the pairwise in-
 242 teraction coefficient, I_s , is calculated for species pairs and used to assess whole-community
 243 coexistence (Kulmatiski *et al.* 2008; Fitzsimons & Miller 2010; Pendergast IV *et al.* 2013; Sud-

ing *et al.* 2013; Kuebbing *et al.* 2015; Smith & Reynolds 2015; Bauer *et al.* 2017; Kandlikar
et al. 2019). However, we have seen that whole-community coexistence is virtually impossible
within the generalized model, and there is no guarantee that the pairwise coexistence condi-
tions for this model will agree with n -species coexistence conditions in other frameworks. For
example, $I_s < 0$ for all species pairs is neither necessary nor sufficient to produce coexistence
in a metapopulation-based model for PSFs (Miller & Allesina 2021).

In contrast to other extensions of the Bever model to many-species communities (Eppinga
et al. 2018; Mack *et al.* 2019), our approach keeps the dynamics of both plants and soil fully
explicit. As such, we make no assumptions about the relative timescales of plant and soil
dynamics, or whether either of these reach equilibrium. This difference likely explains the
discrepancy between our conclusions and previously published predictions for n -species PSFs
(Kulmatiski *et al.* 2011; Eppinga *et al.* 2018; Mack *et al.* 2019).

PSFs as envisioned in the classic Bever model might facilitate coexistence in conjunction
with other mechanisms, such as direct species interactions (Bever 2003), or through long tran-
sient dynamics, but our analysis shows that they cannot produce robust n -species coexistence
in isolation. This finding calls for renewed theoretical investigation of PSFs. One important
consideration is grounding PSF modeling frameworks in more realistic models for absolute
abundances or densities. As various researchers have noted (Kulmatiski *et al.* 2011; Revilla
et al. 2013; Eppinga *et al.* 2018; Ke & Wan 2020), the Bever model and its extensions are in
fact projections (onto the space of relative abundances, or frequencies) of dynamics for plant
and soil *abundances*. Consequently, the projected dynamics can mask unbiological outcomes
in the original model (e.g. relative abundances oscillate around equilibrium while absolute
abundances shrink to zero or explode to infinity). Indeed, the absolute abundance model
(Eq. 4) used to derive our n -species frequency dynamics (Eqs. 5-6) does not generally possess
any fixed points, which is a basic requirement for species coexistence (Hutson 1990; Hutson &
Schmitt 1992). It is usually seen as desirable to study PSFs in the space of species frequencies,
both because this facilitates connections to data, and because frequencies are considered a
more appropriate metric for analyzing processes that stabilize coexistence (Adler *et al.* (2007);
Eppinga *et al.* (2018), but see Kandlikar *et al.* (2019); Ke & Wan (2020)). But models that
introduce frequencies through a natural constraint, such as competition for finite space, will
likely produce more realistic dynamics.

From a broader theoretical perspective, the qualitative change in model behavior that we observe as the number of species increases from two to three or more is a striking phenomenon, but not an unprecedented one. Ecologists have repeatedly found that intuitions from two-species models can generalize (or fail to generalize) to more diverse communities in surprising ways (Strobeck 1973; Smale 1976; Barabás *et al.* 2016). Our analysis provides another illustration of the fact that “more is different” (Anderson 1972) in ecology, and highlights the importance of developing theory for species-rich communities.

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