The ecological and evolutionary assembly of competitive communities in dynamic landscapes

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Needless to say, although the research described here in these pages benefited from all the aforementioned individuals, any mistakes or problems are solely the responsibility of the author.

Contribution of Authors

All parts of this thesis were written by Pradeep Pillai and benefited from Frédéric Guichard's editorial comments.

Abstract

We use metapopulation models based on a classic competition-colonization trade-off in order to 1) study community responses to spatially structured habitat loss on dynamic landscapes when species are assembled by ecological (biogeographic) processes; and 2) to study how species are assembled into communities by evolutionary mechanisms. In the first part of our study we show how the response of species richness to habitat destruction in dynamic landscapes can be driven by the existence of either the spatial structure of habitat dynamics or by life-history trade-offs among species. In the second part of our study we confirm that competitive trade-off models predict runaway evolution towards stochastic extinction, making it impossible for stable multispecies assemblages to evolve. We demonstrate that by relaxing the strict deterministic nature of competitive exclusion in such models species can avoid selection towards extinction, allowing for the possibility of species co-evolution resulting in stable multispecies assemblages.

Résumé

Nous utilisons des modèles de métapopulations basés sur un compromis entre compétition et colonisation afin de 1) étudier la réponse des communautés à la perte d'habitats dynamiques et structurés dans l'espace lorsque les espèces sont assemblées par des processus écologiques (biogéographiques); et 2) étudier l'assemblage des espèces en communautés par des mécanismes évolutifs. Nous démontrons comment la réponse de la richesse spécifique à la destruction de l'habitat peut être influencée par la structure spatiale de la dynamique de l'habitat ou par les compromis de cycles de vie. Nous confirmons que les modèles basés sur un compromis entre compétition et colonisation prédisent une évolution vers l'extinction stochastique, rendant l'évolution d'assemblages multispécifiques stables impossible. Nous démontrons qu'en relâchant la nature strictement déterministe de l'extinction compétitive dans ces modèles, les espèces peuvent éviter la sélection vers l'extinction, ouvrant la possibilité de co-évolution entre espèces et de spéciation résultant en des assemblages multispécifiques stables.

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Chapter 1: Introduction

In the study presented here we explore some of the mechanisms by which species competing for the same resources are able to assemble into communities, as distinct from the mechanisms that simply allow for maintenance of biodiversity and coexistence in the face of competition. As closely related as these two types of mechanisms are it remains important not to conflate the two when attempting to explain the patterns observed in extant communities. For example, Drake (1991) noted how a distinction needs to be drawn between the mechanisms responsible for maintaining the community's structure (interspecific interactions like competition, predation, etc.) and those causal mechanisms, like community-assembly rules, that are ultimately responsible for community organization. In competitive communities coexistence mechanisms help explain how competitive exclusion is often avoided, usually through some form of resource partitioning and limiting similarity (for e.g. Macarthur and Levins 1967), while assembly mechanisms help explain how assemblages arrive at their final community structure determining how abundance distributions and diversity patterns are ultimately achieved; which species are able to co-occur, and in what proportions. The critical difference between the two was put succinctly by Rummel and Roughgarden (1985) when they pointed out that positing mechanisms to explain coexistence like "limiting similarity ... indicates which species cannot coexist (in a community) but neglects the question of which species can coexist."

Community assembly mechanisms often fall into one of two broad categories: *ecological/biogeographic* processes, involving colonization and extinction dynamics, or *evolutionary* processes, involving selection and adaptive niche assembly. When biogeographic processes predominate, diversity will largely result from a balance between immigration and extinction rates. On the other hand if adaptive or evolutionary processes are responsible for maintaining biodiversity species coexistence will likely be the result of *competitive displacement* (Taper and Case 1992) between coexisting types giving rise to the adaptive partitioning of the available habitat. We present here a modelbased study that focuses on different aspects of species assembly due to both ecological and evolutionary processes. Our model assumed a critical role for competitive life-history tradeoffs in partitioning available habitat and allowing coexistence on dynamic landscapes.

Ecological and Evolutionary Assembly Mechanisms

Ecological processes are often non-equilibrium mechanisms of assembly. They lead to the construction of invasion-structured communities that result from constant species immigration into a habitat and subsequent species assortment of residents by competitive interactions. Species assortment occurs when significant niche overlap occurs between invasives and as a result one or more of the competitors are driven to extinction. However two factors can often affect the nature of assortment in ecologically assembled communities. First, because of the uncorrelated nature of species invasions historical contingency plays an important part in invasion-structured communities, allowing chance to help determine species composition through such effects as the sequence, timing and abundance of invasions ("priority effects"; Drake 1991; Belyea and Lancaster 1999). Second, with fast enough immigration rates into a habitat possible niche assembly of the community by species assortment is often preempted by the fact that even maladapted types can potentially be rescued from extinction by recurring immigration back into the habitat. As such, community assembly may simply result from a balance between recurrent immigration and ongoing extinction, and biodiversity simply reflect the equilibrium turnover of species, an idea first suggested by MacArthur and Wilson in their equilibrium model of island biogeography (1963, 1967). The role that both the uncorrelated and the fast temporal scale of the colonization process have in pre-empting adaptive niche assembly may be an important factor in explaining the greater levels of diversity often predicted for invasion-structured communities in comparison to evolutionary-structured assemblages.

Evolutionary or *equilibrium* mechanisms of community assembly are mechanisms that allow species to co-evolve through *character-displacement* in order to minimize competitive interactions between residents. Such co-evolution-structured assemblages are selection driven, usually resulting in a convergent (or attracting) stable state for the community. The end result is thus an adaptive niche assemblage. Several models have

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attempted to show how equilibrium assemblages could come about by slow species introductions and subsequent co-evolution of resident species (Rummel and Roughgarden 1985; Taper and Case 1992) as well as by biodiversity buildup through sympatric speciation and adaptive radiation (i.e. branching processes; Jansen and Mulder 1999; Dieckmann and Doebeli 1999; Kisdi 1999; Bonsall and Mangel 2004; Bonsall *et al.* 2004). Despite their differences, what most models of evolutionary assembly have in common is the expectation that a consistent pattern of limiting similarity, or niche width between types, will ultimately characterize the final steady-state assemblage whenever adaptive dynamics are responsible for filling up the available niche space.

As noted above, an important difference in the predictions made by biogeographic and evolutionary models is the tendency for co-evolutionary mechanisms to limit the potential biodiversity in a community in comparison to ecological processes (Rummel and Roughgarden 1985; Matsuda and Abrams 1994, Bonsall et al. 2004). The limitations that adaptive niche assembly can impose on a community's diversity is perhaps most striking in cases where evolutionary dynamics result in species being driven to "selfextinction" due to runaway evolution to extreme trait values (Matsuda and Abrams 1994). A dramatic example of just such an evolutionary scenario may have been provided by the predictions of Kinzig et al.'s study (1999) describing how evolution in a competitive trade-off community inevitably leads to the extinction of all species and thus preventing any biodiversity buildup whatsoever. Kinzig et al. demonstrated that communities exhibiting a competition-colonization trade-off have predicted equilibrium abundance distributions characterized by unrealistically low species abundances and infinite species packing at the extreme competitive end of the trait spectrum, results that strongly suggest that evolution in such systems ultimately drives species to biologically unrealistic low abundances and hence stochastic extinction.

Competition and Coexistence

As was suggested earlier, the manner in which ecological and evolutionary assembly mechanisms are able to structure a community is largely dependent on the mechanisms purported to maintain coexistence among competitors. Standard explanations for the maintenance of biodiversity and for the observed ability of competing species to coexist in nature have often involved some form of resource partitioning. Resource partitioning as a mechanism to maintain diversity can involve directly dividing up the available niche space (niche-assembly of communities; MacArthur & Levins, 1967), or it can involve the use of competitive life history tradeoffs to divide the available resources in a spatiotemporal manner (Levins and Culver 1971; Levin and Paine 1974; Hastings, 1980; Nee and May 1992; May and Nowak 1994; Tilman, 1994,). These later *metapopulation* models, by assuming that the resource or habitat is spatially subdivided, allow communities structured along a competitive trade-off hierarchy to avoid monodominance, or the absorbing state for the most competitive species, by offsetting competitive ability with such traits as increased mortality or diminished fecundity. The trade-off allows inferior competitors to more efficiently colonize newly available sites or habitat patches in order to escape competitive exclusion by superior competitors that are less efficient or slower colonizers.

Metapopulation models have been important in explaining succession dynamics (Tilman 1988; Rees 1993; Pacala and Rees 1998), and evidence that competitive tradeoffs amongst competitors vying for a common spatially subdivided resource allows coexistence has been suggested by studies of several systems including marine mollusks (Paine 1966,1979), grassland communities (Wedin and Tilman 1993), insects competing for food resources (Hanski 1990; Shorrocks 1991) and Amazonian ants competing for understory plants as habitat sources (Yu *et al.* 2001). Nevertheless there have been some problematic features with both the assumptions and the predicted outcome of many competitive trade-off models. An extreme example being, as mentioned earlier, Kinzig *et al.*'s (1999) demonstration of how standard competition-colonization metapopulation models (based on Tilman (1994)) predicted a potentially unlimited number of species packing into the system at the high competitive/low colonizing end of the trait space.

The relevance of competition-colonization models for explaining plant species communities has also been challenged by several researchers including Yu and Wilson (2001) and Levine and Rees (2002). As a result several attempts have been made to modify or extend such models in order to take into account more of the complexities of natural communities. Levine and Rees (2002) have pointed out how the competitive trade-off model's prediction of communities being dominated by good competitors but

slow dispersers does not match the plant abundance distributions actually observed in natural systems. They did demonstrate however that modifying the model to allow environmental heterogeneity permits the model to predict more realistic distributions. On the other hand Yu and Wilson (2001) showed how the assumptions of the standard competition trade-off models could not apply to perennial plant assemblages because competition in such models did not take into account the life-history stages of plant growth - specifically that competition in real plant communities only occurs between plant seedlings to replace the adults that die on a site (replacement competition) and never occurs directly with the adults themselves (displacement competition) as was assumed in the standard model. Yu and Wilson showed that making the strict competition-colonization trade-off relevant for replacement competition would require that variation in patch density also be incorporated as a niche axis. Alternatively, Kisdi and Geritz (2003) demonstrated that traditional competition-colonization models could actually explain coexistence in perennial plant communities so long as seeds competing for a site were subject to demographic stochasticity. Even more problematically Clark et al. (2004), in a study of forest tree communities, were unable to discern the operation of competitive life-history trade-offs in maintaining biodiversity, and instead proposed that high variability within populations (random individual effects) was a more likely factor responsible for permitting coexistence.

Complicating matters even further have been the various *neutral* models that assume that coexistence arises as a non-equilibrium process due to chance mechanisms, and not by niche partitioning arising from variation in life-history strategies amongst species (Caswell 1976; Hubbell 1979, 2001; Bell 2000, 2001; Chave *et al.* 2002, Chave 2004). Several *neutral* models have pointed to the possibility that extant diversity patterns emerge as a result of demographic stochasticity and drift rather than variation in ecological traits amongst competitors. Furthermore, simulation studies have demonstrated how neutral communities, composed solely of ecologically equivalent species, can display species abundance and distribution patterns that are qualitatively similar to those produced by competitive trade-off structured communities (Chave *et al.* 2002).

Habitat loss and community dynamics

In systems where ecological processes predominate competitive life-history trade-offs may help to facilitate coexistence, but it is how such co-existence mechanisms actually interact with biogeographic processes like extinction that determines how a community will ultimately be structured. Understanding the mechanisms driving extinction then becomes critical to understanding the role of competitive trade-offs in shaping the biodiversity patterns observed in nature. One of the most important factors that have been assumed to drive species extinction in the ecological literature has been that of loss of habitat through destruction or fragmentation (Debinski and Holt 2000). However theoretical studies of habitat loss and extinction have often ignored or downplayed the relevance of two very important features of habitat loss: either the explicit spatial structure of the destroyed habitat, or the temporal dynamics of the destruction.

The role of spatial structure An important study by Tilman et al. (1994, 1997) revealed how habitat loss due to destruction and fragmentation could lead to the biased extinctions of the most competitive species in a community (extinction debt hypothesis). Remarkably enough the same study was also able to demonstrate how the spatial arrangement of the destroyed sites did not appear to affect the nature of species extinction; the same results were shown to obtain whether the habitat was destroyed in large contiguous blocks, or whether the destroyed sites were scattered throughout the landscape. The equivalence between spatially-implicit and spatially-explicit models of habitat loss implied by such results has, however, been undermined by several recent studies demonstrating the importance that the spatial pattern of habitat availability has in affecting extinction. For example, the spatial arrangement or distribution of habitat patches has been shown to be an important determinant in species coexistence and persistence (Neuhauser 1998), as well as for determining extinction thresholds in fragmented landscapes (Bascompte and Solé 1996; Hill and Caswell 1999). What most such studies assumed, whether they were based on spatially explicit or implicit models, was that habitat destruction or loss was static - that there was no recovery of habitat and hence no habitat turnover.

The role of habitat turnover- The effects of disturbance and static habitat loss on species richness and coexistence have been studied extensively – the studies perhaps most relevant to our work being those by Hastings (1980), Nee and May (1992), Tilman (1994), Tilman et al. (1994) and Klausmeier (1998) - all of which demonstrated how habitat loss led to a deterministic and biased extinction of species in the community. Yet studies of the effects of habitat turnover on species coexistence have been far fewer (see for example Levin and Paine 1974), possibly because in most models the temporal scale of landscape dynamics has often been assumed to be much slower than that of the community dynamics. Nevertheless habitat fragmentation can be associated with habitat recovery over relatively short temporal scales. For example empty patches in mussel beds caused by spreading wave disturbances are known to be an important habitat source for macroalgae species, with patches able to open and close over relatively short temporal scales (Paine and Levin 1981). Furthermore, the effects of the temporal dynamics of habitat patch lifespan can be a critical factor in determining population dynamics, as has been demonstrated by studies which showed how the effects of habitat patch lifespan can overwhelm the effects of the spatial scale of patch size in significantly affecting the population size of a single species (Fahrig 1992), or in determining metapopulation persistence and extinctions (Keymer et al. 2000). Similarly Roy et al. (2004) demonstrated how the temporal dynamics of habitat patch turnover can outweigh the effects of habitat availability in determining the richness and abundance patterns of species interacting within competitive hierarchies.

Theoretical framework

In order to explore aspects of both the ecological and evolutionary assembly we studied the behaviour communities structured by a competitive life-history trade-off when subject to the effects of habitat turnover in a dynamic landscape. In the first part of our study (Chapter 2) we explored the role competitive life-history trade-offs have in mediating the extinction responses of species to spatially-structured habitat loss, while in Chapter 3 we studied how competitive interactions between species in a trade-off structured community affect the evolutionary dynamics of community assembly. An overview of the basic landscape and community dynamic models common to both of these studies is provided below in mean-field form. In both chapters lattice-based simulations provided a stochastic version of the mean-field models described below.

Landscape model The landscape in our model was assumed to experience habitat turnover due to disturbance spread and habitat recovery. We also assume in our study that habitat destruction and recovery spread locally in the landscape with probabilities d and c respectively.. The analytical model of the landscape dynamics is presented below in the manner of Guichard *et al.* (2003) and Roy *et al.* (2004). For convenience we adopt throughout this study Roy *et al.*'s (2004) formulation. If x represents the fraction of the landscape that is *available* habitat for colonization and y the fraction of the landscape that is *unavailable*, then the habitat model can be represented by the coupled differential equations:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = (1 - x - y) - dxy + \delta_c y - \delta_d x, \qquad (1a)$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = dxy - cy \left[1 - (x+y)^8\right] - \delta_c y + \delta_d x \,. \tag{1b}$$

The first term in Equation (1a), (1 - x - y), represents the proportion of the landscape undergoing habitat recovery and thus is in transition to becoming *available*, while the second term, *dxy*, represents the loss of habitat due to spreading destruction. In Equation (1b), the second term denotes the proportion of *unavailable* habitat that has *at least one* site within its immediate neighbourhood (nearest eight cells) that is undergoing habitat recovery. The terms $\delta_c y$ and $\delta_d x$ give the density independent creation and destruction of available and unavailable sites respectively. This allows the landscape to avoid the absorbing state for either *available* or *unavailable* habitat (see Guichard *et al.* (2003) for details).

Community dynamics: Trade-off model - Like other classic metapopulation models species in our competitive trade-off community form a transitive hierarchy in competitive ability, with competitively superior species able to displace inferior species in competition for individual sites or patches. Coexistence occurred because colonization or spreading ability, measured in terms of the probability of successful colonization of

available sites, was inversely related to competitive ability. Inferior competitors were more successful at colonizing empty or available sites than superior ones.

The ordinary differential equation model for the metapopulation dynamics of the *i*th species in an n species community can be represented in the manner of Tilman (1994) and Roy et al. (2004) as

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = \beta_i p_i (x - \sum_{j=1}^i p_j) - p_i (\mathrm{d}y) - p_i (\sum_{j=1}^{i-1} p_j \beta_j) + m_i (x - \sum_{j=1}^i p_j).$$
(2)

Here p_i represents the fraction of the landscape occupied by *i*th species, and β_i its colonization rate. It is important to note here that competitive ability decreases with species rank index, *i*, so that the *i*th species is competitively superior to any species *j* with a rank index greater than *i* (i.e. j > i). The first term in (2) tells us the growth of species *i* due to colonization of available habit. Note that all the habitat not occupied by superior competitors, i.e. $(x - \sum_{j=1}^{i} p_j)$, constitutes *available* habitat for species *i*. The second term gives mortality due to spreading habitat destruction and the third term gives mortality arising from competitive displacement or exclusion due to the spread of superior

competitors (j < i) onto sites already occupied by species *i*. The last term in (2) is the frequency of density independent migration onto the landscape by individuals of species *i* from the regional species pool.

Chapter 2 model variations – In order to properly study the role of competitive lifehistory trade-offs in determining community responses to habitat loss we had to develop and test a *neutral* version of the community dynamic model described above. Species in our neutral community model behave in a similar manner to species in the trade-off model save for the fact that all neutral species have equivalent colonizing abilities (i.e. $\beta_1 = \beta_2 = ... = \beta_n$), and are competitively equivalent such that no species can displace any other species already established on a site. The operation of life-history strategies can thus be discerned by comparing the responses of both trade-off and neutral community models to habitat loss.

Chapter 3 model variations – In Chapter 3 evolutionary assembly was studied by extending the trade-off community model such that the clones of all species would now have a chance of undergoing, with each bout of reproduction or colonization, a mutation

in trait value a certain number of steps away from the parental trait value. Each species would thus be subject to selection.

Contribution: Biological Realism

Our model enabled us to study aspects of community assembly when interactions between species could be reasonably described by a competition-colonization trade-off for habitat space. We found that incorporating certain biologically realistic elements into classic metapopulation models profoundly affected the predicted features and properties of species communities: in particular, either how species co-evolved into community assemblages, or how relevant competitive interactions were to determining species responses to habitat loss. Specifically in Chapter 2 we demonstrate how incorporating explicit spatial structure in the habitat changed the predictions of trade-off models in regard to deterministic extinction due to habitat destruction and increasing temporal dynamics, while in Chapter 3 we show how by weakening the deterministic nature of competitive interactions between species allows competition-colonization trade-off models to predict co-evolution of stable evolutionary assemblages. In metapopulation theory competitive life-history trade-offs have an important role in determining community properties like species diversity and distribution patterns, but factors like the spatial structure of the habitat dynamics, or extent of variability within populations can significantly alter that role, or even the relevance life-history trade-offs have in structuring a community.

In the "extinction debt" hypothesis (Tilman *et al.* 1994; Tilman and Lehman 1997) the spatial pattern of habit destruction in static landscapes was shown to be unimportant in affecting the patterns of extinction in a community – the same *deterministic* loss of the best competitors in the community occurred whether increased habitat destruction in the landscape had a spatially-explicit structure or was random (well-mixed). We demonstrate in our study, however, that making the *dynamics* of habitat destruction and recovery a spatially-explicit process reveals how extinction, to a significant degree, represents a *stochastic* loss of species in trade-off communities. This leads to a qualitatively similar response of both trade-off and neutral communities to habitat loss in dynamic landscapes (Chapter 2).

The other element of biological realism we considered was individual differences in competitive ability within species. Because populations in natural systems exhibit significant within population variability in competitive ability (Clark *et al.* 2004) the outcome of competitive interactions between individuals from different species are likely to be far more probabilistic in nature than would be suggested by most competitive trade-off models. In most competitive trade-off models the outcome of competitive interactions between individuals of different species is assumed to result from deterministic processes that always lead to the displacement of the inferior competitive rank. Incorporating into our models individual differences within species leads to competitive uncertainty or probabilistic exclusion when competitors interact. With competitive uncertainty we demonstrate that competitive-colonization trade-off models are able to predict stable evolutionary assemblages – something they were unable to do when exclusion was strictly deterministic in nature (Chapter 3).

We believe the study being presented here demonstrates how extending the standard competition-colonization metapopulation model can help reveal important features of community assembly and organization by both ecological and evolutionary means, and by doing so underscore the continuing relevance of metapopulation theory as a framework for conducting ecological research.

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Chapter 2: Dynamic landscapes reveal the presence of life-history trade-offs in competitive communities

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Abstract

Standard models for studying the effects of habitat loss on species diversity most often involve studying permanent habitat destruction on static landscapes and assume species extinction to be a deterministic process mediated by life-history tradeoffs. Here we show that the response of species richness to habitat destruction in dynamic landscapes can be driven by the existence of either the spatial structure of habitat dynamics or by lifehistory trade-offs among species. We more precisely show that in landscapes without spatial structure, life-history trade-offs are required for the community to be affected by habitat loss, while neutral communities show no response to changes in habitat availability. Our results reveal conditions leading to differential response of neutral and non-neutral communities to habitat availability and suggest a possible approach to testing neutrality of communities in dynamic landscapes.

Key Words: community structure, competition trade-off, extinction, neutral theory, habitat destruction, dynamic landscapes

Introduction

Habitat availability and distribution have been studied within the context of habitat destruction and fragmentation (Tilman *et al.* 1994; Tilman and Lehman 1997; Klausmeier 1998) and have been recognized as major drivers of species extinction (Debinski and Holt 2000). However, most theoretical and empirical progress was made under assumptions of static habitats and was interpreted as a direct consequence of life-history trade-offs. As a result our understanding of the mechanisms of species extinction tends to emphasize the deterministic loss of species that are most susceptible to the loss of habitats. Here we use a community model with life-history trade-offs and spatially-structured habitat dynamics to reveal deterministic and stochastic mechanisms of species extinction.

Size, quality and distribution of habitat patches are often assumed to be the critical factors responsible for determining diversity patterns on destroyed or fragmented habitats (Tilman et al. 1994; Bascompte and Solé 1996; Neuhauser 1998; Hill and Caswell 1999). Ignoring the temporal scale of landscape dynamics was realistic insofar as it corresponded to examples in nature where habitat patch turnover was not comparable to the lifespan of the species inhabiting the environment. However habitat loss can be associated with habitat recovery over relatively short temporal scales. Examples include wave induced gaps in mussel beds acting as habitat sources for subordinate species (Paine and Levin 1981) or plant pathogens being submitted to their host distribution (Mitchell et al. 2002). Under dynamic landscapes the effects of habitat patch lifespan can far outweigh the effects of the patch size in affecting species population size (Fahrig 1992), metapopulation persistence (Keymer et al. 2000), or species diversity in communities based on competition-colonization trade-offs (Roy et al. 2004). Here we show how this determining effect of temporal dynamics can flow from either the spatial structure of landscape processes (i.e. habitat creation and destruction) or from community structure (trade-off vs. neutral).

Life-history trade-offs characterizing resident species are often assumed to be the factor responsible for mediating the response to habitat destruction, resulting in the biased extinction of the most competitive species (*extinction debt*, Tilman *et al.* 1994, Tilman and Lehman 1997). This assumption held not only for studies on static landscapes but

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also for studies where the assumption of static habitat had been relaxed (Keymer *et al.* 2000; Roy *et al.* 2004). Competitive life-history strategies were often assumed to be driving species interactions in spite of the fact that the assumed roles played by such competitive trade-offs in ecological theory have been increasingly challenged by various *neutral* models that, although positing the ecological equivalence of interacting species, are still able to predict diversity and abundance patterns similar to those predicted from niche based theories (Hubbell 1979, 2001; Bell 2000, 2001; Chave *et al.* 2002). This debate was expanded to the case of static habitat fragmentation by Solé *et al.* (2004) demonstrating that competitive trade-offs were not necessary to drive species extinction.

The similarity between predictions made by neutral and competitive trade-off models makes it particularly difficult to empirically test which set of mechanisms is actually in operation (Chave 2004). What we have done here is to study the responses of both competitive trade-off and neutral community models to changing habitat availability on dynamic landscapes, and in the process demonstrate that the non-neutral nature of communities can be revealed under specific habitat dynamics. We more precisely adopt a lattice model of dynamic habitat creation and destruction (Roy *et al.* 2004) and determine habitat area-diversity relationships under (1) well-mixed *vs.* local habitat dynamics, and (2) within communities characterized by species equivalence (*i.e.* neutral) *vs.* competition-colonization trade-offs. Results confirm the dominant effect of habitat turnover rate on species loss previously reported (Roy *et al.* 2004), and more importantly show that extinction can result from either spatially-structured habitat processes *or* from the existence of a life-history trade-off. These results suggest the importance of relevant ecological contexts when testing for the neutral nature of ecological communities.

Mean-field dynamics

We first construct a deterministic model corresponding to a *well-mixed* habitat and community dynamics where species have a well-mixed colonizing ability.

Habitat dynamics - In our model, habitat is constantly created and destroyed through a contact process similar to a spreading forest fire opening up new space for plant colonization (Eversman and Horton 2004) or to a spreading wave disturbance opening up gaps in a mussel bed that provide habitat for colonization by subordinate species (Paine

and Levin 1981). More precisely, habitat creation occurs whenever *unavailable* habitat (e.g. dominant tree) is affected by *restored* habitat (e.g. burning tree) and becomes itself *restored* space that in turn becomes *available* (i.e. empty space) for species colonization. Habitat destruction occurs when unavailable habitat spreads into available habitat, which then becomes unavailable for species colonization. Habitat destruction similarly operates as a dominant species (e.g. mussels, trees) recolonizes disturbed gaps rendering the space unavailable for subordinate species colonization. Changes in the proportions of *available* habitat, *x*, and of *unavailable* habitat, *y*, are more precisely given by (Guichard et al. 2003; Roy et al. 2004):

$$\frac{\mathrm{d}x}{\mathrm{d}t} = (1 - x - y) - dxy + \delta_c y - \delta_d x, \qquad (1a)$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = dxy - cy \left[1 - (x+y)^8\right] - \delta_c y + \delta_d x \,. \tag{1b}$$

where c and d are the creation and destruction rates while δ_c and δ_d give the probability of density-independent habitat creation and destruction respectively. In addition to densityindependent processes the rate of growth of *available* habitat (x), is affected by the proportion (1 - x - y) of *restored* sites that are in transition to becoming *available*, as well as by the proportion of sites that are lost to spreading habitat destruction (*dxy*). Similarly, the growth rate of *unavailable* habitat, (y), depends on the increase in the proportion of *unavailable* habitat sites due to spreading habitat destruction, *dxy*, and to the decrease in the proportion of unavailable sites due to spreading habitat creation in the landscape, $cy[1 - (x + y)^8]$, where 8 is the size of the neighborhood in the spatially-explicit model (see below).

Community dynamics - The dynamics of the community are given by the metapopulation equations for multiple competing species (Levins and Culver 1971; Tilman 1994; Roy *et al.* 2004). For the *trade-off* community model a competitive hierarchy exists amongst species such that species *i* is incapable of displacing or overgrowing a superior competitor species *j*, while the superior competitor, species *j*, is capable of displacing species *i* (here increased competitive ability is denoted by a lower rank index, *i.e.* j < i). Colonizing ability runs in the opposite direction of the competitive

hierarchy, where species of inferior competitive rank have greater colonization rates (denoted by β) than those of superior competitors. That is, $\beta_i > \beta_j$ for all j < i. The rate of change in the proportion of sites occupied by the *i*th species can thus be represented (Tilman 1994, Roy et al. 2004) by the following equation:

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = \beta_i p_i (x - \sum_{j=1}^i p_j) - p_i (\mathrm{d}y) - p_i (\sum_{j=1}^{i-1} p_j \beta_j) + m_i (x - \sum_{j=1}^i p_j).$$
(2)

where m_i is the frequency of density-independent migration onto the lattice by individuals of the *i*th species from the regional species pool. If the probability of migration onto a site is small compared to the probability of the site being destroyed ($m_i \ll d\hat{y}$) then the nonzero equilibrium abundance of the *i*th species, \hat{p}_i , can be shown to be (Tilman 1994):

$$\hat{p}_{i} = \hat{x} - \frac{d\hat{y}}{\beta_{i}} - \sum_{j=1}^{i-1} \hat{p}_{j} (1 + \frac{\beta_{j}}{\beta_{i}}).$$
(3)

The minimum colonization rate, β_{min} , required for a species to persist on the landscape with a *positive* abundance can be determined by noting that in order to persist with a positive density an individual must produce greater than one successful colonization event during the lifetime of the patch it inhabits (where τ = average patch lifespan; Keymer *et al.* 2000). That is

$$\beta_{\min} \cdot \hat{x}\tau > 1,$$
$$\beta_{\min} > \frac{1}{\hat{x}\tau}.$$

When we consider that the *rate of patch turnover* = $1/\tau = d\hat{y}$, we can see that

$$\beta_{\min} > \frac{d\hat{y}}{\hat{x}}.$$
 (4)

Equation (4) gives us the minimum colonization rate of the best competitor allowed by the landscape. We can directly use (4) to define the minimum threshold for persistence, β_0 , where $\beta_0 = d\hat{y}/\hat{x}$. That is the landscape dynamics will deterministically drive towards extinction any highly competitive species whose colonization rate is below the minimum threshold β_0 .

We can now present a *neutral* community version of the metapopulation model. For the *neutral* community model each species *i* is competitively equivalent to any other species *j* and thus is incapable of overgrowing any other species. Similarly each species *i* has a colonization rate β_i that is equal to that of all other species (i.e.

 $\beta_1 = \beta_2 = \dots = \beta_i = \dots = \beta_n$). Thus the rate of change in the proportion if sites occupied by species *i* is given by

$$\frac{dp_i}{dt} = \beta_i p_i (\hat{x} - \sum_j p_j) - p_i (d\hat{y}) + m_i (\hat{x} - \sum_j p_j).$$
(5)

The non-zero equilibrium abundance of all species i in the community can be approximated when m_i is relatively low as:

$$\hat{p}_i = \hat{x} - \frac{d\hat{y}}{\beta_i} - \sum_{j \neq i} \hat{p}_j .$$
(6)

In order for a community composed of such species to persist the colonization rate of all species $\beta_i = \beta$ must be greater than $d\hat{y} / x$; that is, the same condition as equation (4) holds. We now compare these persistence thresholds with results from stochastic simulations on a lattice for each of the well-mixed and spatially-explicit habitat dynamics.

Dynamic landscapes on a lattice

Our simulations implement the mean-field model described above on a 256x256 cell lattice where habitat dynamics (creation and destruction) is implemented as an extension of a lattice model originally created to study mussel disturbance dynamics (Guichard *et al.* 2003). More precisely, each lattice cell can exist in one of four states: (*i*) available for colonization, (*ii*) unavailable state representing destroyed habitat, (*iii*) a cell occupied by an individual of species *i*, or (*iv.*) a restored state that is transitional between unavailable and available and that controls the spatial spread of habitat creation. The model has recently been used as a model of habitat dynamics by Roy et al. (2004), and it has been shown to apply to wind disturbed tropical forests (Schilcht and Iwasa 2006) and to mussel bed dynamics (Guichard et al. 2003), which are known to drive habitat dynamics in intertidal communities (Paine and Levin 1981, Wootton 2001). Interestingly, as long as habitat is connected (available habitat above the percolation threshold; With and Crist 1995), the habitat model we adopt allows varying temporal rates of habitat creation and destruction as well as habitat availability while controlling for the spatial structure of habitat distribution showing scale-invariance with weak variation in the scaling exponent (Pascual *et al.* 2002, Guichard *et al.* 2003)

Habitat dynamics - In the *spatially-explicit* habitat dynamic model the spread of *unavailable* and *available* cells throughout the landscape is a spatially correlated process. Habitat destruction happens when *available* states become *unavailable* habitats through one of 8 neighbours (Moore neighbourhood) spreading from adjacent *unavailable* habitat cells with probability *d*. Habitat creation occurs when *restored* cells spread onto adjacent *unavailable* habitat cells with a probability *c*. Finally, *restored* become *available* within one time step. At each time step one *habitat-creation* and one *unavailable* cell are added to the lattice at random locations (density-independent habitat dynamic model are compared to those obtained from a *well-mixed* dynamic model which involves randomizing the spread of habitat creation and destruction in the landscape.

Community dynamics - Community is defined from a set of n = 1000 species constituting a regional pool. At each time step between 10 and 20 individuals randomly drawn from the regional pool (Chave *et al.* 2002) colonize the lattice at random locations (densityindependent immigration rate onto the lattice). Each individual on the lattice disperses in the immediate neighbourhood (8 cells) if colonization is *local*, or individuals disperse to randomly selected cells if colonization is *well-mixed* (random). Colonization success depends on available habitat and on rules specific to the *neutral* and the *trade-off* community models. In both models, habitat creation and destruction dynamics in the landscape are not affected by the presence of resident species. Community dynamics were simulated using local colonization rules, but runs were also conducted using random (well-mixed) colonization rules (i.e. global dispersal)

In the *neutral* community model, migrant species are indistinguishable with regard to their colonization rate and their relative competitive ability. All species have identical colonization rates (in this case colonization occurs with probability of 1) and are equally competitive. Thus *neutral* species can only spread onto empty cells, and mortality is caused only when a site occupied by an individual is subject to habitat destruction.

In the *trade-off* community model, a trade-off between competitive ability and colonization rate is imposed on species. A transitive competitive hierarchy is defined for all species, where the greater a species' competitive ability the lower its colonization rate (Tilman 1994) Hence a species will be able to colonize an empty cell or a cell occupied by another species defined by a lower competitive value, but not *vice versa*. Mortality of individuals is thus due to either the spreading of better competitors, or to habitat destruction

We ran simulations by systematically varying the habitat destruction spreading rate, d, and the creation spreading rate, c, between 0 and 1 as the parameters of habitat dynamics. Varying c with c>0.5 leads to habitat availability above the percolation threshold of 0.59 (Guichard et al. 2003). This property allowed us to explore habitat-diversity relationships while controlling for fragmentation, by varying habitat availability above the percolation threshold (c>0.5). Simulations were run for 4000 time steps with the first 1000 discarded as transients. The average species richness for the community and the average abundances for each species were measured for each simulation. Spreading processes on the lattice were subject to periodic boundary conditions to avoid edge effects.

Results

Well-mixed landscapes - When habitat creation and destruction processes are well-mixed, the lifespan of habitat patches is positively associated with the overall habitat availability. More precisely, the fraction of available sites in the landscape decreases with increasing destruction rate d (Figure 1A), while the rate of habitat turnover (our measure of temporal dynamics in the landscape) increases (Figure 1B). Thus, habitat availability and turnover are negatively correlated.

Increasing habitat destruction rate leads to the expected decrease in species richness in trade-off communities. This result is robust to local species dispersal and is observed for both *local* (spatially correlated) and well-mixed colonization processes (Figure 2A,C). Since *d* corresponds to both *decreasing* habitat availability and *increasing* patch turnover this result is not surprising. This increasing net loss of species with increasing d can be understood as the result of the same deterministic extinction predicted by equation (4) in the deterministic mean-field model. However, this result is not robust to community type: neutral communities with both well-mixed and local colonization did not show the same discernable response in richness to increasing d above a threshold value matching the analytical condition for persistence of all species in a neutral community (equation (4); Figures 2B and 2D). As such it appears that species loss in response to increasing d on well-mixed landscapes is associated with life-history tradeoffs, and can be explained by both habitat area and lifespan. We now show how spatially-explicit landscapes allow discriminating between these habitat properties as drivers of species loss.

Spatially-explicit landscapes - For spatially-explicit habitats, creation and destruction processes are local (i.e. they spread within a neighborhood). In contrast with well-mixed habitats, available habitat area and turnover are positively correlated over a wide range of *d* values when their dynamics is spatially-explicit (Figure 1C,D). These results can be explained by noting that increasing the destruction rate on spatially-explicit landscapes results in increased connectivity between habitat clusters, which facilitates the local spread of the habitat creation process and counterintuitively leads to higher habitat availability (Guichard *et al.* 2003). This negative coupling between habitat area and lifespan has important consequences for species richness.

All trade-off communities, regardless of dispersal scale (local or global), display a negative richness response to increasing habitat destruction rate d (Figure 3A,C). In contrast, neutral communities (Figure 3B,D) only show a negative response to increasing d when species colonization is local (Figure 3D). Similarly to results on well-mixed habitats, neutral communities with global species colonization show no response to changes in habitat destruction and creation rates when their values meet the minimum habitat lifespan for metacommunity persistence (equation 4) when species colonization is global (Figure 3B). Because total habitat availability and the lifespan of available habitat are now negatively correlated in spatially-explicit landscapes, the negative response of species richness to increasing d should only result from the increased patch turnover driving extinction despite the expected positive effect of increased area previously reported for trade-off communities (see above and Tilman *et al.* 1997). In neutral

communities, no deterministic mechanisms of extinction (*e.g.* extinction debt) are operating in relation to habitat availability or lifespan above the minimum colonization rate (Figure 3B). Our results therefore reveal how spatial correlation in both species and habitat dynamics can constitute a mechanism of stochastic extinction in neutral communities (Figure 3D). They further clarify the relative importance of habitat turnover and habitat area in driving species loss.

Community-level patterns

Species-habitat patterns – When we consider the relationship between connected (*i.e.* above the percolation threshold, see model description) habitat area and diversity (Figure 4) we observe how responses to habitat loss on dynamic landscapes require either the community to be structured along a competitive trade-off, or for there to be spatial correlation between habitat creation/destruction and species colonization. If the spatial correlation is disrupted by randomizing either the landscape processes, or species colonization, then neutral communities are incapable of displaying any discernable response to habitat loss within the limits of percolating habitat. That trade-off communities always show strong habitat-diversity responses is explained by the presence of highly competitive but slow spreading species that are always prone to deterministic extinction with decreasing area and increasing turnover (equation (4); Tilman et al. 1997, Roy et al. 2004).

Total community size - Although no significant effect on species richness can be discerned when habitats with neutral communities are randomly destroyed (well-mixed habitat dynamic model), the total community abundance in neutral communities is generally affected by habitat availbility and lifespan as they vary with rates of habitat dynamics (*c* and *d*; Figure 5B). In contrast with trade-off communities, this loss in overall community abundance is stochastic and affects the abundance of each individual species with no associated decrease in species richness. This suggests some level of independence of neutral communities from the zero-sum assumption (see also Chave et al. 2002).

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Species-rank distributions - The relationship between species richness and habitat area demonstrates that mechanisms of community response to habitat loss in dynamic landscapes are either deterministic (*e.g.* competition-colonization trade-off) or stochastic. Such stochastic processes are here shown to emerge from spatial correlation in habitat and community dynamics. The response of communities to habitat dynamics thus requires the presence of a life-history trade-off or spatial correlation in the dynamics of both habitat and the communities. This conditional response to habitat destruction is partly reflected in the rank-abundance distributions where only trade-off communities consistently show a quantitative response to destruction rate, *d*. However, in contrast with species-habitat relationships described above, qualitative features of the rank-abundance curves appeared to offer little in the way of distinguishing between different community types despite these quantitative differences (see also Chave et al. 2002, Roy et al. 2004).

Discussion

Mechanisms of species extinction - In both neutral and trade-off communities, we found temporal dynamics of patch turnover to be the predominant mechanism driving diversity and extinction (see also Roy et al. 2004). More importantly, we revealed two mechanisms explaining species extinction in dynamic landscapes: (i) competition-colonisation tradeoffs ('extinction debt') and (ii) spatially correlated habitat destruction ('extinction drift'). While recent studies have emphasised the importance of life-history trade-offs in explaining species extinction in response to habitat destruction (Hastings 1980; Nee and May 1992; Tilman et al. 1994; Tilman and Lehman 1997; Klausmeier 1998, Roy et al. 2004), we were able to reveal the contribution of stochastic extinction associated with localised habitat dynamics. In communities characterised by local dispersal, local habitat destruction can result in extinction through correlation in species identity between successive destruction events. In other words, extinction on dynamic landscapes may be largely the result of extinction drift associated with spatial correlation of habitat destruction rather than of the selective extinction of the most competitive species in the community. Extinction drift could not be observed in well-mixed simulations and is also lacking from the deterministic condition for species persistence obtained from mean-field theory. One important consequence of this result is the potential for extinction driven by habitat loss in the absence of any selection against competitive species. An important
goal for future studies remains to separate the relative contributions of both stochastic and deterministic extinction; or more specifically, to quantify the specific role played by spatial-correlation in driving biodiversity loss in model and natural dynamic habitats.

Test of neutrality in dynamic landscapes – Theoretical evidence has long suggested that niche differentiation, acting through competition-colonisation trade-offs, may not be instrumental in determining patterns of species diversity (Caswell 1976; Hubbell 1979, 2001; Bell 2000, 2001; Chave et al. 2002). Simulation studies have shown that communities composed solely of competitively neutral or ecologically equivalent species are capable of producing community-level patterns qualitatively similar to those seen when communities are structured along a competitive trade-off hierarchy (Chave et al. 2002; Wilson and Lundberg 2004). For static habitats it has recently been shown that neutral and trade-off communities also show similar responses to habitat percolation thresholds (Solé et al. 2004) defining the threshold of habitat fragmentation and of species extinction. Here we have demonstrated that in a dynamic habitat neutral and trade-off communities respond similarly to temporal dynamics so long as species colonization and landscape processes (habitat creation and destruction) are spatiallyexplicit and local. One important implication of this result is that well-mixed habitat dynamics, by revealing qualitative differences between habitat-diversity responses of trade-off and neutral communities, can provide the adequate ecological context to test for species equivalence.

An inability to distinguish between the community-level patterns produced by neutral (drift) and non-neutral (trade-off) mechanisms would suggest that positing community structure or assembly rules may be unnecessary in order to explain diversity patterns. If competitive differences between species are unable to manifest themselves through distinct and discernable effects then assuaging the operation of non-neutral mechanisms becomes difficult and testing neutrality becomes problematic from an experimental point of view (Chave 2004). We found, similar to the results of a study by Chave et al.(2002), that rank-abundance distributions were incapable of meaningfully differentiating between neutral and trade-off structured communities, regardless of whether the death processes (due to habitat destruction in our study) were correlated, or uncorrelated as was the case in the study by Chave et al. (2002). However, as we noted before, qualitative differences

between the responses of the two communities were noticeable when we shifted our focus from rank-abundance statistics to the relationship between species richness and habitat area. The problematic nature of using monotonically decreasing rank-abundance distributions as a test for neutral interactions has been further underscored by McGill (2003) and Wootton (2005).

Conclusion

Our results demonstrate how the effects of neutral and non-neutral interactions may only manifest themselves under specific circumstances encountered in natural systems. The fact that we were able to establish conditions under which interspecific variations could be revealed suggests the need to consider the ecological context or overall dynamics at play when determining the *neutral* or *non-neutral* nature of communities. The point then may not be to determine whether species are ecologically equivalent in some generalized *a priori* fashion but to determine whether the range of interspecific variability is relevant given the ecological context (*e.g.* the habitat dynamics at work). Incorporating such a context would improve current predictions from existing neutral models, and allow resolving the relative importance of stochastic mechanisms of extinction in response to dynamic habitat loss. Our work shows that spatial correlation in both habitat and species dynamics can provide such a mechanism.

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Figure 1: Responses of average habitat area (\hat{x}) and turnover as c and d are varied over entire parameter range. Figures show both variation in (A) habitat area and (B) turnover for the well-mixed landscape as well as the (C) habitat area and (D) turnover for spatially-explicit landscapes. Habitat area represents total fraction of landscape that is available for colonization, while turnover is measured as one over the average lifespan (τ) of a single habitat patch or site. Note how in well-mixed landscapes area decreases with increasing d while in spatially-explicit landscapes area increases with increasing d over a significant range. Habitat turnover in both landscape models, on the other hand, decrease with increasing destruction spreading.

Figure 2: Responses of species richness as c and d are varied over the entire parameter range in a well-mixed landscape. The diversity responses are depicted for when species colonization is local or nearest neighbour in (A) trade-off communities and (B) neutral communities, as well as for when species colonization is random or well-mixed in (C) trade-off and (D) neutral communities. In the graphs for both neutral community models (B and D) a line is drawn to indicate the combinations of c and d that give the minimum threshold β_0 predicted by the expression $\beta_0 = d\hat{y}/\hat{x}$. Only when colonization is wellmixed does the line representing β_0 correspond to the large jump or sudden transition in species richness(B). When colonization is local the transition in richness occurs well after the theoretically predicted threshold β_0 due to the fact that locally spreading individuals in such models experience smaller available habitat than the total average \hat{x} experienced by random colonizing species, as a result of the spatial correlation in their spreading. This results in the actual minimum threshold of β required for persistence to be higher than the predicted threshold β_0 . Note how all trade-off communities show negative richness response to increasing habitat destruction spread d, while neutral communities show no significant response above the minimum threshold. Negative response to increasing d

appears to be produced by combined effects of decreasing area and increasing patch turnover on well-mixed landscapes.

Figure 3: Response of species richness as c and d are varied over their entire parameter range in a spatially-explicit landscape. The diversity responses are depicted for when species colonization is local or nearest neighbour in (A) trade-off communities and (B) neutral communities, as well as for when species colonization is random or well-mixed in (C) trade-off and (D) neutral communities. All trade-off communities show negative richness response to increasing habitat destruction spread d, while neutral communities only show a significant response when species colonization is local in nature. Thus on spatially-explicit landscapes with increasing d the adverse effects of increasing patch turnover trumps the effects of increasing area.

Figure 4: Relationship between average richness and available habitat. Figures show the responses of both trade-off communities (filled circles) and neutral communities (empty circles) over significant ranges of habitat availability for models encompassing (A) well-mixed landscapes/ well-mixed colonization, (B) spatially-explicit landscapes/ well-mixed colonization, (C) well-mixed landscapes/local colonization, and (D) spatially-explicit landscapes/local colonization. Trade-off communities on well-mixed landscapes show a positive richness-habitat area relationship due to effects of turnover and area acting in sync, while on spatially-explicit landscape dynamics overwhelming the effects of increased area (as noted by Roy et al. 2004). Neutral communities, in comparison to trade-off communities, show no significant response to available habitat save when colonization is local on spatially-explicit landscape. Well-mixed landscapes shown for c = 0.7 and spatially-explicit landscapes shown for c = 0.9. Range of habitat availability created by varying d.

Figure 5: Change in the total abundance of neutral communities as c and d are varied in a well-mixed habitat landscape. Total abundance represented by the fraction of the total

landscape occupied by all individuals in the community. Results shown for when colonization is (A) well-mixed, and (B) local.

Figure 6: Scaled Rank-Abundance curves for the four different landscape-colonization models. The four landscape-colonization combinations are: (A) well-mixed landscape/ well-mixed colonization, (B) well-mixed landscape/local colonization, (C) spatially-explicit landscape/well-mixed colonization, and (D) spatially-explicit landscape/local colonization. The trade-off community is represented by black curves, while the neutral community is represented by red lines. Solid lines for d = 0.2 and dashed or broken lines for d = 0.8.



Figure 1. Habitat availability and turnover as c and d vary



Figure 2. Average species richness as c and d vary in well-mixed landscapes



Figure 3. Average species richness as c and d vary in spatially-explicit

landscapes



Figure 4. Habitat-Diversity relationship



Figure 5. Total community abundance as c and d varied for well-mixed landscape



Figure 6. Scaled Rank-Abundance curves

Chapter 2 Postscript: Transition Statement

Incorporating explicit spatial structure allowed us to demonstrate, for dynamic landscapes, how loss of diversity due to increased habitat destruction could result in part from stochastic extinction of species as well as from the deterministic extinction of the best competitors in the community predicted by the *extinction debt* hypothesis (Tilman 1994). In Chapter 3 we incorporate yet another realistic feature into the standard metapopulation model: competitive uncertainty or probabilistic outcomes in competitive interactions between individuals of different species due to intraspecific variation in competitive ability. Standard metapopulation models traditionally never account for the random individual differences that actually exist within naturally occurring species, hence the working assumption in competitive trade-off models that competition between two individuals from different species is a deterministic process with a clearly predetermined outcome, where the individual from the competitively superior species always displaces the individual from the competitively inferior species regardless of how close together in average competitive ability the two species are. Accounting for within species variation results in the outcome of competitive interactions between species being less predictable or predetermined: occasionally even individuals from competitively inferior species can be expected to win out over those from superior ones.

In the following chapter (Chapter 3) we modify the classic metapopulation model by relaxing the deterministic nature of competitive interactions between species under the assumption that populations are subject to intraspecific variation in competitive ability, all in order to study the predictions of such models when species are subject to evolutionary dynamics (i.e. mutation and selection).

CHAPTER 3: The evolutionary assembly of competitive communities in dynamic landscapes

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Abstract

We study the evolutionary assembly of a community of species whose interspecific interactions are described by a competition-colonization trade-off in the manner of Tilman (1994). Based on earlier predictions (Kinzig *et al.* 1999) that such models predict runaway evolution and self-extinction for all species, we generalize the metapopulation model by incorporating a competition function controlled by a parameter k that relaxes the strictly deterministic character of competitive interactions between species allowing interactions to be more probabilistic in nature. The generalized metapopulation model is able to prevent species from evolving to the low abundance limit of persistence, thus enabling species to co-evolve into stable communities composed of species with non-trivial abundances and distinct limiting similarity relationships between strategies. The earlier results demonstrating evolution towards stochastic extinction become a special limiting case of our new extended metapopulation model. Furthermore, we observe how for intermediate values of k biodiversity is maximized in the system, and how evolutionary branching due to the persistence of transient mutants becomes observable.

Key Words: evolution, community assembly, competition-colonization trade-off, metapopulation, adaptive dynamics, evolutionary branching

Introduction

Discerning the mechanisms that determine how species competing for the same resources are able to assemble into multispecies communities has been a central concern for ecologists. Assembly mechanisms often fall into one of two broad categories: ecological or evolutionary. While ecological mechanisms often result in non-equilibrium assemblages such as those that arise through a balance between immigration and extinction (e.g. Macarthur and Wilson 1963, 1967), evolutionary mechanisms are assumed to allow for equilibrium assemblages that are more adaptive or stable in nature. Underlying evolutionary mechanisms of assembly are often simple models of resource partitioning involving some form of limiting similarity between competitors arising from niche separation (Macarthur and Levins 1967). Alternatively, coexistence can also arise when there is a spatial subdivision of resources and when competing species exhibit lifehistory trade-offs between competitive ability and some other trait value such as fecundity or mortality (Levins and Culver 1971, May and Nowak 1994; Tilman 1994). We endeavour here to study how species co-evolution in a dynamic landscape can structure a community by extending the standard metapopulation models that describe the coexistence of multiple competitors (Levins and Culver 1971, Tilman 1994, Roy et al. 2004). By allowing species in such models to undergo mutation and selection we can investigate how a system that allows species to coexist through the combined effects of life-history tradeoffs and the spatial subdivision of homogenous habitat resources can assemble communities through evolutionary mechanisms.

Previous theoretical studies of how species co-evolve in the presence of other competitors have demonstrated the way evolutionary mechanisms often limit the potential diversity in a community in comparison to invasion-structured communities through the combined effects of species assortment and character displacement (Rummel and Roughgarden 1983, 1985, Taper and Case 1992). What most previous coevolutionary models assumed was some explicitly defined or predefined relationship between carrying capacity and resource distribution, as well as an assumption that competitive interactions increase with the degree of niche/resource utilization overlap. Greater distance in trait value between two species means less niche overlap and diminished effects of competitive interactions. By minimizing niche overlap (through character displacement) co-evolution often ends up driving certain species in the community to extinction (species assortment). Both of these processes - character displacement and species assortment – together help explain the tendency towards stability and the limits to diversity predicted by these previous models. Both Rummel and Roughgarden (1983, 1985), and Taper and Case (1992) attempted to use such coevolutionary models to study faunal buildup on islands in order to explain the phenomena of taxon cycles (Wilson 1961), particularly those observed for the Anolis lizards (Roughgarden and Pacala 1989). Taxon cycles are patterns of species cycling noted in the fossil record and assumed to be caused when co-evolutionary dynamics in a community, resulting from intermittent species introductions or invasions, pushes one or more species in the community to evolve to extreme trait values and eventual extinction. Matsuda and Abrams (1994) were able to further demonstrate that with intraspecific frequency dependent selection a single species, even in the absence of selective pressure from other competitors, could similarly be driven to extinction (i.e. "self-extinction") so long as the carrying capacity function or resource distribution is non-normal in form.

In contrast to the assumptions of evolutionary resource or niche overlap models, standard metapopulation models describe competitive interactions as being equally strong between species regardless of the difference in trait value. Since trait value is traded off with competitive ability, species with a more advantageous trait value (e.g. higher fecundity or lower mortality) will be competitively excluded by species with a less advantageous trait value in local interactions. Coexistence becomes possible not because of the minimizing of explicit overlap in resource use (the resource is always assumed homogeneous) but by the spatial subdivision of the resource which allows persistence of the poorer competitors at the regional spatial scale despite exclusion at local sites due to the compensating effect of fecundity (or lower mortality; Levins and Culver 1971, May and Nowak 1994, Tilman 1994). Examples include marine mollusks (Paine 1966) grass communities (Wedin and Tilman 1993) or insects partitioning food resources (Hanski 1990; Shorrocks 1991). Although on their own competitive life-history trade-offs have been incorporated into evolutionary studies of species diversification and adaptive radiation in the past, most of the studies were based either on mechanistic models that

were motivated by specific systems (e.g. Jansen and Mulder 1999), or had incorporated the assumptions of niche or resource overlap models (e.g. Bonsall and Mangel 2004). Metapopulation theory in general, however, has not been particularly useful as a framework for exploring evolutionary assembly mechanisms, and has, in fact, displayed unrealistic features that make it particularly problematic for studying adaptive or coevolutionary dynamics.

With large scale invasions followed by species assortment metapopulation models such as Tilman's (1994) have been shown capable of allowing a potentially infinite number of species to pack into the system (Kinzig *et al.* 1999). Kinzig *et al.*'s study further demonstrated that over time species will pack in at the high end of the competitive hierarchy which at the same time given the competition-colonization tradeoff also corresponds to the low end of species abundances. As species accumulate at the high diversity limit of the trait space, their abundances become arbitrarily low, while the overall abundance distribution approximates a -3/2 power law relating abundance to fecundity (Kinzig *et al.* 1999). This prediction of potentially limitless diversity in invasion-structured communities, combined with biologically unrealistic low abundances, poses a challenge to the use of such models when studying equilibrium community assemblages as it would appear to suggest that in such systems species would evolve to the low abundance threshold and thus ultimately to stochastic extinction.

In order to study how evolution would structure a community competing for a spatially subdivided resource and subject to the constraints of a competition-colonization tradeoff we extended the standard metapopulation model of Tilman (1994) to allow for evolutionary processes (trait mutation and selection) in a dynamic landscape. Because we suspected the strongly deterministic nature of competitive interactions, assumed to be in effect in metapopulation theory, was to blame for the biologically unrealistic patterns observed by Kinzig *et al.*, we relaxed the strict nature of competitive exclusion in our evolutionary model, making the outcome of competitive interactions more probabilistic. In doing so we were able to observe the evolution of stable multispecies assemblages as well as the possibility that biodiversity could be built up through species diversification and adaptive radiation caused by the persistence of mutant transients .

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The Model: Population mean-field equations

The basic population dynamics in our model are based on the competition-colonization metapopulation models found in Tilman (1994) and Roy *et al.* (2004). For convenience we adopt the same model formulation as Roy *et al.* (2004).

Habitat Dynamics

The landscape in our model consists of sites that are either available or unavailable for habitation by individuals. Habitat turnover occurs due to destruction and regeneration of sites, leaving at equilibrium an average proportion of sites on the landscape as *available*, \hat{x} , and *unavailable*, \hat{y} . Habitat destruction in this model is a disturbance process that spreads from unavailable (destroyed) sites to available sites with probability *d*. Thus the probability that a site will be destroyed by random habitat destruction spread is $(d \cdot y)$. Habitat regeneration occurs when habitat recovery processes spread into adjacent *unavailable* sites with probability *c*. For a given destruction spreading rate, *d*, and creation spreading rate, *c*, the average proportion of habitat that is available, \hat{x} , and unavailable, \hat{y} , will be determined by the solution to the following coupled differential equations (Guichard *et al.* 2003; Roy *et al.* 2004):

$$\frac{\mathrm{d}x}{\mathrm{d}t} = (1 - x - y) - dxy + \delta_c y - \delta_d x$$

and

$$\frac{\mathrm{d}y}{\mathrm{d}t} = dxy - cy \left[1 - (x+y)^8\right] - \delta_c y + \delta_d x$$

The first term in the first equation, (1 - x - y), represents the proportion of the landscape undergoing habitat recovery and thus is in transition to becoming *available*, while the second term, *dxy*, represents the loss of habitat due to spreading destruction. In the second equation, the second term denotes the proportion of *unavailable* habitat that has *at least one* site within its immediate neighbourhood (nearest eight cells) that is undergoing habitat recovery. The terms $\delta_c y$ and $\delta_d x$ give the density independent creation and destruction of available and unavailable sites respectively. This allows the landscape to avoid the absorbing state for either *available* or *unavailable* habitat (see Guichard *et al.* 2003 for details).

Community dynamics

The dynamics of the community are given by the metapopulation equations for multiple competing species (Levins and Culver 1971; Tilman 1994; Roy *et al.* 2004). In our model the community is structured by a competitive-colonization trade-off, where a transitive hierarchy for competitive ability exists amongst species such that species l > species $2 > \ldots$ species $i \ldots >$ species n. Here increased competitive ability is denoted by a lower rank index such that lower ranking species are always capable of displacing or overgrowing species of a higher rank index, while species of higher rank can never displace species of lower rank. As part of the trade-off a transitive hierarchy for colonizing ability also exists but in the opposite direction such that species l < species $2 < \ldots$ species $i \ldots <$ species n.

Each species *i* has an abundance p_i representing the fraction of the total landscape that is occupied by the species. The rate of change in the proportion of sites occupied by the *i*th species can thus be represented (Tilman 1994; *Roy et al.* 2004) by the following equation:

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = \beta_i p_i (\hat{x} - \sum_{j=1}^i p_j) - p_i (d\hat{y}) - p_i (\sum_{j=1}^{i-1} p_j \beta_j), \qquad (1)$$

where β_i represents the colonizing ability of the *i*th species and \hat{x} and \hat{y} represent the proportions of the total landscape that exist as available or unavailable (destroyed) habitat sites. Equation (1) tells us that the growth in density of the *i*th species is due to the fraction of available habitat successfully colonized (first term in the equation), minus the loss due to habitat destruction (second term in the equation), and the loss due to displacement by superior competitors spreading into sites already occupied by species *i* (third term in the equation). Setting dp_i/dt to zero and solving (1) gives us the non-zero equilibrium abundance of the *i*th species, \hat{p}_i (Tilman 1994),

$$\hat{p}_{i} = \hat{x} - \frac{d\hat{y}}{\beta_{i}} - \sum_{j=1}^{i-1} \hat{p}_{j} \left(1 + \frac{\beta_{j}}{\beta_{i}}\right).$$
(2)

We can use the expression for the equilibrium abundance of the best competitor, $\hat{p}_1 = \hat{x} - d\hat{y}/\beta_1$, to solve for the minimum colonization rate required for persistence on the landscape by setting \hat{p}_1 equal to zero and solving for β_1 . We denote this minimum, or threshold, colonization rate β_0 , where $\beta_0 = d\hat{y}/\hat{x}$. For any species *i* to persist in the landscape its colonization rate must larger than this minimum threshold (i.e. $\beta_i > \beta_0$).

Limiting similarity for the trade-off community

It has been demonstrated for metapopulation models like the one described above that when a community is constructed through immigration onto a landscape followed by species assortment, only those species that have established themselves some minimum distance in trait value away from their immediate competitive superiors will have a chance at persisting (see Tilman 1994; May and Nowak 1994; Kinzig *et al.* 1999). The expression for the limiting similarity expected between species in competitive trade-off models has been derived by Tilman (1994) and May and Nowak (1994). In a manner similar to Tilman (1994) we can use Equation (2) to derive an equivalent expression for limiting similarity. The conditions for limiting similarity, or the minimum distance in trait value that a species must be from its most immediate competitive superior can be represented for species n=2 and higher:

$$\beta_{n} > \beta_{n-1} \left[\frac{\hat{x} - \sum_{j=1}^{n-2} \hat{p}_{j}}{\hat{x} - \sum_{j=1}^{n-1} \hat{p}_{j}} \right].$$
(3)

Each species must thus have a colonization rate β greater than the colonization rate of its immediate competitive superior multiplied by the ratio of the areas left over or available after the immediate two best competitors have established themselves at equilibrium (Tilman 1994).

The Model: Lattice-based simulations

Simulations using our lattice-based model provide a stochastic version of the mean field equations described above. In the lattice simulations habitat is defined on a 256x256 cell

lattice and habitat dynamics (creation and destruction) are implemented as an extension of a lattice model originally created to study mussel disturbance dynamics (Guichard *et al.* 2003).

Habitat dynamics - Habitat destruction and creation spreading occur as explicit processes on the lattice in the manner described in the mean-field model above. As well at each time step one *habitat-creation* and one *unavailable* cell are added to the lattice at random locations (density-independent habitat creation and destruction rates: $\delta_c = \delta_d = 1/256^2$).

Community dynamics – Each possible 'species' or strain in our model is defined by a point between 0 and 1 on the phenotypic gradient of colonizing ability, β . The phenotype space between 0 and 1 is evenly divided with a 1/N gradation, making N the maximum number of species that can be defined in this system. N was chosen to be large enough so as to allow β to approximate a continuously varying trait (here N =1000 for all simulations).

Each cell in the lattice in the *available* state can be potentially occupied by at most one individual at a time. Reproduction occurs whenever individuals on the lattice disperse to randomly selected cells. As population dynamics on the lattice are explicit the total community consists of a discrete countable number of individuals

Species interact according to the trade-off rules described in the mean-field model. Hence a species will be able to colonize an empty *available* cell, or a cell occupied by another species defined by a lower competitive value, but not *vice versa*. The colonization rate, β , defines the probability (between 0 and 1) that an individual can successfully spread onto any one of the cells that are accessible to it. Mortality of individuals is thus due to either the spreading of better competitors, or to habitat destruction.

Community dynamics operate according to the rules described above, but with the added feature that there is a probability, with each bout of reproduction/colonization, of an individual clone undergoing a mutation in its trait value β , a certain number of steps away from the parental trait value. Mutation here is a Poisson process defining the average number of steps (distance) in trait value away from the parent's phenotype for every successful bout of reproduction. The average mutation size in phenotype, μ , is thus

equal to the average number of steps in trait value multiplied by the minimum phenotypic distance between species (i.e. μ = average number of steps*(1/N)). Species in our system will thus be subject to selection and will evolve in a dynamic and stochastic landscape. In simulations where immigration of new species is allowed, species are introduced from the low competitive-high colonizing end of the trait gradient at regular time intervals.

We ran simulations by systematically varying d and c as the parameter of habitat dynamics. Varying c with c>0.5 leads to habitat availability above the percolation threshold of 0.59 (Guichard *et al.* 2003). In all simulations, habitat area was varied above the percolation threshold (0.59) ensuring that the all available habitat sites on the landscape were connected to all other sites via some path through the lattice (i.e. there existed no isolated habitat clusters). For all simulations run the first 1000 time steps were discarded as transients. We used periodic (torus) boundary conditions to avoid edge effects, and at each time step in the simulation all the cells on the lattice are updated asynchronously to approximate a continuous time process (Durrett and Levin 1994).

Relaxing competitive exclusion

Running simulations based on a standard competition-colonization metapopulation model (specifically Tilman 1994), and implementing the model so as to allow mutation and selection leads to the evolutionary extinction of all species introduced. Simulations show that all species tend to evolve towards the minimum trait threshold β_0 , and as they approach this minimum threshold their densities continuously decrease to the point where they are subject to increasing chances of stochastic extinction (Figure 1A). These observations were anticipated by the equilibrium distributions first noted by Kinzig *et al.* (1999). A similar evolutionary drive towards "self-extinction" was observed by Matsuda and Abrams (1994). The results appear robust to the different average mutation rates that were defined for the system. In other words it appears impossible for a stable community assemblage to evolve given the assumptions of the Tilman model. If the average number of mutation steps in trait value are made sufficiently small then it is possible to see a community assemblage evolve that, while giving the appearance of stability, is really

transient as each species slowly drifts towards the low abundance, minimum threshold limit for persistence (Figure 1B).

In Tilman's original model (1994) competitive exclusion was assumed to be a deterministic process, where individuals from species of lower rank index (higher competitive ability) were always able to exclude individuals from species of higher rank index (inferior competitors). The strictly deterministic nature of competitive interactions implied a complete absence of *intraspecific* variation in competitive ability amongst individuals – intraspecific variation that could make competitive interactions less deterministic or more probabilistic in their outcome. The equilibrium abundance distributions of species under these assumptions were shown to suggest that evolution would ultimately drive species towards the minimum threshold for persistence (Kinzig *et al.* 1999).

Given that natural populations exhibit a degree of intraspecific variation or random individual differences in trait values it would be reasonable to expect that the competitive interactions between two individuals of different species would entail some uncertainty in outcome. We decided to relax the strict application of the competitive exclusion principle under the reasonable assumption that intraspecific variation in competitive ability would lead to more competitive uncertainty when individuals interact and that mutations resulting in small differences in colonization ability should not be accompanied by such a drastic all-or-nothing difference in competitive ability as described by the Tilman model. We therefore introduced the following competition function that allowed significant departures from deterministic competitive exclusion:

$$C_{i,j} = C(\Delta \beta_{i,j}) = \frac{1}{1 + e^{-k\Delta \beta_{i,j}}}$$
$$= \frac{1}{1 + e^{-k(\beta_i - \beta_j)}} \quad . \tag{4}$$

Here $C_{i,j}$ gives the probability that species j when attempting to colonize a site already occupied by species i will be able to displace or overgrow species i. Parameter k in the equation indicates the degree of uncertainty in the outcome of competition between two individuals of species *i* and species *j*, and as such signifies the degree to which competitive ability varies between the individuals within populations. In other words high k values indicate a strongly deterministic outcome to competitive interactions due to very little intraspecific variation, while low k values describe competitive interactions that are highly probabilistic due to the large intraspecific variation in competitive ability (Figure 2). Using a similar function to describe asymmetric competition between competitors it had been possible to demonstrate the possibility of co-evolution and stable co-existence of two competitors (Law et al. 1997) as well as speciation and biodiversity buildup through deterministic branching (Kisdi 1999; Jansen and Mulder 1999). Note that when k is very large $(k \rightarrow \infty)$, $C_{i,j}$ behaves like a step function, and approximates deterministic competition as described in the Tilman model:

$$C_{i,j} \approx \begin{cases} 1 & \text{if } i > j \\ 1/2 & \text{if } i = j \\ 0 & \text{if } i < j \end{cases}$$

. . .

Incorporating the competition function into Eqn. (1) generalizes the standard metapopulation model, giving us a modified equation for the population dynamics of the *ith* species:

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = \beta_i p_i \left(\hat{x} - \sum_{j=1}^n (1 - C_{i,j}) p_j \right) - p_i (dy) - p_i (\sum_{j=1}^n C_{i,j} \beta_j) p_j .$$
(5)

Note that since all species now have some non-zero probability of displacing any other species we must consider the competitive effects of every species in the community on species *i*, and not just the effects of those species that are competitively superior to species i (i.e. those of lower rank j < i). We can define the fitness, f, of the ith species as its *per capita* rate of growth, and thus $f_i = (1/p_i) \cdot (dp_i/dt)$. By setting species *i* to its carrying capacity ($f_i = 0$), and noting that $1 - C_{j,i} = C_{i,j}$ we get

$$f_{i} = 0 = \beta_{i}\hat{x} - d\hat{y} - \sum_{j=1}^{n} (\beta_{i} + \beta_{j})C_{i,j}\hat{p}_{j}.$$
 (6)

For a system of n species we can rewrite the n fitness equations as a linear system in matrix form:

$$A\underline{\hat{\mathbf{p}}} = \underline{\mathbf{b}} \tag{7}$$

$$\begin{pmatrix} 2\beta_{1}C_{1,1} & (\beta_{1}+\beta_{2})C_{1,2} & \cdots & (\beta_{1}+\beta_{n})C_{1,n} \\ (\beta_{2}+\beta_{1})C_{2,1} & 2\beta_{2}C_{2,2} & \cdots & (\beta_{2}+\beta_{n})C_{2,n} \\ \vdots & & \ddots & \vdots \\ (\beta_{n}+\beta_{1})C_{n,1} & \cdots & \cdots & 2\beta_{n}C_{n,n} \end{pmatrix} \begin{pmatrix} \hat{p}_{1} \\ \hat{p}_{2} \\ \vdots \\ \hat{p}_{n} \end{pmatrix} = \begin{pmatrix} \beta_{1}\hat{x}-d\hat{y} \\ \beta_{2}\hat{x}-d\hat{y} \\ \vdots \\ \beta_{n}\hat{x}-d\hat{y} \end{pmatrix}$$

If the matrix A is nonsingular (det $A \neq 0$), then matrix A has an inverse ($\exists A^{-1}$) such that $\hat{\mathbf{p}} = A^{-1}\mathbf{b}$. That is, there is a vector of abundances $\hat{\mathbf{p}}$ that is a unique solution to the above system of equations. The solution $\hat{\mathbf{p}}$ however may not be biologically realistic, i.e. it may contain negative abundance values. Thus biological realism requires that the values for all β_i be such that $\hat{p}_i \ge 0$, for all j.

As in the original Tilman (1994) and Roy *et al.* (2004) models, the original equations describing species fitness in our metapopulation model (Equation. (1)) are discontinuous functions with respect to β_i , making them problematic for studying evolutionary or adaptive dynamics. Incorporating the competition function $C_{i,j}$ into the model overcomes the problem by defining continuous versions of the fitness equations that are capable of being differentiated. We now use the competition function, $C_{i,j}$, defined above to analytically study and numerically test the adaptive dynamics of a one and two species system, as well as to study larger ensembles of species using stochastic simulations. Our results show that relaxing the strict application of the competitive exclusion principle allows for the evolution of stable multispecies community assemblages driven by the level of uncertainty in the outcome of competition.

Adaptive dynamics of a one-species system

With a new continuous fitness function, (5), we can now apply the tools of adaptive dynamics or continuous evolutionary game theory (Brown and Vincent 1983; Metz *et al.* 1992; Taper and Case 1992; Geritz *et al.*1998; Doebeli and Dieckmann 2000) to study the evolution of a single species system. We start by considering the fitness, f_m , of a mutant m emerging from a single resident species (*species 1*) at carrying capacity:

$$f_m = \beta_m \hat{x} - d\hat{y} - 2\beta_m C_{m,m} \cdot p_m - (\beta_m + \beta_1)C_{m,1} \cdot \hat{p}_1.$$

Since we are interested in the ability of a mutant to invade and establish itself in a resident population when rare we can assume that the invasive/mutant density is very low $(p_m \approx 0)$, and thus the mutant's fitness equation reduces to

$$f_m = \beta_m \hat{x} - d\hat{y} - (\beta_m + \beta_1)C_{m,1} \cdot \hat{p}_1.$$

The density \hat{p}_1 at carrying capacity can be determined from (6) as $\hat{p}_1 = \hat{x} - d\hat{y}/\beta_1$. Furthermore, for this solution to be biologically relevant (i.e. $\hat{p}_1 > 0$) would require $\beta_1 > d\hat{y}/\hat{x}$.

The gradient of selection, $g(\beta_1)$, when resident β_1 is at its carrying capacity is defined by (Geritz *et al.*1998; Doebeli and Dieckmann 2000)

$$g(\beta_1) = \frac{\partial f_m}{\partial \beta_m}\Big|_{\beta_m = \beta_1}.$$

What we are particularly interested in are those values of β_1^* for which the gradient of selection becomes $g(\beta_1^*) = 0$. At these points in the trait space selection is no longer directional. Such fixed points are referred to as "evolutionary singular" strategies (Geritz et al. 1998; Doebeli and Dieckmann 2000). There are two types of stability associated with singular strategies: If they are evolutionary *attractors* such that evolution pushes nearby strategies in the direction of the singular point then they are "convergent stable";

if the singular strategy is incapable of being invaded by nearby mutants then it is an "evolutionary stable strategy" or an ESS. If a singular point both attracts nearby strategies and prevents further evolution once they arrive (convergent and ESS stable) then the singular point is considered a "continuously stable strategy" or CSS (Eshel 1983; Geritz *et al.*1998; Doebeli and Dieckmann 2000).

In order to determine our evolutionary singular points we have to set the selection gradient $g(\beta_1^*) = 0$. Doing so gives us

$$0 = g(\beta_1) = \frac{\partial f_m}{\partial \beta_m}\Big|_{\beta_m = \beta_1} = \hat{x} - \left(C_{1,1} + 2\beta_1 \cdot \frac{\partial C_{m,1}}{\partial \beta_m}\Big|_{\beta_m = \beta_1}\right) \cdot \hat{p}_1.$$
(8)

Solving for β_1 then gives the singular strategy for a one species community, β_1^* :

$$\beta_1^* = \frac{1}{2} \left(\frac{1}{k} + \frac{d\hat{y}}{\hat{x}} \pm \sqrt{\frac{1}{k^2} + \frac{6}{k} \cdot \left(\frac{d\hat{y}}{\hat{x}}\right) + \left(\frac{d\hat{y}}{\hat{x}}\right)^2} \right). \tag{9}$$

Biologically relevant solutions to the above equation are those where $\beta_1^* > d\hat{y}/\hat{x}$. We can now consider the stability of strategy β_1^* , i.e. whether or not the singular value is convergent and/or ESS stable. For the singular point β_1^* to be an evolutionary attractor the following necessary and sufficient condition would have to be met (Geritz 1998; Doebeli and Dieckmann, 2000):

$$\frac{\mathrm{d}g(\beta_1)}{\mathrm{d}\beta_1}\bigg|_{\beta_1=\beta_1^*} < 0.$$
⁽¹⁰⁾

Since it is the case that

$$\frac{\mathrm{d}g(\beta_1)}{\mathrm{d}\beta_1}\bigg|_{\beta_1=\beta_1^*}=-\frac{1}{2}\bigg(\frac{d\hat{y}}{\beta_1^2}+\hat{x}k\bigg),$$

it is clear that the convergent stable condition always holds and that β_1^* is an evolutionary attractor for all realistic parameter values.

To determine ESS stability a different condition has to be met

$$\frac{\left.\frac{\partial^2 f_m(\beta_m, \beta_1^*)}{\partial \beta_m^2}\right|_{\beta_m = \beta_1^*} < 0.$$
(11)

If this condition holds then the singular point β_1^* is located at a fitness maximum and neighbouring mutants will be unable to invade. Equation (11) is essentially a second derivative test for the fitness function to determine whether the singular point is a local fitness *minimum* or *maximum*. Fitness minimums are of interest because they indicate points in the trait space where branching can occur. It turns out that for a one species system that $[\partial^2 f_m(\beta_m, \beta_1^*)]/\partial \beta_m^2|_{\beta_m = \beta_1^*} = -(1/4) \cdot k \cdot \hat{p}_1$, therefore β_1^* will *always* be located at a fitness maximum and thus will always be a continuously stable strategy (CSS). In other words, in a single species system evolution will always lead towards β_1^* , and once at the singular point evolution will come to a halt.

Since for a large range of k parameter values (k < 100) Equation (9) predicts significant differences in trait value between the singular strategy β_1^* and the minimum threshold for persistence β_0 , it is clear that evolution towards stochastic extinction is no longer inevitable since evolution stops at β_1^* without moving any closer to the low abundance threshold β_0 . When the value of k decreases β_1^* becomes progressively larger, moving further away from the threshold β_0 . Recall how when k is arbitrarily large the competition function $C_{i,j}$ approximates a step function allowing Equation (5) to behave like the equations in the original metapopulation model with perfect competitive exclusion. Looking at Equation (9) for large k values then, we find the solutions for the singular value β_1^* to be

$$\lim_{k \to \infty} (\beta_1^*) = 0, \quad \text{and} \quad \lim_{k \to \infty} (\beta_1^*) = \frac{d\hat{y}}{\hat{x}}.$$

The second (biologically relevant) solution is also the minimum threshold needed for persistence, $\beta_0 = d\hat{y}/\hat{x}$. In other words, once the competitive function starts to approximate perfect competitive exclusion, selection will drive *species 1* towards the minimum threshold where its density will get arbitrarily close to 0. On a stochastic landscape this will result in an evolution of the population towards eventual extinction – runaway selection leading to self-extinction (Matsuda and Abrams 1994). This is in fact what was observed with the original metapopulation model with deterministic competitive exclusion. Figure 3A shows for moderate k values (k = 60) how a single strategy establishes itself at a singular strategy β_1^* , far enough away from the minimum threshold β_0 to avoid extinction.

Adaptive dynamics of a two-species system

For two species we have the following fitness functions when both are at carrying capacity:

fitness of species 1
$$f_1 = 0 = \beta_1 \hat{x} - d\hat{y} - 2\beta_1 C_{1,1} \cdot \hat{p}_1 - (\beta_1 + \beta_2) C_{1,2} \cdot \hat{p}_2$$

fitness of species 2 $f_1 = 0 = \beta_2 \hat{x} - d\hat{y} - (\beta_1 + \beta_2) C_{2,1} \cdot \hat{p}_1 - 2\beta_2 C_{2,2} \cdot \hat{p}_2$

The system of equations represented by equation (7) for n=2, can be used to determine the explicit expressions for the equilibrium densities of \hat{p}_1 and \hat{p}_2 .

We now will consider the fitnesses of mutants arising from both resident species I and 2. First we designate f_{m_1} as the fitness of the mutant/invasive whose trait value is correlated with that of *species 1*, and f_{m_2} as the fitness of the mutant/invasive whose trait value is correlated with that of *species 2*. f_{m_1} and f_{m_2} are defined by the following equations:

$$f_{m_1} = \beta_{m_1}\hat{x} - d\hat{y} - (\beta_{m_1} + \beta_1)C_{m_1,1} \cdot \hat{p}_1 - (\beta_{m_1} + \beta_2)C_{m_1,2} \cdot \hat{p}_2$$

$$f_{m_2} = \beta_{m_2} \hat{x} - d\hat{y} - (\beta_{m_2} + \beta_1) C_{m_2,1} \cdot \hat{p}_1 - (\beta_{m_2} + \beta_2) C_{m_2,2} \cdot \hat{p}_2$$

Each mutant now not only has to compete with its own resident population, but also with that of the other resident. The gradients of selection for the two populations are:

$$g_1(\beta_1) = \frac{\partial f_{m_1}}{\partial \beta_{m_1}}\Big|_{\beta_{m_1}=\beta_1}$$
, and $g_2(\beta_2) = \frac{\partial f_{m_2}}{\partial \beta_{m_2}}\Big|_{\beta_{m_2}=\beta_2}$

The singular strategy $\underline{\beta}^*$ now represents a coalition of strategies, such that $\underline{\beta}^* = (\beta_1^*, \beta_2^*)$. To find the singular strategy $\underline{\beta}^* = (\beta_1^*, \beta_2^*)$ for a two species system we set both the $g_1(\beta_1)$ and $g_2(\beta_2)$ to 0, and solve the resulting system of nonlinear equations in order to find the solutions for trait values β_1^* and β_2^* .

$$0 = g_1(\beta_1) = \hat{x} - \frac{1}{2}(1 + k\beta_1^*) \cdot \hat{p}_1 - \left[C_{1,2} + (\beta_1^* + \beta_2^*) \cdot \left(\frac{\partial C_{1,2}}{\partial \beta_1}\right)\right] \cdot \hat{p}_2, \quad (12a)$$

and

$$0 = g_{2}(\beta_{2}) = \hat{x} - \left[C_{2,1} + (\beta_{1}^{*} + \beta_{2}^{*}) \cdot \left(\frac{\partial C_{2,1}}{\partial \beta_{2}}\right)\right] \cdot \hat{p}_{1} - \frac{1}{2}(1 + k\beta_{2}^{*}) \cdot \hat{p}_{2}, \quad (12b)$$

where \hat{p}_1 and \hat{p}_2 were defined previously, and where

$$\frac{\partial C_{1,2}}{\partial \beta_1} = \frac{\partial C_{2,1}}{\partial \beta_2} = k \Big(e^{1/2k(\beta_{1-}-\beta_2)} + e^{-1/2k(\beta_{1-}-\beta_2)} \Big)^{-2}.$$

The solution to this set of nonlinear equations, $\underline{\beta}^* = (\beta_1^*, \beta_2^*)$, lies on the intersection of the two curves represented by both equations (Figure 4). Although there is no obvious closed-form solution to the system of equations in the manner of the one species system, solutions can be readily estimated using numerical algorithms.

The method for determining ESS stability for a two (or more) species system becomes much more complicated than for a one species system. The general condition described by Equation (11) can be used to determine the ESS stability of each species separately only if the other species in the pair is assumed to already be ESS stable at the singular point and thus not prone to branching (Kisdi 1999). Determining convergence stability to ascertain if the vector $\underline{\beta}^*$ represents an evolutionary attractor for the community may be done (but again, only if both species are ESS stable strategies) by determining whether the real parts of the eigenvalues of the Jacobian matrix of the system, *J*, are negative

$$J = \begin{pmatrix} \frac{\partial g_1(\beta_1, \beta_2)}{\partial \beta_1} & \frac{\partial g_1(\beta_1, \beta_2)}{\partial \beta_2} \\ \frac{\partial g_2(\beta_1, \beta_2)}{\partial \beta_1} & \frac{\partial g_2(\beta_1, \beta_2)}{\partial \beta_2} \end{pmatrix}_{\beta_1^*, \beta_2^*}$$

Using both numerical solutions and simulation results one can once again observe how a range of k values allow species to avoid evolving to the low abundance threshold of the trait space and hence to possible extinction (See Figure 5). Avoiding large parameter values for k appears to facilitate biodiversity buildup. When we consider the case of arbitrarily large k values then it can be easily demonstrated that the limit of the nonlinear system of Equations (12 a-b) as $k \to \infty$ results in the following solution for the singular strategy β^* :

$$\beta_1^* = \frac{d\hat{y}}{\hat{x}}$$
 and $\beta_2^* = \beta_1^2 \left(\frac{\hat{x}}{d\hat{y}}\right)$

The first expression for the first species is also the minimum threshold β_0 while the expression for the second species is actually the limiting similarity condition represented by equation (3) for n = 2 species. Substituting the first expression into the second expression solves for β_2^* at the minimum threshold β_0 . These are precisely the equilibrium values that would be predicted for the special case of perfect competitive exclusion between species. Both species pack infinitesimally close to the minimum threshold β_0 as in the original Tilman model.

Multispecies systems

The system of nonlinear equations for any n species community can be represented in matrix form as follows:

$$\underline{\mathbf{0}} = \underline{\hat{\mathbf{x}}} - Q\underline{\hat{\mathbf{p}}},\tag{13}$$

where

$$\underline{\mathbf{0}} = \begin{pmatrix} 0\\0\\\vdots\\0 \end{pmatrix}, \qquad \underline{\hat{\mathbf{x}}} = \begin{pmatrix} \hat{x}\\\hat{x}\\\vdots\\\hat{x} \end{pmatrix}, \qquad \underline{\hat{\mathbf{p}}} = \begin{pmatrix} \hat{p}_1\\\hat{p}_2\\\vdots\\\hat{p}_n \end{pmatrix},$$

. .

and

$$Q_{n \times n} = \left[q_{i,j} \right] \text{ with } q_{i,j} = C_{i,j} + (\beta_i^* + \beta_j^*) \cdot \frac{\partial C_{i,j}}{\partial \beta_i^*}$$

(Recall from (7) that $\hat{\mathbf{p}} = A^{-1}\mathbf{b}$). Both numerical solutions and lattice simulations (Figure 5) confirm that relaxing competitive exclusion between species strongly facilitates diversity buildup. Species spread out across the entire trait space separated by clear limiting similarities between strategies. As well, species no longer crowd the high competitive/low colonizing end of the phenotypic trait space. The results of the stochastic simulation produce communities where species line up along predicted trait values. The model predicts that each species introduced into the system will evolve to a point some discrete distance in trait space (β) above its immediate competitive superior such that communities are built up by sequentially stacking species until all the available trait space finally fills up. It is important to note that the maximum diversity allowed for the system is determined by the *k* parameter: extreme values of *k* result in very low biodiversity due either to the increased chances of stochastic extinction (for very large *k*), or due to evolution leading to a single species community at the high colonizing end of the trait space (as $k \rightarrow 0$).

It can be demonstrated (see Appendix) that when competitive exclusion is a strictly deterministic process $(k \to \infty)$ the solution to the system of equations described by (13), the singular strategy $\underline{\beta}^* = (\beta_1^*, \dots, \beta_n^*)$, becomes $\underline{\beta}^* = (\beta_0, \dots, \beta_0)$. That is, when $k \to \infty$, (13) predicts that all species will evolve to the minimum abundance threshold and thus towards extinction. The evolutionary behaviour of the Tilman model for an *n* species

community, as observed in the stochastic simulations, thus appears as a special limiting case of our generalized metapopulation model.

The k parameter and multispecies assembly

Competitive uncertainty between individuals can promote greater diversity in communities (Figure 6). The absolute distance in trait value between species at the singular strategy is robust to changes in d and c (Figure 6A). At high k values the two species pack in relatively close to each other, as well as close to the minimum threshold β_0 . At the other end of the spectrum with low k values (before k=0) the community of two species collapses into a community of one as the second species evolves beyond the maximum colonizing ability allowed in the model $\beta = 1$ (i.e. $\beta_2 > 1$). Although theoretically the small limiting similarity between species at large k values should allow for high biodiversity (Figure 6A), stochastic extinction due to extremely low species abundances at this high diversity limit (Figure 6B) would tend to render any natural community unviable. As we reduce the value of k however, larger phenotypic distances between species emerge allowing for equilibrium abundances large enough to avoid stochastic extinction and hence amenable to the construction of viable multispecies communities. Further reductions in k lead to still larger equilibrium abundances, yet to fewer opportunities for coexistence due to the large limiting similarities between strains that restrict the number of species that can exist in the available trait space. As kapproaches zero only one species alone at the maximum colonization end of the trait space can persist as the tradeoff structure of the community is effectively destroyed.

Peak opportunities for community assembly would appear to occur in the intermediate range of k values corresponding to a sufficient enough weakening of the link between colonizing ability and competitive rank through random individual differences or within species variation.

The k parameter and speciation

One important result is the role of the competitive uncertainty parameter k for the onset of sympatric speciation through the accumulation of transients. When stochastic simulations are run the first species in the system evolves to the predicted strategy β_1^* , as expected
(Fig. 3A). However an interesting phenomenon often occurs in those simulations where the average number of mutation steps is set to large values: the single strategy in the system, as it approaches its final convergent stable state, can often be seen branching into two distinct strategies (Fig. 3B). Yet we proved above, using condition (11), that the singular strategy β_1^* is *always* an ESS in a one-species system, and therefore species branching is never supposed to occur for any positive abundance values of the first species, i.e. whenever $\hat{p}_1 > 1$. In simulations, high mutation rates are allowing transients to be produced in large enough numbers such that they are occasionally able to bridge over regions of low fitness and competitive exclusion, avoiding extinction long enough to establish a distinct strategy in the adjacent niche. In other words the species branching witnessed here appears to be a stochastic phenomena arising from the continuous production of mutations, and not the *deterministic* form of branching entailed by violation of the condition established by Eqn. (11). Figure 3B also shows branching of the second species leading to a three species community (n = 3) by Eqn. (13).

A resident strategy that is able to constantly generate a continuous distribution of transient types may be able to produce mutants that can bridge the 'troughs' of low fitness in the adaptive landscape in order to establish themselves in the presence of the resident. This type of sympatric speciation, arising through demographic stochasticity, appears to be the explanation for the haphazard branching seen for the top competitors in our lattice simulations. For us to observe the phenomena required that not only mutation rates should be sufficiently high enough but also that the k parameter values occur (once again) in some intermediate range.

The importance of both sufficiently high mutation rates and intermediate levels of competitive uncertainty can be seen by studying the invasive plots for a one-species system (Fig. 7). By starting near the main diagonal on any of the plots one can see that very small mutations away from the resident strategy will lead one along the diagonal until one arrives at the singular strategy β^* . Drawing a vertical line at this fixed point shows the viability of mutants arising from a resident strategy at this point in trait space (Geritz *et al.* 1998). Mutants that are arbitrarily close to this resident strategy will always be in a region of negative growth regardless of the value of *k*, and will thus be unable to

invade the system. This in fact is a visual confirmation of the ESS condition that we established mathematically for the one-species system earlier. However for certain k values (Fig 7A: k = 60) mutants appearing above the resident phenotype would need to only bridge a relatively small region of negative fitness in order to establish themselves in a region of positive growth. For small values of k the regions of negative fitness above the resident strategy are too large to bridge by normal mutation (Fig 7C: k = 10 and Fig 7D: k=5), while for very large k values (for example k = 100 or higher) β^* is near the minimum threshold β_0 where low abundances of the resident species render the resident population either prone to extinction, or cause the adjacent niche space to occur too close to the resident strategy for the establishment of a distinct species. Once again, only at intermediate levels of competitive uncertainty – this time representing a balance between the need to minimize the distances between niches while maximizing the viability of distinct strains – can one see the possibility of disruptive selection leading to successful speciation.

Discussion

Since its introduction by Levins (1969), metapopulation theory has served, through its various modifications and extensions, as an important theoretical framework for conducting ecological research into the properties and dynamics underlying assemblages of species. Yet the theory showed a complete inability to predict the *evolutionary* buildup of biodiversity in competitive communities. Despite its possible value as an explanatory model for taxon cycles (Wilson 1961; Roughgarden and Pacala 1989), the original metapopulation model's demonstrated tendency towards runaway evolution and self-extinction for all species remained a problematic feature. In response we introduced uncertainty into the interactions between species, allowing the model to obtain realistic species packing and abundance distributions through evolutionary processes. Below we discuss the nature of this competitive uncertainty and how varying degrees of it can determine the extent of biodiversity buildup by preventing evolution to self-extinction, and by permitting disruptive selection and adaptive radiation to fill up available niche spaces.

Evolutionary consequences of competitive uncertainty: Balancing species extinction vs. species packing

The theoretical assumption underlying most competitive trade-off models is the idea that "differences among species overwhelm variability among individuals, so much so that individual differences can be ignored" (Clark *et al.* 2003). In their attempt to test the competition-colonization tradeoff amongst forest trees Clark et al. (2003, 2004) have suggested that *individual differences* within species may actually be the critical factor promoting coexistence and biodiversity. Random individual and temporal effects (RITES) may be important in undermining the competitive advantage one species may have over another, thus weakening the ability of one species to competitively exclude another. Such weakening of competitive exclusion through individual differences has helped explain how competitively inferior *Acer* species can coexist with competitively superior *Liriodendron* in forest tree communities (Clark *et al.* 2004). A similar weakening of the competition-colonization trade-off, but through environmental heterogeneity, has allowed more biologically realistic predictions of species abundance patterns in annual plant assemblages (Levine and Rees 2002).

Accounting for the significant variability often found within species allowed us to extend or generalize the traditional competition-colonization model by incorporating a more probabilistic interpretation of competitive interactions between individuals through a competition function, $C_{i,j}$, that relaxed the deterministic nature of competitive exclusion under the reasonable assumption that naturally occurring variation in competitive ability *within* species would likely increase the uncertainty of competitive interactions between competitors. This new generalized model allowed for evolutionary assembly of communities over a range of values for a new parameter, k, which signified the degree to which within population variability rendered competitive interactions less deterministic or more probabilistic in nature. High k values corresponded to situations where populations exhibited little intraspecific variation and hence more deterministic outcomes when competition occurred between individuals of different species. Low kvalues signified a high variability within populations for competitive ability, weakening the one-to-one link between competitive and colonizing capability and making the outcome of competition between two individuals of different species more uncertain. For sufficiently large k parameter values the model and simulations based on the model converge to previous metapopulation models with strict deterministic exclusion. As such the behaviour and predictions of the standard metapopulation models appear to be a special limiting case of our more generalized model.

Previous attempts at modelling the evolutionary build-up of diversity often relied on mechanistic models motivated by specific biological systems, such as Jansen and Mulder's (1999) study which modelled the population dynamics of seed competition in seasonally reproducing organisms when there was a competition-fecundity trade-off. Similarly Bonsall and Mangel (2004) and Bonsall *et al.* (2004) used studies that utilized trade-offs between competitive ability and such life-history characteristics as longevity and parasatoid attack rate to mechanistically model both the evolutionary assembly of rockfish (*Sebastes*) communities and the evolutionary emergence of polymorphism in parasitoid guilds respectively. In contrast to previous studies we were able to obtain species packing and biodiversity build-up by directly generalizing the original metapopulation model without incorporating features specific to any particular biological system, thus retaining the broad applicability or robustness of the original metapopulation model.

What is particularly noteworthy in our study is how the *degree* of uncertainty in competitive interactions between species determined both the *extent* of biodiversity buildup and the *manner* in which it occurred. Specifically the observation of how intermediate values of k could maximize biodiversity in the community in two ways: (i) by striking a balance between species packing and species abundance (i.e. the ability to avoid extinction), and (ii) by balancing the countervailing effects of genetic distance and species viability on the chances of disruptive selection.

Competitive uncertainty and biodiversity buildup

As has already been noted the values of the k parameter arising from the extended model offered a measure of the degree of uncertainty in competitive interactions, or alternatively, a measure of the amount of intraspecific variation present in populations. Decreasing k values in our model corresponded to situations where population heterogeneity or random individual differences undermined the competition-colonization trade-off. While a very high k value may indicate a strong one-to-one correspondence between colonizing ability,

 β , and competitive rank, lower k values indicate a weakening of this one-to-one mapping between colonizing ability and rank in the competitive hierarchy. A value of k = 0 would denote the complete breakdown of the tradeoff itself. It is precisely because we are able to generalize the standard metapopulation model in a direct or simple manner – a generalization not incumbent on the specific features of any particular system – that the role of k in our model is able to have such a clear interpretation

The evolutionary significance of competitive uncertainty was demonstrated when relaxing competitive exclusion by lowering k allowed species to evolve towards an intermediate value of β instead of towards the minimum threshold for persistence. When the outcome of competitive interactions were made less deterministic in nature there then existed for each species a distinct equilibrium point in the trait space where the gains in competitive rank no longer compensated for the losses in colonizing ability.. Similar functions to our competition function, $C_{i,j}$, have been used to study the effects of asymmetric competition in allowing the co-evolution and stable coexistence of species pairs (Law et al. 1997). Here we generalize these results to the evolution of whole competitive communities. We more preciselly show how the function $C_{i,j}$, interpreted here as a probabilistic model of competitive interactions, can allow biodiversity buildup and the evolution of stable assemblages by affecting how species are distributed in trait space. Specifically, we demonstrate how competitive uncertainty between individuals allow the evolutionary assembly of stable multispecies communities by preventing evolution towards unrealistic packing at the low abundance limit of viability, and by allowing species to co-evolve towards distributions marked by discrete minimum phenotypic distances or limiting similarities between strains, and equilibrium abundances large enough to avoid stochastic extinction.

Through this ability to drive the structure of the community k is able to also determine the extent of diversity buildup. Decreasing the value of k increases the phenotypic distance between strains, thus decreasing the number of species that could potentially pack into the community, while at the same time allowing species to persist or avoid extinction through increased abundances. At increasingly high k values the reduction in limiting similarity increases the potential number of available niches in the trait space but at the cost of lowering species abundances to the point where extinction is inevitable. In other words, extreme values of k decrease the potential diversity in the community, either through increased probability of extinction or through decreased niche availability. The trade-off between species packing and increased extinction risk associated with k means that biodiversity is maximized for intermediate values of k where a balance is effected between these two antagonistic processes

Competitive uncertainty and sympatric speciation: The role of mutant transients

Aside from determining the distribution and level of biodiversity in the community the degree of competitive uncertainty can also explain the occurrence of sympatric speciation and adaptive radiation in the community. For stochastic simulations with high mutation rates speciation was often observed as the first species introduced into the system approached its singular strategy. However the phenomenon was only observed for an intermediate range of k values: extreme values of k were incapable of showing branching regardless of the mutation rate. Yet we had also demonstrated that for a one species system the evolutionary singular strategy β^* was always to be found at a fitness maximum (Eq. (11)) and was thus an ESS, supposedly incapable of being invaded by any neighbouring phenotypes. In other words, the adaptive dynamics of the system supposedly precluded any possibility of speciation, and community assembly could only occur through the invasion and further adaptation of new species.

Biodiversity buildup through sympatric speciation or evolutionary branching has been investigated using several models (Jansen and Mulder 1999; Kisdi 1999; Bonsall *et al.* 2002; Bonsall and Mangel 2004), usually involving some form of asymmetric competition. However in all such studies speciation or evolutionary branching was explored as a *deterministic* process arising from violations of ESS stability at various fixed points in trait space. The speciation observed in the stochastic simulations conducted here occurs due to the accumulation and mutation of transient phenotypes across the regions of negative fitness in trait space.

What is important here is the influence of competitive uncertainty controled by k on the occurrence of sympatric speciation. Our analysis demonstrates how k determines the distance in trait space allowing 2 phenotypes to be involved in disruptive selection. Low k

values result in distances between niches that are too large to be likely bridged by transient mutants, while high k values result in species either packing in too close to each other to be sufficiently differentiated, or in too close to the minimum threshold to avoid extinction. In other words, for stochastic speciation to occur there must be just enough competitive uncertainty, or within population variability, to ensure that species can persist as distinct strategies, without allowing limiting similarity between niches to act as a barrier to transient mutants. Similarly to the effect of competitive uncertainty on community diversity, intermediate k values are key in explaining adaptive radiation in competitive communities with competition-colonization tradeoffs.

The discrepancy between the predicted ESS stability and the stochastic evolutionary branching observed here further highlights the limits of continuous evolutionary game theory and the simplifying assumptions it makes about the dynamics underlying evolutionary processes. One of the assumptions of continuous game theory is that only a single resident and a single mutant confront each other at any given time, and that the mutant is arbitrarily close in phenotype to the resident. There is also the assumption that population dynamics are much faster than evolutionary dynamics such that there is only one of two possible outcomes in a contest between resident and invasive: either the mutant successfully invades and replaces the previous strategy to become the new resident, or it does not. That is to say there exists no period of overlap where multiple transients can coexist before demographic equilibrium or extinction takes place. Of course in natural systems a range of transients can persist for quite some time, producing mutants themselves and affecting the dynamics in a population on their way to eventual extinction. A more realistic model of evolutionary dynamics would approach species not as consisting of a single strategy but as encompassing a continuous distribution of phenotypes, as was the case with the populations in our stochastic simulations. The sympatric speciation observed in the stochastic simulations (and unpredicted by the adaptive dynamics of the system) helped to underscore the importance or impact that long transients can have in ecological or evolutionary models. We believe the demonstration to be particularly relevant given the importance that long transients have recently been shown to have in determining the dynamics or distribution patterns predicted for natural systems (Hastings and Higgens 1994; Scheffer and van Nes 2006), as well as the growing

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recognition that ecological and evolutionary theory's focus on the long-term or the asymptotic behaviour of systems may be undermining an understanding of the true processes structuring natural communities (Hastings 2004). What is striking in our results is the impact of uncertainty in an ecological process (i.e. competition) on the onset of evolutionary processes of sympatric speciation and adaptive radiation in the presence of transient dynamics.

Conclusions

Incorporating a competition function that relaxed the strictly deterministic nature of competitive exclusion between species was found to enable metapopulation models to predict the evolutionary assemblage of competitive communities. The competition function's k parameter was taken as a measure of the degree to which the outcomes of competitive interactions were uncertain or probabilistic in nature. It was also found that intermediate values of the k parameter were required to allow maximum biodiversity buildup. Intermediate values of k also allowed for the possibility of sympatric speciation and adaptive radiation through the persistence of mutant transients that were able to bridge regions of negative fitness between adjacent niches. We interpreted the degree of competitive uncertainty denoted by the k parameter to have a biological basis in the random individual differences or variability present in natural populations. We believe we have demonstrated here how such a probabilistic interpretation of competitive interactions can allow a more generalized metapopulation theory to serve as a viable framework for studying the evolutionary assembly of competitive guilds.

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Appendix

We proceed below to demonstrate that *all* species in an arbitrary *n* species system will evolve to the minimum threshold required for persistence, β_0 , when competitive exclusion is strictly deterministic (i.e. $k \to \infty$). In order to determine the singular strategy of an *n* species community, $\underline{\beta}^* = (\beta_1^*, \dots, \beta_n^*)$, when *k* is arbitrarily large we take the limit as $k \to \infty$ for the system of equations represented by (13), here represented by the *r*th equation:

$$\lim_{k \to \infty} \left\{ \hat{x} - \left[C_{r,1} + (\beta_r^* + \beta_1^*) \cdot \left(\frac{\partial C_{r,1}}{\partial \beta_1} \right) \right] \cdot \hat{p}_1 \cdots - \frac{1}{2} (1 + k\beta_r^*) \cdot \hat{p}_r \cdots - \left[C_{r,n} + (\beta_r^* + \beta_n^*) \cdot \left(\frac{\partial C_{r,n}}{\partial \beta_1} \right) \right] \cdot \hat{p}_n \right\} = 0$$

For any arbitrary species r we can take the limit by first dividing the rth equation by k to get:

$$\lim_{k \to \infty} \left\{ \frac{\hat{x}}{k} - \frac{1}{k} \left[C_{r,1} + (\beta_r^* + \beta_1^*) \cdot \left(\frac{\partial C_{r,1}}{\partial \beta_1} \right) \right] \cdot \hat{p}_1 \cdots - \frac{1}{2k} (1 + k\beta_r^*) \cdot \hat{p}_r \cdots - \frac{1}{k} \left[C_{r,n} + (\beta_r^* + \beta_n^*) \cdot \left(\frac{\partial C_{r,n}}{\partial \beta_1} \right) \right] \cdot \hat{p}_n \right\} = 0$$

$$\lim_{k \to \infty} \left\{ \beta_r^* \cdot \hat{p}_r \right\} = 0$$

$$\beta_r^* \cdot \left(\lim_{k \to \infty} \left\{ \hat{p}_r \right\} \right) = 0$$
(A.1)

The expression for the equilibrium abundance of the *r*th species, \hat{p}_r , can be found by solving equation (5) when $dp_i/dt = 0$, determining the expression for the first species \hat{p}_1 , and then substituting it in to the expression for the abundance of the second species \hat{p}_2 . A process of sequential substitutions can be continued until an expression is determined for the *r*th species. Alternatively, we can solve for the *r*th species abundance using Cramer's rule for the linear system represented by equation (7): $\hat{p}_r = \frac{\det A_r}{\det A}$, where A_r is the matrix *A* with its *r*th column vector replaced with vector **b** from (7).

We thus get

$$\lim_{k \to \infty} \hat{p}_r = \frac{k \to \infty}{\lim_{k \to \infty} \det A_r} \qquad (\text{provided } \lim_{k \to \infty} \det A \neq 0) \qquad (A.2)$$

The expression in the denominator can be shown to reduce to $\frac{\lim_{k \to \infty} \det A = \beta_1 \cdot \beta_2 \cdots \beta_n}{k \to \infty}$ Similarly for the numerator, sequentially taking the Laplace expansion starting on the last column of A_r one can show the solution to be $\frac{\lim_{k \to \infty} \det A = \beta_1 \cdots \beta_{r-1} \cdot \Omega_r \cdot \beta_{r+1} \cdots \beta_n}{k \to \infty}$

where Ω_r represents the expression:

$$\Omega_{r} = (\beta_{r}x - dy) - \sum_{m=1}^{r-1} \left\{ (\beta_{m}x - dy) \cdot \left[(1 + \frac{\beta_{r}}{\beta_{m}}) - \sum_{i=m+1}^{r-1} \left((1 + \frac{\beta_{r}}{\beta_{i}}) \cdot \prod_{j=m}^{i-1} (1 + \frac{\beta_{j+1}}{\beta_{j}}) \right) \right] \right\}.$$
(A.3)

Substituting the numerator and denominator into (A.2) gives us

$$\lim_{k \to \infty} \hat{p}_r = \frac{\beta_1 \cdots \beta_{r-1} \cdot \Omega_r \cdot \beta_{r+1} \cdots \beta_n}{\beta_1 \cdots \beta_r \cdots \beta_n} = \frac{\Omega_r}{\beta_r} \,. \tag{A.4}$$

When we substitute (A.4) into (A.1) we can see the linear system represented by (13) reduces to

$$\Omega_r = 0, \qquad \text{for } 1 \le r \le n. \tag{A.5}$$

Starting with the first species then sequentially solving for β and substituting the values of each β into the expression for the next species, it can be readily seen (also by inspection of (A.3)) that for all species equation (A.5) reduces to $(\beta_r x - dy) = 0$, or alternatively $\beta_r = dy/x$, which is the expression for β_0 , the minimum or zero abundance threshold. That is, the singular strategy $\underline{\beta}^* \rightarrow \left(\frac{dy}{x}, \frac{dy}{x}, \dots, \frac{dy}{x}\right)$ as $k \rightarrow \infty$; therefore all species evolve to the zero abundance threshold when competitive exclusion is a strict deterministic process.

List of Figures

Figure 1: Time-series of lattice simulations depicting evolution of species in dynamic landscape when species are defined by classic competition-colonization trade-off. All species introduced at high colonization (low competitive) end of trait space and allowed to subsequently evolve. All species were found to evolve to the minimum threshold, β_0 , where low abundance resulted in extinction. Results found to be robust to different parameter values of *c* and *d*. In (A) c = 0.7, d = 0.6 and average mutation in trait value β , for every bout of reproduction is $\mu = 0.001^*$ (1/N) (where N = 1000; see text for details). When average mutation in trait value is very small, as shown in time-series (B), the very slow evolution to extinction allows species to accumulate into a *non-equilibrium* assemblage (for (B): c = 0.7, d = 0.6 and $\mu = 0.00001^*$ (1/N)). In both (A) and (B) dashed red lines indicate the location of the minimum threshold β_0 .

Figure 2: Graph of competitive-exclusion function, $C_{i,j}$, for different k values. $C_{i,j}$ represents the probability of species j displacing species i when j moves into a site occupied by species i. The greater the colonizing ability of species i (β_i) compared to species j (β_j), the lower the competitive ability of i relative to j, and thus the greater the chance of species j displacing i. Note as k gets larger, $C_{i,j}$ begins to approximate a step function. When k = 0 the trade-off between competitive and colonizing ability is destroyed and all species have equal probability of displacing each other.

Figure 3: Time-series of lattice simulations depicting evolutionary dynamics in a onespecies system for the extended metapopulation model. All results shown for k = 60. (A) Species now avoid evolution to stochastic extinction by evolving to a singular strategy, β_1^* , some distance above the minimum threshold β_0 (c = 0.7, d = 0.6 and $\mu = 0.001*(1/N)$). (B) With very high average mutations in trait value one sees increased chances of disruptive selection or evolutionary branching as the singular strategy is approached (for sufficiently high k values; see text for discussion). Branching appears to be due to the large number of mutant transients produced that are able to escape competitive exclusion long enough to establish a new strategy sufficiently far enough in trait value from the resident.(Here c = 0.7, d = 0.6 and $\mu = 0.0095^{*}(1/N)$).

Figure 4: Graphical depiction of the possible solutions for the system of nonlinear equations described by (312.a) and (312.b) when k = 10 and parameters d = 0.6 and c = 0.7, giving habitat availabilities of $\hat{x} = 0.653642$, $\hat{y} = 0.248802$. Solutions to the system of equations are represented by the intersection of the curves described by the two equations. Each possible solution is a set of paired values of β_1 and β_2 representing a coalition of strategies. However, in the example shown here only points *a* and *b* represent biologically realistic solutions. Points *c* and *d* give values for β_1 and β_2 that entail biologically unrealistic abundance values – i.e. negative abundances. Since points *a* and *b* are equivalent solutions, with just the values for the two strategies reversed, there only exists one possible singular strategy, $\beta_a^* = (\beta_1^*, \beta_2^*)$, in the example depicted here. The solution for point *a* estimated using a numerical algorithm solver was found to be $\beta^* = (\beta_1^*, \beta_2^*) \approx (0.3853, 0.7752)$.

Figure 5: Time-series of a lattice simulation showing community assembly for a large number of species when c = 0.7, d = 0.6, $\mu = 0.001*(1/N)$ and k = 60. Simulation involved introducing species with trait value $\beta = 0.75$ into the landscape at regular time intervals. Time-series graph demonstrates how over time community assembly results in an equilibrium assemblage of species with distinct phenotypic distances between strategies corresponding to the numerical predictions based on equation (3.13). Also noted is how when an individual strategy is lost due to random extinction or drift all species above it trait value shift downwards one niche space.

Figure 6: (A) Curve depicting phenotypic distance or limiting similarity between two strategies in a two-species system as the value of the *k* parameter is increased. The curve becomes broken or discontinuous at some low *k* value corresponding to the point where the two-species system collapses into a one-species system as increasing distance between the two strategies (and from β_0) pushes one of the strategies beyond the maximum colonization rate allowed for the system ($\beta_{max} = 1$). For high *k* values the curve

asymptotically approaches zero as both species pack arbitrarily close together at the minimum abundance threshold β_0 . The curve was found to be robust to changes in *c* and *d*; the only significant effect of varying the two parameters was to change the point of the discontinuous break in the curve at low *k* values at which the two-species system collapsed into a one-species system. (B) Change in densities of the each species (represented as the proportion of landscape sites occupied) as *k* increases. Solid black curve represents abundance values of the first species (or the superior competitor) p_1 , while the broken red line represents abundance values of the second, inferior, competitor, p_2 . The densities of both species decrease as *k* increases, converging as they asymptote at zero abundance. High *k* values, by decreasing the limiting similarity between species (plot (A)), allow more species to pack into the system, while at the same time the resulting low abundances (plot (B)) significantly increase the risk of extinction for all strategies involved; low *k* values allow species to avoid stochastic extinction through large enough abundances, while simultaneously restricting the number of strategies possible by forcing large limiting similarity relationships between strategies.

Figure 7: Pair-wise invasive plots for resident-mutant combinations when (A) k = 60, (B) k = 30, (C) k = 10 and (D) k = 5. Plots shown for parameter values d = 0.6 and c = 0.7, which give habitat availability relationships of $\hat{x}=0.653642$, $\hat{y}=0.248802$. Lines correspond to resident-mutant trait combinations where growth of both strategies is zero. The regions marked by '+' signs indicate resident-mutant trait combinations where both strategies experience positive growth in the presence of the other strategy when at low abundances, while the '- 'signs indicate regions where both experience negative growth in the presence of the other strategy. Mutants experience positive growth, and residents negative growth in the trait space marked by '+/-', while '-/+' signifies the reverse. Both strategies can only coexist together when each strategy is able to invade a population composed of the other strategy (the point where all zero-growth isoclines intersect) allows one to determine the viability of a mutant arising from a resident at or near the singular strategy (see bold arrow in plot (D)). Plots show, for a given set of parameters, how as k increases the

'negative' region above the singular strategy becomes progressively smaller, increasing the likelihood that it can be bridged by a continuous production of transient mutant strategies.



Figure 1. Evolutionary dynamics of standard metapopulation model



Figure 2. Competition function



Figure 3. Evolutionary dynamics of a one-species system



Figure 4. Graphical depiction of the solutions for a two-species system



Figure 5. Evolutionary assembly of multispecies community



Figure 6. Limiting similarity relation in response to k parameter



Figure 7. Pair-wise invasive plots for various k parameter values

Chapter 4: Conclusions

Summary

Modifying the competition-colonization trade-off model in our study yielded interesting results that helped bring into focus the role competitive interactions have in determining community level patterns and properties. In the study we presented here we implemented the standard competition-colonization trade-off model in a couple of important and realistic ways: first we considered the role of *spatial structure* in determining the responses of communities to dynamic habitat loss; second, by accounting for intraspecific variation in populations we relaxed the deterministic nature of competitive exclusion, allowing greater uncertainty in the outcome of competitive interactions between individuals of different species. In both cases incorporating aspects of biological realism into the model changed the way interactions between species affected either the assembly or the responses of the community.

Role of competitive trade-offs and extinction –Competitive trade-off communities, when subject to static habitat destruction, have been known to experience the biased extinction of the most competitive species in the community ('extinction debt'; Tilman et al. 1994; Tilman and Lehman 1997). This deterministic extinction was shown to be quite robust to differences in the spatial structure of the habitat destruction. However in Chapter 2, for dynamic habitats we demonstrated that when species dispersal was local, locally spreading habitat destruction could lead to a spatial correlation of habitat destruction and species identity between successive destruction events. The result was a stochastic extinction or 'extinction drift' associated with spatial correlation of habitat destruction rather than the selective extinction of the most competitive species in the community. We noted how a significant response to habitat loss in dynamic landscapes required either the community to be structured along a competitive trade-off (deterministic extinction), or for there to be some spatial correlation between local habitat creation/destruction spreading and local species colonization (extinction drift). If the spatial correlation was disrupted by randomizing either the landscape processes or species colonization then extinction drift could no longer be observed, as indicated by fact that neutral communities were

incapable of displaying any significant response to habitat loss; only deterministic extinction was possible under these conditions as was indicated by the ability of trade-off communities to still show a response.

As a result we would expect that in dynamic habitats trade-off communities composed of locally dispersing species are likely to experience significant extinction drift in addition to deterministic extinction. This prediction was only possible when the trade-off community was studied *spatially* – stochastic extinction could not be discerned analytically or in well-mixed models. Thus comparing the responses of both the trade-off and neutral communities in our spatially-explicit model revealed the neutral character of all communities subject to local recruitment and locally spreading habitat destruction. Consideration of the explicit spatial structure of the habitat allowed us to discern a less than deterministic role played by competitive differences between species in structuring communities or determining their properties.

Effect of relaxing competitive trade-off for evolutionary assembly – In Chapter 3 we took a different approach, allowing species whose interspecific interactions were defined by a competitive-colonization trade-off to undergo mutation and selection in order to observe the species assemblages that would be predicted to evolve. As was anticipated by Kinzig *et al.* (1999) a stable community assemblage was found to be simply impossible given a strict competitive-colonization trade-off. All species in the system evolved to unrealistically low abundance values and hence to stochastic extinction. However the evolutionary behaviour of competitive trade-off models changed dramatically when we considered how intraspecific variation in competitive ability could make the outcome of competitive interactions between species more uncertain and less deterministic in nature. Implementing competitive uncertainty in the model allowed our model to predict realistic abundances and distinct limiting similarity relationships within assemblages. We thus generalized the standard metapopulation model in use until now, and showed how the evolutionary behaviour of the original model appears as a special limiting case of our more generalized model.

In metapopulation models competitive exclusion between individuals vying for the same site or patch is a strict all-or-nothing interaction where the superior competitor *always* displaces the inferior competitor, regardless of how close in trait value the two

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individuals are (Levins and Culver 1972; Hastings 1980; Nee and May 1992; Tilman 1994). Realistically however, we would expect the outcome of a competitive contest between individuals to have a less certain, more probabilistic outcome, especially if the two individuals in competition are close together in trait value – the inferior competitor occasionally besting or displacing the superior one. This probabilistic interpretation of competition is an expected consequence of the significant amount of within population variation often found in natural systems. Such random differences between individuals within a population can weaken or blur the competitive dominance one species may have over another.

The degree to which intraspecific variation weakened the deterministic nature of competitive interactions between species was signified by the value for the k parameter in our model. When k was arbitrarily large $(k \rightarrow \infty)$ there existed no intraspecific variation in competitive ability resulting in strictly deterministic competitive interactions and consequently runaway evolution and stochastic extinction of all species in the system. When k became low $(k \rightarrow 0)$ the large amount of random individual differences in competitive ability led to the trade-off structure of the community breaking down and ultimately an evolutionary drive towards a single-strategy community located at the maximum colonization end of the trait space. We found that diversity was maximized for intermediate values of k, representing just enough intraspecific variation to relax competitive exclusion and allow for uncertainty in outcome in competitive interactions, but not enough variation to disrupt or severely weaken the trade-structure of the community. What was particularly interesting was how intermediate levels of competitive uncertainty were able to maximize biodiversity in two ways: first, by allowing species to avoid runaway evolution towards stochastic extinction, and secondly by allowing for the possibility of disruptive selection arising due to the fact that the distances between distinct niche spaces were made small enough that they could be bridged by the continuous production of mutant transients.

Thus the *nature* of the competitive trade-off – specifically the functional relationship between colonizing ability and competitive rank – determined how evolution would

assemble a community, determining both the dynamics and the final species distributions that characterize the final assemblage.

Model limitations and future directions for research

The study presented here explored two aspects of the competition-colonization trade-off in structuring communities: the role (or contextual relevance) of trade-offs in driving diversity patterns, and how the nature of the competitive trade-off can affect evolutionary assembly of communities. Although it was not tested in this study, an alternative trade-off between competition and mortality (or longevity) would likely have produced qualitatively similar results given that previous studies have repeatedly demonstrated that general competition models are often robust (qualitatively speaking) to shifts between both types of trade-offs (for example Tilman 1994; Roy *et al.* 2004).

A more serious limitation to our study is the fact that the results and conclusions obtained from our model are strictly limited to competitive guilds – that is, all species are assumed to be at the same trophic level and are furthermore assumed to be competing for a *single* homogeneous resource. It is questionable how robust the predictions of the model would be if interspecific interactions involved competition for more than one resource, let alone for scenarios involving the effects of more complicated interactions like predation or parasitism. Developing more general models for competitive communities would thus require incorporating trophic interactions as well as competition for multiple resources. The challenge is to do this without making the model too mechanistic or too dependent on the particularities of any one ecological system, and ensuring that the model is general or broad enough in its applicability.

Another obvious direction for future research involves utilizing the generalized model found in Chapter 3, and its assumption of competitive uncertainty, to investigate ecological processes involved in structuring communities and maintaining biodiversity – even revisiting previous theoretical results based on the original metapopulation model. However, using the generalized competition-colonization model presented here to study or model *specific* ecosystems would require an effort at parameterizing the model, specifically the value of k. Since k depends on the functional relationship between

colonizing ability (or some other life-history trait) and competitive ability, determining its value for specific communities would require that the within population variation for the traits in question be accurately assessed for all species. There appears at the moment to be no obvious or compelling reason why this could not be done.

Concluding remarks

Incorporating both biologically realistic ingredients into our model – both the spatial structure of species-habitat interactions, and the continuous competition-colonization trade-off - transformed the manner in which competitive interactions determined properties at the community level. In one case incorporating spatial structure weakened the relevance of competitive differences between species in determining which species will go extinct due to dynamic habitat destruction; while in another, relaxing the deterministic outcome of interactions between individuals of different species, based on the assumption of individual differences within populations, allowed co-evolution towards stable multispecies assemblages. The introduction of both these two realistic features into standard metapopulation theory extended the usefulness of competitioncolonization models as a tool for studying both extinction and co-evolution in dynamic habitats. Our model extensions, like Yu and Wilson's (2001) consideration of patch density as a model parameter, or Levine and Reese's (2002) incorporation of environmental heterogeneity, overcomes, we believe, some of the overly simplistic and problematic assumptions of the standard competition-colonization model, allowing us in Yu and Wilson's pithy words, to affirm that "the competition-colonization trade-off is dead; long live the competition-colonization trade-off"!

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