

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 we use this equivalence 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.

52 Despite the ubiquity of this model, and the fruitful interplay of theory and experiment in the
53 PSF literature, extensions to communities with more than two or three species have appeared
54 only rarely and recently (but see Eppinga *et al.* 2018; Mack *et al.* 2019). While PSF models
55 motivate hypotheses and conclusions about species-rich natural communities, there is much
56 still unknown about the behavior of these models with natural levels of diversity (Van der
57 Putten *et al.* 2013).

58 Here, we extend the Bever model to include any number of plant species, and show that
59 the model is equivalent to a special form of the replicator equation studied in evolutionary
60 game theory (Hofbauer & Sigmund 1998). In particular, this model corresponds to the class of
61 bimatrix games, where there are two players (here, plants and soil components) which interact
62 with asymmetric strategies and payoffs. The replicator dynamics of bimatrix games are well-
63 studied, allowing us to characterize many properties of the Bever model with n plant species.
64 Surprisingly, using this equivalence, we show that coexistence of more than two species in this
65 model is never robust.

66 **2 Results**

67 **2.1 Generalizing a classic PSF model**

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

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

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

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

This model may admit a coexistence equilibrium where

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

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

This coexistence is fragile. Species frequencies oscillate neutrally, similar to the textbook example of Lotka-Volterra predator-prey dynamics. Any stochasticity, external forcing, or time variation in the model parameters can destroy these finely balanced oscillations and cause one species to go extinct (Revilla *et al.* 2013). However, coupled with mechanisms

that buffer the system from extinctions, such as migration between desynchronized patches or the presence of a seed bank, the negative feedbacks in this model might produce sustained coexistence (Revilla *et al.* 2013; Bever 2003).

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

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

From Eq. 4, one can derive the n -species analogue of Eq. 2,

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

giving the dynamics for species and soil component frequencies (Fig. 1). Eq. 5 is conveniently expressed in matrix form as

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

where vectors are indicated in boldface (e.g. \mathbf{p} is the vector of species frequencies $(p_1, p_2, \dots, p_n)^T$ and $\mathbf{1}$ is a vector of n ones) and $D(\mathbf{z})$ is the diagonal matrix with vector \mathbf{z} on the diagonal. We have introduced the matrices $A = (\alpha_{ij})$ and $B = D(\beta_1, \beta_2, \dots, \beta_n)$, specifying soil effects on plants and plant effects on soil, respectively. Because \mathbf{p} and \mathbf{q} are vectors of frequencies, 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

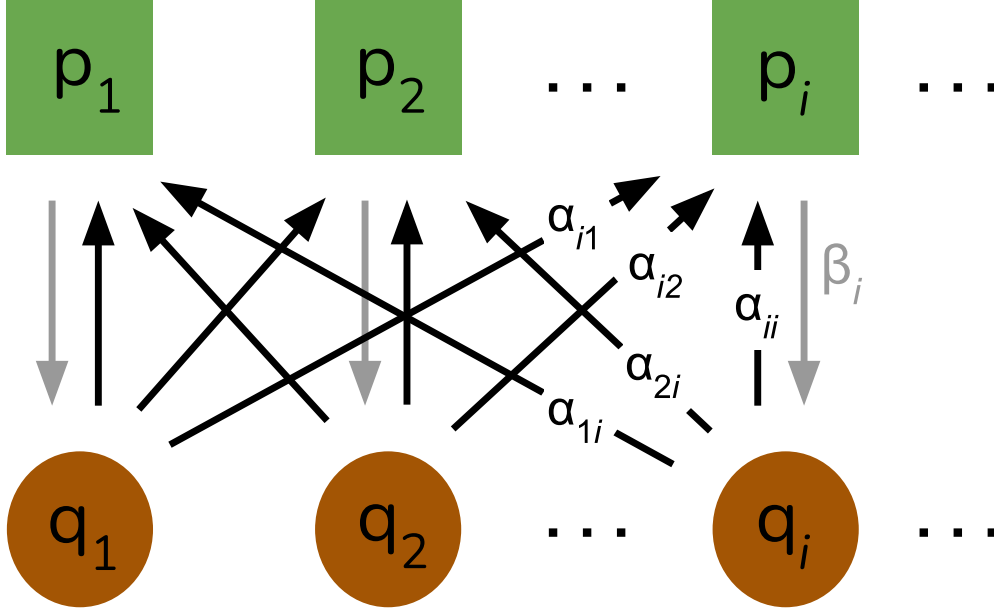


Figure 1: The model described by Eqs. 5-6 is shown here graphically. Plant species (green squares) promote the growth of their respective soil components (brown circles) at a rate β_i (gray arrows). In turn, growth of each plant is governed by the mix of soil components present in the system, with the 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.

111 Bever model (Eq. 2) is a special case of Eqs. 5 and 6 when $n = 2$.

112 2.2 Equivalence to bimatrix game dynamics

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

122 Much is known about bimatrix game dynamics, and we can draw on this body of knowledge
 123 to characterize the behavior of the Bever model with n species. Essential mathematical
 124 background and details are presented in the Supplemental Methods; for a detailed introduction
 125 to bimatrix games, see Hofbauer & Sigmund (1998).

126 Under the mild condition that matrix A is invertible, Eq. 6 admits a unique coexistence
 127 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 $k_q =$
 128 $1/(\mathbf{1}^T A^{-1} \mathbf{1})$ are constants of proportionality that ensure the equilibrium frequencies sum to
 129 one for both plants and soil. Because B is a diagonal matrix, and all β_i are assumed positive,
 130 the equilibrium plant frequencies, \mathbf{p}^* , are always positive, as well. Thus, feasibility of the
 131 equilibrium hinges on the soil frequencies, \mathbf{q}^* , which are all positive if the elements of $A^{-1} \mathbf{1}$
 132 all share the same sign.

133 As we have seen, when the community consists of two species, the coexistence equilibrium,
 134 if feasible, can be either unstable or neutrally stable. In fact, the same is true for the n -
 135 species extension (and, more generally, for any bimatrix game dynamics, Eshel *et al.* 1983;
 136 Selten 1988; Hofbauer & Sigmund 1998). This can be established using straightforward local
 137 stability analysis, after accounting for the relative abundance constraints, which imply $p_n =$
 138 $1 - \sum_{i=1}^{n-1} p_i$ and $q_n = 1 - \sum_{i=1}^{n-1} q_i$. Using these substitutions, Eq. 5 can be written as a
 139 system of $2n - 2$ (rather than $2n$) equations, and the community matrix for this reduced
 140 model has a very simple form (see Supplemental Methods). In particular, due to the bipartite
 141 structure of the model, the community matrix has all zero diagonal elements, which implies
 142 that the eigenvalues of this matrix sum to zero. These eigenvalues govern the stability of the
 143 coexistence equilibrium, and this property leaves two qualitatively distinct possibilities: either
 144 the eigenvalues have a mix of positive and negative real parts (in which case the equilibrium is
 145 unstable), or the eigenvalues all have zero real part (in which case the equilibrium is neutrally
 146 stable). Already, we can see that the model never exhibits equilibrium coexistence, regardless
 147 of the number of species.

148 Another notable property of bimatrix game dynamics is that the vector field defined by
 149 the model equations is divergence-free or incompressible (see Hofbauer & Sigmund 1998, for a
 150 proof). The divergence theorem from vector calculus (Arfken 1985) then dictates that Eq. 6
 151 cannot have any attractors – that is, regions of the phase space that “pull in” trajectories
 152 – with multiple species. This rules out coexistence in a stable limit cycle or other non-

153 equilibrium attractors (e.g. chaotic attractors). Thus, only the relatively fragile coexistence
 154 afforded by neutral oscillations is possible, as in the two-species model.

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

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

160 Using the chain rule and time derivatives in Eq. 2, it is easy to show that $\frac{dH}{dt} = 0$ for any
 161 plant and soil frequencies (see Supplemental Methods). The level curves of H form closed
 162 orbits around the equilibrium when the equilibrium is neutrally stable. Thus, H implicitly
 163 defines the trajectories of the model, and can be used to determine characteristics such as the
 164 amplitude of oscillations arising from particular initial frequencies (Volterra 1926).

165 Because neutral cycles provide the only possible form of coexistence in this model, a key
 166 question becomes whether and when neutral cycles with n species can arise. Do the “negative
 167 feedback” conditions identified by Bever *et al.* generalize in richer communities? Indeed,
 168 they do; however, for more than two species, these conditions are very severe. The model in
 169 Eq. 6 supports oscillations with n species – for any n – if matrices A and B satisfy a precise
 170 relationship (see Supplemental Methods for details). In particular, the model parameters
 171 must satisfy the conditions $\alpha_{ij} = \gamma_i + \delta_j$ for some constants γ_i, δ_i in $i = 1, \dots, n$ (when $i \neq j$),
 172 and $\alpha_{ii} = \gamma_i + \delta_i - c\beta_i$ (where c is a positive constant independent of i). In the language of
 173 bimatrix games, such systems are called *rescaled zero-sum games* (Hofbauer 1996; Hofbauer
 174 & Sigmund 1998). It is a long-standing conjecture in evolutionary game theory that these
 175 parameterizations are the *only* cases where n -species coexistence can occur (Hofbauer 1996,
 176 2011).

177 Ecologically, these conditions mean there is a fixed effect of each soil type and plant
 178 species identity, and the growth rate of plant i in soil type j is the additive combination of
 179 these two, with no interaction effects. The only exception is for plants growing in their own
 180 soil type, which must experience a fitness cost $(\gamma_i + \delta_i - \alpha_{ii})$ exactly proportional to the rate

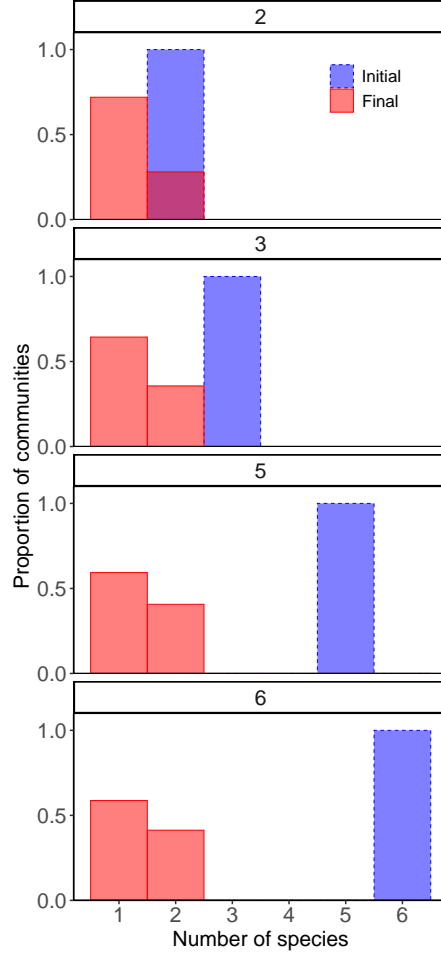


Figure 2: Final community sizes with varying initial richness. We show the distribution of final richness (number of species, in red) for 5000 communities governed by the n -species Bever model, initialized with 2, 3, 5, or 6 plant species. Parameters α_{ij} and β_i were sampled independently from a 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 with one or two surviving species.

181 at which they promote growth of their soil type (β_i). These conditions clearly extend the
182 intuitive notion that each plant must have a disadvantage in its corresponding soil type to
183 allow coexistence. But the parameters of the model are constrained so strongly that we never
184 expect to observe cycles with more than two species in practice. When $n > 2$, a great deal
185 of fine-tuning is necessary to satisfy the conditions yielding a rescaled zero-sum game; the
186 probability that random parameters will be suitable is infinitesimally small. We confirm this
187 numerically with simulations shown in Fig. 2. Although n -species cycles are clearly possible
188 (as in Fig. 3), for parameters drawn independently at random, communities always collapse
189 to one or two species, regardless of the initial richness.

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

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

204 3 Discussion

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

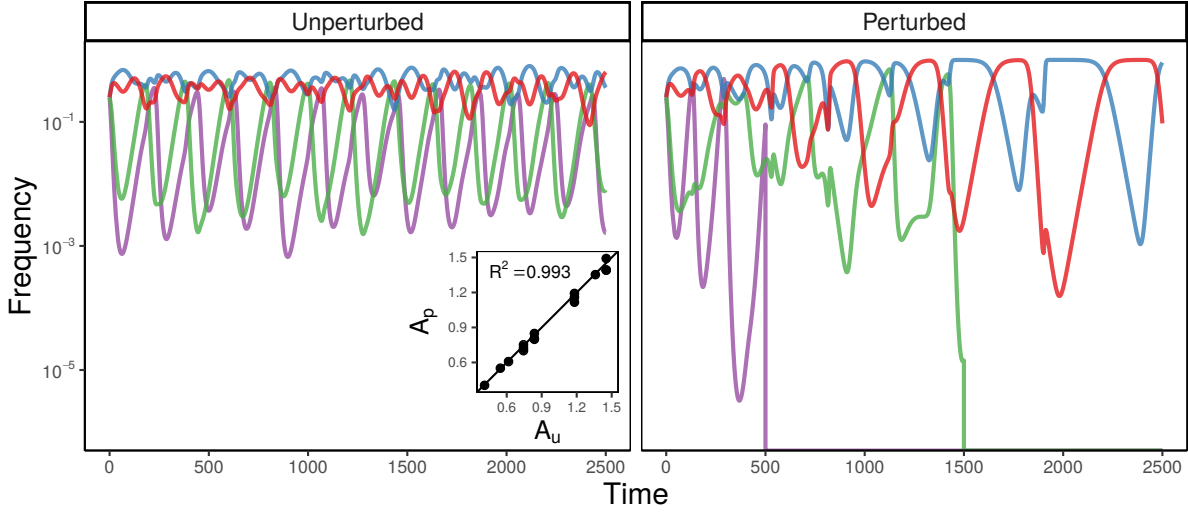


Figure 3: Coexistence of three or more species is not robust. It is possible to obtain neutrally stable oscillations with any number of species if the model parameters constitute a rescaled zero-sum game (see text for conditions). Here, for example, we show sustained oscillations with 4 species using fine-tuned parameters, A_u (left). However, if we randomly perturb A_u by a small amount to obtain new parameters, A_p , the dynamics quickly collapse to a two-species subset (right). Any slight perturbation is enough to disrupt coexistence; for this example, the parameters A_u and A_p are highly correlated (inset) and differ in value by less than 3% on average.

in detail.

Our central finding is that there can be no robust coexistence of plant species in this model. Regardless of the number of species, n , the model never exhibits equilibrium coexistence or other attractors. Coexistence can be attained through neutral oscillations, but these dynamics lack any restoring force and are easily destabilized by stochasticity or exogenous forcing. In this respect, the generalized model behaves similarly to the now-classic two-species system. However, unlike the two-species model, oscillations with $n > 2$ species can only result under very restricted parameter combinations. These parameterizations are vanishingly unlikely to arise by chance, and highly sensitive to small deviations. Thus, coexistence of more than two species is neither dynamically nor structurally stable.

This result may be surprising, because a significant body of experimental evidence indicates that PSFs can play an important role in mediating the coexistence of more than two species in natural communities (Kulmatiski *et al.* 2008; Petermann *et al.* 2008; Mangan *et al.* 2010; Bever *et al.* 2015). Apparently, the picture suggested by the two-species Bever model

224 generalizes in nature, but not in the model framework itself. We note that this framework was
 225 introduced as an intentional simplification to illustrate the potential role of PSFs in mediating
 226 coexistence, not to accurately model the biological details of PSFs. Indeed, the model has
 227 been wildly successfully in spurring research into PSFs. Alongside empirical study of these
 228 processes, other modeling approaches have emerged, accounting for more biological realism
 229 (e.g., Umbanhowar & McCann 2005; Eppstein & Molofsky 2007; Bever *et al.* 2010), or with
 230 the demonstrated capacity to produce multispecies coexistence (e.g., Bonanomi *et al.* 2005;
 231 Miller & Allesina 2021). Some of these are minor modifications of the Bever model framework;
 232 others build on distinct foundations (Ke & Miki 2015; Ke & Wan 2020). Our results suggest
 233 that these various avenues are worth pursuing further.

234 Alternative modeling approaches are particularly important for better integration of the-
 235 ory and data. The predictions of the Bever model are commonly used to guide the design
 236 and analysis of PSF experiments, especially in drawing conclusions about coexistence. Our
 237 analysis cautions that applications of this model in multispecies communities might lead to
 238 incorrect inference. For example, attempts to parameterize the Bever model for three species
 239 using empirical data have produced predictions of non-coexistence in plant communities that
 240 coexist experimentally (Kulmatiski *et al.* 2011). In many other studies, the pairwise in-
 241 teraction coefficient, I_s , is calculated for species pairs and used to assess whole-community
 242 coexistence (Kulmatiski *et al.* 2008; Fitzsimons & Miller 2010; Pendergast IV *et al.* 2013; Sud-
 243 ing *et al.* 2013; Kuebbing *et al.* 2015; Smith & Reynolds 2015; Bauer *et al.* 2017; Kandlikar
 244 *et al.* 2019). However, we have seen that whole-community coexistence is virtually impossible
 245 within the generalized model, and there is no guarantee that the pairwise coexistence condi-
 246 tions for this model will agree with n -species coexistence conditions in other frameworks. For
 247 example, $I_s < 0$ for all species pairs is neither necessary nor sufficient to produce coexistence
 248 in a metapopulation-based model for PSFs (Miller & Allesina 2021).

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

Data accessibility: Code for reproducing the numerical simulations is available at https://github.com/pablolich/plant_soil_feedback.

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