Species diversity reduces invasion success in pathogen-regulated communities

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The loss of natural enemies is thought to explain why certain invasive species are so spectacularly successful in their introduced range. However, if losing natural enemies leads to unregulated population growth, this implies that native species are themselves normally subject to natural enemy regulation. One possible widespread mechanism of natural enemy regulation is negative soil feedbacks, in which resident species growing on home soils are disadvantaged because of a build-up of species-specific soil pathogens. Here we construct simple models in which pathogens cause resident species to suffer reduced competitive ability on home soils and consider the consequences of such pathogen regulation for potential invading species. We show that the probability of successful invasion and its timescale depend strongly on the competitive ability of the invader on resident soils, but are unaffected by whether or not the invader also suffers reduced competitive ability on home soils (i.e. pathogen regulation). This is because, at the start of an invasion, the invader is rare and hence mostly encounters resident soils. However, the lack of pathogen regulation does allow the invader to achieve an unusually high population density. We also show that increasing resident species diversity in a pathogen-regulated community increases invasion resistance by reducing the frequency of home-site encounters. Diverse communities are more resistant to invasion than monocultures of the component species: they preclude a greater range of potential invaders, slow the timescale of invasion and reduce invader population size. Thus, widespread pathogen regulation of resident species is a potential explanation for the empirical observation that diverse communities are more invasion resistant.

The loss of pathogens, herbivores and predators is commonly believed to underlie the success of some exotic plant species in their introduced range (the enemy release hypothesis: Elton 1958, Keane and Crawley 2002, Mitchell and Power 2003, Torchin and Mitchell 2004, Theoharides and Dukes 2007). However, if the loss of natural enemies is presumed to cause unregulated population growth, this implies that native species normally experience natural enemy regulation. This contrasts with the prevailing view of many plant community ecologists who have traditionally emphasised resource-based mechanisms of coexistence (Tilman 1982, Grime 2001, Tilman et al. 2001, Cardinale et al. 2007).

Recent empirical work has shown that native plant species often suffer from negative soil feedbacks, a type of density-dependent regulation imposed by species-specific soil herbivores and pathogens (van der Putten et al. 1993, Bever 1994, Klironomos 2002, De Deyn et al. 2003, Bartelt-Ryser et al. 2005, Kardol et al. 2006). After a given plant species occupies a site for some time, specialist soil pathogens accumulate and reduce the performance of conspecific plants in subsequent generations – a type of Janzen-Connell effect (Janzen 1970, Connell 1971). The strength of these feedbacks is usually measured by comparing the performance of individuals on soils formerly occupied by the same species (home sites) or on soils formerly occupied by other species (away sites). Negative feedbacks have been reported from a variety of communities and vary considerably in strength (Kulmatiski et al. 2008). For example, in field-trained soils, Petermann et al. (2008) found that species from three different functional groups only achieved half the biomass on home soils versus away soils when grown in competition with other functional groups, although others have found weaker effects (Engelkes et al. 2008). Thus, pathogen regulation – in the form of negative soil feedbacks – is sufficiently widespread to warrant serious consideration as an alternative to resource-based mechanisms of coexistence (Kulmatiski et al. 2008, Petermann et al. 2008).

Invasive plants in their introduced range have often been found to suffer weaker negative soil feedbacks than their native competitors, suggesting that a lack of regulation by soil pathogens could be critical to their success (Klironomos 2002, Callaway et al. 2004, but see Beckstead and Parker 2003, Eppinga et al. 2006). For example, some have argued that freedom from negative feedbacks aids expansion of species into new territory (van Grunsven et al. 2007, Engelkes et al. 2008, Menendez 2008, but see Levine et al.

2006, Eppstein and Molofsky 2007). However, because invaders must begin from low population density where home-site encounters are rare, we hypothesise that freedom from negative feedbacks is unlikely to increase the probability of successful invasion. We instead believe that the key ingredient to successfully invading resident communities is good competitive ability on resident soils.

We also hypothesise that soil pathogen regulation might interact with resident species diversity to influence invasion success. If negative feedbacks act on resident species then monocultures are likely to be particularly susceptible to invasion: in monocultures, resident species only encounter home sites where their performance is weakest. In contrast, in diverse communities, each resident species provides away sites on which the remaining residents can compete strongly; hence resident species in diverse communities largely avoid negative soil feedbacks. We might therefore expect that an invader would find it more difficult to invade diverse pathogen-regulated communities. This is consistent with a large body of empirical evidence showing that more diverse communities are indeed more difficult to invade (Knops et al. 1999, Naeem et al. 2000, Hector et al. 2001, Fargione et al. 2003, van Ruijven et al. 2003, Levine et al. 2004). While such results are usually attributed to more complete resource use in diverse communities, the role of soil feedbacks in explaining these patterns has not been explored.

Here we use simple models to explore the requirements for successful invasion when the resident plant community is regulated by negative soil feedbacks. We focus on simulation models because analytical solutions for multi-species systems are difficult, although we do provide analytical support for our invasion conditions (for a detailed theoretical treatment of the two-species case see Eppstein and Molofsky 2007). We first examine the impact of changing the strength of the negative feedback experienced by the invader on its probability of invasion, its rate of population increase and its equilibrium abundance. Second, we consider the effect of changing resident diversity on these same three measures of invasion success.

Methods and results

We consider invasion into a community of 100 000 sites each occupied by a single adult plant, whose dynamics are governed by a weighted lottery (Chesson and Warner 1981). Each year all plants in the community produce the same number of seeds, suffer the same probability of mortality ($d_i = 0.2$) and compete for the sites vacated by the death of adults. The proportion of newly-vacated sites won by a given species is proportional to the product of its relative abundance in the community and its competitive ability, α. The value of α varies between the invader (denoted by an i subscript) and the resident (denoted by an r subscript) and between home and away soils, generating four values: $\alpha_{i, home}$, $\alpha_{i, away}$, $\alpha_{r, home}$, $\alpha_{r, away}$. Sites thereby carry a memory of the former occupant which influences future competitive interactions on that site. Based on the findings of Petermann et al. (2008), we assume that pathogen-driven negative soil feedbacks reduce competitive ability by half on home soils.

Thus, for all simulations, we arbitrarily set the competitive ability of the resident species on away soils, $\alpha_{r, away}$ to be 0.4, and the competitive ability of the resident species on its home soil to exactly half this value, $\alpha_{r, home} = 0.2$ To examine the influence of invader competitive ability on its success, we varied invader performance on away soils, $\alpha_{i, away}$ over the interval 0.15–0.85 in steps of 0.05. To examine the effects of negative feedbacks on invader success, the invader either experienced no negative soil feedback: $\alpha_{i, home} = \alpha_{i, away}$ or, the invader suffered the same magnitude of negative soil feedback as the residents: $\alpha_{i, home} = 0.5 \, \alpha_{i, away}$.

For simplicity, dispersal is global, meaning that the chance of a given species winning a site is a function of its proportion in the community at large, not its local proportion. Strongly limited dispersal would undoubtedly affect model outcomes (Eppstein and Molofsky 2007); however, we previously found that results were unaffected by the inclusion of local dispersal as long as > 50% of the seeds produced by each parent disperse away from the parent site (Petermann et al. 2008). All invasions were initiated with 16 invader individuals (~ 0.02% of the community). For each implementation of the model we recorded 1) whether or not the invasion succeeds; 2) the number of generations required for the invader to reach 1000 individuals (1% of the total community) and 3) the final population size of both the resident and the invader. An invasion is judged successful if at least one individual remains 2000 generations after introduction. For any given set of parameters, we performed 1000 repeated runs from identical starting conditions.

Invasion into a system with a single resident species

In a monoculture, all sites initially consist of home sites for the resident, while a rare invader initially encounters only away sites. As a consequence, whether or not the invader itself possesses a negative feedback has a negligible effect on its probability of successful invasion or the time required to reach 1000 sites (Fig. 1a–b). Of much greater importance is the invader's general competitive ability ($\alpha_{i, away}$), which strongly increases its probability of success (Fig. 1a) and decreases the time required to reach 1000 individuals (Fig. 1b).

However, should the invader satisfy the condition for successful invasion, the equilibrium population size of the invader is much larger when the invader lacks its own negative feedback (Fig. 1c). The equilibrium abundance of the invader is determined by the relative competitive abilities of the invader and the resident on home and away soils (Fig. 1c). For $0.2 < \alpha_{i, away} < 0.4$ the two species coexist, even when the invader lacks soil pathogen regulation; although without soil pathogen regulation the invader is more abundant than the resident. Similarly, an invader without soil pathogen regulation can exclude the resident when $\alpha_{i, away} > 0.4$ because it can outcompete the resident on both home and away sites (the resident's competitive ability never exceeds 0.4). However, a pathogen-regulated invader requires a higher minimum competitive ability on resident soils to exclude the resident, $\alpha_{i, away} > 0.8$. All of these thresholds can be analytically derived for this model, as shown below.
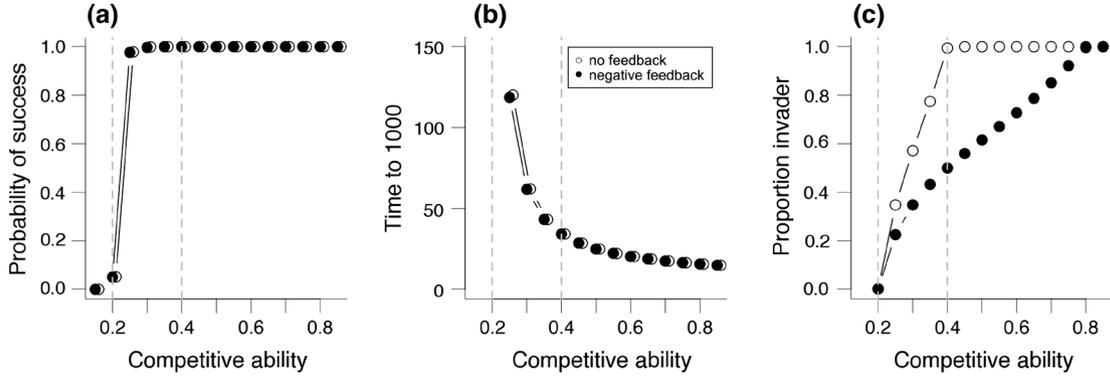
Figure 1. Success of an invader with and without a negative soil feedback and with different competitive abilities on 'away' soils. The probability that the invasion succeeds (a) the time-scale of successful invasion (b) and the proportion invader should the invasion succeed (c) are shown. Dashed lines show the competitive ability of the single resident species on home (0.2) and away soils (0.40). All values are calculated from 1000 repeated runs. The invader population size was calculated 2000 generations after introduction using data from successful invasions only (success constitutes >1 individual after 2000 generations). The timescale is the number of generations required for the invader to reach 1000 individuals.

Analytical conditions for invasion and impact

The simulation results are supported by analytical equations describing the same dynamics but over an infinitely large number of sites. The proportion of sites occupied by the invader, p_i, changes from one time step to the next as follows:

$$p_{i,t+1} = (1-d)p_{i,t} + d\left[p_{i,t}\frac{\alpha_{i,home}p_{i,t}}{\alpha_{i,home}p_{i,t} + (1-p_{i,t})\alpha_{r,away}} + (1-p_{i,t})\frac{\alpha_{i,away}p_{i,t}}{\alpha_{i,away}p_{i,t} + (1-p_{i,t})\alpha_{r,home}} \right] \quad (1)$$

The first term of the sum describes the proportion of invader individuals surviving over the time step, while the second term is the proportion of newly-vacated sites subsequently filled by the invader. The proportion of newly-vacated sites filled by the invader is a weighted average of dynamics on sites that were formerly occupied by the invader (the first term of the bracketed sum) and dynamics on sites formerly occupied by the resident (the second term of the bracketed sum). The invader wins sites in proportion to the product of its abundance and competitive ability, relative to the product of these values for the resident.

To obtain the condition for the invader to increase from rarity, we divide both sides of Eq. 1 by $p_{i,t}$, yielding the per capita growth rate for the invader:

$$\frac{p_{i,t+1}}{p_{i,t}} = (1-d) + d\left[p_{i,t}\frac{\alpha_{i,home}}{\alpha_{i,home}p_{i,t} + (1-p_{i,t})\alpha_{r,away}} + (1-p_{i,t})\frac{\alpha_{i,away}}{\alpha_{i,away}p_{i,t} + (1-p_{i,t})\alpha_{r,home}} \right] \quad (2)$$

When the invader is rare, $p_{i,t}$ is near zero, simplifying the growth rate to:

$$\frac{p_{i,t+1}}{p_{i,t}} = (1-d) + d\left[\frac{\alpha_{i,away}}{\alpha_{r,home}} \right] \quad (3)$$

For the invader to increase when rare, this growth rate must exceed one, and simplifying yields the invasion condition:

$$\alpha_{i,away} > \alpha_{r,home} \quad (4)$$

Thus, the invader can successfully increase when rare if it can outcompete the resident on the resident's home soil. Importantly, condition 4 does not contain $\alpha_{i,home}$ and hence a negative soil feedback for the invader will not affect its probability of successful invasion or its dynamics when rare (Fig. 1a–1b). Condition 4 also explains why the threshold for successful invasion in the simulations is $\alpha_{i,away} > 0.2$ (as $\alpha_{r,home} = 0.2$ in the simulations).

Equations 1–4 above can also be used to describe the dynamics of the resident species by switching the i and r subscripts. We can thus derive the condition for the resident to persist with the invader (as the resident must also be able to increase when rare). This reveals that the resident can increase when rare as long as $\alpha_{r,away} > \alpha_{i,home}$. Thus the invader can displace the resident in our simulations when $\alpha_{i,home} > 0.4$. Notice that, this requires $\alpha_{i,away} > 0.8$ if the invader possesses the same negative feedback as the resident ($\alpha_{i,home} = 0.5\,\alpha_{i,away}$); however if the invader does not possess a negative feedback, displacement of the resident occurs when $\alpha_{i,away} > 0.4$ (Fig. 1c).

Invasion into more diverse communities

It is clear from above that monocultures are particularly susceptible to invasion because all sites are home sites for the resident. However, if the resident community contains more than one species, each suffering from its own specialist soil pathogens, then a greater fraction of newly-vacated sites are away sites for each of the resident species. To evaluate the effect of resident species diversity (D) on invasion success,

we simulated models containing 1, 2, 4, 8 and 16 resident species. In each case, we assumed that all resident species have exactly the same competitive ability on away soils: $\alpha_{r,\,away} = 0.4$, and that they all suffer a negative soil feedback of the same magnitude: $\alpha_{r,\,home} = 0.2$. We further assume that each resident species has its own unique soil pathogens; thus, for each resident species, sites formerly occupied by any other resident species are classified as away sites. This strongly stabilizes dynamics such that residents would coexist indefinitely and at identical abundances were it not for the finite community size.

In our multi-resident simulations, all resident species begin at equal abundance, and are given 500 generations of dynamics prior to the introduction of the invader to 16 sites taken equally from among the resident species. We varied the competitive ability of the invader on away soils over the interval 0.20 to 0.50 in steps of 0.025. We use a narrower interval with finer gradations than in the previous simulations, as it is clear that once $\alpha_{i,\,away} > 0.4$ the invader is a better competitor than all members of the resident community ($\alpha_{i,\,away} > \alpha_{r,\,home}$). We only consider the case where the invader also suffers from a negative soil feedback, which again, is identical in magnitude to that of the residents ($\alpha_{i,\,home} = 0.5\,\alpha_{i,\,away}$).

As hypothesized, increasing resident diversity increases the minimum competitive ability required for successful invasion (Fig. 2a), increases the time-scale of the invasion (Fig. 2b) and reduces the population size of successful invaders (Fig. 2c). The minimum competitive ability on resident soils required for successful invasion increases asymptotically with increasing resident diversity (Fig. 3a), so the largest change is seen when moving from a monoculture to a two-species mixture and each additional resident species has an increasingly small effect (we demonstrate this point analytically below). We therefore predict that weaker competitors are precluded from invading more diverse mixtures, even though they can invade monocultures of all the constituent species. For any given invader, the final population size also declines monotonically with increasing resident species diversity (Fig. 3b), although the time to reach 1000 individuals (the growth rate when rare) increases linearly with species diversity (Fig. 3c). Thus, the different components of invasion success scale differently with increasing resident diversity.
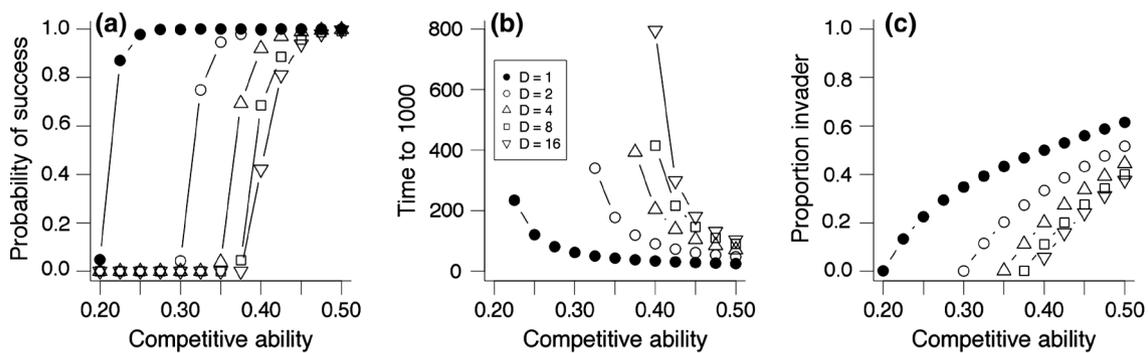
The effects of resident species diversity on invasion success can be shown analytically. If the community contains D resident species, each with identical competitive abilities on home and away soils, then resident species on average have equal abundance; hence each resident species will hold 1/D of the sites not occupied by the invader. Thus, on newly-vacated resident sites, 1/D of the colonizing residents have competitive ability given by $\alpha_{r,\,home}$ and (D-1)/D of the colonizing residents have competitive ability given by $\alpha_{r,\,away}$. We thus replace the resident performance in the second term of the bracketed sum in Eq. 1 with the following:

$$(1-p_{i,t})\left[\frac{\alpha_{i,away}}{\alpha_{i,away}p_{i,t}+\left(\frac{1}{D}\right)(1-p_{i,t})\alpha_{r,home}+\left(\frac{D-1}{D}\right)(1-p_{i,t})\alpha_{r,away}}\right] \quad (5)$$

The condition for the invader to increase when rare now becomes:

$$\alpha_{i,away} > \alpha_{r,away}\left(\frac{D-1}{D}\right)+\alpha_{r,home}\frac{1}{D} \quad (6)$$

Condition 6 reveals that the invader's competitive ability on away soils must exceed a weighted average of the residents' competitive abilities on home and away soils. With D = 1 (a monoculture), the first term of the sum disappears and we return to condition 4. As diversity (D) increases, the second term of the sum decreases, and because $\alpha_{r,\,away} > \alpha_{r,\,home}$, invasion becomes more difficult. Also notice that the greatest decrease in the weighting of $\alpha_{r,\,home}$ (and hence the greatest change in invasion resistance) occurs when D goes from 1 to 2, matching simulations in Fig. 2a and 2b.

Discussion

The loss of natural enemies has often been implicated in the success of exotic species in their introduced range (Keane and Crawley 2002) while the inevitable corollary – that plant populations normally experience natural enemy regulation in their native range – has been largely overlooked. One possible general mechanism for this regulation

Figure 2. Success of an invader introduced into resident communities of different species diversity (D = 1, 2, 4, 8, 16). The resident species always have the same competitive ability on away soils (0.4) and on home soils (0.2). The probability that the invasion succeeds (a) the time-scale of successful invasion (b) and the final abundance of the invader (c) are shown.
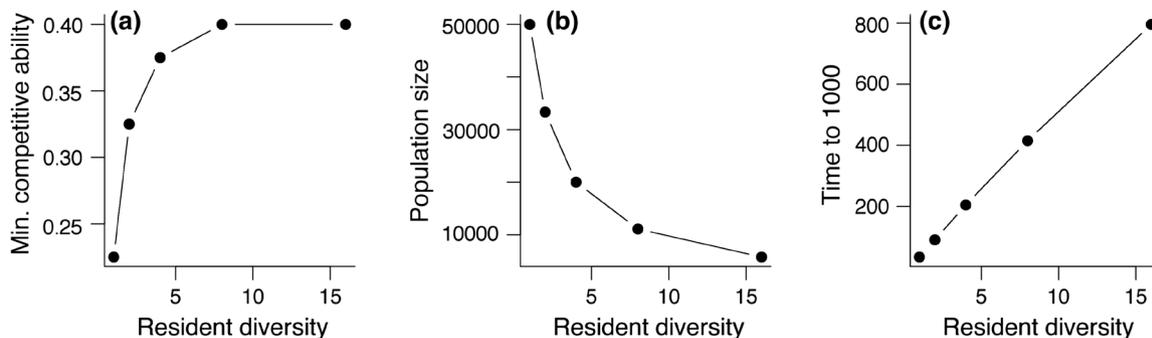
Figure 3. The relationship between resident diversity and the minimum competitive ability required for successful invasion (a). For an invader with exactly the same properties as the resident species, the population size of the invader (b) and the time required to reach 1000 individuals (c) are also shown.

is negative plant-soil feedbacks, where species are disadvantaged on previously-occupied or home sites, analogous to the Janzen-Connell effect. There is widespread empirical evidence for species-specific negative soil feedbacks within plant communities, including evidence that exotic species experience weaker negative feedbacks than native species (Bever 1994, van der Putten and Peters 1997, Klironomos 2002, Bartelt-Ryser et al. 2005, Bonanomi et al. 2005). Several authors have therefore suggested that release from negative feedbacks may allow species to become invasive (van Grunsven et al. 2007, Engelkes et al. 2008).

We used a simple modelling approach to evaluate the potential benefit of escaping regulation by specialist soil pathogens. We found that the loss of a negative soil feedback has no influence on whether or not a given species is able to invade a resident community. Freedom from negative soil feedbacks alone cannot, therefore, allow a species to expand its range or enter new communities. Instead, the probability of successful invasion depends strongly on the competitive ability of the invader on resident soils. This is because, at the start of an invasion, the invader is at low density and so it mainly encounters resident sites. While limited dispersal inevitably changes this outcome to some degree (Bolker and Pacala 1999, Eppstein and Molofsky 2007), it seems unlikely that an invader will be successful if it cannot compete strongly against the residents on resident soils. Invader competitive ability on resident soils is also the primary determinant of the invader growth rate when rare; hence increased competitive ability on away sites also leads to more rapid invasion.

In contrast, if all resident species are affected by a generalist soil pathogen to which an invader is immune (a different form of enemy release), then this could give an invader a competitive advantage on resident soils. Hence, this type of enemy release could increase the probability of invasion success; however, in this case the invader has become successful, not through the loss of regulation, but rather because it has acquired a large fitness differential with respect to resident competitors. Such an effect would be better quantified by comparing the competitive ability of residents versus the invader on sterilised and non-sterilised soil from the introduced range. Notice that in this case we are assigning a rather different role to pathogens in native communities, instead of being species-specific and provid-

ing regulation and stabilisation, they have an equalising role by having a general negative effect on all residents (Chesson 2000). A similar effect is proposed to occur if species lose specialist pathogens or herbivores and as a result are able to evolve increased competitive ability – the EICA hypothesis (Blossey and Notzold 1995).

Invaders freed from negative soil feedbacks tend to achieve higher population densities once successful and are more likely to exclude resident species (Levine et al. 2006, Eppstein and Molofsky 2007). Exclusion of residents is still possible when the invader possesses pathogen regulation, should the invader compete strongly enough on all soil types; however, without pathogen regulation, the invader can reach higher abundance than the resident despite being a poorer competitor on away soils. Comparisons of performance on 'average' soil, compost mixes, or even the invader soil, would therefore be unrevealing. This emphasises the need for carefully controlled experiments on different soil types. Notice that although we used a strong feedback for our simulations, weak negative feedbacks give qualitatively similar results.

Monocultures of resident species which suffer negative soil feedbacks are particularly susceptible to invasion. In a monoculture, all sites are home sites for the resident, reducing the resident's average competitive ability across all available sites. Increasing resident diversity increases community resistance because many of the available sites are now away sites for each of the resident species. This raises the collective competitive ability of the resident community and makes the system more difficult to invade. Increasing resident diversity has diminishing returns; an asymptotic relationship emerged between resident diversity and invader establishment probability. In our models, resident species have identical characteristics, so that the increased invasion resistance of diverse communities is not due to a 'selection' effect by which mixtures are more likely to include species with particularly high resistance to invaders (Loreau and Hector 2001). Thus, a species which cannot invade a diverse mixture could potentially invade monocultures of all the constituent species.

The literature on invasion success in experimental manipulations of biodiversity reveals several patterns consistent with our results. First, the number of invading species and total invader biomass decrease with resident diversity in a non-linear way (Tilman 1997, Knops et al. 1999, Naeem

et al. 2000, Hector et al. 2001, Fargione et al. 2003) and second, several biodiversity experiments report that monoculture performance often declines with time (Pfisterer et al. 2004, Fargione et al. 2007). Although pathogens have not been directly implicated in either of these results, our models suggest that they could play some role. Many biodiversity experiments also reveal that functional group diversity is as important as species diversity in determining ecosystem functioning (Tilman et al. 1997, Hector et al. 1999, Hooper and Dukes 2004, Spehn et al. 2005). Although our models assumed that species possess unique pathogens, such results could be explained if species within the same functional or taxonomic group share pathogens (De Deyn et al. 2003, Gilbert and Webb 2007). For example, the increasing success of phylogenetic distance in explaining a variety of ecosystem performance measures (Cadotte et al. 2008) could also be attributed to pathogens that cross-infect closely-related hosts, as could the observation that species are more successful in invading communities from which their own functional group is absent (Fargione et al. 2003, Turnbull et al. 2005).

Plant ecologists have tended to overlook natural enemies in favour of resource-based explanations for community dynamics and structure (Harpole and Tilman 2007). However, a considerable body of evidence now demonstrates that pathogens, although often unseen, can have large and predictable effects on resident fitness (van der Heijden et al. 2008). Negative soil feedbacks in particular can act in a frequency-dependant manner to promote diversity (Bever 2003) and, as we have shown here, could also endow diverse pathogen-regulated communities with increased invasion resistance.

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