The Role of Consumer Interactions in the Consequences and Causes of Community Phylogenetic Structure

by

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Abstract

Phylogenetic structure measures patterns of evolutionary history within communities – are some communities composed of species more distantly or closely related than expected by chance? Due to common descent, closely related species are more ecologically similar, and so degrees of relatedness in a community may be good predictors of its ecology, more so than the number of species. Whether we are speaking of how phylogenetic structure arises as a consequence of ecological processes, or how phylogenetic structure affects the functioning of communities, the role of consumer organisms has received less attention than the role of resources.

In this thesis, I ask what are the consequences and causes of phylogenetic structure of a potentially multi-level community, focusing on the underappreciated effects of consumer-resource interactions. In Chapter 2, I show how phylogenetic diversity of plant communities predicts the diversity and abundance of arthropods captured in a long-running biodiversity experiment better than species richness alone. In Chapter 3, I show how phylogenetic diversity and species richness interact to explain herbivore damage at a whole community level. In Chapter 4, I explore how phylogenetic structure of old field plant communities differs in plots of
contrasting disturbance history, and speculate as to what factors – such as herbivory – may have contributed to these differences. In Chapter 5, I present a model which incorporates competition – through both resources and consumers of a focal trophic level – and environmental filtering, two factors which are thought to impact phylogenetic structure through their influence on ecological similarity. I show that environmental filtering interacts with competition to determine the coexistence of similar species, and that consumers may have different effects than do resources.

My dissertation provides new insight into the importance of consumers in ecological communities, both through their effect on, and through their response to, patterns of evolutionary history in their prey.
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Chapter 1. Introduction

1.1 Introduction to community phylogenetics


The goals of community phylogenetics can be roughly divided into two broad categories, which I will refer to as the consequences and causes of phylogenetic structure (Cavender-Bares et al. 2009). Phylogenetic structure, broadly defined, is the pattern of evolutionary history, as encapsulated in a phylogenetic tree, of species found together in a community. An important type of phylogenetic structure is phylogenetic diversity, which is a measure of the amount of evolutionary history represented in a community. Though there may be patterns of phylogenetic structure which are not easily encompassed in the term diversity, most research to date has focused on various aspects of diversity, and so in the remainder of this thesis I will refer to phylogenetic structure and phylogenetic diversity interchangeably. There are many different ways of measuring phylogenetic diversity, which depend on how different aspects of a community phylogeny are weighted, and how phylogenetic distances between species pairs are summed up across the whole community (Hardy 2008, Cadotte et al. 2010, Vellend et al. 2010, Pausas and Verdú 2010). If phylogenetic distance can be treated as a useful proxy for evolved ecological distance, then phylogenetic diversity can be treated as a proxy for ecological diversity – or functional diversity, assuming evolved ecological differences between species have led to differences in function, howsoever defined.

It is useful to have a proxy for ecological similarity, because ecological similarity is difficult to define and even more difficult to measure. Though progress is being made in the
measurement and interpretation of species’ traits which relate to their role in ecosystem processes, there may always be aspects of a species ecology which cannot easily be measured, and, as a consequence, the concept of ecological similarity and function will remain nebulous. In contrast, the evolutionary relationship and genetic difference between a pair of species is a concrete concept which can be estimated with high accuracy. Thus, even if the ultimate goal is to understand how organismal traits interact in determining ecosystem assembly and functions, using a proxy for ecological traits, such as phylogeny, will be useful. This is particularly true in a world of rapid change, where there is a need for rapid methods to estimate the nature of ecological relationships.

Phylogenetic distance may also serve as more than just a proxy for one or more types of ecological distance. There may be some cases where phylogenetic information may capture things about species and their interactions that are not evident from their measurable traits. After all, evolutionary history not only tells us about the history of selection and constraint on ecological traits related to fitness, but also tracks aspects of evolution which are unrelated to a species’ traits, such as drift, lineage splitting by vicariance, and other idiosyncratic processes which may be highly contingent. These trait-independent evolutionary factors can sometimes have important impacts on the ecology of species. Though much of ecology can be understood through the traits of organisms, traits are not everything.

1.1.1 Consequences of phylogenetic structure

A major goal of community phylogenetics is to learn about what the phylogenetic diversity of a community can tell us about the properties of that community, including its functioning as a component in a broader ecosystem (Srivastava et al. 2012). Given that there are patterns of phylogenetic structure that vary between communities, whatever their cause, the goal here is to determine how we can use this information to predict things that we want to know about those communities. Most research to date has focused on the effects of phylogenetic structure of species within a single trophic level, so it deals with a sub-community rather than a whole community. I will likewise restrict my discussions in this thesis to single trophic level sub-communities. Expanding theory to encompass whole communities will be an important focus for future progress in this field.

To reiterate this goal of community phylogenetics: given that there are patterns of phylogenetic diversity that vary between communities, the goal is to determine what implications those differences have for the ecology of those communities. The following are some of the important questions related to the consequences of phylogenetic diversity: Do more phylogenetically diverse communities have higher function on average (function being defined on a case-by-case basis) (Maherali and Klironomos 2007, Cadotte et al. 2008, 2009, 2012, Connolly et al. 2011)? Can phylogenetic diversity help us understand how a component community fits into the broader ecological community? Should the preservation of phylogenetic diversity be made a priority in biological conservation?

Chapters 2 and 3 of this thesis have the goal of ascertaining the consequences of phylogenetic structure for the ecology of communities, using plants and their associated herbivore communities as a model system for this approach. To date, this goal of community phylogenetics has received less attention than the goal of understanding the causes of phylogenetic diversity, which I describe below.

1.1.2 Causes of phylogenetic structure

One important goal of community phylogenetics has been to understand what creates patterns of phylogenetic structure (or phylogenetic diversity) within communities of species on a
single trophic level. Much of the work on this question has focused on distinguishing between random and non-random patterns of phylogenetic structure. If there appears to be non-random phylogenetic structure, heuristic explanations are offered for what causes the deviation from randomness. Even if one accepts this procedure, it is a major challenge to find reliable ways to determine that a pattern is not random, a challenge that has yet to be resolved. Part of the problem is that a phylogenetic tree is already a highly non-random pattern, shaped by millions of years of evolution, coevolution, and historical contingency. Given this the challenge is to separate the portion of the community phylogenetic pattern that is related to recent, local, and deterministic ecological forces (Swenson et al. 2006, Kraft et al. 2007, Emerson and Gillespie 2008, Cavender-Bares et al. 2009). To date, the main method used to attempt this separation has been to use null models with hypothesis tests. Null models take the phylogeny of a species pool as a given and then simulate random community assembly from the species pool and calculate phylogenetic diversity metrics. This can give a null distribution of phylogenetic diversity that can be compared to the observed values. The big challenge in this approach is to find ways of simulating community assembly that really are random, and that keep constant factors that are not of interest. There is an enormous literature on the challenges and promises of null models in ecology in general (Connor and Simberloff 1983, 1986, Harvey and Colwell 1983, Quinn and Dunham 1983, Gotelli and Graves 1996, Gotelli 2001, Peres-Neto et al. 2001, Manly and Sanderson 2002, Johnson and Omland 2004), and all of this applies to the use of those models in assessing the role of ecological processes in determining phylogenetic patterns across communities as well (Hardy 2008). In my opinion, such a strong reliance on null models is one of the biggest weaknesses in the field community phylogenetics. This trend may be beginning to change with the development of less heuristic, model-based techniques for community phylogenetic analysis (Ives and Helmus 2011, Chiu and Westveld 2011).

To reiterate this goal of community phylogenetics: given that there are patterns of phylogenetic diversity that vary between communities, the goal is to determine what caused those differences. A few examples of this type of question in community phylogenetics are: Do species differences generated by evolutionary history influence the assembly of communities, thus producing non-neutral assembly? Have certain deterministic forces acted more strongly than others during community assembly? What is the role of historical contingency in community assembly (Peres-Neto et al. 2012)?
I explore some potential causes of phylogenetic and ecological similarity structure of communities in Chapter 4 of this thesis, where I examine empirical patterns of phylogenetic structure in plant communities with contrasting recent history, as well as Chapter 5, in which I use a niche model to ask how the environmental filtering might change the effects of niche similarity on coexistence.

It is also true that the causes and consequences of phylogenetic structure are not likely to be completely independent. That is, if the phylogenetic structure of a sub-community alters its interactions with other sub-communities or its general role in an ecosystem, these changes can feed back to alter the phylogenetic structure of that sub-community. This could lead to negative or positive feedback effects, the outcome of which is currently poorly understood. The interaction between a resource community and its consumers may be an interesting example. In Chapter 4 and 5 I discuss the possibility that high levels of herbivory could suppress the coexistence of closely related plants in a community because of strong apparent competition between them. If this is the case, communities could become more phylogenetically diverse (distantly related species have a higher probability of coexisting). However, in Chapters 2 and 3, I provide evidence that more phylogenetically diverse communities have lower levels of herbivory, and possibly lower abundances of herbivores (see Supplementary material in Chapter 2). This suggests that heavy herbivory could drive changes in the plant community which will lead eventually to conditions unfavourable for herbivores. This is an example of negative feedback, a force that could stabilize herbivore abundances and reduce the likelihood of runaway herbivore outbreaks. Though I do not discuss this idea of feedbacks further in this thesis, I think it will be an area of interesting research in the future, and one which flows naturally from the results I present here.

1.2 The role of consumer interactions in community phylogenetics

In studying both the causes and consequences of phylogenetic structure of communities, much of the theoretical work that forms the basis of current community phylogenetics has concentrated on the interactions of the focal species with their resources. As an example, many studies have attempted to disentangle the relative strength of competitive interactions and environmental filtering on community assembly (some are reviewed in Vamosi et al. 2009). The
idea is that environmental filtering will filter out species whose environmental tolerances do not match the local environment, leading to the coexistence of ecologically similar species, and non-random phylogenetic structure that depends on the relationship between ecological and phylogenetic distance (Webb et al. 2002, Cavender-Bares et al. 2009). On the other hand, classic coexistence theory tells us that there may be a limit on how similar species are to each other in order to coexist, because ecologically similar species compete more strongly (though the general agreement among theoretical ecologists is that there is no absolute limit to similarity (Abrams 1975, 1983; Turelli 1978), only that on average greater similarity in traits related to resource use limits the ranges of other fitness-determining traits that will allow coexistence. This theoretical work is largely based on how species interact with their resources. For example, the classic paper in which the term ‘limiting similarity’ was coined (Macarthur and Levins 1967), showed that species who overlapped in their diets too strongly were limited in the range of competitive ability differences (or fitness differences in modern ecological parlance (e.g. Chesson 1990)), that would allow them to coexist. Much of the work that has followed on from this classic paper has followed suit in defining ecological similarity as the degree to which species consume similar resources (see Abrams 1983 for a review).

More recent theoretical work has shown that the interactions of a group of focal species with their consumers can also have a strong effect on coexistence. Holt (1977) introduced the term ‘apparent competition’ for the phenomenon of species limiting each other through an indirect effect on their shared consumers, rather than their shared resources. The implication is that the effect of shared consumers may be difficult to distinguish from the effect of shared resources. Despite this, most of the community phylogenetics literature has not seriously engaged with the idea of apparent competition (but see Cavender-Bares et al. 2009). Most recent literature does pay lip service to the fact ‘apparent competition’ could have influenced their results, but then often continue their discussion as though resource competition was the main process in play. This may be because empirical and theoretical investigations of the role of consumers in influencing community phylogenetics are still very limited. I explore some of the theoretical side of this question in Chapter 5 of this thesis.

Some recent articles have also noted that consumers could affect phylogenetic structure of their resource species by acting as environmental filters (Cavender-Bares et al. 2009, Yessoufou and Davies 2013). This could happen, for example, if a predator that is very common
in a particular area is particularly adept at catching prey with a particular phylogenetically conserved trait or trait combination. I explore this idea further in Chapter 5 of this thesis.

1.3 The two basic ingredients of community phylogenetics

There are two basic biological requirements that a biological community must have in order for phylogenetic structure to have consequences or to be influenced by ecological causal factors: a) Phylogenetic structure in the traits of organisms must be present and b) the same traits of organisms determine how they interact with the biotic and abiotic environment. One can encapsulate the two ingredients in a single statement: There must be phylogenetic structure in ecologically relevant traits. I will discuss the two ingredients separately below, including how interactions of a focal trophic level with its resources and consumers may influence them.

1.3.1 Phylogenetic structure in species traits

If a group of organisms has phylogenetic structure in a trait, it means that it is possible to partially predict the trait value of an organism based on its position in a phylogeny. But what sort of phylogenetic structure is relevant for ecology? Many tests designed to look for phylogenetic patterns in trait data compare observed data to a null model of ‘random’ evolution across a phylogeny (such as a Brownian motion model (Felsenstein 1985, Freckleton et al. 2002)). In this case, traits can be more conserved than expected, or less conserved than expected, which are two types of phylogenetic structure. This approach is useful when trying to understand the evolution of traits through time in specific clades, but is inappropriate for community phylogenetics (though these tests are still used in community phylogenetics, inappropriately, in my opinion). In community phylogenetics we are simply interested in whether traits are more similar or less similar with increased phylogenetic distance between organisms. For example, if an environment has allowed the coexistence of two similar species, are those species also likely to be closely related? In this case, the deviation from the random model is misleading because most null models of evolution will generate traits which are similar among close relative. Brownian motion models, for example, include phylogenetic inertia. In other words, phylogenetic conservation is what we expect, unless some other force has driven traits to be dissimilar amongst close relatives.
In community phylogenetics, there is phylogenetic structure of traits if there is some statistical association between the phylogenetic distance of species pairs, and their trait differences. The pattern expected in the absence of adaptive responses to ecological interactions is a positive relationship (phylogenetic conservation), but the relationship can also be negative. A negative relationship between phylogenetic distance and trait dissimilarity is often referred to as convergence (Cavender-Bares et al. 2004, 2009), which is misleading for two reasons. First, there can be plenty of convergence in trait evolution across a phylogeny, but the overall pattern of trait similarity and phylogenetic distance could still be completely flat, secondly, other processes besides convergent evolution, such as character displacement amongst close relatives, can generate a negative relationship between trait differences and phylogenetic distance.

There is ample evidence that many ecologically relevant traits are often phylogenetically conserved, though this is by no means universal (Silvertown et al. 2001, Wiens 2004, Wiens and Graham 2005, Silvertown 2006, Losos 2008, Burns and Strauss 2011). Making an estimate of the true frequency of phylogenetic conservation of ecological traits is complicated by the fact that definitions of phylogenetic conservation differ, depending on whether you only require correlation between phylogeny and traits, or that such a correlation exceeds what is expected under some null model, as discussed above. In this area, consumer-resource interactions have great promise as a set of traits which demonstrate relatively predictable relationships with phylogeny.

Consumer interactions have been shown to be phylogenetically conserved under many systems. By this I mean that closely related species tend to share similar diets, and that closely related species tend to have similar assemblages of consumers that feed on them (Ødegaard et al. 2005, Weiblen et al. 2006, Kergoat et al. 2007, Fontaine et al. 2009, Gómez et al. 2010, Chiu and Westveld 2011, Naisbit et al. 2012). There are several reasons why conservation may be very common. The first is that closely related species are likely to be similar in many ways, as discussed above, and so may have similar nutritional requirements. They will also likely provide similar resources for their consumers. A simple example is that many predators are gape-limited and so tend to eat prey of a particular body size. If body size tends to be phylogenetically conserved, then those predators will tend to eat a phylogenetically restricted diet. The second reason is that phylogenetic patterns in an organism’s diet can develop through certain biogeographic and coevolutionary processes that may be partly independent of the species’ traits.
It all adds up to consumer interactions having a fairly predictable relationship with phylogeny, which means that patterns of phylogenetic community structure may be more useful for predictions concerning consumer interactions than for other types of interactions. I examine the phylogenetic structure of the associated arthropod fauna of plants in Chapter 2. One caveat to note, however, is that the degree of phylogenetic conservation of consumer interaction may be strongly dependent on phylogenetic scale (i.e., the depth of the phylogeny of species considered). Phylogenetic conservation is more likely the larger the phylogenetic scale considered. For example, many herbivorous insects tend to feed on plants within the same family (Ehrlich and Raven 1964, Janzen 1980), but when it comes to plant species within a single genus, phylogenetic conservation will often break down (Farrell and Mitter 1998) – which may be because of a recent history of local interaction between plants and insects that occur in the same areas.

1.3.2 Traits determine how organisms interact with the environment

The second ingredient of community phylogenetics is that the traits with phylogenetic structure at least in part determine a species’ interaction with it environment. A classic example is that the sum of potentially many phylogenetically conserved traits leads to a conserved ‘niche’. In other words, closely related species utilize resources similarly and have similar environmental tolerances (Wiens et al. 2010). If this is the case then there are implications for both the consequences and causes of phylogenetic community structure. For example, if distantly related species have less overlap in their resources niches, when found together they may be more efficient at utilizing available resources, leading to greater productivity than when closely related species are found together. This is the basis for much of the recent work on the relationship between the phylogenetic diversity of plant communities and their productivity (Cadotte et al. 2008, 2009, Connolly et al. 2011, Flynn et al. 2011). By the same token, closely related species with similar ‘niches’ are likely to be found in the same area, because environmental conditions may only allow species with certain trait combination to exist. This is the idea of environmental filtering leading to phylogenetic clustering which is common in community phylogenetics. I examine some of these ideas in Chapter 4 of this thesis.

Phylogenetically structured traits may also be involved in a species’ interaction with other species. The classic example is for species in competition. Species with similar traits may
be more likely to compete for the same resources, leading to greater competition amongst close relatives if those traits are conserved (Cahill et al. 2008, Burns and Strauss 2011). Another example is consumer-resource interactions.

If a species’ traits determine its diet, or its suitability as a diet, then these traits will partly determine its interaction with the environment. If these traits are phylogenetically structured, then this will have implication for both the consequences and causes of phylogenetic structure. For example, if a community of plants is composed of distantly related species that share few consumers, then the community of consumers associated with that plant community will be more diverse than for a community composed of plants that are closely related, where many of the plants will share the same consumers. This reflects the effect of of phylogenetic community structure in one trophic level on the structure of another trophic level. This kind of pattern could help us to understand the assembly and functioning of foodwebs at a community scale. I explore this idea in Chapters 2 and 3 of this thesis. In chapter 3, I propose a new term for species whose diet has detectable phylogenetic structure: a cladophage, to distinguish this type of consumers from monophages, oligophages, and polyphages.

Phylogenetically conserved consumer interactions can also influence the causes of phylogenetic structure. For example, species that share consumers will interact indirectly though apparent competition, and could exclude one another via this route. This may be more powerful than resource competition for some organisms. For example, as sedentary organisms, plants only compete strongly for resources with their direct neighbours, whereas they can compete through shared herbivores across much greater distances, because many herbivores are highly mobile. Also, the potential range of a species will be in part determined by the presence or absence and abundance of its resources, so there could also be biotic environmental filtering effects. A more thorough analysis of this issue is found in Chapter 5.

1.4 Thesis Questions

To summarize, I ask two main questions throughout this thesis:

1) Can phylogenetic diversity help to predict ecosystem function?
2) What can we learn about the processes that have acted on ecological community assembly from the patterns of phylogenetic structure left behind?
I study each of these questions through the lens of consumer interactions to some extent and so a third question which runs throughout the thesis might be:

3) What role do consumers play in understanding the phylogenetic community structure of resource communities?

In the remaining chapters of this thesis, I present my own contribution to the field of community phylogenetic, and discuss the appropriate role of community phylogenetics in a modern ecological science.

1.5 Thesis Overview

The following is a brief summary of the last 5 chapters of this thesis and its appendices.

1.5.1 Chapter 2: Diversity of plant evolutionary lineages promotes arthropod diversity

In this chapter my collaborators and I show that indices of phylogenetic diversity are promising as predictors of ecosystem functions. Using a large dataset consisting of arthropod counts collected as part of the big biodiversity II experiment at Cedar Creek Ecosystem Reserve in Minnesota, we show that the phylogenetic diversity of plants is positively correlated with the species richness and abundance of herbivores, parasitoids and predators in a patch. Phylogenetic diversity also interacts with the species richness of plants, such that arthropod richness increases more rapidly with additional plant species in patches with high phylogenetic diversity of plants. These results are robust across different measures of phylogenetic diversity. We discuss the implication of our results for restoration and conservation.

1.5.2 Chapter 3: Species richness and phylogenetic diversity have opposing effects on invertebrate herbivory

In this chapter, I seek to understand how diversity in plant communities influences the occurrence of herbivore damage at the whole community level. In order to measure community-level herbivory, I introduce a mixed model approach using species-level random effects to control for the effects of community composition on average herbivory in a plot. Using this method of analysis, I show that both species richness and phylogenetic diversity of plants in observation plots help to predict herbivory levels measured in those plots. Species richness and phylogenetic diversity of plant interacted to explain herbivory, such that a general positive
relationship between species richness and herbivore damage increased when phylogenetic
diversity was low. I attempt to explain this pattern by suggesting that herbivore’s with
phylogenetically structured diets – for whom I suggest the term ‘cladophage’ – may effectively
be specialists in plant communities with high phylogenetic diversity, or effectively generalists in
plant communities with low phylogenetic diversity. Again, I discuss implications of these results
for restoration and conservation.

1.5.3 Chapter 4: Disturbance alters the phylogenetic composition and
structure of plant communities in an old field system

In this chapter, I was interested in determining whether changes in phylogenetic
composition and structure of communities during succession following disturbance can give us
insights into the community assembly processes. In abandoned agricultural fields, community
composition changes rapidly when a field is plowed, and is thought to reflect a relaxation of
competition due to the elimination of dominant species which take time to re-establish. Several
measures of phylogenetic structure between plant communities were determined in recently
plowed areas and nearby 'undisturbed' sites. There was no difference in the absolute values of
these measures between disturbed and 'undisturbed' sites. However, there was a difference in the
'expected' phylogenetic structure between habitats, leading to significantly lower than expected
phylogenetic diversity in disturbed plots, and no difference from random expectation in
'undisturbed' plots. This suggests that plant species characteristic of each habitat are fairly evenly
distributed on the shared species pool phylogeny, but that once the initial sorting of species into
the two habitat types has occurred, the processes operating on them affect each habitat
differently. This study supports the notion that disturbed plots are more clustered than expected,
suggesting that disturbed plant communities are being more strongly influenced by
environmental filtering of conserved niche traits. I also discuss how herbivory might have
influenced these results.

1.5.4 Chapter 5: The interaction between environmental filtering and
competitive exclusion in a three trophic-level competition model

In this chapter, I develop a mathematical model which incorporates a concept of environmental
filtering into a new version of a classic competition model. The purpose of the model was to shed
some light on a recent debate in community phylogenetics about how competition really should
affect ecological similarity. In the community phylogenetics literature, patterns of clustering and overdispersion are taken to be signs of environmental filtering and competitive exclusion, respectively, when phylogeny is a good proxy for ecological similarity. Competitive exclusion of ecologically similar species is a common expectation based on classic theory on limiting similarity, when ecological similarity refers to niche separation. Critics of community phylogenetics have pointed out that ecological similarity can also lead to similarity in species’ relative competitive ability (or fitnesses), which will actually promote coexistence. This means that the expected effect of competition on ecological similarity is ambiguous. But despite the emphasis on environmental filtering and competition in community phylogenetics, there is no simple mathematical model that incorporates both environmental filters and competition, meaning we cannot easily make predictions about how these factors interact, as opposed to just their independent effects. Therefore, in chapter 5, I present a version of a three-trophic-level competition model – allowing species to compete both through shared resources and shared predators – which incorporates indirect biotic environmental filtering. An analysis of a simplified two species version of the model, suggests that coexistence is maximized at intermediate levels of ecological similarity, and that the strength of environmental filtering effects the position and dispersion of the ideal niche separation. I discuss how the model presented here can serve as an abstract phenomenological model that expresses many of the general characteristics of modern niche concepts.

1.5.5 Chapter 6: Conclusion

In this chapter I summarize the main findings of my thesis and discuss their implications for the field in general. I also discuss possible future directions that could build upon the work I describe in this thesis.

1.5.6 Appendix 1: Bayesian phylogeny for all plant species found at the Koffler Scientific Reserve at Jokers Hill, Newmarket, Ontario, Canada using five barcoding genes.

The effective employment of community phylogenetic techniques to ecological questions requires robust phylogenies for the species that are being studied. In order to facilitate this for studies of plants which occur at the University of Toronto’s field station: the Koffler Scientific
Reserve, I provide as an appendix a phylogenetic tree containing approximately 70% of the plant species found on the reserve. This includes nearly all common plants on the property and was generated using a Bayesian analysis of five barcoding gene region sequences, which were downloaded from Genbank.

1.6 References


Connor, E. F., & Simberloff, D. 1986. Competition, scientific method, and null models in ecology: because field experiments are difficult to perform, ecologists often rely on evidence that is nonexperimental and that therefore needs to be rigorously evaluated. American Scientist 74:155-162.


Chapter 2. Diversity of plant evolutionary lineages promotes arthropod diversity

Russell Dinnage, Marc Cadotte, Nick Haddad, Greg Crutsinger, and David Tilman

This chapter is the result of a collaboration with Marc Cadotte, Nick Haddad, Greg Crutsinger and David Tilman. David Tilman was instrumental in setting up and maintaining the experiment from which the data were drawn, which was started in 1994 and has been running ever since in Minnesota. Nick Haddad, Greg Crutsinger, and David Tilman have all been involved with collecting and compiling the data into more manageable forms and calculating cumulative diversity and abundance measures, as well as helping with the identification of insects and their functional categories. Marc Cadotte calculated much of the initial phylogenetic diversity metrics and generated the phylogeny from which they were calculated (in collaboration with Jeannine Cavender-Bares). I designed and performed all of the analyses presented in the chapter, as well as writing the manuscript. All of the authors contributed comments on the original manuscript. This chapter is published as:


2.1 Abstract

Large-scale habitat destruction and climate change result in the nonrandom loss of evolutionary lineages, reducing the amount of evolutionary history represented in ecological communities. Yet, we have limited understanding of the consequences of evolutionary history on the structure of foodwebs and the services provided by biological communities. Drawing on 11 years of data from a long-term plant diversity experiment, we show that evolutionary history of plant communities – measured as phylogenetic diversity – strongly predicts diversity and abundance of herbivorous and predatory arthropods. Effects of plant species richness on arthropods become stronger when phylogenetic diversity is high. Plant phylogenetic diversity explains predator and parasitoid richness as strongly as it does herbivore richness. Our findings indicate that accounting for evolutionary relationships is critical to understanding the severity of species loss for foodwebs and ecosystems, and for developing conservation and restoration policies.
2.2 Introduction

If the Tree of Life is an apt metaphor for the diversity of organisms on earth and their relationships, then it is being pruned – whole branches at a time. The accelerating loss of species in the last century has motivated ecologists to understand the role of species diversity in ecosystem functioning (Tilman 1997; Knops et al. 1999; Loreau et al. 2001; Balvanera et al. 2006; Cardinale et al. 2006; Haddad et al. 2009; Scherber et al. 2010). But realistic extinctions are often not random with respect to their evolutionary relationships, leading to loss of evolutionary history at a greater rate than expected based on the number of species lost (Heard & Mooers 2000; Purvis et al. 2000; Von Euler 2001; Vamosi & Wilson 2008; Willis et al. 2008; Winter et al. 2009), and resulting in evolutionarily impoverished communities. Indeed, recent studies have shown that anthropogenic disturbance and climate change can lead to sharp reductions in phylogenetic diversity of local communities (Knapp et al. 2008; Willis et al. 2008; Dinnage 2009; Helmus et al. 2010; Silver et al. 2012). Our current understanding of the effects of phylogenetic diversity on community-level properties and the services they provide is poor, though recent research has shown that phylogenetic impoverishment of communities results in a reduction of functions such as plant productivity (Maherali & Klironomos 2007; Cadotte et al. 2008; 2009; Connolly et al. 2011; Flynn et al. 2011). Almost nothing is known about how phylogenetic impoverishment of plants might affect higher trophic levels (e.g. Srivastava et al. 2012).

Phylogenetic conservation of ecologically important traits is common in plants (Futuyma & Agrawal 2009; Weins et al. 2010), leading to the prediction that phylogenetically diverse plant communities represent a larger trait-space and are more likely to contain multiple functional groups – an explanation for why function tends to increase with diversity of all types (Tilman 1997). However, linking different ecosystem functions to particular plant traits is a challenge (Wright et al. 2006), such that interactions among multiple traits and species in shaping ecosystem-level properties may be sufficiently complex that phylogenetic relationships are more efficacious at measuring functional diversity than current methods. Phylogenies have the
advantage of integrating phenotypes – some of which may be unmeasurable – and the influence of past evolutionary events into a single measure (Cadotte et al., 2009; Srivastava et al. 2012).

Most studies of phylogenetic diversity to date have focused on plant communities. As plants support a wide array of herbivore species that feed upon them, as well as the predators that feed on herbivores, the loss of plant phylogenetic diversity should propagate up to consumers. Some studies have shown a positive, but often weak, correlation between plant species richness and the number of animal species inhabiting a community (Murdoch 1972; Root 1973; Southwood et al. 1979; Andow 1991; Siemann et al. 1998; Knops et al. 1999; Mulder & Huss-Daniel 2001; Haddad et al. 2009; Scherber et al. 2010; Schultd et al. 2011). Given the importance of the evolutionary history of plant traits for the animals that use them, we ask whether phylogenetic diversity of plant communities is a better predictor of the diversity and abundance of higher trophic levels than species richness alone.

Phylogenetic diversity may be particularly important for herbivore communities because many herbivores show phylogenetic structure in their diets – they feed on groups of closely related genera or species (Odegaard et al. 2005; Weiblen et al. 2006). This ‘niche hypothesis’ may occur both because closely related plant species may share nutritional or feeding cue traits through common ancestry, or because of a complicated shared evolutionary history between herbivore and plant clades. Patterns of speciation and biogeography can produce phylogenetic patterns in an herbivores’ diet (Jaenike 1990; Brooks & McElennan 2002; Futuyma & Agrawal 2009), creating idiosyncratic relationships between plant traits and herbivore feeding preferences which may be difficult to link from a functional perspective, and so phylogenetic diversity is likely to be important to higher trophic levels as more than simply a proxy for unmeasured trait and functional diversity.

Besides the creation of more arthropod feeding or habitat niches, phylogenetic diversity might affect arthropod diversity indirectly through its effects on plant productivity (‘abundance hypothesis’). Because niche differentiation may be higher in more distantly related plants, more phylogenetically diverse plant communities can achieve higher levels of plant biomass – an effect being documented by a growing literature (Cadotte et al. 2008; 2009; Connolly et al. 2011; Flynn et al. 2011). Such an increase in plant productivity will provide a larger resource base for herbivores, and more habitat volume for predators. This could increase the overall
abundance of arthropods, and consequently increase species richness through abundance based 'sampling' (Colwell and Gotelli 2001).

Using a dataset of over 700 arthropod species and over 110,000 arthropod individuals from the long-term biodiversity experiment conducted at Cedar Creek Ecosystem Science Reserve in Minnesota (Tilman 1997; Haddad et al. 2009), we asked whether phylogenetic diversity and species richness of plants affected the cumulative species richness and abundance of herbivorous and predatory arthropods collected over 11 years in 168 plots. We then ask whether the effects of plant phylogenetic diversity and species richness on arthropods are most likely explained by increases in arthropod feeding and habitat niche diversity, or through a simple abundance effect ultimately caused by plant productivity.

We hypothesized that high phylogenetic diversity in plants would lead to high species richness of arthropods, and that arthropod community composition would be less similar on more distantly related plant species. We also hypothesized that diversity and composition relationships would be weaker, and the 'abundance' hypothesis more likely than the 'niche' hypothesis for predators and parasitoids as compared to herbivores, because predators interact with plants less directly (Scherber et al. 2010; Schuldt et al. 2011).

2.3 Materials and Methods

2.3.1 Experimental set-up and data collection

Arthropod data were collected from a long-term experiment at Cedar Creek Ecosystem Science Reserve, in which species richness of perennial plants was manipulated in 1994 and then maintained since by hand-weeding 3-4 times annually (Tilman 1997). A total of 168, 13x13 m (reduced to 9x9 m in 2000) plots had 1, 2, 4, 8, or 16 plant species, with plant identities chosen at random. Arthropods were collected using annual sweep-net samples from years 1996-2006 (Haddad et al. 2009), in which plots were swept 25 times per sample.

Arthropod data from the 11 years were summed across all years by trophic level (herbivores, predators or parasitoids) for the analysis reported here. We chose to use cumulative
species richness data for our main analysis because it increased the probability of including rarely sampled species. Since the sweep-net technique may miss species in any given year, cumulative species richness will better reflect the true diversity of a plot because of repeated sampling. Although we pooled data for our primary analysis, we also conducted analyses on annual arthropod data, and found results consistent with those of pooled data (see Supplementary Information – Part 1; Table S1-1).

2.3.2 Phylogeny

We generated a maximum-likelihood phylogeny for all 21 plant species that occurred in the plots, using genes (*matK*, *rbcl*, *ITS1* and *5.8s*) downloaded from Genbank (details in Cadotte et al. 2009). The phylogeny was converted to an ultrametric tree, and we standardized branch lengths by dividing them by the maximum distance on the tree (the split between Monocots and Dicots).

2.3.3 Phylogenetic diversity measures

We quantified phylogenetic diversity of plant communities and analyzed its effects using a number of metrics, but here we show the result from a single measure: $H_{aed}$ (Cadotte et al. 2010). We chose this measure because it was not strongly dependent on plant species richness for either its mean value or its variance, and therefore both $H_{aed}$ and species richness of plants could be included in the analysis, and their independent effects separated, without encountering problems with colinearity and heteroscedasticity (See Supplementary Information – Part 2; Figure S1 for details). $H_{aed}$ is an entropic measure integrating the abundance weighted evolutionary distinctiveness of each species in the community. $H_{aed}$ scales evolutionary distinctiveness of a species by its relative abundance, such that diverse communities are those where abundance is proportional to evolutionary distinctiveness, with distinct species having high abundance and those with many close relatives having lower abundance (Cadotte et al. 2010).
We calculated the phylogenetic diversity of plants for each plot within each year for which percent cover data were available (1996-2000) and used the average across all years as the explanatory variable. Since percent cover data were not available for all years, we consider this a temporal sample that reflects the general phylogenetic structure of a plot. Since plant species composition was controlled through hand-weeding, any deviation in this measure subsequent to the year 2000 would be entirely from changes in relative abundance, and would only affect the outcome of our model if different plots responded differently through time. Such divergence appears to be small because a linear mixed model with year and plot as independent crossed random effects explained most of the variation in $H_{\text{arc}}$ (pseudo-$R^2 = 0.86$), leaving only about 14% of the variation for plot*year interaction and error.

### 2.3.4 Effects of Plant Phylogenetic and Species Richness on Arthropod Communities

To test for the effects of plant phylogenetic and species richness on arthropod community richness and abundance, we analyzed data using generalized linear mixed models (GLMMs). Dependent variables included cumulative species richness or abundance of arthropods ($N=122$ plots); independent variables included trophic class, plant phylogenetic diversity, plant species richness and all their interactions as fixed factors and plot as a random effect. Non-significant higher order interactions were dropped from the models. Since both species richness and abundance are count data, we used Poisson distributed errors in both cases. Arthropod species richness showed no sign of overdispersion ($\chi^2$/residual df $= 0.58$), but arthropod abundances did ($\chi^2$/residual df $= 12.68$), and so for this model we included an additional observation random effect to account for it. To improve normality and homoscedasticity of the residuals, we used a log link in the model of cumulative arthropod species richness and a square root link in the model of arthropod abundance. Significance of fixed factors was determined with parametric bootstrapping (Pinheiro and Bates, 2000) with 1000 bootstrap replicates per factor. Monoculture plots were excluded because phylogenetic diversity is undefined for a species richness of one. We tested for non-linearity by including polynomial terms as predictors in separate models for each trophic class. If they significantly improved the model fit, under a likelihood ratio test, we included these quadratic terms in plotting the fitted plane (Figure 2-1).
To compare the effects of plant species richness and phylogenetic diversity on a common scale, and to assess their relative strengths as explanatory variables, we first standardized the regression coefficients by multiplying them by the standard deviations of their respective predictor variable. This puts both species richness and phylogenetic diversity coefficients on a common scale measuring the expected change in arthropod community property per standard deviation of the predictor variable (the coefficient has a unitless denominator). To preserve the interpretability of the species richness coefficient as the change in the dependent variable with an increase of one species in a plant community, we then divided both coefficients by the standard deviation of species richness. This restored the species richness coefficient to its original scale, and transformed the phylogenetic diversity measure to a comparable scale, which we refer to as 'species comparable units'. Species comparable units represent the change in the dependent variable expected when phylogenetic diversity is increased by the same number of standard deviations by which one species would increase species richness.

Additionally, we repeated all the above statistical analyses while excluding all terms including phylogenetic diversity and compared the fit of this reduced model to the full model by calculating the difference in their Akaike Information Criterion (ΔAIC). Generally values of ΔAIC greater than 10 are considered strong evidence that the full model is better than the reduced model.

2.3.5  'Niche' vs. 'Abundance' Hypotheses

To test whether phylogenetic diversity of plants affected arthropod communities through increases in niches or through increases in abundance linked to plant productivity, we performed a number of additional analyses.

In order for there to be an increase in the number of potential niches for arthropods with increasing plant phylogenetic diversity, arthropods must segregate between plant species in such a way that close relatives will have more similar arthropod assemblages. We tested whether we could detect signs of such a segregation using data from monoculture plots (2-3 plots each for 16 species: 35 total). We pruned the phylogenetic tree to include only the 16 herbaceous species that were planted in pure monoculture in this experiment. For each trophic class separately, we
calculated an index of arthropod species overlap – Jaccard's similarity index (Jaccard 1901) – for each pair of plant species and compared it with their phylogenetic distance using a Pearson correlation. We tested the significance of this correlation with a null model randomization, by comparing the observed correlation coefficient to a distribution of correlation coefficients from 1000 datasets, generated by randomly shuffling the tips of the phylogeny. This procedure is identical to that used by Cavender-Bares et al. (2004), only replacing plant species spatial overlap with plant species arthropod assemblage overlap. Correlation was significant if the observed value was equal to or less than 95% of the simulated values. We also performed Mantel tests, and results were consistent with the above null model approach.

Additionally, we used Jaccard's distances (1 - Jaccard similarity) in an hierarchical clustering analysis, using Ward's method, to cluster together plant species in term of their degree of similarity in arthropod species composition. We compared the resulting dendrogram with the phylogram representing phylogenetic relationships, as an informal illustration of their correspondence for different trophic classes.

To test whether higher arthropod species richness could be explained by higher arthropod abundance, we performed an analysis on rarified arthropod species richness, obtained using standard methods (Colwell and Gotelli 2001). Arthropod richness was rarefied to 122, 23, and 8 individuals for herbivores, predators, and parasitoids respectively, which was the minimum abundance found in any plot. The model was the same as described for arthropod species richness and abundance, except the data were no longer count data, and so regular Gaussian errors were modeled. Rarefied richness was square root transformed prior to analysis to improve normality and homoscedasticity of residuals.

Consumer responses to plant phylogenetic diversity or species richness could be caused indirectly through their effects on plant productivity. We tested whether higher plant phylogenetic diversity and species richness increased plant productivity by analyzing square root transformed dry biomass measurements taken from each plot yearly using the same model as described above.
Table 2-1. Model output showing effects of trophic level, plant species richness, plant phylogenetic diversity, and their interactions on cumulative arthropod species richness, abundance, and rarified richness. Back-transformed CI is the 95% confidence interval after performing the inverse link function (lower CI, mean, upper CI). For different trophic classes, the intercept or main effect is included in the estimate and the back-transformed confidence interval, so the CI is based on the actual values, and not the deviations from the average. For plant species richness, plant phylogenetic diversity, and their interactions with trophic class, the back-transformed CI is the change in the dependent variable on the original scale with a increase of one species comparable unit, evaluated at the intercept.

<table>
<thead>
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<th>Dependent Variable</th>
<th>Factor</th>
<th>Estimate</th>
<th>SE</th>
<th>Back-transformed CI</th>
<th>Ch2 Value</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arthropod Species Richness (log link)</td>
<td>Intercept</td>
<td>3.313</td>
<td>0.012</td>
<td>(2.842, 27.471, 28.114)</td>
<td>43986</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Herbivores</td>
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<td>0.012</td>
<td>(81.103, 62.616, 64.168)</td>
<td>43986</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Predators</td>
<td>2.991</td>
<td>0.021</td>
<td>(19.091, 19.896, 20.735)</td>
<td>43986</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Parasitoids</td>
<td>2.812</td>
<td>0.023</td>
<td>(15.909, 16.64, 17.405)</td>
<td>43986</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Plant Species Richness (SR)</td>
<td>0.016</td>
<td>0.002</td>
<td>(0.323, 0.435, 0.547)</td>
<td>50.1</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Plant Phylogenetic Diversity (PD)</td>
<td>0.014</td>
<td>0.002</td>
<td>(0.266, 0.397, 0.527)</td>
<td>32.1</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Diversity Interaction (SR*PD)</td>
<td>0.006</td>
<td>0.002</td>
<td>(0.041, 0.167, 0.293)</td>
<td>6.55</td>
<td>1</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td>TC*SR</td>
<td>Herbivores:SR</td>
<td>0.020</td>
<td>0.003</td>
<td>(0.424, 0.542, 0.66)</td>
<td>5.43</td>
<td>2</td>
<td>0.05</td>
</tr>
<tr>
<td>TC*SR</td>
<td>Predators:SR</td>
<td>0.018</td>
<td>0.004</td>
<td>(0.308, 0.507, 0.706)</td>
<td>5.43</td>
<td>2</td>
<td>0.05</td>
</tr>
<tr>
<td>TC*SR</td>
<td>Parasitoids:SR</td>
<td>0.009</td>
<td>0.004</td>
<td>(0.037, 0.257, 0.476)</td>
<td>5.43</td>
<td>2</td>
<td>0.05</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Herbivores:PD</td>
<td>0.013</td>
<td>0.003</td>
<td>(0.228, 0.364, 0.5)</td>
<td>5.43</td>
<td>2</td>
<td>0.05</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Predators:PD</td>
<td>0.013</td>
<td>0.004</td>
<td>(0.143, 0.356, 0.573)</td>
<td>5.43</td>
<td>2</td>
<td>0.05</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Parasitoids:PD</td>
<td>0.017</td>
<td>0.004</td>
<td>(0.236, 0.47, 0.703)</td>
<td>5.43</td>
<td>2</td>
<td>0.05</td>
</tr>
<tr>
<td>Arthropod Abundance (square root link)</td>
<td>Intercept</td>
<td>12.718</td>
<td>0.144</td>
<td>(154.673, 161.797, 169)</td>
<td>521</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Herbivores</td>
<td>18.794</td>
<td>0.222</td>
<td>(337.07, 353.219, 369.746)</td>
<td>521</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Predators</td>
<td>8.882</td>
<td>0.223</td>
<td>(71.325, 78.886, 86.827)</td>
<td>521</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Parasitoids</td>
<td>10.479</td>
<td>0.223</td>
<td>(100.655, 109.815, 119.157)</td>
<td>521</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Plant Species Richness (SR)</td>
<td>0.121</td>
<td>0.026</td>
<td>(1.806, 3.089, 4.375)</td>
<td>20.6</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Plant Phylogenetic Diversity (PD)</td>
<td>0.116</td>
<td>0.031</td>
<td>(1.404, 2.945, 4.489)</td>
<td>13.3</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Diversity Interaction (SR*PD)</td>
<td>0.076</td>
<td>0.033</td>
<td>(0.279, 1.933, 3.592)</td>
<td>5.13</td>
<td>1</td>
<td>0.028</td>
<td></td>
</tr>
<tr>
<td>TC*SR</td>
<td>Herbivores:SR</td>
<td>-0.058</td>
<td>0.040</td>
<td>(-3.459, -1.486, 0.494)</td>
<td>50.7</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*SR</td>
<td>Predators:SR</td>
<td>0.067</td>
<td>0.040</td>
<td>(-0.293, 1.699, 3.697)</td>
<td>50.7</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*SR</td>
<td>Parasitoids:SR</td>
<td>0.355</td>
<td>0.040</td>
<td>(7.081, 9.099, 11.124)</td>
<td>50.7</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Herbivores:PD</td>
<td>-0.017</td>
<td>0.043</td>
<td>(-2.589, -0.436, 1.724)</td>
<td>29.9</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Predators:PD</td>
<td>0.085</td>
<td>0.043</td>
<td>(0.01, 2.173, 4.343)</td>
<td>29.9</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Parasitoids:PD</td>
<td>0.278</td>
<td>0.044</td>
<td>(4.920, 7.119, 9.317)</td>
<td>29.9</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Rarified Species Richness (square root transformed)</td>
<td>Intercept</td>
<td>3.947</td>
<td>0.018</td>
<td>(14.541, 14.776, 14.975)</td>
<td>1384</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Herbivores</td>
<td>6.316</td>
<td>0.025</td>
<td>(39.298, 30.915, 40.538)</td>
<td>1384</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Predators</td>
<td>3.305</td>
<td>0.025</td>
<td>(10.6, 10.923, 11.251)</td>
<td>1384</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arthropod Trophic Class (TC)</td>
<td>Parasitoids</td>
<td>1.902</td>
<td>0.025</td>
<td>(3.434, 3.619, 3.809)</td>
<td>1384</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Plant Species Richness (SR)</td>
<td>0.020</td>
<td>0.003</td>
<td>(0.112, 0.151, 0.19)</td>
<td>49.9</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Plant Phylogenetic Diversity (PD)</td>
<td>0.012</td>
<td>0.003</td>
<td>(0.048, 0.095, 0.142)</td>
<td>15.8</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Diversity Interaction (SR*PD)</td>
<td>0.002</td>
<td>0.003</td>
<td>(0.035, 0.016, 0.067)</td>
<td>0.39</td>
<td>1</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>TC*SR</td>
<td>Herbivores:SR</td>
<td>0.070</td>
<td>0.004</td>
<td>(0.479, 0.544, 0.612)</td>
<td>185</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*SR</td>
<td>Predators:SR</td>
<td>0.015</td>
<td>0.005</td>
<td>(0.051, 0.119, 0.137)</td>
<td>185</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*SR</td>
<td>Parasitoids:SR</td>
<td>-0.027</td>
<td>0.005</td>
<td>(-0.275, -0.208, -0.14)</td>
<td>185</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Herbivores:PD</td>
<td>0.040</td>
<td>0.005</td>
<td>(0.237, 0.31, 0.363)</td>
<td>64.4</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Predators:PD</td>
<td>0.039</td>
<td>0.005</td>
<td>(-0.003, 0.07, 0.142)</td>
<td>64.4</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TC*PD</td>
<td>Parasitoids:PD</td>
<td>-0.012</td>
<td>0.005</td>
<td>(-0.166, -0.093, -0.021)</td>
<td>64.4</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
2.4 Results

2.4.1 Effects of Plant Phylogenetic and Species Richness on Arthropod Communities

We found that the mean species richness of arthropods is positively associated with both plant richness and plant phylogenetic diversity ($H_{ae}$; hereafter phylogenetic diversity). A significant positive interaction between plant species richness and phylogenetic diversity revealed that increasing species richness of plants has a relatively weak effect on arthropod richness when phylogenetic diversity of plants is low, but has a much stronger effect when phylogenetic diversity is high (Table 2-1; Figure 2-1). After accounting for large trophic class differences in the mean species richness of arthropods, there was also a difference in the strength of the relationship between plant species richness and arthropod species richness that depended on trophic class. This was the result of parasitoids responding to plant species richness around half as strongly as herbivores and predators did, but still positively (Table 2-1; Figure 2-1, 1-2a). On the other hand, plant phylogenetic diversity and the interaction between plant phylogenetic diversity and plant species richness showed consistent effects on arthropod species richness across all trophic classes. All trophic classes were similar in that there was a near doubling of the number of arthropod species from the plots with lowest values of both plant species richness and phylogenetic diversity to the plots with the highest values of both plant species richness and phylogenetic diversity. In all cases, the effect of phylogenetic diversity on the response variables was as strong as that of species richness, as judged by a large overlap in the 95% confidence intervals of both coefficients in species comparable units (Figure 2-2). The full model including plant phylogenetic diversity was a considerably better model than the reduced model excluding phylogenetic diversity ($\Delta AIC = 27.71$).

The relationship between herbivore species richness and plant species richness was non-linear, with a significant second order polynomial term ($\text{Chi}^2=12.422; p=0.0004; \text{Figure 2-1c}$). There was also a trend towards increasing linearity of the plant species richness effect with increasing plant phylogenetic diversity, though this effect was not significant (species richness$^2$ * phylogenetic diversity interaction: $\text{Chi}^2=1.3483, p=0.2456; \text{Figure 2-1c}$). To illustrate this, we included the interaction in the fitted plane in Figure 2-1c.
There was an overall increase in arthropod abundance with both plant species richness and phylogenetic diversity, but these results were dependent on trophic level, and so we treat each trophic group separately below (Table 2-1; Figure 2-2, Figure 2-3). The mean positive response of arthropod abundance to both plant species richness and plant phylogenetic diversity was driven by a strong response of parasitoid abundance to both measures (Table 2-1, Figure 2-2a, 2-3b). Predator abundance also responded positively to plant species richness and phylogenetic diversity, but the response was much weaker (Table 2-1, Figure 2-2bii, 2-3b), with 95% confidence intervals for both slightly overlapping zero. In contrast, herbivore abundance does not increase with either plant species richness or phylogenetic diversity (Table 2-1; Figure 2-2bi, 3c). In all cases, the effect of phylogenetic diversity on abundance was as strong as that of species richness (Figure 2-2). The full model was again a considerably better model than the reduced model excluding phylogenetic diversity ($\Delta AIC = 35.4$).

For arthropod abundances, linear models of herbivore abundance were improved by a second order polynomial term for plant species richness ($\text{Chi}^2=4.5521, p=0.033$; Figure 2-3c). Figure 2-3c

Figure 2-1. The effect of species richness and phylogenetic diversity of plants on the species richness of a) parasitoids, b) predators and c) herbivores. Phylogenetic diversity is measured with the abundance-weighted metric $H_{\text{abund}}$. Fitted plane is based on a linear regression including both factors and their interaction. The fitted plane for herbivores (c) also included a second order polynomial term for species richness and also its interaction with phylogenetic diversity, to illustrate the trend. Including this last term resulted in an improvement in the visual fit of the plane though it was not statistically significant.
shows that herbivore abundance seems to peak at intermediate values of both plant species richness and phylogenetic diversity.

Figure 2-2. The effects of plant species richness and plant phylogenetic diversity on the a) species richness, b) abundance and c) rarefied richness of i) herbivores, ii) predators, and iii) parasitoids. Means are regression coefficients standardized to species comparable units. d) The relationship between the number of arthropods that two plant species share (Jaccard index) and their phylogenetic separation. Open circles are comparisons among Monocot species, solid circles are comparisons among Dicot species, and grey triangles are comparisons between Monocot and Dicot species. e) The phylogeny (left) and dendrogram based on arthropod assemblage overlap (right) for the 16 herbaceous species planted in monoculture. Solid ellipses represent Dicots and open ellipses represent Monocots. Solid lines join the same plant species between the two dendrograms.
### 'Niche' vs. 'Abundance' Hypotheses

For herbivores, the proportion of arthropod species shared between two plant species’ monocultures was negatively related to their phylogenetic distance ($r=-0.66$, randomization test: $p<0.001$; Figure 2-2di). For predators, similarity also declined with plant phylogenetic distance ($r=-0.33$, $p=0.003$; Figure 2-2dii), whereas parasitoids showed no response ($r=-0.062$, $p=0.22$, Figure 2-2diii). When we compared arthropod compositional responses within Monocots and Dicots, we found that herbivore, but not predator or parasitoid, community similarity declined with increasing phylogenetic distance of Dicot host plants ($r = -0.55$; randomization test: $p=0.007$). There was no significant relationship between phylogenetic distance and arthropod community similarity for comparisons within the Monocots for any trophic class. The results of the hierarchical clustering analysis were consistent with the above results. For herbivores, the clustering pattern most consistent with the distribution of pairwise distances between plant species based on arthropod assemblages was

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Figure 2-3. Effects of plant species richness and phylogenetic diversity on the abundance of different trophic levels: a) parasitoids, b) predators, c) herbivores, and d) plant productivity. Phylogenetic diversity is measured with the abundance-weighted metric $H_{ab}$. Fitted plane is based on a linear regression including both factors and their interaction. The fitted plane for herbivores (c) also included a second order polynomial term for species richness. Predator and herbivore abundance is measured as the total number of individuals collected in the plot, whereas plant productivity is measured in grams of biomass. One outlier data point where over 1000 spiderlings were collected on one day was excluded from the abundance data, as it was over 10 times the average predator abundance.
very similar to the phylogeny for the same plant species (Figure 2-3ei), whereas for predators it
was less consistent but still broadly concordant. (Figure 2-3eii). On the other hand, there was
virtually no correspondence between the arthropod assemblage dendrogram and the phylogeny
for parasitoids (Figure 2-3eiii).

In our analysis that uses rarefaction to control for changes in arthropod species richness
due to arthropod abundance, we found that for rarified richness that each trophic class responded
differently to both plant diversity measures (Table 2-1). Both herbivore rarefied richness
(strongly) and predator rarefied richness (weakly) increased with plant species richness, whereas
rarefied richness of parasitoids decreased slightly with increasing plant species richness. Plant
phylogenetic diversity produced similar results, with a strong positive effect on herbivore
rarefied richness, no effect on predator rarefied richness, and a negative effect on parasitoid
rarefied richness (Table 2-1; Figure 2-2c). The full model for rarefied richness including plant
phylogenetic diversity was a better model than the reduced model excluding phylogenetic
diversity by a large margin ($\Delta$AIC = 72.68).

Aboveground plant biomass increased with plant species richness ($t=11.12$, $p<0.001$),
phylogenetic diversity ($t=13.84$, $p <0.001$), and their interaction ($t=2.65$, $p=0.009$; Figure 2-3d).

2.5 Discussion

Our study demonstrates the importance of phylogenetic diversity for predicting the
effects of plant communities on the diversity and structure of higher trophic levels. We found
that the phylogenetic diversity of plant communities had a strong positive influence on the
species richness of both herbivorous and predatory arthropods, and it was just as strong as the
effects of plant species richness. More importantly, we found that species richness interacted
with phylogenetic diversity, so that species richness of plants had a larger positive impact on
arthropod richness when phylogenetic diversity was high (Figure 2-1). Jointly, phylogenetic
diversity and species richness of plants explain arthropod community diversity considerably.
better than plant species richness alone, as judged by large increase in AIC values for the full model over a reduced model excluding phylogenetic diversity.

We hypothesized that the positive effect of plant phylogenetic diversity on arthropods that we observed in this study could be explained through two potential mechanisms: 'niche' or 'abundance' effects. Increasing phylogenetic diversity will only lead to more feeding or habitat niches if arthropods tend to feed on or associate with closely related species – that is, their diet or habitat requirements are phylogenetically structured. In this case, more distantly related plant species are more likely to fall into the host-range of different herbivores, and so phylogenetically diverse communities can support the recruitment and population growth of a wider range of potential herbivores. Given this, adding more plant species to a community will result in smaller increases in arthropod species richness when the plants are closely related than when they are distantly related, because of higher overlap in arthropod assemblages amongst close relatives. Thus we would predict that plant species richness and phylogenetic diversity would interact in explaining arthropod diversity – which is what we observed in this study (Table 2-1; Figure 2-1).

On the other hand, arthropod diversity could be responding to plant diversity indirectly though an 'abundance' effect, whereby increased plant diversity increases the amount of plant biomass in the system, creating more resources for more arthropod individuals, and increasing species richness as a consequence of sampling more rare species (Gotelli and Colwell 2001).

In order to test the plausibility of our phylogenetic 'niche' hypothesis over the 'abundance' hypothesis, we tested whether arthropod assemblages in our study system were influenced by the identity of plant species and their relatedness to other species. We found a negative relationship between the phylogenetic distance of plant species pairs and the degree of overlap in their arthropod assemblages, as measured by arthropods collected from plant species monocultures. As expected, the negative correlation was considerably stronger for herbivores than it was for predators and parasitoids (Figure 2-2d,e). In this study, monoculture plots occurred in an open field embedded within an experiment with many other plant species nearby. As such, there were likely a large number of 'tourists' (sensu Moran and Southwood 1982) in any given plot – species that have no ecological association with plants in the plot but have recently dispersed from neighbouring plots (Haddad et al. 2001). Our results are then conservative, and it may be that the relationship between phylogenetic distance and arthropod community similarity may be considerably stronger than we were able to show.
Given the ecological importance of the evolutionary split between the Monocots and Dicots, it is perhaps not surprising that the relationship between phylogenetic distance and arthropod overlap was heavily influenced by comparisons between these groups (Figure 2-2d,e). However, for herbivores, there was a negative relationship between phylogenetic distance and arthropod community similarity for comparisons just within the Dicots as well. The lack of a relationship in the Monocots is likely due to a smaller sample size as well as a limited range of evolutionary distances in this study, as the common ancestor of all of the Monocots in this study (which were all grasses) is much more recent than the common ancestor of all of the Dicots in the study (Figure 2-2d).

In contrast to herbivores, predator and parasitoid assemblages on plant monocultures have a considerably weaker relationship with phylogenetic distance, which suggests that more phylogenetically diverse plant communities will not necessarily contain more habitat niches for these arthropods. Despite this, predator species richness in polycultures is as strongly explained by plant phylogenetic diversity as herbivore richness is. Though some recent studies have suggested that the effects of plant community diversity on arthropod diversity decline as trophic level increase (Scherber et al. 2010; Schuldt et al. 2011), our study finds that the effects of not only plant species richness but also plant phylogenetic diversity generally do not noticeably weaken at higher trophic levels.

The results of our analysis of rarefied arthropod richness confirm that the mechanisms responsible for increased arthropod species richness with increasing plant diversity – 'niche' or 'abundance' mechanisms – may be different depending on trophic class. When rarefaction was used to remove the influence of abundance on species richness, only herbivore rarefied richness increased with both plant species richness and phylogenetic diversity. Though predator rarefied richness increased slightly with plant species richness, parasitoid rarefied richness actually declined with both plant species richness and phylogenetic diversity (Table 2-1; Figure 2-2ciii). This is consistent with the effects of plant species richness and phylogenetic diversity on arthropod abundances. Since neither plant species richness nor phylogenetic diversity increased herbivore abundance (Table 2-1, Figure 2-3c), abundance could not possibly explain the increase in herbivore species richness. On the other hand, both predator and parasitoid abundance did increase with both types of plant diversity (Table 2-1; Figure 2-3a, 2-3b) and this likely accounted for most of the increase in species richness for these types of arthropods. Taken
together, the evidence is most consistent with the 'niche' hypothesis for herbivores, and the 'abundance' hypothesis for predators and parasitoids as an explanation for why arthropod species richness increases with plant phylogenetic diversity.

Predator and parasitoid abundance are likely responding to plant productivity, which we have shown also increases with both plant species richness and phylogenetic diversity (Figure 2-3d). Herbivore abundance may fail to increase with increased plant productivity because the energy is transferred to the top trophic level, and the abundance of herbivores consequently suppressed by a trophic cascade (Leibold et al. 1997; Haddad et al. 2009).

Positive relationships between plant species richness and ecosystem function are common, but in most cases are saturating at high diversity levels (e.g. Tilman 1997; Knops et al. 1999; Loreau et al. 2001; Balvanera et al. 2006; Cardinale et al. 2006; Haddad et al. 2009; Scherber et al. 2010). We found that the effect of plant species richness could be saturating for herbivore species richness and abundance. At the same time, our results show that the effect of plant phylogenetic diversity is non-saturating for all aspects of arthropod communities that were measured, within the range occurring in this experiment. Figure 2-1c also shows a trend towards increasing linearity of the plant species richness effect with increasing plant phylogenetic diversity. That being said, further studies in other experiments and across a range of phylogenetic diversities in natural systems will be highly valuable to understand if and where the effects of phylogenetic diversity on ecosystem function may begin to saturate within communities.

Our results concerning the effect of phylogenetic diversity on consumer abundance and diversity are likely generalizable to many food webs. We have found that the ability of phylogenetic diversity to explain herbivore richness is related to a correlation between phylogenetic distance and the number of herbivores that are shared amongst plant hosts (Figure 2-2d,e). This pattern will arise whenever consumers have phylogenetic structure in their diets, as is likely the case in many food webs (Ødegaard et al. 2005; Weiblen et al. 2006; Futuyma & Agrawal 2009; Gómez et al. 2010), and can arise from many processes including coevolution, host-switching, and shared biogeographic history, to name a few. In fact, phylogenetic structure of species interactions is not limited to consumer-resource interactions, but also occurs in mutualistic interactions (Fontaine et al. 2009; Gómez et al. 2010). If this holds generally, then
we may expect to see increased mutualist diversity in plots with high phylogenetic diversity as well.

Our study demonstrates that the effects of phylogenetic diversity can have major impacts on communities of herbivorous and predatory arthropods. Our results build upon those studies that have shown that higher phylogenetic diversity increases plant biomass (Maherali & Klironomos 2007; Cadotte et al. 2008; 2009; Connolly et al. 2011; Flynn et al. 2011). Here we show for the first time that phylogenetic diversity of plants influence the structure and diversity of associated communities at higher trophic levels. Furthermore, phylogenetic diversity mediates the effects of species richness on the diversity and abundance of arthropods, so much so that at low plant phylogenetic diversity, plant species richness has virtually no effect. Therefore, incorporating a phylogenetic perspective is vital to understanding the role of diversity for how ecosystems function.

Taken together, the results of our study lead us to posit that the loss of evolutionarily distinct species will have greater impacts on ecosystem function than expected from scenarios of random extinction, particularly in communities where plant species richness is high. The increasing relationship between plant and arthropod richness in phylogenetically diverse systems that we observed likely reflect the fact that the most distantly related plant species have minimal niche overlap – for both their resources and their consumers (Chesson & Kuang 2008) – thus their contributions are more strongly additive (Cardinale 2011). Ultimately, our results show that loss of evolutionary history in basal trophic levels caused by ongoing extinction may have underappreciated effects on other species.

2.6 Acknowledgements

We thank J. Haarstad for his persistence in sampling and identifying all arthropods in this biodiversity experiment for 11 years; J. Knops for his leadership in creating and maintaining the long-term biodiversity experiment; and T. Mielke for maintaining the experiment. MWC is generously supported by an NSERC discovery grant (grant #386151). RD is generously supported by an NSERC CGS-D grant.
2.7 References


2.8 Supplementary Information - Part 1

The following figure S1 shows analyses from 9 different abundance-weighted phylogenetic diversity metrics on the Cedar Creek Arthropod Dataset.

The results were largely consistent for metrics that were based on average branch-length differences across the entire tree (Haed, PSE, Eaed, MPD, Rao's quadratic entropy, and phylogenetic Simpson's index). IAC also showed effects on most arthropod community properties. This index is based on the degree of balance of branches on the tree (and so reflects community tree shape), which may explain why predator abundance shows a stronger response to it than other metrics. Metrics that focus on phylogenetic structure just near the tips of the tree (MNND and PSC), on the other hand, are not strong predictors of any arthropod community property. MPD, Rao's quadratic entropy, and phylogenetic Simpson's index had identical values for all plots in our dataset, so they were combined in figure S1 under MPD.

To evaluate the degree to which different phylogenetic metrics were independent of plant species richness, we performed linear regressions and Breusch-Pagan tests on each of them. A Breusch-Pagan test (1) measures the degree to which the variance in the residuals are correlated by doing a linear regression of the independent variable (in this case species richness) on the squared residuals from an initial linear regression of the independent variable (species richness) on the dependent variable (phylogenetic diversity). For the main paper, we chose to present results from Haed because it had low values of correlation for both tests (linear regression: $r^2 = 0.002$; Breusch-Pagan Test: $r^2 = 0.178$).
Figure S1. Information on the explanatory power and suitability of 9 phylogenetic diversity metrics. For each metric and each dependent variable are plotted regression coefficients and their 95% confidence intervals. Phylogenetic diversity metrics (PD) and species richness (SR) were transformed to species comparable units so that their coefficients could be compared within and across different metrics. Coverage plots show how the metric is related to species richness. PD metrics with good coverage have means and variances that are not strongly related to species richness (SR Mean and SR Variance).
2.9 Supplementary Information – Part 2

2.9.1 Repeated Measures Analysis

To evaluate whether our choice of using cumulative data for all 11 years bias our results, we performed a repeated measures version of the models reported in the main manuscript on the five years of annual arthropod data for which there was corresponding percent cover data for plants.

We performed two analyses, one on arthropod species richness data, the other on arthropod abundance data. We did not perform a repeated measures analysis on rarefied richness of arthropods because the number of individuals in each sample was too low to get reasonable estimates for some of the trophic levels. We analyzed data using generalized linear mixed models (GLMMs). Dependent variables included yearly species richness or abundance of arthropods (N=122 plots); independent variables included trophic class, plant phylogenetic diversity, plant species richness and all their interactions as fixed factors. To control for non-independence of measurements taken in the same year, we included year as a random factor. We also included a plot random factor which was nested within year. Doing so, we allowed there to be a consistent year effect, while allowing the effect of plot to vary from year to year.

Non-significant higher order interactions were dropped from the models. Since both species richness and abundance are count data, we used Poisson distributed errors in both cases with a log link in the model of arthropod species richness and a square root link in the model of arthropod abundance.

The results of the models are broadly consistent with the results of the main manuscript on cumulative data (Table S1) with a few exceptions.

2.9.2 Exception 1

The relative strength of the effects are somewhat different for arthropod species richness. Plant species richness and phylogenetic diversity effects were most strong on predators in the repeated measures analysis, and less strong on herbivores (though still significantly positive). In the analysis on cumulative data presented in the main manuscript, we showed that effects of
plant species richness and phylogenetic diversity were strongest for herbivores, and slightly weaker for predators (though not significantly so). We suspect the reason for this is that herbivore community species richness response is more strongly dominated by the response of rare species. In the cumulative analysis, repeated sampling revealed many of these rare species, but within individual years the samples are more likely to be dominated by common species. If common species tend to be generalists, it is not surprising that the effect of plant species richness and phylogenetic diversity decreased in this analysis, as we hypothesize that their effects are driven by the responses of host-plant specialists, which may be rare and thus less likely to be sampled in any given year.

2.9.3 Exception 2

In the cumulative arthropod abundance analysis in the main manuscript we saw that herbivore abundance was not significantly explained by either plant species richness or plant phylogenetic diversity, but it trended towards a negative relationship. In the repeated measures analysis reported here, both plant species richness and phylogenetic diversity significantly reduced herbivore abundance (Table S1). This may be because of slightly more power in this analysis, because repeated observations lend a greater sample size compared with aggregating the data.

Herbivore abundance may decrease with plant species richness and phylogenetic diversity because of a resource concentration effect (Root 1973). In plots with few plant species, there will be a higher density of any given plant species, and so herbivores may be more likely to find the patch and stay in it. A similar mechanism could act through phylogenetic diversity. If herbivores have phylogenetically structured host associations, then plots with closely related species are more likely to contain multiple plant species that an herbivore can feed on, leading again to higher resource concentration in that patch. And so plant communities with low species richness and low phylogenetic diversity are predicted to have higher densities of herbivores, which is what the negative coefficients observed here imply.

2.9.4 References

Table S1. Repeated measures model output showing effects of trophic level, plant species richness, plant phylogenetic diversity, and their interactions on yearly arthropod species richness, abundance, and rarified richness. Back-transformed CI is the parametric bootstrap 95% confidence interval after performing the inverse link function (lower CI, mean, upper CI). For different trophic classes, the intercept or main effect is included in the estimate and the back-transformed confidence interval, so the CI is based on the actual values, and not the deviations from the average. For plant species richness, plant phylogenetic diversity, and their interaction with trophic class, the back-transformed CI is the change in the dependent variable on the original scale with a increase of one species comparable unit, evaluated at the intercept.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Factor</th>
<th>Estimate</th>
<th>SE</th>
<th>Back-transformed CI</th>
<th>Chi2 Value</th>
<th>df</th>
<th>p-value</th>
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<td>0.091</td>
<td>(5.38, 6.43, 7.685)</td>
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<td></td>
<td>Arthropod Trophic Class (TC)</td>
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<tr>
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<td>Herbivores</td>
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<td>0.091</td>
<td>(12.194, 14.576, 17.425)</td>
<td>8922.1</td>
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</tr>
<tr>
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<td>0.093</td>
<td>(4.085, 4.9, 5.876)</td>
<td>3784.1</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Parasitoids</td>
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<td>0.094</td>
<td>(3.099, 3.722, 4.471)</td>
<td>3784.1</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
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<td>0.002</td>
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<td>0.011</td>
<td>0.003</td>
<td>(0.036, 0.07, 0.104)</td>
<td>15.73</td>
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<td>0.003</td>
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<tr>
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<td>TC*SR</td>
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<tr>
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<td>0.003</td>
<td>(0.016, 0.048, 0.092)</td>
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<tr>
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<td>Predators:SR</td>
<td>0.017</td>
<td>0.004</td>
<td>(0.001, 0.112, 0.162)</td>
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<td>0.003</td>
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<tr>
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<td>TC*PD</td>
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<td>8.27</td>
<td>2</td>
<td>0.016</td>
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<td>0.003</td>
<td>(0.004, 0.04, 0.076)</td>
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<tr>
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<td>(0.006, 0.121, 0.175)</td>
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<td>(0.011, 0.049, 0.108)</td>
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<td>Intercept</td>
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<td>0.324</td>
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<td>Herbivores</td>
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<td>(33.625, 41.618, 50.219)</td>
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<td>Predators</td>
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<td>(8.775, 10.486, 15.004)</td>
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<td>(12.671, 17.598, 23.332)</td>
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<td>Plant Species Richness (SR)</td>
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<td>(0.1, 0.277, 0.454)</td>
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<td>Diversity Interaction (SR*PD)</td>
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<td>(0.079, 0.123, 0.326)</td>
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<td>1</td>
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<tr>
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<td>932.75</td>
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<td>(-0.71, -0.524, -0.338)</td>
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<tr>
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<td>0.010</td>
<td>(-0.05, 0.137, 0.325)</td>
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<td>0.010</td>
<td>(-0.037, 1.227, 1.418)</td>
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<tr>
<td></td>
<td>TC*PD</td>
<td></td>
<td></td>
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<td>513.5</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Herbivores:PD</td>
<td>-0.047</td>
<td>0.011</td>
<td>(-0.639, -0.432, -0.225)</td>
<td></td>
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<tr>
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<td>0.025</td>
<td>0.011</td>
<td>(0.021, 0.23, 0.439)</td>
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<td>0.011</td>
<td>(0.732, 0.942, 1.153)</td>
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<td></td>
<td>TC<em>SR</em>PD</td>
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<td>87.56</td>
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<td>0.012</td>
<td>(-0.321, -0.107, 0.108)</td>
<td></td>
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<td></td>
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<tr>
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<td>Predators:SR:PD</td>
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<td>0.012</td>
<td>(0.017, 0.232, 0.448)</td>
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<tr>
<td></td>
<td>Parasitoids:SR:PD</td>
<td>0.050</td>
<td>0.012</td>
<td>(0.248, 0.463, 0.679)</td>
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Chapter 3. Species richness and phylogenetic diversity have opposing effects on invertebrate herbivory

Russell Dinnage

3.1 Abstract

Long-standing ecological theory proposes that diverse communities of plants should experience a decrease in herbivory. Yet previous empirical examinations of this hypothesis have revealed that plant species richness increases herbivory in just as many systems as it decreases it. In this study, I ask whether more insight into the role of plant diversity in promoting or suppressing herbivory can be gained by incorporating information about the evolutionary history of species in a community. In an old field system in southern Ontario, I surveyed communities of plants and measured levels of leaf damage on 27 species in 38 plots. I calculated a measure of phylogenetic diversity (PSE) that encapsulates information about the amount of evolutionary history represented in each of the plots and looked for a relationship between levels of herbivory and both species richness and phylogenetic diversity using a generalized linear mixed model (GLMM) that could account for variation in herbivory levels between species. I found that species richness was positively associated with herbivore damage at the plot-level, in keeping with the results from several other recent studies on this question. On the other hand, phylogenetic diversity was associated with decreased herbivory. Importantly, there was also an interaction between species richness and phylogenetic diversity, such that plots with the highest levels of herbivory were plots which had many species but only if those species tended to be closely related to one another. I propose that these results are the consequence of interactions with herbivores whose diets are phylogenetically specialized (for which I introduce the term cladophage), and how phylogenetic diversity may alter their realized host ranges. These results suggest that incorporating a phylogenetic perspective can add valuable additional insight into the role of plant diversity in explaining or predicting levels of herbivory at a whole-community scale.
3.2 Introduction

The insect herbivore flies, crawls, hovers, and feeds in a matrix of stems, roots, flowers and leaves. Thousands do this in a typical community of plants in what – to us – is an impenetrably complex tangle of traits, each the product of millions of years of evolution. How then are we to understand the aggregate patterns that emerge from such a community? Indeed, community ecologists have long struggled to understand how the identity and traits of individual plant species add together and interact to determine herbivore communities and the damage they cause.

Though much work on insect herbivory has focused on interactions between single pairs of insect and plant species, it is also important to understand the phenomenon at the level of whole plant communities. After all, many of the consequences of major ecosystem changes will be manifest at the level of the community, and one-to-one interactions may not always be additive (Agrawal, Lau, & Hambach 2006; Agrawal et al. 2007).

One way of understanding herbivory at the community level is to look at the effects of plant species richness. Plant species richness is one of the simplest way to summarize information about many species at the community level, and studies of its role in herbivory link up nicely with the body of literature on the relationship between diversity and ecosystem functioning (Siemann et al. 1998; Haddad et al. 2001; Loreau et al. 2001; Hooper et al. 2005; Cardinale et al. 2006; Balvanera et al. 2006; Cardinale et al. 2007; Scherber et al. 2010a). Insect herbivore damage is a useful reflection of the activities of insect herbivores in plant communities, as well as a phenomenon of interest in and of itself, with implications for the health of a plant community.

There are some clear theoretical predictions about the effects of plant species richness on herbivory, which derive from a simple understanding of direct trophic interactions between plants and insects. Root (1973) suggested that increased plant species richness should lead to a decrease in specialist herbivores, and thus to a decrease in herbivory. The Resource Concentration Hypothesis states that if the number of plant species in a patch is higher, the density of each plant species must be lower, and so specialist herbivores of those species will be less likely to find such a patch, stay in such a patch, and do damage in such a patch. On the other hand, the presence of a wide variety of plant species provides a wide variety of nutritional
resources for generalist herbivores, which may prefer to eat in diverse patches, and may thrive more in them too (Unsicker et al. 2008; Schuldt & Baruffol 2010). I will refer to this idea as the Dietary Mixing Hypothesis (after Bernays et al. 1994).

Unfortunately, previous empirical literature has not provided a clear picture of which of these two hypotheses applies more widely to plant-herbivore systems, because whether plant species richness has a positive, negative, or no relationship with herbivory depends on the system under study. A review of the literature shows that there are roughly equal numbers of studies showing that plant diversity has a positive effect on herbivory as there are showing a negative effect, at least for studies that looked at the effect of species richness on the magnitude of herbivory (Table 2-1). This suggests that the role of plant species richness may sensitively depend on aspects of either the plant or the herbivore community. Based on the Resource Concentration Hypothesis and the Dietary Mixing Hypothesis described above, the relative abundance of generalist vs. specialist herbivores likely plays a role. For example, Lau et al. (2008) were able to separate damage done by specialists and damage done by generalists on Lespedeza capita planted in low and high diversity plots. They found that damage by generalists increased with high plant diversity and that damage from specialists decreased with high plant diversity, in accordance with the predictions of the Dietary Mixing hypothesis and the Resource Concentration Hypothesis, respectively.

Species richness is only a coarse measure of the diversity and structure of a community, and so including other sources of information about communities may help to clarify such simple predictions. Attempts to include more of the natural complexity of plant communities to understand community herbivory include using functional diversity in addition to plant species richness (Siemann et al. 1998; Koricheva et al. 2000; Prieur-Richard, Lavorel, & Linhart 2002; Scherber et al. 2006, 2010b) reducing species composition to low dimensional quantitative measures using ordination (Koricheva et al. 2000; Pfisterer, Diemer, & Schmid 2003; Schaffers et al. 2008), and incorporating information about plant species' evolutionary history, using community phylogenetics. Here, I explore the use of community phylogenetics to understand insect herbivory at the plant community level.

The increasing availability of phylogenetic information on plants and the recent development of sophisticated ways of incorporating this information into diversity measures
(Helmus et al. 2007; Cavender-Bares et al. 2009; Vamosi et al. 2009; Cadotte et al. 2010; Pausas & Verdú 2010), is opening a new avenue of exploration for understanding the effects of plants on ecosystem function at the whole community scale. For example, recent analyses have shown that various measures of phylogenetic diversity are associated with the productivity of plant communities (Cadotte, Cardinale, & Oakley 2008; Cadotte et al. 2009; Connolly et al. 2011; Flynn et al. 2011) and the insect assemblages associated with them (Dinnage et al. 2012; Chapter 2 of this thesis). Here, I show that incorporating phylogenetic diversity into hypotheses about herbivory can provide a useful framework for predicting when species richness may increase or decrease herbivory in plant communities.

Phylogenetic diversity may be particularly important to herbivores and herbivory because of the widespread occurrence of herbivores with phylogenetically restricted diets – they feed on a group of closely related species (Ehrlich & Raven 1964; Janzen 1980; Ødegaard, Diserud, & Østbye 2005; Weiblen et al. 2006; Gossner et al. 2009; Futuyma & Agrawal 2009). Lacking an existing term, I will refer to these species as cladophages, from the Greek klados for 'branch', and the Greek phagein for 'to eat' – thus 'branch-eater', or an organism that feeds preferentially on just one of the branches of the tree of life that is available to them. The act of feeding in this manner can be called cladophagy.

In this study I asked whether the phylogenetic diversity of old-field plant communities can predict the amount of herbivore damage on plants at a community-scale.
Table 3-1. Literature review of previous studies on the role of plant diversity in promoting or suppressing herbivory. Type refers to whether the species richness was manipulated (Experimental), natural species richness variation was taken advantage of (Observational), or the conclusion was based on estimates from previous literature (Meta-analysis). Consumer effect refers to whether the study estimated a measure of the amount of interaction between plants and consumers (Magnitude) – usually a damage measurement, or estimated the effect that interaction had on the plants’ fitness (Impact) – usually by measuring biomass in the presence or absence of herbivory. A positive relationship means that the study found that the magnitude or impact of herbivory increased with increasing plant diversity, a negative relationship means the study found that herbivory decreased with plant diversity. No relationship means the study found no relationship between herbivory and plant diversity. No study that was used in the referenced meta-analyses is repeated in this table.

<table>
<thead>
<tr>
<th>Study</th>
<th>Type</th>
<th>Species Richness Range</th>
<th>Measured</th>
<th>Measured On</th>
<th>Consumer effect</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lau et al. 2008</td>
<td>Experimental</td>
<td>1 vs. 16</td>
<td>Leaf damage from generalists</td>
<td>1 Legume sp</td>
<td>Magnitude</td>
<td>Positive</td>
</tr>
<tr>
<td>Mulder &amp; Huss-Danell 2001</td>
<td>Experimental</td>
<td>1, 2, 4, 8, 12</td>
<td>Leaf damage</td>
<td>Community</td>
<td>Magnitude</td>
<td>Positive</td>
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<td>Plath et al. 2011</td>
<td>Experimental</td>
<td>1 vs. 3</td>
<td>Leaf damage</td>
<td>1 Rosea tree</td>
<td>Magnitude</td>
<td>Positive</td>
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<td>Prieur-Richard et al. 2002</td>
<td>Experimental</td>
<td>3, 6, 18</td>
<td>Leaf damage</td>
<td>2 Conyza spp.</td>
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<td>Positive</td>
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<td>Scherber et al. 2006</td>
<td>Experimental &amp; 60</td>
<td>1, 2, 4, 8, 16, 16</td>
<td>Leaf damage by Mollusks</td>
<td>All species + 3</td>
<td>Magnitude</td>
<td>Positive</td>
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<td>25 – 68</td>
<td>Leaf damage</td>
<td>10 tree spp</td>
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<td>Meta-analysis</td>
<td>1 vs. Several (Oak &amp; Alder)</td>
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<td>Experimental</td>
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<td>Leaf damage by Mollusks</td>
<td>All spp</td>
<td>Magnitude</td>
<td>None</td>
</tr>
<tr>
<td>Sobek et al. 2009</td>
<td>Observational</td>
<td>Natural range across German deciduous forest</td>
<td>Leaf damage by insects</td>
<td>2 Maple spp</td>
<td>Magnitude</td>
<td>None</td>
</tr>
<tr>
<td>Study</td>
<td>Type</td>
<td>Species Richness Range</td>
<td>Measured</td>
<td>Measured On</td>
<td>Consumer effect</td>
<td>Relationship</td>
</tr>
<tr>
<td>------------------------------</td>
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</tr>
<tr>
<td>Yguel et al. 2011</td>
<td>Observational</td>
<td>Natural range across managed French forest</td>
<td>Leaf damage</td>
<td>1 Oak sp.</td>
<td>Magnitude</td>
<td>None</td>
</tr>
<tr>
<td>Jactel &amp; Brockerhoff 2007</td>
<td>Meta-analysis</td>
<td>1 vs. Several</td>
<td>Leaf damage</td>
<td>Many individual spp.</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>Lau et al. 2008</td>
<td>Experimental</td>
<td>1 vs. 16 from specialists</td>
<td>Leaf damage</td>
<td>1 Legume sp</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>Massey et al. 2006</td>
<td>Experimental</td>
<td>1 vs. 5</td>
<td>Leaf damage</td>
<td>1 Shorea sp</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>McNaughton 1985</td>
<td>Observational</td>
<td>Natural range across Serengeti</td>
<td>% Biomass consumed</td>
<td>Community</td>
<td>Magnitude</td>
<td>Negative</td>
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<tr>
<td>Petermann et al. 2010</td>
<td>Experimental</td>
<td>1, 2, 3, 4, 6, 9</td>
<td>Infestation by aphids</td>
<td>Community</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>Sobek et al. 2009</td>
<td>Observational</td>
<td>Natural range across German deciduous forest</td>
<td>Leaf damage by insects</td>
<td>1 Beech sp</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>Unsicker et al. 2006</td>
<td>Observational</td>
<td>18 – 45</td>
<td>Leaf damage</td>
<td>Many individual spp.</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>Vehviläinen, Koricheva &amp; Ruohomäki 2007</td>
<td>Meta-analysis</td>
<td>1 vs. Several</td>
<td>Leaf damage by insects</td>
<td>1 Birch sp</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>Wilsey &amp; Polley 2002</td>
<td>Experimental (manipulated Evenness)</td>
<td>1 – 4</td>
<td>Infestation by spittlebugs</td>
<td>Solidago canadensis</td>
<td>Magnitude</td>
<td>Negative</td>
</tr>
<tr>
<td>Mulder &amp; Huss-Danell 2001</td>
<td>Experimental</td>
<td>1, 2, 4, 8, 12</td>
<td>Reduction of biomass in insecticide plots</td>
<td>Community</td>
<td>Impact</td>
<td>Positive</td>
</tr>
<tr>
<td>Scherber et al. 2010</td>
<td>Experimental</td>
<td>1, 2, 4, 8, 16, 60</td>
<td>% reduction of biomass in insect exclusions</td>
<td>Community</td>
<td>Impact</td>
<td>None</td>
</tr>
<tr>
<td>Study</td>
<td>Type</td>
<td>Species Richness Range</td>
<td>Measured</td>
<td>Measured On</td>
<td>Consumer effect</td>
<td>Relationship</td>
</tr>
<tr>
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<td>---------------------------------------------------------------------------</td>
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</tr>
<tr>
<td>Hillebrand &amp; Cardinale 2004</td>
<td>Meta-analysis</td>
<td>1 - 60</td>
<td>Absolute and % reduction of phytoplankton biomass in grazer exclusion</td>
<td>Community of phytoplankton</td>
<td>Impact</td>
<td>Negative</td>
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<tr>
<td>Lanta 2007</td>
<td>Experimental</td>
<td>1, 2, 4, 6</td>
<td>Reduction of biomass in Mollusk exclusions</td>
<td>Community</td>
<td>Impact</td>
<td>Negative</td>
</tr>
<tr>
<td>Narwani &amp; Mazumder 2010</td>
<td>Experimental</td>
<td>1 vs. 4</td>
<td>Biomass consumed</td>
<td>Community of phytoplankton</td>
<td>Impact</td>
<td>Negative</td>
</tr>
<tr>
<td>Pfisterer, Diemer &amp; Schmid 2003</td>
<td>Experimental</td>
<td>1, 2, 4, 8, 32</td>
<td>% reduction of biomass in insect exclusion</td>
<td>Community</td>
<td>Impact</td>
<td>Negative</td>
</tr>
<tr>
<td>Stein et al. 2010</td>
<td>Observational</td>
<td>15 – 37</td>
<td>% reduction of biomass in insect exclusions</td>
<td>Community</td>
<td>Impact</td>
<td>Negative</td>
</tr>
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</table>
3.3 Materials and methods

3.3.1 Data collection

The study was conducted at the Koffler Scientific Reserve (KSR) at Joker's Hill (King City, Ontario, Canada; [http://www.ksr.utoronto.ca/jh.html](http://www.ksr.utoronto.ca/jh.html)), a 350 hectare property containing a mix of primary forest, secondary forest and open habitats, including a large area of old field sites.

3.3.2 Species survey

I haphazardly selected 38 10 x 10 meter plots spread across the available old field habitat at KSR. In early August, I surveyed each plot within four randomly placed 1x1 meter quadrats, one in each of the four quadrants of the larger plot. I noted the presence or absence of each forb species within the quadrats and combined the data from all four quadrats into a low resolution measure of abundance (ranging from 0-4) for each species within each 10x10 meter plot. I decided to focus on forbs to the exclusion of grasses for several reasons. Herbivory from chewing insect is difficult to measure on grasses but is obvious on forbs. There were only two common species of grass which occurred in nearly every one of the plots surveyed, and so inclusion of grasses in the phylogenetic diversity measures would have only diluted the signal from the forbs. I hypothesized that phylogenetic diversity amongst forbs would be the most important to understanding herbivory on forbs. This is because grasses and forbs share few herbivores, except for the most generalist. As an example, Dinnage et al. (2012) showed that the largest difference in arthropod communities collected from different prairie plant species was between grasses and forbs.

Using these data, I calculated the species richness and abundance-weighted phylogenetic diversity for all 38 plots.
3.3.3 Herbivory survey

In order to quantify the amount of herbivore damage in the plots, I selected 27 of the most common species at KSR to measure damage (Figure 3-1). These species acted as phytometers to capture the overall herbivore pressure in the plot. In late August – over a period of approximately two weeks – I measured herbivore damage rates in the 38 plots. For each of the phytometer species that occurred in a given plot, I sampled 10 individual plants by counting the number of damaged leaves and the number of total leaves on each one. The dataset then consisted of 1862 datapoints, each from an individual plant.

3.3.4 Phylogeny and diversity indices

I created a phylogenetic tree containing all the most common old field species found at my site using methods previously described (Dinnage 2009). I then pruned the tree so that the remaining species matched those found in the plots used for this study (Figure 3-1).

Using this phylogeny I calculated an index of abundance-weighted phylogenetic diversity for each plot. There are several such indices available – I chose Phylogenetic Species Evenness (PSE; Helmus et al. 2007). PSE measures the amount of evolutionary history represented in a community by calculating the expected variance in a hypothetical continuous trait modeled as evolving through Brownian motion across the community phylogeny, and is standardized by the expected variance of the same modeled trait on a star phylogeny – where phylogenetic distances among all species are equal. This captures one of the fundamental features of interest in phylogenetic diversity, that it may encapsulate information about the ecological similarity of species in a community. I chose PSE for this reason, and because it is theoretically (and empirically in this study) independent of species richness. Thus, by using it, I could evaluate the independent contributions of species richness and phylogenetic diversity without the problems of co-linearity and heteroscedasticity common to many other phylogenetic diversity indices (e.g. Schweiger et al. 2008; Pio et al. 2011). PSE ranges between 0 and 1, where high values are associated with high phylogenetic diversity. Low values are associated with low phylogenetic diversity, or phylogenetic clustering – small average phylogenetic distances among species in the community.
I used species richness rather than an abundance-weighted measure because I was interested in the effects of adding or subtracting species. This combined with the phylogenetic diversity measure can give a statistical measure of adding species of different phylogenetic distances from the species already present. In addition, abundance weighting is easily interpretable for a measure like phylogenetic diversity, because in essence it is a weighted average, and phylogeny is made from continuous measures of branch length. On the other hand, abundance weighted measures like the Shannon-Weaver index are abstracted quantities with no simple interpretation biologically, as abundance weighting of a discrete count measure is less...
intuitive. I did calculate evenness for the plots and it was not correlated with phylogenetic diversity, and so the phylogenetic diversity measure, though abundance-weighted, was not confounded with species evenness. In addition, evenness was not a significant predictor of herbivory when included as a factor in the model described below, and so I did not use it.

3.3.5 Statistical analysis

In order to account for variation in species composition across plots, I used a generalized linear mixed model (GLMM) with crossed random effects, to disentangle species and plot-level effects on herbivory. The number of damaged leaves on a plant can be modelled as a binomial distribution, with a damaged leaf considered a Bernoulli success (for the herbivores) and an undamaged leaf a failure. Factors that may influence the probability of a leaf being damaged were incorporated into the model with a logit link.

I used a logit-normal-binomial statistical model to analyze the data, as follows:

\[
\text{Damaged}_i \sim \text{Binomial}(p_i, N_i)
\]

\[
\text{Logit}(p_i) = \alpha + \mu^1_{\text{species}[i]} + \mu^2_{\text{plot}[i]} + \mu^3_{\text{obs}[i]} + \beta_{\text{pd}}PD_{\text{plot}[i]} + \beta_{\text{sr}}SR_{\text{plot}[i]} + \beta_{\text{pd}sr}(PD*SR)_{\text{plot}[i]} + \beta_{\text{date}DATE_{\text{plot}[i]}}
\]

\[
\mu^1_{\text{species}[i]} \sim \text{Normal}(0, \sigma^2_{\text{species}}), \quad \mu^2_{\text{plot}[i]} \sim \text{Normal}(0, \sigma^2_{\text{plot}}), \quad \mu^3_{\text{obs}[i]} \sim \text{Normal}(0, \sigma^2_{\text{obs}})
\]

Where \(\text{Damaged}_i\) is the number of damaged leaves on individual plant \(i\), \(p_i\) is the probability of any given leaf on plant \(i\) being damaged, and \(N_i\) is the total number of leaves on plant \(i\). \(\text{PD}_{\text{plot}[i]}\) and \(\text{SR}_{\text{plot}[i]}\) are the phylogenetic diversity and the species richness, respectively, for the plot in which plant \(i\) was found. \(\text{DATE}_{\text{plot}[i]}\) is the date on which I sampled the plot, to control for any increases in herbivory that may have occurred while the sampling was ongoing. \(\mu^1_{\text{species}[i]}\) and \(\mu^2_{\text{plot}[i]}\) are the random effects for species and plot, respectively. \(\mu^3_{\text{obs}[i]}\) is a random effect for the individual observation which was included to account for any over- or under-dispersion in the
data since the binomial distribution contains no variance parameter. The $\alpha$ (intercept) and $\beta$ parameters are the fixed effects.

I used the lme4 package (Bates, Maechler, & Bolker 2011) for R statistical environment (R Development Core Team 2010) to fit the model.

Plot level herbivory (after accounting for species-level variation, sampling date, and observation) can then be estimated as the best linear unbiased predictors (BLUPs) – sometimes referred to as the conditional modes – of $p_i$ (hereafter estimated proportional leaf damage). For plot $j$, this is equal to $p_j = \text{Logit}^{-1}(\alpha + \mu_j^2 + \beta_{pd}PD_j + \beta_{sr}SR_j + \beta_{pd*sr}(PD*SR)_j)$. Likewise, herbivory of species $k$ (after accounting for plot-level variation, sampling date and observation) is $p_k = \text{Logit}^{-1}(\alpha + \mu_k^3)$. These values were used for plotting (Figs 3-2 and 3-3).

Significance of the relationships between estimated proportional leaf damage and the fixed factors was determined using a parametric bootstrap approach. For each fixed factor, data was simulated under a simplified model without the fixed factor of interest. The full model was then fit to the simulated data and the z statistic was calculated. The observed z statistic from the full model was then compared to the distribution of z values obtained from 1000 such simulations, and a p value determined as the percent of simulated z values whose absolute value was greater than or equal to the absolute value of the observed z-value (Pinheiro & Bates 2000).

To make sure that abundance weighting of phylogenetic diversity did not bias my results, I also ran the analysis described below with PSV (unweighted phylogenetic diversity) in place of PSE.

### 3.4 Results

The average percentage of leaves damaged in this study was 53.6%. The species of the plant had a large effect on the estimated proportional leaf damage, with estimated variance for the species random effect of 2.4 compared with 0.26 for the plot random effect and 0.82 for the observation random effect (equivalent in this model to residual variance). Leaf damage rates ranged from 5% for the non-native highly defended *Euphorbia cyparissias* to close to 98% for the (also non-native) forage legume *Medicago sativa* (Figure 3-2). Most of the common, native
species such as *Solidago canadensis*, *Asclepias syriaca* and *Symphyotrichum spp.* had intermediate to high levels of herbivory (Figure 3-2).

Sampling date was positively related to estimated proportional leaf damage but not significantly so (z = 1.05, p = 0.334; Table 3-2).

![Figure 3-2. The 27 species for which herbivore damage measurements were taken. On the left is the phylogenetic relationships of the species with branch length representing time since divergence. On the right is a barchart whose bars represent the best linear unbiased predictors (BLUPs) or conditional modes of the estimated proportional leaf damage for each species. Error bars are based on the conditional variance-covariance matrix generated by the model fitting procedure (lmer function in the lme4 package for R) and are conditional mode +/- 1 conditional standard deviation.](image)

After accounting for species composition, I found a significant positive main effect of species richness (z = 2.26, p = 0.042), and a marginally significant negative main effect of phylogenetic diversity (z = -0.19, p = 0.055) on herbivory at the plot-level (Table 3-2, Figure 3-3). There was also a significant negative interaction between phylogenetic diversity and species...
richness of plants ($z = -2.27$, $p = 0.043$; Table 3-2, Figure 3-3), so that the positive effect of species richness on herbivory decreased with increasing phylogenetic diversity. This means that the plots with the highest estimated proportional leaf damage were plots with many species which tended to be closely related. Plots with few species and plots with more distantly related species tended to have lower herbivory (Figure 3-3). Plots with the lowest phylogenetic diversity and the highest species richness had about twice as much proportional leaf damage (~80%) as plots with high phylogenetic diversity and low species richness (~40%, Figure 3-3).

Using phylogenetic diversity unweighted by abundance (PSV) in place of PSE, the results are similar, except there is a much weaker main effect of phylogenetic diversity ($\beta_{pd} = -0.017$, $z = -0.031$, $p = 0.97$). However, the species richness effect ($\beta_{sr} = 0.048$, $z = 2.336$, $p = 0.019$) and the important interaction between phylogenetic diversity and species richness ($\beta_{sr*pd} = -0.44$, $z = -2.25$, $p = 0.024$) are significant and of similar magnitude to those in the model using abundance weighting. The model with abundance weighted phylogenetic diversity fits slightly better based on its AIC score (12814 vs. 12816). Therefore the important results of this study do not depend on abundance weighting. For the remainder of the chapter, I base my inferences on the results of the abundance weighted model.

Table 3-2. Statistics for the fixed effects in a generalized linear mixed model (GLMM) with binomial family and logit link. $Pr(|z|_{obs} < |z|_{sim})$ is the p-value generated from a parametric bootstrap on the $z$ values. * $z$ value is significant at the alpha = 0.05 level.

| Parameter | Name of Factor                        | Estimate | $z$ value | $Pr(|z|_{obs} < |z|_{sim})$ |
|-----------|---------------------------------------|----------|-----------|-----------------------------|
| $\alpha$  | Intercept                             | 0.032    |           |                             |
| $\beta_{date}$ | Sampling Date                   | 0.029    | 1.05      | 0.334                       |
| $\beta_{sr}$ | Plant Species Richness          | 0.038    | 2.26      | 0.042*                      |
| $\beta_{pd}$ | Plant Phylogenetic Diversity (PSE) | -0.87    | -2.10     | 0.055                       |
| $\beta_{sr*pd}$ | Plant Diversity Interaction  | -0.51    | -2.27     | 0.043*                      |

### 3.5 Discussion

The results of this study show that phylogenetic diversity is a useful measure for predicting the level of herbivory in plant communities. I have shown that community-level
herbivory tends to increase with plant species richness, consistent with some past studies, and in contrast to other past studies (Table 3-1). On the other hand, I also showed, for the first time, that high phylogenetic diversity of plant communities is associated with overall lowered levels of herbivory. Even more importantly, there was an interaction between plant species richness and phylogenetic diversity, such that with increasing phylogenetic diversity, the positive effects of species richness on herbivory decrease.

Figure 3-3. Two figures showing the relationship between estimated proportional leaf damage and plot-level plant species richness and phylogenetic diversity. a) Points represent best linear unbiased predictors (BLUPs) or conditional modes of plots. The size of the points is proportional to the species richness of the plot so that large points are speciose communities. Error bars are based on the conditional variance-covariance matrix generated by the model fitting procedure (lmer function in the lme4 package for R) and are conditional mode +/- 1 conditional standard deviation. Fitted lines are back-transformed predicted values from the full generalized linear mixed model, for four different pre-set values of species richness (3,6,12,&17) representing the full range of species richnesses in this study. b) A heatmap which shows the back-transformed fitted surface of the full generalized linear mixed model. Points are the plot BLUPs, their colour represents their value as per the legend. Points that are darker than the surrounding colour fall below the predicted surface; points which are lighter fall above it.
3.5.1 The effects of plant species richness on herbivory

The positive effect of plant species richness on herbivory found here is the opposite of early ecological predictions (Elton 1958; Root 1973), but is not surprising given the frequency with which this pattern has been found in other systems (e.g. Mulder & Huss-Danell 2001; Prieur-Richard et al. 2002; Scherber et al. 2006; Vehviläinen, Koricheva, & Ruohomäki 2007; Lau et al. 2008; Schuldt et al. 2010; Plath et al. 2011; see Table 3-1). Theory predicting decreased levels of herbivory in speciose communities was based on the idea that specialist herbivores would be less likely to find and more likely to abandon diverse patches because abundance of their preferred hosts would necessarily be low in such communities (the Resource Concentration Hypothesis : Root 1973). However, this theory is dependent on the herbivore species being monophagous. Thus, in systems where monophages are rare or do not constitute the most damaging class of herbivores, the Resource Concentration Hypothesis is unlikely to apply. Another theory for why herbivore abundance and thus herbivory may be low in speciose plant communities is the Enemies Hypothesis (Elton 1958; Root 1973), which suggests that predators will be more abundant in diverse plant communities, and they will suppress herbivore populations. However, several recent empirical tests of this hypothesis have shown little direct relationship between plant species richness and predator abundance (Scherber et al. 2010a; Schuldt et al. 2011).

Theory for potential causes of a positive relationship between species richness and herbivory, on the other hand, is less developed and less frequently cited. Some authors have suggested that this may be the result of nutritional advantages to generalist herbivores who have access to a variety of food resources in diverse patches (Bernays et al. 1994; Unsicker et al. 2008; Schuldt & Baruffol 2010), which I refer to here as the Dietary Mixing Hypothesis. Other authors have suggested that spillover from preferred to less preferred host species could explain the effect, sometimes referred to as ‘associational susceptibility’ (White & Whitham 2000).

3.5.2 The effects of plant phylogenetic diversity on herbivory

The likelihood of the Resource Concentration Hypothesis, the Dietary Mixing Hypothesis, or associational susceptibility being a factor may be related to the phylogenetic
structure of the plant community, because many herbivore species, and especially insect herbivores, have phylogenetic structure in their diet – they feed on few or many species which tend to be closely related (Ehrlich & Raven 1964; Janzen 1980; Ødegaard et al. 2005; Weiblen et al. 2006; Gossner et al. 2009; Futuyma & Agrawal 2009). And so theory which is based on the dichotomy of specialist vs generalist herbivores is likely to be too simplistic to adequately describe real systems. Instead it is more useful to use three categories of herbivore which may inhabit a plant community: 1) True specialists or monophages – which feed on only a single plant species, 2) Phylogenetic specialists or cladophages – which feed on a group of related plant species, and 3) true generalists or polyphages – which feed on a group of plant species which has no pattern with respect to phylogeny at some relevant phylogenetic scale. Phylogenetic scale is important because almost any species can be considered a cladophage at some phylogenetic scale. For example, all insect herbivores are cladophages at the scale of the tree of life, because they only eat plants – a monophyletic clade. And so to properly define these categories, the phylogenetic scale of interest must also be defined. Practically speaking, for the study of herbivory, this will usually be based on the phylogenetic tree containing all the plant species present in the study, which will usually be the most appropriate for understanding local ecological dynamics (Cavender-Bares et al. 2009).

Using this framework we can begin to make hypotheses about the effects that phylogenetic diversity might have on herbivory in plant communities. It is clear that neither monophages nor polyphages should be affected by phylogenetic diversity of plants, at least directly – though nutritional effects are possible in generalists. On the other hand, cladophages are likely to respond to phylogenetic diversity of plants due to direct interactions with their host-plants (Dinnage et al. 2012). In a plant community with low phylogenetic diversity, if one host capable of supporting a particular cladophage is present, there are likely to be other suitable hosts as well (assuming the presence of at least moderate species richness). On the other hand, in plant communities with high phylogenetic diversity, if any hosts are suitable for a particular cladophage, it is likely to be the only one. This means that cladophages present in low phylogenetic diversity plant communities will be 'effective polyphages'; cladophages present in high phylogenetic diversity plant communities will be 'effective monophages'. Therefore, in plant communities with low phylogenetic diversity, cladophages are more likely to be able to take advantage of dietary mixing effects (as per the Dietary Mixing Hypothesis), and so species
richness should have a positive effect. This is consistent with the negative effect of phylogenetic diversity on herbivory observed in this study, and also may explain why the positive effect of species richness increased at low phylogenetic diversity.

In plant communities with high phylogenetic diversity, cladophages will usually only be able to feed on one or a very few species, and so they may respond according to the Resource Concentration Hypothesis, that is, increasing the number of species in the plant community will make it more difficult for them to find their preferred host. Though in this study, the effect of species richness never became negative even at the highest level of phylogenetic diversity, it did become very nearly flat (Figure 3-3). It is possible that the relationship would have become negative if there had been plots in this study with even higher phylogenetic diversity than observed.

There are several reasons why the relationship between plant species richness and herbivory may not become completely negative at the highest phylogenetic diversity of plants. For one, the effects of cladophages will be overlaid on the effects from monophages and polyphages. If the polyphage effect is more important in the system, then positive effects of plant species richness will likely predominate. Another possibility is that low species richness can sometimes have a negative effect on monophages, instead of the expected positive effect according to the Resource Concentration Hypothesis. These effects have been termed 'resource dilution effects' (Otway, Hector, & Lawton 2005), and the commonness of their occurrence has yet to be established.

Though no study to date has studied the role of phylogenetic diversity *per se* on rates of herbivory in plant communities, my results are consistent with the results of Jactel & Brockerhoff (2007), who found in a meta-analysis that reductions in herbivory for focal trees grown in mixed stands instead of monoculture stands were stronger when the associated tree species in the mixed stand was taxonomically unrelated to the focal species.

### 3.5.3 The role of cladophages in ecological systems

The relative abundance of cladophages in this system is unknown, but it is likely that they occur regularly in most systems. It has been noted that the tendency for herbivores to feed on
several closely related species is widespread (Ehrlich & Raven 1964; Janzen 1980; Futuyma & Agrawal 2009). If so, it is predicted that insect herbivore assemblages should be more similar in closely related plant hosts than in more distantly related ones. This pattern has been found in several recent studies in different systems (Ødegaard et al. 2005; Weiblen et al. 2006; Gossner et al. 2009). For example, in a tropical system, Weiblen et al. (2006) found that approximately half of the herbivore species they studied could be categorized as phylogenetic specialists.

The widespread existence of cladophages is also an assumption underlying the hypothesis that invasive species which are more distantly related to native species should experience higher levels of enemy release and thus lower levels of herbivory (Mitchell et al. 2006). This pattern, too, has been found in several recent studies (Dawson, Burslem, & Hulme 2009; Hill & Kotanen 2009; Ness, Rollinson, & Whitney 2011). Native species have also been shown to experience lower herbivory when growing with neighbours which are distantly related (Yguel et al. 2011; Ness et al. 2011), further suggesting not only that cladophages are common, but that they exert important influence in ecological systems.

### 3.5.4 Alternative explanations

There are several alternative explanations for why phylogenetic diversity might indirectly affect herbivory. It has been suggested that phylogenetic diversity is a good proxy for unmeasured trait or functional diversity of a community (e.g. Cadotte et al. 2008; Cavender-Bares et al. 2009). It is possible that functional diversity may be responsible for reduced herbivory. It is not clear why functional diversity would decrease herbivory directly, but it is possible that increased functional diversity could promote predator recruitment and abundance, which in turn could suppress herbivores. Functional diversity could increase the architectural complexity of a plot, allowing more hunting niches, nesting sites, and places to hide and stalk for predators (Andow & Prokrym 1990; Coll & Botrell 1996; Beals 2006; Woodcock et al. 2007). For example, Dinnage et al. (2012; Chapter 1 of this thesis) found that in an experimental prairie system, predator abundance increased strongly with phylogenetic diversity. However, in the old field system at my study site, there was little variation in structural forms. Most species grew with tall stalks, and leaves parallel to the ground along their entire height. There were a few understory species (rosettes), a few vines, and a few tree or shrub saplings. Most plots had all of
these, regardless of phylogenetic diversity (personal observation). These growth forms occurred across the phylogenetic tree without any obvious patterns. However, I cannot rule out this explanation without further information on the abundance of predators. The effect may also have been the result of a combination of factors, that is, both increased predator abundance and reduced diet breadth are jointly responsible for the decrease in herbivory.

It is possible that a correlation between phylogenetic and functional diversity contributes to the patterns I observed in addition to the effects of cladophagy, but it does not offer a good explanation for the interaction between phylogenetic diversity and species richness, or the effect of species richness itself. This is because functional diversity is also expected to – and usually observed to – increase with species richness, and in fact this is often the explanation offered for why species richness affects various ecosystem functions (Tilman 1997; Loreau et al. 2001; Hooper et al. 2005; Cardinale et al. 2006; Balvanera et al. 2006; Duffy et al. 2007; Cadotte et al. 2009; Fornara & Tilman 2009; Cardinale 2011; Connolly et al. 2011). Given this, we should expect to see a synergy between phylogenetic diversity and species richness, rather than a negative interaction.

Though the observational nature of this study gives it the advantage of realism, it also means I cannot completely rule out all confounding factors that may explain my results. If, for example, there were abiotic conditions which influenced both species richness and phylogenetic diversity, and also affected herbivory, and which varied sufficiently across my sites, this could spuriously generate the observed correlations. Though all the plots in this study came from a small geographic area and from a single habitat type, and thus likely do not vary much in environmental conditions, it is possible that some soil characteristics may have varied between the plots. Though environmental correlates of species richness have attracted much interest in the past, especially at large spatial scales, little is known about what environmental factors might influence phylogenetic diversity. Since it is often supposed that phylogenetically closely related species will compete more strongly, it is possible that plots with conditions that suppress competition amongst plants are the only ones where many species which are closely related can coexist. An example of this might be an environment with very mild restrictions on a species’ fitness, which I show in Chapter 4 can reduce competitive exclusion of closely related species. If such conditions also promoted high herbivory, then this could lead to high herbivory in plant communities with high species richness and low phylogenetic diversity, as observed. To fully
understand the role of phylogenetic diversity in ecosystem function will require conducting large-scale experiments where phylogenetic diversity is explicitly manipulated, but observational studies in natural settings such as this will remain invaluable.

3.5.5 Limitations of this study: Measuring the impact of herbivory

This study shows that many plants may receive lower herbivore damage in phylogenetically diverse communities. This result is similar to those of Yguel et al. (2011) who found that oak trees that grew amongst distantly related trees experienced lower herbivory. Yguel et al. (2011) suggested that this may produce a selective benefit that could promote the evolution of a strategy to grow amongst distant relatives. This is an intriguing possibility, but studies which only measure the magnitude of damage on plants cannot draw this conclusion, unless they also measure the impact of damage on the plants. In order to understand how selection might affect a plants' preference for its phylogenetic neighbourhood, we need to know how the fitness of the plants are affected.

Damage is generally thought of as a negative impact on plant fitness, but many plants are able to tolerate large amounts of damage without sustaining large reductions in fitness (Rosenthal & Kotanen 1994; Strauss & Agrawal 1999). To understand fitness impacts of herbivory generally requires measuring plant performance in the presence and absence of herbivory. In Table 3-1, I show that although many studies that looked at the magnitude of herbivory found that plant species richness increased herbivory, all but two studies that looked at the impact of herbivory found a negative association with plant species richness, such that speciose communities had a smaller difference in biomass between herbivore exclusion and control treatments. This suggests that plant diversity may provide benefits in terms of a plant's ability to tolerate herbivory, which more than makes up for any increases in the actual amount of herbivore damage.

I therefore cannot conclude that any reduction in herbivory due to high phylogenetic diversity necessarily results in an advantage to plants growing with their distant relatives. However, the only way this would not be the case is if plants growing in low phylogenetic diversity communities were more tolerant of damage than plants growing in high phylogenetic
diversity communities, and this increase in tolerance fully compensated for the increase in herbivore damage. This seems unlikely, but cannot be ruled out without herbivore exclusion studies. It is possible, for example, that plants growing with distant relatives will tend to be in more marginal habitat, since abiotic niche requirements also may be similar for close relatives (Cavender-Bares et al. 2009). Plants in marginal habitat may be impacted by herbivory more.

3.5.6 Implications for other studies

As I show in Table 3-1, the results of previous studies are inconsistent about the relationship observed between herbivory and species richness. The interaction I observed between phylogenetic diversity and species richness in this study may offer an explanation. That is, the degree and even direction of the relationship between species richness and herbivory may depend on the difference in phylogenetic diversities of the communities that are compared. Though I observed such a relationship at a local scale, between individual plots, it may also apply on a larger scale. For example, it is possible that I may have observed an overall positive main effect of species richness in my study because there was generally a low amount of phylogenetic diversity in this system compared with other systems. Old fields tend to be dominated by species in the family Asteraceae, and the one I studied is no exception. Other systems where the question has been studied may draw from a larger pool of evolutionary history, where negative effects may perhaps be more likely.

Of course, the relative abundance and importance of monophages, polyphages, and cladophages present and active in the plant communities may also alter the observed effect of plant diversity. For example, simplified ecosystems such as agricultural systems – where we often see negative diversity-herbivory relationships (Andow 1991) – may be dominated by monophages, because monocultures on very large scales may discourage polyphages (or even many cladophages). Whereas polyphages need not be less common compared with monophages in monocultures that are imbedded in a more diverse landscape (as is the case for most biodiversity experiments), as long as the scale of the plots does not exceed the dispersal capability of the polyphages.
3.5.7 Conclusion

Here I have shown that incorporating measures of phylogenetic diversity can improve our understanding of the role of plant diversity in promoting or suppressing herbivore damage. Phylogenetic diversity was negatively correlated with herbivory in an old field system, and determined the degree to which species richness influenced herbivory as well. If we consider a reduction in herbivore damage as a positive outcome at the community scale, as is often the case in agricultural ecosystems, then we may wish to prioritize the conservation and restoration of phylogenetic diversity, perhaps even at the expense of some species richness.

3.6 Acknowledgements

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Chapter 4: Disturbance alters the phylogenetic composition and structure of plant communities in an old field system

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4.1 Abstract

The changes in phylogenetic composition and structure of communities during succession following disturbance can give us insights into the forces that are shaping communities over time. In abandoned agricultural fields, community composition changes rapidly when a field is plowed, and is thought to reflect a relaxation of competition due to the elimination of dominant species which take time to re-establish. Competition can drive phylogenetic overdispersion, due to phylogenetic conservation of 'niche' traits that allow species to partition resources. Therefore, undisturbed old field communities should exhibit higher phylogenetic dispersion than recently disturbed systems, which should be relatively 'clustered' with respect to phylogenetic relationships. Several measures of phylogenetic structure between plant communities were measured in recently plowed areas and nearby 'undisturbed' sites. There was no difference in the absolute values of these measures between disturbed and 'undisturbed' sites. However, there was a difference in the 'expected' phylogenetic structure between habitats, leading to significantly lower than expected phylogenetic diversity in disturbed plots, and no difference from random expectation in 'undisturbed' plots. This suggests that plant species characteristic of each habitat are fairly evenly distributed on the shared species pool phylogeny, but that once the initial sorting of species into the two habitat types has occurred, the processes operating on them affect each habitat differently. This study supports the notion that disturbed plots are more clustered than expected, rather than 'undisturbed' plots being more overdispersed, suggesting that disturbed plant communities are being more strongly influenced by environmental filtering of conserved niche traits.
4.2 Introduction

After a disturbance which removes vegetation, plant communities are reset. From bare ground new communities sprout up and change over time as the forces of seed bank dynamics, colonization, environment and interspecific interactions act upon them. Studying successional dynamics often yields insight into these processes, which is why the process of succession in plant communities has remained an important focus of research in community ecology [1,2]. A relatively new method of analyzing community data examines how the evolutionary history (phylogeny) of species influences community structure. I hope to show that the techniques of community phylogenetics have potential for expanding our understanding of succession.

Disturbance can change the balance of forces acting on the local community. By eliminating species and thus freeing space and resources, disturbance usually will temporarily reduce the impact of interspecific competition [3,4,1]. As succession occurs, the original strength of competition is gradually restored. Change in the strength of competition is thought to be one of several important drivers of changes in community composition during early succession [1]. In general, this process of recurring disturbance and successional change should promote coexistence of competing plants if there is a trade-off between competitive ability and colonization efficiency or resistance to disturbance [5].

Any change in competition can also affect the phylogenetic structure of communities [6-9]. Competition and 'environmental filtering' affect the degree of similarity in the ecological roles ('niches') of species in communities, and phylogenetic distance can be treated as a proxy for this similarity – more closely related species being assumed to be more alike. The concept of limiting similarity [10,11] proposes that similarity in the resource requirements and usage by consumer species limits their ability to coexist. On the other hand similar species will also share environmental tolerances, meaning that more similar species will be more likely to coexist in any given area [12]. Thus the processes of competition and environmental filtering act in opposite directions. By using phylogeny to explore such patterns of similarity it may be possible to distinguish which process played a stronger role in that community. The balance of competition and environmental filtering is expected to change during the process of succession, and should therefore produce predictable changes in phylogenetic structure.
The strength of competition should be weaker in communities where a recent disturbance has eliminated or reduced the abundance of competitive dominants. It is known that succession occurs in abandoned agricultural fields, changing communities from a bare plowed field through to the grassland, herbaceous mixed community we usually refer to as ‘old field’, and eventually to woodlands [13,14]. Succession from bare ground to a semi-stable old-field community occurs quickly – on the order of a few years – making it an ideal system to study succession. In eastern North American old fields, the difference between communities of plants before and after a disturbance is thought to result partially from the elimination of competitive dominant species which include several common grass species (Poa spp., Bromus spp., etc.) and a few large herbaceous dicots such as Solidago spp., and Aster spp., [15,16]. In this study I evaluate whether the phylogenetic structure of an old field herbaceous plant community changes in a predictable manner following elimination of these dominant species. I predict that sites that have been recently disturbed will be more phylogenetically ‘clustered’ than those that have not, because reduced competition following disturbance will relax limiting similarity. In addition, disturbance might select for disturbance tolerance traits which could be phylogenetically conserved. The purpose of this study is to test this prediction of competition theory.

Several other studies have attempted to quantify the effect of a disturbance on patterns of relatedness among species. Most, however, have used taxonomic measures of relatedness and have found mixed results, with some finding that disturbance increases average relatedness [17-19], but others finding no difference [20]. One study found that plant communities tended to have lower phylogenetic diversity in urban areas [21], but this study encompassed the entirety of Germany, and so was conducted on a very large scale. The study described here is concerned with what happens at the patch scale within a single habitat type. This allows control of differences in habitat that might be confounded with disturbance when compared across large scales. This is important because certain types of habitat may be selected for by humans when creating anthropogenic disturbance.

I distinguish two approaches to incorporating phylogenetic information: analyzing the phylogenetic composition and the phylogenetic structure of communities. Phylogenetic composition simply incorporates phylogenetic relatedness information into traditional methods of studying communities – for example: ordination approaches – which normally treat all species as independent. Phylogenetic structure, on the other hand, is a summary of the phylogenetic information contained in each community, analogous to measures of diversity in traditional
analyses [22]. Phylogenetic structure is analyzed with phylogenetic diversity indices (several are reviewed in reference 23). Phylogenetic structure can be divided into phylogenetic alpha diversity (within site) and phylogenetic beta diversity (between site) [24]. I only look at phylogenetic alpha diversity in this study, however, the concept of comparing phylogenetic composition is related to phylogenetic beta diversity, because site differences can be compared, however, the method of calculating distances between sites is different.

The questions addressed here are: 1) Are recently disturbed old field communities different than undisturbed communities both in species composition and phylogenetic composition?; 2) Is the phylogenetic structure of recently disturbed communities systematically different than that of undisturbed communities? If so, is there evidence that reduced competition after disturbance allows communities to be more phylogenetically 'clustered'?

### 4.3 Methods

#### 4.3.1 Data Collection

I was granted permission to conduct the study on the Koffler Scientific Reserve (KSR) at Joker's Hill (King City, Ontario; http://www.ksr.utoronto.ca/jh.html), a 350 hectare property containing a mix of primary forest, secondary forest and open habitats, including a large area of old field sites. Many areas of the reserve are plowed for experiments and agriculture. I chose fields that had been plowed within the last 2 seasons as examples of recently disturbed systems (R. Dinnage, personal observation). I located 19 of these recently disturbed fields that were separated from each other by at least 50 meters. Most were separated by 100 meters or more, and were spread throughout the old field habitat on the reserve. In each of these fields a 10x10 meter plot was placed haphazardly within 10 meters of the edge of the plowed area. Each of these 'disturbed' plots was then paired with an 'undisturbed' plot of the same size from just outside the plowed area.

The community composition of herbaceous forbs was measured by surveying the presence or absence of species within four 1x1 meter quadrats placed within the four quadrants of each plot. The data from the four quadrats were later combined to the plot level, with the number of quadrats in which each species was found acting as a coarse measure of frequency (0-
The survey was conducted between August 24-31, 2007. All analyses were based on this survey data combined with a phylogeny for all species found in the samples. The raw sample data and the phylogeny are included as supplementary information files.

4.3.2 Phylogeny generation

I created a phylogeny for all the herbaceous old field plants I surveyed by combining a backbone tree based on the APG phylogeny (http://www.mobot.org/MOBOT/research/APweb/) generated by Phylomatic (http://www.phylodiversity.net/phylomatic/phylomatic.html) with subtrees created using downloaded sequences. I made three such trees for three families that lacked resolution on the backbone tree (Asteraceae, Lamiaceae, and Brassicaceae), using all species from these families found in the samples plus several other species which had divergence estimates between them [25].

The internal transcribed regions (ITS1 and ITS2; but not 5.8S) for each species in these sub-trees plus an outgroup species (from the hypothesized sister family) were downloaded from GENBANK [26]. After downloading I aligned them using MAFFT alignment [27] with default settings, concatenated them, then analyzed them with maximum parsimony using the PHYLIP 3.47 [28] software package (dnapars program) with default settings.

Branch lengths for the backbone tree were calculated with the BLADJ program included with Phylocom 3.41 [29]. This program assigns ages to nodes that were estimated in reference 25, and then estimates the ages of remaining nodes so that they spread evenly between the dated nodes. This method loses some phylogenetic information, but is better than simply using number of nodes separating taxa as an estimate of phylogenetic distance, especially for community phylogenies which are highly incomplete.

Branch lengths on the three subtrees were calculated from the maximum parsimony analysis and then converted into age estimates using rate smoothing in the software package r8s [30]. The estimated age of divergence of the family was assigned according to reference 25. Several taxa that were included either in reference 25 or 31 – which estimated divergence times for groups within the Asteraceae – were included in the subtrees so that an estimated age could be assigned to the common node between them and improve the accuracy of the r8s estimate of intervening nodes. Species not occurring in the samples were then trimmed off, before I grafted these subtrees onto the backbone tree. This final tree is a nearly fully resolved (to the genus
level) ultrametric tree with branch lengths in units of time (millions of year) – i.e., a community chronogram (Figure 4-1). Measures of community phylogenetic structure were based on this phylogeny. *Thuja occidentalis* was an unusual occurrence in one plot and was removed from subsequence analysis as a extreme outlier (very large branch length and very rare). Inclusion of *Thuja* did not change the results of the analysis.

### 4.3.3 Comparison of disturbed and undisturbed plots

I compared disturbed and undisturbed plots using several measures of community structure, both traditional and phylogenetic. All analyses were performed using R Statistical Language Environment [32].

### 4.3.4 Species composition

I looked for a difference in species composition between disturbed and undisturbed sites using non-metric multidimensional scaling (NMDS)[33] using the metaMDS function in the *vegan* package [34]. NMDS is an ordination technique which graphically arranges communities according to their similarity in species composition. I used Bray-Curtis distance because it has been found to perform well in simulations for ecological data [35]. Plots which occur close together on the NMDS generated axes are similar in composition. For analysis I used three axes, which fit the data well and resulted in a stress of 15.1%. To test the difference between disturbed and undisturbed plots I used the envfit function from *vegan*, with plot type as a categorical factor variable. Envfit will calculate centroids for each factor level and calculate the difference between centroids. Significance of this difference is calculated using 1000 random permutations of the factor levels. If the observed difference in centroids is greater than more than 95% of the randomly permuted datasets, we can reject the null hypothesis of no difference at an alpha of 0.05.

### 4.3.5 Phylogenetic composition

To test for differences in phylogenetic composition between disturbed and undisturbed plots I again used NMDS, but instead of species composition as the input I used a representation of the phylogenetic nodal structure of each community. To do this I used the node-as-factor
function in Phylocom [29]. This function generates a matrix with a different column for every node in the input phylogeny – then for each plot sample it fills in what nodes are present in that community, weighted by their frequency. In order for a node to be considered present in a community, at least one species from the clade subtending that node must be present. The result is similar to a standard community matrix, but with columns representing phylogeny nodes instead of species. This allows the incorporation of phylogenetic information into ordination, by allowing communities that share nodes to be considered similar. In an ordinary ordination species are treated independently. For example, if two closely related species have disjunct distributions, they could cause communities to be very different on a traditional ordination. However, using a node-as-factor approach, their close relationship will cause these communities to be more closely clustered. I used three axes resulting in a stress of 11.7%. Again, envfit was used to test the difference between disturbed and undisturbed plots using 1000 permutations.

4.3.6 Phylogenetic structure

I used two methods to compare phylogenetic structure amongst habitats, and take concordance between the results to be a sign of robustness.

4.3.6.1 Method 1

First, I calculated a phylogenetic diversity index for all the plots that could be compared amongst them. I chose two related phylogenetic diversity indices: phylogenetic species variability (PSV) and phylogenetic species evenness (PSE) [36]. PSV is calculated as the expected variation within a community for a trait that is evolving neutrally at a fixed rate (i.e. under brownian motion sensu Felsenstein [37]). This method was useful for comparing between habitats because it is unbiased with respect to species richness [36,38]. This is desirable because disturbed and undisturbed habitat are likely to differ in species richness. PSE allows for the incorporation of abundance data into PSV. I used species frequency as a measure of abundance.

PSV and PSE, like all phylogenetic diversity indices, are dependent on the shape of the input phylogeny, which is a function of the species pool considered. In other words, every species pool will have a unique 'expected' phylogenetic diversity for plots of differing species richness. Therefore, phylogenetic diversity indices must be interpreted in terms of deviation from the expected in order to make inferences about forces acting on the plot scale (i.e. independent of
the forces which created the species pool). I therefore compare phylogenetic diversity in two ways. First I compare the raw diversity values, which can tell us about the overall pattern of phylogenetic diversity amongst habitat types. I do this with a simple paired t-test for PSV and PSE. However, since raw PSV and PSE incorporate information both about the structure of the overall species pool of the habitat, in addition to structure at the plot scale, this comparison cannot distinguish the forces that are at work within each different habitat, unless we take the species pool for each habitat to be the same. Therefore, I compare how plots in each habitat deviate from their expected phylogenetic diversity based upon the species pool for that habitat by generating null distribution based upon a simple null model of community assembly.

Null distributions were generated for PSV and PSE using the *phylostruct* function in the R package 'Picante' [39]. This function generates null communities by randomly assembling them from the observed species pool. The null model I used randomly placed species into communities so that each species maintained its original frequency among plots. Results using other possible null models were similar. Null distributions of mean PSV and PSE were generated for 1) all plots 2) just disturbed plots, and 3) just 'undisturbed' plots, to which the observed mean PSV and PSE were compared.

### 4.3.6.2 Method 2

I compared the degree to which phylogenetic distance amongst species pairs was correlated with their degree of co-occurrence (as in reference 7). I used the *comm.phylo.cor* function in the R package 'picante' [39]. This function calculates pairwise phylogenetic distances among species using an input phylogeny and then compares this to an index of species co-occurrence using correlation. I used Schoener's index of co-occurrence ('cij' [40]), following reference 7. For visualizing the results I placed species pairs into 'bins' based on their phylogenetic distance from one another. Each bin spanned approximately 10-15 million years. I calculated the mean and standard error of the co-occurrence indices within each phylogenetic distance bin and plotted this (Figure 4-5). The raw data was used to calculate statistics for hypothesis testing.

The test was repeated for: 1) all plots, 2) just disturbed plots, and 3) just 'undisturbed' plot. Traditional Pearson correlation statistics were produced for each, however, the assumption of this statistic are violated. Because the comparison was conducted on pairwise measures, and each species is compared to every other species, datapoints are not independent. To control for
this violation, I performed a randomization test [7]. Because I was interested in the effects of phylogeny, species were randomly shuffled amongst the tips of the phylogeny 1000 times and the Pearson correlation recalculated each time. This produced a null distribution of correlation coefficients to which the observed values could be compared. This procedure is essentially similar to a 'Mantel' test. I could also test if the Pearson correlation value differed significantly between habitats by calculating the difference between generated correlations for the disturbed


(https://www.mobot.org/MOBOT/research/APweb/)
habitat and those for the 'undisturbed' habitat for each 1000 iterations. This creates a null
distribution for the difference between habitats in their correlation between phylogenetic distance
and co-occurrence. If the actual difference is greater than 95% of the generated values, then I can
conclude that it is significant at the $a = 0.05$ level. Since I expected disturbed plots to be more
phylogenetically clustered, and thus have a more negative correlation between phylogenetic
distance and co-occurrence I performed a one-tailed test of this hypothesis.

4.4 Results

4.4.1 Species composition

Disturbed plots had nearly 70% more species than undisturbed plots (p<0.001). Nonmetric multidimensional scaling plots showed strong segregation between disturbed and undisturbed plots. The two environments separated mostly on axis 1 and axis 3 – only these axes are shown in the plot (Figure 4-2a). The difference in centroids was significant (p<0.001).

4.4.2 Phylogenetic composition

NMDS using the phylogenetic node structure of the plots showed even stronger separation between disturbed and undisturbed plots, with no overlap of the standard

Figure 4-2. Non-metric multidimensional scaling scores for disturbed and undisturbed plots. Plot of the nonmetric multidimensional scaling scores for the two most important axes for all plots using the a) species composition data, or b) phylogenetic nodal structure data. The centroids for disturbed and undisturbed plots are labelled and linked to all points with radiating lines. Ellipses represent 1 standard deviation. Size of the points represents the relative number of species found in the plots.
deviation ellipses (Figure 4-2b). This time most of the separation occurred in the first two axes, which were plotted (Figure 4-2b). The centroids were significantly different (p<0.001).

Most of the major clades have a relatively even representation in both habitat types. This can be seen in Figure 4-3, as the major division in the tree used here (rosids, asterids, Asteraceae) fall along the dividing line between disturbed and undisturbed habitat. Within these major groups, each smaller clade seems to dominate in one habitat or the other. On the other hand, it is very rare that two species which are each others' closest relative on the tree are found in different

![Figure 4-3. Non-metric multidimensional scaling scores for all phylogenetic nodes with reference to habitat occurrence tendency. Ordination plot for the phylogenetic ordination shown in figure 3-2b but with plot points removed and phylogenetic node vectors displayed. For clarity, only important or non-redundant nodes are displayed. Filled bubbles are a rough representation of the branching structure of the nodes from one another. Dark filling represents more association with undisturbed plots whereas lighter filling represents more association with disturbed plots. Dotted ellipses represent the centroids and 1 SD area as a reference for where disturbed and undisturbed plots fall on the diagram. Nodes which are referred to can be seen on figure 3-1.](image-url)
habitats. Therefore, habitat preference seems to be phylogenetically conserved at an intermediate phylogenetic scale.

4.4.3 Phylogenetic structure

There was no significant difference in PSV ($t = -0.67$, $df = 18$, $p = 0.51$) or PSE ($t = -0.49$, $df = 18$, $p = 0.63$) between habitats, though they were both slightly lower in the 'undisturbed' habitat (Figure 4-4).

However, habitats differed in how they deviated from expected PSV and PSE. When looking at plots across both habitats, on average both PSV and PSE were significantly lower than expected by chance under a null model of community assembly (PSV: $p < 0.001$; PSE: $p < 0.001$; Figure 4-4). When considered separately, however, disturbed plot were on average significantly phylogenetically clustered – PSV and PSE were lower than expected (PSV: $p = 0.008$; PSE: $p < 0.001$; Figure 4-4). On the other hand, 'undisturbed' plots had a random phylogenetic structure, with no difference between observed PSV/PSE and expected based on the null mode (PSV: $p = 0.59$; PSE: $p = 0.68$; Figure 4-4). This result was corroborated by a significant negative correlation between co-occurrence and phylogenetic distance between species in the disturbed plots (corr = -0.21, $p$
= 0.003; Figure 4-5), but no significant correlation in the 'undisturbed' plots (corr = -0.03, p = 0.32; Figure 4-5). The difference in this correlation between habitats was also significant (p = 0.017).

4.5 Discussion

Community composition differed between disturbed and undisturbed plots. Disturbed plots had higher species richness, consistent with previous results in old field systems [e.g

Figure 4-5. Relationship between co-occurrence and phylogenetic relatedness for disturbed and undisturbed plots. Plots showing the relationship between phylogenetic distance of species and their degree of co-occurrence for disturbed and undisturbed plots. Co-occurrence index is Schoener's index [40]. Line of best fit is included for illustrative purposes, and is based on least-squares.
Nonmetric multidimensional scaling confirmed that the two habitat types differed in their species composition. This difference was exaggerated in the analysis incorporating the phylogenetic node structure of the plots. This means that disturbed plots are quite phylogenetically distinct from undisturbed plots, with each type of plot represented by different terminal clades. This can be seen visually in Figure 4-1 and 4-3.

Recently disturbed plots displayed larger variation in phylogenetic ordination scores than undisturbed plots. This is likely because most species and clades that are dominant in undisturbed habitats are also found to a lesser degree in disturbed plots. Several factors are likely responsible for this, including the fact that many are perennial plants which can resprout from rhizomes after the plots were plowed. In addition there is probably a large propagule pressure from old field dominants entering into the disturbed plots. On the other hand, very few species or clades characteristic of disturbed habitats were also found in undisturbed habitats. This may be because most are annual weeds which cannot easily establish under the conditions of high density and shading in the undisturbed plots, because they are adapted to open habitats.

Overall, I found that when all plots were considered together, they were on average significantly clustered phylogenetically, when compared to a null model. This was true both for PSV, and PSE when compared to a null model of species assembly. It was also true when pairwise co-occurrence values were correlated with phylogenetic distance. This is consistent with many other studies of phylogenetic structure in plant communities, most of which have found phylogenetic clustering when structure was found [reviewed by 41,42]. However, simulation studies have found that these tests can be liberal under several circumstances [43], including cases of spatial autocorrelation due to limited dispersal, and phylogenetic structure in the experiment-wide abundances. Abundance Phylogenetic Deviation index (APD [43]) measures the clustering of species abundance on the phylogeny by comparing the mean phylogenetic distance of species in the experiment, with the abundance-weighted mean phylogenetic distance. Positive values suggest clustering of abundances, whereas negative values suggest overdispersion of abundances. In this study the APD value for undisturbed plots was 0.08 and for disturbed plots it was 0.10 – slight clustering. This could have made the overall test liberal, however, it is the comparison among habitat types which is the important result. Since the APD values are close, there is little reason to suspect that the test for the disturbed sites is more liberal than that for the undisturbed sites, and so there should not be a higher probability of finding significant results in the disturbed plots.
Despite no difference between disturbed and undisturbed habitat types in phylogenetic diversity indices, there was a difference in how they deviated from their expected phylogenetic diversity, based on null models of community assembly (Figure 4-4). Disturbed plots were significantly more 'clustered' than expected under a null model of community assembly, whereas undisturbed plots did not deviate from random expectation. This could only have come about if the 'expected' phylogenetic structure of each habitat differed.

In this study, I found that the available species pool for disturbed and undisturbed habitat differed, and that the phylogenetic diversity of each pool also differs. The average phylogenetic diversity expected under a null model of community assembly is reflective of the underlying phylogenetic structure of the species pool. Disturbed plots had a higher expected phylogenetic diversity, suggesting that at a regional scale disturbed areas contain lineages that are less related than in undisturbed areas. This is contrary to my expectation, as it is usually thought that disturbance should select closely related species. One possible explanation is that the undisturbed communities actually constitute a harsher environment for species due to their high level of competition, and that there may be a suite of traits that make species suited to this environment which are phylogenetically conserved. On the other hand, since I essentially only have a single sample for each habitat's pool of species, this difference may be due to chance alone. It is impossible to assess the generality of this pattern because most studies which have found higher clustering in disturbed habitats have failed to distinguish between regional species pool differences and more local plot level differences [18,19,21].

The results at the plot-level within each habitat type were different. Disturbed plots were more phylogenetically clustered than expected by chance, so that individual plots had, on average, lower phylogenetic diversity than their regional habitat pool. In undisturbed habitat, phylogenetic diversity in individual plots did not differ significantly from the regional habitat pool. A weaker competitive environment in recently disturbed plots could lead to more phylogenetic clustering than expected in several ways. If the environmental tolerances of species are phylogenetically conserved, then differences in the environment could act as a filter, and closely related species will be more likely to coexist. A heavy disturbance such as plowing could create a harsh or unique environment that selects for species that can tolerate these conditions [17,44].

Stripping away dominant vegetation could lay bare environmental variation which was masked before. This could happen if the competitive stresses of the environment are strong
enough that they become more important than anything else, and so in a sense, homogenize the environment. If so, such a competitive environment will act as an initial filter, reducing the species pool, but thereafter species are distributed randomly with respect to phylogeny. This could also happen if traits relating to competition are less phylogenetically conserved than those involved with dealing with abiotic stresses which may be more prevalent in recently disturbed environments.

Another possible explanation is that both environments are experiencing forces that promote phylogenetic clustering, but in the undisturbed environment there are also strong counteracting forces promoting phylogenetic overdispersion. This would happen if ecological traits related to niche partitioning were phylogenetically conserved, and that the stronger competition in undisturbed plots led to stronger niche differentiation. Opposing processes that counteract each other's effect on phylogenetic structure has been demonstrated before. One study found that when environmental factors were statistically removed from sunfish communities, phylogenetic overdispersion was revealed [38]. An argument against this possibility is that phylogenetic conservation of niches has been difficult to demonstrate in plants. For example a study of meadow communities showed that phylogenetic distance was not correlated with niche separation along several axes of soil conditions [45]. Another study came to the conclusion that the intensity of competition between plant species pairs was only weakly correlated with phylogenetic distance in a meta-analysis of pot experiments, and only for certain taxa [46].

Though competition and environmental filtering are often thought of as dominant forces in the structuring of communities, there are other factors that could come into play in this system and others. Predation, or herbivory in this case, could be involved in the structuring of communities. Herbivory could promote phylogenetic overdispersion if herbivores fed on more than one species, and those species tended to be closely related, through the action of 'apparent competition' [47], in a manner analogous to resource competition. Theory has shown that apparent competition can act very similarly to resource competition [48], and so limiting similarity may act here as well, only in this case the similarity is in shared predators rather than shared resources. This effect can also be thought of as a phylogenetic extension of the Janzen-Connell hypothesis [49,50] as described in a recent review of community phylogenetics [8]. Such “Janzen-Connell” effects could be stronger in the undisturbed plots. Though it is unlikely that herbivore pressure differs greatly between the habitats (given their close spatial proximity), herbivore effects would likely be gradual and only result in significant difference in community
structure over many years – years which the undisturbed plots have experienced and which recently disturbed plots have not.

Predation could also act as a filter. Though smaller specialized herbivores such as insects may not vary between the habitats, deer herbivory may. Deer are common on the property on which I conducted my surveys and they may impose pressure on old field plant communities. The increased exposure of disturbed fields makes plants more apparent, and so deer could be a stronger force in recently disturbed plots. If traits that lead to deer-resistance are phylogenetically conserved, deer could act as a filter leading to phylogenetic clustering in areas where deer are more common.

Many of the effects discussed above vary in the timescale over which they act. Most of the filters promoting clustering will act immediately, whereas those thought to promote overdispersion will act gradually. It may be useful to define filters as density-independent effects on fitness, whereas competitive effects (including both resource and 'apparent') are density-dependant, in that they become stronger in high densities. It may be then that disturbance exposes plant communities to environmental filters which leads to greater than expected phylogenetic clustering at low densities, after which communities gradually return to their 'expected' level of phylogenetic structure, through the action of weak dispersion promoting forces, such as limiting similarity and Janzen-Connell effects, which become important as densities increase. It is particularly interesting to note however, that in this system this process leads to no difference in the absolute phylogenetic diversity of the different habitats, due to differences in their species pool and therefore differences in the expected phylogenetic structure of each habitat.

This could have implications for conservation. It is becoming clear that phylogenetic diversity has consequences for ecosystem functioning [51,52]. If so, reductions in phylogenetic diversity could have negative effects that may be independent of the effects of species richness. Indeed, one study found that urban areas (assumed to be more disturbed) actually had higher species diversity of plants but that phylogenetic diversity was lower [21]. This likely reduces the positive aspects of increased species richness. Consistent with many other studies [17-19,21], I demonstrated the ability of disturbance to decrease the phylogenetic diversity of an area, however, I also show that whether this leads to an absolute difference in phylogenetic diversity between disturbed and undisturbed habitats is dependant on the pool of available species in each habitat. In this case, disturbed areas had the potential for higher phylogenetic diversity than
undisturbed areas, but clustering at the plot level led to statistically indistinguishable values for phylogenetic diversity in each habitat.

4.5.1 Conclusion

Factors that influence ecological succession may act in a biased manner with respect to phylogeny, because of a correspondence between phylogeny and ecological similarity. Therefore, phylogenetic information should be useful in understanding these forces. In this study I found phylogenetic information could be used to get a fuller picture of compositional changes in plant communities. In particular, disturbed plant communities were more phylogenetically clustered than expected by chance, suggesting the action of environmental filters on phylogenetically conserved traits. Importantly, this led to no difference in phylogenetic diversity between disturbed and undisturbed plots, because the underlying species pool for disturbed plots had a higher phylogenetic diversity. This suggests that processes that structure communities can have different effects on phylogenetic diversity at different scales, from the regional to the plot level. This necessitates the careful choice of null models when comparing phylogenetic diversity indices amongst habitats. Analyzing differences in phylogenetic structure and composition at different scales can lead to useful insights into habitat differences in community composition.

4.6 Acknowledgements

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4.7 References


Chapter 5. The interaction between environmental filtering and competitive exclusion in a three trophic-level competition model

5.1 Abstract

In the community phylogenetics literature, patterns of clustering and overdispersion are taken to be signs of environmental filtering and competitive exclusion, respectively, when phylogeny is a good proxy for ecological similarity. Competitive exclusion of ecologically similar species is often assumed to be an expectation of classic theory on limiting similarity, where ecological similarity refers to niche separation. Critics of community phylogenetics have recently pointed out that coexistence theory shows that ecological similarity can also lead to similarity in species’ relative competitive ability (or fitnesses), which will actually promote coexistence. This means that the expected effect of competition on ecological similarity is ambiguous. To fully understand the implications of this issue for community phylogenetics and related fields, however, requires incorporating a concept of environmental filtering, which is expected to promote coexistence of ecologically similar species by only allowing the inclusion of species with suitable traits for an environment, into a model of competition, allowing a full exploration of how these factors interact to determine coexistence. Here, I present a continuous version of a three trophic level competition model – allowing species to compete both through shared resources and shared predators – which incorporates indirect biotic environmental filtering. An analysis of a simplified two species version of the model, suggests that coexistence is maximized at intermediate levels of ecological similarity, and that the strength of environmental filtering affects the position and dispersion of the ideal niche separation. I discuss how the model presented here can serve as an abstract phenomenological model that expresses many of the general characteristics of modern niche concepts.

5.2 Introduction

There has been a recent surge of interest in understanding the effects of niche-based competition and environmental filtering on local community assembly (Adler et al. 2007,
HilleRisLambers et al. 2012, McInerny and Etienne 2012). Niche-based competition includes mutually negative effects of two or more species on each other through indirect interaction with resources or predators, which may in some cases limit their ability to coexist in the same environment. Environmental filtering, on the other hand, is a phenomenon where only some species are able to exist in certain environments, through an interaction between the conditions of that environment and the traits possessed by the species – e.g. only species that possess traits or trait values that are appropriate to an environment can survive and thrive there. Much of the increased interest in these topics has followed from advances in our understanding of coexistence theory, and the development of new tools for testing hypotheses of community assembly relating to coexistence (phylogenetic and trait-based community ecology: Webb et al. 2002, Ackerly and Cornwell 2007, Prinzing et al. 2008, Cavender-Bares et al. 2009, Kraft and Ackerly 2010).

Community phylogenetics, for example, includes the study of patterns of phylogenetic clustering or overdispersion in local communities. Treating phylogeny as a proxy for trait difference, phylogenetic community ecologists hypothesize that clustering is a sign of environmental filtering of species with similar traits, and that overdispersion is the result of similar species competing more strongly, via indirect interactions with other species, and thus competitively excluding each other (Cavender-Bares et al. 2009). There has been much recent criticism of this idea (e.g. Mayfield and Levine 2010, HilleRisLambers et al. 2012, Kunstler et al. 2012), which has largely been driven by recent reinvigoration of certain theoretical insights (Chesson 2000, Adler et al. 2007), suggesting that coexistence is not just mediated by niche differences amongst species (termed stabilizing effects) but also by relative differences in species-level fitness (termed equalizing effects). For example Mayfield and Levine (2010) argue that if certain traits help determine a species’ overall competitive ability, then similar traits could lead to similar fitness, and thus promote coexistence, rather than depress it, as is traditionally assumed. This means that trait clustering (or by proxy, phylogenetic clustering) could be the outcome of either environmental filtering of similar species, or the result of competitive equality of similar species.

This is by no means a new insight, however. Although Chesson’s (2000) review clarified and simplified the concept, helping to renew interest in it, the basic idea is imbedded in some of the earliest coexistence models (Volterra 1928, Macarthur and Levins 1967). For example, Abrams (1986) made more or less the same point as Mayfield and Levine, decades before the
first community phylogenetics paper, referring to studies looking at taxonomic measures of clustering rather than phylogenetic ones, but the principle is the same (the criticism is also discussed more thoroughly and more generally in Abrams 1976, 1983, 1990). However, the potential power and promise of community phylogenetics as a path to drawing more ecological inferences from observational data makes it important to carefully reconsider the predictions of coexistence theory with respect to trait similarity. Therefore, the renewed interest in equalizing and stabilizing mechanisms of coexistence is timely.

Besides consideration of stabilizing and equalizing coexistence mechanisms, there are many other issues to consider as well, some of which are summarized in a recent review by HilleRisLambers et al. (2012). When trying to understand how the environment and competition interact with a species, we also need to understand not just the independent effects of filters and local competition, but how they can interact with each other. This effort has been hindered by a lack of theoretical models which simply and explicitly incorporate both environmental filtering and competition in a way that can be broken down into stabilizing and equalizing mechanisms. It is one of the goals of this chapter to develop such a model. The other goal of the model developed here is to incorporate a view of the niche in terms of the modern view that it can consist of both the effect of a species on its environment, as well as the environment's effect on a species (the effect and response niches respectively, but also allowing that the niche can be a facet of the environment as well as a facet of an organism (McInerny and Etienne 2012). Putting these different niche concepts together into a single model, I show that stabilizing niche differences and equalizing fitness variation can be linked through the interaction of the effect and the response niches of different species, and the niche of the environment. Additionally, the model includes both interactions that are driven by resources and by predators, and thus reveals some interesting differences in how positive and negative effects of environmental filters might influence coexistence of species that have distinct types of their niche differences.

5.3 The Model

The model is based on a three trophic level version of Macarthur’s classic competition model (Macarthur 1970) where he derived competition coefficients of the Lotka-Volterra competition model from a consumer-resource model, based on resource consumption overlap between different species. Chesson and Kuang (2008) extended Macarthur’s consumer-resource
model by adding a third trophic level, where there are predators which eat the focal consumers, which in turn share a set of resources. This set-up allows the focal species to compete through both shared resources and shared predators (‘apparent competition’: Holt 1977). In this chapter I develop a version of this three trophic level model with continuous resource and predator spectrums, where the sets of resource and predator species equations are each replaced by a single equation which represents an abstract density along a ‘niche’ axis. The main purpose of this abstraction is to reduce the number of equations to be solved, and to eliminate the choice of resource and predator species numbers. (Usually, models that replace individual species with continuous spectra will closely approximate similar models with many discrete species.) This also allows me to add a process of ‘environmental filtering’ to the model, expressed as a continuous function of the niche axes. I will discuss how this more abstract model can help elucidate modern niche concepts.

5.3.1 Resource and predator densities

I start by describing a series of hypothetical axes which define a niche-space in which resource and predator species exist. In this model I postulate two separate biotic niche volumes, one to represent resources, the other to represent predators. The biotic niche axes could represent different traits of the resources and predators, such as body size, running speed, or toxicity, as examples. So far this is not different from Chesson and Kuang (2008), except that they limit their discussion to a single niche axis each for resources and predators. I begin with many potential axes for a general discussion of the model, but later reduce this to one dimension each for predators and resources in order to simplify analysis. In Chesson and Kuang (2008) there are multiple equations representing the growth of multiple resources and predators. Each resource and predator is assigned a unique position on their respective niche axes. These many equations for resources and predators are combined with equations for two focal species in competition, and the whole system of equations is solved to derive coexistence criterion for the two competing focal species. It is common in the consumer-resource version of this model (without predators) to replace the series of individual resource equations with a single equation which describes the growth of resource as a continuous density along niche axes. In fact Macarthur’s original version of this model (MacArthur and Levins 1967) used a continuous concept of resources, though the form of competition based on these continuous densities was not justified.
mechanistically from resource growth equations until MacArthur (1970). In this model, I also replace a set of predator species with a continuous density across a niche-space.

The density of resources and predators along their respective niche axes is determined by a logistic differential growth equation, which is modified by the effect that the focal species has on them, as follows:

\[
\frac{dR[x]}{dt} = \left( r_R \left( 1 - \frac{R[x]}{K_R} \right) - \sum_j C_j[x]N_j \right) R[x]
\]

\[
\frac{dP[y]}{dt} = \left( r_P \left( 1 - \frac{P[y]}{K_P} \right) + \sum_j w_jA_j[y]N_j \right) P[y]
\]

Where \( x \) and \( y \) are vectors representing \( \{x_1, x_2, ..., x_n\} \) and \( \{y_1, y_2, ..., y_n\} \) respectively: the \( n \) variables making up the \( n \)-dimensional niche-axes of the resource and predation niche volumes. \( R[x] \) and \( P[y] \) are functions giving densities of resources and predation, respectively. \( K_R \) and \( K_P \) are the carrying capacities for the resources and predators respectively – their equilibrium densities in the absence of the focal species. For now we assume that carrying capacities are constant across all niche axes. \( r_R \) and \( r_P \) are the per capita rates of growth for resources and predators; these inherent rates of growth determine how quickly their densities return to their carrying capacities after being perturbed by the presence of a focal species. For simplicity, we assume that \( r_R \) and \( r_P \) are constants with respect to resource and predation niche-space. This formulation means that the density of resources or predators at each point in niche-space evolves according to a logistic equation, which is appropriate for functions meant to represent interactions with self-reproducing aspects of the environment (generally other biological species). However, the density equations can take other forms depending on what they are meant to represent. A chemostat type of growth might be appropriate in some cases, or a modified logistic with nonlinear density dependence. \( w_j \) is the value of focal species \( j \) – how much the predator per capita growth rate increases with a unit increase in its consumption of this focal prey. \( C_j[x] \) is analogous to the consumption curve in the classic Macarthur-Levins competition model and those derived from it (Chesson 1990, Abrams et al. 2008, Chesson and Kuang 2008) –
it is a function describing the per capita consumption rate of resource by species \( j \) along all resource niche axes. \( A_j[\mathbf{y}] \) on the other hand is a ‘loss curve’ – it is a function describing the amount of biomass or population loss the focal species experiences as a proportion of predator density at different points in niche-space, or the predator attack rates. Lastly, \( N_j \) is the population size of the \( j \)th focal species, the summation sums up the effects of all focal species on the resource and predator densities.

A logistic growth equation with a constant carrying capacity is a natural and popular choice for the growth of resources, where the carrying capacity represents the limits of the environment to support the resource species (though see Abrams et al 2008 for some criticisms of the logistic growth function). Because they are self-reproducing, it is assumed that the resources are themselves consuming another resource which is what limits their growth. That consumption is represented indirectly by the fact that the resources have density-dependent growth. A significant assumption underlying this representation is that the resources themselves do not share lower-level resources, as they would otherwise compete with each other. Using logistic growth for predators, on the other hand, is more difficult to justify. Chesson and Kuang (2008) justified this choice by suggesting that the predators have other prey besides the focal species, which are able to maintain the predators at some carrying capacity even in the absence of the focal prey. This is somewhat problematic because, if some of the predators are being sustained on the same non-focal prey species, then they should be competing with each other, and the model cannot handle this possibility. This, however, is also true for the resources. Essentially this model assumes that resources and predators do not interact within their own trophic level. Ultimately, assuming a constant carrying capacity for predators is a choice of mathematical convenience, as it allows there to be an equilibrium density of predators in the absence of focal species, meaning we do not need to worry about the effects of predator extinction. Basically I am setting up the model so that predation can be considered a background process, with the details of how predator remain at a given density, independent of the focal species, being unknown. Incorporating more of these details will be an important future consideration for the further analysis of this question, as Abrams and Nakajima (2007) have shown that competition within a lower trophic level can influence the outcome of competition between consumer species. For this chapter, including predator carrying capacities in the model
presented here is also useful because it allows me to incorporate environmental filters for both predators and resources through an effect on carrying capacities.

5.3.2 The focal species equations

The population dynamics of focal species j can be described with the following differential equation:

\[
\frac{dN_j}{dt} = \left( \int_D b_j C_j[x] R[x] \, dx - \int_D A_j[y] P[y] \, dy - d_j \right) N_j
\]

\( \int_D f[x] \, dx \) is an abbreviation for the multiple integral \( \int \cdots \int f[x_1, x_2, \ldots, x_n] \, dx_1 \cdots dx_n \) across \( n \) niche-axes. \( b_j \) is the efficiency of focal species \( j \) – how much biomass it is able to produce from the amount it depresses resource density. \( d_j \) is the death rate of species \( j \), which is sometimes called the maintenance requirement of species \( j \), because it is the minimum net amount that a species needs to gain from its interactions with the resources in the absence of predators in order to maintain a non-negative growth rate. The effects across all of niche-space on the focal species are summed up by integrating across all values of \( x \) and \( y \). By removing the predator equation and the predation terms, this consumer equation becomes equivalent to that presented in Abrams et al. (2008).

5.3.3 Incorporating environmental filters

I add environmental filters to the model, as biotic indirect filters. That is to say, the ability of either of the two focal species to exist in the absence of the other is determined by the resource and predator populations sustained by that environment. This makes the environmental effect on the focal species indirect. It would also be possible to incorporate a direct environmental filter on the focal species, but this would necessitate adding a third niche volume to represent conditions on the focal species growth rate. This could be incorporated by modifying the death rate \( d_j \) to be a function of another series of niche axes. For simplicity, in this model I only explore indirect environmental filters. In other words, in this model, the ability of the focal species to exist in an
environment is completely dependent on the densities of its resources and predators – its biotic environment.

I incorporate biotic environmental filters by modifying the carrying capacity terms of the resources and predators so that they are functions of the resource and predation niche axes. It should be made clear that these carrying capacity functions should be considered facets of the environment. They represent the relative ability of the environment to support resources or predators that exist in different regions of niche-space. Where the functions have high values the associated resources or predators have high densities in the absence of focal species. Because carrying capacities in this model are independent of the focal species, their indirect effects on the focal species will, in turn, be independent of the focal species densities. This is important because a good working definition of an environmental filter is a density-independent effect on the fitness of a species.

To reinforce the idea that the carrying capacity functions are facets of the environment I place a subscript k on them -- $K_{R_k}[x]$ and $K_{P_k}[y]$ for resources and predators respectively, meaning that these are the carrying capacity functions for environment k. These functions can of course vary depending on the environment to be modelled. I then multiply the constant carrying capacity terms (which are a facet of the non-focal organisms) in the resource and predator equation by these environmental carrying capacity functions to get new carrying capacities combining the intrinsic carrying capacity of the resource or predator species and the proportional change caused by the environmental conditions. Since the organismal carrying capacities are constant, we can simply absorb this term into the environmental carrying capacity function. For simplicity's sake, when studying a single environment, there is no advantage to maintaining the organismal and environmental carrying capacity function as separate parameters, so they can be merged.

In the rest of the chapter I will refer to the environmental carrying capacity functions as the environmental niche functions. This is because these functions can be thought of as a mathematical representation of the ‘environmental niche’, a concept close to the original conceptions of the niche, as a ‘recess’ in the environment to be filled by species with particular traits (often associated with Grinnell 1917). The niche concept is more often thought of nowadays as being a facet of an organism, representing either the effect of a species on its
environment, or its response to it (e.g. Chase and Leibold 2003). In fact, a full understanding of the niche probably requires both perspectives, one only needs to be careful to be clear which concept one is referring to when using the term niche. The outcome of the interaction of organisms with their environment is the product of both the organismal niches and the environmental niche. In a recent special issue of the Journal of Biogeography, McInerny and Etienne (2012) argue that just such a merging and simultaneous delimitation of the niche is what is needed to revive the niche concept from relative decline and make it useful once again for understanding ecology. It turns out the simple model presented here can be expressed in terms of these different niche components, providing an interesting mathematical example of the framework laid out by McInerny and Etienne (2012).

5.3.4 Reparameterizing to represent effect and response niches

We can reparameterize the model so that it is a function of the previously discussed environmental niche functions and two organismal niche functions for each niche space. The two organismal niche functions reflect the idea that the organismal niche can be divided into two components: the effect niche – which describes the effect of an organism on its environment, and the response niche – which describes the response of an organism to its environment. This conception of the niche is associated with Elton (1927) and was later formalized by Chase and Leibold (2003). McInerny and Etienne (2012) also use this in their recent synthesis of the niche concept in ecology.

It turns out there are natural analogs of the concept of the effect and response niche in the model presented here. The resource effect niche of the focal species is described by their consumption curve, which tells us how it depletes different parts of resource niche space of resources. Likewise, the resource response niche is also related to the focal species’ consumption curve, as the way the focal species’ density is affected by resources across resource niche space is described by how much it depletes the resource times the value of those resources in terms of conversion to focal species’ biomass. So we can define organismal niche functions for both the resource and predation niche spaces as follows:

**Resource Effect Niche Function:**

\[ c_j^{Eff}[x] = -c_j[x] \]
Resource Response Niche Function: \[ C_j^{\text{Res}}[x] = b_j C_j[x] \]

Predation Effect Niche Function: \[ A_j^{\text{Eff}}[y] = w_j A_j[y] \]


The negative sign in the resource effect niche expresses the direction of the effect (the resource is negatively affected by the presence of the focal species). Likewise, the negative sign in the predation response niche reflects that the response of the focal species to the density of predators is negative. The other two niche functions reflect positive responses or effects.

We now have three niche functions for each of the two biotic niche spaces, all expressed across the same niche axes: the environmental niche function and the two organismal niche functions. Substituting these new functions back into our original equations, we get a system of differential equations that describe the behaviour of the model. The first two equations describe the change through time of functions of niche space, giving us continuous densities of resources and predators. The third is an equation describing how the density of one or more focal species changes through time. For a given environment \( k \), the system of equations is:

\[
\frac{dR_k[x]}{dt} = \left( r_R \left( 1 - \frac{R_k[x]}{K_R k[x]} \right) + \sum_j C_j^{\text{Eff}}[x] N_{jk} \right) R_k[x]
\]

\[
\frac{dP_k[y]}{dt} = \left( r_p \left( 1 - \frac{P_k[y]}{K_P k[y]} \right) + \sum_j A_j^{\text{Eff}}[y] N_{jk} \right) P_k[y]
\]

\[
\frac{dN_{jk}}{dt} = \left( \int_D C_j^{\text{Res}}[x] R[x] \, dx + \int_D A_j^{\text{Res}}[y] P[y] \, dy - d_j \right) N_{jk}
\]
Where $R_k[x]$ and $P_k[y]$ are functions describing the density of resources and predators over their respective niche spaces in environment $k$, and $N_{jk}$ is the density of a focal species $j$ in environment $k$. Since I only deal with a single environment at a time in the remainder of this chapter, I drop the $k$ subscripts from here on for simplicity. Figure 5-1 shows an example of a two dimensional resource and predator niche function, solved at equilibrium with two focal species. The continuous density functions resemble a ‘field’ which has been perturbed by the presence of the focal species. These perturbations can then feed back onto the focal species.

**Figure 5-1. Visualization of the concept of ecological niche functions. A)** From left to right: A environmental resource niche function with no species (I also refer to this as an environmental filter in this chapter), the same niche field with two focal species (their position in niche-space represented by black spheres) which are not too close in their organismal effect niches, and the same field with two species with very similar effect niches. The species’ effect niches suppress the resource density surrounding the species. The functions are plotted at their equilibrium values for the given focal species density. Environmental niche filters and species’ niche functions are Gaussian. Parameter values are: $r_R = 1; M_{KR(1)} = M_{KR(2)} = 4; \delta_{KR(1)} = 8; \sigma_{KR(2)} = 18; \mu_{KR(1)} = \mu_{KR(2)} = 0; M_{CI(1)} = M_{CI(1)} = M_{CI(2)} = M_{CI(2)} = 2; \sigma_{CI(1)} = \sigma_{CI(1)} = \sigma_{CI(2)} = \sigma_{CI(2)} = 3; N_i = N_j = 0.5$; Middle Panel: $\mu_{CI(1)} = 4; \mu_{CI(1)} = -6; \mu_{CI(2)} = 8; \mu_{CI(2)} = -1$; Right Panel: $\mu_{CI(1)} = 6; \mu_{CI(1)} = -1; \mu_{CI(2)} = 8; \mu_{CI(2)} = 6$. **B)** The same as in A, but showing the predation niche function. The species’ effect niches increase the predator density surrounding them. Parameter values: $w = r_P = 1; M_{KP(1)} = M_{KP(2)} = 4; \sigma_{KP(1)} = 8; \sigma_{KP(2)} = 18; \mu_{KP(1)} = \mu_{KP(2)} = 0; M_{AI(1)} = M_{AI(1)} = M_{AI(2)} = M_{AI(2)} = 2; \sigma_{AI(1)} = \sigma_{AI(1)} = \sigma_{AI(2)} = \sigma_{AI(2)} = 3; M_{AI(2)} = M_{AI(2)} = 3; \sigma_{AI(2)} = \sigma_{AI(2)} = 3; M_{AI(1)} = M_{AI(1)} = 8; \mu_{CI(2)} = -6; \mu_{CI(2)} = -3; \mu_{CI(1)} = 3; \mu_{CI(1)} = 3; \mu_{CI(2)} = 2; \mu_{CI(2)} = -2.$
5.4 A simple analysis of the model

In Macarthur’s original (1970) analysis of this model, with consumers (the focal species) and resources, he assumed that the dynamics of the resources were faster than those of the consumers, and so the density of the resources in the focal species equation could be approximated by their consumer-dependent equilibrium values. Here I use a similar method, although most predators (and some types of resources) usually exhibit slower dynamics than their prey. Parasites fit the assumption, but often require different dynamical models. This being the case, by approximating the predator and resource densities by their focal species-dependent equilibrium values, the resulting model will not exhibit accurate dynamics. However, if we only assume that there does exist a stable equilibrium with positive densities of all resource and predator components, then we can ask questions about the behaviour of the model near equilibrium. Coexistence is generally discussed in terms of equilibrium. Chesson and Kuang (2008) also present several reasons why this 'quasi-equilibrium' approximation can be reasonable for addressing questions of coexistence.

By setting \( \frac{dR[x]}{dt} \) and \( \frac{dP[y]}{dt} \) to zero, isolating the \( R[x] \) and \( P[y] \) terms, and substituting them into equation 2, we get a single differential equation describing the dynamics of a single species within the focal species group (using the original parameterization).

\[
\frac{dN_i}{dt} = 
\left( b_i \int_D \left( K_R[x] - \frac{K_R[x]}{r_R} \sum_j C_j[x]N_j \right) C_i[x] \, dx 
- \int_D \left( K_P[y] + \frac{K_P[y]}{r_P} \sum_j w_j A_j[y]N_j \right) A_i[y] \, dy - d_i \right) N_i
\]

This equation can be rearranged into a classic Lotka-Volterra form as follows:

\[
\frac{dN_i}{dt} = \left( k_i - \sum_j a_{ij} N_j \right) N_i
\]

where

\[
k_i = b_i \int_D K_R[x] C_i[x] \, dx - \int_D K_P[y] A_i[y] \, dy - d_i
\]

and
The above equation is a continuous version of the model presented in Chesson and Kuang (2008), or the Chesson and Kuang model can be considered a discretization of the above idealization. One can generate any particular discrete version of the above model by randomly assigning point niche values for a number of discrete resources and predators and assigning consumption and loss values as the deterministic density at each resource or predators point in niche-space, according to the resource consumption and predator loss curves. Then you would need differential equations for every resource and predator species, rather than simply modelling the combined effect of hypothetical resources and predators, as we do in this model. Finally the integrals in the focal species equation will be replaced by summations across all resource and predator species.

I will analyse a version of the above model with two focal species to explore patterns of coexistence in the presence of both competition and environmental filtering, and by doing so shed some light on some recent debates about community assembly, in particular, arguments in the fields of community phylogenetics and trait-based ecology (Mayfield and Levine 2010, HilleRisLambers et al. 2012, Kunstler et al. 2012). In Lotka-Volterra form, a two-species version of the model is:

$$\frac{dN_i}{dt} = (1 - \alpha_{ii}N_i - \alpha_{ij}N_j)N_i$$

Where $\alpha_{ii}$ and $\alpha_{ij}$ are, respectively, the absolute intraspecific competition coefficient and the absolute interspecific competition coefficient, and where, in this model (assuming for simplicity that all $b_i$ and $w_i$ are equal):

$$\alpha_{ii} = \frac{b \int_D \frac{K_R[x]}{r_R} C_i[x] C_i[x] \; dx + w \int_D \frac{K_p[y]}{r_p} A_i[y] A_i[y] \; dy}{b \int_D K_R[x] C_i[x] \; dx - w \int_D K_p[y] A_i[y] \; dy - d_i}$$

$$\alpha_{ij} = \frac{b \int_D \frac{K_R[x]}{r_R} C_i[x] C_j[x] \; dx + w \int_D \frac{K_p[y]}{r_p} A_i[y] A_j[y] \; dy}{b \int_D K_R[x] C_i[x] \; dx - w \int_D K_p[y] A_i[y] \; dy - d_i}$$
Volterra showed that two species can coexist in a Lotka-Volterra system, by the mutual invasion criterion, if \( a_{jj} > a_{ij} \) and \( a_{ii} > a_{ji} \). Following Chesson (1990), we can put the above equation into the following form:

\[
\frac{dN_i}{dt} = (k_i - a_{ii}N_i - a_{ij}N_j)N_i
\]

Where

\[
k_i = b \int_D K_R[x] C_i[x] dx - w \int_D K_P[y] A_i[y] dy - d_i
\]

\[
a_{ii} = b \int_D \frac{K_R[x]}{r_R} C_i[x]^2 dx + w \int_D \frac{K_P[y]}{r_P} A_i[y]^2 dy
\]

\[
a_{ij} = b \int_D \frac{K_R[x]}{r_R} C_i[x] C_j[x] dx + w \int_D \frac{K_P[y]}{r_P} A_i[y] A_j[y] dy
\]

The conditions for coexistence can then be described by two parameters: \( \rho \) – which represents the degree of niche-overlap of species \( i \) and \( j \), and \( \frac{\kappa_i}{\kappa_j} \) -- the ratio between the two species’ density independent fitness (defined as their growth rate at zero density of all focal species divided by the square root of the species’ competitive effect on itself). Both species coexist when

\[
\rho < \frac{\kappa_i}{\kappa_j} < \frac{1}{\rho}
\]

Chesson (1990) showed that

\[
\rho = \frac{a_{ij}}{\sqrt{a_{ii}a_{jj}}}
\]

And that

\[
\kappa_i = \frac{k_i}{\sqrt{a_{ii}}}
\]
And so the conditions for coexistence become:

\[
\frac{a_{ij}}{\sqrt{a_{ii}a_{jj}}} < \frac{\sqrt{a_{jj}k_i}}{\sqrt{a_{ii}k_j}} < \frac{\sqrt{a_{ii}a_{jj}}}{a_{ji}}
\]

5.4.1 Caveats to following Chesson’s decomposition of the Lotka-Volterra model

In the following section I use Chesson’s framework of dividing the analysis of coexistence into a niche overlap factor (\(\rho\)), and a fitness ratio factor (\(\frac{k_i}{k_j}\)), in order to frame the analysis in terms of the arguments of Mayfield and Levine (2010) and others, who have claimed that community phylogenetics has focused too much on competition vs. environmental filtering and have not considered the viewpoint of Chesson (2000). However, it should be noted before we proceed that the above and below analysis depends on the assumption that the focal species’ competitive effects are linear, that is, they do not depend on the density of the focal species. Otherwise, we would not be able to neatly separate the focal species density from the rest of the equation to derive the classic Lotka-Volterra form. This means that it would be impossible to split the coexistence conditions analytically into a niche overlap and a fitness ratio component. What’s more, it is unclear how one might decompose coexistence into these two factors from a numerical standpoint using data on the densities of interacting competitors.

Some of these non-linearity issues are explored in Abrams (1980), Abrams et al (2008) and Abrams and Rueffler (2009). An important way that such non-linearity can come into this type of model is when resources go extinct (although there are other ways to get non-linear competition amongst focal species in other models, where per capita resource growth may be nonlinear or predators have nonlinear functional responses, or the three trophic levels interact in other ways, such as anti-predator behavior affecting resource acquisition). In the context of this model, the resource and predator density functions cannot fall below zero at any point in their respective niche space (except perhaps parts of niche space that have no effect on the focal species – e.g. the focal species’ response niche is zero in these regions). Basically, the following analyses depend on the assumption that the resource and predator density functions remain positive for all values of the their niche-axes. This means that the analysis presented here will be
valid for some parameter combinations, but there will be some parameter combination where it will be invalid. All else being equal, the range of parameter values where the resource density function remains positive will be greater in this model with predation than one that lacks predation (such as that presented by Abrams et al. 2008). This is because the predators suppress the focal species, which are then less able to suppress the resource densities, leading to fewer or no negative values. In this model, the predator densities cannot fall to zero or lower because of the logistic form of the predator densities with a constant carrying capacity. If we were to replace this form with a form where predator densities only depended on the focal species, then we would also have to worry about the possibility of predator extinction. There are also other ways for non-linearity to enter the equations, as mentioned above. Exploring these effects is a major next step for testing the generality of the conclusions I make in this chapter, since it has been shown that non-linearity in competition can have important effects (Abrams 1980; Abrams et al. 2008; Abrams and Rueffler 2009). In the mean time, linear competition of the focal species should be considered a strong assumption of this model in the following analysis, which allows me to analyse the model more comprehensively for the special case of linear competition.

5.4.2 Analysis of the Gaussian Case

In order to analyse the model further, it is necessary to make some assumptions about the shapes of the effect and response niche functions, as well as the environmental niche functions. First, we will reduce our multi-dimensional niche spaces down to a single niche axis for the resource niche and a single axis for the predation niche. Along those single niche-axes we will assume that both the environmental niche functions and the effect and response niche functions of the focal species take on a general Gaussian form. For example the function describing the environmental niche field for resources is:

$$ K_R[x] = M_{KR}e^{-\frac{(x-\mu_{KR})^2}{2\sigma_{KR}^2}} $$

Where $\mu_{KR}$ is the mean (and mode) of a Gaussian distribution, $\sigma_{KR}$ is related to the width of the distribution (the inflection points occur at $\mu_{KR} - \sigma_{KR}$ and $\mu_{KR} + \sigma_{KR}$). $M_{KR}$ is the height of the curve’s peak. The subscript $KR$ refers to which function is being invoked, e.g. $KR$ is the environmental niche function for resources, $KP$ would be the environmental niche function for predators, $C_j$ would be the consumption curve for species $j$, etc. I will also assume that the $M$ and
σ parameters of the functions for consumption and loss rates of the two species i and j are identical, eg. \( \sigma_{ci} = \sigma_{cj} = \sigma_c \), and \( A_{ci} = A_{cj} = A_c \). For simplicity, I also assume that \( b \) and \( w = 1 \). The Gaussian form was chosen to represent features of environmental and organismal niches that are often assumed in coexistence theory. For example, it is generally assumed that species specialize to some degree on some part of adjacent niche space, which makes a unimodal function like a Gaussian ideal. Likewise, environmental filters are often conceptualized as a region of niche space where persistence is permitted, outside of which species cannot exist – they do not have the right traits to live there. Again, a unimodal function reproduces this type of effect, with high density in one particular area, and near-zero density in other places. There are many possible unimodal functions, but a Gaussian has convenient mathematical properties, allowing a more thorough analytical analysis. There are also disadvantages to using a Gaussian function (some are outlined in Abrams et al. 2008), and so a future numerical analysis should be conducted to explore the consequences of this assumption.

Substituting Gaussian expressions into the equation for \( \rho \) gives us:

\[
\rho =
\int \left( \frac{M_{KRE}}{r_R} \frac{e^{-\frac{(x-\mu_{KR})^2}{2\sigma_{KR}^2}}}{M_C e^{-\frac{(x-\mu_{CI})^2}{2\sigma_{C}^2}}} \right) dx + \int \left( \frac{M_{KPe}}{r_P} \frac{e^{-\frac{(y-\mu_{KP})^2}{2\sigma_{KP}^2}}}{M_A e^{-\frac{(y-\mu_{AI})^2}{2\sigma_{A}^2}}} \right) dy
\]

By taking advantage of the fact that the product of Gaussians is Gaussian, and the Gaussian integral

\[
\int ae^{-\frac{(x-b)^2}{c^2}} = a|c|\sqrt{\pi}
\]
In this case, \( c \) is always greater than zero, so the Gaussian integral is \( ac\sqrt{\pi} \).

Given this

\[
\rho = \frac{1}{r_R} M_{KR} M_C^2 \left( \frac{1}{2} \frac{\sigma_C^2 \sigma_{KR}^2 \pi}{\sigma_C^2 + \sigma_{KR}^2} e^{-\frac{(\mu_{Ci} - \mu_C)^2}{4\sigma_C^2}} e^{\frac{-(\mu_{KR} - (\frac{\mu_{CI} + \mu_C}{2}))^2}{2\left(\frac{1}{2}\sigma_C^2 + \sigma_{KR}^2\right)}} \right)
+ \frac{1}{r_P} M_{KP} M_A^2 \left( \frac{1}{2} \frac{\sigma_A^2 \sigma_{KP}^2 \pi}{\sigma_A^2 + \sigma_{KP}^2} e^{-\frac{(\mu_{Al} - \mu_A)^2}{4\sigma_A^2}} e^{\frac{-(\mu_{KP} - (\frac{\mu_{AI} + \mu_A}{2}))^2}{2\left(\frac{1}{2}\sigma_A^2 + \sigma_{KP}^2\right)}} \right)
\]

We can eliminate some of the parameters with some change-of-variables. We can express the predation terms \( r_p \), \( M_{KP} \), and \( M_A \) as a proportion of their resource counterparts:

\[
r_p = \theta_r r_R
\]

\[
M_{KP} = \theta_{MK} M_{KR}
\]

\[
M_A = \theta_{MA} M_C
\]

Giving us:
\[ \rho = \sqrt{\frac{\sigma_C^2 \sigma_{KR}^2}{\frac{1}{2} \sigma_C^2 + \sigma_{KR}^2}} e^{-\frac{(\mu_{CI} - \mu_{CJ})^2}{4\sigma_C^2}} e^{-\frac{\left(\frac{\mu_{KR} - (\mu_{CI} + \mu_{CJ})}{2}\right)^2}{2\left(\frac{1}{2}\sigma_C^2 + \sigma_{KR}^2\right)}} + \frac{1}{\theta_r} \theta_{MK} \theta_{MA}^2 \frac{\sigma_A^2 \sigma_{KP}^2}{\frac{1}{2} \sigma_A^2 + \sigma_{KP}^2} e^{-\frac{(\mu_{KP} - \mu_{A})^2}{4\sigma_A^2}} e^{-\frac{\left(\frac{\mu_{KR} - (\mu_{A} + \mu_{AJ})}{2}\right)^2}{2\left(\frac{1}{2}\sigma_A^2 + \sigma_{KP}^2\right)}} \]

\[ = \left( \begin{array}{c} \frac{\sigma_C^2 \sigma_{KR}^2 \pi}{\frac{1}{2} \sigma_C^2 + \sigma_{KR}^2} e^{-\frac{(\mu_{KR} - \mu_{C})^2}{4\sigma_C^2}} e^{-\frac{\left(\frac{\mu_{KR} - (\mu_{CI} + \mu_{CJ})}{2}\right)^2}{2\left(\frac{1}{2}\sigma_C^2 + \sigma_{KR}^2\right)}} \\ \frac{\sigma_A^2 \sigma_{KP}^2 \pi}{\frac{1}{2} \sigma_A^2 + \sigma_{KP}^2} e^{-\frac{(\mu_{KP} - \mu_{A})^2}{4\sigma_A^2}} e^{-\frac{\left(\frac{\mu_{KR} - (\mu_{A} + \mu_{AJ})}{2}\right)^2}{2\left(\frac{1}{2}\sigma_A^2 + \sigma_{KP}^2\right)}} \end{array} \right) \]

5.4.3 Just the Resource Niche

It is difficult to go much further than this with the two different environmental niche functions in the equation, but we can further analyse it if we look at the resource and predation niches one at a time. First let us look at a system with only the resource niche and no predation niche. This simply means that all of the predation field related terms are removed from the consumer equations:

\[ \rho = \sqrt{\frac{\sigma_C^2 \sigma_{KR}^2 \pi}{\frac{1}{2} \sigma_C^2 + \sigma_{KR}^2}} e^{-\frac{(\mu_{CI} - \mu_{CJ})^2}{4\sigma_C^2}} e^{-\frac{\left(\frac{\mu_{KR} - (\mu_{CI} + \mu_{CJ})}{2}\right)^2}{2\left(\frac{1}{2}\sigma_C^2 + \sigma_{KR}^2\right)}} = e^8\sigma_{KR}^2 + 4\sigma_C^2 e^{-\frac{(\mu_{CI} - \mu_{CJ})^2}{4\sigma_C^2}} \]
This appears to be a spread-out Gaussian with respect to the distance between the focal species' consumption curve peaks. The degree to which the Gaussian is 'spread-out' is determined by the sigma parameter of the ecological niche function. The more permissive the environment is (that is, a larger width along the niche axis has high resource carrying capacity), the closer the competition value becomes to Macarthur’s classic result. In the limit of infinite niche-width (which is equivalent to having a constant value for carrying capacity across the entire niche axis, the traditional assumption) the first term cancels and what we are left with is a familiar Gaussian relationship between niche separation and competition:

\[ e^{-\frac{(\mu_{Ci} - \mu_{Cj})^2}{4\sigma_C^2}} \]

(Macarthur and Levins 1967). With very low environmental niche width, the Gaussian relationship gets ‘smeared-out’. This makes sense because as the two species niches are separating along the axes, their overlap is decreasing, but the amount of resources available is falling (as the Gaussian niche function values decrease in either direction on average), which makes competition more intense. For very strict environments with small niche width then, competition will be important over larger distances than more permissive environments.

For the fitness ratio we have:

\[
\frac{\kappa_i}{\kappa_j} = \left( \left( \int \frac{M_{KR} e^{-\frac{(x-\mu_{KR})^2}{2\sigma_{KR}^2}}}{r_R} \left( M_C e^{-\frac{(x-\mu_{Cj})^2}{2\sigma_C^2}} \right)^2 dx \right) \right)^{-1} \left( \left( \int \frac{M_{KP} e^{-\frac{(x-\mu_{KP})^2}{2\sigma_{KP}^2}}}{r_P} \left( M_A e^{-\frac{(x-\mu_{Aj})^2}{2\sigma_A^2}} \right)^2 dy \right) \right)^{\frac{1}{2}}
\]

\[
= \left( \left( \int M_{KRE} e^{-\frac{(x-\mu_{KR})^2}{2\sigma_{KR}^2}} M_C e^{-\frac{(x-\mu_{Cj})^2}{2\sigma_C^2}} dx \right) \right)^{-1} \left( \left( \int M_{KPE} e^{-\frac{(x-\mu_{KP})^2}{2\sigma_{KP}^2}} M_A e^{-\frac{(x-\mu_{Aj})^2}{2\sigma_A^2}} dy \right) \right)^{\frac{1}{2}}
\]

\[
= \left( \left( \int M_{KRE} e^{-\frac{(x-\mu_{KR})^2}{2\sigma_{KR}^2}} M_C e^{-\frac{(x-\mu_{Cj})^2}{2\sigma_C^2}} dx \right) \right)^{-1} \left( \left( \int M_{KPE} e^{-\frac{(x-\mu_{KP})^2}{2\sigma_{KP}^2}} M_A e^{-\frac{(x-\mu_{Aj})^2}{2\sigma_A^2}} dy \right) \right)^{\frac{1}{2}}
\]

\[
= \left( \left( \int M_{KRE} e^{-\frac{(x-\mu_{KR})^2}{2\sigma_{KR}^2}} M_C e^{-\frac{(x-\mu_{Cj})^2}{2\sigma_C^2}} dx \right) \right)^{-1} \left( \left( \int M_{KPE} e^{-\frac{(x-\mu_{KP})^2}{2\sigma_{KP}^2}} M_A e^{-\frac{(x-\mu_{Aj})^2}{2\sigma_A^2}} dy \right) \right)^{\frac{1}{2}}
\]
Making the same substitution as discussed previously, and the following additional one: \( d_i = d_j = d = mM_{KR}M_c \) (expressing the death rate as a proportion of the product of the maximum heights of the niche function and the consumption curve, and making it equal for both species.)

\[
\frac{\kappa_i}{\kappa_j} = \left( \frac{\sigma_c^2 \sigma_{KR}^2 \pi}{1 \sqrt{\sigma_c^2 + \sigma_{KR}^2}} \right) \frac{-(\mu_{KR} - \mu_C)^2}{e^{2(\frac{1}{2}\sigma_c^2 + \sigma_{KR}^2)}} + \frac{1}{\theta_r} \theta_{MK} \theta_{MA} \frac{\sigma_A^2 \sigma_{KP}^2 \pi}{1 \sqrt{\sigma_A^2 + \sigma_{KP}^2}} e^{2(\mu_{KR} - \mu_A)^2} \left( \frac{2\sigma_c^2 \sigma_{KR}^2 \pi}{\sigma_c^2 + \sigma_{KR}^2} \right) \frac{-(\mu_{KR} - \mu_A)^2}{e^{2(\sigma_c^2 + \sigma_{KR}^2)}} - m \right)
\]

Again, we can analyse this further if we consider the resource and predation niches independently. The fitness ratio of two focal species that interact only with resources is

\[
\frac{\kappa_i}{\kappa_j} = \left( \frac{\sigma_c^2 \sigma_{KR}^2 \pi}{1 \sqrt{\sigma_c^2 + \sigma_{KR}^2}} \right) \frac{-(\mu_{KR} - \mu_C)^2}{e^{2(\frac{1}{2}\sigma_c^2 + \sigma_{KR}^2)}} + \frac{1}{\theta_r} \theta_{MK} \theta_{MA} \frac{\sigma_A^2 \sigma_{KP}^2 \pi}{1 \sqrt{\sigma_A^2 + \sigma_{KP}^2}} e^{2(\mu_{KR} - \mu_A)^2} \left( \frac{2\sigma_c^2 \sigma_{KR}^2 \pi}{\sigma_c^2 + \sigma_{KR}^2} \right) \frac{-(\mu_{KR} - \mu_A)^2}{e^{2(\sigma_c^2 + \sigma_{KR}^2)}} - m \right)
\]
\[
\frac{(\mu_{CI} - \mu_{CJ})(\mu_{KR} - (\mu_{CI} + \mu_{CJ}))}{e^{\frac{1}{4}\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}} = \left(\frac{2\sigma_C^2\sigma_{KR}^2\pi}{\sigma_C^2 + \sigma_{KR}^2}\right) \frac{e^{\frac{1}{4}\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}}{e^{\frac{1}{4}\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}}
\]

For large \(\sigma_{KR}\) (or \(\sigma_C\)) or small \(m\), the second term becomes dominated by the ratio

\[
\frac{\left(\frac{2\sigma_C^2\sigma_{KR}^2\pi}{\sigma_C^2 + \sigma_{KR}^2}\right) e^{\frac{1}{4}\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}}{e^{\frac{1}{4}\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}} = \left(\frac{\mu_{KR} - (\mu_{CI} + \mu_{CJ})}{\sigma_{KR}^2}\right) e^{\frac{1}{4}\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}
\]

And so:

\[
\frac{\sigma_{KR}^4(\mu_{CI} - \mu_{CJ})(\mu_{KR} - (\mu_{CI} + \mu_{CJ}))}{4(\sigma_{KR}^4 + \frac{1}{2}\sigma_C^2\sigma_{KR}^2\sigma^4)} = \frac{\left(\mu_{CI} - \mu_{CJ}\right)(\mu_{KR} - (\mu_{CI} + \mu_{CJ}))}{4\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}
\]

As \(m\) becomes large, the ratio converges to

\[
e^{\frac{1}{4}\left(\frac{1}{2}\sigma^2 + \sigma_{KR}^2\right)}
\]

In either case the exponent \(\left(\mu_{CI} - \mu_{CJ}\right)(\mu_{KR} - (\mu_{CI} + \mu_{CJ}))\) tells the story. \(\mu_{KR} - (\mu_{CI} + \mu_{CJ})\) is a measure of how far the average value of the two consumption peaks are from the peak of the environmental niche function. If this is positive, the two species are on average skewed right, if negative, they are skewed left. The further away from the peak they are the larger the ratio of their fitness becomes (or smaller, depending on whether species \(i\) or \(j\) is closer to the niche peak). \(\left(\mu_{CI} - \mu_{CJ}\right)\) shows that as the two peaks of the consumption curves get further away from each other, the more extreme the fitness ratio becomes. This makes sense because if the two consumption curve peaks are asymmetrically arranged with respect to the environmental niche function peak, then as they get further away they will be at very different parts of the curve. In the extreme case, one species will occupy the peak of the environmental niche function, while the other species is out on one of the tails, where fitness will likely be very low (on the
other hand competition may be very low too). In the opposite extreme, if both species are perfectly symmetrically positioned with respect to the niche peak, then they can be as far apart as they like, and they will still have equal fitness, due to the symmetrical nature of the Gaussian curve. Non-symmetrical curves for the niche-field, obviously, would not always imply these responses. However, the general effect of niche separation should apply to any niche field function that is more-or-less unimodal.

In all, we can infer that the effect of niche separation can have two effects on coexistence. By decreasing the competition coefficient, niche separation promotes coexistence. On the other hand, if the species are not perfectly symmetrically arranged with respect to the environmental peak of the niche field, then niche separation leads to an increased difference in the fitness of the two species, which should suppress coexistence. So even in the context of species competitive interactions, the effect of having different niches is not simple, and not linear. This will be explored further with numerical analysis of the full model in the next section.

5.4.4 Just the Predation Niche

We can repeat all of the above for the case where we only have a predation niche and no resource niche. However, in this model, resources are the only source of positive growth for the focal species, so we cannot remove resources entirely. Alternatively we can simply reduce the influence of resource competition to a negligible level, so we can focus on the effects of the predation niche. The simplest way to do this is to make the growth rate of the resources $r_R$ very high compared to the predator growth rate $r_p$. If resources replenish themselves at a high rate compared to the predators, the contribution of resources to completion becomes small. As $r_R \to \infty$, $k_i$, $a_{ii}$, and $a_{ij}$ become:

$$k_i = b \int_D K_R[x] C_i[x] dx - w \int_D K_P[y] A_i[y] dy - d_i$$

$$a_{ii} = w \int_D \frac{K_P[y]}{r_P} A_i[y]^2 dy$$
Using these terms the competition term for predation is

\[ \rho = e^{B\sigma_{KP}^2 + 4\sigma_A^2} e^{-(\mu_{AI} - \mu_{AJ})^2} \]

By assuming that \( r_N = b \int_D K_R[x] C_i[x] dx = b \int_D K_R[x] C_j[x] dx \), the fitness ratio is

\[ \frac{(\mu_{AI} - \mu_{AJ})(\mu_{KP} - (\mu_{AI} + \mu_{AJ}))}{\sqrt{\frac{2\sigma_A^2 \sigma_{KP}^2 \pi}{\sigma_A^2 + \sigma_{KP}^2} e^{2(\sigma_A^2 + \sigma_{KP}^2)} - (r_N - d)}} \]

These are more or less identical to the equations based on the resource field alone (with \( m \) replaced with \( (r_N - d) \)), confirming that the effects of predation on coexistence are difficult to distinguish from those of resource competition (Chesson and Kuang 2010). Although, it should be noted that the above is only an approximation, as making the resource growth rate very high also has the effect of making the focal species practically limited only by the predators. So in the absence of significant predation, the focal species can grow to extremely high densities. This makes this version of the model unrealistic, though there is no reason to suspect that the dynamics of predator mediated competition should not be compatible with the dynamics in a more realistic model. A numerical analysis later in the chapter shows that the general results of this approximation are compatible with a model with realistic resource growth rates.

5.4.5 The different types of environmental niche filter effects on species

Here, I have shown that the effects of an environmental filter, as expressed by a focal species’ independent Gaussian environmental niche function, can have effects on the coexistence of two species. However, all of the above only applies if both species have positive densities when they are growing alone.
The effects of an environmental filter on coexistence through competitive interactions, as discussed above, differs from the more common way that a filter is thought to influence coexistence, – that is, having a density independent effect on fitness. This leads to some species being unable to have positive growth, regardless of the presence or absence of other species. In this case the filter effect can be described by what we might call the ‘existence’ criterion:

\[ k_i > 0 \]

The ’no-existence’ criterion is

\[ k_i < 0 \& k_j < 0 \]

This basically amounts to saying that in order to exist at all, a species growth rate must be positive in the absence of a competitor, when at zero density. Failure to satisfy this criterion in this model means that the requirements for a species to survive are not present in the environment. This is the traditional way of thinking about a filter. In this model I incorporate an environmental filter through an environmental niche function, which described how the carrying capacity of resources and predators change through niche space. This results in the filtering out of focal species when the equilibrium density of the resources is too low or the density of predators to high to support any focal species in a particular range of niche space. Therefore, whether a species is filtered out is a function of the environmental niche and the focal species’ organismal niches (e.g. a focal species’ consumption curve falls mostly in a region of niche space with low resource carrying capacity). This is how a filter is defined in the following section.

Put together this means there are 6 relevant states of a two consumer species system when thinking about the combined effects of niche separation and the presence of a filter:

1. Coexistence – Both species have positive densities at equilibrium and so they do not competitively exclude each other, and they both are suited to the environmental filter.
2. Filter-mediated coexistence – Both species have positive densities at equilibrium and so they do not competitively exclude each other, however, one of the species would have excluded the other in the absence of a filter. This means the filter affected either the competition coefficient or the fitness ratios, such that coexistence became possible where it was not before.
3. Competitive exclusion – Only one species has positive density, but each species could have a positive density in the absence of the other. They would have excluded each other even with no filter present.

4. Filter-mediated competitive exclusion - Only one species has positive density, but both species could have positive density in the absence of the other. However, the species would not have been competitively excluded if there had been no filter present. This means the filter affected either the competition coefficient or the fitness ratios, leading to exclusion.

5. Filter exclusion of one species - Only one species has positive density, because one of the species falls outside the environmental filter.

6. Filter exclusion of both species (‘No-existence’) – Neither species has positive density, regardless of the presence or absence of the other, because neither is suitable for the environment.

If any of outcomes 3-6 occur due to the effects of niche distance (or any other parameter), then niche distance will potentially affect the species composition of an environment. This considerably enriches the possibilities over just the idea of ‘environmental filtering’ vs ‘limiting similarity’. Basically, this framework implies that competition or coexistence effects and environmental filters do not have independent effects, but interact in interesting ways.

I will explore outcomes 1, 4, 5, and 6 in this paper because for simplicity I assume that all focal species have equal fitness in the absence of the environmental niche filters, which means that when the ‘filter’ is not present, all species will coexist, regardless of their niche overlap. Though this assumption is useful because it simplifies the analysis, I argue that it is actually not an unreasonable assumption. This is because, although the model does contain a parameter which affects fitness independently of any niche requirement – the death rate or maintenance requirement of the species – it is mainly included in models as a way to incorporate fitness differences whose causes are unknown. The idea of a fitness parameter that was truly independent of the environment does not make sense. Certainly, much of evolutionary biology is predicated on the idea that all fitness is dependent on the environment. If there were traits that were independent of the environment, we can only assume that natural selection would have tuned them to their maximums in all species, such that there would be no variation amongst species in them, except where there was considerable genetic constraint. In the end, I only argue
that it is reasonable to assume that all fitness of a species is environmentally dependent to some
degree, the only additional assumption I make is that this dependence on the environment is fully
described by the ecological niche field functions of the model. However, in a more realistic
model, there may also be random differences between species in their fitness due to things like
gene flow that are not determined by the environmental conditions. Higher niche separations
would need to be maintained for coexistence in the presence of such random fitness differences.

In order to explore the effect of niche separation on the above outcomes, and also look at
the interactive effects of the predation and resource niches simultaneously (as opposed to
separately as we did in the previous section), I conduct numerical analyses of the parameters of
the model relevant to coexistence.

5.5 Numerical Analysis of the Model

In order to understand more fully the implications of the model, I evaluate the
coeexistence coefficients $\rho$, $k_i$, and the fitness ratio $\frac{k_i}{k_j}$, and determine the predicted coexistence or
lack thereof when I vary the niche-related parameters of the model. In particular, I am interested
in the effects of niche separation on coexistence, here defined as the distance between two
species’ consumption or loss curves, which will affect both the species’ effect and response
 niches.

To do so I vary the niche distance between two species, and their average distance to an
environmental niche peak, and see how these interact to determine coexistence outcomes, first
for a model with only a resource niche, and second for a model with only a predation niche.
Since I am mainly interested in either the coexistence or exclusion of both species, or the
exclusion of one species, and am not concerned which of the two species is excluded, I can fully
characterize the outcome by shifting the two species’ consumption or loss curves from the centre
of the environmental niche peak (which I arbitrarily assign the value of zero) in one direction,
keeping the order of the two species along the niche axis the same. This is because the only thing
that matters for coexistence is that one species is closer to the peak than the other, and it doesn’t
matter which is the closer one. Reversing the positions of the species will yield the same
outcome, as will shifting the curves in the other direction with respect to the environmental niche
peak, because it is symmetrical.
Unless otherwise noted, for the numerical analyses I used the following parameters:

\[ b = w = r_R = r_P = M_{KR} = M_{KP} = M_{Cl} = M_{Aj} = \sigma_{Cl} = \sigma_{Cj} = \sigma_{AI} = \sigma_{Aj} = 1 \]

\[ \sigma_{KR} = \sigma_{KP} = 2; m = (r_N - d) = 0.25; \theta_r = \theta_{MK} = \theta_{MA} = 1. \]

Since both niche separation and distance to the environmental niche peak can go from zero to infinity, I had to choose a range over which to evaluate the model. The range I chose for the maximum distance between niche peaks in the resource only model was from zero to the width of the environmental niche Gaussian curve (measured by the distance between the two positions where it is five percent of its maximum height, which is determined by \( 2\sqrt{4\ln20}\sigma_{Kz} \)).

For the resource-only model the maximum distance from the environmental niche peak was half this value. For the predation-only model I used three times the full width for both the maximum niche separation and the maximum distance to the environmental niche peak, because there were interesting patterns that emerged at greater separations. Looking at further distances than these confirmed that observed trends continued indefinitely due to the self-similarity of the Gaussian function.

To look at just the effect of niche separation just on coexistence, I integrated across all distances to the environmental niche peak that were analysed by averaging over all measurements taken at each niche separation value. The resulting value is the proportion of distances from the environmental niche peak where coexistence occurred (or the probability of coexistence at a certain niche separation if the distance from the environmental niche peak is random according to a uniform distribution across the range that was evaluated).

Lastly, I analyze the model with both a resource and a predation niche. For simplicity, I only look at the effects of niche separation in the two niche-axes (resource and predation axes), and so I integrate across the different combinations of distances to the two environmental niche peaks. To do so I evaluate 100 different niche peak distances on a grid of predation distance and resource distances. In this case the order of the two species on the niche axes does matter, because in one case a species position may be low on both environmental niche fields (and the other species high on both), or one species could be high on one peak and low on the other. So I evaluate all possible arrangements of the two species with the same niche separation and take the average. This again gives a probability of coexistence marginalized with respect to the distance.
from the environmental peaks, but conditional on the range of values evaluated. Increasing the maximum distance to the niche peaks evaluated will change the absolute values of the coexistence probabilities, but it won’t change the overall relative relationship between the coexistence probabilities and the niche separation.

5.5.1 The effects of resource niche separation on coexistence in the presence of an environmental filter.

First, I explore the behaviour of the model when only a resource niche is considered, and no predation niche.

When the distance between two species consumption curves is varied, along with the distance that the two species are from the environmental niche peak, in general, I find that coexistence first increases with initial niche separation and then decreases (Figure 5-2). This depends to some degree on the distance of the two species from the environmental niche peak. Coexistence is promoted by small distance from the niche peak. After this point, the further away from the niche peak the two species are, the smaller the range of niche separations that can support coexistence. Dividing up the areas where no coexistence is possible into filter-mediated competitive exclusion and one- and two-species filter exclusion clarifies the mechanisms behind this result. The initial increase in coexistence with niche separation is due to decreasing competition between the species as their effect niche overlap gets smaller. Coexistence then declines with further niche separation.

Figure 5-2 Left-hand column: Regions for different coexistence outcomes in the resource only model for different values of the environmental niche filter width ($\sigma_{KR}$). Green = Two-species coexistence; Orange = Filter-mediated competitive exclusion; Light Red = One species excluded; Dark Red = Both species excluded. Niche separation and Niche peak distance are measured as the proportion of the total width of the Gaussian niche filter function at 5% of the maximum. Middle column: Plot of the probability of coexistence vs. niche separation on the proportional scale (distance from the niche peak is factored out by numerical integration). Right Panel: Plot of the probability of coexistence vs. Niche separation on the original scale, to facilitate comparison.
because one or both of the species response niches now no longer overlap the environmental niche strongly enough to maintain positive growth rates. This is the environmental filter effect that is expected under standard community phylogenetics theory for example. So far, competitive effects and environmental filtering have their expected effects, with competition making similar species exclude each other and environmental filtering promoting coexistence between similar species. However, in this case, the competitive effect is partly mediated by fitness differences. This is because in this model there are no fitness differences that are independent of the environment. Closely related species have similar fitness because they are close together with respect to the environmental niche. This means that in order for competition to overcome this similarity in fitness and exclude species, similarity in fitness needs to decline more rapidly with niche separation than the competition coefficient does. This only happens if the environmental filter is very strong.

By changing the variance parameter of the environmental filter function, I can vary the strength of the filter. With small values the suitability of the environment declines very rapidly away from the peak position and with large values it declines very shallowly. This can be seen in Figure 5-2, where with high values of environmental variance parameter (permissive environments), the range of niche separations in which competitive exclusion occurs gets smaller. This makes sense because in an environment with very strict requirements for growth, being even slightly different from the ideal competitor could result in substantial decreases in fitness. At the limit of no environmental filter,
in this model, no competitive exclusion can occur. In such a world, we would expect that the probability of coexistence should decrease linearly with niche separation, leading to clustering of traits in all cases. This leads to the somewhat counterintuitive notion that strong environmental filters are required in order for competitive exclusion to occur, and that the stronger the environmental filter, the more likely it is to see exclusion of similar species. This means that rather than inferring environmental filters from trait clustering, what perhaps we should be looking for is a narrowing of the range of trait distances, from both directions. Figure 5-3 also shows the effect of the density (and niche) independent fitness parameter (death rate) $d$ on these effects. The general result is the same, increasing the death rate merely decreases the range of niche separations and niche peak distances that can maintain positive densities. On the other hand, decreasing the death rate to too low a value means that the probability of resource extinction becomes high, and if that occurs, the results of this analysis will be invalid. In a model accounting for the possibility of resource extinction, varying the death rate of the focal species may lead to more complicated conclusions regarding niche separation and coexistence.

Figure 5-4. Left-hand column: Regions for different coexistence outcomes in the predation only model for different values of the environmental niche filter width ($\sigma_{K_P}$). Green = Two-species coexistence; Orange = Filter-mediated competitive exclusion; Light Red = One species excluded; Dark Red = Both species excluded. Niche separation and Niche peak distance are measured as the proportion of the total width of the Gaussian niche filter function at 5% of the maximum. Middle column: Plot of the probability of coexistence vs. Niche separation on the proportional scale (distance from the niche peak is factored out by numerical integration). Right Panel: Plot of the probability of coexistence vs. Niche separation on the original scale, to facilitate comparison.
5.5.2 The effects of predation niche separation on coexistence in the presence of an environmental filter.

I repeat the above numerical analysis with the model which only includes the predation field, and no resource field. Though the coexistence criterion based on the previous analytical analysis suggested that resource and predation fields had very similar effects on coexistence, a consideration of the filter effects make the outcome considerably different for this version of the model compared with the resource only model.

Figure 5-4 shows that coexistence tends to increase with niche separation when initial separation is low. However, contrary to the resource case, coexistence does not strongly decline with larger increases in separation. In fact, it tends to increase until the probability of coexistence reaches a maximum and then remains there. The maximum reached in this case is related to the distance from the niche peak that I integrated out to. If I could extend the integration out indefinitely, it would asymptote towards a probability of 1 (the light red strip indicating one of the two species was filtered out will extend to infinity but it will become a smaller and smaller proportion of the outcomes). The general increase in coexistence with niche separation can be explained by the fact that the filter for a predator niche acts most strongly close to the environmental niche peak, rather than further away from it. This is because the predation field is a negative filter – species are filtered out if they are too close to the predation niche peak, rather than too far away, as is the case for the resource niche. This means that at low niche separation and low distances from the niche peak, one or both species are excluded by the filter. Once species are far enough from the environmental niche peak to maintain positive density, only then do competitive effects kick in. When the species are far from the predation filter peak, but have similar effect niches, competitive exclusion can sometimes occur (upper left area of Figure 5-5). With further niche separation, at large niche peak distance, coexistence occurs. Likewise, at large niche separation and very short average distance to the environmental niche peak (species niche peaks are equidistant on either side of the environmental niche peak), coexistence occurs because the filter is weak out there and so is competition.

In the absence of a filter the coexistence conditions would look very similar to the resource case, but the filter leads to a general increase in coexistence probability with niche separation. The reduction in coexistence at low niche separation is caused by a combination of competitive exclusion and filter-based exclusion. Thus, when I increase the width parameter of
the environmental filter, creating a more permissive environment, the apparent competition effect becomes weaker, eventually leaving only the filter effect (Figure 5-4: bottom row), just as in the resource only model.

5.5.3 The effects of resource and predation niche separation on coexistence in the presence of environmental filters.

An evaluation of the coexistence outcomes with respect to both resource and predation niche separations shows that the overall pattern is one of increasing coexistence with niche separation followed by a decline with large niche separation (Fig 5). For the same degree of environmental filtering (the same width parameter for both predation and resource fields), the effect of predation is stronger in suppressing coexistence at small niche separations. Changing other parameters of the model leads to the same basic pattern – a triangular coexistence region at intermediate niche separation – but with the position and size of the triangle changing. The second coexistence region that we saw in the predation niche only model at large niche separations (and low distance from the niche peak) does not reappear in the model with both resources and predation. This is because that coexistence region depended on low competition at high niche separation on the predation niche. When the resource field is also present, at low resource niche separation, higher competition for resources cancels the low competition (apparent competition) from predation. On the other hand at high separation for the resource niche, the low competition from predators is overwhelmed by the strength of the resource-based filter at those niche separations.
5.6 Discussion and Conclusions

The model is a general model of niche-based coexistence between different species (or genotypes) of a group of focal species. The model incorporates an abstract representation of the niche, which includes the modern idea that the niche consists of both the effect of the environment on a species, and the effect of the species on its environment (Chase and Leibold 2003, McInerny and Etienne 2012). It also allows that the niche can refer to a property of the environment, as well as a species (McInerny and Etienne 2012).

Figure 5-5. Contour plot showing the probability of two-species coexistence for different predation and resource niche separations, and different combinations of values for the niche filter width parameters for both predation and resources. Niche separation is measured on the original scale. Distance from the niche peaks is factored out with numerical integration.
An analysis of a simple version of this model has shown that environmental filtering influences the outcome of competition by altering the degree to which species differ in their niches and their fitnesses. In particular, strong environmental filters tend to increase the likelihood of competitive exclusion because they drive large differences in fitness with only small differences in niche position. The model also makes clear that both resources and predators can act as filters to some degree if their density is at least in part independent of the focal species. It is noteworthy that, if predators are abundant and/or effective in a particular region of niche space, this will act as a ‘negative’ filter on the focal species, meaning that focal species that fall in the region of niche space where predation pressure is strong will be less likely to survive. The added implication of this is that only when two species have similar predation niches could they be co-excluded, meaning there is a higher probability of two focal species coexisting if they have dissimilar predation niches. Some of these results could change substantially, however, if predators have higher-order predators or there is direct density dependence among the predators, in which case there can be positive indirect effects between prey that share predators (Abrams and Matsuda 1996).

The distinction between positive and negative filters has not been well-considered in the trait-based and phylogenetic ecology literature. In one sense, the distinction is trivial, in that any negative filter can be converted to a positive one by inverting it – that is, if an environment prevents species with a certain trait from existing there we can just as easily think of the environment as permitting species to exist with traits other than the negative trait in question. However, such technicalities will certainly hinder our understanding of the mechanisms of the filter. There is a difference between certain traits being beneficial in an environment compared with certain traits being harmful, even if they are hard to tell apart. In this model we treated the filters as Gaussian distributions, which means if we inverted the strong negative filter caused by predation on a certain part of niche-space, we would get a distribution that was highly bimodal. In higher dimension we would get a bowl-shape, which looks like a scoop was removed from the niche function. Likewise, some abiotic environmental conditions likely act in this way as well.

The recognition of negative environmental filters is important because this model shows that their presence can suppress the coexistence of similar species. The paradigm in community phylogenetics, as an example, is that filters promote coexistence among similar species, and competition suppresses coexistence among similar species. It has already been shown that
competition can lead to similar species being more or less likely to coexist depending on whether the traits involved lead to high niche overlap or high fitness similarity (e.g. Abrams 1983, Mayfield and Levine 2010). Here, I show that an environmental filter can lead to similar species being more or less likely to coexist depending on whether the filter is positive or negative.

Another interesting result of analyzing this model is that the strength of competitive exclusion depends on the strength of the environmental filter. Stronger environmental filters mean that the amount of niche-space in which fitness is maximized is low, so that it only takes a small difference in response niche to lead to a large decrease in fitness. The large disparity in fitness among species that are close to the environmental niche peak is likely the reason for strong competitive exclusion at close niche proximity, however, the analytical results also showed that the competition coefficient itself is also affected by the strength of the filter.

5.6.1 Interpretation of the model

By making both the resources and predators a continuous density function across niche space, the model becomes a very abstract version of the Lotka-Volterra equations. This has its advantages and disadvantages. One disadvantage is in applying a biological interpretation. How should we think about a continuous density distribution across a niche space? One way is to speak of the notion of an ‘ecological field’. This is because the density functions through a multi-dimensional space, akin to Hutchinson’s niche hypervolumes (Hutchinson 1958), can be analogized to the concept of a field in physics, such as a gravitational field. The concept is useful because a field both affects objects and is affected by them. A gravitational field, for example, is a curvature in space-time which influences the motion of bodies, and yet it is the presence of bodies that creates the curvature (above any background curvature, perhaps created by bodies outside the realm being considered in a particular case). Likewise, a species in an environment creates an influence on that environment that extends out from it. Those remote effects alter the dynamics of other species and can then feedback onto the same species that created them (see Figure 5-1). And so this ecological field concept captures the essence of the way we think of species in their environments, without modelling the specifics of individual interactions. In this sense, the model is phenomenological – it is capturing in a loose way the essence of an ecological interaction. This means however, that the model may only be useful for asking very general questions, whose answer does not depend on the particulars of a system, but only on the
general structure of the system – that is, a collection of agents who only interact through their mutual effects on some underlying environmental medium (in this case abstracted resources and predators). Therefore, more thorough investigations using discrete predator and resource species versions of the model should be conducted before applying any results of this model to real systems.

Another possible way to interpret the model is as an approximation to the expected outcome of a stochastic version of the model. We can imagine an arena, into which we are going to throw two species to compete. Each bout of competition the arena is stocked with a random set of N discrete resources and predators. The niche position of these resources is drawn from a uniform distribution across all valid niche space. What is the expected outcome of competition averaged across thousands of such bouts? The integrals in the focal species equations are the equivalent of an average of the niche functions, but this won’t tell us what the average outcome is, because of Jensen’s inequality. However, as the number of resources and predators drawn in each bout, N, gets large, the variance between different bouts decreases, meaning that the function of the average will more closely approximate the average of the function. However, with low N, there could be substantial disagreement between a stochastic discrete version of the model and the continuous version presented here. More fully exploring the differences and similarities between this model and a stochastic version will be an interesting extension of the model.

When I analyzed the model with both the resource and predation niches, the overall pattern was one of maximal coexistence at intermediate niche separation. Interestingly, the predation niche produced stronger declines in coexistence at low niche separation, due to the negative filter effect. Perhaps then we should look more closely at enemy interactions as a potential explanation when we discover communities with over-dispersed traits, though this result likely depends to some degree on the shape of the predation filter. On the other hand, the Gaussian function doesn’t seem like a bad model for this type of interaction. An example would be where predators of a certain body size tend to feed on prey of a certain body size. This mean that a focal species of a certain size will preferentially be fed upon by predators which do not fall below or above some size (predator body size could be a predation niche axis), and probably resembles a Gaussian in shape. This prey species will compete more strongly with other prey around the same size, and if the predators are particularly abundant in an area then prey of a
certain body size may become rare. This will lead to a community composed of species too large for those common predators to eat easily, and those too small to bother with. Thus we end up with trait over-dispersion for body size through a negative filter, rather than apparent competition amongst the focal species.

Why should this effect of predation be considered a filter, rather than standard apparent competition? Because the effect is density-independent, that is, the predators are there regardless of the individual density of the species being excluded. Though the predator may respond to the density of the focal species, they need not do so in order to exclude them. This might be considered a rather small distinction in the case of predation. One can certainly argue that to be present in the environment at all the predators need to be feeding on something, and so ultimately, this filter effect is apparent competition, just apparent competition with species other than the focal species of interest. In this case, the degree to which a biotic factor influences the existence of a focal species in a filter-like (density-independent) manner will depend on the degree to which the biotic factor is dependent or independent of the focal species. This could be expressed as a continuum rather than either it is a ‘filter’ or it is ‘competition’. Ultimately, there is no simple prediction for what effect a filter or competition should have on ecological similarity of coexisting species.

For any of the predictions of this model and others to affect the trait-based and phylogenetic similarity of species in real communities, the abstract effect and response niches of species in the model need to be linked to traits of real species. As long as there are traits that affect the mean, mode, or dispersion of the niche functions then this will be the case. However, the representation of the niche in the simple model presented here does not encompass all of the traits that might affect a species' interaction with its resources and predators.

In the model presented here, I assumed that the niche-axes of the predation and resource niches were independent of one another, but this need not be the case. Some niche-axes may be shared amongst different ecological niche fields, and a fuller model would have just one master niche-field that combined all influences into one master function. Doing this would put the model in a form that would allow the inclusion of niche functions with covariance between different niche-axes. Then it would be possible to explore the possibility that predators and resources may be correlated between different environments. It is also possible of course, that a
focal species’ niche functions are correlated between resources and predation, or other hypothetical ecological niches. This can be incorporated by allowing the modes and widths (for example) of different niche functions to covary amongst species (or within species by replacing the independent univariate niche functions with multivariate ones).

Overall, the model presented here is a flexible and abstract model that has connections with many useful concepts in ecological theory. I hope to explore several other variations of the model, including models with non-linear competition, different niche function shapes, and more than two focal consumer species.

5.7 References


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Chapter 6. Conclusions

In the introduction to this thesis I laid out two major questions which I would seek to answer during my thesis. The two questions were:

1) Can phylogenetic diversity help to predict ecosystem function?
2) What can we learn about the processes that have acted on ecological community assembly from the patterns of phylogenetic structure left behind?

6.1 Can phylogenetic diversity help to predict ecosystem function?

This thesis has provided ample evidence that the answer to this question is yes. In Chapter 2 I show that including measures of phylogenetic diversity could improve a statistical model designed to predict arthropod diversity in experimental plots of plants nearly two fold over a model which only utilized species richness of plants as an explanatory variable. Likewise, in Chapter 3 I show that phylogenetic diversity interacted with species richness of plants to better explain patterns of herbivory at the community level in an observation study. This was in keeping with the hypothesis that herbivore diets have some phylogenetic structure, which makes herbivores vulnerable to variation in phylogenetic structure in the plant communities they inhabit.

In a recent study, Pellissier et al. (2013) showed that Lepidoptera in the Swiss Alps had high phylogenetic structure to their host plant diets, and that Lepidopteran communities along altitudinal gradients responded to phylogenetic diversity of the local plant communities. Unlike the study I describe in Chapter 2, however, Pellissier et al. (2013) showed that alpha phylogenetic diversity was not a strong predictor of alpha diversity of Lepidoptera – alpha diversity meaning the number of species or lineages in single area. Rather, phylogenetic beta diversity was strongly associated with beta diversity of the Lepidoptera – beta diversity meaning the amount of turnover in species or lineages between different spatial locations. However, this is not surprising given the dispersal capability of butterflies and moths. It should not be forgotten that high beta diversity can be expressed as high alpha diversity measured at a sufficiently large
scale. This result suggests that the response of butterfly community structure to structure in communities of their food-plants is expressed at a larger scale than what was initially measured in this study. Taking a whole group such as arthropods as a focal group then will lead to a mosaic of structure that resolves itself at different scales for different species, depending on their degree of mobility.

This recent work is certainly encouraging about the prospects of phylogenetic diversity having a useful contribution to our understanding of diversity-functioning relationship in ecosystems, but these ideas have yet to be tested in an experiment that is designed specifically to isolate the effects of evolutionary history on aspects of community functioning, at least in macro-organisms. A study using micro-organisms in microcosms showed that communities which were experimentally constructed to have high phylogenetic diversity had higher community productivity, but only when the microorganisms were not subjected to heavy artificial selection prior to community assembly (Gravel et al. 2012). Interestingly, a recent history of experimentally imposed selection pressure obscured the historical effects of phylogeny, causing the relationship between phylogenetic diversity and ecosystem function to break down. This suggests that phylogenetic history may be most important to the functioning of ecosystems in ecosystems which have remained fairly stable over recent evolutionary time, or those where community members are only recently exposed to new environmental conditions, before they have not yet had a chance for new selection pressures to impose idiosyncratic relationships between phylogenetic positions and organismal traits. Either way, anthropogenic climate change and species migrations may have important implications for how phylogenetic diversity influences ecosystem function. This should be a major new avenue of research in the coming years.

6.2 What can we learn about the processes that have acted on ecological community assembly from the patterns of phylogenetic structure left behind?

In Chapter 4 I showed that sites with contrasting histories of disturbance have different phylogenetic structure when compared to their species pools. However, the exact cause of this difference remains ambiguous, as evidenced by the discussion in Chapter 4, which outlines a large number of possible explanations for the pattern. This suggests that the answer to the
question of what we can learn about processes from phylogenetic patterns should be: “not much”. However, I think it is still too earlier to unequivocally dismiss this approach. As I will discuss more thoroughly in the next section, we may still be able to learn more about processes from pattern by moving towards fitting models, rather than the heuristic methods I use in Chapter 4. At the least, the model fitting approach may be able to rule out certain possibilities. In Chapter 5 I presented a model, which could be one possible model to start narrowing our expectations on the production of patterns in species’ ecological similarity. Importantly, the model predicts that we should expect a range of niche similarities to coexist, but that species with intermediate ecological similarity are the most likely to coexist. This suggests that perhaps we can gain more insight into phylogenetic structure by modelling the distribution of branch lengths between community members, rather than relying on metrics which summarize the information by averaging. There may be as much information in the variance in branch lengths as there is in the average branch length.

6.3 Future Directions

The field of community phylogenetics, though young, has made some interesting contributions to modern ecology. However, there are many places where the theory and practice of community phylogenetics can be improved. In the next section I discuss my own ideas for where the field should be heading in the coming years.

6.3.1 Moving away from heuristic measures and null-model based hypothesis testing and towards fitting of multiple process-based models to data

In the introduction, I discussed how phylogenetic community structure is often determined by comparing observed measures of phylogenetic structure to null distributions generated by simulation (and I conducted some of these tests in Chapter 4). This forms a hypothesis test of a sort, where a ‘significant’ result is a community which has higher or lower phylogenetic diversity than expected under the null model. But in order to have phylogenetic structure in communities, as described in introduction, you need two things: phylogenetic
structure in at least some traits, and that some of those same traits determine the species’ interaction with the environment. Therefore, if the null hypothesis in these tests is not rejected, it could be either because one or the other of these two ingredients is missing, or both are missing, with no way to tell which. And so the test is really testing the combination of two hypotheses rather than a single hypothesis.

When we do reject the null hypothesis, the two ingredients also cause problems. If communities are clustered, we do not know whether there is phylogenetic conservation of traits with environmental filtering, or phylogenetic convergence of traits with competitive exclusion of similar species (Cavender-Bares et al. 2009). The double hypothesis is severely underdetermined by the data. Because of this, some authors have suggested we need to measure traits and determine what phylogenetic structure they have (Cavender-Bares and Wilczek 2003). Then we know if we see clustering or overdispersion, we have an idea of what may have caused that structure (e.g. environmental filtering of a phylogenetically conserved trait). But if one does this, we are not really testing any hypothesis unique to community phylogenetics anymore. This is because if one knows, for example, if certain traits are phylogenetically conserved, then in order to observe phylogenetic clustering of communities, there must be environmental filtering on those traits (or other traits correlated with the measured traits). But since the traits are already measured, we could simply test whether those traits are associated with co-occurrence directly. And so the test of phylogenetic clustering just becomes a less direct way of testing the association of traits with environments. What this general method of community phylogenetic analysis does provide is more insight into how deep evolutionary history interacts with local recent ecological forces to determine community assembly. This is a very interesting, but in essence, what we are talking about here is a descriptive science.

I think that community phylogenetics is a descriptive, or pattern-based science for the most part (though experimental approaches are being developed), but that descriptive science is very important. Hypothesis testing may be inappropriate when applied to descriptive science, but what it does give us is a wealth of new information that we can use to fit models to, and thus make better predictions, and at the very least, to circumscribe a smaller set of probable models for how the world actually works from a larger set. I therefore think that we should largely abandon null hypothesis testing in the field of community phylogenetics. The truth is that their main use is to provide a p-value to satisfy the editors of journals, when really they are nearly
meaningless. Many of the current criticisms of community phylogenetics stem around the over-
interpretation of null hypothesis rejections, in light of out still limited knowledge about how
different processes interact to create phylogenetic patterns. If we stop pretending that we really
can infer all such processes just from patterns, many of the criticisms would die away.

I would compare the current state of community phylogenetics to the current state of
genomic science. Many early genomics advocates oversold the ability of genomics to infer
biological processes. It has become increasingly realized that there are so many processes acting
and interacting on genomes, that disentangling the effects they have from the patterns they leave
behind in sequences is impossible (Travisano and Shaw 2013). But the power of genomes, as is
the power of community phylogenetics, is the increase in information density they provide,
which can, in conjunction with experiments, and theory, lead us to narrow our range of
hypotheses about mechanisms underlying observed patterns. They are both part of the movement
that is happening all over biology and science in general, the move towards big data science. But
it shouldn’t be forgotten that big data can only lead to true progress in understanding when
partnered with its more traditional counterparts of experiment and theory.

We must not oversell community phylogenetics. It is never a magic bullet. Many of the
statistics used to date are deeply flawed, and merely provide a veneer of statistical rigour to mask
the difficulty of inferring process from pattern, especially when experimental and theoretical
studies in this area are severely wanting. At its heart community phylogenetics is a descriptive
science, but which nonetheless will be very important in the coming years for understanding
ecological processes, and ultimately in fulfilling the promise of making ecological predictions. I
believe descriptive science includes the fitting of quantitative models to data, and this is where
we will achieve more insight in the years to come. It is encouraging that more model-based
approaches to understanding phylogenetic community data are being developed recently. For
example Ives and Helmus (2011) developed a model for testing community phylogenetic
structure using a hierarchical statistical model, though this is still lacking in process-based
modelling. Likewise Chiu et al. (2011) describe models for incorporating phylogenetic
information into network-based analysis of foodwebs by modelling networks in a latent-variable
space. This approach has promise for improving our understanding of trophic interactions with a
phylogenetic perspective.
Moving away from rejecting a fairly arbitrary null model of community assembly (which in general we already know is false), and instead fitting a series of alternate model of community assembly to data will allow us to incorporate more of the complexity of ecological processes which can potentially influence phylogenetic structure. It is this lack of a simple link between a few factors and a few simple effects on phylogenetic structure that has led to some criticism of community phylogenetics as a bit of a fool’s errand. I address a few of these criticisms in the next section.

6.3.2 Community phylogenetics needs more theory and experiments

As a young field, community phylogenetics is underdeveloped in theory and experiment. In a sense, the field has developed in a non-standard way, with applications to analysis of empirical data being developed before the theoretical underpinnings. This has led to some major criticisms, many of which have been expressed in an argument about whether community phylogenetics theory, undeveloped as it is, ignores so-called ‘modern’ coexistence theory, which is often a reference among empirical ecologists to the ideas espoused in Chesson (2000), and which I will refer to in the following section as ‘Chessonian’ coexistence theory.

6.3.3 Does ‘Chessonian’ coexistence theory undermine community phylogenetics and expose it as a bandwagon, or is Chessonian coexistence itself ecology’s latest bandwagon?

Several recent commentators have suggested that community phylogenetics as a field has not adequately absorbed the lessons of so-called modern coexistence theory (Mayfield and Levine 2010), as described in Chesson (2000). I argue that what has come to be described as modern coexistence is neither modern, nor as complete or enlightening as it is often made out to be by ecologists. It is not modern, because the basic insight of Chesson (2000), that coexistence in classic Lotka-Volterra and similar competition models is co-determined by the degree of similarity in two species’ resource consumption (or ‘niches’), and the degree to which they differ in their intrinsic competitive ability (or ‘fitness’), has been apparent since the original formulation of these models by Lotka and Volterra. Chesson’s (2000) contribution was to give these two coexistence ‘mechanisms’ new names (I use quotations because it is unclear whether in fact these can both be considered mechanisms in the traditional sense (Loreau et al. 2012)), ‘stabilizing’ and ‘equalizing’ respectively, and to derive a re-parameterization of the Lotka-
Volterra models which makes this dichotomy clearer. Despite this idea being derived from a very simple, though admittedly influential and important competition model, and under pretty unrealistic assumptions, ecologists have seized upon this framework with an enthusiasm which borders on recklessness.

Nevertheless, the basic insight of two types of differences between species interacting to determine coexistence is a good one – and one which was been pointed out long ago (e.g. Armstrong 1976; Abrams 1976, 1983, 1986, 1990). To me however, this only suggests the general weakness of community phylogenetics, in which it has largely based on the application of simple models to data in a highly heuristic way, with no attempt to built up the mathematical basis of the ideas, using for example, model-fitting and simulations. In other words, Mayfield and Levine’s (2010) argument leads merely to the naive application of a new model, without a detailed mathematical exploration of its likely consequences. Basically, mathematical theory work is very useful to explore the factors which may be important in a particular system, but when it comes to actually evaluating the potential importance of a factor in a real system, and what will lead to important empirically measurable differences in those systems, mathematical theory by itself is not enough. Experimental and simulation studies will help to translate the abstract quantities in model parameters into real-world effects. This unfortunately has not been done in community phylogenetics.

Given the lack of studies at the interface of mathematical theory and empirical field studies concerning organism similarity and coexistence, in many cases arguments for the greater adoption of the viewpoint of Chesson (2000) amount to little more than replacing one inadequate oversimplified dichotomy – environmental filtering vs. limiting similarity in community phylogenetics theory (Mayfield and Levine 2010), or selection vs. complementarity effects in biodiversity-functioning theory (Carroll et al. 2010, Loreau et al. 2012) – with another inadequate oversimplified dichotomy – equalizing vs. stabilizing mechanisms in Chessonian coexistence theory. It should be noted, however, when I refer to Chessonian coexistence theory, I refer to the simplified stabilizing vs. equalizing concept presented as part of Chesson (2000), which is based largely on the work in Chesson (1990), whereas the full paper of Chesson (2000) presents a much more full and subtle view of coexistence theory in its entirety. However, it is largely the stabilizing vs. equalizing concept which has been taken up by other ecologists,
particularly empirical ecologists, who seem to be attracted to dichotomies as organizing themes for empirical research.

 Though Chessonian coexistence theory has much to recommend it as an aide to understanding certain classes of competition models (I use the framework myself in Chapter 5, though that was partially to frame my argument in the same terms that ecologists are increasingly using), but as a basis for an ongoing bandwagon of empirical research in ecology there is much to be wary of. A recent major review of the coexistence theory in ecology, HilleRisLambers et al. (2012), has called for the greater adoption of the dichotomy espoused by Chesson (2000), as a central organizing thesis in the empirical study of coexistence, which I think does injustice to the full subtlety and complexity that has been revealed by theoreticians studying this problem. Rather, the full subtlety of true modern competition and coexistence theory should be integrated with the insights of these other fields, to forge a research program which is in line with the full complexity of ecological phenomena. I attempted a very crude step in this direction in Chapter 5, in which I attempted to integrate concepts from both coexistence theory and community phylogenetics together, in this case by taking “environmental filtering” and “limiting similarity” and by splitting “limiting similarity” into its stabilizing and equalizing components. Even though this still ignores the further complexity of stabilizing and equalizing factors possibly being a false dichotomy, this exercise makes a small contribution to merging the concepts contained within community phylogenetics with those of the broader coexistence literature. Before this can be applied properly to help generate empirical insights, however, the full complexity of coexistence theory needs to be integrated, and simulation studies conducted to see what we really should expect when these factors interact to generate some phylogenetic structure if any. Unfortunately, I was unable to get to this point during the course of this thesis, but it remains an important follow-up goal to build on the results of chapter 5.

 Stabilizing and equalizing mechanisms is probably a false dichotomy, in the sense that in practice it is impossible to unambiguously separate the two (that is, outside a simplified model). In order to express the criteria for coexistence into the relationship among two parameters, one of which represents niche differences and the other fitness differences, Chesson needed to make a large assumption. The assumption is that competition between a focal species and a competitor species is completely linear, that is, it does not depend on the density of the focal species itself. This is unlikely to be the case in real systems. Without this assumption, there is no way to isolate
the two parameters in the way that Chesson does, suggesting that equalizing and stabilizing ‘mechanisms’ are not actually separable and distinct mechanisms in most systems (Loreau et al. 2012). It is telling that in a major review (HilleRisLambers et al. 2012) recounting the use of stabilizing and equalizing concepts in empirical studies, the authors could find no examples where experimenters had been entirely successful at isolating these mechanisms experimentally. It may not be possible, in fact. Even putting the non-linearity argument aside, both terms contain some of the same parameters of the Lotka-Volterra equations, suggesting that manipulations that affect any parameter of the original competition model will likely affect both equalizing and stabilizing mechanisms, meaning that the meaningful separation of them using experiments becomes even more dubious. Given this, it is difficult to see the utility of attempting to ‘categorize’ empirical systems into stabilizing and equalizing coexistence, as has been suggested by some commentators (HilleRisLambers et al. 2012). Certainly this would at least require stabilizing and equalizing mechanisms to be additive (so they can be decomposed properly), which they certainly are not (Loreau et al. 2012).

In practice, though it is correct to point out that similarity in fitness can help increase the probability of coexistence, and therefore it could potentially lead to coexistence of species with similar traits, if those traits are involved in ‘fitness’, there are important caveats which may make this of limited importance in real systems. One of the most important caveats, is that this effect of fitness similarity may be very weak in comparison to ‘niche’ differences. As just one example, only species whose fitnesses are exactly the same, cannot be excluded by each other in the absence of unequal evolutionary change in those species. This is not likely to ever be the case. Likewise, since it is impossible for the fitness difference of two species to be infinite, fitness differences can never guarantee a lack of coexistence either. On the other hand, it is possible for two species to have no niche overlap, which does guarantee coexistence when existence is possible. This alone, I argue, makes niche separation a more powerful force in coexistence. One piece of evidence in favour of this view comes from Carroll et al. (2010), who use Lotka-Volterra competition models to model the effects of niche separation and fitness differences amongst community members on community productivity. This does not specifically look at coexistence, but it has been shown that there is a connection between the production of mixtures of species, and the coexistence of those species in competition (Loreau 2004), and this was the motivation for the study. Though they make much of the fact that fitness differences do indeed
affect community productivity, examination of their figures reveals that the effect of fitness differences is much weaker than that of niche differences. I believe this will translate to coexistence likelihoods as well.

6.3.4 Experiments

Community phylogenetics has been hampered by its relative lack of experiments. Much of the literature focuses on analysing observational data, but to anchor these analyses we need to confirm and flesh out our expectations. Above I spoke about how we can do this with mathematical theory, but nothing can teach us about the veracity of our expectations better than performing experiments. Now, we all know that it is very difficult to conduct manipulative experiments at a scale relevant to ecology, but a few recent studies are showing that experiments can make a valuable contribution to the study of community phylogenetics (e.g. Maherali and Klironomos 2007, Cahill et al. 2008, Gravel et al. 2012). In Chapter 4 I took advantage of a sort of ‘natural’ experiment (natural in the sense that I did not impose it myself, but it was anthropogenic in origin) to look at the effect of a manipulation on phylogenetic structure. More comparative studies such as this will shed more light on the relationship between community phylogenetic structure and ecological processes.

6.4 Phylometrics: The study of phylogenetic diversity measures

6.4.1 Pitfalls and Promises

The basis of many of the questions in community phylogenetics is the metrics which are used to measure the phylogenetic structure of communities. These metrics take phylogenetic information about relationships among species and information about how those species gather together into communities and try to boil it down into a simple measure which captures elements of both. They attempt to measure the diversity of a community while taking into consideration the lack of independence of species due to common ancestry. Much of the future work of community phylogenetics, both for understanding causes and consequences, will be in refining and understanding the properties and interrelationships of the different ways of measuring phylogenetic diversity, of which there are a huge and growing number. Here I discuss some of the pitfalls and promises of the emerging subfield of what I sometimes call phylometrics.
(although variometrics might be a more general term to apply to all metrics which attempt to capture non-independence of entities by their similarity of lack thereof).

6.4.1.1 Pitfalls

There are several issues with phylogenetic diversity measures that need to be solved for the field of community phylogenetics to move forward. Most importantly is that there is a large and growing number of them (Hardy 2008, Schweiger et al. 2008, Vellend 2010, Pausas and Verdú 2010), leading to the question of which metric should we use in a given situation? I solve this issue in Chapter 2 by repeating my analysis for a large number of different metrics to see whether they told similar stories. This is not a solution that will work all of the time, as you need a large sample size, and it does not lead to any better understanding of what the differences in the metrics may mean. In Chapter 3 I chose a metric using a priori criteria. Many metrics seem to contain similar information, suggesting the choice between these metrics may not be so important. On the other hand, some metrics seem to be very different from others (e.g. see Cadotte et al. 2010). These potentially represent different aspects of phylogenetic information which may be complementary to each other. Exploring the meaning of such differences will be an important project for community phylogenetics in the future.

A few studies have attempted to compare different metrics for various properties (Schweiger et al. 2008). One issue with many metrics is that they don’t obey the set monotonicity criteria, which means that extinction of species should decrease the metric (Schweiger et al. 2008). This criterion may make sense from a conservation or restoration perspective, but metrics that obey this criterion tend to be spuriously correlated with species richness. Metrics that are not correlated with species richness are desirable if we want to disentangle the effects of phylogenetic diversity from that of species numbers. It is unlikely that any metric has both set monotonicity and is uncorrelated with species richness, making this one consideration that can help narrow down the choice of metrics, depending on the goal of the research.

Ultimately, the fact that different metrics seem to capture different aspects of phylogenetic information suggests that a fruitful avenue may to develop more multivariate metrics that capture more of this variation. This of course will always be in tension with the
desire for single numbers which capture as much as possible, for the purposes of management for example, where speed and simplicity is an asset.

Many new metrics also include the ability to weight by relative abundance of species, leading to the added pitfall that it is difficult to tell what part of the signal in the metric is caused by phylogenetic information and which is caused mainly by abundance distributions. Rather than trying to wrap all these aspects of community diversity into a single measure, I believe the best approach is to retain species richness, abundances, and phylogenetic diversity as separate and statistically independent measures whenever possible, and incorporate the possibility of interactions between these facets of biodiversity by explicitly including interactions in the statistical models employed. I derived important insights which otherwise would have been obscured by taking this approach with species richness and phylogenetic diversity in Chapters 2 and 3.

6.4.1.2 Promises

The added information density that phylometrics can add to our measurements opens up a lot of promise for biodiversity science. We are entering an era of rapid environmental change that coincides with an era of rapid technological change. The rapid technological development can help us to understand the consequences and opportunities of these rapid environmental changes. Phylometrics will be only useful so long as they can keep up with the technology. Phylogenetic information is increasingly available for more and more organisms, making phylometrics a possibility in new systems all the time. A lot of the increase in the availability of phylogenetic information is due to the explosion of next generation sequencing technology which is making the sequencing of genetic material cheaper and faster than ever before. Still, in order to use phylometrics on communities, it is necessary to identify all organisms, gather genetic data for each, align sequences, and then run phylogenetic algorithms to generate a phylogeny, all before we can calculate any phylogenetic diversity measure. Some of these steps are becoming more challenging simply due to the incredible increase in the amount of data. For example, multiple sequence alignment methods increase in difficulty exponentially as you add more species and more sequence length, to the point where now we are getting whole genome data for many species, but sequence alignment of entire genomes is almost impossible for more
than a few species at a time, not to mention that in more distantly related species, genomic rearrangements makes alignment unrealistic. Identifying homology, a necessary step in building phylogenies becomes increasingly challenging with more species and more sequence length as well. Increasing the speed of this pipeline will be an important step going forward, and several developments will help this happen.

One of the easiest ways to generate phylometrics (or variometrics) faster would be to cut out some of the steps. Often when we calculate phylogenetic diversity, we are using phylogeny as a proxy for ecological distinctiveness. This being the case, we do not necessarily need a phylogeny at all. In practice most phylogenetic diversity measures only utilize branch lengths between species rather than tree topology, and so the tree is superfluous in any case. That being said, most genetic distance algorithms still require a multiple sequence alignment, which can be time-consuming (and often inaccurate). This is where new alignment-free methods may be perfectly suited to community phylogenetics (e.g. Vinga and Almeida 2003, Sims et al. 2009, Comin and Verzotto 2012). Alignment-free methods for phylogeny construction are usually based on a pairwise matrix of genetic distances between species calculated without alignment, often by counting the numbers of shared ‘words’ between sequences, without considering the relative positions of those words (so-called ‘k-mer’ methods (Chor et al. 2009)). These distance matrices can then be submitted to a neighbour-joining or other clustering algorithm to build a phenetic tree. In many case these trees can get very close to the phylogeny built using multiple alignment, especially when using whole genomes. It would seem the added information density in the entire genome may be enough to compensate for the lack of homology information in these alignment-free techniques. It is just as well, as alignment-free methods are really the only method that can currently be applied to large numbers of species with whole genomic data, simply because they are so much less computationally expensive. In community phylogenetics, when we are looking simply for a proxy of genetic distance, which in turn is a proxy for ecological distance, these methods hold great promise.

These methods will be particularly useful as we enter the age of metagenomics, in which environmental samples are sequenced for whole genomes. In this case the only information we may have on organisms (particularly when they are microscopic) is this genetic data. A major new avenue for phylometrics will be how to extract as much information about a community
from patterns of genetic similarity and dissimilarity within and between samples (Koyano and Kishino 2010, O’Dwyer et al. 2012).

6.4.2 Summary statistics for advanced model fitting

Another useful avenue of research in the application of phylometrics is how they can be used as promising data to help fit ecological models. There has been an increasing emphasis on ecology to create mechanistic models which can then be fit to patterns of real data. This effort has been hampered to date by a narrow focus on the type of data being fitted. For example, when Hubbell (2001) showed that a simple model in which all species were ecologically equivalent could generate patterns in species abundance curves similar to those found in nature, it prompted the development of great numbers of models, to which species abundance curves could be fit (reviewed in McGill et al. 2007). However, species abundance curves represent a pretty poor sample from the pool of available ecological data, which can be used to fit models.

A large class of studies attempt to fit models of ecological environmental interactions to data on the distribution of organisms (Elith and Leathwick 2009). These species distribution models represent another example of fitting models to data, but again the data utilized is nowhere near the full extent of data available. As an example very few of these models utilize community-level information, and just treat species distributions as independent inputs to the model. One notable exception would be Mokany et al. (2011), who modelled patterns of alpha and beta diversity across a landscape as a function of environmental variables. It is this type of model where phylometrics may help to distinguish models.

Though there are very few examples so far in ecology, a method of model-fitting which is becoming increasingly popular, particularly in fitting models to genomic data, is approximate Bayesian computation (ABC) (Beaumont 2010). I have compared community phylogenetics to genomics already in this chapter, and here is another place I think community phylogenetics (and observational ecology in general) could take a cue from genomics. ABC fits models by minimizing the difference between simulated data and observed data in certain summary statistics, which capture relevant aspects of the data. Phylometrics offer an important new source of summary statistic for this purpose.
6.4.3 Conservation and Restoration

A recent review in TREE started a conversation about how phylogenetic diversity should be used in conservation and restoration (Winter et al. 2012, 2013, Rosauer and Mooers 2013). If it is true that phylogenetic diversity plays a role in promoting ecosystem function, then this adds a new reason for the protection of phylogenetic diversity. It had been previously suggested that protecting phylogenetic diversity was valuable, in that it preserves genetic and evolutionary heritage, which cannot be regained once lost (at least not within a reasonable timescale) (Faith 1992). A fuller understanding of how phylogenetic diversity influences ecosystem functioning will add helpful information to the discussion around whether and how to include phylogenetic diversity in conservation triage decisions.

6.5 References


Appendix 1. Bayesian Phylogeny for the plants of Koffler Scientific Reserve
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