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Coexistence, saturation and invasion resistance in simulated plant assemblages

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A popular hypothesis is that species-rich systems are less susceptible to invasion. This hypothesis is based on the idea that species richness correlates with community saturation so that establishment by a new species is more difficult in saturated communities. Little attention has been focussed on how changing assumptions about the processes regulating species richness will alter community properties such as invasion resistance. Here, we simulate plant community assembly using four models that have different underlying coexistence mechanisms (and so differ in the amount of available niche space) and subject them to invasion. We created species richness gradients by comparing between models or by considering the output of a single model with different parameter values. We found that the relation between species richness and invasion resistance depends critically on the model considered and the cause of the species richness gradient. Overall, our results suggest that species richness does not necessarily correlate with saturation and is likely to be a poor predictor of invasion resistance. These results provide a possible explanation for the variety of outcomes reported in recent experimental and observational studies that examine the relationship between species richness and invasion resistance. We conclude that consideration of the processes regulating species richness is crucial for a successful understanding of invasion resistance along species richness gradients.

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What processes and attributes determine the success of an invading species? Historically, the focus has centred on the attributes of the introduced species, but it is increasingly acknowledged that the attributes of the community into which species are introduced are also important (Fox and Fox 1986, Crawley 1987, Lodge 1993, Williamson 1996, Prieur-Richard and Lavorel 2000). Important factors likely to affect the outcome of invasion include, the abundance of natural enemies, competitors and mutualists in the new environment (Crawley 1987), the disturbance regime (Crawley 1987), unutilised resource availability (Davis et al. 2000) and propagule supply (Levine 2000).

A significant amount of both theoretical (Rummel and Roughgarden 1985, Case 1990, Gilpin 1994, Morton et al. 1996) and empirical (Crawley 1987, Robinson et al. 1995, Burke and Grime 1996) attention has focussed on how plant communities or assemblages develop resistance to invasion as a community attribute. In particular, work has concentrated on the search for relationships between species richness and invasibility. The idea is that more species rich assemblages have most niches occupied and are thus more saturated and difficult to invade. In contrast, little attention has been paid to the effect that different mechanisms of coexistence acting within

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a community may have on properties such as invasion resistance.

We propose that the underlying assumption that more species rich systems are more saturated with species is likely to be false if the processes that regulate species richness differ from assemblage to assemblage. Therefore the hypothesised relationship between species richness and invasion resistance is also unlikely to hold if comparisons are made between different assemblages. Indeed, it seems likely that some species rich systems may be more invasible than species poor systems.

The hypothesis that species rich systems are more resistant to invasion rests primarily on the apparent susceptibility of islands to invasion (Elton 1958, Williamson 1996; see also Lodge 1993) as well as theory based on saturating models of coexistence (Case 1990, 1995, Kokkoris et al. 1999). Island susceptibility to invasion is normally attributed to their reduced species richness relative to similar mainland communities, which is due to the limited colonisation opportunities on islands. As such, island communities are considered to be unsaturated, with many vacant niches. Similar logic has been applied to species-poor assemblages in general. However, it is not clearly established that mainland species-poor systems are correspondingly empty. Low species richness may also be due to competitive dominance of only a few species rather than a lack of species to occupy empty niches. For example, decreased diversity in high grasslands is attributed to the competitive dominance of a few species mediated by increased productivity and competition for light, which results in the exclusion of low growing species (e.g., Milberg 1992, Mountford et al. 1993, Mitchley et al. 1996, Crawley 1997, Kleijn and Snoeijing 1997, Foster and Gross 1998).

Theoretical support for the hypothesis that species richness confers invasion resistance rests on coexistence models that saturate with increasing species richness, particularly those based on the Lotka-Volterra competition equations (Case 1990, Kokkoris et al. 1999). A classic feature of these model communities is that as species richness increases they become increasingly saturated. Case (1990) has shown that randomly assembled Lotka-Volterra systems show increased resistance to invasion from species with parameters chosen from the same range as species richness increases. However, Lotka-Volterra models describe a very particular view of nature. Empirical studies (Rees et al. 1996, Hubbell et al. 1999) and theory developed to provide mechanisms for coexistence (Tilman and Pacala 1993, Bengtsson et al. 1994, Palmer 1994, Pacala 1997) all suggest that species richness can be maintained by a variety of mechanisms, many of which are not captured by simple Lotka-Volterra models. Many processes have been postulated to facilitate coexistence both at the level of competitive interactions (Pacala 1986, Chesson 1994, Huston and DeAngelis 1994, Loreau 1996) and incorporating different processes such as herbivory and other higher trophic level interactions (Holt 1977, Crawley 1983, Jeffries and Lawton 1984) as well as regional processes and patch dynamics driven by colonisation and extinction (Hastings 1980, Shmida and Wilson 1985, Pulliam 1988, Holt 1993, Loreau and Mouquet 1999). More detailed models to represent these different mechanisms of coexistence have been developed. Models focussed on competitive interactions include additional processes such as spatial (or temporal) segregation, recruitment limitation or trade-offs between competitively important attributes. Many of these coexistence mechanisms do not lead to saturated communities or assemblages; indeed in many of the models there are no theoretical limits to species richness (Cornell and Lawton 1992, Tilman 1999, Loreau 2000). Therefore, previous conclusions on the vulnerability of communities to invasion based on standard Lotka-Volterra models may be inappropriate when applied to many real assemblages.

Species richness in natural plant communities may be affected by changes in the following factors: species identity, adaptive history of the regional species pool, environmental conditions and the mechanisms of coexistence. Here, we use two methods to generate species richness gradients in simulated plant assemblages.

The first method alters the underlying model of community interactions, and so changes in species richness reflect a fundamental change in the way species interact and coexist in a community. We represent these changes by altering the underlying assumptions describing the interactions between species. Changing these assumptions can result in a change in the total amount of niche space available and hence the maximum number of species that can coexist. Hence, using different models we can simulate assemblages of the same species richness but differing in saturation.

The second method is to alter the parameters within a model and represent those cases in which changes in species richness can be attributed to changes in species adaptive history or the environmental conditions under which the community is assembled. Examples include changing the size of the regional species pool, the level of resource availability or the maximum fecundity of the species. This variation can be modelled by changing parameters within a given model structure and does not require changing assumptions about how the species interact.

In this paper, we examine the effect of changing assumptions about what determines coexistence on the invasion resistance of model communities. The effect of different mechanisms of coexistence on ecosystem properties, such as productivity, have been discussed in a separate paper (Mouquet et al. unpubl.). We use models based on previously published models of coexistence to simulate community assembly and invasion. We use these models to examine the relationship between species richness and invasion resistance. In addition, we compare the effect of changes in species richness on invasion resistance when the changes are driven by model changes or parameter changes.

We focus on two coexistence mechanisms that regulate species richness in different ways; the competition-colonisation trade-off (Tilman 1994) and resource heterogeneity in the environment (Pacala and Tilman 1994, Hurtt and Pacala 1995). For both mechanisms we consider the case when recruitment is limiting and also the case when recruitment is effectively infinite to give four models in all. These models are described in detail below.

Methods

Models of assembly and invasion

Mechanistic lottery models are often used to model spatially structured systems in which competition for vacant sites (each of which can contain a single individual) occurs between juveniles. Early models assumed that species compete through a recruitment process where each site is allocated in proportion to the number of propagules of each species (Sale 1977, Skellam 1991). These models have been extended to incorporate more elaborate kinds of competition in the recruitment process including recruitment limitation and spatial variation in the suitability of sites (e.g., Chesson 1985, Pacala and Crawley 1992, Pacala and Tilman 1994, Hurtt and Pacala 1995). These models are readily simulated and have been extensively studied (e.g., Chesson and Warner 1981, Shmida and Ellner 1984, Armstrong 1989). Hence, they provide a useful framework into which a wide range of coexistence mechanisms can be incorporated.

General model

Consider an environment which consists of an infinite number of cells each of which can contain at most one adult. Competition occurs between juveniles to occupy cells made vacant by the death of an adult. If there are N plant species then

$$\Delta X_i = VG_i - d_i X_j \tag{1}$$

where, X_i is the fraction of cells occupied by species i at time t, d_i is the adult death rate of species i, ΔX_i is the change that occurs between the fraction of space occupied by species i between times t and $t+1$, V is the amount of free space and G_i is the probability that a propagule of species i successfully establishes in an unoccupied cell. The amount of free space has two components; those cells just vacated ($\Sigma\, d_i X_i$) and those cells that have been unoccupied for more than a single time step ($1 - \Sigma\, X_i$). Hence,

$$V = \sum d_i X_i + 1 - \sum X_i. \tag{2}$$

In the analysis and simulations that follow we assume that death rate, d, is density independent and the same for all species. There is no age structure in any population, all individuals are assumed to reach reproductive age in a single time-step. We assume that dispersal is global, so that all seeds produced are pooled and then distributed with equal probability among cells. In this respect the models presented here are not spatially explicit.

It is through the recruitment process G_i that species compete. Different coexistence mechanisms are developed by altering the assumptions about the process driving recruitment and by altering the spatial heterogeneity of the system. Four scenarios are considered. Competition for a single limiting resource, a trade-off between competitive ability and fecundity, resource heterogeneity in the environment and resource heterogeneity in the environment with uniform recruitment limitation (referred to as the recruitment limitation model).

Single limiting resource (SLR)

This mechanism is included as an extreme case where coexistence is not possible. Consider a habitat that is homogeneous in which all species are competing for a single limiting resource. Let R_i be the level of resource R at which species i is the superior competitor. We assume that each species R_i value is chosen at random from a uniform distribution in the interval (0, 1). Using the results of Tilman (1982), we assume that the level of the resource in any cell is reduced to the level of the best competitor present in a cell. This species will consequently win the competition for recruitment into that cell. The best competitor is that species with the lowest R_i value. In addition, we assume that there is no recruitment limitation, that is, each species is guaranteed to disperse a propagule into every unoccupied cell in the habitat at each time-step. Hence, the recruitment function G_i is simply,

$$G_i = \begin{cases} 1.0 & \text{if } R_i = \min(R_1, R_2, \ldots, R_N), \\ 0.0 & \text{otherwise.} \end{cases} \tag{3}$$

It is clear that only one species will ever persist in the habitat and that the persisting species will be the one with the lowest R_i value.

Competition-colonisation trade-off (CC)

The competition-colonisation trade-off model is based on the assumption that there is a trade-off between allocation to biomass (root and/or shoot) that results in high competitive ability for resources and allocation to reproductive structures resulting in the production of an increased number of propagules. The environment is considered to be spatially homogeneous and species again compete for a single resource with the best competitor having the lowest R_i value. However, in this model, species are recruitment limited and so there is a finite probability that propagules of any particular species will not reach every cell. It is assumed that seeds are distributed as a Poisson process. This model is based on that of Hastings (1980) and Tilman (1994). However, in the model presented here competition occurs only for empty space relaxing the assumption in previous studies that juveniles can displace established individuals that are poorer competitors.

Let the species be ranked from 1 to N with species 1 being the best competitor (having the lowest R_i value). If more than one species attempts to colonise the same cell then the best competitor always prevails. Juveniles cannot displace adults of any species regardless of their competitive ability. With these assumptions,

$$G_i = \exp\left(- \sum_{j=1}^{i-1} F_j X_j \right)(1 - \exp(F_i X_i)) \tag{4a}$$

where

$$F_i = -F_{mn} \ln(1 - R_i); \quad R_i \in (0, 1], \tag{4b}$$

and F_{mn} is the asymptotic mean fecundity of all species in the assemblage. As F_{mn} tends to infinity, competitive species are no longer recruitment limited and this model collapses to the model of a single limiting resource described above.

Resource heterogeneity in the environment (RH)

This model focuses on resource heterogeneity as a mechanism to facilitate coexistence and is based on the approach of Pacala and Tilman (1994). Each species is assumed to be the best competitor for a particular level of resource availability. Hence, each species can be considered to have a different realised niche positioned along a spectrum of resource availability.

The environment of each cell is represented by a value H_k, which is chosen for each cell by a random draw from the uniform distribution over the interval (0,1). There is no correlation between the H_k values of different cells and the value does not change with time. A species is considered to be the best competitor for a cell with environment, H_k, if its R_i value is closest to the H_k value of the cell. If, in addition, we assume that there is no recruitment limitation, then $G_i = P_i$ where P_i is the probability that species i is the best competitor for a randomly chosen cell, and

$$P_i = \int_{\varphi_i} B(h)\, \mathrm{d}h, \tag{5}$$

where $B(h)$ is the probability density function of H_k and φ_i is the set over which species i is the best competitor. As R_i and H_k are uniformly distributed random variables over the interval (0, 1) then, for N species in the initial species pool,

$$G_i = \int_{\varphi_i} 1\, \mathrm{d}h = \varphi_i \tag{6}$$

and so

$$G_i = \begin{cases} \dfrac{3}{2(N+1)} & \text{if } R_i \text{ is closest to 0 or 1,} \\ \dfrac{1}{N+1} & \text{otherwise.} \end{cases} \tag{7}$$

It can be easily shown that equilibrium values for each species are given by $X_i^* = G_i$ for all species. The species closest to the endpoints have a larger average niche width. However, there is no qualitative difference in being at the endpoint and so this does not affect the behaviour of the model. As H_k can take any value between (0, 1) the number of niches are infinite and consequently so is the number of species that can coexist.

Resource heterogeneity with uniform recruitment limitation (RLU)

The recruitment limitation model relaxes the assumption of infinite fecundity in the previous model. Recruitment is limited through limits to fecundity. All species are presumed to be uniformly recruitment limited and so produce F_{mn} propagules per individual per time step. If F_{mn} is small then it is unlikely that propagules of all species will reach all cells in a single time step.

The recruitment limitation model is

$$G_i = \left(P_i + (1 - P_i) \exp\left(- F_{mn} \sum_{j \neq i} X_j \right) \right) \times (1 - \exp(-F_{mn} X_i)), \tag{8}$$

where P_i is as defined previously and F_{mn} is the same value as was used in the trade-off between competition and colonisation.

Model simulation

The family of models were simulated using a variety of parameter values to explore the effect that different coexistence mechanisms and parameter changes have on the invasion resistance of the resulting assemblages.

The habitat is set to 4900 cells, the maximum number of individuals that the habitat can support. For each simulation, a regional pool of species is chosen at random. A species is completely defined by its R_i value which determines its competitive ranking for the single limiting resource model, its colonisation coefficient for the competition-colonisation model and its optimal niche for the resource heterogeneity and recruitment limitation models. The habitat is initialised with an equal number of seeds of all species, such that 2/3 of the habitat are initially occupied. The system is then iterated for 1000 time-steps four times. Each time a different coexistence model is used. The initial species pool is the same for all the assemblages constructed using the different coexistence models. A time-step begins with mortality and is followed by the recruitment process after which the population is censused. Mortality rate is the same for all species and in the simulations presented here, the probability that an individual dies in a single time-step, d, is 0.4.

Next, we simulate recruitment. We use the same procedure for the single limiting resource, resource heterogeneity and recruitment limitation models. Each species has a probability of reaching a cell, S_i, which depends on the abundance of the species and is calculated during the seed rain event. For each species and each cell we chose a random number in the interval (0,1) from a uniform distribution and consider that the species has reached the cell if this number is lower than the probability S_i. Competition for the site then occurs between the seedlings present in a particular cell, with the species with the highest competitive ability for the conditions encountered in that cell winning the competition and occupying the cell. If no individuals reach a cell, it remains empty. For the competition-colonisation model, species are ranked according to their competitive abilities (R_i values). For each cell, a random number is drawn between 0 and 1 in a uniform distribution to see if the best competitor has reached the cell (eq. 4). If it has, then it wins the cell. If not, another random number is drawn to see if the second best competitor reaches the cell. This process is iterated until the cell is occupied or no species has successfully reached the cell, in which case it remains empty.

Each assembled community (four in all) is then subjected to ten invasion attempts by 10 randomly chosen species, which have an initial propagule density of 0.01 per cell. The invading propagules compete with resident propagules for the empty space. Typical initial population sizes of invading species are 10–20. The identity of the invaders, as defined by their R_i value, is the same for all the community types, facilitating direct comparison between coexistence mechanisms. The invaders are chosen from the same distribution of attributes as the species and so can be considered to originate from the same species pool. The outcome of each invasion attempt is recorded after 500 time-steps, which is sufficient for any transient dynamics to have disappeared.

The entire simulation process was repeated fifty times for each combination of parameters. The results presented below are an average of these fifty replicates. We classified the outcome of an invasion into two categories. We consider an invasion *successful* if the invader persists or a *failure* if the invader does not persist. We subdivide success into two components (Case 1990). *Augmentation*, the invader persists and joins the community and so species richness increases and *replacement*, the invader persists but its success results in the extinction of one or more species.

Results

It is possible to predict the relationship between species richness and invasion resistance for the two models that assume no limit to fecundity. In the single limiting resource model only a single species can persist. Hence, an invading species will only persist if it is a better competitor than the resident species and can successfully displace it. If there are N species in the initial species pool, then the probability that a new species has a R_i value lower than that of all the other species is $1/(N+1)$ which decreases as the size of the initial species pool increases.

In contrast, in the resource heterogeneity model there is no limit to species richness. Unless species richness is sufficiently great that the size of the habitat is limiting (in this case ~ 1000 species), invasions are always successful. The position of each species on the niche axis (and hence its available niche space) is chosen independently from a uniform distribution. Hence, the invader is not disadvantaged as it has the same probability distribution of niche widths as any other species. In an infinite habitat, G_i is > 0 for all possible values of N, so $X^*_{N+1} > 0$ and any invader will be successful. The addition of a new species reduces the expected amount of habitat available for every species, although in any given realisation it will only affect a maximum of two resident species. Hence, these assemblages are both very species-rich and highly invasible, although in a finite habitat, as N gets very large, population levels will be small and species will be more vulnerable to demographic extinction.

Parameter driven changes in species richness

Size of the regional pool

The species richness of the simulated assemblages all increased when the initial regional pool of species was increased in size, with the exception of the single limiting resource model (Fig. 1a). However the magnitude of the changes in local species richness were very different for the different coexistence mechanisms. The maximum number of coexisting species was maintained by the resource heterogeneity model.

All models showed evidence of increasing saturation with increasing species richness (Fig. 1a) except for the resource heterogeneity model, which shows no evidence of saturation over the range of parameters considered here. Although both the competition-colonisation and recruitment limitation models show evidence of saturation, the competition-colonisation model is more saturated than the recruitment limitation model which, although saturating, has not yet reached complete saturation (i.e. a plateau as species richness increases in Fig. 1a). Thus, we observe a saturation gradient that is maximum in the single limiting resource model and minimum in the resource heterogeneity model.

Patterns of invasibility also changed considerably as the size of the regional pool increased (Fig. 2a). In particular, the invasion resistance of the recruitment-limited system was noticeably greater in species-rich systems. The mechanism is quite simple. As the number of species increases both the number of optimal sites for an invader and the probability of finding these sites decrease.

Effect of changes in fecundity

Changes in mean fecundity, F_{mn}, of species in the regional pool (including invaders) affects two classes of coexistence mechanisms, but in different ways (Fig. 1b). For the competition-colonisation mechanism, F_{mn} defines the rate of increase in colonisation ability as competitive ability changes. This means that when F_{mn} is high, then the colonisation ability of any given species is greater, and in particular, that poor competitors are considerably more fecund than when F_{mn} is low.

The parameter F_{mn} also affects the recruitment-limited system. In this case, F_{mn} is the per plant fecundity for all individuals of all species. In consequence, as F_{mn} increases, the degree of recruitment limitation decreases and the system approaches the resource heterogeneity model.

The effect of changing F_{mn} on the ability of species to invade is shown in Fig. 2b. Again, different coexistence mechanisms respond differently. That the recruitment limitation model tends to the resource heterogeneity model as fecundity increases is also evident in the decrease in invasion resistance as fecundity increases. In contrast, the competition-colonisation model shows an increase in invasion resistance as fecundity increases, which can be attributed to the increased fecundity of the dominant competitor.

Model driven changes in species richness

Comparing the different models for a given set of parameters (i.e. changing our assumptions about the mechanism of coexistence) also produces assemblages of different species richness (Fig. 3a). The gradient ranges from communities of one species, when no coexistence mechanism is incorporated, to communities where the number of species coexisting is equal to the size of the regional species pool, when the resource heterogeneity mechanism (with no recruitment limitation) is invoked. These results are consistent with expectations of previous analytic and theoretical work on these coexistence mechanisms (Goldwasser et al. 1994, Pacala and Tilman 1994, Tilman 1994, Hurtt and Pacala 1995).

The outcome of 10 invasion trials for each type of assemblage is shown in Fig. 3b. Invaders are more successful when coexistence mechanisms that promote species richness are functioning. If we compare results between models we see a positive correlation between species richness and invasibility. The positive correlation contrasts with previous hypotheses because it violates the assumption that species-rich communities are more saturated. In the simulations presented here the most saturated community is the single limiting resource model in which only a single species can persist. Hence, a new invader can only succeed if it is better competitor for the resource than the current occupant. This is illustrated by the decline in degree of replacement (more As relative to Rs) that occurs in the more species-rich communities, indicating that in this example saturation decreases with increasing species richness.

The relationship between species richness and invasion success

If we plot invasion resistance as a function of local species richness then it is clear that there is no consistent relationship (Fig. 4). In Fig. 4 we consider only those cases where local species richness changed with changing parameters. It is clear that the direction of the

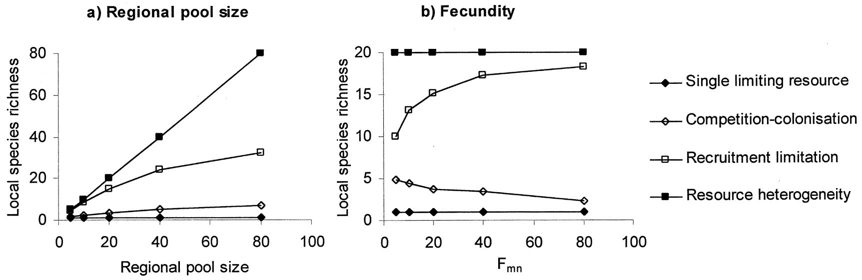
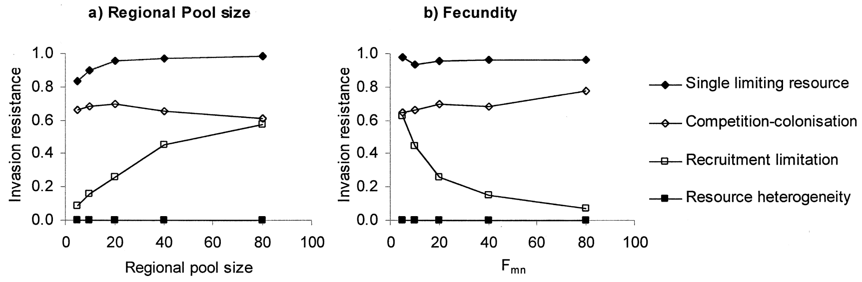


Fig. 1. The effect of the initial size of the regional pool and changing the fecundity parameter (F_{mn}) on the resulting species richness of the assemblages for the four different coexistence mechanisms. Each point represents the average value of 50 simulations. Error bars of one standard error are smaller than the symbols and so have not been included (all standard errors <0.25).

Fig. 2. The effect of the initial size of the regional pool and changing the fecundity parameter (F_{mn}) on invasion resistance of the invader for the four different coexistence mechanisms. Invasion resistance is calculated as (1 − the proportion of successful invasions). Each point represents the average value of 50 simulations. Error bars of one standard error are smaller than the symbols and so have not been included (all standard errors <0.05).



relationship depends on whether changes in local species richness are due to changes in the regional species pool, mean fecundity or the model of coexistence considered. If we plot all these results together it is clear that there is no overall global trend between species richness and invasibility (Fig. 4c).

A positive relationship between species richness and invasion resistance was only evident in the recruitment limitation model when species richness changes are driven by changes in regional pool size (Fig. 4a). The behaviour of the recruitment limited model can be attributed to a decrease in niche size and hence population size combined with limited fecundity, which means that it is uncertain whether a species can find those parts of the habitat for which it is best adapted. In this case, low species richness results in more inefficiently utilised (i.e. effectively empty) niche space and so invasion resistance increases with increasing species richness. In contrast, when changes in species richness are driven by changes in fecundity, the recruitment limitation model displays the opposite behaviour. Increases in fecundity reduces recruitment limitation, increases local species richness and decreases invasion resistance, since success depends on being able to find those pieces of habitat in which the invader is the best competitor. As fecundity increases, the recruitment-limited model becomes more like the resource heterogeneity model in which invasion resistance is insensitive to local species richness (Fig. 2).

The behaviour of the competition-colonisation model is the least intuitive. When changes in species richness are driven by changes in fecundity, this model shows a weak decrease in invasion resistance with increasing species richness, which is exactly the opposite to that which is predicted by saturating models of competition. This is due to the upper bound in the simulations on the parameter, R (<1), which effectively limits the maximum fecundity that any species in the community can have. Tilman (1994) has shown for deterministic models that are similar to the competition-colonisation mechanism that the required increase in fecundity increases rapidly as the number of superior competitors increases. This means that if the maximum possible fecundity value is bounded (as is the case in our models) then the number of species that can coexist with a dominant will decrease as the fecundity of the dominant increases (Kinzig et al. 1999). This results in a decrease in species richness as fecundity increases (Fig. 2b), and in the extreme case in which fecundity ceases to be limiting, species richness declines to one. Hence, in this case, higher species richness is associated with a dominant species that is more fecundity limited and hence less abundant. Consequently there is more available niche space in which an introduced species can potentially coexist and so the probability of an invader being successful increases accordingly.

Deterministic models similar to the competition-colonisation model can be transformed into Lotka-Volterra equations by a simple change of variable (Hastings 1980). Hence, we would expect the dynamics to be similar. That these results contradict those of the Lotka-Volterra models implies that an additional constraint is acting in the competition-colonisation model that limits the development of invasion resistance. This constraint is due to the extremely specific nature of the trade-off between competitive ability and fecundity and the highly asymmetrical nature of competition between the species due to the addition of a strict competitive hierarchy.

Discussion

Our results demonstrate that increases in species richness do not necessarily result in an increase in community saturation. Hence, the classic assumption that invasion resistance increases with species richness does not hold. This is not to say that such a relationship will never be observed, simply that there is no a priori reason to expect it to be the case. In particular, our results suggest that the nature of the relationship between species richness and invasion resistance depends critically on the underlying cause of the species richness gradient.

Changes in species richness driven by changes in coexistence mechanisms drive large variations in invasion resistance of resulting communities which may not conform to the classic assumption of increasing saturation with increasing species richness. We have illustrated that species richness and saturation do not necessarily correlate by constructing a species richness gradient in which saturation (and consequently invasion resistance) declines with increasing species richness. We suggest that mechanisms which are likely to result in high levels of species richness may well be less saturated and so be more easily invaded.

Model differences also affect the way in which within-model changes in local species richness affect invasion success. When changes in local species richness are driven by the parameters, there is no consistent trend in the resulting relationship between species richness and invasion resistance. Both the direction and the strength of the resulting relationship depend on the underlying model of coexistence as well as the identity of the parameter driving the changes (i.e. the cause of the species richness gradient). It was noteworthy that there was only a single case when the hypothesised positive relationship between species richness and invasion resistance was produced by our models.

In natural systems changes in species richness are likely to be driven by both the underlying processes regulating species richness (the model), the identity of the species involved and the particular conditions they experience (the parameters). Determining whether a change in species richness in real systems is due to a change in the coexistence mechanism or a change in conditions is not a trivial problem. Intuitively, small scale variation in species richness can probably be attributed to variation in conditions within a given coexistence mechanism, while large scale changes, and particularly variation between different community types, are likely to be due to changes in the mechanisms that are acting. However, it can often be more complicated than this. For example, changes in conditions may well result in changes in the way species interact and hence to changes in available niche space. We suggest that no consistent pattern exists between species richness and invasion resistance when we sample natural systems unless we can control for the mechanisms regulating species richness in different communities. Indeed, our results are consistent with the wide variety of empirical results that have been reported.

Many observational studies compare invasion success between different vegetation types of varying species richness. In these studies, the number of exotic species present in assemblages is often higher in species-rich systems (Damascos and Gallopin 1992, Knops et al. 1995, Planty-Tabacchi 1997, Stohlgren et al. 1998, 1999). If we assume that the number of exotic species is correlated with the probability of successful invasion, such results support our hypothesis that processes likely to produce species-rich assemblages will also tend to be vulnerable to invasion. As expected from our results, other empirical studies indicate that species-poor vegetation has a greater chance of being invaded (Woods 1993, Prober and Thiele 1995, Pysek and Pysek 1995). It should be noted that invasion by exotics often reduces the species richness of the invaded flora (Damascos and Gallopin 1992, Holmes and Cowling 1997, Rose and Fairweather 1997, Gremmen et al. 1998, Morgan 1998). As these studies did not collect data over time, it is impossible to tell whether the correlations between low species richness and invasion success are driven by species richness or are the result of invasion.

Empirical studies considering responses within a single vegetation type indicate a variety of relationships between species richness and invasion resistance. For

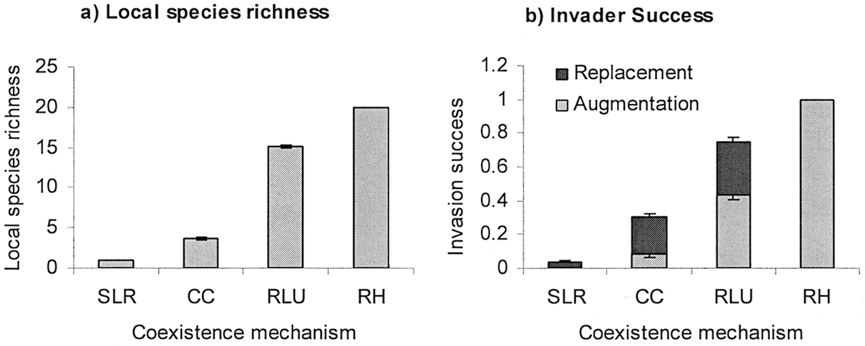


Fig. 3. The effect of coexistence on the species richness and invasion success (1 − invasion resistance) of an assemblage averaged over 50 simulations. Each assemblage was subjected to ten invasion trials and the outcome recorded after 500 time-steps. Invasions resulting in a species appending the community are classified as A and if the result was replacement of a species they are classified as R. The outcomes are displayed as the proportion of successful invaders out of ten trials. Each assemblage was initiated with the same 20 species and invaded by the same ten species. Maximum fecundity was set at 20. The coexistence mechanisms are defined as follows. SLR; Single limiting resource, CC; competition colonisation, RLU; recruitment limitation and RH; resource heterogeneity. The error bars are one standard error.

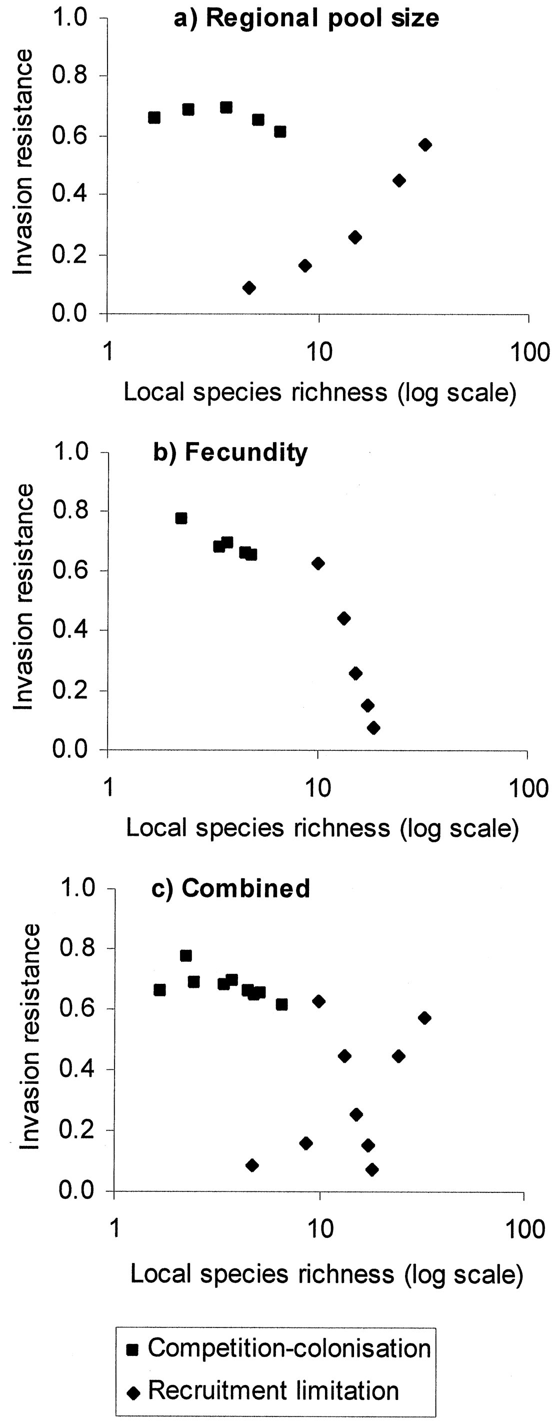


Fig. 4. The relationship between species richness and invasion resistance for ten randomly chosen invaders and two different models (competition-colonisation and recruitment limitation) for a) changes driven by regional pool size, b) changes driven by fecundity and c) both sets combined. Each point represents the average value of 50 simulations. Error bars are smaller than the symbols and have been omitted (all standard errors < 0.05). Note that species richness is plotted on a logarithmic scale for clarity. Invasion resistance is (1 – the proportion of invaders that were successful out of ten).

example, in a long-term study, Wiser et al. (1998) recorded the invasion of the exotic plant *Hieracium lepidulum* over 23 years in New Zealand mountain beech forest. They found that the probability of invasion increased with increasing species richness. Similarly, in a 13-year study of invasion by predominantly C3 exotics into C4 dominated tallgrass prairie in the United States (Smith and Knapp 1999), native and exotic species diversity were strongly positively correlated independent of the disturbance regime. However, small-scale (1-m^2 plots) studies of Californian grasslands (Harrison 1999) found that native species richness and the proportion of exotic species was negatively correlated suggesting that these assemblages may show increased invasion resistance with increasing species richness.

Experimental work examining species richness and invasion resistance can be divided into two broad categories: first, seed addition experiments of invaders into naturally occurring richness gradients and second, experiments using constructed and manually maintained species richness gradients. The results of the seed addition studies are contradictory. Robinson et al. (1995) found a negative relationship between species richness and the invasion resistance of the native (but previously absent) California poppy in annual grasslands in California. In contrast, studies by Tilman (1997) that examined the success of 54 experimentally introduced species in Minnesota grasslands found the opposite trend.

The majority of the constructed gradient studies have found a positive relationship between species richness and invasion resistance (Naeem et al. 1998, Knops et al. 1999, Levine 2000, Symstad 2000). However, no relationship (Crawley et al. 1999) and a negative relationship (Palmer and Maurer 1997) have also been reported. These experiments provide the best evidence for a positive relationship between species richness and invasion resistance. Since these experiments 'isolate' the effect of richness (or diversity), they are also often considered definitive. However, experimentally produced species richness gradients are predominantly constructed as depauperate versions of the natural communities present at the field site. Given that the natural richness is higher, this reduction in species richness probably results in the creation of empty niches. Hence, these experimental communities become increasingly saturated (in terms of niche space occupied) with increasing species richness and so it makes sense that a positive relationship is often found.

Our models suggest that a positive relationship between species richness and invasion resistance will be found if two conditions are met. First, that there is niche complementarity between species (Loreau 1998), i.e. species are not functionally redundant, and second, that the process creating the species richness gradient will result in unoccupied (or inefficiently exploited) niches. An obvious candidate for a process that will maintain empty niches at low levels of species richness is recruitment limitation. Many of the experiments that show a negative relationship between species richness and invader success were carried out at the Cedar Creek Natural History Area in Minnesota, USA (Naeem et al. 1998, Knops et al. 1999, Symstad 2000). Other experiments have provided evidence that this system is recruitment limited (Tilman 1997). Also, that some niche complementarity occurs between species at the site is implied by functional effects on ecosystem processes (Tilman and Downing 1994, Symstad et al. 1998).

Our models also support the hypothesised conditions for a positive relationship. The only model considered here that produced a positive relationship was the recruitment limitation model in which species have different niches and are recruitment limited. In addition, the positive relationship was only produced when the gradient was caused by changes in the size of the regional species pool (analogous to manually manipulating species richness in experimental plots). Clearly, the generality of this hypothesis requires further work. In particular, the effect of the strength of niche complementarity in the community on the strength of the relationship and other processes that may produce species richness gradients in which low species richness is associated with empty niches or inefficient resource use need to be examined.

The empirical studies and our results suggest that it is important to identify and differentiate between assemblages with low species richness which have empty niches (e.g., isolated assemblages and experimental gradients) or fully occupied niches (e.g., grass dominance in fertile grasslands).

The models presented here are examples and are by no means exhaustive. There are many other mechanisms that facilitate coexistence at the level of competitive interactions (Pacala 1986, Chesson 1994, Huston and DeAngelis 1994, Loreau 1996), incorporating higher trophic level interactions (Holt 1977, Crawley 1983, Jeffries and Lawton 1984) as well as regional processes and patch dynamics driven by colonisation and extinction (Hastings 1980, Shmida and Wilson 1985, Pulliam 1988, Holt 1993, Loreau and Mouquet 1999). We can expect that different models will produce different relationships between species richness and available niche space and different patterns of invasion resistance with changing species richness. The form of any relationship between species richness and invasion resistance is highly dependent on the process regulating species richness in the community and the cause of the species richness gradient.

Our simulations were run until any transient dynamics disappeared. However, in natural systems, transient dynamics can play an important role in determining plant assemblage composition and structure and may well alter the outcome of invasion, particularly in early successional assemblages maintained by frequent disturbance. The results presented here focus on the long-term outcome of an invasion; short-term theoretical and empirical outcomes may be different.

In our models, species are introduced only once at the beginning of an assembly sequence or invasion trial. Plant assemblages are constantly receiving propagules not only from their member species but also from other species nearby. Therefore, some species may be able to persist through immigration alone. Other species may only be able to establish after other species have previously been established or become extinct. Incorporating propagules from the regional pool at all time-steps will likely result in an increase in species richness. It has been shown that assembly order may affect the composition of the community (Law and Morton 1996). Variation in assembly sequence in the models presented here is more likely to simply increase species richness because some species will be maintained in the community through immigration (Shmida and Wilson 1985, Loreau and Mouquet 1999). As species maintained by immigration alone are likely to be poor competitors according to the assumptions of the models considered here, their persistence is unlikely to have a significant effect on an assemblage's level of invasion resistance as they have little influence on the structure of the community.

We do not differentiate between the regional species pool from which the initial community is assembled and the pool from which potential invaders are chosen. Hence, we do not incorporate any effect due to co-adaptation of the coexisting species or the fact that exotic species may well have a different adaptive history, with a different set of adaptive constraints. Allowing species within a community to co-evolve and reach 'optimal' niche partitioning is likely to reduce the effect of the size of the regional pool on species richness and will lead to invasion resistance of assemblages to species from the same regional pool (Loreau et al. 2001). However, the ability of a species to invade from another pool is more difficult to predict. The adaptive constraints of an invader may result in failure due to poor adaptation, increased growth and fecundity rates due to competitive release or reduced natural enemy densities (Crawley 1987, Noble 1989). Likewise, new selection pressures may result in an increase in its competitive ability and its impact on the existing assemblage (Blossey and Notzold 1995).

None of these complications and elaborations are likely to alter the simple conclusion of the present work that the processes maintaining species richness will drastically alter our predictions about community level attributes such as invasion resistance. We conclude that efforts to identify communities at risk of invasion based on species richness are unlikely to be successful. The relationship between species richness and invasion success can only be interpreted in the context of the mechanisms of coexistence acting in the assemblages and the cause of the observed species richness gradient. Including these factors in our conceptual model of invasion resistance will do much to advance our understanding of invasion resistance in plant communities.

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