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SPECIAL FEATURE

PLANT–SOIL FEEDBACKS IN A CHANGING WORLD

Consequences of plant–soil feedbacks in invasion

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Summary

1. Plant species can influence soil biota, which in turn can influence the relative performance of plant species. These plant–soil feedbacks (PSFs) have been hypothesized to affect many community-level dynamics including species coexistence, dominance and invasion.

2. The importance of PSFs in exotic species invasion, although widely hypothesized, has been difficult to determine because invader establishment necessarily precedes invader-mediated PSFs. Here, we combine a spatial simulation model of invasion that incorporates PSFs with a meta-analysis that synthesizes published case studies describing feedbacks between pairs of native and exotic species.

3. While our spatial model confirmed the link between positive soil feedbacks (‘home’ advantage) for exotic species and exotic species spread, results were dependent on the initial abundance of the exotic species and the equivalence of dispersal and life history characteristics between exotic and native species.

4. The meta-analysis of 52 native–exotic pairwise feedback comparisons in 22 studies synthesized measures of native and exotic performance in soils conditioned by native and exotic species. The analysis indicated that the growth responses of native species were often greater in soil conditioned by native species than in soil conditioned exotic species (a ‘home’ advantage). The growth responses of exotic species were variable and not consistently related to species soil-conditioning effects.

5. *Synthesis.* Overlaying empirical estimates of pairwise PSFs with spatial simulations, we conclude that the empirically measured PSFs between native and exotic plant species are often not consistent with predictions of the spread of exotic species and mono-dominance. This is particularly the case when exotic species are initially rare and share similar dispersal and average fitness characteristics with native species. However, disturbance and other processes that increase the abundance of exotic species as well as the inclusion of species dispersal and life history differences can interact with PSF effects to explain the spread of invasive species.

Key-words: coexistence, determinants of plant community diversity and structure, native–exotic pairwise feedback, positive feedback, priority effects, soil legacies, soil pathogens and mutualists, stabilizing and destabilizing mechanisms, transient dynamics

Introduction

Widespread evidence indicates that individual plant species can influence soil biota, which can differentially affect the performance of plant species (Ehrenfeld, Ravit & Elgersma 2005; Kulmatiski *et al.* 2008; Bever *et al.* 2010). The direction of these plant–soil feedbacks (PSFs) can be either negative or positive, depending on the balance of the negative effects of soil-borne pathogens, herbivores and parasites compared to the positive effects of beneficial soil organisms such as mycorrhizal fungi and nitrogen fixing bacteria (Westover & Bever 2001; Klironomos 2002). Because these interactions can differ in intensity between host plant species (Bever *et al.* 2009) and neighbouring plant species (Hausmann & Hawkes 2009), PSFs are thought to play key roles in plant community dynamics, including succession (Kardol, Bezemer & van der Putten 2006), invasion (Callaway *et al.* 2004; Wolfe & Klironomos 2005) and restoration (Eviner &

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Hawkes 2008). However, associating measures of PSFs with community dynamics is challenging (Reynolds *et al.* 2003; van der Putten *et al.* 2009). Here, we explore how PSF estimates for native and exotic species in uninvaded (native-conditioned) and invaded (exotic-conditioned) soils can be extrapolated to invasion dynamics, and specifically, to the spread and dominance of exotic species.

A number of reviews have focused on how to interpret PSF effects and their influence on plant community structure (Bever 2003; Reynolds *et al.* 2003; Bever *et al.* 2010). These reviews, along with theoretical work on PSFs (Bever, Westover & Antonovics 1997; Eppinga *et al.* 2006; Eppstein, Bever & Molofsky 2006; Turnbull *et al.* 2010), emphasize the need to view feedbacks as frequency-dependent interactions between multiple species. PSF models often build upon the two-species Lotka-Volterra framework (Bever 2003; Eppinga *et al.* 2006), where the relative effects of the soil communities can differentially influence the population growth of two plant species. At the community level, positive feedback generally has a destabilizing impact, resulting in one species either dominating a community or in a patchy mosaic of alternative states that depend on initial conditions. Negative feedbacks favour faster population growth when rare, but reduce population growth rates when species become more abundant, leading to coexistence (Bever, Westover & Antonovics 1997).

Negative PSFs are often thought to play an important role in coexistence between native species due to the accumulation of species-specific soil pathogens over time. In contrast, exotic species are thought to affect the soil biota to their own advantage (Bever *et al.* 2010). Exotic species may promote soil communities that increase their resource acquisition, suppress native symbiont communities and promote native pathogen communities, whilst escaping soil pathogens from their home range (Hawkes *et al.* 2005; Wolfe & Klironomos 2005; Eppinga *et al.* 2006). Thus, a common prediction relating PSFs to invasion is that spread and dominance (the replacement of native species by exotic species, following the establishment or arrival stage of an invasion) will occur when the exotic species has a greater ‘home’ advantage and experiences less negative PSFs than native species.

While this mechanism is commonly invoked as an explanation for monotypic dominance of invasive species, lack of PSF experiments that take a pairwise comparative approach has precluded testing the generality of this hypothesis (e.g., Kulmatiski *et al.* 2008). However, in the last several years, there has been a rapid increase in studies that compare feedback strengths using a pairwise species–soil approach (i.e., assessment of species response to reciprocal soil-conditioning treatments).

Capitalizing on recent work on this front, we combine a spatial simulation model of invasion with a meta-analysis of feedbacks involving paired native and exotic species. We ask two questions: (i) how do the feedbacks experienced by both the native and the exotic species contribute to post-establishment invasion dynamics (i.e., replacement of natives by exotics)? (ii) Within a particular invasion, do resident native species experience more negative (or less positive) feedbacks than the invading exotic species? To examine the first question, we use a spatially explicit model to describe the hypothetical effects of PSF for pairs of native and exotic species, exploring how the different effects of invaded and uninvaded soil communities on native and exotic species can contribute to invasion patterns. To examine the second question, we use a meta-analysis of net pairwise PSFs of native and exotic species and compare these feedback estimates with the modelled predictions of invasion dynamics.

Materials and methods

SPATIAL INVASION MODEL

We developed a stochastic cellular automata model in which individuals of two species – a native and an exotic – are able to generate PSFs by modifying the ‘soil state’ of the cell they occupy. We used a 100 × 100 cell lattice, where cells can be occupied by either the native or exotic species or can be unoccupied (e.g., following mortality). Boundaries of the lattice are absorbing (cells on one edge are considered neighbouring cells for cells on the opposite edge), and the state of all cells in the lattice is updated synchronously. The model assumes that the environment is initially homogeneous and that species are identical in their environmental requirements.

Feedback parameters (f_n and f_e for native and exotic species, respectively) describe a species’ performance in its own-conditioned soil (*Nn* and *Ee* for native and exotic species, respectively) compared to soil conditioned by the other species (*Ne, En*). Positive feedback occurs when a species performs better in its own-conditioned soil than in soil conditioned by the other species (i.e. a home advantage: $Nn > Ne$ or $Ee > En$). Negative feedback occurs when a species performs better in soil conditioned by the other species than in own-conditioned soil (i.e. an away advantage: $Nn < Ne$ or $Ee < En$). Because feedback parameters for both species are included in this model, species soil-conditioning has the potential to influence its own performance (either positively or negatively) as well as to influence the performance of the other species (either positively or negatively).

Spatial heterogeneity in soil condition arises over time as species generate effects on the soil state *S* of each cell, which affects the probability of establishment and survival by the next recruiting individual. Effects on the soil state of a cell are cumulative and reversible: feedbacks grow in magnitude the longer an individual maintains occupancy of a cell, up to a maximum set value. If the cell becomes occupied by the other species, the soil state can be progressively reversed as the second species continues to occupy the soil. The soil state can have values from −1 to +1; the sign for the soil-state gradient is unrelated to whether feedback effects are negative or positive, but instead reflects the occupying species (natives positive, exotics negative). For example, as an exotic species persists for a longer time in a given location, it modifies the soil-state gradient in the negative ‘exotic’ direction. If the native species replaces the exotic species, the presence of the native species will begin reversing the state gradient in the opposite ‘native’ direction (*S* will become more positive over time). The magnitude of the soil state (*S*) for each cell changes (positive direction for native species; negative direction for exotic species) by 25% of the maximum value per time step of occupancy by the same species, up to the maximum value set by the soil feedback parameters f_i (f_e for the exotic, f_n for the native).

An individual's probability of survival s_i (s_e indicates the probability for exotic species, s_n for native species) depends on whether a species has a soil-dependent home or away advantage (f_i), the sign of this feedback, and the soil state (S):

$$s_e = (1 - \text{sign}(f_e) \cdot S)/2 \qquad \text{eqn 1}$$

$$s_n = (1 + \text{sign}(f_n) \cdot S)/2 \qquad \text{eqn 2}$$

where home advantage occurs for positive values of f_i and away advantage for negative values of f_i. For example, an exotic with a strong positive home-advantage ($f_e = +1$) that has occupied a cell for many time steps ($S = -1$, the negative sign indicates a fully conditioned exotic soil state) will have a survival probability of 100% (e.g., $s_e = (1 - (+1)\cdot(-1))/2 = 1$). Similarly, an exotic species with a weaker positive feedback ($f_e = +0.4$) that has recently invaded native-conditioned soil (and as a result, its soil effects have had less time to accumulate; $S = +0.2$) will have a survival probability < 10% for the next time step (e.g. $s_e = (1 - (+0.4)\cdot(+0.2))/2 = 0.06$). Survival s_i scales from a minimum of 0 to a maximum of 1. The variable s_i adds to a species' baseline mortality rate m_i and an individual dies when $m_i + (1 - s_i)$ is greater than a random draw from a uniform distribution $\sim U(0,1)$.

Mortality creates a vacant cell that can be colonized by either species. We initially set baseline mortality (m) to 0.05 per time step. We initially assume seed dispersal is local (determined by seed production of the nearest eight neighbouring cells plus the occupant of the previous time step), with no differences in per capita seed production between exotic and native individuals. We also assume no long-term seed banking: all seeds come from individuals occupying cells in the previous time step. The colonization probability p for each species is proportional to its relative seed production (c) weighted by its soil state-dependent survival probability s (where c for each species is its seed production summed over the eight nearest neighbouring cells plus the current cell, if occupied):

$$p_e = c_e \cdot s_e/(c_e \cdot s_e + c_n \cdot s_n), \text{and}\, p_n = 1 - p_e \qquad \text{eqn 3}$$

To simulate the scenario of invasion following the initial establishment of an exotic species, we started each simulation with exotic species occupying 5% and natives 95% of the cells and set the initial soil state to the maximum feedback value for the native (f_n). We ran the model over all combinations of PSF parameters f_i (from -0.8 to $+0.8$ for both native and exotic species). For our initial simulations, we followed the abundance of exotic and native species over 100 time steps for different combinations of PSFs (f_e and f_n). Native and exotic species were functionally equivalent in all respects other than PSF effects. We first assume functional equivalence in these other important life history characteristics because our objective is to tie our modelling results directly to empirically measured PSFs (described later); these studies often do not report mortality rates or seed production for the species.

Following these initial simulations, we examined the role of PSFs in an additional case where the exotic species is shorter lived but a better colonizer than the native species; in this set of model runs, we assumed that the exotic species dispersed globally rather than locally and that it produced twice as much seed per capita and experienced twice the rate of baseline mortality as the native species. We also ran simulations where we held feedback estimates constant for both species ($f_n = f_e = 0.3$) and varied the sign of feedback effects (positive and negative) and baseline mortality rates to investigate interactions between life history and PSFs. Our model was written in C and output figures generated with R.

META-ANALYSIS

We compiled a data set from previously published studies that compared PSFs for native and exotic species, and compared these results to the outcomes portrayed by our model. Our criterion was the inclusion of plant performance measures of at least one native and one exotic species, with each species growing in own-conditioned (conspecific) soil (e.g. *Nn, Ee*) and in the soil conditioned by the other species (e.g. *Ne, En*).

Experiments to quantify plant–soil PSFs generally follow a multistep process. Plants first influence the composition of the soil community, which is called soil conditioning. This stage can be based on soil collected from the field or on soil trained by both native and exotic plant species grown in the greenhouse. We allowed soil conditioning to include soils in which the species were grown previously (most often in the greenhouse) or in soils that are representative of a particular community, generally dominated by adults and most often in a field setting. The second stage of a PSF experiment evaluates the effects of conditioning by assessing plant growth responses to both self-conditioned soil and soil conditioned by the other species. The testing of plant responses in this second stage was generally performed in the greenhouse with a soil inoculation to isolate soil biota effects.

Manuscripts were identified by searching keywords in the Web of Science for the combination of terms describing PSF (soil legacy, plant–soil feedback) and invasion (invasive, invasion, invader, exotic). Search terms were truncated to allow for singular or plural forms of the keywords. We excluded manuscripts that only examined the effects of a subset of the microbial community (e.g. just pathogens) or the effects of soil conditioning relative to sterile soil conditions. We did not include studies comparing the performance of one species in soils from its native and invaded range. We augmented this data set with four unpublished data sets from the authors that met the above criteria as well as papers that met our criteria but were not identified by our keyword search. In total, we located 22 studies describing PSF among 52 native–exotic species pairs (Table S1 in Supporting Information).

We treated each exotic–native species pair as a separate comparison (Gurevitch, Curtis & Jones 2001); some studies conducted more than one exotic–native comparison and, in these cases, they often quantified PSFs of many native species relative to one exotic species. Different response measures determined in the same study were excluded, as were measurements in multiple years. Above-ground biomass was the most commonly measured response variable. As few studies varied the relative abundance of species to assess the frequency dependence of soil effects, we treated soil effects as a categorical variable (own-conditioned, other-conditioned). Because we were specifically interested in the reciprocal comparison between native and exotic species in the context of invasion, we did not use studies where growth in other-cultivated soils included soil conditioning from a mix of native and exotic species. We were not able to additionally evaluate the net effects of soil biota (after Reinhart & Callaway 2006) involving comparisons between sterile and non-sterile soil, as too few studies reported growth under sterilized conditions.

Several methods of calculating PSF effects have been proposed (Brinkman *et al.* 2010). For the purposes of this review, we calculated feedback for both native and exotic species as effect sizes using Hedges' d (Hedges & Olkin 1985): the mean performance of a species in own-cultivated soil minus its performance in the other-cultivated soil, divided by the pooled variance of the two cases. For example, a native PSF effect size calculation would compare a native plant grown in own-conditioned soil (*Nn*) relative to exotic-conditioned soil (*Ne*).

For each native–exotic comparison, two PSFs were calculated, one for native species (*Nn* vs. *Ne*) and one for exotic species (*Ee* vs. *En*). Because some studies compared multiple native species with one exotic species, we also calculated effect size for each study based on the averaged response of native and exotic species. A positive effect size indicates that the species grew better in its own (self-cultivated) soil than in other-cultivated soil, whereas a negative value indicates better growth in the soil conditioned by the other species. Effect sizes were calculated in METAWIN (version 2.1).

Bever, Westover & Antonovics (1997) developed a net pairwise feedback calculation, called interaction strength (*Is*), that takes into account both individual feedback estimates. In the case of our study comparisons, this calculation would be $Nn - En - Ne + Ee$. However, as Hedges' d calculates effect size as differences between soil effects for one species (i.e. $Nn - Ne$) relative to pooled variation, we interpret the sum of effect sizes for a native and exotic species pair as a meta-analytical pairwise feedback estimate approximate to the interaction strength (*Is*).

We analysed PSF effect sizes in three ways. First, to test whether PSFs differed consistently between native and exotic species, we used a mixed-factor ANOVA model with study and species pair (nested in study) as random factors and origin as a fixed factor. This analysis tested the prediction that exotic PSFs (*Ee* vs. *En*) are consistently less negative than native PSFs (*Nn* vs. *Ne*) within a native–exotic species pair. To begin to assess whether life-history and growth-form differences may influence PSF, we also described species pairs by whether they shared life history or growth form. While this first analysis takes into account study as a random factor, some PSF measures were used in more than one species-pair comparison within a study (e.g. for a study that compares three native species to one exotic species, the measure *Ee* is used in three native–exotic comparisons and thus in three effect sizes). To take into account this level of non-independence, we also averaged all performance measures for a given species–soil combination (e.g., *Nn*) within a study, and calculated study-level effect sizes ($n = 22$). In this second analysis, we used a mixed-model ANOVA with study as a random factor and origin as a fixed factor, and also examined how study design (collection of soil inoculum, community or individual-level assessment) and the inclusion of the four unpublished data sets affected our results. Lastly, we qualitatively assessed how these estimates of feedbacks fell within the feedback space described by the simulation model. Statistical analyses were conducted in SAS (version 9.3).

Results

SPATIAL INVASION MODEL

Simulating a range of PSF effects indicates the general prevalence of predictions of native resistance to exotic invasion, regardless of exotic PSFs, when exotic species are initially rare (Fig. 1). Natives were predicted to dominate anywhere they grew better in their own-conditioned soil, regardless of the strength or sign of soil effects for the exotic species (Fig. 1a). One exception was where the positive 'home' advantage for the exotic species was greater than the 'home' advantage for the native species (Fig. 1a, region c), resulting in a net positive feedback that allowed exotic species to expand into native-dominated areas and slowly increase in abundance (Fig. 2c).

When natives grew better in exotic-conditioned soil than in their own-conditioned soil, the model predicted that exotic species would increase and dominate if they grew better in native-conditioned soils or when the negative effects of their 'home' soils were weak in comparison with the natives 'home' soil effect (Fig. 1a, regions d–f). Exclusion occurred slowly for weakly positive exotic PSFs, taking more than 1000 time steps (results not shown).

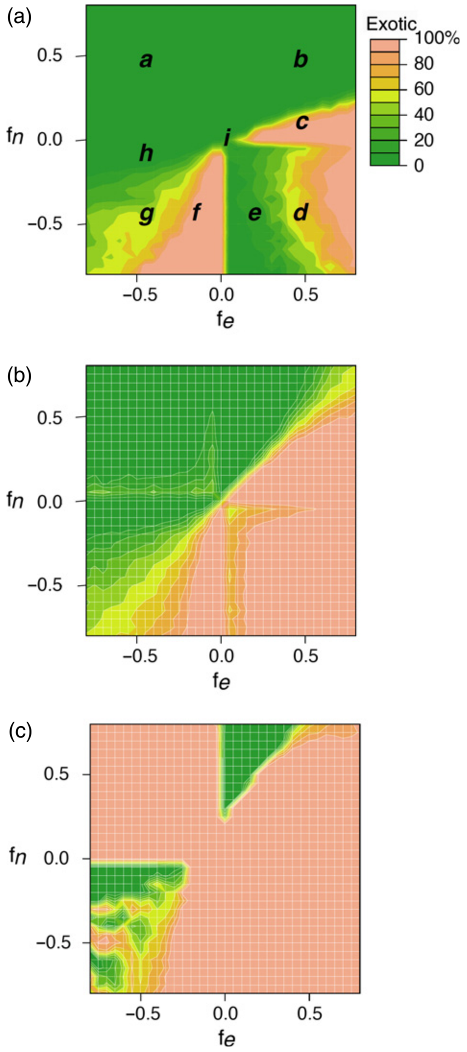

Fig. 1. Simulation model results showing predicted abundance based on exotic plant–soil feedback (PSF) (*fe* magnitude of exotic soil feedback effect, positive sign indicating a 'home' advantage) and native PSF (*fn*, magnitude of native soil feedback effect): native dominance is indicated by green, areas of coexistence or slower, incomplete exclusion in yellows and orange, and areas where exotics are predicted to dominate are indicted in red. (a) A baseline case where the exotic species has established but is rare (5% abundance), dispersal is assumed to be local, and mortality and seed production are held equal between species. Letters in the panel refer dynamics shown in Fig. 2. (b) If simulations begin with equal abundance of exotics and natives on neutral soil states, the dynamics proceed towards equilibrium more quickly. (c) If species differ in dispersal and life history, the outcomes for various combinations of *fe* and *fn* shift towards increased dominance of the exotic species (here, the exotic produces twice as many seeds, disperses globally and has twice the mortality rate of the native).

Natives and exotics were predicted to coexist over a fairly large range of PSF values when they both have negative val-

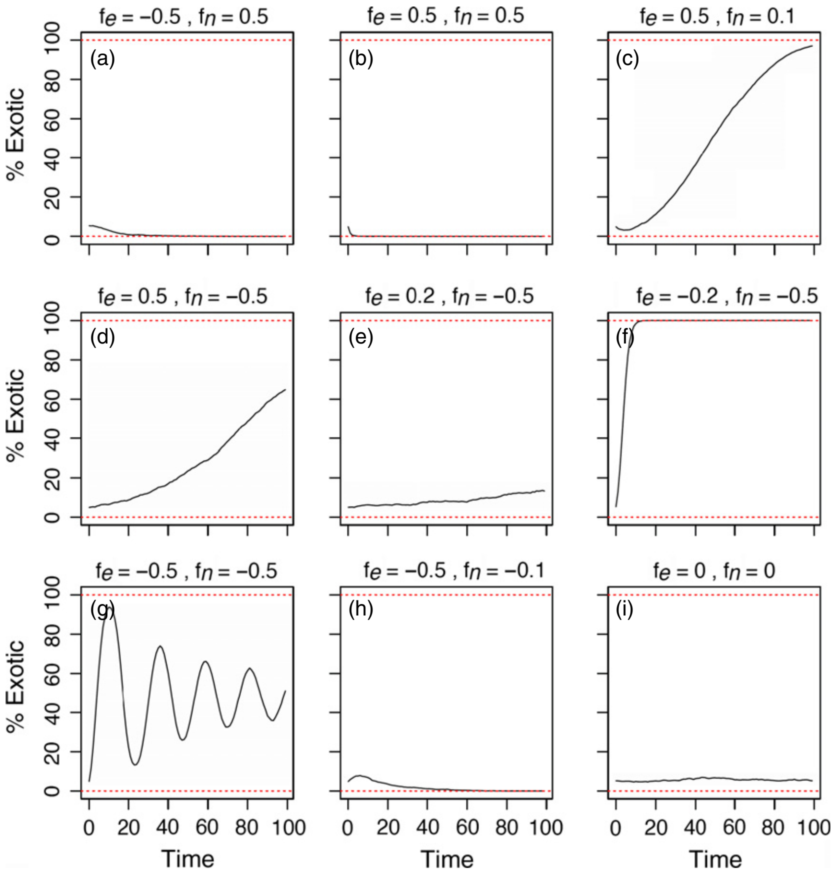

Fig. 2. Simulation model results showing dynamics of exotic relative abundance over 100 time steps for the various combinations of *fe* and *fn* indicated on Fig. 1a by lower-case letters a–i.

ues of a similar magnitude (approximate range of f_e:f_n ratios 0.3–3.3) (Fig. 1a, region g). This is an example of stabilizing coexistence producing damped oscillations where each species has a larger negative effect on itself than its competitor (Fig. 2g).

Natives were able to maintain dominance even when they performed better in exotic-conditioned soils if exotics experienced an even stronger disadvantage on their own-conditioned soils (Fig. 1a, region h). Under equal starting conditions (when both species start at 50% abundance), the dynamics proceed more quickly towards equilibrium, and exotics are predicted to dominate in areas where they have greater positive feedback than the native (Fig. 1b, upper right quadrant).

The model is sensitive to the assumption of functional equivalence of the native and exotic species. When this assumption was relaxed to reflect species differences and tradeoffs in addition to PSF, either species was able to exclude the other depending on their relative performance advantages in the regions where one species had a home PSF advantage and the other had an away PSF advantage (i.e. where they both did best in the same soil) (Fig. 1c). For the case where exotics were shorter lived but better colonizers (i.e. with global dispersal and double the seed output and mortality rate of native species), the native species maintained dominance in only two cases: when the native had a much stronger positive 'home' advantage than the exotic and when the native was less inhibited by its 'home' soil compared to the exotic species in its 'home' soil (Fig. 1c).

To further investigate the effects of species life history on the effects of PSFs (e.g. Fig. 1c), we varied baseline mortality rates of the two species while holding PSFs equal (Fig. 3). Baseline mortality describes the average life span of a species, and thus can be interpreted as a species trait that influences the time over which plant–soil effects can accumulate and the frequency with which cells become available for colonization. When both species have short life histories (high baseline mortality rates), invasion rate increases due to decrease in the strength of soil legacy effects caused by long-term occupancy (Fig. 3b). Stochastic formation of alternative states was greatest when species were allowed to disperse globally (Fig. 3c): when mortality rates were > 50% on soils with weak PSFs, stochastic processes shifted the modelled outcome, unpredictably, to either exotic- or native-dominated systems (Fig. 3c).

META-ANALYSIS

The 52 pairwise native–exotic species comparisons examined represent a small subset of plant species (33 native and 25 exotic species) and are biased towards greater representation of species with certain characteristics: the majority of the studies focused on herbaceous species (over 70%), predominately graminoids. Exotic species tended to be annuals (44%), whilst natives tended to be perennials (94%) in our data set, resulting in a third of the native–exotic species comparisons involving a shorter-lived exotic. Of the 22 studies, four

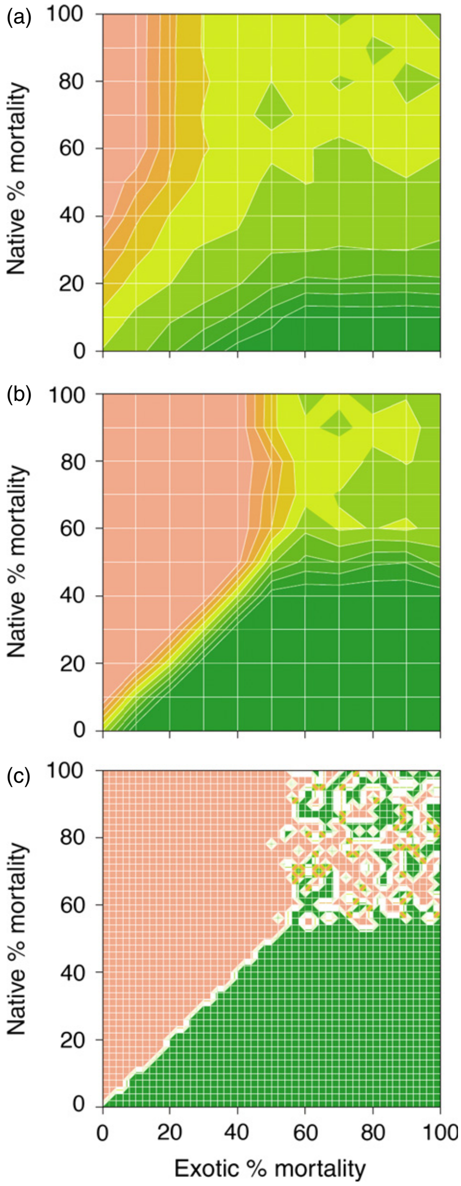

Fig. 3. Effects of life span on coexistence. Results when both exotic and native species are identical with same sign and magnitude of feedback effects, dispersal and seed production, but when baseline mortality parameters are allowed to vary. (a) Exotic and native species produce negative feedback ($f = -0.3$; similar to region g, Fig. 1a) and disperse locally. (b) Exotic and native species produce positive feedbacks ($f = 0.3$; similar to region b, Fig. 1a) and disperse locally. High mortality delays exclusion in both the case of negative (a) and positive (b) feedbacks. (c) Exotic and native species produce positive feedback and disperse globally, illustrating formation of alternative states due to stochasticity when both species have high mortality (note higher resolution of c compared to panels a and b). Colors as in Fig. 1.

assessed effects at the community-level (e.g. in multi-species assemblages) rather than at the species level. While species performance was generally measured in the greenhouse, over half of the studies (12) used soil conditioned in the field. Most studies focused on grassland habitats (13), with other studies focusing on invasions in woodlands, coastal dunes and wetlands.

Feedback estimates differed among studies ($F_{18,26} = 3.52$, $P = 0.002$) and within species pairs across studies ($F_{17,27} = 7.13$, $P = 0.01$). Mean soil feedback tended to be positive for native species ($d = 0.30$, 95% CI 0.01–0.59) and neutral (not significantly different from zero) for exotic species ($d = 0.014$) (Fig. 4, Table 1), although soil PSFs did not consistently differ between native and exotic species ($F_{1,27} = 0.78$, $P = 0.39$). The inclusion of the four unpublished studies did not affect the results (mean effect size estimate changed by < 0.04 standard deviation units). Study design did not appear to affect feedback estimates: the one exception was a non-significant trend towards studies that used field-collected soil as inoculum finding more positive feedbacks for native species ($F_{1,21} = 2.56$, $P = 0.10$). Summing effect size across native and exotic comparisons in each study (equivalent to Is), pairwise feedbacks were generally positive ($d = 0.31$) but not significantly different from zero.

Overlaying the empirical results with the model results (Fig. 5), empirical PSF estimates most often predict dominance of the native species or exotic species rather than coexistence. However, the majority of PSF estimates occurred in regions where initial starting abundances are important: in the case where exotic species are initially rare (e.g., Fig. 1a), model results indicate that native species should dominate with PSFs measured in most of the studies included in the meta-analysis. While the surveyed literature did not provide quantitative estimates of dispersal and longevity of the species included in the meta-analysis, the bias towards shorter-lived exotic species suggests that predictions of dominance of exotic species would increase if these species differences were also considered (e.g. Fig. 1c).

Discussion

Our aim was to test the expectation that positive PSFs for exotic species, where an exotic species benefits more than native species from its ‘own’ soil biota, can lead to a spread of the exotic species and monotypic dominance. While our spatial simulation model produced results consistent with the positive feedback expectation, dynamics were dependent on the assumptions of an initially mixed community (50% native, 50% exotic species) and both species having similar life history (life span, dispersal) attributes. Meta-analysis of feedback comparisons between native and exotic species pairs indicated that the growth of native species was greatest in soil conditioned by native species (a home advantage), while growth of exotic species did not differ consistently in soils conditioned by native or exotic species.

Two types of plant–soil interactions could result in this ‘home’ advantage for native species (a positive PSF): exotic species could affect soil communities in a way that leads to reduced growth for native species, and native species may affect soil communities in a way that boosts growth for themselves (e.g., be more dependent on mutualists). While we cannot distinguish which of the two interactions predominate, the spatial invasion model predicts that the resulting feedback

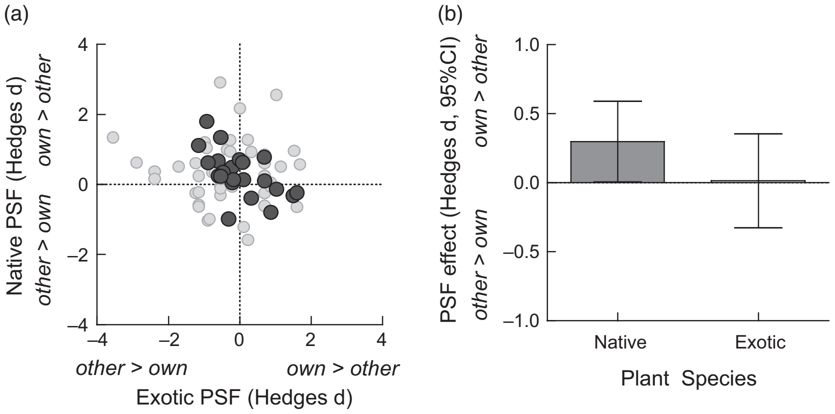

Fig. 4. (a) Effect size of plant–soil feedbacks (PSFs) across the 22 studies (black symbols) and 52 species pairs (grey symbols) for native and exotic species where positive values indicate greater plant performance (all studies measured growth) in self-conditioned soil ('own') and negative values indicate greater performance in the soils conditioned by the other species. Units of Hedges' d are in terms of standard deviations. (b) Mean effect sizes among the 22 studies with 95% confidence intervals: on average, native PSF effects were significantly > 0 while exotic PSFs were not different from zero.

Table 1. Studies included in the meta-analysis comparing native and exotic species growth in native- and exotic-conditioned soil. Species number indicates the number of natives (N) and exotic (E) species in each study; asterisks indicate the use of multiple-species communities rather than individual species. Plant–soil feedback (PSF) effect size (Hedges d) is the comparison of the effect of soil conditioned by conspecifics vs. the other species: a positive value for a native species, for example, indicates that species grew better in their own-conditioned soil vs. exotic-conditioned soil. PSFs listed are the mean estimate of each study; when a study compared more than one native and one exotic species, growth estimates were averaged across native and exotic species prior to calculation of effect size. Table S1 presents PSFs for each species pair. Inoculum source indicates the source of the soil inoculum for the plant response (i.e. phase II) portion of the feedback experiment: 'Grnhse' indicates studies that used soil conditioned by plants grown in greenhouse, and 'Field' indicates studies where soil was collected in invaded and uninvaded field sites.

Study	Habitat type	Species number (N/E)	PSF effect (Hedges d)		Inoculum Source
			Native	Exotic	
August-Schmidt (unpub)	Grassland	1/1	0.49	−0.22	Field
Batten, Scow & Espeland (2008)	Grassland	2/1	0.67	−0.60	Grnhse
Bennett, Thomsen & Strauss (2011)	Grassland	1/1	1.80	−0.92	Field
Carvalho *et al.* (2010)	Coastal dune	2/1	0.35	−0.46	Field
Grman & Suding (2010)	Grassland	1*/1*	0.71	−0.01	Grnhse
Harnden, MacDougall & Sikes (2011)	Grassland	1/1	0.78	0.69	Field
Jordan, Larson & Huerd (2008)	Grassland	3/1	0.11	−0.53	Grnhse
Jordan, Larson & Huerd (2011)	Grassland	3/3	0.24	0.70	Grnhse
Kulmatiski & Beard (2011)	Shrub-steppe	1/1	1.34	−0.89	Field
Larios & Suding (unpub)	Grassland	1/1	0.62	0.11	Field
Nijjer, Rogers & Siemann (2007)	Woodland	4/1	0.14	−1.15	Field
Niu *et al.* (2007)	Mixed forest	3/1	1.12	0.87	Field
Rodriguez-Echeverria *et al.* (2009)	Coastal dune	2/1	−0.80	1.50	Field
Scharfy *et al.* (2010)	Wetland	3*/1	−0.32	−0.60	Grnhse
Shannon, Flory & Reynolds (2012)	Woodland	1*/1	0.24	−0.21	Grnhse
Smith & Reynolds (2012)	Woodland	1/1	0.05	1.60	Grnhse
C. Stein (unpub)	Grassland	2/1	−0.24	−0.18	Field
C. Stein and W. Harpole (unpub)	Grassland	2/2	0.14	−0.31	Field
van der Putten *et al.* (2007)	Coastal dune	1/1	−0.98	0.32	Grnhse
van Grunsven *et al.* (2007)	Grassland	3/3	−0.39	0.08	Grnhse
Vogelsang & Bever (2009)	Grassland	1/1	0.63	1.03	Grnhse
Yelenik & Levine (2011)	Coastal sage	2/1	−0.14	−0.53	Field

should result in invasion resistance when exotics are rare: native species maintain dominance in the community because their soil advantage alongside local dispersal will reduce the chance of exotic spread.

NATIVE SPECIES GROW BETTER IN THEIR 'HOME' SOIL

Most studies have found PSFs of species to be generally negative (Bever 1994; Kulmatiski *et al.* 2008; Petermann *et al.*

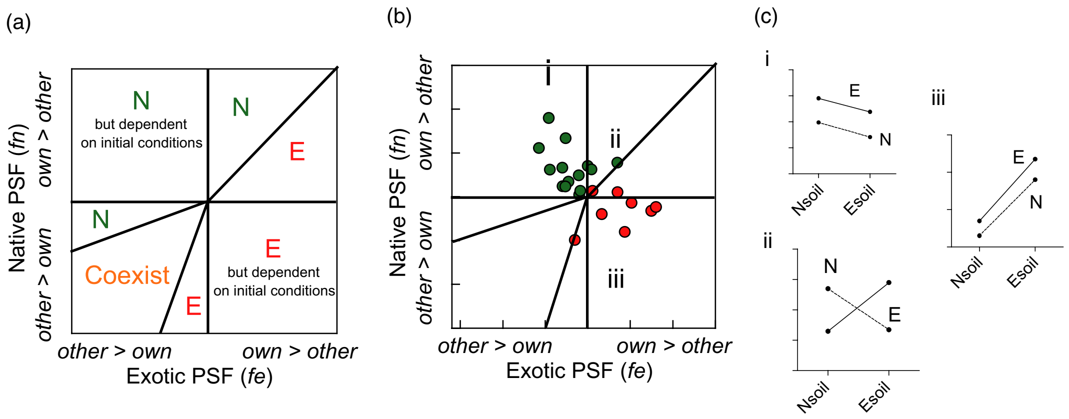

Fig. 5. Plant–soil feedback (PSF) space as described by the feedback of exotic species (*fe*) and the feedback of native species (*fn*). (a) Pairwise coexistence and dominance outcomes generalizing the spatial simulation results (and after Eppstein, Bever & Molofsky 2006). N = native species; E = exotic species. (b) The same feedback space with PSF estimates from the meta-analysis. Each symbol represents a study; colour-coding reflects classification according to panel a. (c) Examples of the types of plant performance responses that characterize the feedback estimates, where E and N are exotic and native species, respectively, and Nsoil and Esoil are the corresponding soil-conditioning treatments. Regions in feedback space are annotated i–iii in panel b: (i) growth of both species is greater in native-conditioned soil, (ii) species respond differently to soil-conditioning and (iii) growth of both species is greater in exotic-conditioned soil. Note that average growth rate differences are also visible in panel c; although they may contribute to average fitness differences; feedback estimates just reflect relative differences in response (i.e. the slope of the lines).

2008). Extrapolating this general finding to the case of invasion, we would expect that native species would grow better in exotic-conditioned soil than soil conditioned by conspecifics. However, many studies we reviewed found that native species grew better in their 'home' soil than in 'invaded' soil. This pattern generally indicates that exotic species can markedly affect soil in a way that is distinct from native species within a community (Ehrenfeld 2010). It is consistent with several hypotheses, including the degraded mutualist hypothesis (Stinson *et al.* 2006; Vogelsang & Bever 2009; Bever *et al.* 2010; Kulmatiski & Beard 2011) where exotic species are thought to suppress native symbiont communities. For example, Batten, Scow & Espeland (2008) found that a native species, *Lasthenia californica*, was negatively affected by soil conditioned by an invasive grass (*Aegilops triuncialis*), while *Aegilops* growth was unaffected when grown in invaded vs. native-conditioned soil. The 'home' advantage for native species is also consistent with the novel weapons hypothesis (Callaway *et al.* 2008) that exotic species may produce allelopathic or antimicrobial root exudates, and the hypothesis of Eppinga *et al.* (2006) that exotic species can accumulate local pathogens but suffer less from those pathogens than native species.

Our use of pairwise comparisons (native vs. exotic species pairs) to specifically address patterns in invasion differs somewhat from the more generalized multiple species approach that compares growth in 'own' soil to the average response to soils conditioned by 'others' as an array of more than two plant species (Klironomos 2002; MacDougall, Rillig & Klironomos 2011). Although the pairwise approach gives specific predictions about relative dominance and invasion spread that is most comparable with models of community dynamics that involve two species, it does not address interactions of more than two species or compare effects of native vs. exotic soil with effects among the native species community. Thus, the result that natives often grow better in their 'own' soils than in exotic-conditioned soil does not indicate how these same native species would grow in their 'own' soils relative to soil conditioned by other native species; it is this feedback that is most often found to be negative in prior studies (Bever *et al.* 2010).

EXOTIC SPECIES VARY IN THEIR RESPONSE TO INVADED AND UNINVADED SOILS

We found that exotic species, on average, did not respond differently in 'home' and 'away' soil. While there were some studies that did find strong PSFs for exotic species, our overall results contradict the widespread expectation that exotic species affect the soil biota in a way that benefits their own performance (Reinhart & Callaway 2006; Bever *et al.* 2010). This result is consistent with a previous review (Levine *et al.* 2006) that also found little evidence of strong positive feedbacks.

Only a few studies examined here indicated that an exotic species may grow better in soil conditioned by conspecifics (a 'home' advantage). These few studies are consistent with the expectation that net positive interactions with soil biota may be limited to cases where the exotic species evolves 'novel' mutualisms with native mutualists or is accompanied by a mutualist from their home range (Pringle *et al.* 2009; Bever *et al.* 2010). It could also occur in cases where natives accumulate pathogens that affect the exotic species.

However, other studies in our data set found that particular exotic species grow better in soil conditioned by natives (an 'away' advantage) (Nijjer, Rogers & Siemann 2007; Scharfy *et al.* 2010). These results are consistent with the expectation that exotic species may inhibit mutualists or other soil biota, negatively affecting the growth of both exotic and native plant species. This mechanism depends on the species specificity of the plant–mutualist interaction: we know of several cases where efficacy differs between species and cases where exotics are less dependent on mutualists (Richardson *et al.* 2000; Vogelsang & Bever 2009). Greater time since introduction may increase the chance of soil pathogens arriving from their home range (Hallett 2006), which may cause exotic–soil biota interactions to become increasingly negative over time (Diez *et al.* 2010; Lankau 2011). Frequency-dependent effects of plant species on the soil other than soil biota – for instance, resource availability – could also influence these dynamics (Ehrenfeld 2003); these effects are important but beyond the scope of this study.

IMPORTANCE OF INITIAL CONDITIONS AND SPECIES DIFFERENCES

When interpreting PSFs in the context of community dynamics, assumptions of starting abundances – when PSFs begin to affect community dynamics – are critical (Kardol *et al.* 2007; Turnbull *et al.* 2010; Elgersma *et al.* 2011). Under starting conditions where both exotic and native species are abundant, outcomes follow the expectation that exotic species increase in abundance and dominate when the exotic modifies soil to its own relative advantage (e.g., below the 1 : 1 line in Fig. 1b). However, frequency dependence is essential to consider: in a community dominated by natives, the native community is able to resist invasion in cases even when the exotic species has a greater positive feedback. This resistance occurs because the invader encounters soils conditioned by native species when it is rare. These dynamics can create alternative stable states or transient ‘waves’ of invasion depending on the speed at which exotic and native abundances approach equilibrium (Fukami & Nakajima 2011) (Fig. 2g).

Due to dependence on starting abundance, the net pairwise approach described by Bever, Westover & Antonovics (1997) may best apply in cases where the exotic and native species are both abundant. Predictions of community change that depend on species turnover and spread, such as succession and invasion scenarios, require that initial abundances of species in the community, and thus initial soil legacy effects, be considered. In these cases, interactions will depend on the strength and direction of these starting conditions, in essence weighing one individual feedback over another, creating historical contingencies (Kardol *et al.* 2007; Turnbull *et al.* 2010; Elgersma *et al.* 2011). The chance of PSF conferring invasion resistance has been appreciated (Suding, Gross & Houseman 2004; Kardol *et al.* 2007); here we show that it can occur within the range of empirically measured PSFs under some circumstances. Our results also indicate that positive PSFs alone cannot account for successful invasion: another process (such as disturbance) must allow the exotic species to establish and reach abundance levels necessary for its effects on soil biota to translate into spread and persistence.

Modelling also revealed strong dependencies in life history and dispersal, cautioning against interpretation of particular invasion dynamics without consideration of these other factors (also see Eppstein, Bever & Molofsky 2006). When we incorporated a common life history difference between species in the data set – that exotics had a shorter life history and were better dispersers than natives (see also Hamilton *et al.* 2005; Pysek *et al.* 2009) – PSF estimates from the meta-analysis resulted in the spread and dominance of exotic species. Thus, our results suggest that it is essential to combine knowledge of PSFs with consideration of trait differences and abundance of the exotic to understand invasion dynamics.

Conclusions

Combining the simulation model with meta-analysis results, we found that the expectation that positive exotic species–soil feedbacks allow populations of exotic species to spread into native communities and form mono-dominant stands was not borne out by the empirical feedback estimates. Of 52 native–exotic pairwise comparisons of PSF in 22 studies, less than a third estimated feedback strengths consistent with this prediction (Fig. 5). Instead, the majority of comparisons described feedback where natives grew better on native soil, resulting in the dominance of native species when exotics are initially rare in our simulation model. We find that these same feedbacks could lead to dominance of exotic species in cases where exotics also have a dispersal or competitive advantage, or in cases where a disturbance or another factor allows the exotic species to establish at high abundances.

As has been emphasized by other reviews on the subject, taking empirical estimates of PSFs and translating them to community-level patterns is conceptually complex. Here, we initially explore PSFs and how they may relate to invasion dynamics using a pairwise approach. Our empirical findings are based on a small data set: these pairwise comparisons represent just a very small snapshot of the plant invasions occurring in natural communities today. Our understanding will grow as pairwise studies continue to accumulate and we integrate PSFs with effects related to other species differences such as dispersal characteristics and life-history traits, as well as how PSFs interact with processes such as resource competition (Shannon, Flory & Reynolds 2012). Community-level tests of the role of feedbacks (van de Voorde, van der Putten & Bezemer 2011) and measures of frequency dependence (Elgersma & Ehrenfeld 2011) can complement our spatial simulation modelling technique to better translate PSFs between native and exotic species to invasion dynamics at the community level.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Native and exotic pairwise feedback comparisons used in the review; all compared native and exotic growth in native- and exotic-conditioned soil.