Patterns of invasions
and the mechanism behind invasion resistance

Why are communities differently susceptible for invaders?

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1. Introduction

1.1 Motivation

Invasion of habitats by exotic species is a global phenomenon that can bring about serious damage to biodiversity, ecosystem functioning and economic systems (Vitousek et al. 1997, Pimentel et al. 2000, Chapin et al. 2000, Mack et al. 2000, Sakai et al. 2001). The number of invasions is accelerating due to increased trade and transport. After habitat destruction and fragmentation, invasive species are considered the most important cause of loss of biodiversity. No ecosystems are preserved from invasive species and species from across all taxa are known to potentially become invasive. Despite the deleterious effects, invasions do occur and can be regarded large-scale natural experiments that could give insight in the population biology of invasive species and in the community ecology of invaded ecosystems. If the mechanisms behind the process of invasions can be understood, much damage can possibly be prevented or repaired.

Characteristics of the invader in question, propagule pressure and the susceptibility of the invaded ecosystem influence the establishment- and invasion success of the exotic species. Much effort has been put into studying patterns between invasiveness and life history traits, evolutionary history and ecology of the invasive species. Such patterns would be particularly interesting to conservationists due to the predictive power that would emanate from such studies (Kolar and Lodge 2001). On the other hand it is thought that the susceptibility of ecosystems to invasive species could be an emergent property that depends on the community's diversity, competitive ability of residents and disturbance-regime (Elton 1958, Mack et al. 2000, Davis et al. 2000).

In spite of the effort, until today we have a poor understanding of the mechanisms behind invasion resistance and we don't know why ecosystems are differently invasible, not to mention the disability of science to predict invasions.
In this essay I will explore theory and empiry to get insight in the functioning of communities and ecosystems regarding invasions. The focus will be on plant communities because most of the theoretical and experimental research has been performed on this trophic level. Furthermore, if the mechanisms acting on this level are not understood it is impossible to understand the more complex whole system. Specifically, I will try to answer the question: *"What is the mechanism behind invasion resistance of plant communities and what is its effect?"* Furthermore I will investigate patterns of invasibility and see how well these can be explained by our current knowledge of community ecology.

1.2 Process of invasion

To be able to understand the mechanisms influencing invasive species it is important to know the different transitions in the invasion sequence (fig. 1). All invasions start with an exotic[1] species that is transported outside its native range into a new

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[1] The basic processes that admit exotic plant species are essentially the same as those that facilitate colonizations by native species (Thompson et al. 1995). Therefore, exotic can be regarded as "non-existent in that particular community" as well.

ecosystem. For establishment and growth, a species must be able to increase in abundance at the invaded locality. This depends on the opportunities that the particular invaded community provides for the invader in question (Shea and Chesson 2002) and on characteristics of the species itself. If it has established a population it may continue to expand its range and attain the invasive status or remain viable but not expand its range (Sakai et al. 2001). Invasive species differ in the impact that they may have on the ecosystem. Some exotic invaders displace other species and may change ecosystem function whereas others appear to have little effect (Levine 2003).
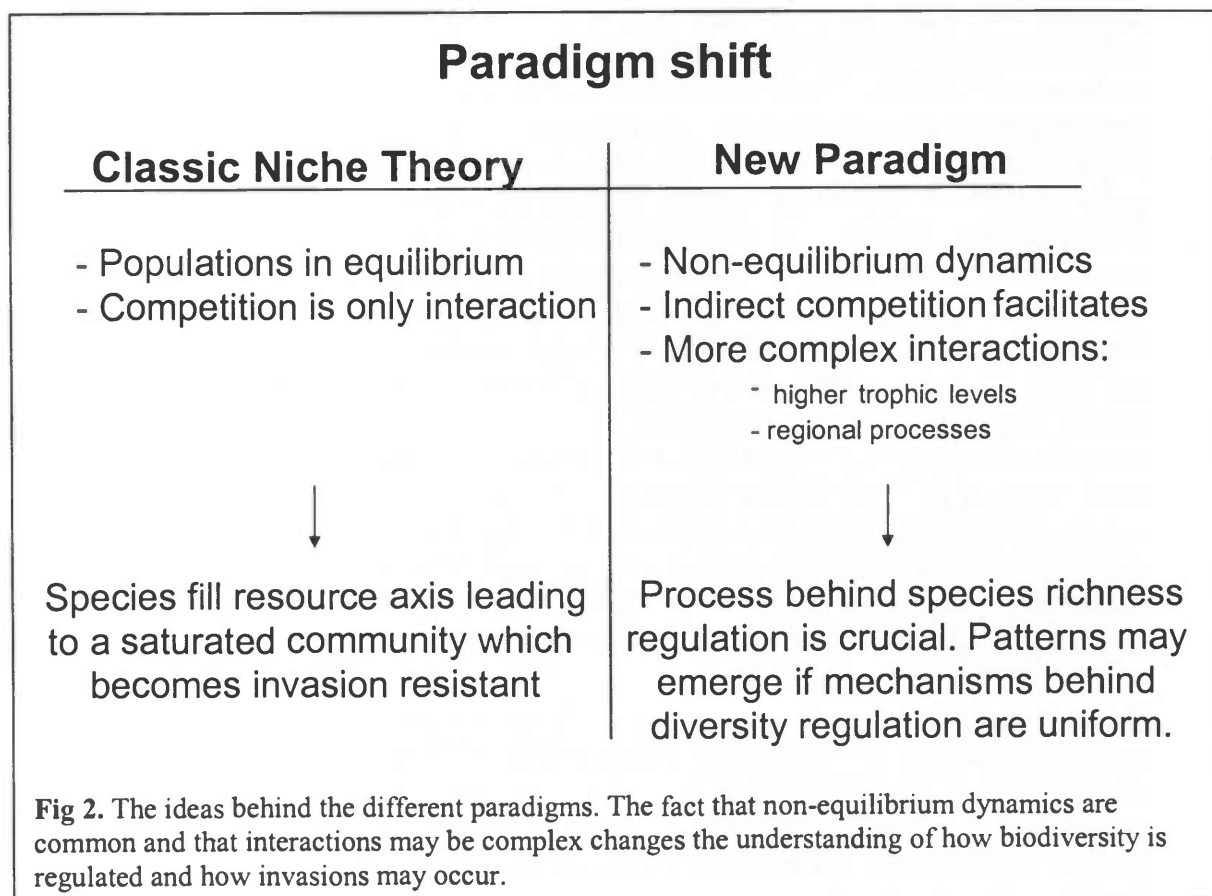
Process of invasion

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 ┌──────────┐      ┌──────────────┐      ┌──────────┐      ┌─────────┐
 │ propagule│─────▶│ establishment│─────▶│ spreads  │────▶│ high    │
 │ arrival  │      │ of population│      │ (invasive)│     │ impact  │
 └────┬─────┘      └──────┬───────┘      └────┬─────┘      └─────────┘
      │                   │                   │
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 ┌──────────┐      ┌──────────────┐      ┌─────────┐
 │establishment│   │ population   │      │ low     │
 │ fails    │      │ remains viable│     │ impact  │
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Fig 1. Process of invasion of an exotic species. Invasions start with the arrival of a propagule in a new ecosystem. It may either succeed to establish a population or fail. Subsequently it may expand its range (invasive) or just remain viable at low population density. And last, invasive species differ in the way they impact the environment. Some invaders may displace native species or alter community functioning while other species persist without causing damage (low impact).

1.3 Theory against historical background

No communities are impenetrable to invasion by exotic species (Usher 1988, Cohen and Carlton 1998, Sakai et al. 2001). However, communities differ in their susceptibility to invasion as well as in their ecological and evolutionary responses to these invasions. It is widely believed that diverse communities are less easily invaded by exotic species. However, new paradigms and theory are changing this view (fig. 2).
As far as known, Elton (1958) was the first to argue that "the balance of relatively simple communities of plants and animals are more easily upset than that of richer ones; that is more subject to destructive oscillations in populations ... and more vulnerable to invasions." He had observed that simple ecosystems such as island communities and agricultural monocultures show high vulnerability to invasions (in Levine and D'Antonio 1999). Classic ecological theory has contributed to the belief that more diverse systems are less invasible. In the classic view, it is assumed that communities are structured by competition and that populations are in equilibrium (Tilman 1982). Invasibility of a site depends on the availability of the resources that

limit the growth of the invading species. Therefore, natural communities that are rich in species have limited niche space and are less invasible than species-poor systems. In general the paradigm suggests that the more species occupy a resource axis, the more fully resources are monopolized, and the more difficult it becomes to insert new (exotic) species. This classic theory has been modeled by simple Lotka-Volterra equations (e.g. Case 1990, 1991, Law and Morton 1996). These models simulating single and multi-trophic interactions suggest that invasibility decreases with diversity.

Paradigm shift

Classic Niche Theory	New Paradigm

- Populations in equilibrium
- Competition is only interaction
	- Non-equilibrium dynamics
	- Indirect competition facilitates
	- More complex interactions:
	   - higher trophic levels
	   - regional processes

↓	↓
Species fill resource axis leading to a saturated community which becomes invasion resistant	Process behind species richness regulation is crucial. Patterns may emerge if mechanisms behind diversity regulation are uniform.

Fig 2. The ideas behind the different paradigms. The fact that non-equilibrium dynamics are common and that interactions may be complex changes the understanding of how biodiversity is regulated and how invasions may occur.

Yet, the assumptions that populations are in equilibrium and that communities are structured by competition alone, as modeled by the Lotka-Volterra models, are extremely strict and wrong. First, it is known that populations may cycle or show chaotic fluctuations. In fact, populations that are in equilibrium probably don't exist. Secondly if competition is the only structuring mechanism in a community it means that each species suffers from the presence of all other species. However, it is known that competitors along a resource axis may indirectly facilitate one another via competing with shared competitors (for overview see Bruno et al. 2003). Indirect facilitation occurs when the indirect positive effect of one species on another, via the suppression of a shared competitor, is stronger than the direct competitive effect. Stone and Roberts (1991) showed that when fluctuations in interaction effects (between species and between species and environment) are included in models, this results in 20-40% beneficial interactions so that species may profit from the presence of other species. Competition in the way that all species suffer from each other can only occur when the environment is nearly constant and when all species are similar; both of which are implausible (Stone and Roberts 1991). Empirical evidence for indirect interactions is emerging. Levine (1999) showed that in a riparian community,

the sedge *Carex nudata* had direct competitive effects on other plant species, as well as indirect facilitative effects, by suppressing a second competitor, the common monkey-flower *Mimulus guttatus*. Because facilitation through indirect competition plays an important role in the diversity of communities, it logically follows that species-rich communities not necessarily are more resistant against invaders than species-poor communities.

Another problem of the Lotka-Volterra models is that well-mixed populations are assumed, such that all species interact with a potential invader. Because heterogeneity increases with scale, the predictions from these models can only apply to small spatial scales. Diversity of plants can be explained by adding heterogeneity into their environment. Chesson (1994) showed that species-specific responses to fluctuating resources might promote diversity. In a theoretical study, Huston and DeAngelis (1994) show that a large number of species can coexist on a single limiting resource under steady-state conditions. For this, they needed to incorporate low transport rates or high input fluxes of resources that generate heterogeneity in the environment. Such circumstances would apply to terrestrial but not aquatic systems. Huisman and Weissing (1999) propose a possible solution to the plankton paradox (Hutchinson 1961) by showing that competition for 3 or more resources may generate oscillations and chaos. Such non-equilibrium dynamics allow for a greater number of coexisting species than there are limiting resources.

Furthermore, theoretical (Fagerström 1988, Moore et al. 2001) and empirical (Levine 2000, Bruno et al. 2003) studies have shown that communities are shaped by more complex interactions than competition alone. A large body of explanations for the diversity observed in nature incorporate higher trophic level interactions such as predation and parasitism (Holt 1993). A third category of explanations incorporates regional processes and patch dynamics driven by colonization and extinction (Pulliam 1988, Loreau and Mouquet 1999).

Moore et al. (2001) show in a theoretical study that the process of species-richness regulation is crucial for a successful understanding of invasion resistance along species-richness gradients. Hence, in order to understand why ecosystems differ in invasibility it is important to clearly differentiate between communities of single and multiple trophic levels and to determine the mechanism behind the coexistence. Therefore, they predict that general relationships between species-richness and invasibility are only to exist for systems that have uniform mechanisms behind coexistence.
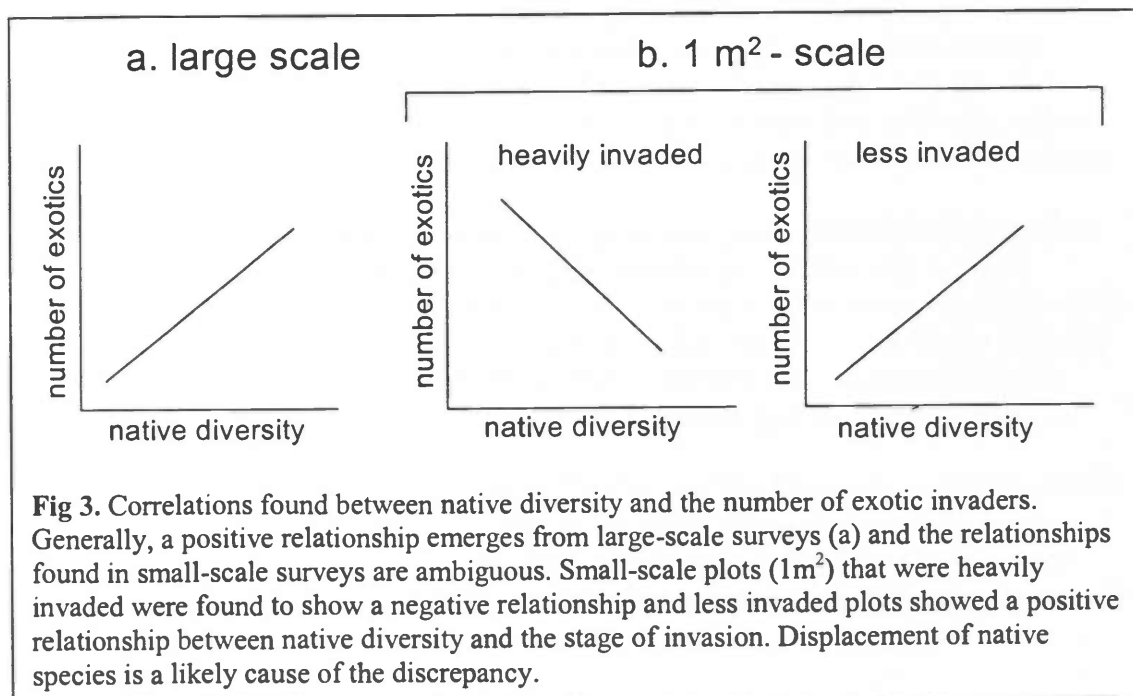
Summarizing, recent research shows that indirect interactions are common and more general, that many systems are loosely structured and not at equilibrium. Secondly, classic niche theory is based on a homogeneous environment that is rarely found in nature. This observation discredits the classic niche space paradigm. Furthermore, a large body of theory shows that mechanisms other than competition exist behind the regulation of biodiversity, including higher trophic level interactions and regional processes. Relationships between species-richness and invasibility will therefore only be found in communities that have the same mechanisms behind the regulation of biodiversity.

2. Natural patterns of species diversity and invasion

Despite Elton's (1958) observations and the results from the theoretical investigations of community richness and invasion resistance based on Lotka-Volterra models, nature most commonly shows a positive correlation between biodiversity and the number of exotic species (Levine and D'Antonio 1999). The studies showing this relationship are based on correlative surveys between native diversity and the number of exotics that reflect both the effects of diversity as well as the effects of processes covarying with diversity. It must be noted that simple documentation of community structure in invaded and uninvaded areas reveals little about the underlying mechanisms.

Fox and Fox (1986) analysed species lists from well-defined areas, such as reserves to explore patterns of diversity and invasion. The data were re-analysed by Levine and D'Antonio (1999) and shows a positive relationship between the number of native and exotic species for shrubland sites and a non-significant relationship for heathland sites. Stohlgren et al. (1999) investigated the relationship between species-richness and number of invasions in the Rocky Mountains and in Grasslands in the Great Plains in the USA. On a large scale, they found more exotic species in communities with high biodiversity. On the scale of $1m^2$ they found that species-rich grassland communities contained fewer exotic species than their species-poor counterparts.

Brown and Peet (2003) investigated exotic and native species diversity of vascular plants across five spatial scales in riparian and upland plant communities in the southern Appalachians. A positive relationship was found between species diversity and the number of exotic species in riparian areas at large scales ($100 m^2$), which graded into a negative relationship at small scales ($0.01 m^2$). In uplands, there was a slight positive relationship between native and exotic species diversity at both scales of observation.

Nevertheless, other studies show a negative relationship between invasibility and native species richness (Prober and Thiele 1995, Pysek and Pysek 1995). However, in all the cases investigated the invasibility of the systems were covarying with other factors of influence on the exotics making it impossible to study the mechanistic effect of diversity on invasibility.

Fig 3. Correlations found between native diversity and the number of exotic invaders. Generally, a positive relationship emerges from large-scale surveys (a) and the relationships found in small-scale surveys are ambiguous. Small-scale plots ($1m^2$) that were heavily invaded were found to show a negative relationship and less invaded plots showed a positive relationship between native diversity and the stage of invasion. Displacement of native species is a likely cause of the discrepancy.

Despite the reports of Stohlgren et al. (1999) and Brown and Peet (2003), the relationship between species-richness and number of exotic species may become ambiguous at smaller scales (fig. 3). Stohlgren et al. (1999) also reported that $1m^2$ plots placed in more heavily invaded communities showed negative correlations between native and exotic diversity, while those in less invaded areas showed positive relationships. Damascos and Gallopin (1992) found that species-rich and lightly disturbed communities were more often invaded than their species-poor, undisturbed counterparts. When, in later stages of invasion, the communities became dominated by the invader (*Rosa eglanteria*) the species-richness decreased. These observations indicate that native species may be displaced by the exotic species in a later stage of the invasion. It illustrates that correlations between the number of exotics and the native diversity should be interpreted with care.

Furthermore, correlations between diversity and invasibility do not reflect invasibility when different biogeographic regions are compared (as in Fox and Fox 1986) because factors influencing invasion success that are independent from the invaded community such as propagule pressure and characteristics of the invader are not considered.

In order to study the effect of diversity itself, it becomes inevitable to perform experiments where covarying factors can be controlled.

3. Experimental evidence

This chapter shows results from field experiments where the relation between community diversity and invasion resistance is studied more mechanistically. The experiments include invasions of exotic species in artificially constructed and natural grasslands where neighbourhood effects are examined. The distance to the next neighbour is assumed to affect resource density. Therefore, neighbourhood properties themselves do not influence the success of an invader but they act via resources.

Invasions at Cedar Creek, Minnesota
Knops et al. (1999) performed an experiment in which they created plots with different plant community richness. Exotic plants were allowed to invade from seed rain. They showed that species diversity and invasion (numbers and size) were negatively correlated. Secondly, they showed that resource availability (extractable soil nitrate in the rooting zone and light penetration) was positively associated with the total biomass of the invading species. This suggests that high species richness caused a decline in resource density which reduced the susceptibility of the community. Their findings support the hypothesis that the increased use of limiting resources that occurs at higher levels of plant richness is a mechanism that inhibits invasion by other plant species. Kennedy et al. (2002) showed that increases in the number of species planted lead to more crowded and diverse neighborhoods, and smaller nearest neighborhood distances. Secondly they showed that invaders became established in neighborhoods that were significantly less crowded than randomly chosen neighborhoods. The performance of individual invaders was negatively affected by the degree of neighborhood crowding and diversity. Invaders in neighborhoods that are crowded and diverse will never get very large compared to invaders in neighborhoods that are uncrowded and species-poor.

Nash's Field, Silwood Park
Crawley et al. (1999) performed an experiment in which they wanted to test the effect of species richness on invasibility in productive grasslands. Vegetative fragments of perennial herbs and and the seedbank were killed by a methyl bromide treatment prior to sowing. Four perennial grass species were grown in monoculture, pairwise mixtures and a four-species mixture, while a species-rich plot was sown with 80 species of dicots, giving four levels of initial species richness (1,2,4 and 80). There were three different liming treatments. Nonsown species were free to invade, either from seed production of sown species on adjacent plots, or by immigration of species from outside the experiment.
It was found that for productive, small-scale grassland plots, species identity matters more than species-richness in determining the number of invaders and the total biomass of invasives. The plots that were sown with high initial species richness were better resistant against invasive species. However, this effect was not due to diversity itself. The pattern arose by the "sampling effect": the larger the sample of species sown, the more likely it is that the competitive dominant species will be present on any given plot.
Species differ, and it is because species differ that one might expect to observe effects in experiments where the number of species is varied. When an increasing number of different, complementary species are added, niche space is filled up. Crawley et al. (1999) conclude that a small-scale community that is rich in complementary species is

resistant against invaders. The results are consistent with the idea that interspecific competition is the most important process resisting plant invasion.

Leek Spring Meadow, Sierra Nevada, California

Lyons and Schwartz (2001) performed a field study in which they wanted to test the hypothesis that less common species can influence the colonization of exotics. This approach offers supplementary testing of theory following the work of Knops et al. (1999) and Kennedy et al. (2002). The experiment was conducted in a natural plant community wherein species diversity was lowered by removal of less abundant species. The resulting disturbance was controlled for by removal of an equivalent amount of biomass of the most common species from paired plots. Seeds from the exotic species *Lolium multiflorum* were sown into manipulated plots differing in species richness. Only one invader was used so that it was avoided to put invaders in competition with one another.

They found that exotic species establishment was higher in plots in which diversity was successfully reduced. In addition they showed that exotic establishment was inversely related to species-richness. Their results indicate that interspecific competition plays an important role in invasion resistance in plant communities. Furthermore, these results demonstrate that less dominant species can significantly influence invasion success.

Nelson Environmental Studies Area, University of Kansas

Foster et al. (2002) performed a seedling experiment along a natural gradient of plant diversity in a successional grassland in the prairie-forest ecotone of northeastern Kansas. The objective of this study was to examine the dependence of community invasibility on plant diversity and on extrinsic factors correlated with diversity. Seeds of 34 different grassland species were added to plots differing in extrinsic factors (soil disturbances and light availability) which affected the species diversity. It was found that community susceptibility to invasion was greatest in high diversity microsites. This effect was suggested to be due to the direct influence of extrinsic factors that contribute to spatial variation in diversity, not to any direct effect of diversity per se.

South Fork Eel river, California

Levine (2000 and 2001) performed an experiment along 7 km in a riparian system where he investigated the effect of plant diversity on invasion success on tussocks. He showed that, as manipulated species richness increased, the proportion of spontaneously arriving propagules that germinated and survived the growing season significantly declined. Furthermore he showed that the size of the largest individual per tussock significantly declined. Even including the spatial variability of a natural system, diversity could significantly enhance resistance to biological invasions. Due to correlation between cover and diversity, cover may have mediated the effect. He suggested that the decreased success of invaders is due to failure in the germination/seedling stage, a stage that is particularly vulnerable to shading by plant cover (Goldberg and Miller 1990).

Conversely, when Levine looked at tussocks along the entire stretch of river, he found invading species to be more abundant on the most diverse tussocks. On community scale, the patterns of diversity and invasion do not reflect the intrinsic effects of diversity operating at neighborhood scales. Hence, factors covarying with diversity, such as propagule pressure are likely determinants of species richness and invasibility.

It was found that the downstream tussocks were the most diverse and the most invaded indicating that seed supply determined community patterns.

Levine conducted a second experiment in which he planted the same number of seeds on all tussocks under study. He chose 190 natural tussocks of a range of diversities all along the seven-kilometer study site. He added large numbers of seeds to each tussock to cancel out the effect of natural recruitment from the stream. If a factor, other than the seed supply drove the community invasion patterns, one would expect positive correlations between natural diversity and the success of the added propagules. However, Levine found that the recruitment on all tussocks was about equal, suggesting that the observed pattern was due to the supply of seeds and not resource availability or some other characteristic of the tussock.

Kerr Center for Sustainable Agriculture, Oklahoma

Palmer and Maurer (1997) performed an experiment where they planted annual crop species in mono- and polyculture. They found that species richness of weeds in the polycultures were highest, whereas the species composition of the communities were similar among treatments. This supports the idea that "diversity begets diversity". The patterns resulted from differential recruitment from the seedbank, growth and survival. Increased environmental microheterogeneity in polycultures could account for the higher level of diversity of weeds.

The crops were grown in densities that yield optimal production. Such density is typically lower than the density of plants in nature. Therefore, competition for resources is weak between crops and weeds. Instead of interacting competitively, the crop species may facilitate for weed species by creating a heterogeneous microclimate, which results in a species-rich weed community.

Synthesis

From the experiments where extrinsic factors are controlled and the plants are sufficiently similar, it becomes evident that more diverse plant communities are more resistant against plant invasions. From the work of Knops et al. (1999) it appears that the resistance arises via competition for resources. This observation is supported by the study of Kennedy et al. (2002) that shows that the success of an invader decreases when the distance to its neighbours becomes shorter. Crawley et al. (1999) show that species identity of the community determines the resistance against invasions. Furthermore, their research indicates that the "sampling effect" may play an important role. Resistance against invaders may not be a consequence of diversity itself but may arise through the increased chance that a suitable competitor is abound in a large sample. Different species fill up niche space making a community resistant against invaders. Lyons and Schwartz (2001) show that even though some species are low in abundance they may play an important role in community resistance. In all these experiments the extrinsic factors were controlled and only the effect of diversity is measured. This conclusion is illustrated by the experiment of Foster et al. (2002) where extrinsic factors were allowed to vary and the effects of competition could no longer be observed.

Levine (2000, 2001) shows that diversity may enhance invasion resistance in a natural riparian system as well. Furthermore, when diversity – invasion patterns are studied on a community scale, secondary factors that drive diversity also may promote invasion. This observation illustrates why sites that are high in diversity may be found to contain many exotic invaders.

The experiment performed by Palmer and Maurer (1997) appears to contradict that diversity, on neighbourhood scale, resists invasions. However, the conditions under which the experiment was performed were not suitable to be able to detect competitive exclusion. The species used were functionally different and were grown in low density. Theory only predicts competitive exclusion when the species in competition are similar and when they are grown in close distance from each other. Moreover, on account of the dissimilarity of the species facilitation instead of competition was more likely to occur.

Species loss at small scales may reduce invasion resistance. However, on community scale, the effects of ecological factors spatially covarying with diversity, such as propagule supply, make the most diverse communities most likely to be invaded. Furthermore, facilitative effects are possible between plants, making it more difficult to find straightforward patterns.

4. Reflection on theory

Experimental manipulations of diversity and models have supported the hypothesis that diverse communities better resist biological invasions. In contrast, studies of natural patterns examining invasion of natural gradients tend to find that the most diverse areas are the most invaded. This apparant conflict between observational studies and experimental work on the relationship between diversity and invasion resistance has been resolved in different ways by several authors. One mode of explanation for the observed patterns is based on the idea of increasing heterogeneity and effect of extrinsic factors when the scale of observation is enlarged. Another type of argumentation is based on the availability of resources for invading species and how the availability changes with disturbance of the community and adaptation of the residents.

4.1 Matter of scale

Huston (1999) argues that the relative contributions of local versus regional processes may be the key to understanding global patterns of biodiversity. It is crucial to find the appropriate scale to detect the effects of local processes. Effects of competition, which is a local process, can be detected when species are sufficiently similar and considered the same functional type. Secondly, the size of the local area must be small enough for individuals of different species to interact with each other. And thirdly, the conditions must be suitable for equilibrium to be achieved because that is when competitive exclusion may occur (Tilman 1982). Because heterogeneity and variation of environmental conditions increase with scale, large-scale samples fail to show evidence for competitive exclusion.
In accordance with Huston (1999), Levine and D'Antonio (1999) hypothesized that the contradiction between the observations of natural patterns and the experimental evidence is the result of factors that promote diversity of native species diversity as well as the invasion of exotic species. Exotic species are likely to profit from conditions that are favorable for endemic species.
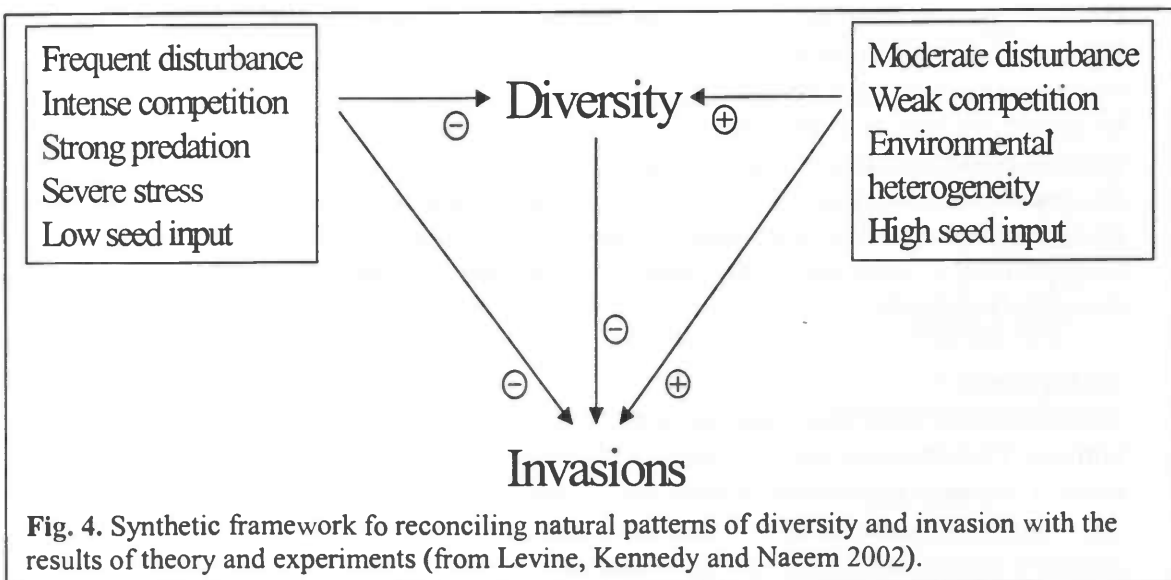

Fig. 4. Synthetic framework fo reconciling natural patterns of diversity and invasion with the results of theory and experiments (from Levine, Kennedy and Naeem 2002).

Levine, Kennedy and Naeem (2002) developed this idea to what they call a 'synthetic framework'. The intrinsic, causal effect of diversity (via competition) on invasions is negative and represented by the vertical arrow in fig 4. However, there are also positive effects such as environmental heterogeneity and moderate disturbance of which both diversity and exotic invaders take advantage. On the other hand there are restricting effects such as severe stress and low seed input that negatively affect native diversity and exotic invasions. Due to these covarying factors that affect diversity and invasions, the direct relationship between diversity and invasion resistance is obscured.

The consequence of this is that if areas with low native species diversity are also associated with unfavorable conditions, they might also be difficult to invade. In contrast, areas with high biodiversity indicate favourable conditions for species richness and exotic invaders. Thus diverse areas may be susceptible to invaders despite the causal effect of species-richness operating on neighbourhood scales.

4.2 Resources

Davis et al. (2000) propose, what they call, a mechanistic and quantitative theory in which fluctuations of resource availability is the key factor controlling invasibility. The theory is stated as follows: *A plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources.* The theory is based on the assumption that an invader must have access to resources and that invasion is feasible when it encounters resources in sufficient quantity (resource opportunity). It logically follows that any factor that increases the availability of limiting resources will increase the vulnerability of a community to invasion.

This idea can be regarded as an extension of Tilman's $R*$ (Tilman 1982) rule that predicts that invasion will occur if the resident's $R*$ is greater than the invader's $R*$. However, different interactions and processes may affect the $R*$-value of a species. Invasive species may through escape from their natural enemies allocate resources towards competitive ability and thereby attain a lower $R*$-value. Resource opportunities may be created by interactions such as allelopathy or by functionally changing the environment as well. The net outcome of such different interactions determines the magnitude and nature of the niche opportunities provided by the community and created by the invader.

Invasions are hard to predict because the release of resources occur intermittently and must coincide with the availability of propagules. Furthermore, disturbances and fluctuations in communities most commonly occur unpredictably, which decreases the predictability of invasions further. An important consequence is that a community's susceptibility to invasion is not a static or permanent attribute, but a condition that can fluctuate over time.

Disturbance

Disturbance of ecosystems and communities occur naturally or may be induced by humans. Disturbances may introduce additional resources into the community or cause a decrease in resource uptake due to mortality or weakening of the resident community. A general effect is that disturbances disrupt the historical pattern of resource supply and consumption. When environmental conditions are altered the adaptations of the native species are sub-optimal and resource opportunities for

exotics arise. However, disturbances may differ in size and effect. Large-scale disturbances may alter ecosystem function and create opportunities for invaders which they may become dominant (Vitousek et al. 1997). Small-scale disturbances are likely to create local patches of unexploited resources and thereby facilitate invasions on a smaller scale.

Community maturity

Based on the resource competition of Tilman (1982) and Davis (2000) I demonstrate how evolution and community maturity affect resistance against invasive species. Different species may vary in competitive ability and their degree of specialization. Trade-offs between competitive abilities for different resources have the effect that plants become specialized to a narrow range of circumstance. A group of such specialized plants may more efficiently deplete resources to a lower level than one generalist species in the same environment. Communities that have had less time to assemble, and less time for their constituent species to evolve specializations, are likely to contain fewer species with broader niches (Fig. 5). Such communities are expected to be less resistant against invasions than "older" communities. Furthermore, communities with a long evolutionary history may be better resistant against invasive species than a "younger" community of equal species diversity. Note that this argument is only valid when the environment is heterogeneous and all species competitively interact (see chapter 2).
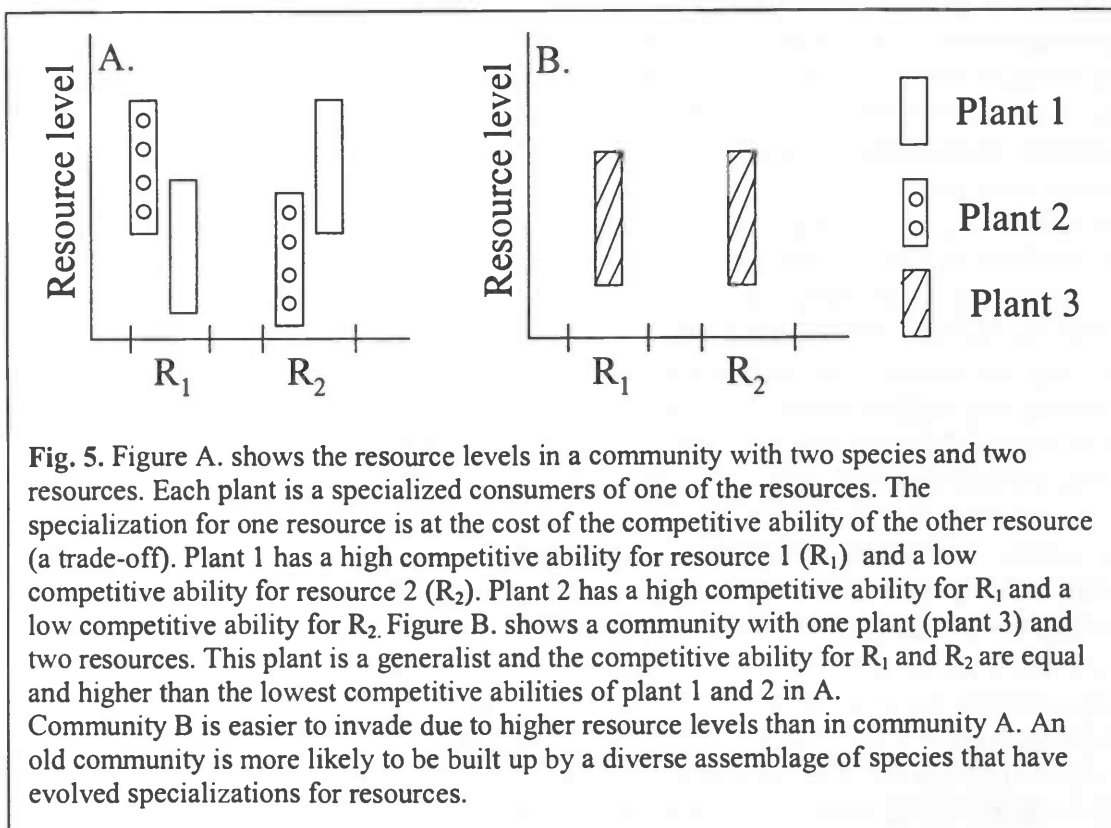

Fig. 5. Figure A. shows the resource levels in a community with two species and two resources. Each plant is a specialized consumers of one of the resources. The specialization for one resource is at the cost of the competitive ability of the other resource (a trade-off). Plant 1 has a high competitive ability for resource 1 (R_1) and a low competitive ability for resource 2 (R_2). Plant 2 has a high competitive ability for R_1 and a low competitive ability for R_2. Figure B. shows a community with one plant (plant 3) and two resources. This plant is a generalist and the competitive ability for R_1 and R_2 are equal and higher than the lowest competitive abilities of plant 1 and 2 in A.
Community B is easier to invade due to higher resource levels than in community A. An old community is more likely to be built up by a diverse assemblage of species that have evolved specializations for resources.

5. Conclusions and discussion

One result from this research has been the finding of an explanation to the conflicting patterns between species diversity and invasion resistance (Levine and D'Antonio, 1999). Models and experiments show that species-rich communities are better resistant against invasive species than species-poor communities, whereas positive correlations between species-richness and the number of exotic species are generally found in surveys performed in natural areas. Under a narrow range of conditions plant communities are able to resist invasions of other plant species through competition. Competition for resources between plants works on the neighbourhood scale. When the soil is homogeneous, the populations well mixed and the resource consumption of the species sufficiently similar, invasion resistance by competition may be noticeable. Invasive species are deterred when the resource requirements are similar and the combined competitive ability of the community is lower than the competitive ability of the invader.

Despite the claim of authors (Levine, Kennedy and Naeem 2002) to have developed a "synthetic framework" their synthesis merely puts the effect of competition in a larger whole of mechanisms that also affect invasions. The other mechanisms leave room for hindsight and ad hoc explanations. Due to the variability of nature any non-trivial, falsifiable hypotheses can not be deduced from this framework.

Nature is heterogeneous and that is why competition for resources (with the exception of space) is unlikely to play an important role in invasion resistance of natural systems. Most natural plant communities are built up by a larger number of functionally different species than managed grasslands and therefore exhibit more heterogeneity. Within such heterogeneous plant communities it is likely that more complex interactions occur than just competition. Generally, combinations of interactions result in loose structure and a complex community with a diverse array of microhabitats, which support the establishment of exotic species. To explain that invasibility of communities increases with diversity converges to the general problem of explaining biodiversity. Factors promoting biodiversity are likely to also positively affect the success of invading species. Propagule pressure, migration, facilitation, grazing and abiotic disturbances are examples of factors that positively affect species-richness and establishment of exotic species. If neutral processes play a dominant role in the assemblage and structuring of communities, it is unlikely to find strong invasion resistance in any system.

In addition to the limited explanation of natural patterns of the "synthetic framework" there are some problems with the experiments performed at Cedar Creek. Even though it was managed to isolate the effect of diversity, it was not managed to simulate invasion resistance of natural grasslands. The species-richness gradients were constructed as depauperate versions of the natural communities at the field site (Levine, Kennedy and Naeem, 2002). 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 with increasing Species richness and so it makes sense that a positive relationship is often found.

Davis et al. (2000) proposed a "general theory" in which fluctuations in resource availability is identified as the key factor controlling invasibility. Fluctuations are caused by factors that alter the supply and consumption of resources. There is little doubt that a system with high levels of fluctuating resources is less resistant against

invasions than a system that keeps resource levels low and constant. However, the theory does not pinpoint which mechanisms in a community control the resource levels. Furthermore, the theory neglects the causes behind the spatial heterogeneity in resource levels.

The provided "theory" (Davis et al. 2000) and "synthetic framework" (Levine et al. 2002) are probably true but can only be used to explain trivial observations. The room for ad-hoc explanations within their theory and framework illustrate that, due to an innumerable number of species, ecosystems and interactions that "everything is possible". It is unlikely that a general theory of invasion resistance will ever emerge. Every invader is different and so will invasion success in different communities differ. Yet, the fact that detailed mechanisms become more difficult to detect in multi-trophic communities does not rule out the possibility that certain patterns can emerge from such systems.

Future research:

Recruitment limitation
The only pattern easy to find in heterogeneous natural systems is the correlation between natural species diversity and the number of invasive species. The processes that are responsible for the species richness gradient, such as disturbance and environmental heterogeneity, also create empty niches. If invasive species are to succeed they must find empty niches which are likely to exist in species-rich areas. Only, when recruitment is limited, it may be possible to find empty niches in species-poor areas as well. I expect that research that examines the effect of recruitment limitation on invasibility of a community could show a pattern in invasion resistance.

Identifying important resources
It is expected that the positive relationship between diversity and invasion observed in nature would be even stronger were it not for the effects of competition. Therefore, research that explores the significance of the small-scale experimental results for the invasibility of entire communities is desperately needed.
General patterns in how competition works on community scale may be found if one was to investigate which resource most commonly is limiting. Due to the distribution of light and space, I hypothesize that these two resources often play an important role in determining the success of invasive plants in undisturbed ecosystems such as forests and productive grasslands. Which resource is likely to mostly affect the community's resistance can be tested by directly manipulating hypothesized factor in an experimental design. Furthermore I expect allelopathy to play a considerable role in preventing exotic species to invade.

Impact of invaders as a parameter of susceptibility
Some species may invade but cause little harm to the native community while other invaders may alter the community composition or ecosystem functioning (Vitousek et al. 1997). Invaders are known to have changed community assemblage by the replacement of native species or have altered the ecosystem functioning. In fact, from a conservation point of view, the impact that an invasive species has is more important than the establishment itself. An important question from both fundamental and conservation points of view is why do some invaders have large impacts on some systems but not on others (Levine et al. 2003)? Interestingly, this important question

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has received little attention. Even though an effect of community characteristics on invasion remains elusive, it might be that community characteristics clearly affect the impact that invasive species have. The models of Case (1990, 1991) predict that not only will diversity act to enhance invasion resistance, but it will also act to prevent the displacement of resident species after invasions. In some of the only empirical work in this area, Dukes (2001) found that community evapotranspiration was less impacted by invasion in more diverse California grassland microcosms.

On the other hand it may be the case that certain species characteristics are responsible for the severe impacts they have. Several investigators have observed that successful invaders, particularly ones with large impacts, tend to have qualitatively different traits than the resident species (Vitousek 1990 and Chapin et al. 1994). Nitrogen fixation in combination with positive feedback in nitrogen poor environments is an example of how an invasive plant can have severe effects on the invaded community. Enhanced predictability is likely to come from matching invader traits against those of the resident community.

Trophic interactions

The theory and empiry discussed in this essay was based on plant communities. It is expected that higher-level trophic interactions may qualitatively change the behavior of a community.

Diversity begets diversity is a trivial result of host specificity when multiple trophic levels are regarded. It is likely that the positive relationship between diversity and invasion becomes stronger when multiple trophic levels are considered. However, I expect that detecting patterns in community resistance becomes increasingly difficult when interactions with herbivores and predators are included. For example, if an exotic plant arrives in a new community where its potential competitors suffer predation from specialist herbivores it will result in competitive advantage for the invader. As the resident competitor needs to invest in defense against the herbivores, the invader may allocate its resources to competition. On the other hand, host switching by specialist herbivores may occur which results in a disadvantage for the invader because it has not adapted a strategy against its new enemy.

Implications for conservation

The fact that the most diverse areas are found to be the most invaded ones and that competition is the only mechanism by which communities can resist invasions raises concerns. First, the most diverse assemblages might be at the greatest risk of invasion, an important point for managing invasive species. Second, loss of species may result in creation of empty niches making it easier for exotic species to establish a population.

Due to the greenhouse effect the climate of the world is changing. Such changes are likely to result in sub-optimal adaptation of resident species whereby increased resource opportunities arise for exotic species. Therefore it is expected that the rate at which invasions occur will further increase.

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