

Plant-soil feedbacks buffer plant communities from extinction risks in unpredictable environments

Tancredi Caruso (✉ tancredi.caruso@ucd.ie)

University College Dublin <https://orcid.org/0000-0002-3607-9609>

Matthias C Rillig

Freie Universität Berlin

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Abstract

Theory and experiments have demonstrated that negative plant-soil feedback promotes coexistence between plant species. Plants and soils, however, face the challenge of an increasingly unpredictable environment due to multiple global change factors, including but not limited to climate change. Environmental stochasticity generally reduces the space for coexistence between competing species and it induces fluctuations that increase the variability and unpredictability of community properties such as total productivity. In this paper, we formulate a stochastic version of a classical plant-soil feedback deterministic model, which describes the outcome of plant species competition in the presence of soil feedback. If the soil feedback is negative, the deterministic expectation is that pulse perturbations to the system (e.g. a drought episode) cause plants and soil to move away from their equilibrium to eventually return to it through periodic and exponentially decaying fluctuations. Environmental stochasticity alters this expectation: the system can either settle into a fluctuation regime around the deterministic expectation, or some components of the system may go extinct. Our model results show that while the probability of extinction predictably increases with environmental stochasticity, the more negative the soil feedback, the more it can counteract the increase in extinction probability caused by increased environmental stochasticity, which can be empirically tested. The impact of plant-soil feedback, however, depends on the type of interactions that link soil to plants. These results suggest that plant communities in which strong negative soil feedbacks operate are better placed to withstand the risk posed by increased environmental stochasticity.

Introduction

Very many factors structure plant communities (Tilman 1998; Rees et al. 2001; Hille Ris Lambers et al. 2002; Adler 2007; HilleRisLambers et al. 2012) but in the last three decades the so called plant-soil feedback has been increasingly investigated at multiple levels, from theory and in silico modelling studies (Bever 2003; Bonanomi et al. 2005; Bever et al. 2010) to experiments and combined experimental and field studies, and metaanalysis (Crawford et al. 2019; in't Zandt et al. 2021). At a theoretical level, plant-soil feedback can be defined as the net contribution of the soil community to the dynamics of a pair of competing plant species (Bever et al. 1997). The plant species, too, exert effects on the soil community, hence the term "feedback". If plant species A and B compete, there are two ways to ensure they coexist (Bever 2003): one is the classic one (Case 2000) that intraspecific competition should be larger than interspecific competition, with the necessary condition that the product of competition coefficients (cA and cB) should be smaller than 1. The other way is a net negative soil feedback, which can allow coexistence even under strong interspecific competition that would otherwise cause competitive exclusion (Bever et al. 1997, 2010; Bever 2003). There are at least four terms that are needed to describe the plant soil feedback I_s . For a simple description, but without loss of generality, those four terms are easier to define under the assumption that the soil community can be described by a multivariate axis S (Bever 2003). That axis may range from an arbitrary value, say S_a , which represents the soil community

characteristic of plant A, to another value, say S_B , which represents the soil community characteristic of plant B.

Experimentally, the “characteristic” soil community is the one associated with two generations of plant monoculture grown on the same soil, often defined as “home” soil. If the soil axis is standardised to vary between 0 and 1, the four terms that describe the soil feedback can then be defined in terms of the impact that the soil community S_A typical of A has on its home plant A (α_a) and on the other plant B (α_b) and also in terms of the impact that the soil community typical of B ($S_B = 1 - S_A$) has on its own plant B (β_b) as well as on plant A (β_a). With these assumptions, the soil feedback $I_s = \alpha_a - \alpha_b - \beta_a + \beta_b$. The space for coexistence is greatly expanded when $I_s < 1$, even for $cA \times cB > 1$ (Fig. 3 of Bever 2002). Also, as PSF I_s depends on 4 terms that can be either positive or negative, it (or better, the underlying model from which it is derived) allows describing multiple types of combined positive, negative, direct and indirect effects of soil on plants, which ultimately describe the impact of soil pathogens, mutualists and also saprotrophs on plants. There are two main features that are characteristic of the dynamics determined by plant-soil feedback: they cause systematic and predictable fluctuations around the equilibrium of the system (Bever 2003), and they can greatly expand the space for coexistence between plants that would otherwise coexist under a very limited range of conditions, or not even coexist at all (Bever 2003; Bever et al. 2010). There are also many other implications of plant-soil feedback dynamics, which have been analysed extensively in the last 10 years (Van der Putten et al. 2013; van der Putten et al. 2016)

The classic theoretical approach to plant-soil feedback, and the relevant expectations that have informed much plant-soil feedback research, is based on fully deterministic models. But natural systems are facing increasingly more unpredictable environments, especially in relation to multiple, interacting global change factors (Rillig et al. 2019). In this paper, we thus offer an expansion of the classic models that incorporates environmental stochasticity and reformulates the expectation of plant-soil feedback models in a stochastic framework, that is in terms of probability of extinction and coexistence or, more generally, the probability distribution of species relative abundances that emerge from stochastic dynamics (Lande et al. 2003; Allen 2010). In general, increasing levels of stochasticity decreases long term population growth rates (Lande et al. 2003; Tuljapurkar 2013) and may decrease the space for coexistence even when the average dynamics, that is the deterministic part of the stochastic dynamics, implies coexistence (May 1973; Gravel et al. 2011). We here explored the tension between the destabilising force of stochasticity and the stabilising effect of the plant-soil feedback as well as of the balance between different types (positive and negative) of plant-soil interactions. We introduce a general stochastic model for plant-soil feedback dynamics, we numerically explore some aspects of the models to formulate expectations on probability of coexistence and extinction, and how the plant-soil feedback affects this probability, and finally discuss the implications of our analysis for future models and experiments.

Methods

The deterministic model

We start from the classic Bever deterministic model (Bever 2003) that couples the population dynamics of two competing plant species, A and B, to their soil, S_A and $S_B = 1 - S_A$. The system of coupled ordinary differential equations (ODE) that describes this model is (Eqs. 1):

$$\begin{cases} \frac{dA}{dt} = A(r_A - m_A A - c_{BA}B + \alpha_A S_a + \beta_A(1 - S_A)) \\ \frac{dB}{dt} = B(r_B - m_B B - c_{AB}A + \alpha_B S_a + \beta_B(1 - S_A)) \\ \frac{dS_A}{dt} = S_A(1 - S_A) \left[\frac{A}{A+B} - v \frac{B}{A+B} \right] \end{cases}$$

Where A and B are the population size of species A and B, and S_A is the soil axis variable that reaches its maximum value when the soil communities equal the one associated to a monoculture of plant A. The parameter r and m are the intrinsic growth rate and logistic term of the classic logistic population model, and the terms “ c ” are the competition coefficients. Note that while r , m and c are strictly positive, the parameters α_a , α_b , β_a and β_b are either positive or negative. The two alpha parameters (α_a and α_b) describe the net effect of soil of A on plant A and B, while the beta parameters (β_a and β_b) describe the net effect of the soil of B on plant A and B. The soil state variable thus can fluctuate between the soil typical of A and that typical of B. Finally, the parameter v describes the impact of B on the soil of A. The behaviour of this model is well known (Bever, 2003), and in the supplementary materials (RScript_Bever_Model_Stochastic.R) we provide an R script that reproduces the behaviour of the model with an example based on the same parameters originally presented by Bever (2003). If the system starts away from the equilibrium values, and the combination of parameters is such that the system allows plant coexistence, the trajectories of the system will be characterised by sinusoidal oscillations that quickly dampen until the system reaches the equilibrium, which is stable (Fig. 1a).

Stochastic model: formulation

We introduce environmental stochasticity to the ODE system of Eqs. 1 through the Itô calculus formalism for continuous stochastic differential equations (SDE). SDEs for interacting populations are constructed by combining the deterministic component (the ODE of Eqs. 1 for us), which represents the “drift” term, and either a continuous time Markov chain describing probabilistic transitions within the population due to demographic stochasticity (Allen 2010) or an external source of random variability due to environmental fluctuations (Allen 2010; Dobrow 2016), or a combination of both demographic and environmental stochasticity (Lande et al. 2003). Here, we are mostly interested in broad scale population dynamics, where the impact of demographic stochasticity is likely to be minor given the size of the population under consideration and considering that, typically, demographic stochasticity scales as the inverse of population size (Lande et al. 2003). We thus consider a general model with environmental stochasticity

only, which can in the future be expanded to include also demographic stochasticity. The general SDE model then is:

$$dN = \mu(N)dt + \Sigma dW$$

Where the bold notation indicates vectors, and so N is a vector with population sizes A , B and the soil state variable, dW is a vector of independent Wiener processes (often referred to as white noise in ecology), which we use as the source of environmental stochasticity (Lande et al. 2003; Dobrow 2016), and the matrix Σ is the diffusion matrix, which quantifies the intensity of stochasticity for each state variable. The drift term μ , which is a function of population size, corresponds to the deterministic structure of our ODEs, that is the classic Bever model (Bever 2003). If plant A , B and Soil were affected by independent environmental stochasticity, the diffusion matrix would simply be

$$\Sigma = \begin{bmatrix} \sigma_A & 0 & 0 \\ 0 & \sigma_B & 0 \\ 0 & 0 & \sigma_S \end{bmatrix}$$

And the corresponding SDEs then is

$$\left\{ \begin{array}{l} dA = [A (r_A - m_A A - c_{BA} B + \alpha_A S_a + \beta_A (1 - S_A))] dt + \sigma_A dW_1 \\ dB = [B (r_B - m_B B - c_{AB} A + \alpha_B S_a + \beta_B (1 - S_A))] dt + \sigma_B dW_2 \\ dS_A = \left[S_A (1 - S_A) \left[\frac{A}{A+B} - v \frac{B}{A+B} \right] \right] dt + \sigma_S dW_3 \end{array} \right.$$

This model can be made more realistic by introducing correlations in the source of environmental stochasticity, and so to the responses of plants and soil to environmental fluctuations, which are most likely correlated. For example, a flood event will modify water availability, but also produce physical disturbance and produce anoxic conditions, at the same time. The individual effects of all these factors on the different plants and soil may differ, but the resulting responses of the state variables might be correlated. The more general model thus accounts for correlation in the three stochastic terms via a covariance matrix

$$K_{ij} = \begin{bmatrix} \sigma_A^2 & \sigma_A \sigma_B \rho_{BA} & \sigma_A \sigma_S \rho_{SA} \\ \sigma_A \sigma_B \rho_{BA} & \sigma_B^2 & \sigma_S \sigma_B \rho_{SB} \\ \sigma_A \sigma_S \rho_{SA} & \sigma_S \sigma_B \rho_{SB} & \sigma_S^2 \end{bmatrix}$$

where the variance terms σ^2 for plant A and B and soil S reflects the strength of environmental stochasticity, and the terms ρ are the correlations. Note that this matrix is symmetric, simply because the covariance between variable i and j is the same as the covariance between j and i . We used Cholesky factorization (Allen 2010; Kloeden et al. 2012) of the covariance matrix K_{ij} to define the diffusion matrix that accounted for correlated environmental fluctuations in our matrix. The diffusion matrix now

becomes: $\Sigma =$

$$\begin{bmatrix} \sigma_A & 0 & 0 \\ \sigma_B \rho_{BA} & \sigma_B \sqrt{1 - \rho_{BA}^2} & 0 \\ \sigma_S \rho_{SA} & \frac{\sigma_S (\rho_{BS} - \rho_{AS})}{\sqrt{1 - \rho_{BA}^2}} & \sigma_S \sqrt{1 - \rho_{AS}^2 - \frac{(\rho_{BS} - \rho_{AS})^2}{1 - \rho_{BA}^2}} \end{bmatrix}$$

Note that if the correlation terms ρ are set to zero, the matrix returns to the special case of independent Wiener processes, with variance terms in the diagonal equal to the three σ terms for A, B and S and all the off-diagonal elements equal to zero.

Computation

The key goal of the analysis of a stochastic process is the characterization of the probability distribution that describes how the population changes with time (Karlin and Taylor 1975). The variation of the population is not deterministic, meaning that given the same initial conditions, the population can take many different paths or trajectories. The population of size N is thus best described by a probability distribution $P_{(N,t)}$ that quantifies the key features of the collective behaviour of the paths. The mean and variance of N over time t are some of these key features. Another important feature is the probability that the population goes below a certain value, for example below zero (i.e. extinction). Or also, the probability for the population to be at a certain value (for example two times the initial population size, or zero) after a certain amount of time (i.e. hitting time). For simple processes, the probability distribution $P_{(N,t)}$ has an analytically close form that can be derived by the Fokker-Planck equation that corresponds to the Itô SDE. Our system, however, has a complex form, and we could not resolve it analytically. We thus simulated it numerically, using the Euler-Maruyama method (Allen 2010; Dobrow 2016), and we provide the full R script that implemented this method for our system (RScript_Bever_Model_Stochastic.R).

We analysed multiple scenarios, starting from the same parameters as in (Bever 2003), apart from equating the carrying capacity of the two plant species (which we did just for convenience, and with no effect on the final results). First, we compared a scenario in which the stochastic components of the process are not correlated with a scenario in which they are correlated and, within each of these two scenarios, we also compared a scenario where the variances of plant A and B were relatively high with a scenario in which the variances were low (results in Fig. 2). Also, we compared a scenario in which only the variance of A was high (or low) with the opposite scenario (results in Fig. 3). Finally, we also

investigated how variance controls the probability of extinction at different level of soil feedback I_s (results of Fig. 4). We replicated the simulation of each scenario 1000 times, and estimated the probability of a certain outcome (e.g. unfeasible system, that is at least one species goes extinct) as the frequency of that outcome over 1000 independent replicates of the same process. In the scenarios in which we changed the soil feedback $I_s = \alpha_a - \alpha_b - \beta_a + \beta_b$, we set to negative the PSF by keeping three parameters ($\alpha_b, \beta_a, \beta_b$) and decreasing the other parameters (α_a). But PSF being the same, we expected that the probability of extinction changed with different combination of parameters. We thus also explored scenarios in which we kept the PSF positive, constant, and compatible with coexistence at low level of variance, and then progressively increased the difference between parameters α_b and β_a .

Results

First, we verified that the Euler-Maruyama method of our SDEs with zero variance and zero correlation returned an accurate approximation of the trajectory expected under the deterministic model, which was the case (Fig. 1a). To explore the behaviour of the model qualitatively, we then plotted 10 paths of two parameterizations of our SDE: one with no correlation, and the other one with correlation (Fig. 1b, we report just the one with correlation). As qualitatively visible across the 10 trajectories plotted in Fig. 1b, the system rapidly converges towards the deterministic equilibrium but it then keeps fluctuating indefinitely around the equilibrium, with plant A and B out of phase, and with the soil variable with a phase intermediate between that of plant A and B. A key metric to describe the asymptotic behaviour of the system is the long-term value of the ratio between plant A and plant B population size. For the parameters of the deterministic model based on (Bever 2003), this ratio is 0.8, and the two plants coexist although plant B is the superior competitor. Stochasticity alters this expectation in two ways: first, depending on the variance level, a fraction of the simulation returned unfeasible configurations, which we defined as those where one of the plant populations went either extinct or to infinity. Second, when the system could settle into a feasible configuration for the time span analysed in our simulation, the distribution of plant A to plant B ratio slightly shifted to the right, that is above 0.8, and so in favour of plant A (Figs. 2 and 3).

When plotting probability of extinction (defined as the fraction of trajectories that returned an unfeasible system, with one of the two plants going extinct) as a function of environmental stochasticity (with the variance terms of both plant A and B ranging from 0.5 to 10) and five different levels of plant soil feedback (PSF: ranging from slightly positive, as in the parameters choices of the example given in Bever 2003, to slightly and more decisively negative) we observed a clear stabilising effect of PSF (Fig. 4a): the more negative the PSF the higher the level of variance needed to increase probability of extinction. The details of these results, however, depend on the combination of parameters used in these scenarios, in which we changed the soil feedback $I_s = \alpha_a - \alpha_b - \beta_a + \beta_b$ by keeping three parameters ($\alpha_b, \beta_a, \beta_b$) constant and decreasing the parameters α_a . But there are also combinations for which, PSF being the same, probability of extinction varies depending on the ratios between the 4 parameters. We give an example, among the infinite number of possibilities, in Fig. 4b, where PSF is positive, constant, and compatible with

coexistence at low level of variance, and then progressively increased the difference between parameters α_b and β_a . This set of simulations shows how the details of the PSF parameters matter in determining probability of extinctions and the response of this probability to increased levels of stochasticity.

Discussion

New predictions

Much experimental evidence on species coexistence theories come from plant communities (Vellend 2010; Gravel et al. 2011; HilleRisLambers et al. 2012) and is rooted in classical ecological theory based on the niche concept (Tilman 1982; Chase and Leibold 2003). Stochastic versions of the classic niche framework were formulated already early in the history of ecology (May 1973), and have been reframed more recently following input from neutral theories (Tilman 2004; Adler 2007; Vellend 2010). In the conservation biology literature, models that embrace stochasticity are the norm simply because time series of any natural population are characterised by fluctuations that can, at least at first, appear erratic and that result from the interaction of many unknown events, which are best modelled using probability distributions (Lande et al. 2003). The main contribution of stochasticity to deterministic models is that coexistence may no longer be guaranteed even when, on average, the expectation for the system is coexistence. This is important in our view because models and experiments that have formalised and investigated the impact of soil biota on plant populations show that negative plant soil feedback (PSF) may increase the space for coexistence, and that plant species may actually not coexist in the absence of PSF (Bever 2003). We, thus, investigated how a general model that incorporates environmental stochasticity modifies the classical expectation of PSF theory. Indeed, we observed that a stochastic equivalent of a general PSF model may result in a fraction of trajectories along which one plant species goes extinct. In that sense, stochasticity reduces the space for coexistence, despite the deterministic expectation being coexistence. Stochastic models account for the realistic fact that in nature, especially under the influence of temporally dynamic and multiple global change factors (Rillig et al. 2019), there are sources of environmental variance that are difficult to predict and that are thus best modelled stochastically (Lande et al. 2003; Allen 2010). Under global change, the impact of environmental variance on soil biota, for example in the form of unpredictable weather events, is expected to increase (Bardgett and Caruso 2020), which implies fluctuations in community dynamics that involve PSF.

Our key result, however, goes beyond the obvious verification of the fact that, given a set of conditions, stochasticity reduces the space for coexistence: our simulations collectively show that the more negative the PSF, the higher stochasticity needs to be to generate a sizeable probability of extinction. Our theoretical model thus generalises the key expectation from the classical PSF model: the new expectation we propose is that PSF buffers plant-soil systems from the negative impact that environmental stochasticity has on the ability of plant species to coexist. It is, however, important to clarify a crucial point: the impact of an increasingly more negative PSF on probability of extinction can be evaluated when experimental conditions are relatively strongly controlled, which in our simulations is represented by

keeping three out of the three parameters that control the PSF constant and varying PSF by decreasing/increasing the fourth parameter, which is left free to vary. For example, consider the following two combinations of parameters for $I_s = \alpha_a - \alpha_b - \beta_a + \beta_b$: i) $\alpha_a = 0.35$, $\alpha_b = 0.2$, $\beta_a = 0.2$, and $\beta_b = 0.2$; and ii) $\alpha_a = 0.35$, $\alpha_b = 0.3$, $\beta_a = 0.1$, and $\beta_b = 0.2$. In both cases, the total PSF equals 0.15. But in case 1, which is the same as in Fig. 4a for PSF = 0.15, the system rapidly becomes unfeasible for moderate levels of environmental variance, while in case 2 probability of extinction is comparable to some of the negative PSF explored in Fig. 4a. The implication is that PSF being the same, the nature and intensity of the interaction between soil and the plant species matters, meaning that a positive (or negative) PSF exerted through, say, just positive mutualistic interactions can impact probability of extinction very differently from a positive (or negative) PSF exerted through negative or a mixture of negative and positive interactions. The biology of the system does matter, and the compound metrics used to quantify the PSF helps, but it is alone not sufficient to predict how environmental variance may impact the probability of extinction.

Experimental tests

Our predictions can be tested experimentally using classical PSF experiments (Van der Putten et al. 2013; Crawford et al. 2019) on pairs of plant species but with the addition of an experimental regime that should incorporate environmental variance. The environmental variables to consider for manipulation should be any that have an impact on the growth rate of the plants involved in the experiment. It could be temperature, it could be a physical disturbance imposed on the system (drought, flood). The variance regime should be a factor in the experiment, ranging from low to high variance, as per the x-axis of Fig. 4. This “variance factor” can be either continuous or categorical. The variance factor would have been effective if it could be shown to alter the probability that the two species coexist. This may require pilot studies to identify the amount of environmental variance that can trigger a shift in the regime of the system, as in Fig. 4, where there is a range of variances for which the system rapidly goes from relatively low levels of extinction to the certainty that the plants cannot coexist. As the prediction is probabilistic, the result of the experiment can be recorded in terms of number of experimental units for which a certain outcome is observed. This is useful, because the key observation is not a time series of the plant population, but rather the frequency at which coexistence or extinction are observed over a relatively long but well-defined period of time. Measurements of plant-soil feedback can also be related to the outcome of the experiment to validate the expectation that the PSF is associated with a positive relationship between environmental variance and probability of extinction.

General implication of stochasticity for plant-soil feedback

Negative PSF can predict the relative abundance of species in tropical forests (Mangan et al. 2010) and has recently be shown to be linked to fluctuations in the relative abundance of plant species in diverse mountain meadows (in't Zandt et al. 2021). In these very species rich system, PSF is hypothesised to be a key factor maintaining species diversity. Through its link to plant coexistence, PSF could also control the biodiversity-productivity relationship (Forero et al. 2021). If time series are available (e.g. in't Zandt et al., 2021), they can be modelled as stochastic processes (Brouste et al. 2014; Iacus and Yoshida 2018). For

example, our equations can be fitted to plant time series using the formalism of SDEs through the R package Yuima (Brouste et al. 2014; Iacus and Yoshida 2018). If the negative implications of stochasticity can be controlled through some of the elements of the deterministic component of the system, such as the PSF and the type of biotic interactions that determine the PSF (e.g. purely mutualist vs. purely pathogenic effects), then it is in principle possible to harness the natural system to boost its ability to resist or recover from the perturbation regime continuously created by environmental stochasticity. Controlling the plant soil feedback would, however, require a mechanistic knowledge of the biological interactions that underpin the total PSF (van der Putten et al. 2016), and these interactions are at least of two kinds, positive and negative, and notoriously very challenging to harness. Another alternative is the plant community itself, because the PSF depends on the mutual interaction that links plant to soil biota, and different pairs of plants will thus be associated with different types of PSF. Our model suggests that, all else being the same, plant communities with strong negative PSF are more resilient to environmental stochasticity. One future experimental challenge will be to quantify negative PSF at the entire community level but we suggest that land management should then aim at actions that promote these more resilient plant communities with more negative PSF to counteract the impact of an increasingly more unpredictable environment.

Declarations

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References

1. Adler PB (2007) A niche for neutrality. *Ecol Lett* 10:95–104. <https://doi.org/10.1111/j.1461-0248.2006.00996.x>
2. Allen LJ (2010) An introduction to stochastic processes with applications to biology. CRC press
3. Bardgett RD, Caruso T (2020) Soil microbial community responses to climate extremes: resistance, resilience and transitions to alternative states. *Philos Trans R Soc B Biol Sci* 375:20190112. <https://doi.org/10.1098/rstb.2019.0112>
4. Bever JD (2003) Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytol* 157:465–473
5. Bever JD, Dickie IA, Facelli E et al (2010) Rooting theories of plant community ecology in microbial interactions. *Trends Ecol Evol* 25:468–478. <https://doi.org/10.1016/j.tree.2010.05.004>
6. Bever JD, Westover KM, Antonovics J (1997) Incorporating the Soil Community into Plant Population Dynamics: The Utility of the Feedback Approach. *J Ecol* 85:561–573
7. Bonanomi G, Giannino F, Mazzoleni S (2005) Negative plant–soil feedback and species coexistence. *Oikos* 111:311–321

8. Brouste A, Fukasawa M, Hino H et al (2014) The yuima project: A computational framework for simulation and inference of stochastic differential equations. *J Stat Softw* 57:1–51
9. Case TJ (2000) *An illustrated Guide to Theoretical Ecology*. Oxford University Press, New York
10. Chase JM, Leibold MA (2003) *Ecological Niches: Linking Classical and Contemporary Approaches*. Chicago University Press, Chicago, IL
11. Crawford KM, Bauer JT, Comita LS et al (2019) When and where plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecol Lett* 22:1274–1284
12. Dobrow RP (2016) *Introduction to stochastic processes with R*. John Wiley & Sons
13. Forero LE, Kulmatiski A, Grenzer J, Norton JM (2021) Plant-soil feedbacks help explain biodiversity-productivity relationships. *Commun Biol* 4:1–8
14. Gravel D, Guichard F, Hochberg ME (2011) Species coexistence in a variable world. *Ecol Lett* 14:828–839
15. Hille Ris Lambers J, Clark JS, Beckage B (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417:732–735. <https://doi.org/10.1038/nature00809>
16. HilleRisLambers J, Adler PB, Harpole W et al (2012) Rethinking community assembly through the lens of coexistence theory. *Annu Rev Ecol Evol Syst* 43:227–248
17. Iacus SM, Yoshida N (2018) Simulation and inference for stochastic processes with YUIMA. *Compr R Framew SDEs Stoch Process Use R*
18. in't Zandt D, Herben T, van den Brink A et al (2021) Species abundance fluctuations over 31 years are associated with plant–soil feedback in a species-rich mountain meadow. *J Ecol* 109:1511–1523
19. Karlin S, Taylor HM (1975) *A first course in stochastic processes*. Academic Press, San Diego
20. Kloeden PE, Platen E, Schurz H (2012) *Numerical solution of SDE through computer experiments*. Springer Science & Business Media
21. Lande R, Engen S, Saether B-E (2003) *Stochastic population dynamics in ecology and conservation*. Oxford University Press on Demand
22. Mangan SA, Schnitzer SA, Herre EA et al (2010) Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466:752–755
23. May RM (1973) Stability in randomly fluctuating versus deterministic environments. *Am Nat* 107:621–650
24. Rees M, Condit R, Crawley M et al (2001) Long term studies of vegetation dynamics. *Science* 293:650–655
25. Rillig MC, Ryo M, Lehmann A et al (2019) The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science* 366:886. <https://doi.org/10.1126/science.aay2832>
26. Tilman D (1998) *Plant Strategies and the Dynamics and Structure of Plant Communities*
27. Tilman D (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ

28. Tilman D (2004) Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc Natl Acad Sci U S A* 101:10854–10861. <https://doi.org/10.1073/pnas.0403458101>
29. Tuljapurkar S (2013) *Population dynamics in variable environments*. Springer Science & Business Media
30. Van der Putten WH, Bardgett RD, Bever JD et al (2013) Plant–soil feedbacks: the past, the present and future challenges. *J Ecol* 101:265–276
31. van der Putten WH, Bradford MA, Pernilla Brinkman E et al (2016) Where, when and how plant–soil feedback matters in a changing world. *Funct Ecol* 30:1109–1121
32. Vellend M (2010) Conceptual synthesis in community ecology. *Q Rev Biol* 85:183–206

Figures

Figure 1

In panel a), numerical solution to the deterministic plant-soil feedback (PSF) model of Bever (2003). The parameters are the same as in Bever (2003) but with equal carrying capacity for the two plants (set to 100), and starting initial conditions set at 50 (0.5 for soil, which ranges from zero to 1). The numerical solution has been derived from applying the Euler-Maruyana algorithm to our system of stochastic differential equations (SDEs) but with variance and correlation set to zero (which collapses our system of SDEs to Bever's ODEs model). In panel b, ten trajectories or paths (each colour correspond to one simulation for the coupled equations of the three populations) for plant A, Soil and plant B from ten independent simulation of our system of SDEs. Environmental stochasticity puts the system into a series of periodic fluctuations around the expectation for the deterministic equilibrium. The 10 trajectories represent a system over a period of time for which a quasi-equilibrium is reached. For high level of stochasticity, the system may exit this quasi-equilibrium state to become unfeasible.

Figure 2

Frequency distribution (histograms, y-axis) of the ratio (x-axis) between the population size of plant A and plant B. The vertical blue line (at 0.8 on the x-axis) shows the ratio for the deterministic model (and for the parameters used in Bever (2003), which are the same as in Figure 1a). In general, stochasticity shifts the ratio to the right (that is >0.8) and correlation seems not to affect this shift. The shift is particularly pronounced ($>95\%$ of stochastic path have a ratio >0.8) for scenarios with high variance in both species A and B, meaning that, for this combination of parameters, stochasticity tends to favour the inferior competitor (species A). Each distribution is calculated from 1000 simulations of the system. A certain

fraction of simulation returned a fraction of unfeasible configurations (one species extinct), which was removed.

Figure 3

Same as Figure 2, but with variance in A either higher (panel a and b) or lower (panel c and d) than variance in B. This time, in all cases stochasticity markedly shift the ratio to the right of the deterministic expectation, regardless of which species is affected by the highest level of stochasticity.

Figure 4

Relationship between variance (i.e. strength of stochasticity, x-axis) and the probability of extinction (y-axis) estimated as the number of unfeasible configurations over 1000 simulations of the same system. Each data point thus corresponds to 1000 simulations. Both in panels a) and b), eleven levels of variance, ranging from 0.5 to 10 were considered. For each level, the 1000 simulations of panel a) were run for each of the 5 different level of plant soil feedback (PSF), marked with the different colours and symbols. In panel a), the scenario in orange, with the diamond symbol, corresponds to a PSF of +0.15, that quickly leads to extinction for moderately high level of stochasticity. But all the scenarios in figure a) keep the impact of soil A on plant B, that of soil B on plant A, and that of soil B on plant B constant, and negativizes PSF by making the impact soil A on plant A more and more negative. In panel b), instead, we kept PSF constant (at 0.15) and also kept the impact of plant A on soil A and that of plant B on soil B constant. The scenarios in panel b) differ in the difference between the impact of soil A on plant B and that of soil B on plant A. As this difference increases, higher variance is required to lead the system to extinction.

Supplementary Files

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- [RScriptBeverModelStochastic.R.r](#)