IDEA AND PERSPECTIVE

Plant–soil feedbacks and invasive spread

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Abstract

Plant invaders have been suggested to change soil microbial communities and biogeochemical cycling in ways that can feedback to benefit themselves. In this paper, we ask when do these feedbacks influence the spread of exotic plants. Because answering this question is empirically challenging, we show how ecological theory on 'pushed' and 'pulled' invasions can be used to examine the problem. We incorporate soil feedbacks into annual plant invasion models, derive the conditions under which such feedbacks affect spread, and support our approach with simulations. We show that in homogeneous landscapes, strong positive feedbacks can influence spreading velocity for annual invaders, but that empirically documented feedbacks are not strong enough to do so. Moreover, to influence spread, invaders must modify the soil environment over a spatial scale larger than is biologically realistic. Though unimportant for annual invader spread in our models, feedbacks do affect invader density and potential impact. We discuss how future research might consider the way landscape structure, dispersal patterns, and the time scales over which plant–soil feedbacks develop regulate the effects of such feedbacks on invader spread.

Keywords

Dispersal, exotic plant, feedbacks, invasions, soil biota, spread.

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INTRODUCTION

Biological invasions by exotic plants incur tremendous economic and environmental impacts worldwide (Vitousek *et al.* 1997, Wilcove *et al.* 1998, Pimentel *et al.* 2000). However, the fraction of introduced plant species that spread through and impact native ecosystems is surprisingly small, often estimated at around 1 % (Simberloff 1981, Williamson & Fitter 1996). This finding has motivated many ecologists to search for the key traits characterizing the most successful and damaging plant invaders (Baker 1974, Rejmánek & Richardson 1996). Recently, positive plant–soil feedbacks have been proposed as important factors explaining plant invasiveness. These feedbacks occur when plants change the mutualistic and pathogenic components of the soil microbial community in ways that benefit themselves (Klironomos 2002, Bever 2003, Callaway *et al.* 2004a). Positive feedbacks can also arise through more direct changes in soil biogeochemistry including invader effects on nutrient and litter dynamics (Ehrenfeld *et al.* 2001, Scott *et al.* 2001, Lenz *et al.* 2003) and the production of allelopathic compounds (Vivrette & Muller 1977, Callaway & Aschehoug 2000). Because native species are often harmed by the changes they induce in the soil environment

(negative feedbacks) (Van der Putten 2002, Reinhart *et al.* 2003, Bever 2003), positive plant–soil feedbacks may strongly favour invasion success.

In a landmark study, Klironomos (2002) showed that five of North America's most damaging exotic plant invaders modified the soil microbial community in ways that benefit themselves (positive feedbacks), whereas five rare native plants all experienced negative plant–soil feedbacks, a result hypothesized to explain the differential growth, dominance, and spread of these species. Similarly, Callaway *et al.* (2004a) found a switch from negative to positive plant–soil feedbacks for spotted knapweed when moving from its native to exotic range. In these and other studies, negative feedbacks are thought to arise from the accumulation of specialist pathogens after plants occupy a soil for some period of time. These negative feedbacks overpower the positive feedbacks arising through the accumulation of soil mutualists (Van der Putten 2002, Reinhart *et al.* 2003, Bever 2003).

These results are consistent with an emerging below-ground view of the enemies release hypothesis, where invaders suffer less negative effects of specialist soil predators and pathogens in their exotic vs. native range (Reinhart *et al.* 2003, Knevel *et al.* 2004, but see Beckstead & Parker 2003). Under this hypothesis, negative soil feedbacks mediated via

the accumulation of specialist pathogens should be weak for invaders, allowing positive feedbacks to dominate (Klironomos 2002, Van der Putten 2002, Reinhart *et al.* 2003, Callaway *et al.* 2004a,b). Moreover, even if positive feedbacks fail to develop, simply the loss of negative feedbacks could provide an important advantage for invaders.

Despite rapidly growing interest in plant–soil feedbacks as a control over invasiveness, our empirical understanding of this relationship is based largely on short-term greenhouse experiments (Wolfe & Klironomos 2005). Consequently, it is 'difficult to predict how plant feedbacks with soil biota can affect the long-term spread and persistence of exotic plant species (Wolfe & Klironomos 2005)'. Understanding how feedbacks affect spread is particularly complex because exploring this relationship requires integrating feedbacks with other stages in the invader life-cycle, namely dispersal. Because such an integration is empirically challenging, we argue that incorporating models of population spread is key to understanding how plant–soil feedbacks affect the spread of invaders. Pursuing this understanding is important because spread is the process distinguishing successful from unsuccessful invasions (Daehler 2001).

In this paper, we raise the question of when do feedbacks with the soil environment influence the spread of exotic plants. We first describe scenarios in which feedbacks should and should not influence invader spread, and identify their parallels to the 'pushed' and 'pulled' invasions described by theoreticians. To demonstrate the value of this theory for determining when feedbacks influence spread, we incorporate soil feedbacks into models for annual invaders. We then derive the conditions under which soil feedbacks affect invader spread, support our approach with simulations, and compare our conditions to empirically documented feedbacks. We discuss how future research might consider the way landscape structure, dispersal patterns, and the time scales over which plant–soil feedbacks develop regulate the effects of soil feedbacks on invader spread.

ARE INVASIONS WITH FEEDBACKS —PUSHED OR —PULLED?

Although empirical work on plant–soil feedbacks has focused on invader growth and dominance, a number of studies have suggested that feedbacks affect the 'spread' or 'expansion' of invasions (Ehrenfeld *et al.* 2001, Scott *et al.* 2001, Klironomos 2002, Lenz *et al.* 2003, Callaway *et al.* 2004a). Such hypotheses follow reasonable intuition. If as invasions proceed, plants modify the soil such they grow better and produce more seeds, and those seeds are responsible for moving the invasion forward, feedbacks affect spread (Fig. 1a). Complexity arises, however, because feedbacks take time and invader density to develop. Recently colonized individuals at the front of an invasion
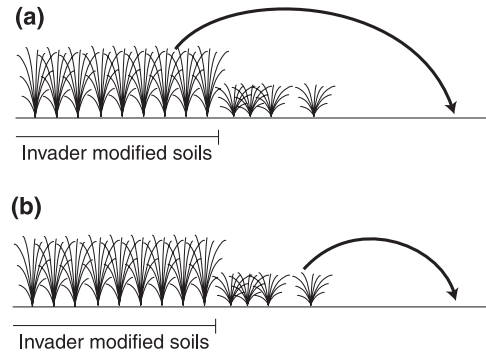
Figure 1 (a) A 'pushed' invasion where individuals in the interior of the invasion, occupying soils modified to their benefit, produce most of the seeds dispersing ahead of the invasion. (b) A 'pulled' invasion, where individuals at the front of the invasion, too sparse and recently arrived to benefit from positive plant–soil feedbacks, produce most of the seed dispersing ahead of the invasion.

grow in soils they have yet to modify. If these individuals produce the seeds moving the invasion forward, feedbacks that later develop are unimportant for spread (Fig. 1b).

Fortunately, ecological theory provides the tools to distinguish these two alternatives, tools the form the basis of our work here. The first alternative, where well-established interior individuals at higher densities drive the spread of the invasion, describes a 'pushed' invasion (Fig. 1c) (Lewis & Kareiva 1993, Kot *et al.* 1996, Wang *et al.* 2002, Hastings *et al.* 2005). The second alternative, where spread is driven by the demographic performance of individuals when rare at the front of the invasion, describes a 'pulled' invasion (Fig. 1b). The key point is that if plant–soil feedbacks affect invader spread, they must cause invasions to be pushed. If not, the invasions are pulled by recently colonized, leading-edge individuals and feedbacks do not affect spread. Because of this, we can use the ecological theory that predicts whether invasions are pushed or pulled, to also predict whether plant–soil feedbacks affect the spread of invaders.

PLANT INVASION MODEL WITH SOIL FEEDBACK

To demonstrate our approach, and provide the critical first step in asking whether plant–soil feedbacks influence the spread of invasions, we examined models for annual invaders that modify the soil environment, such as yellow star thistle (*Centaurea solstitialis*) or cheatgrass (*Bromus tectorum*). Specifically, we added a soil feedback to an integrodifference equation model for invasions (Kot *et al.* 1996, Hastings *et al.* 2005):

$$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y)g[N_t(y)]F_t(y)\,dy \tag{1}$$

$$F_{t+1}(x) = h[N_t(x)]$$

$N_{t+1}(x)$ is the density of the invader population at location x and time $t + 1$. It is the summed contribution of the seeds produced at all locations y, multiplied by the probability a seed disperses from y to x. $F_{t+1}(x)$ is the fractional increase or decrease in fecundity due to soil modification, a function h of $N_t(x)$. The term $g[N_t(y)]$ describes how seed production rises with density in the absence of the feedback, and when multiplied by $F_t(y)$, describes the feedback-influenced seed production. $k(x - y)$ is the dispersal kernel, describing the probability that a seed moves between locations x and y.

Growth and soil feedback functions

We used a common annual plant population model (Watkinson 1980, Pacala 1986, Levine & Rees 2002) for the growth function g:

$$g(N) = \frac{\lambda N}{1 + aN}. \tag{2}$$

Invader density in next generation equals that in the current generation, times λ, the intrinsic rate of increase or fecundity, divided by intraspecific competition. The rate at which intraspecific competition increases with density is regulated by a, which can be interpreted as the proportional area occupied by a solitary individual at a given location (Watkinson 1980).

The feedback function h specifies how invader density modifies the microbial community or biogeochemical processes in ways that 'feed back' to affect the performance of future generations. For annual plants, we define feedbacks as changes in plant fecundity that occur after soil has been modified by the previous generation. Thus, the feedback in eqn 1, $F_{t+1}(x)$, is a function of the previous year's invader density $N_t(x)$. In our formulation, we incorporate a feedback term φ, often defined in the empirical invasions literature as the difference in invader performance on previously invaded vs. uninvaded soils, divided by performance on invaded soils (Klironomos 2002, but different than I_s of Bever 2003). Positive feedbacks result when invaders grow better on soil they have modified, and can range from 0 to 1, while negative feedbacks occur when invaders grow more poorly on their modified soil, and range from $-\infty$ to 0.

We examined two different relationships between feedbacks and density (Fig. 2). In both, there is no feedback near zero density and the feedback reaches φ at high density, but the two forms differ in whether the transition is continuous or abrupt. In the latter, a threshold density is required for the feedback to develop. Note that with φ defined as above, $1/(1-\varphi)$ describes the ratio of performance (fecundity in our model) on invaded to uninvaded soils.
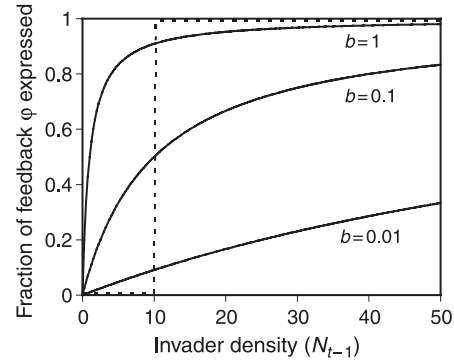
Figure 2 Alternative relationships for how feedbacks increase with plant density. The solid lines show feedback strength rising continuously with plant density as described by eqn 3. Different lines show relationships with different values of b, the spatial scale over which individual plants modify soils. The dashed line shows a thresholding feedback (eqn 4) where below a critical density or cover, no feedback is expressed, while above that value, the entire feedback is expressed.

We formulated the continuous feedback function following from the way plants fill space in the growth function (eqn 2):

$$h(N) = \frac{1}{1 - \varphi\left(\frac{bN}{1+bN}\right)}. \tag{3}$$

Analogous to a in the growth function (eqn 2), b is the proportion of area at a given location over which an individual plant modifies the soil to exert feedback φ, and regulates the rate at which feedbacks develop with density (Fig. 2). While in the growth function (eqn 2), $\frac{aN}{1+aN}$ is the fraction of the potential seed production actually produced, $\frac{bN}{1+bN}$ is the fraction of the feedback φ actually produced.

The spatial interpretation of a also underlies our formulation of the alternative, thresholding feedback function, which is expressed as follows:

$$h(N) = \begin{cases} 1 & \text{if } aN < c \\ \frac{1}{1-\varphi} & \text{if } aN \geq c \end{cases} \tag{4}$$

where c is the critical invader cover above which the feedback φ is expressed. Because a specifies the fractional area occupied by a single plant (Watkinson 1980), aN corresponds to a measure of plant cover.

CONDITIONS FOR FEEDBACKS TO INFLUENCE INVASION VELOCITY

In analysing the effects of feedbacks on invasion velocity, we take advantage of work by mathematical ecologists proposing a series of conditions under which integrodifference equation models of invasions are linearly determinate

or 'pulled'. For such invasions, the asymptotic spread velocity is controlled only by the invader's growth rate when rare and ability to dispersal. Given that feedbacks do not affect the performance of plants when they first colonize and are rare, invasions that are linearly determinate or 'pulled', should have asymptotic invasion velocities that are unaffected by feedbacks (see Appendix for more formal proof). Thus, the conditions for invasions to be pulled are also the conditions under which plant–soil feedbacks have no effect on the speed of spread.

One key condition for invasions to be pulled is that the per capita growth rate of the invader is maximized when it is rare (Weinberger 1982, Kot *et al.* 1996). Theory for co-operative systems (Weinberger *et al.* 2002) shows that invasions described by eqn 1 will be 'pulled' (Fig. 1b), if the following condition holds (Appendix):

$$g(N)h\left(\frac{N}{\lambda}\right) \leq \lambda N \quad \text{for all } N. \tag{5}$$

For such pulled invasions, spread is controlled by the dispersal kernel and population growth rate when rare, but not the plant–soil feedback. Different dispersal kernels can change the speed of the invasion, but will not cause feedbacks to influence velocity. If the condition in eqn 5 does not hold, the invasion is 'pushed' by seeds dispersed from individuals on previously modified soils (Fig. 1a), and feedbacks affect spread. In the Appendix, we suggest that condition five should be conservative for predicting invasion speed independent of feedbacks, a point confirmed through simulations below.

Substituting in the growth and continuous feedback functions (eqns 2 and 3) into condition 5, yields the following inequality (Appendix), which outlines the condition under which feedbacks have no effect on invasion velocity for our model:

$$\varphi \leq \frac{a\lambda}{b}. \tag{6}$$

Thus, invasion rates are unaffected by the feedback (expression 6 holds) in the following three cases. (1) The feedback is negative. Negative feedbacks always satisfy eqn 6 because the right-hand side is always positive (*a*, *b*, and *λ* are all positive) and thus greater than any negative *φ*. (2) Plants modify soils over an equal or lesser area than they occupy (*a* ≥ *b*). This condition satisfies eqn 6 because when *a* ≥ *b* and *λ* > 1, the right-hand side of eqn 6 always exceeds the strongest mathematically possible positive feedback (+1). (3) Invaders modify soils over an area greater than they occupy (*b* > *a*), but have high fecundity (*λ*). The three cases have intuitive interpretations if we recall that eqn 6 basically specifies when invader per capita growth rates are greatest at low density. This occurs when feedbacks are negative, invader growth rates decline rapidly with

density (*a* is large), positive feedbacks develop more slowly with density (*b* is small), or when the population that favourably modified the soil in the previous generation is much smaller than that in the current generation exerting negative intraspecific effects (*λ* is large).

Taken together, conditions 1–3 place severe constraints on when plant–soil feedbacks influence the speed of spread for an annual invader. Our results suggest that the loss of negative feedbacks when moving from native to exotic ranges should not increase invader spread, especially when positive feedbacks fail develop. Moreover, positive feedbacks of any magnitude should not increase invasive spread when the area over which plants interact competitively is similar or greater than the area over which they modify the soil. Only if plants modify soils over larger areas than they occupy can feedbacks influence invasion velocity, and then only for invaders with low population growth rates and strong positive soil feedbacks.

Simulations

We used simulations of our model to (1) confirm that the theory-based analytical result predicts when plant–soil feedbacks affect invasion speed; (2) examine invasion velocities when these conditions are violated; and (3) examine the robustness of our results to different functional relationships between soil modification and density. We simulated invasions using numerical integration of the system of eqn 1 with the growth and feedback functions specified in eqns 2–4. For the dispersal kernel, we used a negative exponential (Willson 1993), though the analytical results are independent of the kernel as long as it possesses a moment generating function bounded below by one (Appendix). Following eqns 1–3, our model for simulation is written:

$$N_{t+1}(x) = \int_{-\infty}^{\infty} \frac{m}{2} e^{-m|x-y|} \frac{\lambda N_t(y)}{1 + aN_t(y)} F_t(y)\, \mathrm{d}y$$

$$F_{t+1}(x) = \frac{1}{1 - \varphi\left[\frac{bN_t(x)}{1+bN_t(x)}\right]}, \tag{7}$$

where *m* is the parameter from a negative exponential kernel. This model includes feedbacks rising continuously with density (eqn 3), but the same simulation approach was also applied to the thresholding feedback (eqn 4).

We wrote simulation code in R version 1.8.1, allowing us to calculate the population densities for a determined number of generations on a linear array of a specified distance, equally divided into 1000 points. We initialized the simulations with a density of one individual at the leftmost point along the array. For each generation and for each

spatial coordinate, we first calculated the seed production with the growth and feedback functions. Seeds were then redistributed using the dispersal kernel, and the contribution of seeds to all points in the array was calculated using the trapezoidal approximation of the integral in eqn 7. The velocity of the invasion was measured as its displacement in the last half of the simulation, where locations with a threshold density > 0.01 were considered occupied. The boundaries of the simulated landscape were absorbing. We ran simulations enough years for a stable wave to develop and move across the landscape, and ended simulations if the last point in the array was occupied.

Simulation results

Simulations (Fig. 3a) confirmed our analytically solved condition for feedbacks to have no effect on invasion velocity. Consistent with condition 6, with $a \geq b$ or negative feedbacks, the feedback has no effect on the simulated invasion velocity, regardless of dispersal or fecundity (Fig. 3a). Simulations also showed that when invaders were capable of modifying soils over an area 10 times greater than they occupy ($b = 10a$), feedbacks more positive than +0.5 could increase spread for invaders with low fecundity (Fig. 3a). Note that a feedback of +0.5 is greater than that predicted to violate condition 6 based on parameter values (shown by the points in Fig. 3a), supporting our assertion in the Appendix that the condition is conservative for predicting no effect of feedback. Lastly, we note that even when plant–soil feedbacks do exert changes in invasion velocity, these changes are small in comparison with those resulting from changes in invader fecundity (λ) or dispersal (m).

Our results were robust to the specific functional form of the feedback $b(N)$. With the alternative thresholding feedback function (eqn 4), negative feedbacks did not influence invasion speed in simulations with a wide range of thresholds (Fig. 3b). Even for invaders with a low threshold cover ($c = 0.10$), feedbacks stronger than +0.5 were required to influence invasion velocity (Fig. 3b).

Should empirically documented plant–soil feedbacks influence invader spread and density?

To compare the conditions under which plant–soil feedbacks influence invasion rates in our models to empirical plant–soil feedback studies, we quantified the distribution of feedback magnitude and direction in the empirical literature. We reviewed experiments comparing exotic plant performance on uninvaded soils to performance on soils modified by prior exotic plant occupation or inoculated with the soil microbial community cultivated by the exotic plant. This review yielded 56 experiments from eight studies (Bever
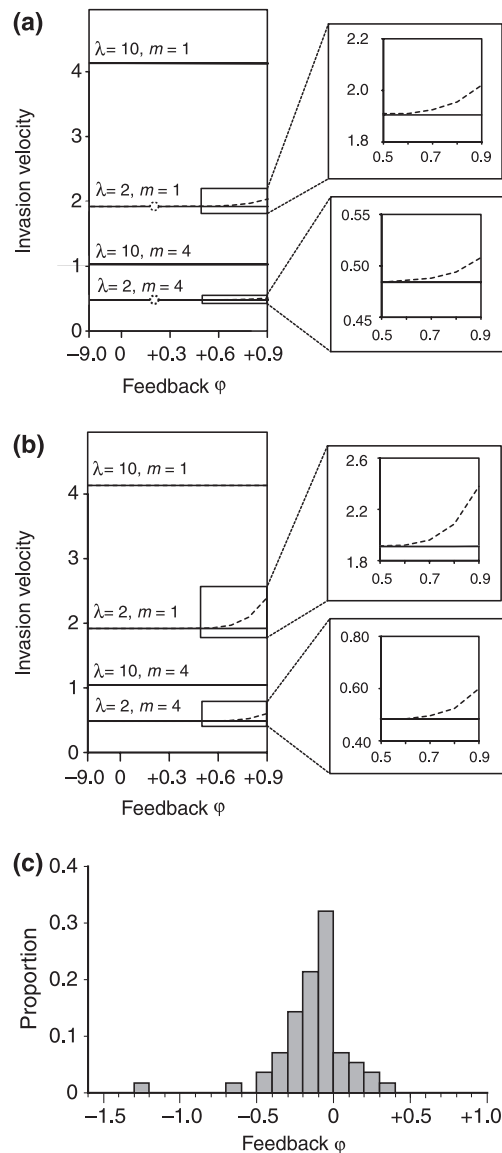

Figure 3 Relationship between plant–soil feedbacks and invasion velocity (m/year) in model simulations. (a) Feedbacks rise continuously with density, or (b) exert in full but only after a threshold invader cover is reached. λ is the intrinsic growth rate of the invader, and m is the parameter from a negative exponential dispersal kernel. In (a), $a = 0.01$, and the dashed, solid black, and solid grey lines correspond to $b = 10a$, $b = a$, and $b = \frac{a}{10}$, respectively, though the grey line is hidden by the black. The points correspond to the minimum feedback violating eqn 6 for the case where $b = 10a$ and $\lambda = 2$ (for the other parameter combinations, that minimum violating feedback $\geq +1$). In (b), the dashed, solid black, and solid grey lines correspond to threshold covers (aN) of 0.1, 0.5 and 0.9, respectively, though the grey line is hidden by the black. Note the different scales of the negative and positive x-axis. (c) Histogram of empirically documented feedbacks observed for exotic plants.

1994, Westover & Bever 2001, Bever 2002, Klironomos 2002, Reinhart *et al.* 2003, Reinhart & Callaway 2004, Callaway *et al.* 2004a,b), though more than half of the experiments came from one large study (Klironomos 2002). In cases where the feedback was not calculated as explained in the 'Growth and Feedback Functions' section, we calculated φ ourselves. Note that the empirical studies typically measured exotic plant biomass. We thus assume that changes in biomass are comparable with changes in fecundity when comparing the fecundity-based feedbacks in our model to those in the empirical literature, a good assumption for annual plants (Rees & Crawley 1989).

Our simulations showed that even when we accept the unlikely case where low fecundity ($\lambda = 2$), annual invaders modify the soil environment to exert feedback φ over an area 10 times greater than that which they occupy ($b = 10a$), positive feedbacks stronger than +0.5 are still required to influence invasion velocity. Such feedbacks exceed the strongest documented empirically for exotic plants (Fig. 3c), suggesting that observed feedbacks should not influence the spread of an annual invader. Although our simulations and models suggest that empirically documented feedbacks are unlikely to affect annual invader spread, these same feedbacks can strongly affect invader density in their already occupied range (Fig. 4).

DISCUSSION AND FUTURE DIRECTIONS

Growing empirical evidence that invasive plants can modify the soil environment in ways that facilitate their own growth has raised the question of whether such feedbacks influence the spread of the invader (Ehrenfeld *et al.* 2001, Scott *et al.* 2001, Klironomos 2002, Lenz *et al.* 2003, Callaway *et al.* 2004a, Wolfe & Klironomos 2005). Answers thus far have been based largely on intuition, in that they did not involve a
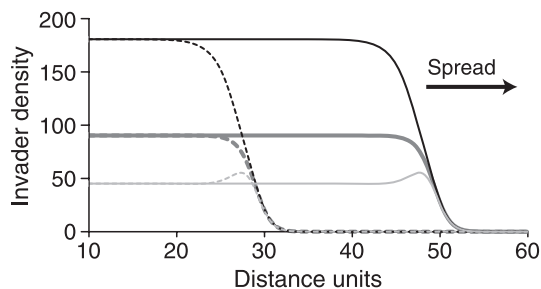
Figure 4 Simulated invasions with continuous density-feedback functions at 20 (dashed lines) and 30 years (solid lines) after the initiation of the invasion. Black, thick grey and thin grey lines correspond to invasion fronts produced with strong positive ($\varphi = 0.5$), no ($\varphi = 0$), or strong negative ($\varphi = -1$) feedbacks. $\lambda = 10$, $a = b = 0.1$ and $m = 4$, where m is the parameter from a negative exponential seed dispersal kernel.

formal connection between soil modification, plant fecundity, dispersal and invasive spread. The relatively simple models we examined here suggest that formalizing this connection is essential to predicting when feedbacks do or do not affect spread. In models of annual invaders moving though homogeneous environments, biologically reasonable plant–soil feedbacks did not influence the speed of the invasion. By the time local populations were established enough to significantly influence the soil environment, the invasion had spread to even further locations, where no soil modification has taken place. Nonetheless, as we hypothesize below, this general result might change with more realistic patchy landscapes, perennial invaders, and more complex dispersal, each of which generates important questions for future research.

Over what spatial and temporal scales do plant–soil feedbacks develop?

Our modelling results highlight the importance of understanding the spatial and temporal scales over which plant–soil feedbacks operate in order to predict their influence on the spread of invasions. Feedbacks did not affect spread in our models when invaders generated their empirically documented soil feedbacks over a spatial scale, *b*, comparable with or less than that over which they drew resources, *a*. That *a* and *b* are of comparable spatial scales is a reasonable first approximation for plant–soil feedbacks because the mechanisms of competition and the mechanisms of soil modification are both operating within the rhizosphere or plant canopy. Incorporating similar reasoning, empirical studies typically quantify feedbacks with invader modified soils collected directly underneath well-established individuals. Our work suggests that going a step further and better quantifying the spatial scales over which exotic plants modify the soil environment would be important for predicting feedback effects on spread. Indeed, for processes that allow positive feedbacks to be generated over much larger scales than those over which plants compete (e.g. feedbacks between fuel loading and fire), positive feedbacks should increase invasion rates.

We also assume that it takes time (one growing season) for plants to accumulate soil pathogens or mutualists, or modify soil biogeochemistry via soil inputs. This assumption is consistent with the underlying processes, and matches those made by empirical studies on plant–soil feedbacks. Studies quantifying feedbacks compare invader growth on soils previously cultivated by the invader to growth on uncultivated soils or soils cultivated by other species (Bever 1994, Klironomos 2002, Callaway *et al.* 2004a). Without a time lag in the development of plant–soil feedbacks, these studies would not find differing invader growth across soils with different plant compositional histories. In fact, some

empirical studies (Fig. 3c) use several generations of plant occupancy to modify the soil community. Nonetheless, some invader feedbacks may develop rapidly, and these are the ones most likely to influence spread. Similarly, spread might be affected by generalist soil biota present in the environment prior to invader arrival (as opposed to biota locally cultivated by invader-soil feedbacks). These points suggest that better quantifying the time course of feedback development in nature would greatly enhance our ability to predict the impact of such feedbacks on the spread of invasions.

The importance of understanding the rate at which feedbacks develop also emerges when applying our annual invader results to perennials. We focused on annuals because this life history characterizes many problematic invaders and is consistent with the assumptions of the integrodifference equation model we examined. Still, our results generate interesting hypotheses for perennial invaders. The main result of our annual model is that feedbacks fail to influence spread because invaders have already dispersed by the time local populations become established enough to experience the effects of soil modification. Via the same logic, the timing of seed production relative to soil modification should dictate the effects of feedbacks on the spread of perennial invaders. If perennials only experience the effects of soil modification once they are well established, and after they produce their first seed crops, we might expect their plant–soil feedbacks to be unimportant for spread. By contrast, if they modify the soil environment well before seed production, and soil modification affects early seed output, such effects may influence invasion velocity. How rapidly invaders modify soil biogeochemical cycles and microbial communities is not entirely clear, especially in relation to the time required to reach reproductive maturity. Nonetheless, because annuals take relatively little time to reproduce, we expect soil feedbacks to have greater effects on the spread of perennial invaders.

Competitive interactions with resident species

The feedback φ in our model very broadly describes the change in plant performance on invaded vs. uninvaded soils. The invader could be spreading through an unvegetated landscape such as a lava flow, or invading a landscape occupied by resident plants insensitive to invader-induced changes in the soil community. In the latter case, φ is interpreted as the difference in invader performance on soils modified by the invader vs. resident species. λ is the growth rate of the invader when it is rare and the residents are at equilibrium, prior to invader modification of the soil. Because we assume $\lambda > 1$, the invader is a superior competitor to the residents even before soil modification.

In order to examine cases where the resident species also grow differentially well on invaded and uninvaded soils, or the feedback causes the invader to switch from competitively inferior to superior, the more complex modelling approach developed by Bever (2003) could be incorporated. Bever has developed a powerful modelling framework incorporating competition between species and pairwise interactions between each species and soils they cultivate to examine coexistence and community structure.

Landscape structure and dispersal

One of the more important assumptions of the model we explored is that the landscape is spatially homogeneous. Our results thus best apply to the spread of invasive species within habitats that are relatively uniform in their suitability for invader growth. A large scale, real world example could be provided by yellow starthistle (*Centaurea solstitialis*) moving across the grasslands that dominate California.

Nonetheless, some of the most important questions for future research concern how feedbacks affect the spread of plant invaders in heterogeneous landscapes. This is especially true for invaders spreading through a network of suitable and unsuitable patches via rare, long distance dispersal events. Even if positive feedbacks do not increase the spread of such invaders within their local patches, they will elevate local density and seed production (as in Fig. 4). This greater production could in turn increase the likelihood that rare events move invaders the longer distance between suitable patches. Alternatively, those long dispersing seeds may still originate from recently colonized individuals at the front of the invasion, dispersed prior to feedback development. Quantitatively examining these alternatives will require spatial simulations more complex than those explored here, incorporating finite kernels (Clark *et al.* 2003).

CONCLUSIONS

Our work presents a quantitative framework for understanding how plant–soil feedbacks influence the spread of exotic plant invaders, one that places constraints on when empirically documented feedbacks can influence invader spread. This, however, does not preclude such feedbacks from being important at other stages of the invasion process. In fact, our models invariably show that feedbacks influence the density of invaders in their already occupied range. This result is consistent with other theoretical work on plant–soil feedbacks in communities in general (Bever 2003), and is consistent with the suggestion that such feedbacks may regulate the dominance and impact of invaders on native plant communities (Klironomos 2002, Callaway *et al.* 2004a). More generally, our results encourage better integrating

theory on the spread of biological invasions with leading empirical questions in the discipline (Kot *et al.* 1996, Neubert & Parker 2004). Doing so will allow researchers to connect what have been largely greenhouse studies of plant–soil feedbacks with invasion processes that are dynamic in natural settings. Because this connection proves theoretically complex, our work also emphasizes the need to examine plant–soil feedbacks in the context of other ecological interactions and demographic processes.

ACKNOWLEDGEMENTS

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APPENDIX

In this section, we first show that the invasion velocity for our model linearized about zero is independent of the feedback term *h*. We then use results from Weinberger *et al.* (2002) to find the conditions under which the asymptotic expansion speed of the model is the same as that of its linearization, meaning that speed is independent of the feedback. These conditions are more easily solved by letting $L_{t+1}(x) = N_t(x)$. Therefore, $F_t(y) = h[L_t(y)]$, and the system of eqn 1 from the text can be equivalently expressed:

$$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y)g[N_t(y)]h[L_t(y)]\,\mathrm{d}y$$
$$L_{t+1}(x) = N_t(x) \tag{A1}$$

Let $n_t(x)$ and $l_t(x)$ be small deviations of $N_t(x)$ and $L_t(x)$ from the zero equilibrium. The linearization of this system about zero is

$$n_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y)[g'(0)h(0)n_t(y) + g(0)h'(0)l_t(y)]\,\mathrm{d}y$$
$$l_{t+1}(x) = n_t(x) \tag{A2}$$

Substituting in $g(0) = 0$ and $h(0) = 1$, which is true for our growth (eqn 2) and feedback (eqn 3) functions, leads to

$$n_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y)g'(0)n_t(y)\,\mathrm{d}y$$
$$l_{t+1}(x) = n_t(x) \tag{A3}$$

The speed of spread in this system is governed by the growth rate of $n_t(x)$, i.e. $g'(0)$, and does not include the feedback term *h*. Thus the linearized system advances at a speed independent of the feedback.

For systems with positive feedbacks, where *g* and *h* are monotonically increasing functions of *N* and *L* [with $g(0) = 0$ and $h(0) = 1$], the system of eqn A1 satisfies all conditions stated in Weinberger *et al.* (2002). It is a cooperative system because as $N_t(x)$ increases, $L_t(x)$ increases and as $L_t(x)$ increases $N_t(x)$ increases. In our formulation, this system also satisfies all necessary conditions stated in hypotheses 2.1 in Weinberger *et al.* (2002). In theorem 3.1, the authors state that if an additional condition

holds, then the spread rate is driven by invader growth rate when rare (i.e. it is linearly determinate). This condition, as applied to our model is $g(\tilde{N})h(\tilde{L}) \leq \lambda\tilde{N}$ for some special values of $\tilde{N}$ and $\tilde{L}$, where λ is the intrinsic rate of increase. Rather than deriving these specific $\tilde{N}$ and $\tilde{L}$, which depend on the dispersal kernel, we consider the stronger condition where $L = \frac{N}{\lambda}$:

$$g(N)h\left(\frac{N}{\lambda}\right) \leq \lambda N \quad \text{for all } N. \tag{A4}$$

This condition is stronger, and our results are conservative for predicting no effect of feedback, as long as the moment generating function for the dispersal kernel is bounded below by one. This condition holds for commonly used kernels including the negative exponential and Gaussian. If condition A4 holds, the asymptotic invasion speed of our system is equivalent to its linearization, i.e. independent of the feedback.

Notice that eqn A4 (eqn 5 from the text), a key condition for the invasion to be linearly determinate for a cooperative system, is similar to the linear conjecture of Weinberger (1982). It is often assumed that if such conditions hold, the invasion is pulled. This is important because to our knowledge, mathematical proofs for when our model with a negative feedback $\{h[N_t(x)]$ is not monotonically increasing$\}$ is linearly determinate do not currently exist. Thus, we make the assumption, and support it with simulation, that if condition A4 holds, the wave is linearly determinate, even with a negative feedback. Indeed, under these conditions, simulated invasion velocities (Fig. 3a) equaled those predicted for the linearization of our model, where, following Kot *et al.* (1996) and Neubert & Parker (2004):

$$\text{velocity} = \min_{s>0}\left\{\frac{1}{s}\ln\left[\lambda\frac{m^2}{m^2-s^2}\right]\right\}, \tag{A5}$$

where *s* is the term from the moment generating function $[M(s)]$ for a negative exponential dispersal kernel.

Next, we show how eqn A4 (eqn 5 from the text), including the growth and density-mediated feedback functions in eqns 2 and 3, respectively, yields expression 6 in the text. Substituting in eqns 2 and 3 into eqn 1 yields:

$$\left[\frac{\lambda N}{1 + aN}\right]\left[\frac{1}{1 - \varphi\left(\frac{b\frac{N}{\lambda}}{1+b\frac{N}{\lambda}}\right)}\right] \leq \lambda N \quad \text{for all } N. \tag{A6}$$

Rearranging gives

$$\varphi \leq \frac{a\lambda + abN}{b + abN} \quad \text{for all } N. \tag{A7}$$

Given a maximum possible φ of 1, condition A7 can only constrain φ if

$$\frac{a\lambda}{b} < 1. \tag{A8}$$

If A8 holds, condition A7 is most severe, meaning the right side of is smallest, when N is near zero (the derivative with respect to N of the right hand side of eqn A7 is always positive). With N near zero, condition A7 is:

$$\varphi \leq \frac{a\lambda}{b}. \tag{A9}$$