The phylogenetic structure of ecological communities under change

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Declaration of Originality

Except where acknowledged in the text of my thesis and where mentioned below, all work within this thesis is my own.

I collected none of my own ecological data, and provide references in the text to the sources of the data I used. I also cite computer software where it was written by others.

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Abstract

Darwin first noticed that closely-related species tend to be more similar, and that this brings them into more severe competition with one another. In my thesis, I use information on the phylogenetic relatedness of species to help understand the processes that structure ecological assemblages. I start with a review of how phylogenetic structure is useful to ecologists (chapter one), and the methodological tools available to study it (chapter two). I then re-analyse the Barro Colorado Island dataset, finding shifts in phylogenetic structure across extremely fine spatial and phylogenetic scales that previously used measures were unable to detect (chapter three). I outline a new tool that automatically generates phylogenies for ecologists, making use of online DNA sequence databases (chapter four). Using trait and phylogenetic data, I examine marine benthic invertebrate assemblages (chapter five), and characterise the structure of British birds and butterflies (chapter six). I then prioritise British plant conservation according to a new scheme that includes evolutionary distinctiveness, species threat and our degree of uncertainty about species threat (chapter seven), and conclude by considering future directions for the study of the phylogenetic structure of ecological communities (chapter eight).

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Chapter 1

Introduction: why study the phylogenetic structure of ecological communities?

Community phylogenetics is an attempt to combine the fields of community ecology and evolutionary biology, asking how the phylogeny of species can shed light on processes of community assembly and interspecific competition. I can find no useful rigid definition of the field, but I consider Webb (2000) to be the foundation of it. While Webb (2000) is not the first study to incorporate phylogeny into ecology (Warwick, 1995; Tofts & Silvertown, 2000, are notable for this), Webb's NRI/NTI family of dispersion measures quickly gathered momentum and have become well-established. Community phylogenetics is not typically concerned with intraspecific processes (genealogical perspective on these falls under community genetics; see Rowntree *et al.*, 2011), nor is it an attempt to understand how past ecological forces shaped the evolution of a clade. The dominant paradigm examines whether an area's biota is phylogenetically clumped or overdispersed, where the former's close phylogenetic relatedness between species is assumed to reflect habitat filtering according to shared traits, and in the latter these same shared traits bring close relatives into excluding competition.

If we accept Webb (2000) as the first true 'community phylogenetic' paper, then

it is valid to ask what the field has achieved in over ten years, and whether it shows any promise for the next ten. This chapter will briefly review the field's history, describe the contributions community phylogenetic studies have made to the wider literature, and then outline the major themes of this thesis. Although I will make some general comments about possible future work, a more rigorous discussion is saved for the final chapter.

1.1 History

> *As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera.*
>
> Darwin (1859), chapter three.

It was Darwin who first noticed the relationship between species' taxonomic proximity and competitive interactions. Foreshadowing discussions of niche conservatism, he argued that, because congeners are more similar, competition should be strongest among them. While Darwin was interested in how this increasing competition would affect natural selection, decades later scientists would ask what the number of congeners present in the community could reveal about the ecological processes structuring it.

Jaccard (1901) first calculated the ratio of the number of genera present in a community to the number of species present, and related the results to competitive interactions between species. While numerous workers (reviewed in Järvinen, 1982) showed the approach was flawed and overly sensitive to community diversity, the idea that ecological processes could be detected in the taxonomic structure of the community took hold. Species-genus ratio analyses continued, albeit at a reduced pace, until a taxonomic diversity concept was formulated by Warwick (1995), who argued that counting the mean number of taxonomic ranks between community members was a meaningful shorthand for taxonomic

proximity. Taxonomic methods continue to be used in marine ecology circles to this day; over 150 articles with 'marine' in their keywords on `Web of Knowledge` (`www.webofknowledge.com`) cite Warwick (1995). This is likely because of the difficulties inherent in producing phylogenies for marine assemblages, which commonly contain several Linnean kingdoms (Paine, 2010).

Bacterial ecologists, meanwhile, have favoured measures with less emphasis on hierarchical phylogenetic relationships, explicitly acknowledging the difficulty of even distinguishing species (e.g., Singleton, 2001). Strangely, their most popular approach (UniFrac; Lozupone & Knight, 2005) has been ignored by most large-organism ecologists, and despite being highly cited (over 480 citations on `Web of Knowledge`) is ignored in all reviews of community phylogenetics I can find (Schweiger *et al.*, 2008; Vamosi *et al.*, 2009; Pausas & Verdú, 2010; Pavoine & Bonsall, 2011; Vellend *et al.*, 2011), bar a passing mention in Cavender-Bares *et al.* (2009).

The mainstream of ecology prefers to use Webb's (2000) *NRI* and *NTI* measures (and the family of measures developed from them; see the next chapter), and it is for this reason that I consider Webb (2000) as the beginning of modern community phylogenetics. They examine the 'dispersion' of a community—whether its species are more (phylogenetically clustered, or underdispersed) or less (phylogenetically overdispersed) related than would be expected given random assembly from the species that constitute its source pool. Invoking niche conservatism (reviewed in Wiens *et al.*, 2010), phylogenetic clustering is assumed to reflect habitat filtering according to shared traits, while overdispersion reflects those shared traits causing species to competitively exclude one another. The preference for the *NRI*/*NTI* family may be because these measures use null distributions already widely used in community ecology (reviewed in Gotelli, 2000) and can also be applied to trait data (e.g., Kraft & Ackerly, 2010), thus fitting more snugly with conventional ecological analyses. Once the `Phylomatic` tool for automated construction of informal phylogenetic supertrees from species lists (Webb & Donoghue, 2005) was released, it became possible to examine the phylogenetic structure of existing datasets without collecting any additional data.

There was a rush to apply this new framework to diverse taxa (e.g., plants–

Cavender-Bares *et al.*, 2004, birds–Graham *et al.*, 2009, fishes–Helmus *et al.*, 2007, and yeasts–Anderson *et al.*, 2004) and to assess changes in dispersion across ecologically meaningful processes and scales (e.g., growth and recruitment–Webb *et al.*, 2006; Letcher, 2009, pre/post invasion–Lessard *et al.*, 2009; Schaefer *et al.*, 2011, and across disturbance regimes–Helmus *et al.*, 2010). However, as the number of measures and publications grew, the dominant paradigm was challenged. Valiente-Banuet & Verdú (2007) demonstrated that facilitation, not only competition, between distantly related species could lead to overdispersion, while in a more serious blow Mayfield & Levine (2010) questioned whether phylogenetic distance could plausibly be related to ecological distance, given the likely prevalence of convergent evolution and widespread variation in how traits evolve.

The general consensus seems to be that explicit incorporation of trait data into studies of phylogenetic dispersion will solve these problems (e.g., Cavender-Bares *et al.*, 2006), and recently-developed techniques can examine traits and phylogenetic structure simultaneously (e.g., Pillar & Duarte, 2010; Ives & Helmus, 2011). Community phylogenetics is difficult to define precisely because it encompasses so many different aspects of ecology: even if the Webb paradigm is rejected, I find it hard to believe that the field will be entirely lost.

1.2 What phylogenetic structure can help us understand

Filtering processes

Many ecologists think of community assembly as a process of filtering, where the species in an assemblage are somehow selected from a potential set of species (the 'source pool') by a series of 'filters', such as environmental tolerances and competitive interactions with species already present in the assemblage. As described above, phylogenetic dispersion is plausibly related to these filters, and so provides a new way to examine fundamental ecological processes. While phylogenetically clustered, overdispersed, and random assemblages have all been documented, a

systematic review reported that the majority (18 of 24) of studies find phylogenetic clustering (Vamosi *et al.*, 2009). This is a major achievement; we know that assemblages tend to consist of closely-related species, and so the field can be said to have answered one its own fundamental questions (as posed by Webb *et al.*, 2002).

However, while there has been work on spatial scaling in community phylogenetics (e.g., Swenson *et al.*, 2006), studies rarely test for multiple filtering processes, instead assuming that a single dispersion measure is sufficient for a study. Thus there is more work to be done examining the precise spatial and phylogenetic scales across which phylogenetic clustering and overdispersion dominate. Chapter three shows how varying the spatial delimitation of assemblages and source pools helps reveal different filtering processes, and how there is systematic variation among clades' dispersion values.

Patterns of diversity

Most ecologists have an intuitive concept of biodiversity and are interested in how it varies in time and space, but acknowledge that biodiversity is intrinsically multidimensional; for example, we are not just interested in species richness, but also the evenness of species' abundances (Purvis & Hector, 2000; Magurran, 2004). There are probably hundreds of proposed diversity measures, but major advances include deriving the general class of 'Hill numbers' (Hill, 1973), and that diversity can be additively partitioned into α, β, and γ components (Lande, 1996). A number of measures have been extended to incorporate phylogenetic information (described in the next chapter), often as generalisations of classic ecological diversity measures. Notably, the *PCD* family (Ives & Helmus, 2010) can distinguish between contributions to dissimilarity from communities' shared and non-shared species, essentially distinguishing between non-phylogenetic and phylogenetic components respectively.

The explosion of phylogenetic diversity measures suggests biologists want to incorporate phylogenetic information into studies of diversity, but I can find few general themes in the approach. That phylogenetic β-diversity should be demon-

strable is interesting, but too few studies have used the same methodologies for strong conclusions to be drawn. However, since an `R` library implementing many common measures was released only two years ago (Kembel *et al.*, 2010), this may be changing.

The general approach of incorporating phylogenetic information into diversity measures has led to the *EDGE* lists (Isaac *et al.*, 2007, 2012), which have contributed to the public's understanding of phylogenetic diversity. Chapter seven of this thesis shows an extension of such lists to incorporate uncertainty in estimates of risk and phylogenetic structure.

Functional traits

Functional traits are an established part of the ecological literature, and it is perhaps unsurprising that functional trait and phylogenetic structural analyses are often seen as complementary given phylogenetic dispersion is often described in terms of phylogenetically conserved traits. Various comparative tools exist to quantify traits' phylogenetic signal (the tendency for closely related species to resemble once another; commonly used tools include Blomberg's K—Blomberg *et al.*, 2003 and Pagel's λ—Pagel, 1999; Freckleton *et al.*, 2002), and they are often used to try and validate assumptions of niche conservatism (e.g., Kraft *et al.*, 2007).

Assessing functional traits in the context of phylogenetic structure has provided additional insight, since phylogeny can 'fill in' for traits where they are insufficient to explain a system (e.g., Graham, 2012), or at the very least suggest where additional trait data are required. There are a number of frameworks (e.g., Pillar & Duarte, 2010; Ives & Helmus, 2011) that compare the contributions of phylogenetic and trait data to assemblage structure, and some of the earliest community phylogenetic studies incorporated species' traits (e.g., Tofts & Silvertown, 2000). In chapters five and six, I ask how trait and phylogenetic data are able to explain ecosystem function and compositional changes.

Ecosystem function

While little work (so far) has related phylogenetic structure to ecosystem function, what has been done suggests phylogenetic structure is at least as good a predictor of function than functional trait data (Cadotte *et al.*, 2008, 2009; Flynn *et al.*, 2011). Chapter five is an attempt to examine how well functional traits and phylogenetic structure explain ecosystem function.

Comparisons between unrelated groups

It can be difficult to usefully compare profoundly different study systems, since it is hard to infer process from many diversity measures, while species' traits can be too specific. For example, it is difficult to determine much about butterfly and bird assembly processes from the measurement of five butterfly species and seven bird species at the same site, and hard to meaningfully compare average wing length between these two taxa. Phylogenetic structure can be measured among most taxa, and because the underlying concepts, such as phylogenetic niche conservatism, can be separately tested, general inferences can be drawn. Phylogeny forms a backbone upon which various methodologies can be hung, and allows fundamental questions to be answered in a common framework.

Interactions between evolutionary biology and ecology

Biologists openly acknowledge the interconnections of the "*ecological theatre and the evolutionary play*" (Hutchinson, 1965), and the titles over 15% of the sessions at the '*Evolution 2012*' meeting in Canada included the word 'ecology'. The more exchange between ecology and evolutionary biology fuelled by empirical results, the better. Phylogenetic structure provides another direct link between these two fields, and it requires data (e.g., DNA sequences) and has outputs (e.g., phylogenies) that are useful to both.

1.3 Overview of this thesis

My thesis examines how phylogenetic structure helps us understand how ecological communities are structured, and how that structure can change, and begins in earnest with a review of how phylogenetic structure is measured (chapter two). I then demonstrate that a measure more explicitly linked to trait evolution theory describes the spatial and phylogenetic scales of ecological assemblage definitions more sensitively than an alternative that does not (chapter three). I describe an automated phylogeny generation program for use in community phylogenetic studies (chapter four), and then use it to examine ecosystem structure and function in invertebrate benthic systems (chapter five). I explore how phylogenetic and functional trait dispersion has changed in British bird and butterflies communities (chapter six), and my final analysis (chapter seven) describes an extension to the *EDGE* approach to conservation prioritisation. I conclude by summarising my thesis, and suggesting some future areas of research (chapter eight).

Chapter 2

A review of the measurement of phylogenetic structure in ecological assemblages

2.1 Abstract

There are many measures of phylogenetic structure, but no satisfactory theoretical framework within which to classify them. I suggest that most community phylogenetic measures are concerned with one of four aspects of phylogenetic structure: *shape*, *diversity*, *dispersion*, and *dissimilarity*. These categories are strongly linked with existing ecological and evolutionary literature, and I place almost 40 distinct measures of assemblages' phylogenetic structure into them. I then comment on the importance of phylogeny construction, null models, and trait data in community phylogenetic studies. To conclude, I suggest general recommendations for how to conduct a community phylogenetic study.

2.2 Overview

Chapter one outlined some of the ways in which phylogenetic structure has been used in ecological studies, but did not attempt to review how phylogenetic structure is measured. There have been at least seven attempts to review community phylogenetics and its methods (Emerson & Gillespie, 2008; Schweiger *et al.*, 2008; Kembel, 2009; Vamosi *et al.*, 2009; Pausas & Verdú, 2010; Pavoine & Bonsall, 2011; Vellend *et al.*, 2011), and I am unwilling to make that list any longer. However, the "jungle" of measures of phylogenetic structure (Pausas & Verdú, 2010) has become so thick that I think it is vital to re-examine what phylogenetic structure actually is. While Vellend *et al.* (2011) define two "types" of measure of phylogenetic diversity according to how they are *calculated*, I feel it is more useful to define community phylogenetic measures in terms of what they *measure*.

I propose that most community phylogenetic measures assess one of four components of assemblages' phylogenetic structure: *shape*, *diversity*, *dispersion*, and *dissimilarity*. *Shape* measures describe an assemblage phylogeny's topology, branch lengths, size, and how closely related its species are, and are mostly taken from phylogenetic literature that pre-dates community phylogenetics. The *diversity* measures, on the other hand, reflect how evenly species' abundances are distributed throughout a phylogeny; I term these diversity measures because they are extensions of existing (typically entropy-based) measures of species diversity. Additionally, some *diversity* measures attempt to partition diversity according to some hierarchy (akin to α, β, and γ diversity). The absolute values of shape and diversity measures provide little information in of themselves—it is their comparison with possible values that is most informative.

Dispersion measures are the most commonly used of the measures, and attempt to match phylogenetic pattern with mechanism. They ask whether variance in an observed measure, such as the mean phylogenetic distance between species (which is a shape measure), is greater or lesser than would be expected under a given null model. They measure whether a particular assemblage's species (or individuals) are more, or less, phylogenetically related to one another than would be expected under random assembly; thus they are intrinsically scaled and

their absolute value has meaning. Finally, phylogenetic *dissimilarity* measures compare the composition of species (and their abundances) among assemblages. Incorporating phylogeny allows comparison of assemblages even when they have no species in common.

In addition, there are a number of issues that cut across most community phylogenetic studies, such as the choice of null model with which a dispersion measure is calculated, the relevance of trait data, and how an assemblage phylogeny should be constructed. This latter point is rarely discussed in the literature, despite the obvious importance of a sufficiently accurate phylogeny in a community phylogenetic study. Indeed, there have been few attempts to incorporate phylogenetic uncertainty in community phylogenetic studies, unlike comparative analysis where posterior predictive methods (reviewed in Bollback, 2005) have become popular.

The remainder of this chapter will categorise measures into these four classes, discuss the three over-arching issues mentioned above, and then conclude by providing general advice for undertaking community phylogenetic study. I do not attempt a novel assessment of the sensitivity and accuracy of these measures, although I examine theoretical concerns with some of them.

2.3 Classification of measures

While I have tried to categorise as many measures as possible, this is by no means an exhaustive list. In particular, many imbalance statistics (reviewed in Mooers *et al.*, 2007) have been omitted, and I examine few of the methods that count the number of nodes in a phylogeny. Such 'nodal' measures are biased by rapid evolutionary radiations, slowly speciating lineages, and incomplete taxon sampling, and are largely unnecessary given the large number of phylogenies now available. I also mention a number of 'approaches' and 'plots' in the tables below; these do not generate measures and so do not strictly belong in a review of measures of phylogenetic structure, but I record them in order to reflect the current state of the field.

In the text below, I make reference to a number of measures using only their acronyms (e.g., I refer to *PD*, not phylogenetic diversity). Each section is intended to be read alongside its table of measures; all measures and their acronyms are briefly defined in these tables.

Shape

The *shape* measures in table 2.1 assess the structure of a phylogeny alone, and can be calculated in the absence of any ecological data other than a species list. *PD* and *MPD* are notable in that they could be applied to any kind of dendrogram or distance matrix respectively, and as such could be used with functional trait data. The γ statistic is biased by non-random taxon sampling (Pybus & Harvey, 2000); this bias is essentially what a study of phylogenetic assemblage structure examines and so it is unclear how to safely interpret a γ value. The same is likely to be true of *LTT* plots and many other of these measures that were originally derived for complete, not assemblage, phylogenies. Heard & Cox (2007) circumvent these problems by comparing observed Colless' index (I_c; also derived for complete phylogenies) values with values calculated across a set of ecologically-meaningful null phylogenies. Davies *et al.* (2012) go further, and compare observed assemblages' joint distributions of I_c and γ against those from simulated assemblages.

Diversity

While a *shape* measure requires no data beyond a phylogeny, a *diversity* measure incorporates species' abundances, and most are extensions of existing measures of ecological diversity. Many have an intrinsic sense of *hierarchy* and distinguish between different levels (e.g., α and β) of diversity (table 2.2; reviewed in Graham & Fine, 2008), while other (*non-hierarchical*) measures do not (table 2.3). Ecological diversity has a number of equally valid definitions and many have been extended to incorporate phylogeny. *PSE* is probably the most frequently used measure, and by comparison with null distributions is used in much the same way

as a *dispersion* measure (see below); however, it is sensitive only to the degree of phylogenetic clustering and so cannot detect overdispersion (e.g., chapter six).

Dispersion

Phylogenetic *dispersion* describes whether assemblages contain species (or individuals, if assessing abundance) that are more (underdispersed; clustered) or less (overdispersed) closely related to one another than would be expected under random assembly; this comparison with some null expectation is key to their calculation. *NRI* and *NTI* are the most popular measures, and distinguish between structure detectable across the whole phylogeny (*NRI*) and among close-relatives (*NTI*). However, *NRI* and *NTI* are shown (in chapter three) to be less sensitive than *D*, and to be incomparable among assemblages.

There is confusion in the literature over the definition of *NRI* and *NTI*, perhaps because Webb *et al.* (2002) re-defined them two years after their initial publication (Webb, 2000). While the use of branch lengths instead of nodal distance in the second definition is an improvement, many authors cite their first definitions when using their second definition. To add further confusion, Kembel (2009) also define SES_{MPD} and SES_{MNTD}, which are intended to be the negation of *NRI* and *NTI* (Webb *et al.*, 2002) respectively. *INND* and *MIPD* (Ness *et al.*, 2011) are interesting extensions of the general approach, using the inverse of phylogenetic distance to test whether phylogenetic distance linearly scales with ecological distance. All of these measures can be abundance-weighted by considering the mean of individuals' distances, rather than mean species distances (although their names remain the same, e.g., '*NRI*' in Swenson *et al.*, 2012). Since these measures are defined with direct reference to one another, I refer to them as the '*NRI* family' (table 2.4), and describe other dispersion measures in table 2.5.

Dissimilarity

Dissimilarity measures (table 2.6) examine the differences in assemblages' compositions, incorporating phylogenetic information so that species are not treated

as identically distinct units. This is particularly useful when comparing more than two assemblages that have no shared species; they need not be identically dissimilar when the phylogenetic distance among species is taken into account. In this regard, special attention should be drawn to *PCD*, since it distinguishes between dissimilarity based on species overlap and shared evolutionary history. The *P Test* is unlikely to be appropriate for most community phylogenetic studies because it is based around a cladistic method; adopting maximum parsimony to examine a phylogeny derived from a maximum likelihood or Bayesian approach seems inconsistent.

Comparison with other classifications

As mentioned in the overview, there have been many reviews of community phylogenetics, many of which do not focus on reviewing the measurement of assemblages' phylogenetic structure (Emerson & Gillespie, 2008; Vamosi *et al.*, 2009; Cavender-Bares *et al.*, 2009), or provide advice on the use of measures but do not attempt to classify them (Pausas & Verdú, 2010). While Pavoine & Bonsall (2011) do not classify phylogenetic measures, the analogies they draw between trait and phylogenetic measures goes a long way towards linking these related fields.

Existing analytical investigations support much of this review. My claim that *D* should be used in preference to members of the *NRI* family is partially supported by power analyses showing SES_{MPD} is insensitive to overdispersion (Kembel, 2009), and my grouping of measures is consistent with Cadotte *et al.*'s (2010) hierarchical cluster analysis of measures. However, I disagree with Schweiger *et al.* (2008), who prefer taxonomic (nodal) measures because they think them unbiased with respect to species richness. Fixing phylogeny age but allowing species number to vary in their simulations actually demonstrates the sensitivity, not bias, of phylogenetic methods to changes in structure when close-relatives co-exist, and the relative insensitivity of taxonomic methods to fine-scale changes in phylogenetic structure.

Vellend *et al.* (2011) attempt to categorise phylogenetic diversity measures by

splitting them into two 'types' according to how they are calculated. This has the advantage of being rigidly defined, but the arbitrary nature of the names ('type I' and 'type II') reflects the fact that the measures do not reflect anything of *a priori* biological interest. As an analogy, we do not distinguish quantile regressions from general linear models on the basis that quantile regression typically involves the use of linear programming algorithms and general linear models do not. Instead, we distinguish on the basis of their asking philosophically different questions; I feel this is more useful and intuitive, and prefer to attempt the same with community phylogenetic methods.

Measure	Reference	Description	Notes
Colless' Index (I_c)	Colless (1982)	Comparison of the number of tips either 'side' of each node with the number in a perfectly balanced tree	A measure of phylogenetic imbalance
PD (Phylogenetic Distance)	Faith (1992)	Sum of the branch lengths in a phylogeny	A phylogenetic version of species richness
MPD (Mean Phylogenetic Distance)	Unknown	The mean of PD	
γ	Pybus & Harvey (2000)	γ values < 0 suggest internal nodes are closer to the root than expected	The converse cannot be tested with γ
LTT (Lineages Through Time) Plot	Martin (2002)	Number of lineages through time in a phylogeny; Martin (2002) assumed departure from a Yule curve indicates over dispersion or clustering	Suggested for use, but not derived by Martin (2002)
PSV (Phylogenetic Species Variability)	Helmus *et al.* (2007)	Compares branch lengths of species with the variance expected under the Brownian motion of a neutral trait across a phylogeny	Claims specifics of the model are independent of Browian model
PSR (Phylogenetic Species Richness)	Helmus *et al.* (2007)	Product of PSV and phylogeny size	

Table 2.1: Phylogenetic *shape* measures.

Measure	Reference	Description	Notes
F_{ST}	Martin (2002)	Standard population genetics method, showing how differentiated samples are	Re-purposed by Martin (2002) for use in concert with the *P test*, to study the phylogenetic scale of clustering
P_{ST}	Hardy & Senterre (2007)	An extension of Simpson's index to incorporate phylogenetic relatedness. Assesses how much of a site's diversity is explained by turnover within sites	
Π_{ST}	Hardy & Senterre (2007)	As P_{ST}, but looks at turnover of species, not individuals	
H_α, H_β, H_γ	Mouchet & Mouillot (2010)	An extension of the phylogenetic entropy concept of Allen *et al.* (2009), using the Shannon relationship ($\beta = \gamma - \alpha$) to generate a hierarchy of phylogenetic entropy measures	

Table 2.2: *Hierarchical* phylogenetic *diversity* measures.

Measure	Reference	Description	Notes
Quadratic Diversity	Rao (1982)	Sum of the product of the proportions of sites where two species are present, and their phylogenetic relatedness	Generalisation of the Simpson Index
Δ (taxonomic diversity index)	Warwick (1995)	Extension of the Shannon index, with weighting according to the absolute taxonomic distance between individuals	Motivated by dislike of other measures not distinguishing between three different genera being present in the system, as opposed to three kingdoms
Phylogenetic Entropy	Allen *et al.* (2009)	The product of two species co-occurring and their natural logarithm of their phylogenetic relatedness	Generalisation of the Shannon Index
PSE (Phylogenetic Species Evenness)	Helmus *et al.* (2007)	As PSV, but with polytomies with branch lengths of zero and sizes equal to the frequency of members of the community added to the phylogeny	
Pavoine *et al.* (2009)	I_a	A generalisation of PD and Quadratic Entropy	
${}^qPD(T)$	Chao *et al.* (2010)	Splits a phylogeny at time T, and calculates the Hill number (Hill, 1973) of the present-day abundances in each lineage at age T	Designed to obey the 'replication principle', and suggests a way of averaging the measures across possible values of T

Measure	Reference	Description	Notes
AED (Abundance-weighted Evolutionary Distinctiveness)	Cadotte *et al.* (2010)	Family of measures based around the sum of the ratios of terminal branch lengths to the number of individuals for each species	
IAC (Imbalance of Abundances at higher Clades)	Cadotte *et al.* (2010)	The sum of the deviation from the expected number of species per node, scaled according to the number of nodes in the phylogeny	The null model is based on measures developed to quantify clade imbalance in phylogenies

Table 2.3: *Non-hierarchical* phylogenetic *diversity* measures.

Measure	Reference	Description	Notes
NRI (Net Relatedness Index)	Webb (2000)	Mean pairwise *nodal* distance between members of a community scaled by the maximum mean pairwise distance possible for that dataset, all subtracted from 1	Designed for ease of use with super trees; based on *nodal distance*
NTI (Nearest Taxa Index)	Webb (2000)	Mean of the smallest *nodal* distance for each present species with between it and it's nearest neighbour, scaled by the greatest possible mean for that dataset, all subtracted from 1	Designed to be a more 'local' measure when compared with *NRI* (Webb, 2000)
NRI (Net Relatedness Index)	Webb *et al.* (2002)	The negation of the mean pairwise *phylogenetic* distance between members of a community subtracted from the mean phylogenetic distance under null randomisations, scaled by the standard deviation of those null randomisations	
NTI (Nearest Taxa Index)	Webb *et al.* (2002)	The negation of the mean of the smallest *phylogenetic* distance for each present species with between it and it's nearest neighbour, subtracted from the mean smallest phylogenetic distance under null randomisations, scaled by the standard deviation of those null randomisations	Designed to be a more 'local' measure when compared with *NRI* (Webb *et al.*, 2002)

Measure	Reference	Description	Notes
SES_{MPD} (Standardised Effect Size of Mean Phylogenetic Distance)	Kembel (2009)	The negation of *NRI* (Webb *et al.*, 2002)	
SES_{MNTD} (Standardised Effect Size of Mean Phylogenetic Distance)	Kembel (2009)	The negation of *NTI* (Webb *et al.*, 2002)	
INND/*MIPD* (Inverse Nearest Neighbour Distance/Mean of Inverse Pairwise Distances)	Ness *et al.* (2011)	As *NRI*/*NTI* (Webb *et al.*, 2002), but using the *inverse* of phylogenetic distance.	Assumes nonlinear relationship between ecological and phylogenetic distance

Table 2.4: The *NRI* family of dispersion measures. All these measures can be calculated according to the mean distance among individuals, and there is no precedent in the literature for distinguishing between these definitions using different names. Other dispersion measures are described in table 2.5.

Measure	Reference	Description	Notes
Δ^+ (taxonomic distinctiveness index)	Warwick (1995)	Essentially Δ (Warwick, 1995) divided by the value of Δ given the simplest possible taxonomic structure (all species in the same genus)	More complex null models could be used for comparison
'Dispersion Regression'	Cavender-Bares *et al.* (2006)	Species pairs' (often co-occurring and not co-occuring) phylogenetic distances are plotted against ecological similarity and compared with a null expectation	Assess ecological and evolutionary models simultaneously
PAE (Phylogenetic Abundance Evenness)	Cadotte *et al.* (2010)	A scaled measure of the product of species frequency and each species' terminal branch length	Significance assessed by permutation
D	Fritz & Purvis (2010)	Sum of differences in independent contrasts of species' presence/absence, scaled according to random and Brownian expectation	See chapter three for a discussion of its scaling and sensitivity
D_C	Chapter five	As D, but with a continuous variable	

Table 2.5: Phylogenetic *dispersion* measures. Names in inverted commas are the author's invention; note that the '*NRI* family' are described in table 2.4.

Measure	Reference	Description	Notes
P Test	Maddison & Slatkin (1991); Martin (2002)	Compares distribution of sequences unique to each community within the phylogeny and compares the number of evolutionary transitions required for this distribution with a null model	Adapted from the cladistic literature by Martin and based on parsimony, which is often not how the phylogenies themselves were generated
Γ^+	Izsak (2001); Clarke *et al.* (2006)	Mean of the smallest taxonomic distances between species in each sample	Can be shown to be related to the Bray-Curtis index
Θ^+	Clarke & Warwick (1998); Clarke *et al.* (2006)	As Γ^+, but each samples minimum distances are kept listed separately and then averaged	Can be shown to be related to the Bray-Curtis index
Δ_C	Singleton (2001)	Compares curves of number of unique sequences within a sample against a cut-off for sequence dissimilarity	Designed for bacterial systems and rRNA
UniFrac	Lozupone & Knight (2005)	The fraction of total branch length that two communities share. Can thus create a distance matrix for all communities to which one can apply multivariate statistics	Widely used by the microbiological community, but ignored by the wider ecological community. In some ways a generalisation of *PD*
PCD	Ives & Helmus (2010)	An extension of *PSV* (Helmus *et al.*, 2007) that partitions dissimilarity into phylogenetic and non-phylogenetic components	

Table 2.6: Phylogenetic *dissimilarity* measures.

2.4 Over-arching issues

Phylogeny construction

The structure of a phylogeny is as important as the ecological data it is used to analyse. It is beyond the scope of this review to suggest how phylogenies can be accurately constructed, but any phylogeny used should have branch lengths proportional to time. Some may debate community phylogenetics' implicit assumption that evolutionary divergence is proportional to ecological divergence, but fewer would argue the number of mutations at a limited number of genetic loci, which is the alternative, is ecologically relevant. Few (if any) phylogenies are perfect, and collapsing poorly supported clades and posterior predictive methods (reviewed in Bollback, 2005) can be used to investigate the dependence of results on a particular phylogenetic topology.

Some of the above methods can use taxonomies or DNA distance matrices as well as phylogenies. Methods based on taxonomy assume that dissimilarity scales predictably with taxonomic rank, which may not be appropriate if species are delimited according to morphological details such as sexual organ structure. Use of distance matrices based on DNA distance data assume, like a phylogeny not scaled according to divergence time, that divergence of that DNA is related to ecological function.

Making a phylogeny is difficult, so many use the program `Phylomatic` (outlined in figure 2.1; over 190 citations on `Web of Knowledge`; Webb & Donoghue, 2005) to produce a community phylogeny based on the taxonomy of their study species and a reference phylogeny. While the approach is extremely powerful, great care must be taken over the following aspects:

- Topological Accuracy
  Beyond the obvious point that the reference phylogeny must be a reasonably well-supported hypothesis, the way species are grafted into the phylogeny can cause problems. While *NRI* may be fairly robust to deep polytomies introduced at and above the family-level (Swenson, 2009), the same may not

be true of terminal polytomies (particularly when assessing overdispersion), or for other measures.

- Dating Accuracy
  Spacing undated nodes equally between dated parts of a phylogeny (the `bladj` algorithm; Webb & Donoghue, 2005) is a fair guess, but it can produce incorrectly dated trees (Ricotta *et al.*, 2012). Figure 2.1 shows how `Phylomatic` can systematically introduce errors into its output.

- Taxonomic Certainty
  Many reference phylogenies use only one representative of each genus; if this genus is no longer thought to be monophyletic, or the genus undergoes taxonomic revision, that reference phylogeny may not be appropriate for that study system. This may not be a common an issue, but the black-box use of any phylogeny without checking its provenance leaves a study open to it. Note that, since the publication of the Davies *et al.* (2004) angiosperm phylogeny bundled with `Phylomatic`, there has been a major revision of angiosperm taxonomy APG III (2009).

An alternative to `Phylomatic` that automatically creates phylogenies for ecologists using DNA sequence data (with estimates of phylogenetic uncertainty; `phyloGenerator`) is described in chapter six.

Null models and scaling

Ecologists have long been aware that their choice of null model can determine the outcome of their study (reviewed in Gotelli, 2000), and this is reflected in the wide variety of options available when calculating SES_{MPD} in `Picante` (Kembel *et al.*, 2010). Ignoring the other issues I will raise in chapter three, SES_{MPD} and SES_{MNTD} values cannot easily be compared among studies because the choice of null distribution determines their absolute value. Thus it is difficult to conduct a meta-analysis of phylogenetic dispersion, and Vamosi *et al.* (2009) were forced to simply count how many studies were phylogenetically clustered, overdispersed, and random.

This is indicative of a more general problem: the scaling of community phylogenetic measures. Taking another example, *PSE* (Helmus *et al.*, 2007) is constructed using *PSR*, which is intended to be a measure of phylogenetic shape, such that any *PSE* value is a function of both phylogenetic shape and diversity, and thus not easy to compare among study systems. To compare among study systems, a measure must be scaled according to phylogenetic structure, but what one means by structure varies among measures. The randomisations of SES_{MPD} are intended to control for phylogenetic structure, and in a sense they fail because they do so too well: figure 2.2 shows how SES_{MPD} is not affected by phylogenetic transformation, unlike *D*. Which is the most appropriate form of scaling will depend on the question being asked.

Traits

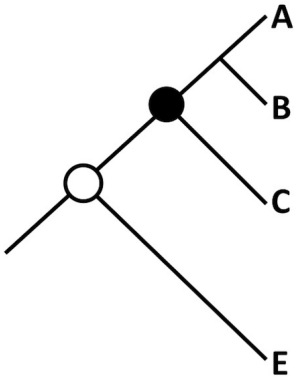
Community phylogenetic methods often invoke niche conservatism to explain their patterns (some would say erroneously, see Mayfield & Levine, 2010), and so it is surprising that there are relatively few methods that allow the direct comparison of phylogenetic and trait data. Important exceptions are Ives & Helmus (2011), who explicitly compare the ability of phylogenetic and trait data to predict assemblage composition, and Pillar & Duarte (2010), who correlate matrices of phylogenetic and trait data to understand meta-community dynamics. Neither method calculates anything that can satisfyingly be called a dispersion measure (and are no worse for that), but as both methods examine the correlation between species' phylogenetic distance and their likelihood of community presence, neither can detect overdispersed phylogenetic structure.

More fundamentally, by comparing which of phylogenetic or trait data best explain assemblage structure, both methods seem based around the idea that phylogenetic data can be replaced by some combination of trait data, or vice-versa. I think the use of detailed environmental, trait, and phylogenetic data to examine competing models of ecological assembly processes that incorporate *interactions* between ecological and evolutionary processes (e.g., Rabosky *et al.*, 2011) would be more interesting.

2.5 Recommendations

There is unlikely to be a single 'best' community phylogenetic measure, but a few simply pieces of advice can be given:

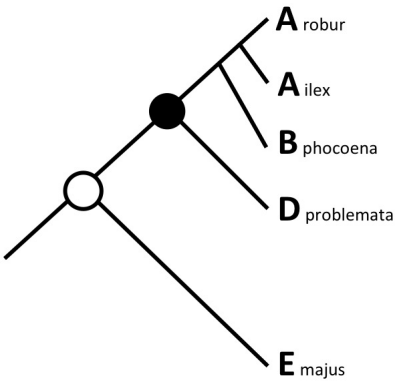
- Comparing assemblages on the basis of diversity or shape measures requires careful consideration of null distributions.
- Use D (Fritz & Purvis, 2010) and D_C when examining phylogenetic dispersion; D is more sensitive than alternatives (chapter three), and D_C is sensitive to overdispersion (chapter six).
- Use the *PCD* family (Ives & Helmus, 2010) when comparing assemblages; it distinguishes between the effect of phylogeny and species identity.
- Compare assemblages' phylogenetic and trait structures. Check trait data for phylogenetic inertia, for example with Pagel's λ (Pagel, 1999; Freckleton *et al.*, 2002) or Blomberg's K (Blomberg *et al.*, 2003).



(a) Reference phylogeny

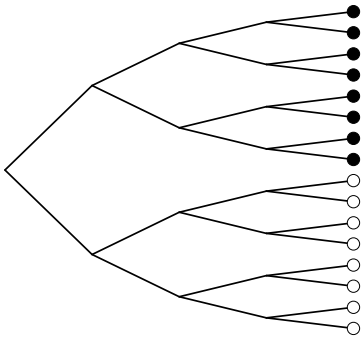
Family	Genus	Species
●	A	robur
●	A	ilex
●	B	phocoena
●	D	problemata
○	E	majus

(b) Community list

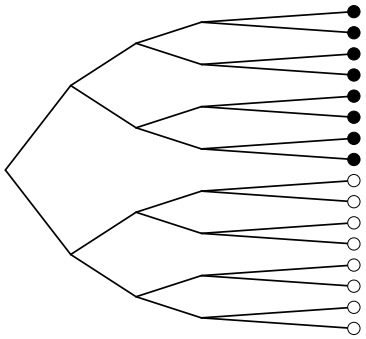


(c) Phylomatic's resulting phylogeny

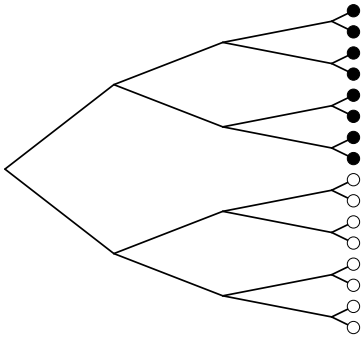
Figure 2.1: How Phylomatic generates a community phylogeny. (A) shows the 'reference' phylogeny, whose structure is used to turn the species list (b) into a phylogeny (c). First, genus C is not in the community list, so it is removed from the reference phylogeny. Next, because genus D is not in (a), but representatives of its family (●) are, genus D is added at the age of the ● family. This inappropriately that implies the divergence order of the A, B, and D genera are known. Two representatives of genus A are present, and so an additional clade is added, with the node (following the `bladj` algorithm) halfway between the presumed date of genus 'A' In the phylogeny: the present (time zero) and the split between genera A and B.



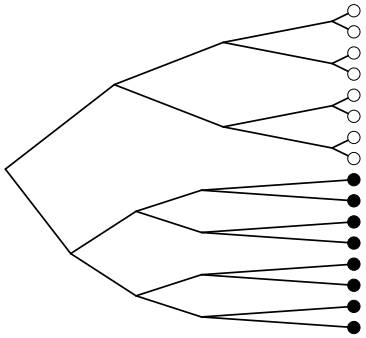
(a) Equal branch lengths. $MPD = 6.57$, $SES_{MPD} = 0.46$, $D = -0.62$



(b) $\lambda = 0.75$. $MPD = 6.93$, $SES_{MPD} = 0.44$, $D = -1.41$



(c) $\lambda = 1.25$. $MPD = 6.21$, $SES_{MPD} = 0.44$, $D = 0.01$



(d) Mixture of $\lambda = 0.75$ and $\lambda = 1.25$. $MPD = 6.57$, $SES_{MPD} = 0.42$, $D = -0.41$

Figure 2.2: Phylogenetic transformation and the scaling of phylogenetic dispersion. (A) shows a phylogeny with equal branch lengths (all set to 1), (b) and (c) the same phylogeny with λ (Pagel, 1999) transformations of 0.75 1.25 respectively, and (d) half of (b) and (c) bound together. Filled circles represent species that are present in an assemblage, clear circles absent species. Note how SES_{MPD} values (calculated under the 'richness' null model) are invariant to profound changes in structure, whilst D, which is scaled according to an evolutionary null model, is not.

Chapter 3

Barro Colorado Island's phylogenetic assemblage structure across fine spatial scales and among clades of different ages

3.1 Abstract

Phylogenetic analyses of assemblage membership provide insight into how ecological communities are structured. However, despite the scale-dependency of many ecological processes, little is known about how assemblage and source pool size definitions can be altered, either alone or in concert, to provide insight into how ecological diversity is maintained. Moreover, while studies have acknowledged that different clades within an assemblage may be structured by different forces, there has been no attempt to relate the age of a clade to its community phylogenetic structure. Using assemblage phylogenies, and spatially-explicit data on trees from Barro Colorado Island (BCI), I show that larger assemblages, and

assemblages with larger source pools, are more phylogenetically clustered. I argue this reflects competition, the influence of pathogens, and chance assembly at smaller spatial scales, all operating within the context of wider-scale habitat filtering. While the commonly used measure SES_{MPD} is unable to detect these differences, a community phylogenetic measure that is based on a null model derived explicitly from trait evolution theory, D, is. I also detect a moderate tendency for increased phylogenetic clustering in younger clades, which suggests coarse analyses of diverse assemblages may be missing important variation among clades. These results emphasise the importance of spatial and phylogenetic scale in community phylogenetics, and show how varying these scales can help to untangle complex assembly processes.

3.2 Introduction

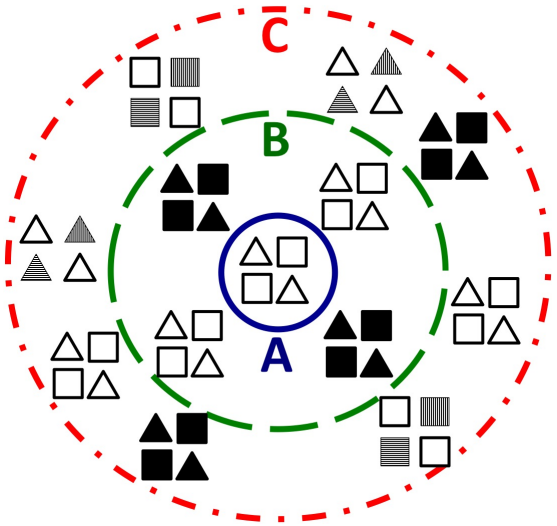
A major challenge for ecology is to understand how abiotic, biotic, and stochastic factors interact to filter a source pool of potential colonists down to an ecological assemblage (Vellend, 2010), and to understand the spatial and temporal scales at which these processes operate (Levin, 1992). This is driven, in part, by a need to explain how it is possible for so many species to coexist in highly diverse regions such as tropical forests. Among the theories that explain the maintenance of high diversity in tropical forests are Janzen-Connell effects (Janzen, 1970; Connell, 1971), the intermediate disturbance hypothesis (Connell, 1978), stochastic drift (Hubbell, 2001), and niche partitioning along environmental gradients (Schoener, 1974). Most ecologists would acknowledge that it is unlikely any single process can explain highly diverse assemblages, and that separating their relative contributions is difficult.

Community phylogenetic studies typically assess these processes within an evolutionary context by asking how closely related species within an assemblage are, given a list of species that could plausibly be in that assemblage (the 'source pool') (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009). Thus, under the assumption of niche conservatism (reviewed in Wiens *et al.*, 2010), niche

partitioning and habitat filtering produce phylogenetic clustering. In contrast, interspecific competition, and lineage-specific pathogens (e.g., Gilbert & Webb, 2007; Goßner *et al.*, 2009) are expected to lead to phylogenetic overdispersion, and stochastic neutral processes to random phylogenetic structure. By changing the spatial scale (size) of our definition of assemblage (Swenson *et al.*, 2007; Kraft & Ackerly, 2010) or source pool (Kembel & Hubbell, 2006; Swenson *et al.*, 2006; Webb *et al.*, 2006; Lessard, 2012), community phylogenetic studies can detect the spatial scales over which these processes that create phylogenetic structure operate. However, to my knowledge no study has examined the effect of varying both the size of an assemblage and its source pool simultaneously, which is likely to be important if the relevant spatial scales of assembly processes are to be dissected and fully understood.

Assemblage and source pool size can influence the inference of community phylogenetic patterns (figure 3.1). Consider a small assemblage with a source pool defined by its immediate neighbours (case *1* in figure 3.1). Case *1* is phylogenetically overdispersed: its members are less closely related to each other than would be expected given chance assembly from its source pool. However, the same assemblage in the context of a larger source pool (case *2*) is more phylogenetically clustered. Its members are now more closely related to each other than would be expected, because the source pool contains more habitat types and the clades adapted to them. This pattern of phylogenetically conserved habitat preferences is commonly found (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2006; Willis *et al.*, 2010; Lessard, 2012). Source pools are often defined using species' range data, but finer-scale data allow us to define source pools that highlight smaller-scale environmental variation and account for dispersal limitation.

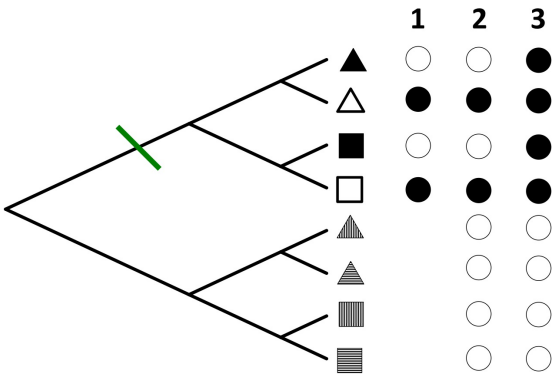
There is an interplay between source pool and assemblage definitions, and in case *3* (figure 3.1) a larger assemblage within the larger source pool is the most strongly phylogenetically clustered case of all. Simultaneously varying the spatial scale of assemblage and source pool can be more informative, and is so in this case because the source pool now contains those species that have a higher probability of dispersing propagules locally into an assemblage. In this case, we have isolated the local neigbourhood of plants' interactions by increasing the size of



(a) Species' Distributions

Case	Assemblage	Source Pool
1	A	B
2	A	C
3	B	C

(b) Assemblage Definitions



(c) Phylogeny

Figure 3.1: The two components of spatial scale. (a) shows the distributions of eight species in space, with three concentric circles used to delimit the assemblages defined in (b). (c) shows the phylogeny of those species, and has three columns to its right for each of the assemblages in (b). In each column, species present in an assemblage's source pool have open circles, while species also present in that assemblage have closed circles. These assemblages are referred to and described in the text.

the assemblage beyond the scale at which competition, lineage-specific pathogens, and stochasticity are detectable. Assemblage size often receives little attention (but see Swenson *et al.*, 2006; Lessard *et al.*, 2009), perhaps because when considering a smaller assemblage the necessarily smaller number of species results in a decrease statistical power (Heard & Cox, 2007).

In recognising that an increase in source pool size can increase the number of clades and lead to phylogenetic clustering, we implicitly acknowledge that the phylogenetic scale (the age of the clade) across which we are calculating dispersion values has changed. For example, if case *2*'s dispersion value were calculated across the clade marked on figure 3.1c in green, that value would be equal to that of case *1*. This assemblage has not been formed by one process; local-scale competition has taken place within the context of wider habitat-filtering, and the different results at different phylogenetic scales reflect this. Using a phylogeny containing all species in a given source pool assumes that processes act identically throughout that phylogeny; yet researchers look for influential clades (e.g., Parra *et al.*, 2010), and acknowledge different patterns of trait evolution across different phylogenetic scales (e.g., Ackerly *et al.*, 2006; Uyeda *et al.*, 2011). Greater phylogenetic clustering in higher taxonomic groups has been found in a meta-analysis (Vamosi *et al.*, 2009), but it is unknown whether this holds within a single community.

The 50 hectare (ha) forest dynamics plot on Barro Colorado Island (BCI; Panama) offers a unique opportunity to study spatial processes, as the locations and species' identities of all individuals greater than 1 cm in diameter at breast height within it are known (Condit, 1998; Hubbell, 1999; Hubbell *et al.*, 2005). BCI has well-documented spatial variation in density dependence (Comita *et al.*, 2010), spatial aggregation (Condit *et al.*, 2000), and dispersal ability (Muller-Landau *et al.*, 2008). In addition, small-scale variation in habitat and soil types (Harms *et al.*, 2001; John *et al.*, 2007) and variation in phylogenetic dispersion across these habitat types (Kembel & Hubbell, 2006; Kress *et al.*, 2009; Schreeg *et al.*, 2010) has been described. Yet previous community phylogenetic studies in BCI have found no relationship between assemblage size and phylogenetic dispersion (Kembel & Hubbell, 2006; Swenson *et al.*, 2007), and have found relationships between

source pool size and dispersion only at regional scales (Swenson *et al.*, 2006).

Here, I evaluate the effect of spatial scale on phylogenetic structure by simultaneously varying the focal assemblage size and the size of the source pool from which the assemblage is drawn. I use a recently proposed measure of trait dispersion (D; Fritz & Purvis, 2010) that scales the observed measure of phylogenetic structure with simulated expectations under a null model based on an explicit evolutionary process (Brownian evolution of an underlying trait) and random assembly. I find D is more sensitive to shifts in phylogenetic structure within BCI than a previously-used measure (SES_{MPD}, Kembel, 2009). I find evidence of increasing phylogenetic clustering in larger assemblages and assemblages with larger source pools across ecologically meaningful scales (i.e., measured in meters), and that younger clades are more phylogenetically clustered than one would expect from models of random assembly.

3.3 Methods

Ecological data

The BCI community data are freely available online (Hubbell *et al.*, 2005), and were described in detail by Hubbell (1999). In brief, the data consist of the location (to within 10 cm) and species identity of every woody plant with a stem diameter $\geqslant$ 1 cm at breast height within the entire 50 ha plot. Data on plants recorded as alive during the 2005 survey were downloaded and used for analysis. I split the dataset into continuous (but not overlapping) circular assemblages, with concentric source pool circles around them (see figure 3.2 and table 3.1), but used the entire species list for the 'global source pool' results. Thus each assemblage had a list of species that made up its source pool, and for each of those species a binary variable indicated its presence or absence in that assemblage. Note that assemblages on the edge of BCI often have their source pools cut by the edge of the plot. Since measures of phylogenetic community structure are uninformative for assemblages where presence or absence of species in an assemblage is is the

Assemblage Radius (m)	Source Pool Radii (m)
5	50, 100, all of study site
10	50, 100, all of study site
50	100, all of study site

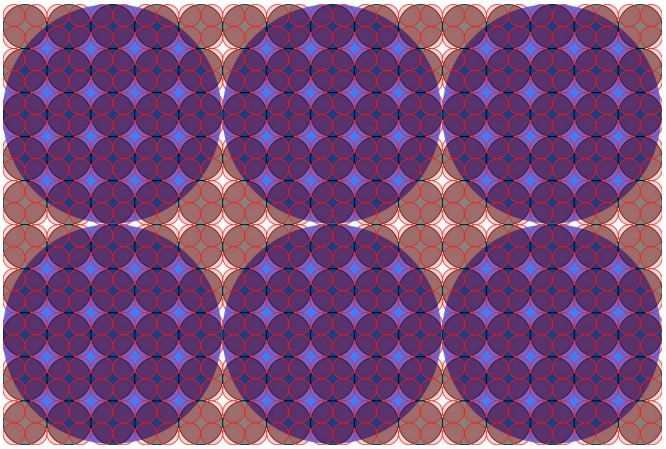
Table 3.1: Assemblage and source pool radii combinations used in these analyses. I define an assemblage as the list of species found within a particular circle, and its source pool as the list of species found within another concentric circle around that. References to the size of assemblages or source pools in the text refer to these circles' radii.

same for all, or all bar one, species in the source pool, I excluded the three such assemblages from this analysis.

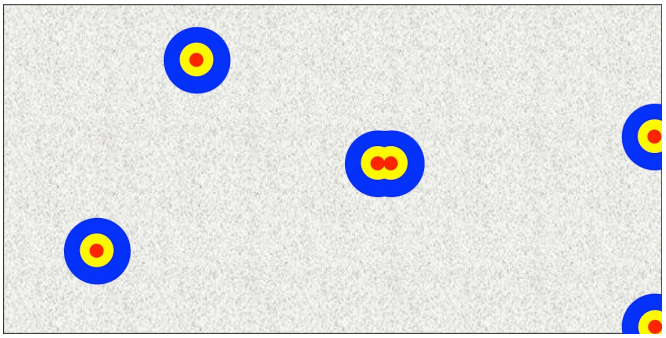
Phylogeny construction

Previous community phylogenetic studies have shown that results are sensitive to the phylogenetic structure of their source pool phylogeny (Kress *et al.*, 2009; Swenson, 2009), but the most accurate complete phylogeny available (from Kress *et al.*, 2009) was missing some taxa, possibly introducing an ecological bias. Thus I used three different phylogenies: one modified from Kress *et al.* (the 'Kress phylogeny'; 2009), another taken from `Phylomatic` (Webb *et al.*, 2008) containing all the species in BCI but with less phylogenetic resolution (the 'Phylomatic phylogeny'), and finally one with only the species in the Kress phylogeny but with the resolution of the Phylomatic tree (the 'control phylogeny').

The Kress phylogeny was not ultrametric, a possible source of error as its branch lengths were proportional to the rate of evolution at the three loci used to construct it. To make the tree's branch lengths proportional to divergence times, I rate-smoothed it using the Penalised-Likelihood method of Sanderson (2002) as implemented in `r8s` (Sanderson, 2003) with its `Powell` algorithm, under the constraint that the root age was 1. The smoothing parameter of 0.1 was derived from cross-validation across six possible parameter values (0.1, 1, 10, 100, 1000 and 10000). The final solution was found after twenty sets of perturbations with nudging parameters of 0.05 and 0.1, and had a flat solution gradient.



(a) Assemblage Definitions



(b) Source Pool Definitions

Figure 3.2: Assemblage and source pool definitions. (a) is to scale but not of the whole site, and shows how the assemblages (5m, 10m and 50m radius circles in red, black and blue, respectively) are nested within each other. (b) is to scale and of the entire study site, and shows a 10m radius assemblage (the black circle) and three possible source pools around it: 100m and 200m radius circles (in yellow and blue respectively) and all the study site (the speckled box surrounding them all). Note that in some cases the circular source pools are cut by the limits of the BCI plot, which was accounted for in the analyses (see text).

The Phylomatic phylogeny was made with `Phylomatic` (Webb *et al.*, 2008) using the Davies *et al.* (2004) phylogeny as a reference. The control phylogeny was created in the same way, but using only those species also present in the Kress phylogeny. All three phylogenies are shown in the supplementary materials.

Choice of dispersion metric

There are currently many measures of community phylogenetic dispersion, but no general consensus as to which is the best (but see Kembel, 2009; Vellend *et al.*, 2011, for reviews). A dispersion metric should be sensitive to both under- and over-dispersion, and scaled such that it is comparable between study systems. Ideally, its observed values should be comparable with null distributions that are relevant to the questions of a study. I used two metrics: SES_{MPD} (Kembel, 2009) and D (Fritz & Purvis, 2010).

SES_{MPD} (Kembel, 2009) is perhaps the most commonly-used measure of phylogenetic dispersion, and is directly related to the popular NRI measure (Webb *et al.*, 2002). It is known to have difficulty detecting strong phylogenetic clustering (Kembel, 2009), and below I describe how it can perform poorly when comparing among assemblages. As equation 3.1 shows, SES_{MPD} compares the observed Mean Phylogenetic Distance (MPD) with the mean value observed under some null hypothesis (MPD_{rnd}), correcting for the standard deviation of that mean ($SD_{MPD_{rnd}}$). This is intended to control for mean changes in phylogenetic structure, and in essence calculates a test statistic; SES_{MPD} can tell us when there has been a significant departure from a null distribution, but not the magnitude of that departure. By analogy, to assess the significance of differences in the means of two distributions one would divide that difference by its standard error to calculate a t-statistic, but there is no unique mapping of a t-statistic onto the differences in those means. Groups cannot be compared on the basis of test statistics, and so SES_{MPD} values cannot be compared between assemblages.

$$SES_{MPD} = -1 \times \frac{MPD - MPD_{rnd}}{SD_{MPD_{rnd}}} \tag{3.1}$$

D (Fritz & Purvis, 2010) offers an alternative that can compare dispersion values among assemblages. Originally proposed in another context, D is the only measure of phylogenetic dispersion based upon two null distributions: one in which community presence is phylogenetically random, and one in which it is determined by the value of an underlying continuous variable that evolves along the branches of a phylogeny by Brownian motion. I consider this a better way to control for phylogenetic structure; while SES_{MPD} averages out phylogenetic structure once its null distributions have been constructed, D incorporates phylogenetic structure when generating its Brownian null model.

A full account of D is available in Fritz & Purvis (2010), and it is defined in equation 2. Briefly, the method is based on the calculation of phylogenetically independent contrasts (Felsenstein, 1985), whereby each node in a phylogeny is valued according to the mean of its descendent nodes, these having been weighted according to the lengths of the branches leading to them. These calculations are performed once for the observed values, giving each species in the assemblage a value of 1 and those species absent from the assemblage but present in the source pool a value of 0; the sum of these observed contrasts is denoted d_{obs}. A maximally clumped trait will be in the same character state in all related species whereas a maximally overdispersed trait cannot, causing d_{obs} to be lowest for clumped communities and highest for overdispersed communities. Two random distributions are then generated, the first by permuting the observed values across the phylogeny and summing its contrasts (to obtain d_r). For the other, the evolution of many continuous traits are simulated along the phylogeny under Brownian motion, a threshold applied to each trait to produce a series of binary traits with the same prevalence as the observed community presences (a Brownian threshold model; Felsenstein, 2005), and the contrasts again summed to obtain d_b. D is therefore independent of the shape and size of the phylogeny. D values greater than one, lesser than one, or lesser than zero, indicate greater than random, less than random, or less than expected under a Brownian model of trait evolution, levels of phylogenetic dispersion respectively.

$$D = \frac{\sum d_{obs} - mean(\sum d_b)}{mean(\sum d_r) - mean(\sum d_b)} \tag{3.2}$$

Analysis

All analyses were conducted using `R` (R Core Team, 2012). For the spatial analyses, D values were calculated using the `phylo.d` function in the package `CAIC` (Orme *et al.*, 2009), while for the phylogenetic scale analyses I wrote the function `phylo.d.subsets` for the package `caper` (Orme *et al.*, 2011). SES_{MPD} values were calculated using the `ses.mpd` function in the package `picante` (Kembel *et al.*, 2010) under the `richness` null model. This null model is most similar to those of D and is appropriate for comparisons between assemblages with different source pools. The analyses were split into two parts: whether assemblage and source pool size affect phylogenetic dispersion (spatial scale), and the relationship between the age of a clade and its phylogenetic dispersion (phylogenetic scale).

Spatial scales

Mixed-effects models were used to account for spatial pseudo-replication and nestedness in D and SES_{MPD}, with assemblage and source pool size treated as fixed effects, and the nesting of the 50, 10, and 5 m circles fitted as random effects (using `lmer`; Bates & Maechler, 2010). While model estimates were computed under restricted maximum likelihood (REML), I compared models including assemblage and source pool size with null models containing only the random effect terms under maximum likelihood (ML), using likelihood ratio tests (LRT) and comparing models' AIC values.

I used quantile regressions (in `quantreg`; Koenker, 2011) to show whether assemblage and source pool size affect the distribution of D and SES_{MPD}, using the Frisch-Newton interior point method due to the large size of the dataset. I estimated the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} quantiles, and used the 'rank' method to calculate their standard errors.

A separate analysis was performed, excluding those assemblages whose source pools were constrained by the edge of the plot, and using fewer quantiles in the quantile regression (the 25^{th}, 50^{th}, and 75^{th}) because there was less data. The results were qualitatively identical to those of the complete analysis, and

are presented in the supplementary materials. In addition, simulations looking at the distribution of D values in assemblages with very few species were performed. These show that D performs well in small assemblages (fewer than five species) and source pools (fewer than 25 species), and are presented in the supplementary materials.

Phylogenetic scale

The large number of clades in each phylogeny meant calculating dispersion values for all clades in all assemblages was not feasible. D values were thus calculated for a random subset of each assemblage size, picking 30 assemblages from each assemblage size or the total number of assemblages of that size, whichever was smaller. In total I chose 105 assemblages.

D has less statistical power in extremely small phylogenies (Fritz & Purvis, 2010), so clades containing fewer than 10 nodes were excluded from the analyses. As D's variance is greater in smaller clades it is difficult to make solid inferences about changes in dispersion across clade age, since I might expect younger clades to have fewer species. Thus the observed relationship between clade age and dispersion in each assemblage was compared with five random assemblages with the same number of, but randomly assigned, present species (525 in total).

I fitted a Generalised Least Squares (GLS) model with an exponential error structure based on clade age, and fixed effects of the interaction between clade age, whether the data were observed or simulated, and the assemblage from which the data were taken. While model estimates were calculated under REML, I compared this model under ML with a null model where dispersion was a function of clade age and its interaction with the assemblage from which the data were taken. Rejection of the null model, according to LRT and AIC values, indicates that phylogenetic dispersion was related to the phylogenetic scale across which it was calculated.

3.4 Results

Spatial scales

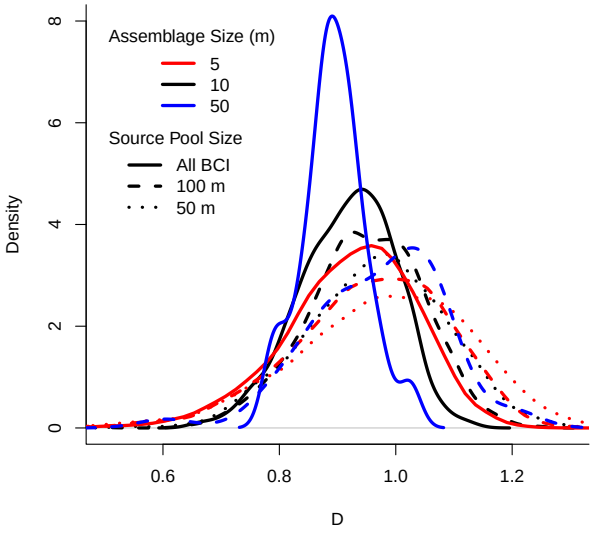
The results using each of the three phylogenies were qualitatively identical, and so the results from the Phylomatic and control phylogenies are presented in the supplementary materials. D values were lower in larger assemblages and assemblages with larger source pools, reflecting an increase in phylogenetic clustering (figure 3.3a). SES_{MPD} values do appear to significantly depart from zero (tables 3.2 and 3.3b), but their departures showed no systematic pattern with regard to assemblage or source pool size (figure 3.3b).

Mixed-effects models support an increase in phylogenetic clustering in larger assemblages and source pools, albeit with small effect sizes (table 3.2). The upper bounds of the D distributions increase in smaller assemblages and source pools, with a reasonable proportion of their values being greater than 1, while the lower bounds remain relatively constant. Quantile regressions statistically support these distributional changes, and generally show larger effects sizes than the mixed effects models (table 3.3a). However, they do not show a systematic effect of spatial scale on SES_{MPD} (table 3.3b).

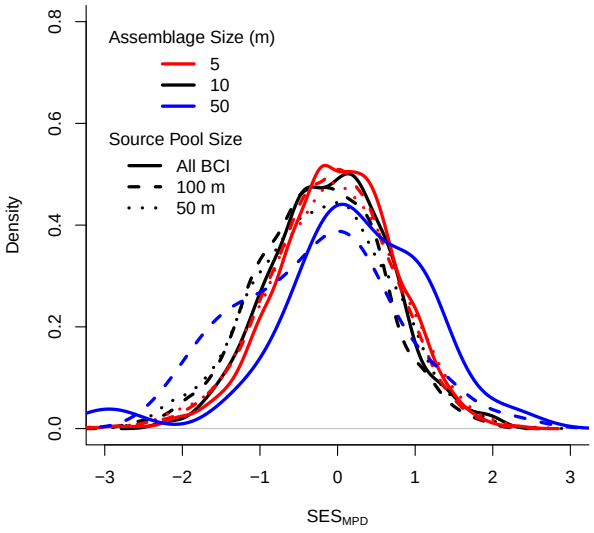
Phylogenetic depth

There is a negative relationship between variance and clade age in both the simulated and observed assemblages, as expected (figure 3.4). In the Kress phylogeny each assemblage's linear slope of D against clade age is greater in the observed data than the simulated, supporting a (modest) tendency for more phylogenetic clustering in younger clades (figure 3.5a). This trend is not present in the Phylomatic and control phylogenies (figure 3.5b). Note the scales of the plots in figure 3.5 are very different, and that the slope estimates come from the GLS models reported below.

For the Kress phylogeny, a GLS fitting separate slopes and intercepts for observed



(a) D



(b) SES_{MPD}

Figure 3.3: Smoothed density plots of D and SES_{MPD}. In (a), smaller assemblages and source pools have greater D values, consistent with a shift from assemblages dominated by phylogenetic clustering, to assemblages dominated by phylogenetic overdispersion and random assembly. However, in (b), there is no shift in dispersion value according to assemblage size or source pool size. See text for details. The legend is common to both sub-figures, and is split across the two.

Assemblage	Source Pool	D	SES_{MPD}
5	50	0.98 ± 0.0059	-0.05 ± 0.0247
5	100	0.95 ± 0.0059	-0.08 ± 0.0247
5	All BCI	0.92 ± 0.0059	0.02 ± 0.0247
10	50	0.97 ± 0.0083	-0.17 ± 0.0369
10	100	0.95 ± 0.0083	-0.21 ± 0.0369
10	All BCI	0.92 ± 0.0083	-0.04 ± 0.0369
50	100	0.97 ± 0.0160	-0.17 ± 0.0977
50	All BCI	0.89 ± 0.0160	0.29 ± 0.0968

Table 3.2: Mixed effects models of D and SES_{MPD} values across BCI. Estimates of mean values (± SE) for each assemblage/source pool combination, with a different table for each dispersion measure, subdivided within each table according to the phylogeny used. Smaller assemblages and source pools have greater D values. D (AIC — -27732 vs. -26643; p-value of likelihood ratio test < 0.0001) and SES_{MPD} (AIC — 39861 vs. 39997; p-value of likelihood ratio test < 0.0001) models showed statistically significant effects of source pool and assemblage size when compared with a null model containing neither variable.

and simulated assemblages fits the data significantly better than a model where they had the same slopes (AIC — 4072.41 vs. 4360.03; p-value of likelihood ratio test < 0.0001). While the same was true of the Phylomatic (AIC — 2299.26 vs. 2278.93; p-value of likelihood ratio test < 0.0001) and control phylogenies (AIC — 2329.09 vs. 2281.08; p-value of likelihood ratio test < 0.0001), the differences in AIC values are much smaller.

3.5 Discussion

I have presented evidence that larger assemblages and assemblages with larger source pools are more phylogenetically clustered. This suggests a model of ecological assembly where competition and chance colonisation take place in the context of wider-scale habitat filtering. While these patterns are common in community ecology, this is the first demonstration of the simultaneous and opposing influences of assemblage and source pool definition on phylogenetic community structure. This explanation is contingent on niche conservatism, but tree functional traits

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
5	50	0.78	0.88	0.99	1.09	1.16
5	100	0.78	0.87	0.97	1.05	1.12
5	All BCI	0.77	0.85	0.93	1.00	1.06
10	50	0.81	0.89	0.97	1.05	1.12
10	100	0.82	0.88	0.95	1.02	1.07
10	All BCI	0.81	0.86	0.92	0.98	1.02
50	100	0.81	0.86	0.89	0.92	0.96
50	All BCI	0.82	0.89	0.98	1.04	1.09
Range		0.05	0.04	0.10	0.17	0.20

(a) D Values

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
5	50	-1.14	-0.62	-0.05	0.50	0.98
5	100	-1.10	-0.61	-0.07	0.43	0.89
5	All BCI	-0.98	-0.50	0.00	0.51	0.96
10	50	-1.29	-0.80	-0.18	0.39	0.87
10	100	-1.24	-0.80	-0.23	0.31	0.70
10	All BCI	-1.05	-0.59	-0.07	0.43	0.83
50	100	-1.58	-0.93	-0.16	0.35	1.08
50	All BCI	-0.91	-0.27	0.20	0.91	1.25
Range		0.67	0.66	0.43	0.60	0.55

(b) SES_{MPD} Values

Table 3.3: Quantile regression of D values across BCI. Estimates for each of the five measured quantiles (τ stands for 'quantile') of the distributions of D values in each of the three phylogenies. Note the range of estimates (given in the final row of each table) is greater for higher quantiles of D, but not SES_{MPD}. Standard errors are shown in the supplementary materials.

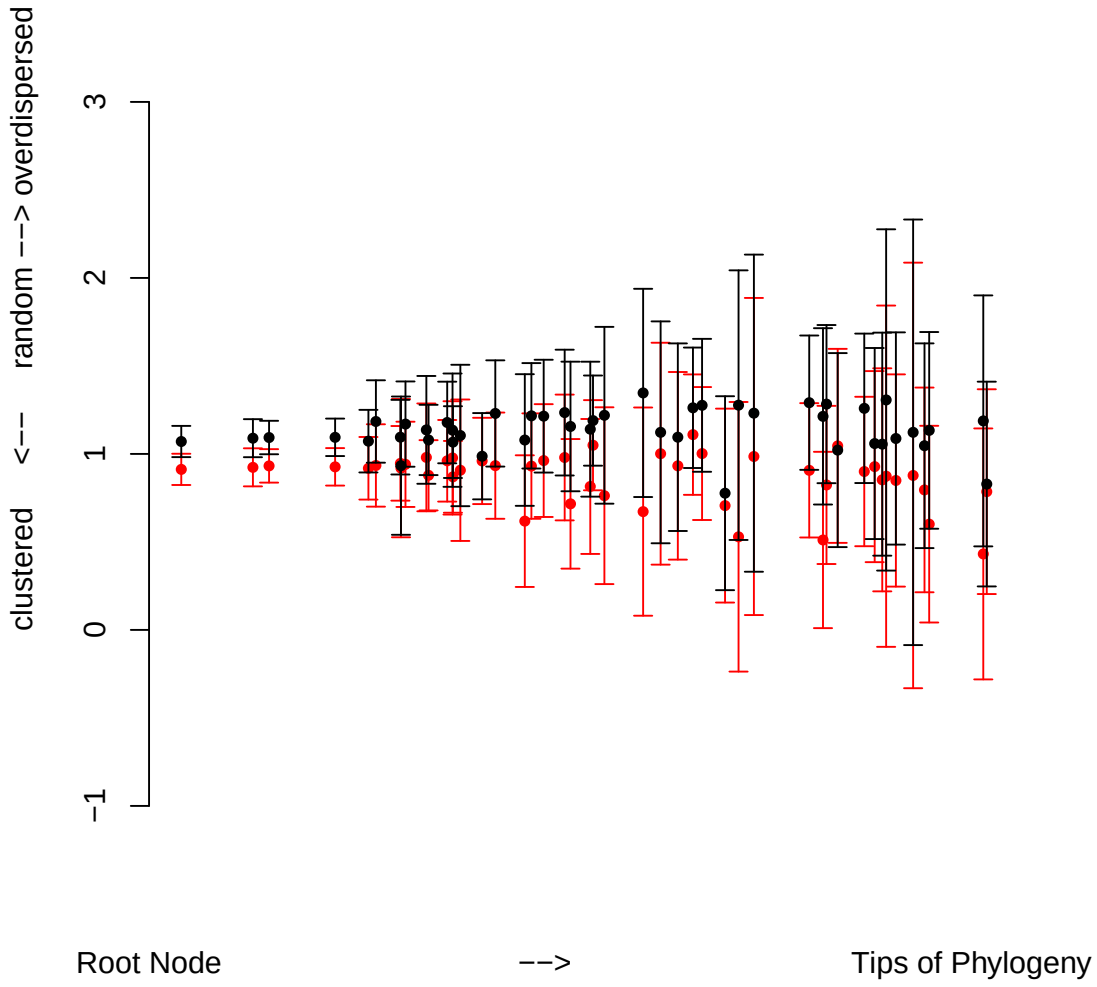
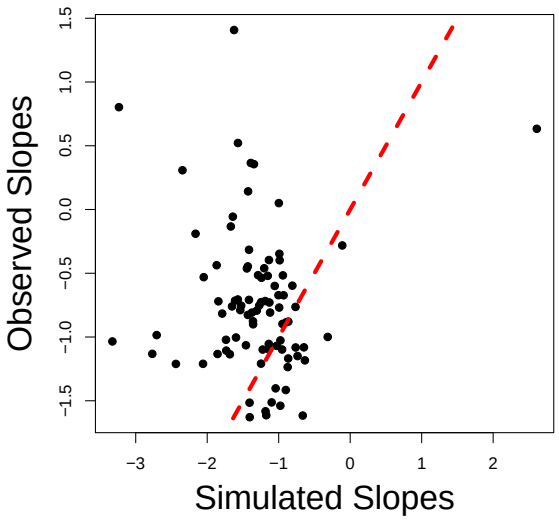
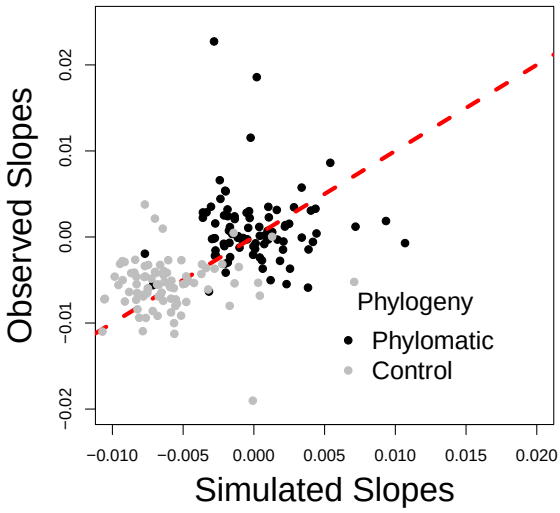


Figure 3.4: Phylogenetic depth plots of D for the observed and simulated assemblages in the Kress phylogeny. The randomised assemblages are plotted in black, the real data in red. Each circle represent's a clade's median values, and error bars represent the standard deviations of the data. The differences between the two distributions are slight, but a tendency for lesser D values in the observed is noticeable, as is the predicted decrease in variance with clade age.



(a) Kress Phylogeny



(b) Phylomatic and control Phylogenies

Figure 3.5: Plot of observed and simulated slopes for regressions of D on clade age. The red dashed line passes through the origin with a slope of 1 (the null expectation). That so many of the Kress phylogeny's observed slopes are greater than the simulated slopes suggests more phylogenetic clustering in younger clades in BCI, even accounting for the increase in variance in younger clades (a). This pattern is not detectable in the Phylomatic and control phylogenies (b), which also do not appear to demonstrate much of a trend in either the simulated or observed slopes. Note that the scales are very different for the two figures.

are known to be phylogenetically conserved in BCI (Swenson *et al.*, 2007). Thus phylogenetic distance is plausibly related to ecological distance, suggesting that phylogenetic clustering reflects habitat filtering; overdispersion reflects competition or lineage-specific pathogens, and that random structure reflects stochastic drift or a mixture of clustering and overdispersion. In addition, I show that younger clades are weakly, but significantly, more phylogenetically clustered.

Spatial scale

Within the context of larger source pools, assemblages are more phylogenetically clustered. While the effect sizes in my mixed effects models may seem small, fitting a level of the random effect term for each five, ten, and fifty meter assemblage is an extremely conservative way of dealing with spatial autocorrelation, and is likely to reduce the variation attributable to assemblage and source pool size. BCI's plant composition is known to vary with soil nutrients (John *et al.*, 2007), and there is documented community type variation (Harms *et al.*, 2001), so my result supports the idea that niche partitioning and habitat filtering may play a role in maintaining BCI's high diversity. Dispersal limitation might be expected to affect my results at scales beyond 100m, especially as this is beyond the mean dispersal distance of most species modelled by Muller-Landau *et al.* (2008). However, dispersal limitation should be random with respect to phylogeny: dispersal limitation reflects the chance spatial arrangement of individuals, and thus cannot be responsible for increases in phylogenetic patterning.

The greater overdispersion within smaller assemblages suggests that density dependent processes, including inter-specific competition and lineage-specific pathogens, may help maintain diversity within BCI. I are unaware of a BCI study that detects a shift in dispersion at spatial scales as fine as these (*c.f.* Swenson *et al.*, 2007; Kraft & Ackerly, 2010). Density-dependent recruitment is well-demonstrated within BCI (e.g., Harms *et al.*, 2000; Comita *et al.*, 2010), although distinguishing between competition and Janzen-Connell effects is difficult. Lineage-specific pathogens, which are within the spirit of the Janzen-Connell-hypothesis, have been found in BCI (Gilbert & Webb, 2007). Using only

these phylogenetic data, it is difficult to distinguish between competition and lineage-specific pathogens, and the widening of smaller assemblages' dispersal distributions in figure 3.3a makes it unlikely that the same processes are taking place in each assemblage. Indeed, the larger number of D values close to one in smaller assemblages would be consistent with neutral dynamics at smaller scales (Hubbell, 2001). Note that these results come from presence-absence data, so are not at odds with previous demonstration of intra-specific aggregation in BCI (Condit *et al.*, 2000).

It is unlikely that the overdispersion at finer scales is driven by facilitation between ecologically distinct, distantly related species (*sensu* Verdú & Valiente-Banuet, 2008; Verdú *et al.*, 2009). Facilitation is classically associated with severe environments, such as deserts and alpine regions (Brooker *et al.*, 2008), or where there is particularly high consumer pressure or physical stress (Bertness & Callaway, 1994); BCI is not such a system. Common mycorrhizal networks also facilitate growth between species, but usually operate across larger spatial scales than those in which overdispersion was observed (Selosse *et al.*, 2006) and so should not be driving patterns in only the smallest assemblages.

These results are unlikely to be an artefact of lower replication at high spatial scales; fifty 50 meter diameter assemblages is a reasonable level of replication for an ecological study. In addition, tests of dispersion values in smaller assemblages show that the fewer species in each smaller assemblage are unlikely to have biased the results (supplementary materials). Were the smaller assemblages' results entirely random, there would be no effect of source pool size on these assemblages. It is, however, worth noting that this study ignores below-ground diversity, which can be high in BCI (Jones *et al.*, 2011), and that plants can interact below ground over large spatial scales.

Choice of dispersion measure

In keeping with previous work on BCI (Swenson *et al.*, 2006), SES_{MPD} plots showed no consistent pattern across these fine spatial scales; D values, however, did. Additionally, D's spatial scale results were consistent across all three phylo-

genies, whereas there is no apparent pattern to SES_{MPD}, suggesting D was better at extracting signal from the BCI dataset. This may be because the detected differences were in the degree of phylogenetic clustering; D is based around an explicit model of phylogenetic similarity (the Brownian model), while SES_{MPD} detects overdispersion better than clustering (Kraft *et al.*, 2007).

Phylogenetic scale

The tendency for younger clades to show more phylogenetic clustering shows that the effect of phylogenetic scale is not restricted to meta-analyses. The trend is weak, but is unlikely to be a statistical artefact of the ecological data because it is absent from the Phylomatic and control phylogenies results, which are based on the same ecological data. While all three phylogenies had significant LRT, the difference in AIC between the models with the Kress phylogeny (288) is much greater than with the Phylomatic and control phylogenies (21 and 48, respectively), and figure 3.5 shows much more signal in the Kress results. This shows that there is evidence of a trend in the Kress phylogeny, but limited support for a trend in the other phylogenies.

I therefore argue that the more resolved Kress molecular phylogeny permits a more sensitive test. Stronger filtering among younger clades leads to the near-complete inclusion or exclusion of subclades from an area, resulting in clades that contain too little variation for us to assess their dispersion. While such clades will still influence dispersion values calculated in older (and so more inclusive) clades, identifying the age at which this takes place requires a bifurcating tree, hence the lack of power in the Phylomatic and control phyloenies.

A greater tolerance of close relatives in younger clades suggests, under niche conservatism, that younger clades may more finely partition their niche requirements, moving themselves out of direct competition with one another. If so, this relationship is likely to change depending on the cause of that clade's radiation: clades driven by ecological speciation, as opposed to species brought back in secondary contact after allopatric speciation, would likely have different dispersion-age relationships. This work is complementary to that of Parra *et al.* (2010), who showed

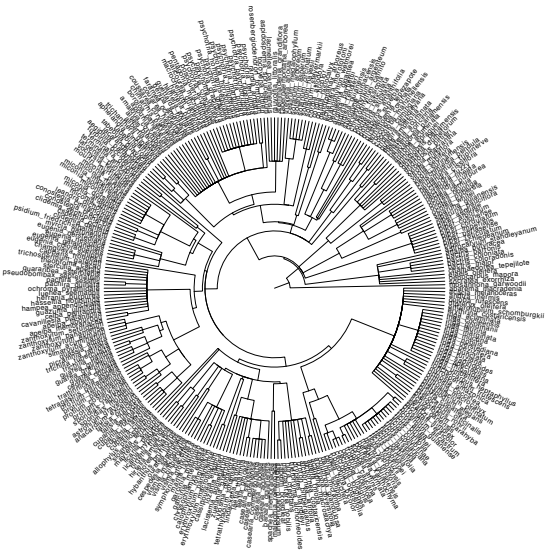
that particular clades can drive a dispersion value, and Schreeg *et al.* (2010), who found variation in clades' responses to soil and habitat types within BCI. For a particular clade to be different from the rest of the phylogeny necessarily implies variation amongst clades, and I extend their results by showing that filtering processes can extend throughout an entire community phylogeny, even increasing in strength in younger clades.

Conclusion

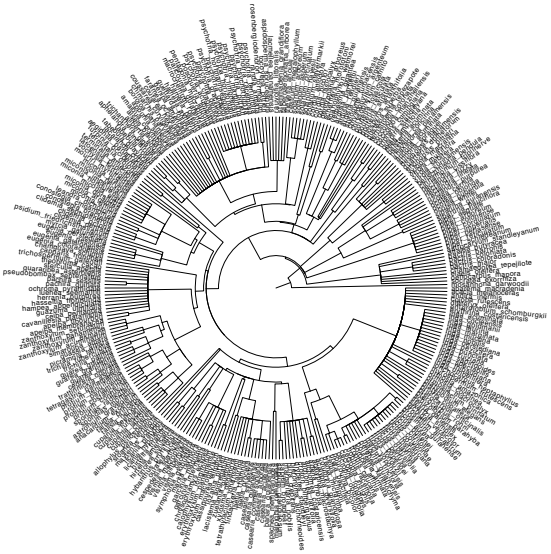
Ecologists delimit the communities they study both spatially and phylogenetically. That a single dispersion value for a single definition of assemblage or a single taxonomic delimitation of study species (e.g., 'the plants') does not capture the variation across all spatial scales community is unsurprising. However, it is likely that only well-resolved, molecular phylogenies will have the power to detect fine-scale phylogenetic scale effects. I have demonstrated that community phylogenetic tools have the power to pull apart the processes operating across spatial scales, but whether they hold across other systems and with other taxa is an open question.

3.6 Supplementary materials

(a) Kress phylogeny

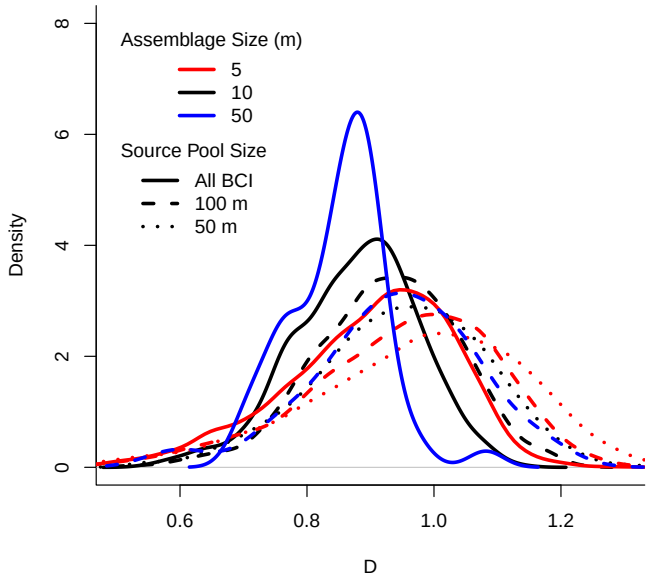


(b) Phylomatic phylogeny

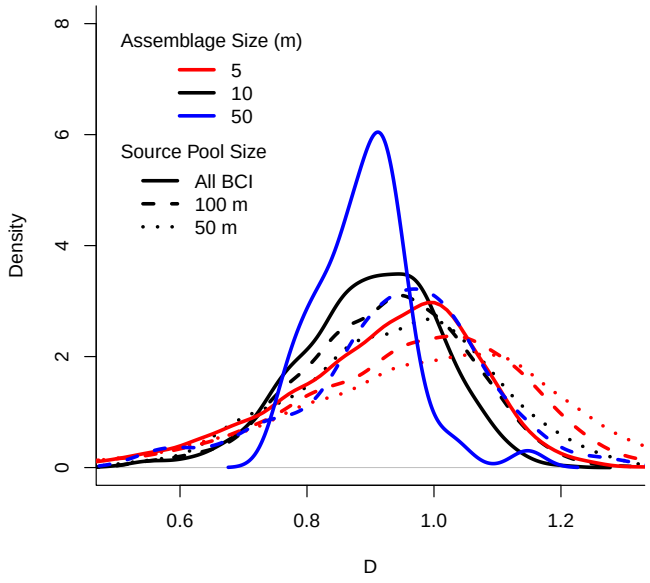


(c) Control Phylogeny

Figure 3.6: The three phylogenies used in the study. Note the lack of resolution in the Phylomatic (b) and control (c) phylogenies, as compared to the Kress phylogeny (a).

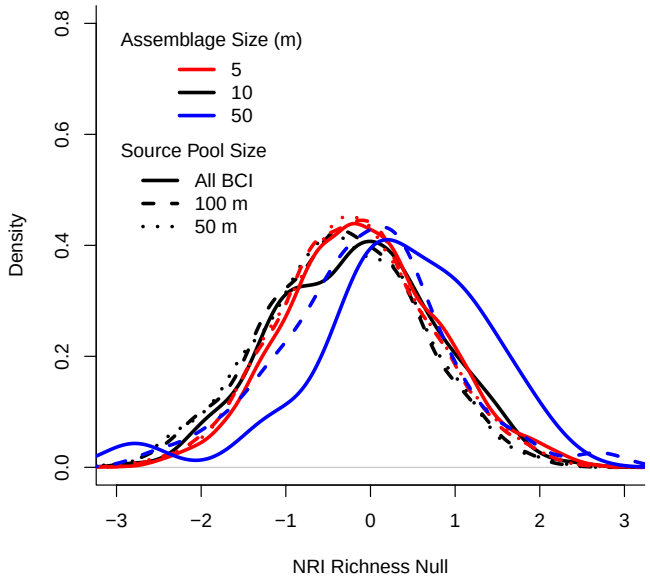


(a) Phylomatic Phylogeny

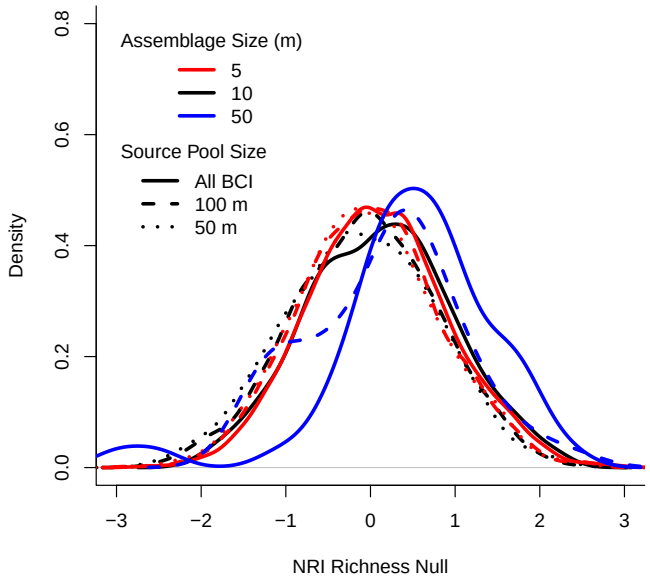


(b) Control Phylogeny

Figure 3.7: Density plots of D with different assemblage and source pool sizes in the Phylomatic and Control phylogenies.



(a) Phylomatic Phylogeny



(b) Control Phylogeny

Figure 3.8: Density plots of SES_{MPD} with different assemblage and source pool sizes in the Phylomatic and control phylogenies.

Assemblage	Source Pool	Phylomatic	Control
5	50	0.97 ± 0.0052	0.97 ± 0.0070
5	100	0.95 ± 0.0052	0.95 ± 0.0070
5	All BCI	0.90 ± 0.0052	0.90 ± 0.0070
10	50	0.95 ± 0.0074	0.93 ± 0.0074
10	100	0.92 ± 0.0074	0.91 ± 0.0074
10	All BCI	0.88 ± 0.0074	0.89 ± 0.0074
50	100	0.94 ± 0.0181	0.93 ± 0.0154
50	All BCI	0.86 ± 0.0181	0.88 ± 0.0154

(a) D Values

Assemblage	Source Pool	Phylomatic	Control
5	50	-0.13 ± 0.0215	0.03 ± 0.0290
5	100	-0.13 ± 0.0215	0.06 ± 0.0290
5	All BCI	-0.03 ± 0.0215	0.16 ± 0.0290
10	50	-0.30 ± 0.0394	-0.01 ± 0.0409
10	100	-0.30 ± 0.0394	0.05 ± 0.0409
10	All BCI	–0.11 ± 0.0394	0.23 ± 0.0409
50	100	-0.10 ± 0.1099	0.39 ± 0.1026
50	All BCI	0.40 ± 0.1089	0.73 ± 0.1017

(b) SES_{MPD} Values

Table 3.4: Mixed effects model estimates of of mean values (± SE) of D and SES_{MPD} values across BCI in the Phylomatic and control phylogenies. D Phylomatic (AIC — -22886 vs. -21496; p-value of likelihood ratio test < 0.0001) and control (AIC — -24604 vs. -22896; p-value of likelihood ratio test < 0.0001) models showed statistically significant effects of source pool and assemblage size when compared with a null model containing neither variable. SES_{MPD} Phylomatic (AIC — 44678 vs. 44848; p-value of likelihood ratio test < 0.0001) and control (AIC — 41518 vs. 41778; p-value of likelihood ratio test < 0.0001) models showed statistically significant effects of source pool and assemblage size when compared with a null model containing neither variable.

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
5	50	0.74	0.87	0.99	1.10	1.18
5	100	0.74	0.86	0.97	1.06	1.13
5	All BCI	0.71	0.82	0.92	1.00	1.05
10	50	0.78	0.87	0.95	1.04	1.11
10	100	0.78	0.85	0.93	1.01	1.06
10	All BCI	0.75	0.81	0.89	0.95	1.00
50	100	0.76	0.86	0.95	1.03	1.08
50	All BCI	0.75	0.80	0.86	0.89	0.92
Range		0.07	0.07	0.13	0.21	0.26

(a) Phylomatic Phylogeny

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
5	50	0.71	0.85	1.00	1.12	1.22
5	100	0.72	0.85	0.98	1.08	1.17
5	All BCI	0.70	0.82	0.94	1.02	1.09
10	50	0.73	0.84	0.95	1.04	1.12
10	100	0.75	0.84	0.93	1.01	1.08
10	All BCI	0.75	0.83	0.91	0.98	1.03
50	100	0.74	0.87	0.96	1.03	1.12
50	All BCI	0.79	0.84	0.89	0.92	0.97
Range		0.09	0.05	0.11	0.20	0.25

(b) Control Phylogeny

Table 3.5: Quantile regression of D values across BCI in the Phylomatic and control phylogenies.

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
10	50	0.0080	0.0054	0.0042	0.0042	0.0053
10	All BCI	0.0091	0.0065	0.0054	0.0048	0.0064
10	100	0.0093	0.0066	0.0060	0.0055	0.0068
5	50	0.0090	0.0062	0.0050	0.0049	0.0062
5	All BCI	0.0088	0.0058	0.0046	0.0046	0.0057
5	100	0.0090	0.0062	0.0050	0.0047	0.0058
50	All BCI	0.0383	0.0124	0.0085	0.0119	0.0059
50	100	0.0279	0.0112	0.0134	0.0144	0.0087

(a) Kress Phylogeny

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
5	50	0.0105	0.0067	0.0059	0.0053	0.0064
5	100	0.0102	0.0064	0.0057	0.0051	0.0063
5	All BCI	0.0099	0.0063	0.0056	0.0050	0.0062
10	50	0.0088	0.0055	0.0051	0.0046	0.0057
10	100	0.0103	0.0074	0.0069	0.0063	0.0074
10	All BCI	0.0098	0.0071	0.0061	0.0056	0.0074
50	100	0.0533	0.0109	0.0149	0.0069	0.0329
50	All BCI	0.0248	0.0194	0.0122	0.0046	0.0074

(b) Phylomatic Phylogeny

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
10	50	0.0069	0.0062	0.0060	0.0052	0.0078
10	100	0.0094	0.0079	0.0073	0.0072	0.0090
10	All BCI	0.0086	0.0080	0.0071	0.0059	0.0089
5	50	0.0097	0.0080	0.0072	0.0060	0.0085
5	100	0.0090	0.0073	0.0068	0.0060	0.0083
5	All BCI	0.0086	0.0072	0.0065	0.0056	0.0081
50	100	0.0149	0.0077	0.0217	0.0089	0.0678
50	All BCI	0.0305	0.0158	0.0170	0.0054	0.0261

(c) Control Phylogeny

Table 3.6: Standard errors of quantile regression of D values across BCI in all three phylogenies.

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
5	50	-1.34	-0.80	-0.20	0.40	0.98
5	100	-1.34	-0.79	-0.21	0.39	0.96
5	All BCI	-1.24	-0.71	-0.12	0.51	1.10
10	50	-1.56	-0.96	-0.36	0.31	0.84
10	100	-1.54	-0.98	-0.34	0.28	0.85
10	All BCI	-1.36	-0.87	-0.14	0.49	1.08
50	100	-1.45	-0.62	-0.07	0.40	1.12
50	All BCI	-1.09	-0.18	0.32	1.03	1.66
Range		0.47	0.80	0.68	0.75	0.82

(a) Phylomatic Phylogeny

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
5	50	-1.12	-0.62	-0.06	0.52	1.08
5	100	-1.07	-0.58	-0.01	0.55	1.10
5	All BCI	-0.96	-0.48	0.08	0.63	1.20
10	50	-1.29	-0.76	-0.13	0.50	1.02
10	100	-1.19	-0.66	-0.04	0.52	1.04
10	All BCI	-1.00	-0.51	0.12	0.70	1.24
50	100	-1.19	-0.51	0.27	0.65	1.23
50	All BCI	-0.44	0.08	0.56	1.04	1.73
Range		0.85	0.84	0.69	0.54	0.71

(b) Control Phylogeny

Table 3.7: Quantile regression of SES_{MPD} values across BCI in the Phylomatic and Control phylogenies.

Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
10	50	0.0454	0.0373	0.0320	0.0339	0.0272
10	100	0.0588	0.0522	0.0465	0.0459	0.0455
10	All BCI	0.0565	0.0478	0.0429	0.0463	0.0409
5	50	0.0492	0.0405	0.0350	0.0372	0.0315
5	100	0.0500	0.0401	0.0347	0.0359	0.0317
5	All BCI	0.0491	0.0399	0.0351	0.0367	0.0317
50	100	0.0539	0.4235	0.1351	0.0462	0.1549
50	All BCI	0.3776	0.0726	0.0837	0.1402	0.1055

(a) Kress Phylogeny

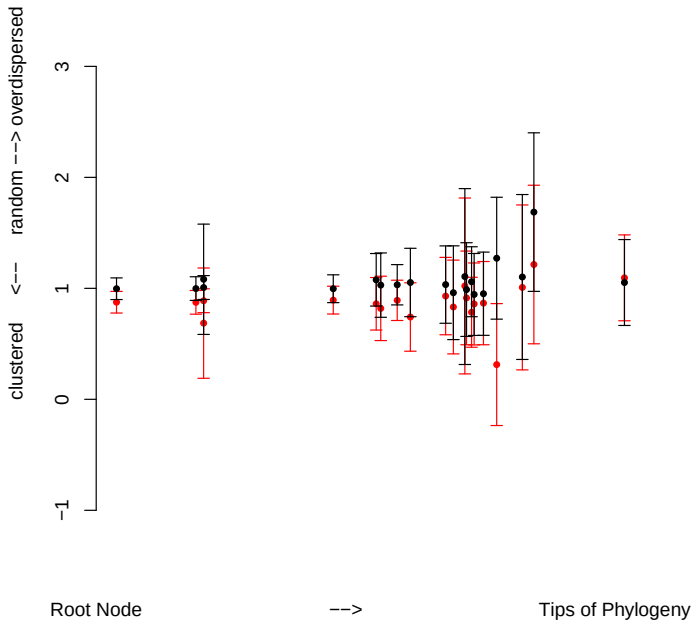
Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
10	50	0.0382	0.0370	0.0300	0.0333	0.0537
10	All BCI	0.0614	0.0571	0.0451	0.0450	0.0670
10	100	0.0652	0.0534	0.0421	0.0465	0.0772
5	All BCI	0.0430	0.0407	0.0343	0.0386	0.0583
5	50	0.0425	0.0408	0.0339	0.0373	0.0580
5	100	0.0428	0.0409	0.0339	0.0385	0.0567
50	100	0.1061	0.2361	0.1103	0.0396	0.2841
50	All BCI	0.2991	0.0693	0.1907	0.0512	0.4082

(b) Phylomatic Phylogeny

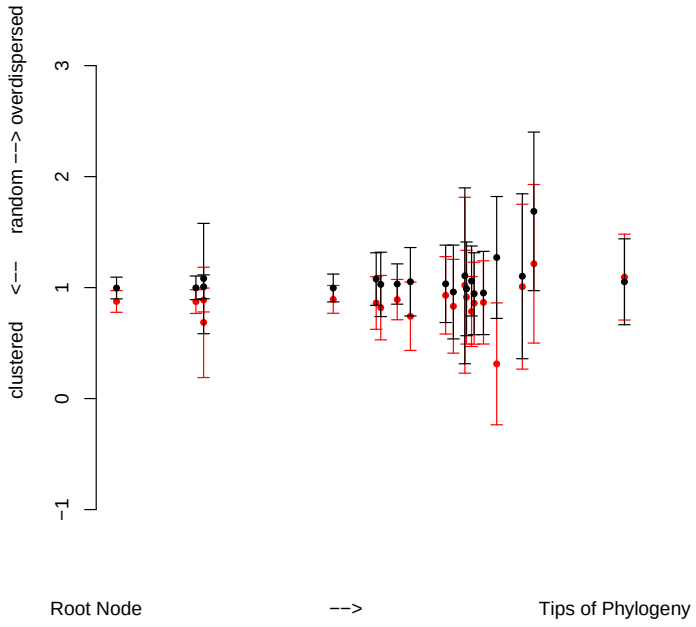
Assemblage	Source Pool	τ=0.10	τ=0.25	τ=0.50	τ=0.75	τ=0.90
10	50	0.0440	0.0366	0.0352	0.0277	0.0402
10	100	0.0658	0.0542	0.0437	0.0466	0.0640
10	All BCI	0.0593	0.0513	0.0451	0.0457	0.0600
5	50	0.0472	0.0398	0.0383	0.0331	0.0466
5	100	0.0484	0.0392	0.0382	0.0314	0.0460
5	All BCI	0.0480	0.0394	0.0386	0.0326	0.0470
50	100	0.0697	0.1562	0.1165	0.0905	0.0908
50	All BCI	0.1424	0.0753	0.0732	0.0405	0.2588

(c) Control Phylogeny

Table 3.8: Standard errors of quantile regression of SES_{MPD} values across BCI in all three phylogenies.

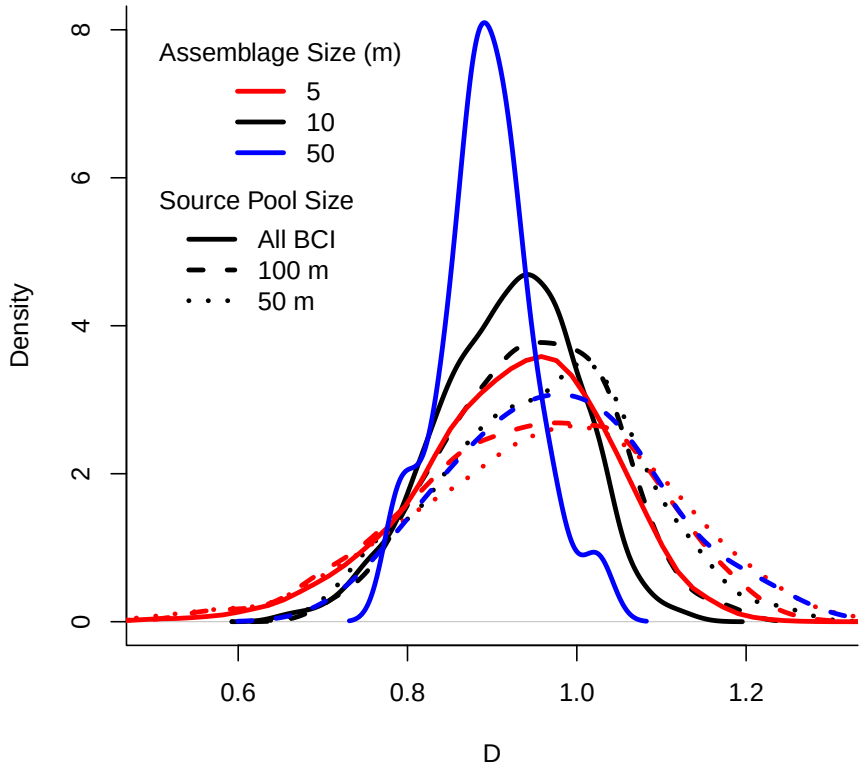


(a) Phylomatic Phylogeny

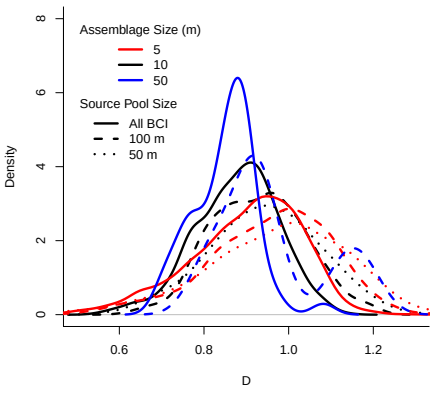


(b) Control Phylogeny

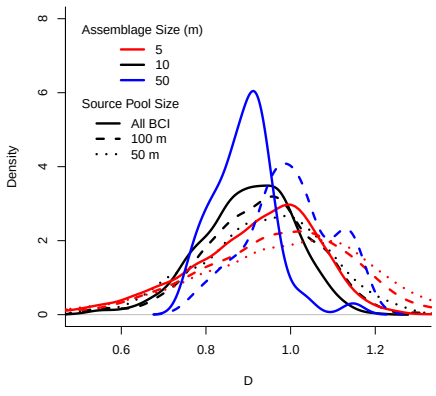
Figure 3.9: Phylogenetic depth plots of D for the observed and simulated assemblages in the Phylomatic and Control phylogenies. These plots seem much more discrete than those of the Kress phylogeny, reflecting the poor resolution of both these phylogenies.



(a) Kress Phylogeny

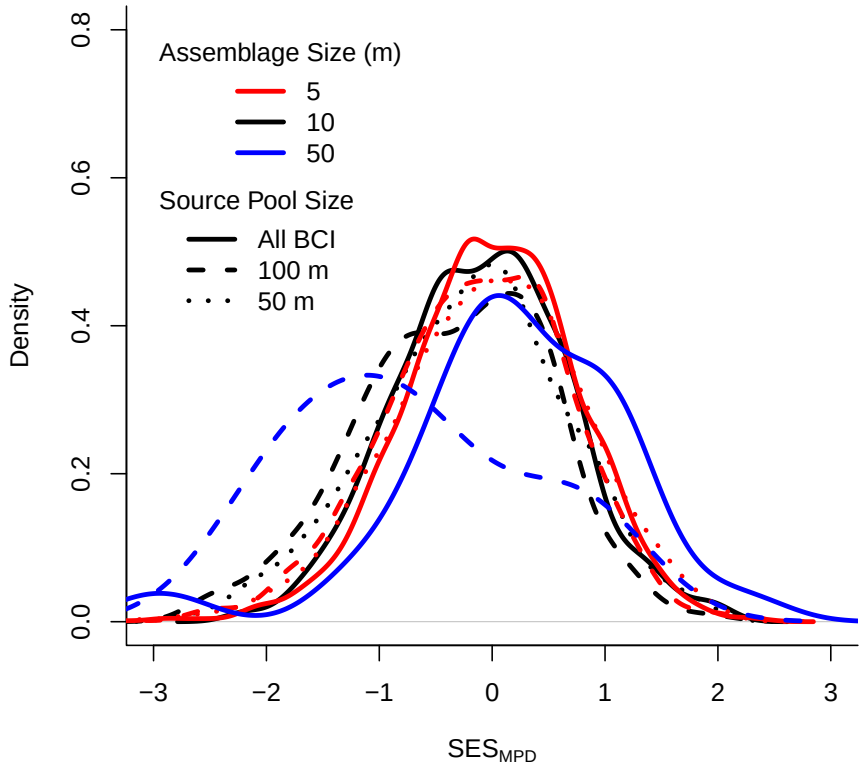


(b) Phylomatic Phylogeny

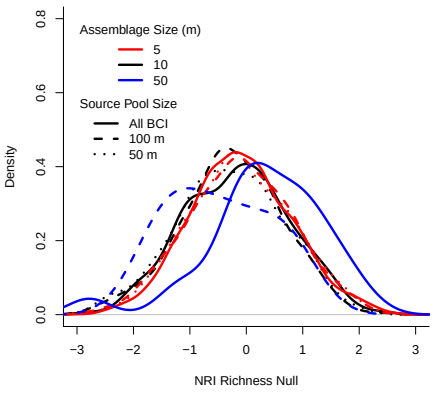


(c) Control Phylogeny

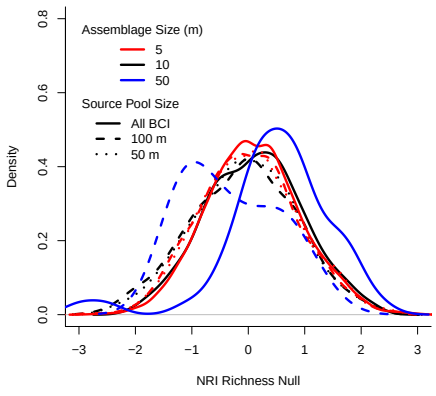
Figure 3.10: Density plots of D with different assemblage and source pool sizes in all three phylogenies, with assemblages whose source pools that cross the boundary of BCI removed from the analysis.



(a) Kress Phylogeny



(b) Phylomatic Phylogeny



(c) Control Phylogeny

Figure 3.11: Density plots of SES_{MPD} with different assemblage and source pool sizes in all three phylogenies, with assemblages whose source pools that cross the boundary of BCI removed from the analysis.

Assemblage	Source Pool	Kress	Phylomatic	Control
5	50	0.96 ± 0.0059	0.96 ± 0.0055	0.97 ± 0.0073
5	100	0.94 ± 0.0060	0.95 ± 0.0058	0.95 ± 0.0075
5	All BCI	0.92 ± 0.0057	0.90 ± 0.0052	0.91 ± 0.0071
10	50	0.96 ± 0.0087	0.94 ± 0.0079	0.92 ± 0.0080
10	100	0.94 ± 0.0093	0.92 ± 0.0088	0.91 ± 0.0086
10	All BCI	0.92 ± 0.0084	0.89 ± 0.0073	0.89 ± 0.0077
50	100	0.95 ± 0.0247	0.94 ± 0.0302	1.02 ± 0.0254
50	All BCI	0.89 ± 0.0143	0.86 ± 0.0162	0.90 ± 0.0169
AIC_{model}		-15196	-13604	-13816
AIC_{null}		-14855	-13131	-13109

(a) D Values

Assemblage	Source Pool	Kress	Phylomatic	Control
5	50	0.02 ± 0.0227	-0.19 ± 0.0240	-0.10 ± 0.0283
5	100	-0.00 ± 0.0255	-0.18 ± 0.0266	-0.07 ± 0.0306
5	All BCI	0.17 ± 0.0204	0.04 ± 0.0220	0.14 ± 0.0265
10	50	-0.03 ± 0.0420	0.05 ± 0.0425	0.12 ± 0.0450
10	100	-0.05 ± 0.0487	0.13 ± 0.0489	0.20 ± 0.0511
10	All BCI	0.23 ± 0.0379	0.44 ± 0.0387	0.52 ± 0.0413
50	100	0.26 ± 0.1909	0.38 ± 0.1863	0.70 ± 0.1886
50	All BCI	-0.13 ± 0.0987	0.80 ± 0.0968	1.03 ± 0.0987
AIC_{model}		20043	23656	21641
AIC_{null}		20175	23792	21819

(b) SES_{MPD} Values

Table 3.9: Mixed effects models of D and SES_{MPD} values across BCI, with assemblages whose source pools that cross the boundary of BCI removed from the analysis. Estimates of mean values (± SE) for each assemblage/source pool combination, with a different table for each dispersion measure, subdivided within each table according to the phylogeny used. AIC values and LRT p-values for each model are given the last two rows of each table. All likelihood ratio tests had p-values < 0.0001.

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.86	0.97	1.07
5	100	0.85	0.95	1.04
5	All BCI	0.85	0.93	1.00
10	50	0.88	0.97	1.04
10	100	0.87	0.95	1.01
10	All BCI	0.86	0.92	0.98
50	100	0.89	0.96	1.05
50	All BCI	0.86	0.89	0.92
Range		0.04	0.08	0.15

(a) Kress Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.86	0.99	1.09
5	100	0.86	0.97	1.06
5	All BCI	0.82	0.92	1.00
10	50	0.85	0.94	1.03
10	100	0.85	0.93	1.01
10	All BCI	0.81	0.89	0.95
50	100	0.86	0.92	0.97
50	All BCI	0.80	0.86	0.89
Range		0.06	0.13	0.20

(b) Phylomatic Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.85	1.00	1.12
5	100	0.84	0.97	1.09
5	All BCI	0.82	0.94	1.02
10	50	0.84	0.94	1.04
10	100	0.85	0.94	1.01
10	All BCI	0.83	0.91	0.98
50	100	0.94	0.98	1.04
50	All BCI	0.84	0.89	0.92
Range		0.12	0.11	0.20

(c) Control Phylogeny

Table 3.10: Quantile regression of D values across BCI in all three phylogenies, with assemblages whose source pools that cross the boundary of BCI removed from the analysis.

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.0060	0.0045	0.0047
5	100	0.0059	0.0055	0.0039
5	All BCI	0.0023	0.0020	0.0020
10	50	0.0082	0.0089	0.0059
10	100	0.0080	0.0075	0.0077
10	All BCI	0.0035	0.0036	0.0025
50	100	0.0055	0.0209	0.0272
50	All BCI	0.0144	0.0082	0.0135

(a) Kress Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.0057	0.0047	0.0056
5	100	0.0057	0.0052	0.0045
5	All BCI	0.0031	0.0022	0.0020
10	50	0.0071	0.0074	0.0068
10	100	0.0085	0.0108	0.0105
10	All BCI	0.0049	0.0033	0.0032
50	100	0.0704	0.0365	0.3063
50	All BCI	0.0340	0.0178	0.0103

(b) Phylomatic Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
10	50	0.0088	0.0075	0.0073
10	100	0.0074	0.0062	0.0077
10	All BCI	0.0052	0.0040	0.0028
5	50	0.0060	0.0050	0.0037
5	100	0.0077	0.0053	0.0053
5	All BCI	0.0038	0.0027	0.0020
50	100	0.0417	0.0331	0.1345
50	All BCI	0.0127	0.0250	0.0013

(c) Control Phylogeny

Table 3.11: Standard errors of quantile regression of D values across BCI in all three phylogenies, with assemblages whose source pools that cross the boundary of BCI removed from the analysis.

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	-0.60	-0.02	0.53
5	100	-0.65	-0.09	0.43
5	All BCI	-0.50	0.00	0.51
10	50	-0.75	-0.15	0.36
10	100	-0.89	-0.27	0.30
10	All BCI	-0.59	-0.07	0.43
50	100	-1.41	-0.77	0.56
50	All BCI	-0.27	0.20	0.91
Range		1.14	0.97	0.61

(a) Kress Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	-0.77	-0.14	0.54
5	100	-0.75	-0.11	0.53
5	All BCI	-0.71	-0.12	0.51
10	50	-0.92	-0.30	0.37
10	100	-0.80	-0.26	0.35
10	All BCI	-0.87	-0.14	0.49
50	100	-1.15	-0.44	0.25
50	All BCI	-0.18	0.31	1.03
Range		0.97	0.73	0.78

(b) Phylomatic Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	-0.60	0.02	0.62
5	100	-0.60	-0.02	0.57
5	All BCI	-0.48	0.08	0.63
10	50	-0.68	-0.03	0.57
10	100	-0.74	-0.03	0.60
10	All BCI	-0.51	0.12	0.70
50	100	-1.03	-0.23	0.51
50	All BCI	0.08	0.54	1.04
Range		1.11	0.77	0.53

(c) Control Phylogeny

Table 3.12: Quantile regression of SES_{MPD} values across BCI in the Phylomatic and Control phylogenies, with assemblages whose source pools that cross the boundary of BCI removed from the analysis.

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.0261	0.0252	0.0263
5	100	0.0352	0.0305	0.0179
5	All BCI	0.0149	0.0142	0.0140
10	50	0.0546	0.0489	0.0533
10	100	0.0650	0.0785	0.0577
10	All BCI	0.0325	0.0291	0.0318
50	100	0.3056	0.0328	1.6307
50	All BCI	0.0964	0.1107	0.1489

(a) Kress Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.0278	0.0252	0.0347
5	100	0.0341	0.0327	0.0367
5	All BCI	0.0164	0.0164	0.0199
10	50	0.0491	0.0542	0.0551
10	100	0.0771	0.0590	0.0782
10	All BCI	0.0432	0.0354	0.0326
50	100	0.4939	0.0984	0.3733
50	All BCI	0.2130	0.2350	0.1455

(b) Phylomatic Phylogeny

Assemblage	Source Pool	τ=0.25	τ=0.50	τ=0.75
5	50	0.0281	0.0289	0.0290
5	100	0.0277	0.0333	0.0320
5	All BCI	0.0147	0.0153	0.0165
10	50	0.0760	0.0597	0.0479
10	100	0.0766	0.0450	0.1025
10	All BCI	0.0339	0.0300	0.0340
50	100	0.2534	0.4484	0.0257
50	All BCI	0.1436	0.0899	0.0787

(c) Control Phylogeny

Table 3.13: Standard errors of quantile regression of SES_{MPD} values across BCI in all three phylogenies, with assemblages whose source pools that cross the boundary of BCI removed from the analysis.

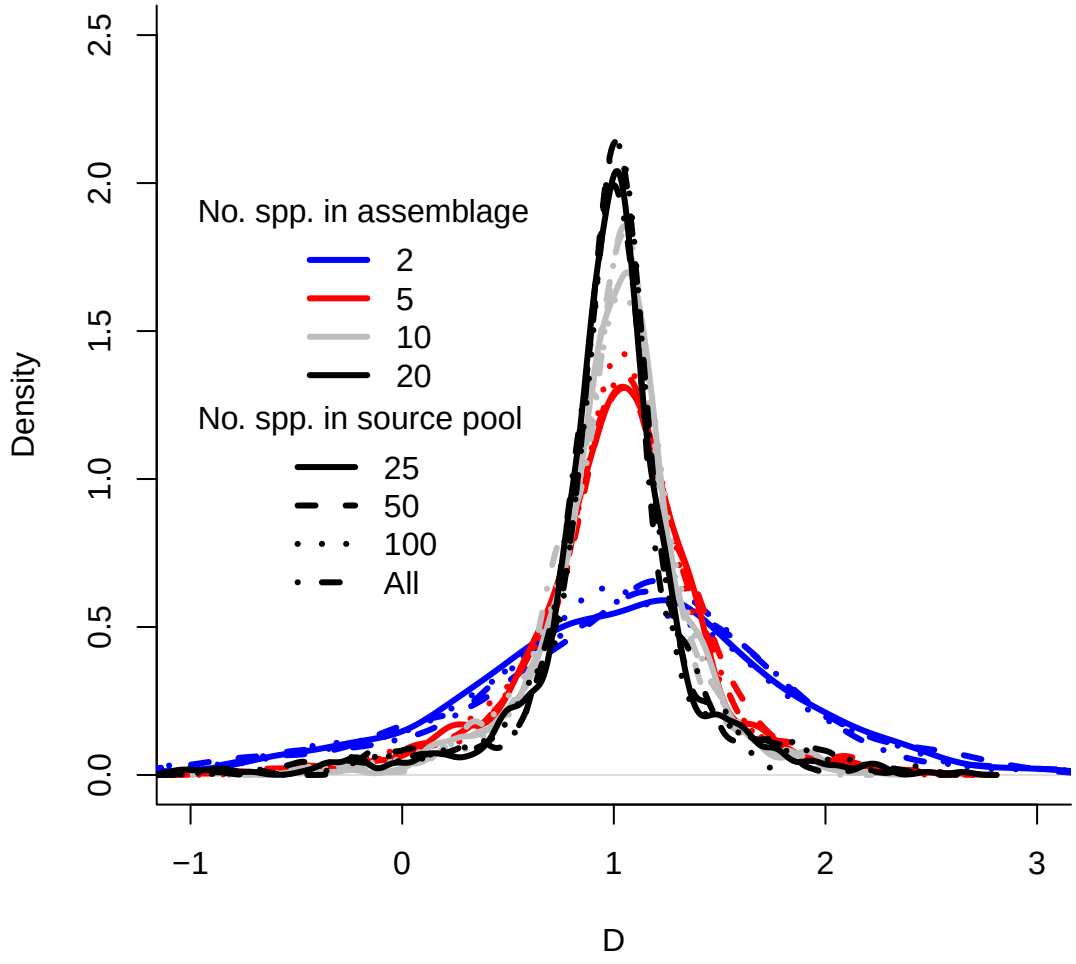


Figure 3.12: Simulated small assemblages' D values. 30 randomly selected source pools containing 25, 50, 100, and all species in BCI, within with 30 different assemblages containing 2, 5, 10, and 20 species were created. D values were calculated for all 14400 assemblages, and are plotted above. A two-way ANOVA of D against assemblage and source pool size was significant ($F_{15,14384} = 1.739$), but only had an r^2 of 0.18%. This likely reflects the poorer resolution of D in assemblages containing only two species.

Chapter 4

phyloGenerator: an automated phylogeny generation tool for ecologists

4.1 Abstract

1. Ecologists increasingly wish to use phylogenies, but are limited by the technical challenge of phylogeny construction.
2. I present `phyloGenerator`, an open-source, stand-alone Python program that makes use of pre-existing sequence data and taxonomic information to largely automate phylogenetic construction.
3. It allows non-specialists to quickly and easily produce robust, defensible phylogenies, without requiring an extensive knowledge of phylogenetics. Experienced phylogeneticists will also find it useful as a tool to conduct exploratory analyses.
4. `phyloGenerator` performs a number of 'sanity checks' on the user's output, but users should still check their outputs carefully. The program gives some advice on how to do this.

5. By linking a number of tools in a common framework, `phyloGenerator` is a step towards an open, reproducible phylogenetic workflow.

6. Bundled downloads for `Windows` and `Mac OSX`, along with the source code, can be found at `http://willpearse.github.com/phyloGenerator` (note the capital 'G').

4.2 Introduction

Ecologists have long recognised the importance of incorporating phylogenetic data in their work. Entire areas of study, such as community phylogenetics (Webb *et al.*, 2002; Vamosi *et al.*, 2009; Cavender-Bares *et al.*, 2009) and comparative analysis (Felsenstein, 1985; Harvey & Pagel, 1991), require detailed phylogenetic, as well as ecological, information. Despite vast amounts of sequence data, progress in these fields has been slowed by the level of expertise required to create reliable phylogenies. While there has been a recent explosion in the creation of extremely large phylogenies with many species (e.g., Smith *et al.*, 2009; Izquierdo-Carrasco *et al.*, 2011), there is often a mismatch between the species sequenced to build such trees and the species in which ecologists are interested. Moreover, while projects such as the '*Open Tree of Life*' (`http://opentreeoflife.wordpress.com/`) aim to create a phylogeny of all life on Earth, as yet no such tree exists for the non-specialist to use.

Ecologists capable of conducting phylogenetic analyses are rewarded with estimates of phylogenetic uncertainty and the ability to work with novel sequence data. Ecologists without these skills must rely on programs such as `Phylomatic` (Webb & Donoghue, 2005), which allows anyone to generate a phylogeny by adding missing species into a reference phylogeny on the basis of taxonomy, and (conservatively) cannot generate a result that conflicts with the user's phylogeny or taxonomy. `Phylomatic` has been used almost exclusively for plant studies, largely because the software has always been bundled with an excellent family-level phylogeny (Davies *et al.*, 2004), though the latest online version (3 at the time of writing) features the Bininda-Emonds *et al.* (2007) mammal supertree.

`Phylomatic` is extremely robust and powerful, but when faced with taxa not in its reference phylogeny its output may contain many polytomies, and its `bladj` algorithm, which dates unknown clades by interpolating from dated clades, can produce inaccurately dated phylogenies (Ricotta *et al.*, 2012).

The rapid uptake of `Phylomatic` suggests there is a need for a method that combines `Phylomatic`'s ease of use with the flexibility and accuracy of *de novo* tree construction. `phyloGenerator` takes a list of species, candidate genes, and (optionally) taxonomic information, and from them creates a novel phylogeny using established phylogenetic methods. In contrast with other automated methods (e.g., Peters *et al.*, 2011), `phyloGenerator` allows the non-specialist to produce a defensible phylogeny with minimal effort.

4.3 A non-technical overview of *phyloGenerator*

It is beyond the scope of this chapter to review the entire of phylogenetics, and in the brief overview below I assume basic familiarity with the concepts of DNA sequences, phylogenies (or 'trees'), and Bayesian inference. A phylogenetic study attempts to find the phylogeny that is most likely given a particular DNA *alignment*. An alignment is intended to represent the same locus in the genome of all species under study, and phylogenies are judged according to how likely they are to produce that alignment under a given model of DNA evolution. I strongly encourage any user to manually inspect their output phylogeny despite the checks `phyloGenerator` performs, since many common problems are clear even to a novice phylogeneticist upon inspection.

First, `phyloGenerator` downloads DNA sequence from `GenBank` (Benson *et al.*, 2009) for particular species and genetic locus, and then *aligns* the sequences to determine how each species' sequence relates to the others (see figure 4.1). The choice of locus is important; an expressed gene may be under selective pressures that are difficult to model, while a neutral region that isn't under selection is harder to align since it can vary more freely. Moreover, if a locus' mutation rate

is too slow there will be insufficient variation for analysis, but if it is too fast then multiple mutations at the same position could confound analysis. A search program constructs a phylogeny from an alignment by calculating the likelihood of a candidate phylogeny given that alignment, and then rearranging that phylogeny in an attempt to improve its likelihood score.

For almost all phylogenies it is not feasible to evaluate all possible trees (there are over two million possible phylogenies containing only ten species), and so no guarantee of finding the best estimate of a phylogeny. Maximum likelihood (ML) methods (`phyloGenerator` uses `RAxML`; Stamatakis, 2006) can be run multiple times from different starting trees to maximise the chances of finding a good tree, and recording how many times a particular clade is found during these searches can provide an estimate of the credibility of a clade. A Bayesian approach (`phyloGenerator` uses `BEAST`; Drummond *et al.*, 2006; Drummond & Rambaut, 2007; Drummond *et al.*, 2012) can also make use of multiple starting trees, but support comes from the resulting posterior distribution of trees. Most Bayesian methods use Markov Chain Monte Carlo methods to estimate this posterior distribution and so require that the Markov Chain has *converged* on a distribution of likely phylogenies. There are many ways of assessing convergence, and the user should only use a Bayesian method if they are comfortable judging convergence.

All of these search strategies can be *constrained*, restricting the phylogeny search to trees that do not conflict with a given constraint phylogeny. The user is encouraged to restrict their search to conform to well-known clades (e.g., taxonomic families), and then estimate the unknown relationships within these clades. *Long branch attraction*, a common problem where DNA sequences extremely dissimilar to the rest of the phylogeny group together on long branches. This problem is usually immediately apparent if the user visually inspects their output, and, as it often results from poor-quality sequences download from `GenBank`, can be corrected by downloading different sequences with `phyloGenerator`.

The maximum likelihood phylogenies produced by `RAxML` have branch lengths proportional to the rate of evolution at the loci used, not divergence date among species. Molecular dating techniques can be used in `phyloGenerator` to transform these branch lengths to be proportional to divergence time, either by es-

sentially averaging out variation in branch lengths (using `PATHd8`; Britton *et al.*, 2007), or a `BEAST` run where the phylogeny's topology is constrained to that of the ML phylogeny and only branch lengths are estimated.

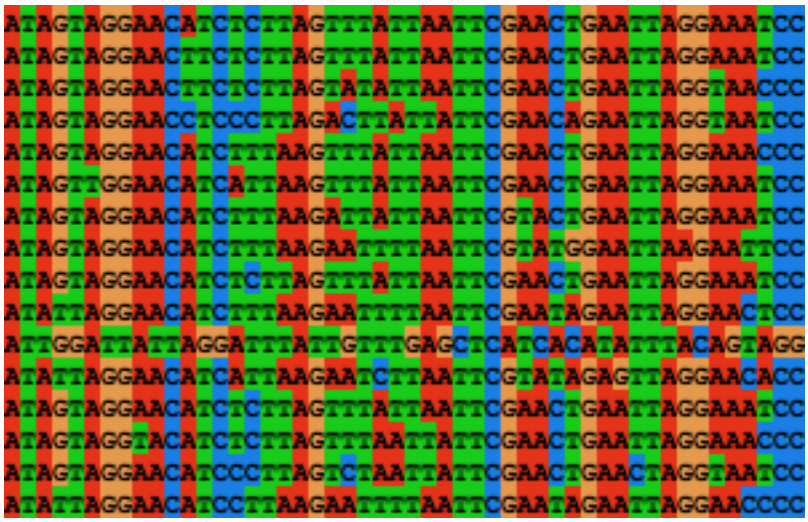
4.4 A more technical description of *phyloGenerator*

`phyloGenerator` is a command-line application that uses and extends the `BioPython` framework (Cock *et al.*, 2009). It combines many phylogenetic tools in one distribution, under a single interface; no customisation or setup, beyond downloading the program, is required for use. Users are guided through the process of making a phylogeny by a series of questions, while the advanced user can pre-select options from the command line. Thus the tool may be used within an automated workflow, providing a step towards an open framework of repeatable phylogenetic methods.

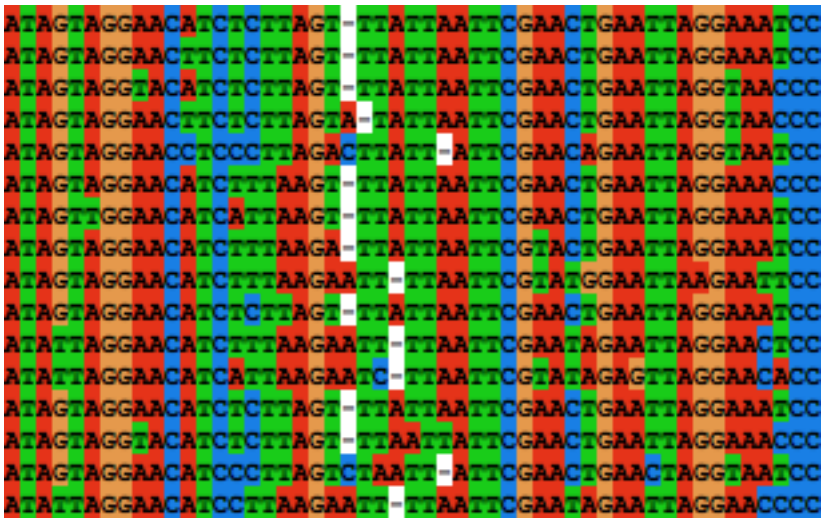
The program's procedures can easily be customised, and the source code itself has been written to facilitate user modification. Phylogeneticists can use its features, such as the `replace` method and `BEAST` analysis templates, within their own pipelines. I wrote the program in `Python` to allow for this easy integration with advanced users' scripts, while also permitting `phyloGenerator` to function as stand-alone software. My hope is that user preferences and future methodological advances can be incorporated into its workflow, such that novice phylogeneticists can benefit from the skills of others. Bundled downloads for `Windows` and `Mac OSX`, along with the source code, can be found at `http://willpearse.github.com/phyloGenerator` (note the capital 'G'). An outline of the program's workflow is shown in figure 4.2.

DNA sequence download and cleaning

The user provides a list of species and candidate genes, which `phyloGenerator` downloads from `GenBank`, choosing between multiple sequences either at random,



(a) Unaligned DNA sequences



(b) Aligned DNA sequences

Figure 4.1: Description of a DNA alignment. In (a), 16 unaligned DNA sequences are displayed (one per row), while in (b) the same sequences are displayed, but they have now been *aligned*. Gaps ('—') have been inserted into some sequences, and represent where additional base pairs have been inserted (or removed) from the DNA sequences. In the aligned sequence, because each species' nucleotides can be compared with the nucleotides at the same position in every other species, models describing mutation from one nucleotide to another can be fit across the data.

according to the median, maximum, or minimum length of sequences on `GenBank`, or with reference to a target gene length. `phyloGenerator` can search for open reading frames in any sequence, and extract a gene of interest from annotated sequences. Not all the genes searched for need be used in the final phylogeny; if the user only wishes to use a certain number of genes, `phyloGenerator` can select the set of genes that maximises species coverage. If no match is found for a particular species' gene, a relative's gene can be used instead, but only if the `NCBI taxonomy` indicates the species and its replacement would form a monophyletic clade within the phylogeny (the `replace` method). If no such replacement can be found for (a) species, the user can `merge` the missing species with another species that has sequence data; in the final output the species will form a polytomy dated according to the `bladj` algorithm. Users should be aware that not all `GenBank` sequences are labelled in the same way; searches for '*Internal Transcribed Spacer*', '*ITS*', '*ITS1*', and '*ITS2*' will not necessarily yield the same results. `phyloGenerator` attempts to search both sequence annotations and sequence descriptions for specified genes.

DNA sequence alignment

DNA data can be aligned using `Clustal-Ω` (Sievers *et al.*, 2011), `MAFFT` (Katoh *et al.*, 2005; Katoh & Toh, 2008), `MUSCLE` (Edgar, 2004), and `Prank` (Löytynoja & Goldman, 2005). There is no general consensus on how to identify the most accurate alignment, so several options are offered to help the user choose among `phyloGenerator`'s candidate alignments. Alignments are compared according to their number of gaps, and 'difficult' regions can be removed with `trimAl` (Capella-Gutiérrez *et al.*, 2009). Alignments can be directly compared with each other (using the *SSP* metric of `MetAl`; Blackburne & Whelan, 2012), or by their impact on tree searches (the mean Robinson-Foulds distances between `RAxML` searches with each alignment). The user can reload sequences and align those sequences as many times as they wish, and is advised to visually inspect any alignment before proceeding to build a phylogeny.

Phylogeny construction and molecular dating

Using `RAxML`, a tree can be found with bootstrapped confidence intervals, and sub-optimal trees are retained if the search was performed more than once. If desired, molecular dating can be performed using `PATHd8`, or with a `BEAST` search where the topology has been constrained to that of the best tree found by `RAxML`.

`BEAST` can also be used for the entire search process, in which case the resulting phylogeny already has branch lengths proportional to evolutionary divergence and no molecular dating is required. I do not know of a fool-proof automated way to detect a lack of convergence in a `BEAST` run, and so the user is responsible for checking the convergence of their search(es). `AWTY` (Nylander *et al.*, 2008) and `Tracer` (Rambaut & Drummond, 2012) are excellent tools for checking for convergence, and `phyloGenerator` outputs `BEAST`'s log file and posterior distribution of trees for use with them.

Some may be concerned at the idea of a non-specialist building a phylogeny from sequence data. To counter this, the user is encouraged to constrain their tree search using existing phylogenetic knowledge, and `Phylomatic` can be used to do so. The data's agreement with a constraint can be assessed by comparing tree searches with and without the constraint tree (using the mean Robinson-Foulds distances between `RAxML` tree searches). If the user provides a constraint tree with named clades, those clades' ages are set as strong priors (a normal distribution with the given age as the mean, and a standard deviation of one) during a `BEAST` search. By constraining their phylogeny according to known phylogenetic relationships, and dated clades (using `Phylomatic` if desired), the user can be certain that their phylogeny cannot conflict with established phylogenetic relationships. `phyloGenerator` attempts to auto-detect sequence alignment problems, but the user is strongly advised to visually inspect all output from the program, and to take heed of estimates of clade credibility.

4.5 Example and comparison with existing methods

Figure 4.3 shows a phylogeny generated using `Phylomatic` (in black) of plant species in an experiment at Silwood Park (Berkshire, United Kingdom). Of the 33 species in the phylogeny, 13 descend from polytomies, suggesting a lack of phylogenetic information for these species. I used this phylogeny as a constraint for `phyloGenerator`, and generated a completely resolved phylogeny (in red on figure 4.3) using the *rbcL* and *matK* genes. `phyloGenerator` has automatically set strong priors on the ages of all named clades (marked on figure 4.3, dating other clades using DNA data. Phylogeny construction itself takes approximately twenty minutes on a 2.66Ghz Intel Core 2 Duo MacBook Pro laptop, and DNA download under five minutes, but these steps are automated and do not require user intervention. A tutorial video on the `phyloGenerator` website explaining and demonstrating the user input required to build this phylogeny lasts less than five minutes.

A number of other automated phylogenetics workflows exist, but `phyloGenerator` is the only one designed specifically for novice phylogeneticists, and requires the least user intervention. Table 4.1 compares and contrasts some methods, but is not an exhaustive list. The methods that do not require the user to already have DNA data are suitable only for trained phylogeneticists; Peters *et al.*'s method (2011) consists of over twenty separate `Ruby` scripts, `ape` (Paradis *et al.*, 2004) requires manual setup of command line tools and for the user to script their own workflow, and `GeneFinder` (Lanfear & Bromham, 2011) requires the user to already know the `GenBank taxon IDs` of the species for which they want DNA data. The other programs that align DNA and perform tree searches for the user are also unsuitable for novice phylogeneticists: `rPlant` (Banbury *et al.*, 2012) is essentially a command line interface to the `iPlant` servers, while SATé-II (Liu *et al.*, 2012) is a simultaneous alignment-phylogeny estimation program and not a complete phylogenetic workflow.

Program	DNA Download	DNA Alignment	Tree Search	One-click	Local	Sanity Checks
`ape` (Paradis *et al.*, 2004)	✔	✔	✗	✗	✔	✗
`Phylomatic` (Webb *et al.*, 2008)	*NA*	*NA*	*NA*	✔	✔	✗
Peters *et al.* (2011)	✔	✔	✔	✗	✔	✗
`rPlant` Banbury *et al.* (2012)	✗	✔	✔	✔	✗	✗
`GeneFinder` (Lanfear & Bromham, 2011)	✔	✗	✗	✗	✔	✗
SATé-II (Liu *et al.*, 2012)	✗	✔	✔	✗	✔	✗
`phyloGenerator`	✔	✔	✔	✔	✔	✔

Table 4.1: Programs with features similar to `phyloGenerator`. In order from left to right, each column describes whether a program: downloads DNA data from the Internet, aligns that DNA data, heuristically searches for an acceptable phylogeny, doesn't require the user to manually run its different sub-components, conducts analyses on the user's computer, and checks the user's data and output for obvious sources of error. In each column, ✔ and ✗ indicate whether a program does or does not have a feature respectively; `Phylomatic` does not attempt to build a novel phylogeny, and so is listed as *NA* under some columns. More details about each program are given in the text.

4.6 Conclusion

`phyloGenerator` offers a way for non-specialists to quickly make phylogenies, using real sequence data and cutting-edge techniques. It is safer than alternatives, since it is easily constrained with taxonomic information and gives estimates of uncertainty, but I do advise users to manually check their output. It also acts as a tool that experienced phylogeneticists can use to rapidly search for sequences and conduct exploratory analyses. It is not designed to replace phylogeneticists, but it is intended to facilitate the rapid and broad dissemination of their expertise to those who badly need phylogenies in their work. I hope it is a step towards an open, reproducible way of describing, sharing and implementing phylogenetic methods.

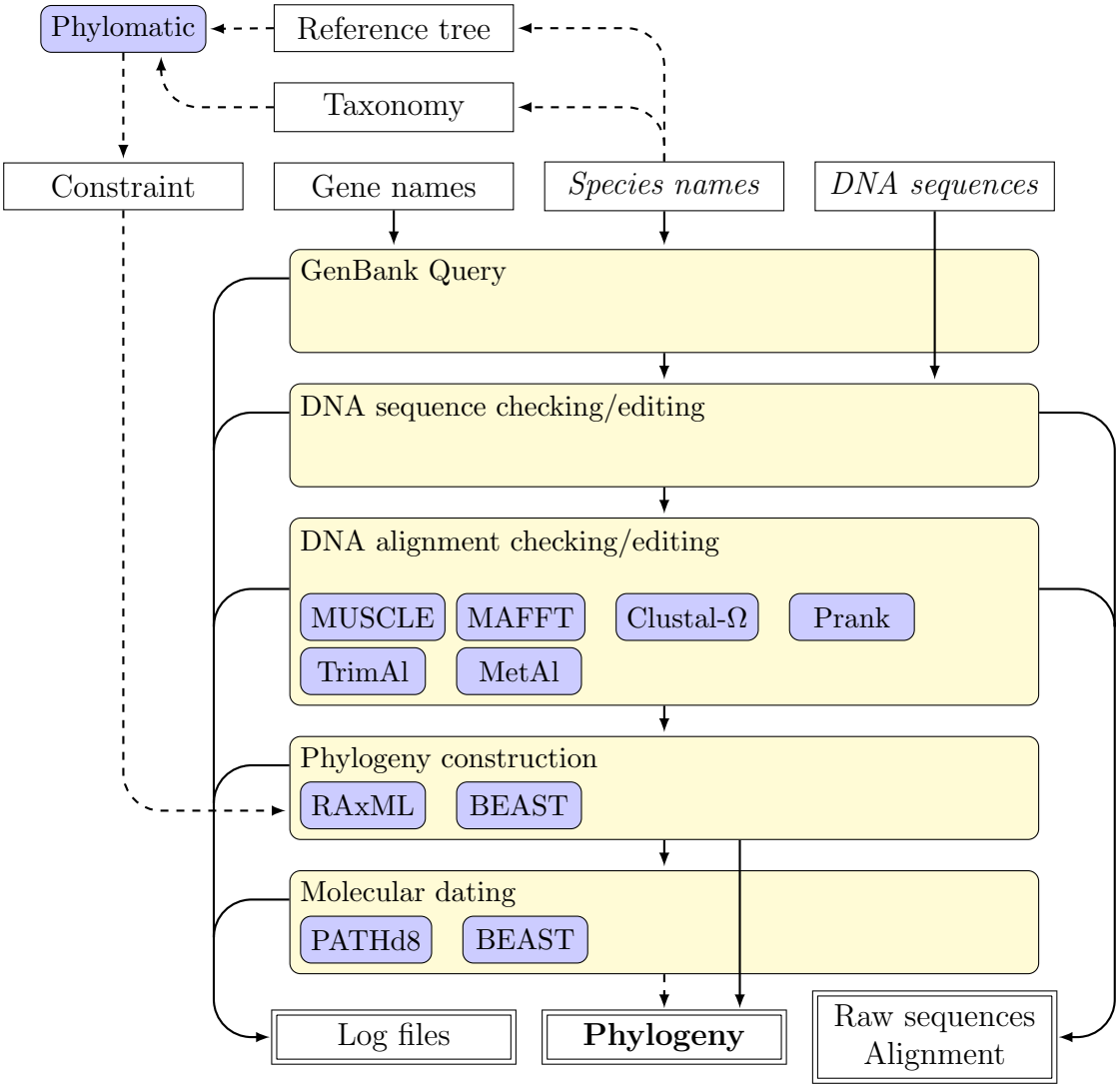


Figure 4.2: Outline of `phyloGenerator`'s workflow. Stages of the program are coloured yellow, programs used are blue, inputs are white, and outputs are white with two lines around them. Optional steps have dashed lines. The user must provide either DNA sequences or species names, but not both (in italics). A constraint tree can either be provided by the user, or generated from a reference tree and taxonomic information using `Phylomatic`.

Figure 4.3: Phylogenies of a plant dataset made using `Phylomatic` (black) and `phyloGenerator` (red). Nodes whose age was constrained in `phyloGenerator` are marked with circles. `phyloGenerator` has produced a phylogeny very similar to that of `Phylomatic`, but without any polytomies. This example is included in the `phyloGenerator` distribution.

Chapter 5

Phylogenetic structure and ecosystem productivity in marine benthic assemblages

5.1 Abstract

Ecosystem function studies are dominated by studies of grassland communities, yet marine benthic assemblages provide important ecosystem services and are under increasing threat. Studies taking a community phylogenetic approach to ecosystem services are comparatively rare, and the high phylogenetic diversity of benthic assemblages—typically containing many phyla—poses a particular challenge. In this chapter, I produce two assemblage phylogenies for two existing marine benthic datasets, using them to both examine the assemblages' phylogenetic structure and dispersion, and to test whether phylogenetic dispersion and species' traits predict ecosystem function as measured by sediment mixing depth. I show that more disturbed assemblages are more phylogenetically clustered, but that neither traits not phylogenetic dispersion are good predictors of ecosystem function. Instead, species richness and environmental perturbation drive ecosystem function.

5.2 Introduction

The study of ecosystem function is an important part of ecology, providing a framework to study ecosystem processes such as nutrient cycling (Hooper *et al.*, 2005) and to give ecosystems monetary value (Costanza *et al.*, 1997; Balmford *et al.*, 2002). A major aim of ecosystem function experiments has been to understand the importance of species composition, notably in artificially assembled grassland communities (e.g., Naeem *et al.*, 1994; Tilman *et al.*, 1997; Roscher *et al.*, 2005; Hector *et al.*, 2011), though some studies use natural gradients (reviewed in Fukami & Wardle, 2005).

Most studies have examined grassland ecosystems (∼57%; Balvanera *et al.*, 2006), yet most of the world's surface is covered by ocean: ocean floor assemblages have therefore been greatly under-represented. These benthic communities are also under threat, notably from trawling (Thrush & Dayton, 2002; Tillin *et al.*, 2006), but also from organic enrichment (Pearson & Rosenberg, 1978; Weston, 1990; Conlan *et al.*, 2004), though UK legislation has mitigated much of this threat (Rees *et al.*, 2006). Benthic ecosystems have important functions: they are major determinants of atmospheric CO_2 levels (IPCC, 2007), deep-sea productivity (Danovaro *et al.*, 2008), bacterial decomposer and primary producer communities (Kristensen, 2000), and nutrient flux (Norling *et al.*, 2007). Bioturbation (the reworking of sediment) controls sediment mixing depth, and so, in turn, the rate of these key ecosystem processes. Recent technological advances make measurement of natural benthic community composition and sediment mixing depth (and so bioturbation) straightforward (reviewed in Solan *et al.*, 2003), facilitating detailed examination of benthic ecosystem function.

Community phylogenetic approaches are rarely used to assess ecosystem function, but where tested, phylogenetic structure has been shown to explain function as well (Flynn *et al.*, 2011) or better (Cadotte *et al.*, 2008, 2009) than functional trait data. These findings relate primarily to grassland ecosystems but, if general, are good news for benthic ecologists—collecting life-history data on species that live in underwater sediment is difficult, and many benthic species' morphologies are difficult to compare quantitatively (polychaete worms and brittlestars, for

instance). Furthermore, the large taxonomic diversity in the oceans compared with terrestrial systems (Paine, 2010) could give phylogenetic approaches high discriminatory power in benthic assemblages.

In this chapter, I relate bioturbation to species composition in invertebrate datasets from two previously-published studies, using novel assemblage phylogenies and trait data. In year-long time series data taken from two sites (one disturbed, the other pristine; Solan *et al.*, 2004), I find that the sites have phylogenetically distinct species composition, but both ecosystem function and species turnover are random with respect to phylogenetic structure and species' traits. Along an organic enrichment gradient (Godbold & Solan, 2009), I find greater phylogenetic clustering in more disturbed assemblages, and that species' traits and phylogenetic dispersion are poor predictors of bioturbation when compared with degree of enrichment and species richness.

5.3 Methods

This study is concerned with how well phylogenetic dispersion can predict ecosystem function and species turnover in marine benthic invertebrate assemblages. I used two different datasets and phylogenies, first assessing their phylogenetic composition and dispersion, and then attempting to explain ecosystem function (sediment mixing depth) with phylogenetic dispersion and trait data. All analyses, apart from phylogenetic construction and the assessment of ecological nestedness, were conducted in `R` (v. 2.15.1; R Core Team, 2012); all other named pieces of software are `R` packages.

Ecological data

The 'time series' data (Solan *et al.*, 2004) were collected from two sites on the West Coast of Ireland (Galway Bay); one was a relatively disturbed site at a depth of 9m, perturbed by freshwater and sewage discharges from on-shore (the 'disturbed' site), while the second (the 'intact' site) was at a depth of 22m and

is designated as 'pristine' by the European Community programme. Monthly macro-invertebrate samples (five 0.1 m^2 van Veen grabs per site per month) were taken from December 1996—November 1997, apart from February 1997 when storm conditions were too intense for sampling.

The 'enrichment gradient' data (Godbold & Solan, 2009) were taken from Loch Creran (Scotland), along an organic enrichment gradient caused by a commercial salmon farm. Seven sites were set up approximately 50m from each other moving away from the fish farm (site 1 being closest to the farm), and at each site five samples (depth 10 cm, diameter 10 cm) of species were taken and identified. The total organic carbon concentration (TOC) of the sediment was determined by loss on ignition of 1.05 ± 0.01 g of dry sediment after combustion for one hour at 525°C.

In each dataset, sediment mixing depth was quantified using a sediment profile camera, and trait data on species' mobility and ability to rework sediment were scored (1–5, integer values) with reference to literature. Abundance-weighted means of these traits were calculated for each sample from each dataset. Mixing depths are plotted as positive values, such that a site with a mixing depth of six centimetres is recorded as '6cm'; this differs from Godbold & Solan (2009), where such a depth would be recorded as '-6cm'.

Phylogenetic data

I constrained each phylogeny according to the taxonomic information listed in the supplementary information. Both trees were based on *cytochrome c oxidase subunit I* sequences downloaded from `GenBank` (Benson *et al.*, 2009), trimmed to their open reading frames, and then aligned with `MAFFT` (Katoh *et al.*, 2002, 2005; Katoh & Toh, 2008), all using `phyloGenerator` (chapter three). Since many of the species in the dataset do not have representative sequences on `GenBank` (Benson *et al.*, 2009), replacement sequences were found using `phyloGenerator`'s `replace` method. In cases where no replacement that formed a monophyletic clade with the target species could be found, no direct replacement for that target species was included in the alignment; this was the case for 41 out of 146 species in the

time series dataset, and 36 out of 95 species in the enrichment gradient dataset.

The resulting alignments were then used for five separate `BEAST` analyses (Drummond *et al.*, 2006; Drummond & Rambaut, 2007; Drummond *et al.*, 2012), each using a different random starting tree, a relaxed lognormal clock, running for ten million generations, and sampling every 10 000 generations. I used a GTR+γ (with four rate categories) DNA substitution model for each analysis, and checked that the runs had converged, mixed, and achieved estimated sample sizes greater than 300 for each parameter using `Tracer` (Rambaut & Drummond, 2012). I then combined each alignment's runs, using a 10% burn-in for each, and used their maximum clade credibility tree for further analysis. Species missing from the trees were inserted into the phylogeny according to their taxonomy, with branch lengths manually adjusted following `phyloGenerator`'s `merge` method. Both phylogenies are shown in the supplementary materials (figures 5.8 and 5.9).

Statistical analysis

Assemblage composition

To compare samples' species compositions, in both datasets I calculated *PCD* (phylogenetic community dissimilarity; Ives & Helmus, 2010), and Rao's quadratic entropy (which, unlike *PCD*, accounts for species' abundances; Rao, 1982) standardised to account for within-assemblage diversity (H). H is defined in equations 5.1 and 5.2 (modified from `picante`'s help files; Kembel *et al.*, 2010), where x_{ki}/x_{lj} is the relative abundance of species i/j in assemblage k/l, and t_{ij} is half the the phylogenetic distance between species i and j. *PCD* and H were calculated using the functions `PCD` and `raoD` respectively in `picante`, and then hierarchically clustered using `hclust`'s `complete linkage` method. Combined with a hierarchical cluster analysis, both measures provide a good way to detect and visualise compositionally similar communities. I compared the mean dissimilarity among samples taken from the same and different sites with *t-tests*, and compared the observed t values with 1000 null t values where the identity of sites were randomly permuted. In the enrichment gradient analysis, I extended this to compare dis-

similarity among samples taken from neighbouring and more distant sites.

$$D_{kl} = \sum (t_{ij} \cdot x_{ki} \cdot x_{lj}) \tag{5.1}$$

$$H_{kl} = D_{kl} - \frac{D_{kk} + D_{ll}}{2} \tag{5.2}$$

In the enrichment gradient dataset, the measures *NODF* (*nestedness* metric based on *overlap* and *decreasing fill*; Almeida-Neto *et al.*, 2008) and *WNODF* (an abundance-*weighted* form of *NODF*; Almeida-Neto & Ulrich, 2011) were used to assess the nestedness of species losses across the organic enrichment gradient. *NODF* is very sensitive to whether depauperate assemblages contain subsets of the most species-rich assemblages (Ulrich *et al.*, 2009), and distinguishes between species compositional (site; row) and species occupancy (species; column) nestedness. Before analysis the site-species matrix was sorted by the number of assemblages in which each species was present, but site order reflected the enrichment gradient and so was not changed. When calculating *NODF*, an independent swap null model (31500 swaps, 1000 randomisations) was used to assess significance, and 1000 row/column weight-fixed randomisations were used to assess *WNODF*'s significance. All calculations used the program `NODF` (Almeida-Neto & Ulrich, 2011).

Assemblages' phylogenetic dispersion

D (Fritz & Purvis, 2010) values were calculated using the total species lists of each dataset as source pools, to assess the dispersion of species present in each sample. A modified form of *D*, which I denote D_C (a *continuous* measure of *dispersion*), was used to assess the dispersion of species' abundances, using a source pool of only those species present in each assemblage. D_C is very similar to *D*, but species' actual abundances are used when calculating independent contrasts. The random simulations are otherwise identical, and in Brownian randomisation a continuous trait is simulated as in *D*, only each species' trait value is then ranked, replaced by the observed abundance having that rank, and then the sums of their independent contrasts calculated. Code to calculate D_C is soon to be integrated into the `R`

package `caper` (Orme *et al.*, 2011) as the function `phylo.d.c`.

Changes in D and D_C through the time series data were modelled according to the site from which they were measured and time. D_C values of turnover in species' abundances (the difference between species' abundances in one month and the previous month at each site) were calculated for all temporally contiguous months, which I denote as D'_C. A D'_C value less than one would indicate phylogenetic conservatism of turnover, perhaps because whole clades have increased/decreased *en masse*, while a value greater than one would indicate overdispersion of turnover and so some kind of phylogenetic compensation. D and D_C were also regressed against distance along the enrichment gradient.

Prediction of ecosystem function

I used mixing depth as a measure of ecosystem function, as it is directly affected by bioturbation and, by altering sediment structure, controls bacterial productivity (Kristensen, 2000) and nutrient flux (Norling *et al.*, 2007). In the time series dataset, mixing depth was modelled as a function of site and (in separate models) D, D_C, and the abundance-weighted means of species' mobility and reworking abilities. To test the significance of the measures, each model was compared using an ANOVA against a model containing only the site from which each measurement was taken.

Previous work on the enrichment gradient (Godbold & Solan, 2009) has compared the relative importance of TOC and species richness as predictors of mixing depth, and so these were assessed along with the D, D_C, and the abundance-weighted means of species' mobility and reworking abilities. However, unlike Godbold & Solan (2009), I incorporated position along the enrichment gradient (as a continuous variable) in the analysis. I measured relative importance following Lindeman *et al.* (1980), conducting partial linear regressions and averaging over all orderings of sequential r^2s to calculate each variable's contribution to model fit (named LMG by Grömping, 2006). I used the `boot.relimp` function in `relaimpo` (Grömping, 2006) to calculate LMG for each variable, and estimate their bootstrapped 95% confidence intervals.

	Slope	r^2	r^2_{null}	F	p
D	-0.0077	0.11	0.06	1.04	0.32
D_C	0.0066	0.67	0.66	0.70	0.41
D'_C	-0.012	0.32	0.31	0.40	0.54
Reworking	-0.0079	0.14	0.02	2.79	0.11
Mobility	-0.0083	0.23	0.02	5.14	0.035
Mixing depth	-0.15	0.88	0.68	29.54	< 0.0001
Species richness	0.78	0.95	0.93	7.98	0.01

Table 5.1: Changes in variables through the time series dataset. The second and third columns describe models of each measure as a function of site and time, while the fourth describes the r^2 of models incorporating each measure and site alone. The last two columns describe ANOVAs between models of the measures as functions of site and time, and models containing only site. Plots of these relationships are shown in figure 5.2.

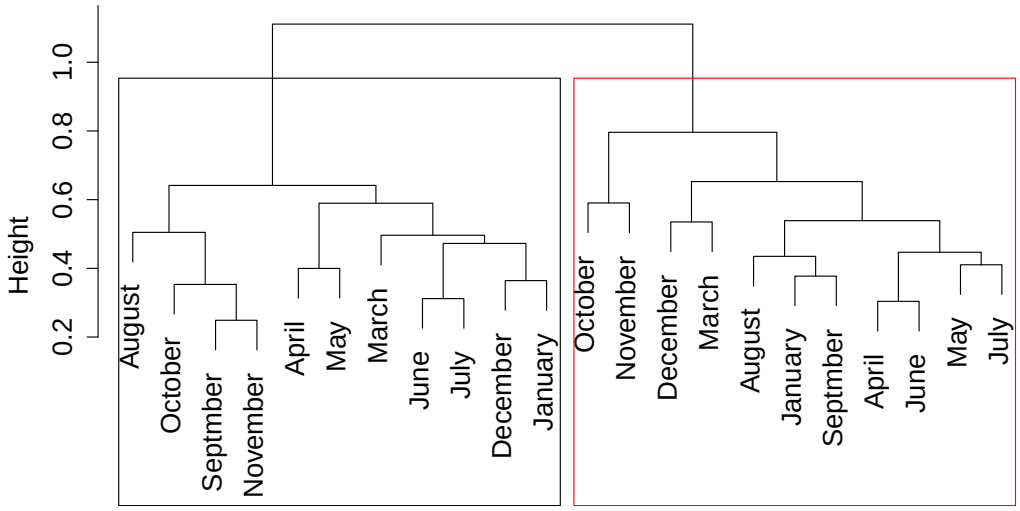
5.4 Results

Time series

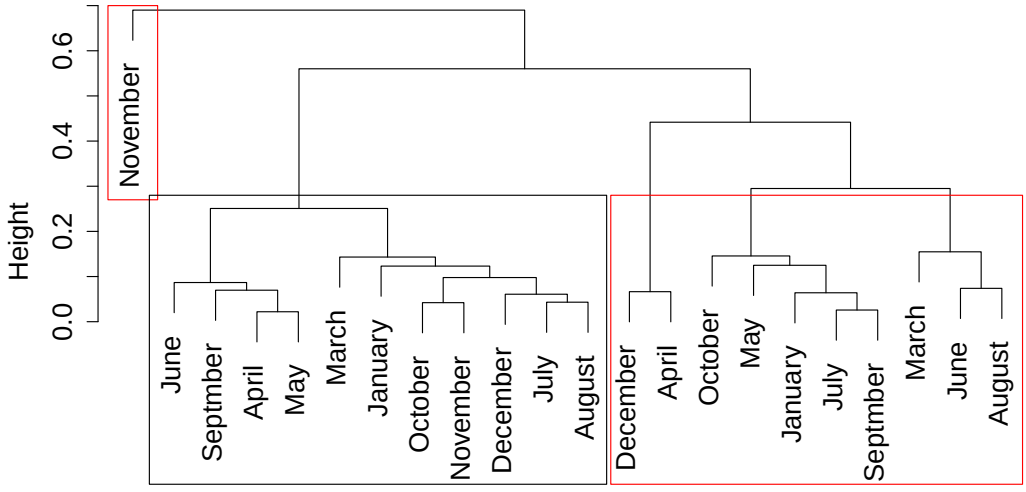
The two sites in the time series dataset are phylogenetically distinct (figure 5.1). While the disturbed site is more phylogenetically clustered than the intact site, there is no evidence that any of the dispersion measures changed through time (figure 5.2, table 5.1). Note that the unusually phylogenetically clustered disturbed November D'_C value is also an outlier in figure 5.1. Aside from a marginally significant relationship between mixing depth and species' mobility, there is no evidence that mixing depth is significantly related to anything other than site and species richness (table 5.2, figure 5.3).

Enrichment gradient

Assemblages nearby along the enrichment gradient have phylogenetically similar species' compositions (figure 5.4), and there is no evidence of nested species composition (figure 5.5). D remains relatively stable across the gradient, and while D_C is generally lesser closer to the source of organic enrichment, the most

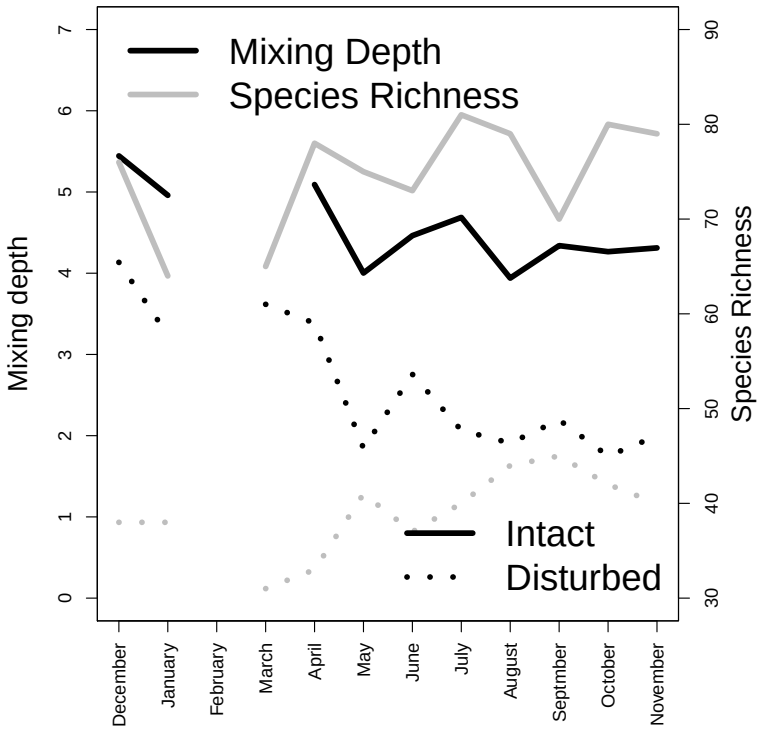


(a) *PCD*

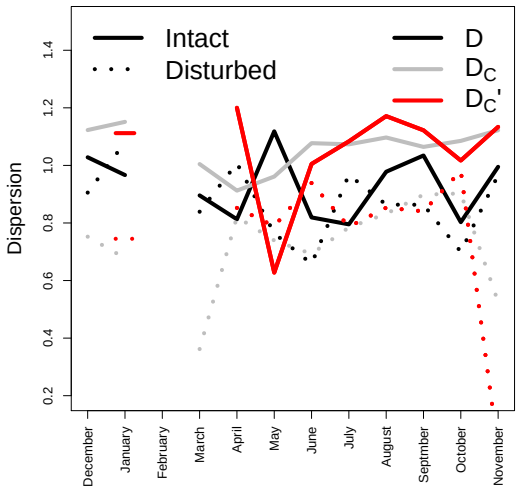


(b) *H*

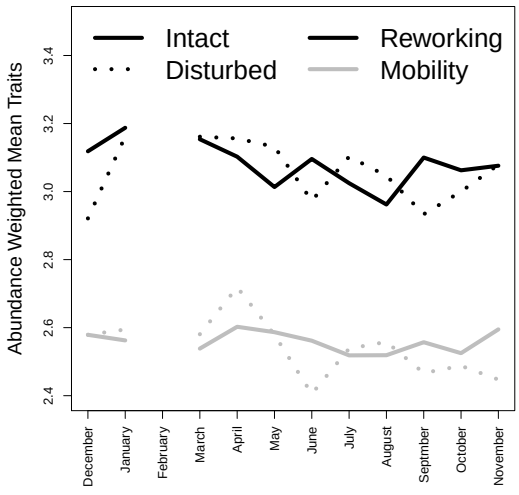
Figure 5.1: Hierarchical cluster dendrograms, grouping the time series data according to phylogenetic similarity. The intact sites are boxed by a black line, the disturbed by a red, and the labels indicate the month of sampling. (a) is based solely on species' presences (*PCD*), while (b) takes into account species' abundances (*H*), as discussed in the text. Both *PCD* ($t_{observed} = 48.6$, greatest $t_{null} = 3.00$) and *H* ($t_{observed} = 15.6$, greatest $t_{null} = 3.43$) are significantly smaller within sites than among sites.



(a) Mixing depth and species richness

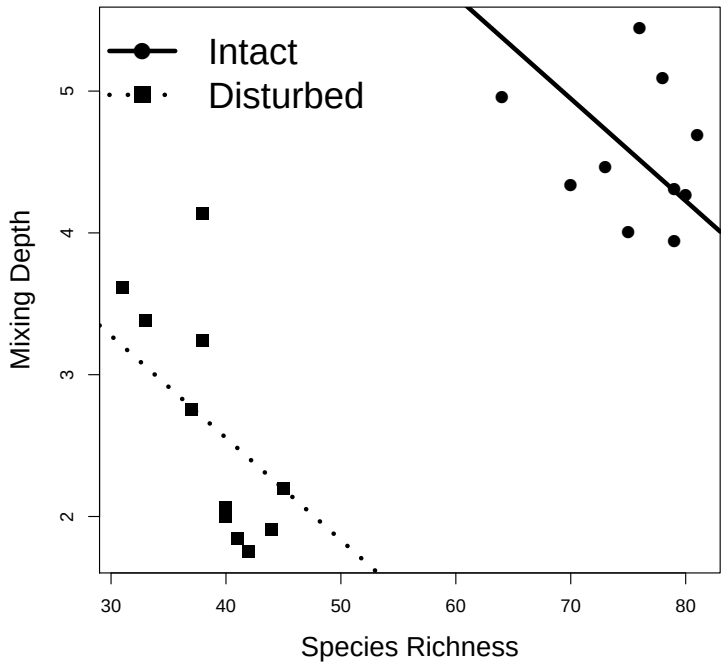


(b) Phylogenetic dispersion

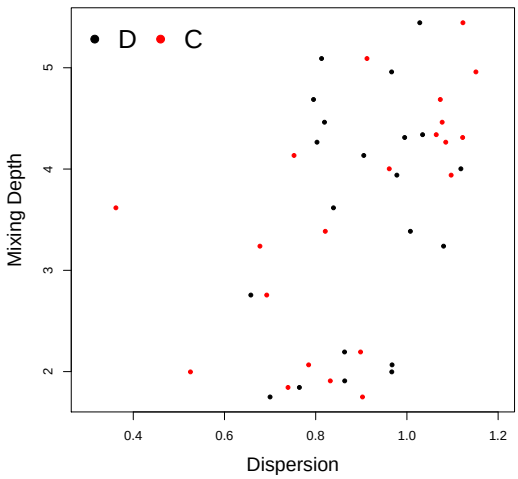


(c) Traits

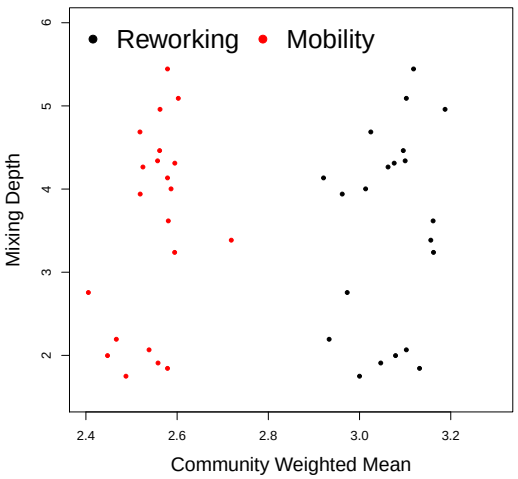
Figure 5.2: Change in variables through the time series dataset. Note that there is no mixing depth data for the month of April from the intact site. Regressions for each of these variables through time are described in table 5.1.



(a) Species richness



(b) Phylogenetic dispersion



(c) Traits

Figure 5.3: The drivers of mixing depth in the time series dataset. Regression estimates are given in table 5.2

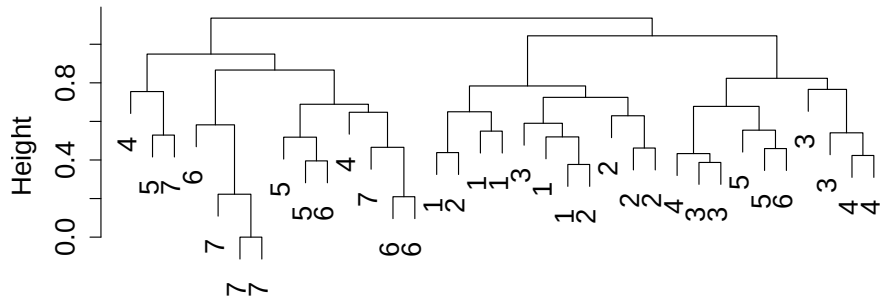
	Slope	r^2	r^2_{null}	F	p
Site	*NA*	0.68	*NA*	40.23	<0.0001
D	0.85	0.69	0.68	0.43	0.52
D_C	-1.55	0.71	0.68	1.60	0.22
Reworking	1.94	0.70	0.68	0.93	0.35
Mobility	4.69	0.74	0.68	4.52	0.048
Species richness	-0.07	0.76	0.68	5.86	0.03

Table 5.2: Models of mixing depth in the time series dataset. The second and third columns describe models of each measure as a function of site and time, while the fourth describes the r^2 of models incorporating each measure and site alone. The last two columns describe ANOVAs between models of the measures as functions of site and time, and models containing only site. The exception is the first row, which describes a model containing only site being compared with a null model consisting of a single overall mean. Plots of these relationships are shown in figure 5.3.

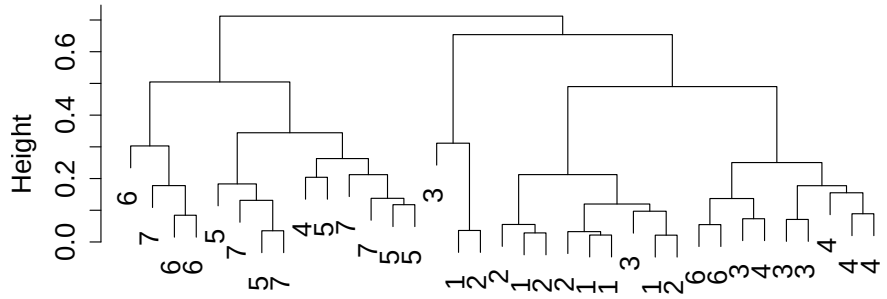
disturbed site has phylogenetically random species abundances (figure 5.6). Position along the enrichment gradient was the most important predictor of mixing depth, followed by species richness and TOC; phylogenetic dispersion was the worst predictor of mixing depth. Species' mean reworking and mobility scores were negatively correlated with ecosystem function (i.e., assemblages with species whose mean reworking abilities were *greater* had *lesser* mixing depth; table 5.3, figure 5.7).

5.5 Discussion

I have presented evidence that both datasets show phylogenetic structure (figures 5.1 and 5.4), and that the phylogenetic dispersion of species' abundances changes along an environmental stress gradient (figure 5.6). Ecosystem function correlates most strongly with site (table 5.2) and position along the enrichment gradient (table 5.3) in the time series and enrichment gradient datasets respectively. Phylogenetic dispersion and species' traits were relatively poor predictors of ecosystem function.

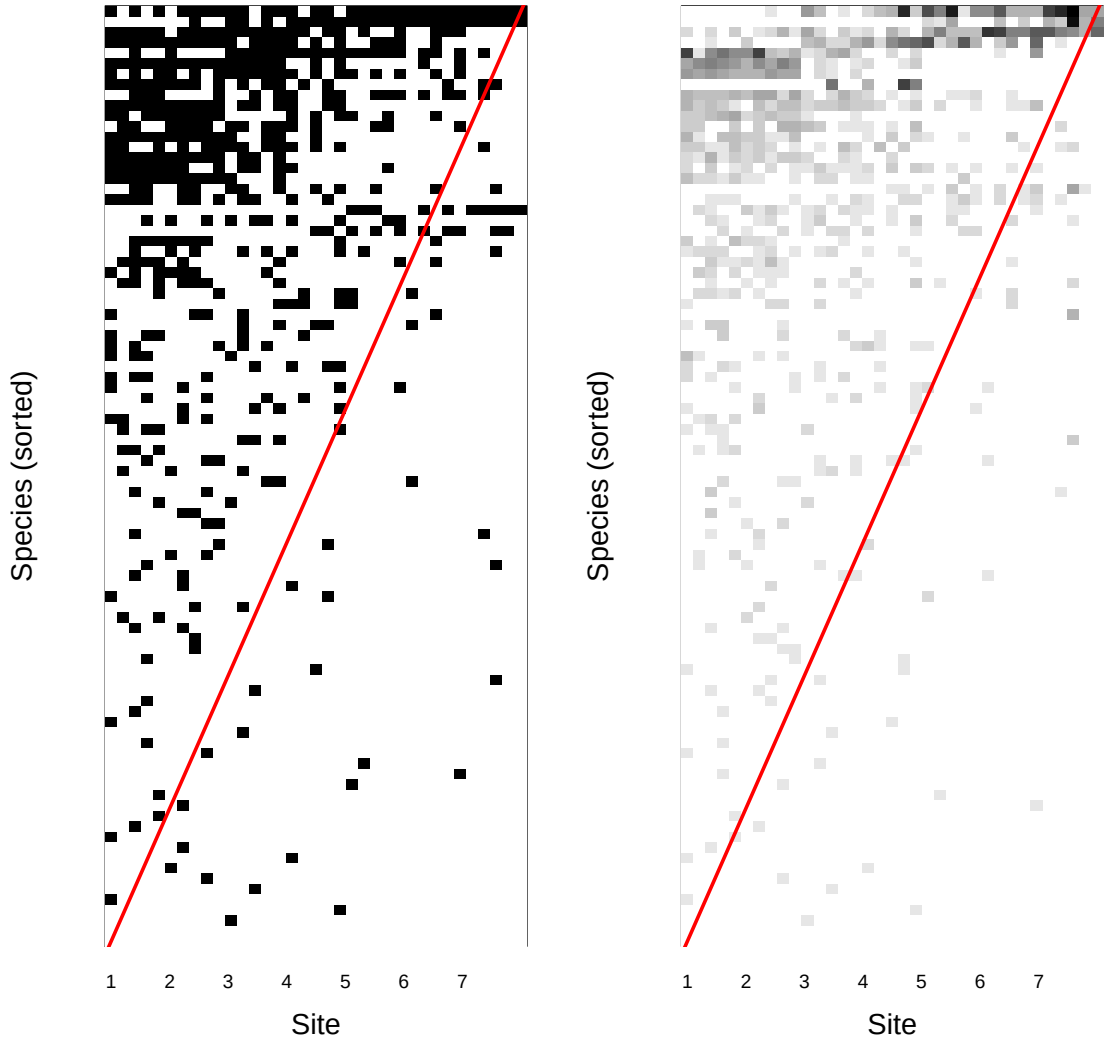


(a) *PCD*



(b) *H*

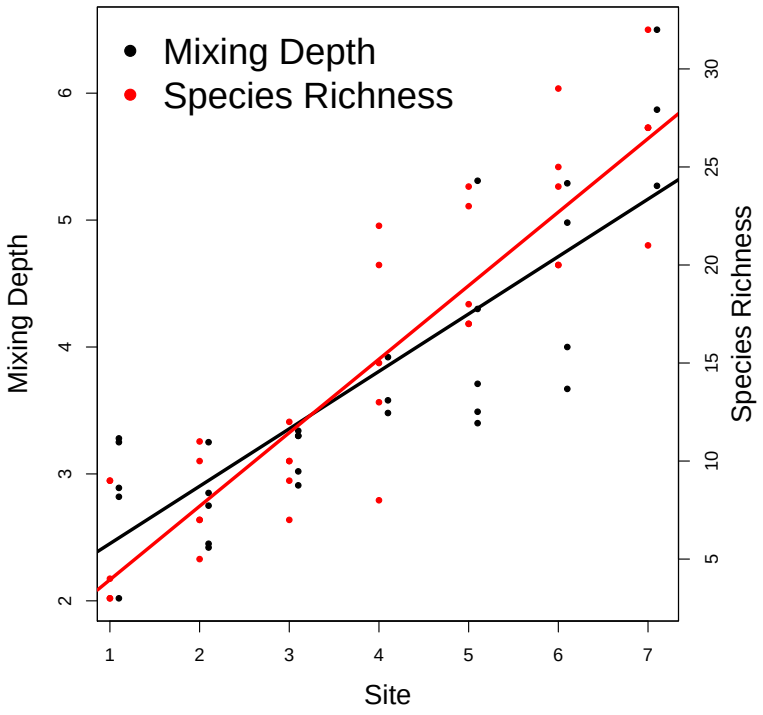
Figure 5.4: Hierarchical cluster dendrograms of the enrichment gradient data, showing assemblages with phylogenetically similar compositions. Numbers at tips indicate the site from which a sample was taken; site '1' is closest to the source of organic enrichment. (a) is based solely on species' presences (*PCD*), while (b) takes into account species' abundances (H), as discussed in the text. Both *PCD* ($t_{observed} = 13.7$, greatest $t_{null} = 3.02$) and H ($t_{observed} = 14.2$, greatest $t_{null} = 3.45$) are significantly smaller within sample sites along the gradient than among sample sites. The same is true when neighbouring sites' dissimilarities are compared with more distant sites (*PCD*: $t_{observed} = 23.9$, greatest $t_{null} = 2.99$; H: $t_{observed} = 22.0$, greatest $t_{null} = 3.39$).



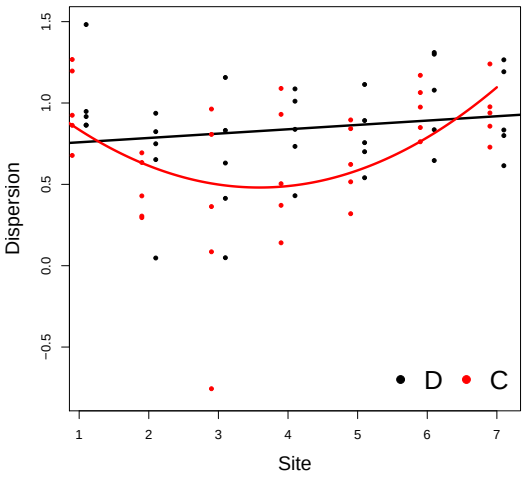
(a) Presence

(b) Abundance

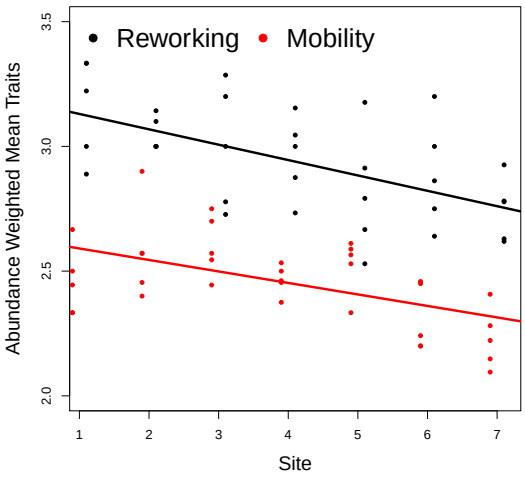
Figure 5.5: Species-site matrices of enrichment gradient data, where each row is a species and each column a sample. Sites are also marked; site '1' is closest to the source of organic enrichment. In (a), black squares indicate species that were present in an assemblage, and there is slight, non-significant suggestion of nested species occupancy ($NODF_{obs.row} = 31.36$, $NODF_{sim.row} = 30.60$, $p = 0.094$) and significantly less nestedness of species composition than under the null model ($NODF_{obs.col} = 41.45$, $NODF_{sim.row} = 44.15$, $p = 0.0011$). In (b), shading indicates species' abundances (twenty Jenk's quantiles from `classInt`; Bivand *et al.*, 2012a), and there is essentially random nestedness of species occupancy ($WNODF_{obs.col} = 41.45$, $WNODF_{obs.col} = 46.17$, $p = 0.055$) and less nestedness of species composition than expected under the null ($WNODF_{obs.row} = 31.36$, $WNODF_{sim.row} = 49.67$, $p < 0.0001$). Each matrix's minor diagonal drawn in red.



(a) Species richness and mixing depth

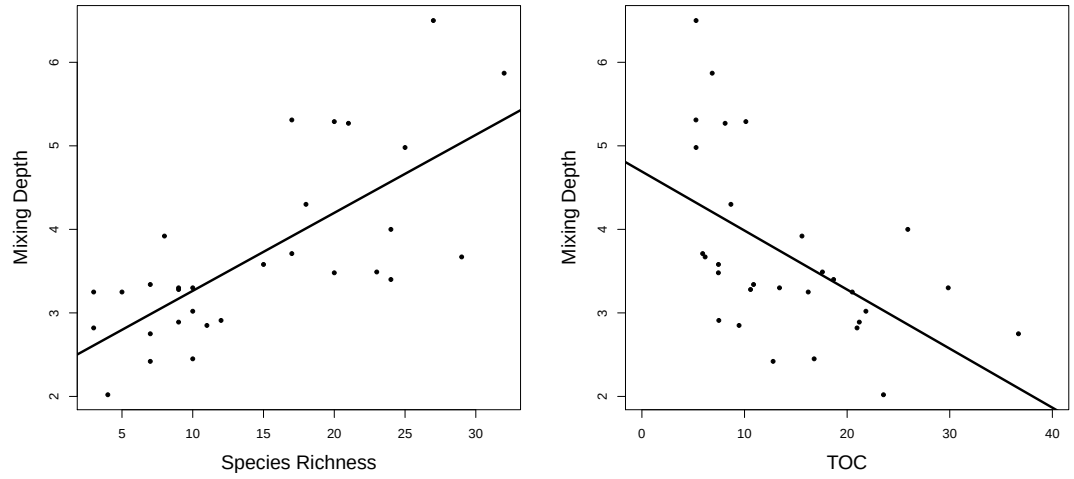


(b) Dispersion



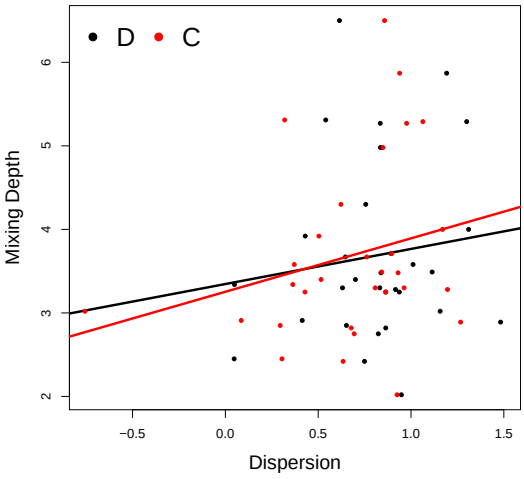
(c) Traits

Figure 5.6: Change across the enrichment gradient. Site 1 is closest to the source of organic enrichment; small variation has been introduced in the horizontal axis to avoid over-plotting. In (a), the trend (and strong correlation) between mixing depth and species richness is apparent, while in (b) and (c) it is evidence that dispersion and trait measures respond less strongly. D_C (in b) has had a quadratic curve fitted to it; this curve is a significantly better fit than a straight line (ANOVA $F_{1,32} = 9.18$, $p = 0.0048$, model $r^2 = 0.26$).

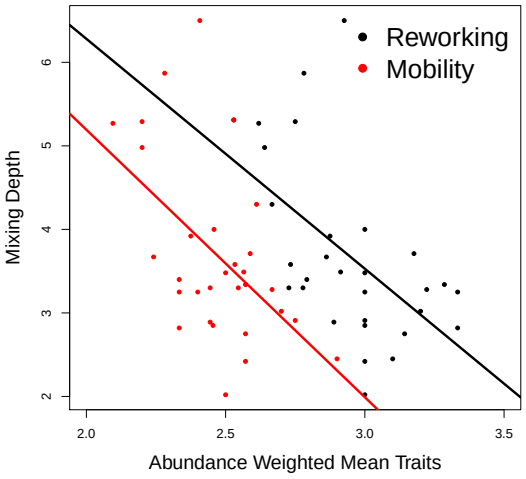


(a) Species richness

(b) TOC



(c) Phylogenetic dispersion



(d) Traits

Figure 5.7: Mixing depth plotted against various measures in the enrichment dataset. In (a) and (b) the strong correlations with species richness and TOC are apparent, while in (c) and (d) the smaller influences of phylogenetic dispersion and trait values can be seen. The importance of each of these variables is described in table 5.3.

	LMG	95% CI
Gradient	0.33	0.18–0.41
Species richness	0.18	0.10–0.25
TOC	0.11	0.05–0.18
Reworking	0.09	0.02–0.19
Mobility	0.05	0.02–0.15
D	0.02	0.00–0.15
D_C	0.01	0.01–0.11

Table 5.3: Importance of explanatory variables in the enrichment gradient analysis. The most important predictor of mixing depth is distance along the enrichment gradient, after which species richness and TOC are most important. Species traits, in particular reworking ability, are of some importance, but phylogenetic dispersion is a poor predictor. Note that Godbold & Solan (2009) have already shown that species richness and TOC are statistically significant predictors of bioturbation. These relationships are plotted in figure 5.7.

Assemblages phylogenetic dispersion and composition

The time series dataset shows very little change in phylogenetic dispersion; D and D'_C values fluctuate close to 1.0 (the null expectation, indicating no phylogenetic signal of assemblage membership or abundance) in both sites, though D_C is more phylogenetically clustered in the disturbed site (figure 5.2). However, the two sites' species are phylogenetically distinct (there is no site overlap in figure 5.1). A taxonomically diverse range of species found at the intact site are either rare or almost entirely absent from the disturbed site, such as *Amphiura filiformis* (the burrowing brittlestar), *Cerianthus lloydii* (the lesser cylinder anemone), and *Turritella communes* (the common tower shell). The final measurement of the disturbed site reveals extremely phylogenetically clustered species turnover (figure 5.2b), and the same sample is most phylogenetically distinct from all other measurements when abundances are considered (figure 5.1b). Dispersal between local communities is common in benthic assemblages (Covich *et al.*, 2004), so this may reflect a sudden immigration of novel species, but without further data it is impossible to know whether this was a stable shift to a new regime or something more transient.

Assemblages nearby along the enrichment gradient have phylogenetically simi-

lar compositions (figure 5.4), which is consistent with Godbold & Solan's (2009) suggestion that sites can be fuzzily grouped along the enrichment gradient. The quadratic relationship between enrichment and D_C suggests the most disturbed site has random phylogenetic dispersion, possibly reflecting a lack of power in species-poor assemblages (some have only three species; figure 5.6). Indeed, the most species poor assemblages contained only polychaete worms, suggesting phylogenetically biased filtering was taking place, and when site 1 is excluded, D exhibits a stronger change across the gradient (supplementary materials, figure 5.10). However, extremely organically polluted benthic sites can have more variable species' compositions (Conlan *et al.*, 2004), and the non-linearity of D_C across the gradient may be a response to environmental drivers over than eutrophication. For instance, large debris in the immediate vicinity of the fish farm could cause local disruption to sediment, altering species composition.

Ecosystem function is driven by species richness

Site-level variation drives the majority of variation in mixing depth in the time series dataset and the (marginally significant) effect of mobility is small in comparison with site (figure 5.3 and table 5.2). Though species richness was an important determinant of ecosystem function (as found by Godbold & Solan, 2009) in the enrichment gradient dataset, the gradient itself was the predominant driver of the system, and there was little effect of phylogenetic dispersion. That total organic carbon (TOC) was less important than species richness does not imply that species richness is a dominant driver to enrichment. Chemical measures of enrichment from fish farms do not perfectly correlate with enrichment levels (Weston, 1990) and so distance from the fish farm may be a better measure of disturbance than TOC, particularly if the fish farm is a source of other kinds of contaminants and damage. The importance of species' traits is debatable given that species' predicted reworking ability was *negatively* correlated with mixing depth (figure 5.7c). This is likely to be a sampling effect; the enrichment gradient filters species according to traits other than reworking ability, and so when species richness increases, so too does the variation in species' traits, implying that these

weighted abundances are simply another way of measuring species richness.

Productivity in the time series data is known to be driven by the ecosystem engineer *Amphiura filiformis* (Solan *et al.*, 2004); its abundance is two orders of magnitude greater in the intact site, and so productivity is greater in the intact site. The negative relationship between species richness and mixing depth *within* the sites could be an artefact of temporal autocorrelation (see the decrease in mixing depth through time in the disturbed site in figure 5.3a), or it could reflect the impact of competition. In particular, sites crowded with filter-feeding species would have reduced bioturbation if those filter-feeders are attached to the sediment and thus hold it in place.

5.6 Conclusion

Quantifying the functional responses of benthic invertebrate assemblages is difficult, because they are such a taxonomically and morphologically diverse group that they are difficult to measure on a common scale. While I have been able to show that benthic assemblages have different phylogenetic compositions, phylogenetic dispersion (and trait data) fail to explain variation in ecosystem function. These results suggest that environmental variation and ecosystem engineers, perhaps followed by interspecific competition, control ecosystem productivity.

5.7 Supplementary information

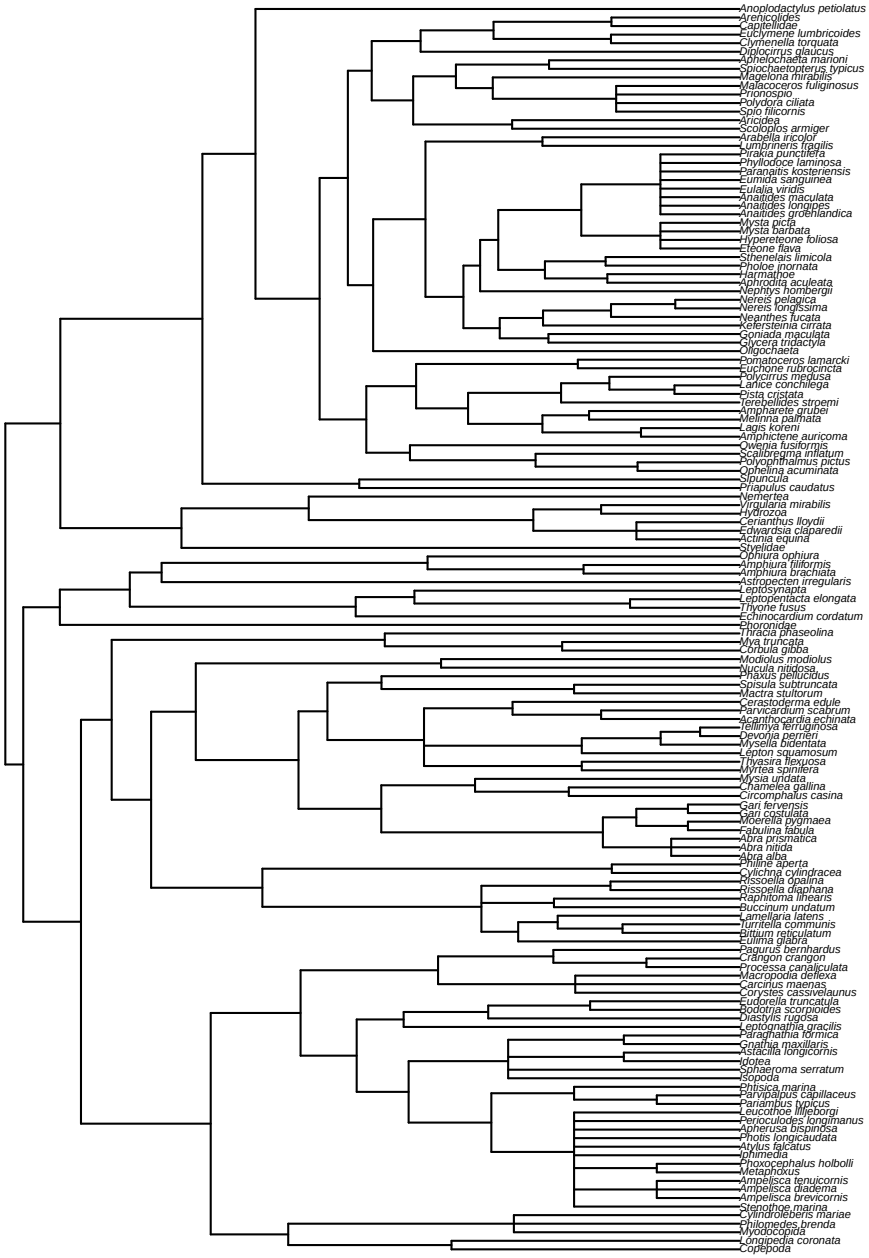


Figure 5.8: Phylogeny of the time series data, created as described in the text.

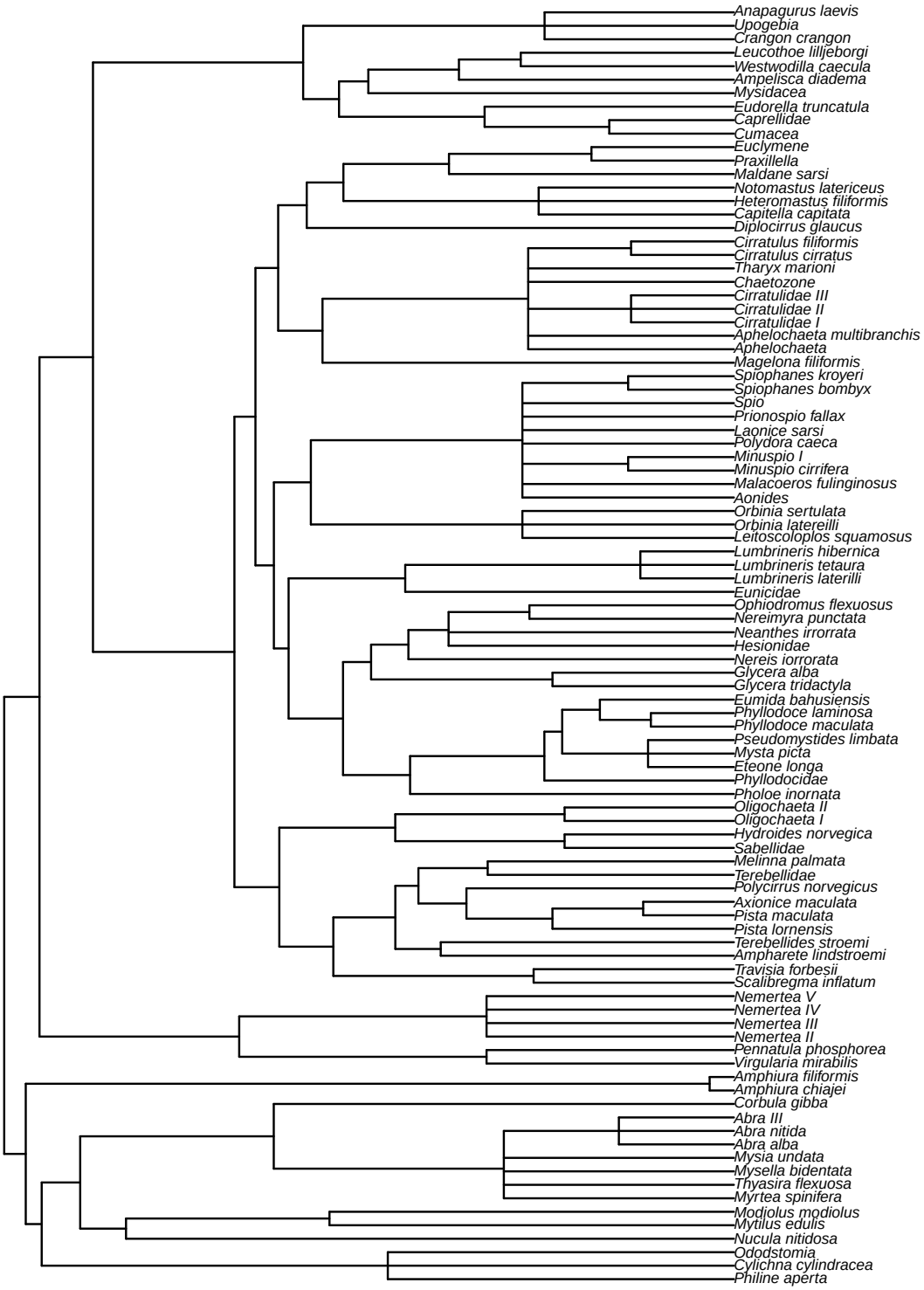


Figure 5.9: Phylogeny of the gradient data, created as described in the text.

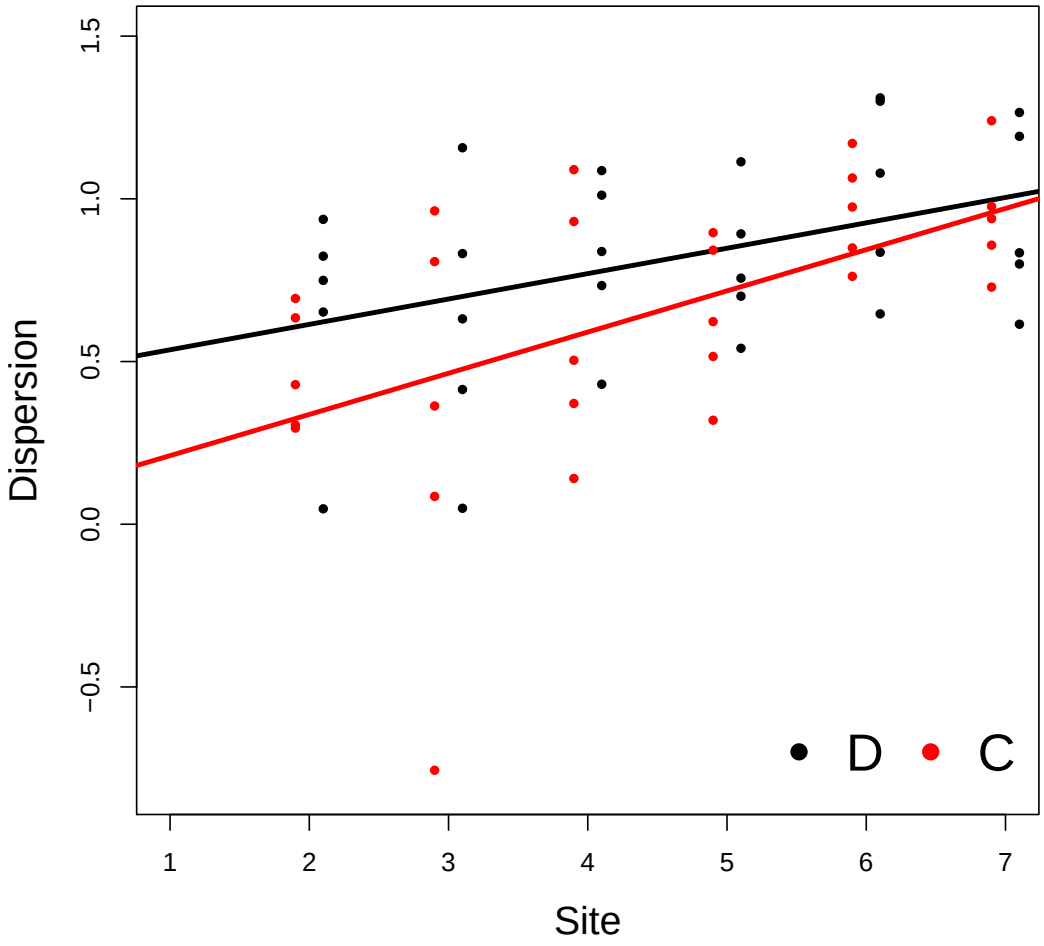


Figure 5.10: Change in phylogenetic dispersion across the organic enrichment gradient, excluding the most impacted site. Each line is a linear regression; note that the D regression has a greater slope (0.029 vs. 0.078) than in figure 5.6b.

Time Series Data Taxonomy

Phylum CNIDARIA
Superclass HYDROZOA
Hydrozoa sp.
Superclass ANTHOZOA
Class OCTOCORALLIA
Order PENNATULACEA
Family Virgulariidae
Virgularia mirabilis (Müller, 1776)
Class HEXACORALLIA
Order CERIANTHARIA
Suborder SPIRULARIA
Family Cerianthidae
Cerianthus lloydii (Gosse, 1859)
Order ACTINIARIA
Suborder NYNANTHEAE
Family Actiniidae
Actinia equina (Linnaeus, 1758)
Family Edwardsiidae
Edwardsia claparedii (Panceri, 1869)

Phylum NEMERTEA
Nemertea spp.

Phylum PRIAPULIDA
Family Priapulidae
Priapulus caudatus (Lamarck, 1816)

Phylum SIPUNCULA
Sipuncula spp.

Phylum ECHIURA
Order ECHIURIDA
Family Echiuridae
Thalassema thalassemum (Pallas, 1766)

Phylum ANNELIDA
Class POLYCHAETA
Order PHYLLODOCIDA
Superfamily APHRODITOIDEA
Family Aphroditidae
Aphrodita aculeata (Linnaeus, 1758)
Family Polynoidae
Harmathoe spp. (Kinberg, 1855)
Family Pholoidae
Pholoe inornata (Johnston, 1839)
Family Sigalionidae
Sthenelais limicola (Ehlers, 1864)
Superfamily PHYLLODOCOIDEA
Family Phyllodocidae
Subfamily Eteoninae
Eteone flava/longa (Fabricius, 1780)
Hypereteone foliosa (Quatrefages, 1866)
Mysta barbata (Malmgren, 1865)
Mysta picta (Quatrefages, 1866)
Subfamily Phyllodocinae
Anaitides groenlandica (Oersted, 1842)
Anaitides longipes (Kinberg, 1866)
Anaitides maculata (Linnaeus, 1767)
Eulalia viridis (Linnaeus, 1767)
Eumida sanguinea (Oersted, 1843)

	Paranaitis kosteriensis	(Malmgren, 1867)
	Phyllodoce laminosa	(Lamarck, 1818)
	Pirakia punctifera	(Grube, 1860)
Superfamily GLYCEROIDEA		
Family Glyceridae		
	Glycera tridactyla	(Schmarda, 1861)
Family Goniadidae		
	Goniada maculata	(Oersted, 1843)
Superfamily NEREIDOIDEA		
Family Hesionidae		
Subfamily Hesioninae		
	Kefersteinia cirrata	(Keferstein, 1862)
Family Nereididae		
	Neanthes fucata	(Savigny, 1820)
	Nereis longissima	(Johnston, 1840)
	Nereis pelagica	(Linnaeus, 1758)
Superfamily NEPHTYOIDEA		
Family Nephtyidae		
	Nephtys hombergii	(Savigny, 1818)
Order EUNICIDA		
Family Lumbrineridae		
	Lumbrineris fragilis	(Müller, 1776)
Family Oenonidae		
	Arabella iricolor	(Montagu, 1804)
Order ORBINIIDA		
Family Orbiniidae		
	Scoloplos armiger	(Müller, 1776)
Family Paraonidae		
	Aricidea sp.	(Webster, 1879)
Order SPIONIDA		
Superfamily SPIONOIDEA		
Family Spionidae		
	Malacoceros fuliginosus	(Claparède, 1868)
	Polydora ciliata	(Johnston, 1838)
	Prionospio spp.	(Malmgren, 1867)
	Spio filicornis	(Müller, 1766)
Superfamily MAGELONOIDEA		
Family Magelonidae		
	Magelona mirabilis	(Johnston, 1865)
Superfamily CHAETOPTEROIDEA		
Family Chaetopteridae		
	Spiochaetopterus typicus	(Sars, 1856)
Superfamily CIRRATULOIDEA		
Family Cirratulidae		
	Aphelochaeta marioni	(Saint-Joseph, 1894)
Order FLABELLIGERIDA		
Family Flabelligeridae		
	Diplocirrus glaucus	(Malmgren, 1867)
Order CAPITELLIDA		
Family Capitellidae		
	Capitellidae spp.	
Family Arenicolidae		
	Arenicolides sp.	(Mesnil, 1898)
Family Maldanidae		
Subfamily Euclymeninae		
	Clymenella torquata	(Leidy, 1855)
	Euclymene lumbricoides	(Quatrefages, 1866)
Order OPHELIIDA		
Family Opheliidae		
Subfamily Ophelininae		
	Ophelina acuminata	(Oersted, 1843)
	Polyophthalmus pictus	(Dujardin, 1839)
Family Scalibregmatidae		
	Scalibregma inflatum	(Rathke, 1843)
Order OWENIIDA		

Family Oweniidae
Owenia fusiformis (Chiaje, 1842)

Order TEREBELLIDA
Family Pectinariidae
Amphictene auricoma (Müller, 1776)
Lagis koreni (Malmgren, 1866)
Family Ampharetidae
Subfamily Melinninae
Melinna palmata (Grube, 1869)
Subfamily Ampharetinae
Ampharete grubei (Malmgren, 1866)
Family Trichobranchidae
Terebellides stroemi (Sars, 1835)
Family Terebellidae
Subfamily Amphitritinae
Lanice conchilega (Pallas, 1766)
Pista cristata (Müller, 1776)
Subfamily Polycirrinae
Polycirrus medusa (Grube, 1850)
Order SABELLIDA
Family Sabellidae
Euchone rubrocincta (Sars, 1861)
Family Serpulidae
Subfamily Serpulinae
Pomatoceros lamarcki (Quatrefages, 1866)
Class OLIGOCHAETA
Oligochaeta spp.

Phylum CHELICERATA
Class PYCNOGONIDA
Family Phoxichilidiidae
Anoplodactylus petiolatus (Kryer, 1844)

Phylum CRUSTACEA
Class MAXILLOPODA
Subclass COPEPODA
Copepoda spp.
Order HARPACTICOIDA
Suborder POLYARTHRA
Family Longipediidae
Longipedia coronata (Claus, 1863)
Class OSTRACODA
Order MYODOCOPIDA
Myodocopida sp.
Family Philomedidae
Philomedes brenda (Baird, 1850)
Family Cylindroleberididae
Cylindroleberis mariae (Baird, 1850)

Class EUMALACOSTRACA
Subclass PERACARIDA
Order AMPHIPODA
Suborder GAMMARIDEA
Superfamily EUSIROIDEA
Family Eusiridae
Apherusa bispinosa (Bate, 1856)
Superfamily OEDICEROTOIDEA
Family Oedicerotidae
Perioculodes longimanus (Bate & Westwood, 1868)
Superfamily LEUCOTHOIDEA
Family Leucothoidae
Leucothoe lilljeborgi (Boeck, 1861)

Family Stenothoidae		
	Stenothoe marina	(Bate, 1856)
Superfamily PHOXOCEPHALOIDEA		
Family Phoxocephalidae		
	Metaphoxus sp.	(Bonnier, 1896)
	Phoxocephalus holbolli	(Kryer, 1842)
Superfamily STEGOCEPHALOIDEA		
Family Iphimediidae		
	Iphimedia sp.	(Rathke, 1843)
Superfamily DEXAMINOIDEA		
Family Dexaminidae		
	Atylus falcatus	(Metzger, 1871)
Superfamily AMPELISCOIDEA		
Family Ampeliscidae		
	Ampelisca brevicornis	(Costa, 1853)
	Ampelisca diadema	(Costa, 1853)
	Ampelisca tenuicornis	(Liljeborg, 1855)
Superfamily COROPHIOIDEA		
Family Isaeidae		
	Photis longicaudata	(Bate & Westwood, 1862)
Suborder CAPRELLIDEA		
Infraorder CAPRELLIDA		
Superfamily CAPRELLOIDEA		
Family Caprellidae		
	Pariambus typicus	(Kröyer, 1845)
	Parvipalpus capillaceus	(Chevreux, 1888)
Superfamily PHTISICOIDEA		
Family Phtisicidae		
	Phtisica marina	(Slabber, 1769)
Order ISOPODA		
	Isopoda sp.	
Suborder GNATHIIDEA		
Family Gnathiidae		
	Gnathia maxillaris	(Montagu, 1804)
	Paragnathia formica	(Hesse, 1864)
Suborder FLABELLIFERA		
Family Sphaeromatidae		
	Sphaeroma serratum	(Fabricius, 1787)
Suborder VALVIFERA		
Family Idoteidae		
	Idotea sp.	(Fabricius, 1798)
Family Arcturidae		
	Astacilla longicornis	(Sowerby, 1806)
Order TANAIDACEA		
Suborder TANAIDOMORPHA		
Superfamily PARATANAOIDEA		
Family Anarthruridae		
Subfamily Leptognathiinae		
	Leptognathia gracilis	(Kröyer, 1842)
Order CUMACEA		
Family Bodotriidae		
Subfamily Bodotriinae		
	Bodotria scorpioides	(Montagu, 1804)
Family Leuconiidae		
	Eudorella truncatula	(Bate, 1856)
Family Diastylidae		
	Diastylis rugosa	(Sars, 1865)
Subclass EUCARIDA		
Order DECAPODA		
Suborder PLEOCYEMATA		
Infraorder CARIDEA		
Superfamily ALPHEOIDEA		
Family Processidae		
	Processa canaliculata	(Leach, 1815)
Superfamily CRANGONOIDEA		

Family Crangonidae
Crangon crangon (Linnaeus, 1758)
Infraorder ANOMURA
Superfamily PAGUROIDEA
Family Paguridae
Pagurus bernhardus (Linnaeus, 1758)
Infraorder BRACHYURA
Section OXYRHYNCHA
Superfamily MAJOIDEA
Family Majidae
Subfamily Inachinae
Macropodia deflexa (Forest, 1978)

Section CANCRIDEA
Superfamily CANCROIDEA
Family Corystidae
Corystes cassivelaunus (Pennant, 1777)
Section BRACHYRHYNCHA
Superfamily PORTUNOIDEA
Family Portunidae
Subfamily Carcininae
Carcinus maenas (Linnaeus, 1758)

Phylum MOLLUSCA
Class GASTROPODA
Subclass PROSOBRANCHIA
Order MESOGASTROPODA
Superfamily CERITHIACEA
Family Cerithiidae
Subfamily Bittiinae
Bittium (Bittium) reticulatum (da Costa, 1778)
Family Turritellidae
Subfamily Turritellinae
Turritella (Turritella) communis (Risso, 1826)
Superfamily LAMELLARIACEA
Family Lamellariidae
Lamellaria latens (Müller, 1776)
Superfamily EULIMACEA
Family Eulimidae
Eulima glabra (da Costa, 1778)
Order NEOGASTROPODA
Superfamily MURICACEA
Family Buccinidae
Subfamily Buccininae
Buccinum undatum (Linnaeus, 1758)
Superfamily CONACEA
Family Turridae
Subfamily Daphnellinae
Raphitoma linearis (Montagu, 1803)
Order HETEROSTROPHA
Superfamily RISSOELLACEA
Family Rissoellidae
Rissoella (Rissoella) diaphana (Alder, 1848)
Rissoella (Jeffreysina) opalina (Jeffreys, 1848)

Subclass OPISTHOBRANCHIA
Order CEPHALASPIDEA
Superfamily PHILINACEA
Family Cylichnidae
Cylichna (Cylichna) cylindracea

(Pennant, 1777)
Family Philinidae
Philine (Philine) aperta (Linnaeus, 1767)
Class PELECYPODA
Order NUCULOIDA
Superfamily NUCULACEA
Family Nuculidae
Subfamily Nuculinae
Nucula (Nucula) nitidosa (Winckworth, 1930)
Order MYTILOIDA
Superfamily MYTILACEA
Family Mytilidae
Subfamily Modiolinae
Modiolus (Modiolus) modiolus
(Linnaeus, 1758)
Order VENEROIDA
Superfamily LUCINACEA
Family Lucinidae
Subfamily Myrteinae
Myrtea spinifera (Montagu, 1803)
Family Thyasiridae
Subfamily Thyasirinae
Thyasira (Thyasira) flexuosa
(Montagu, 1803)
Superfamily GALEOMMATACEA
Family Leptonidae
Lepton squamosum (Montagu, 1803)
Family Montacutidae
Subfamily Montacutinae
Devonia perrieri (Malard, 1904)
Tellimya ferruginosa (Montagu, 1808)
Subfamily Mysellinae
Mysella bidentata (Montagu, 1803)
Superfamily CARDIACEA
Family Cardiidae
Subfamily Cardiinae
Acanthocardia (Acanthocardia) echinata
(Linnaeus, 1758)
Parvicardium scabrum (Philippi, 1844)
Subfamily Laevicardiinae
Cerastoderma edule (Linnaeus, 1758)

Superfamily MACTRACEA
Family Mactridae
Subfamily Mactrinae
Mactra (Mactra) stultorum (Linnaeus, 1758)
Spisula (Spisula) subtruncata
(da Costa, 1778)
Superfamily SOLENACEA
Family Pharidae
Phaxus pellucidus (Pennant, 1777)
Superfamily TELLINACEA
Family Tellinidae
Subfamily Tellininae
Fabulina fabula (Gmelin, 1791)
Moerella pygmaea (Lovén, 1846)
Family Psammobiidae
Subfamily Psammobiinae
Gari (Psammobella) costulata
(Turton, 1822)
Gari (Psammobia) fervensis
(Gmelin, 1791)
Family Semelidae
Abra alba (Wood, 1802)
Abra nitida (Müller, 1776)
Abra prismatica (Montagu, 1808)

Superfamily VENERACEA
Family Veneridae
Subfamily Venerinae
Circomphalus casina (Linnaeus, 1758)
Subfamily Chioninae
Chamelea gallina (Linnaeus, 1758)
Family Petricolidae
Mysia undata (Pennant, 1777)
Order MYOIDA
Suborder MYINA
Superfamily MYACEA
Family Myidae
Subfamily Myinae
Mya (Mya) truncata (Linnaeus, 1758)
Family Corbulidae
Subfamily Corbulinae
Corbula (Variocorbula) gibba (Olivi, 1792)
Order PHOLADOMYOIDA
Superfamily THRACIACEA
Family Thraciidae
Thracia (Thracia) phaseolina (Lamarck, 1818)

Phylum PHORONIDA
Family Phoronidae
Phoronidae sp.

Phylum ECHINODERMATA
Class ASTEROIDEA
Family Astropectinidae
Astropecten irregularis (Pennant, 1777)
Class OPHIUROIDEA
Order OPHIURIDA
Family Amphiuridae
Amphiura brachiata (Montagu, 1804)
Amphiura filiformis (Mller, 1776)
Family Ophiuridae
Ophiura ophiura (Linnaeus, 1758)
Subphylum ECHINOZOA
Class ECHINOIDEA
Order SPATANGOIDA
Family Loveniidae
Echinocardium cordatum (Pennant, 1777)
Class HOLOTHURIOIDEA
Order DENDROCHIROTIDA
Family Phyllophoridae
Thyone fusus (Müller, 1776)
Family Cucumariidae
Leptopentacta elongata (Duben & Koren, 1845)
Order APODIDA
Family Synaptidae
Leptosynapta sp. (Verrill, 1867)

Phylum CHORDATA
Subphylum TUNICATA
Class ASCIDIACEA
Order PLEUROGONA
Suborder STOLIDOBRANCHIATA
Family Styelidae
Styelidae sp.

Gradient Data Taxonomy

Phylum CNIDARIA
Superclass ANTHOZOA
Class OCTOCORALLIA
Order PENNATULACEA
Family Virgulariidae
Virgularia mirabilis (Müler, 1776)
Family Pennatulidae
Pennatula phosphorea (Linnaeus, 1758)

Phylum PLATYHELMINTHES
Platyhelminthes spp.

Phylum NEMERTEA
Nemertea spp.

Phylum ANNELIDA
Class POLYCHAETA
Order PHYLLODOCIDA
Superfamily APHRODITOIDEA
Family Pholoidae
Pholoe inornata (Johnston, 1839)
Superfamily PHYLLODOCOIDEA
Family Phyllodocidae
Subfamily Eteoninae
Eteone longa (Fabricius, 1780)
Mysta picta (Quatrefages, 1866)
Pseudomystides limbata (Saint-Joseph, 1888)
Subfamily Phyllodocinae
Phyllodoce maculata (Linnaeus, 1767)
Eumida bahusiensis (Bergstrom, 1914)
Phyllodoce laminosa (Lamarck, 1818)
Superfamily GLYCEROIDEA
Family Glyceridae
Glycera alba (Müler, 1776)
Glycera tridactyla (Schmarda, 1861)
Superfamily NEREIDOIDEA
Family Hesionidae
Hesionidae spp.
Subfamily Hesioninae
Nereimyra punctata (Müler, 1788)
Ophiodromus flexuosus (Chiaje, 1827)
Subfamily Nereididae
Neanthes irrorrata (Malmgren, 1867)
Superfamily NEPTHYOIDEA
Family Nepthyidae
Nepthys incisa (Malmgren, 1865)
Order EUNICIDA
Family Eunicidae
Eunicidae spp.
Family Lumbrineridae
Lumbrineris latereilli (Audouin & Milne-Edwards, 1833)
Lumbrineris tetaura (Schmarda, 1861)
Order ORBINIIDA
Family Orbiniidae
Leitoscoloplos mammosus (Mackie, 1987)
Orbinia latereilli (Audouin & Milne-Edwards, 1833)
Orbinia sertulata (Savigny, 1820)
Family Paraonidae
Cirrophorus sp. (Ehlers, 1908)
Oder SPIONIDA

Family Spionoidea		
	Aonides sp.	(Claparède, 1864)
	Laonice sarsi	(Soderstrom, 1920)
	Malacoeros fulinginosus	(Claparède, 1868)
	Minuspio cirrifera	(Wiren, 1883)
	Polydora caeca	(Oersted, 1843)
	Prionospio fallax	(Soderstrom, 1920)
	Spio sp.	(Fabricius, 1785)
	Spiophanes bombyx	(Claparède, 1870)
	Spiophanes kroyeri	(Grube, 1860)
Order MAGELONOIDEA		
Family Magelonidae		
	Magelona filiformis	(Wilson, 1959)
Order CIRRATULOIDEA		
Family Cirratulidae		
	Cirratulidae spp.	(Blake, 1991)
	Aphelochaeta sp.	(Blake, 1991)
	Aphelochaeta multibranchis	(Grube, 1863)
	Chaetozone sp.	(Malmgren, 1867)
	Cirratulus cirratus	(Müler, 1776)
	Cirratulus filiformis	(Keferstein, 1862)
	Tharyx sp.	(Webster & Benedict, 1887)
Order FLABELLIGERIDA		
Family Flabelligeridae		
	Diplocirrus glaucus	(Malmgren, 1867)
Order CAPITELLIDA		
Family Capitellidae		
	Capitella capitata	(Fabricius, 1780)
	Heteromastus filiformis	(Claparède, 1864
	Notomastus latericeus	(Sars, 1851)
Family Maldanidae		
Subfamily Maldaninae		
	Maldane sarsi	(Malmgren, 1865)
Subfamily Euclymeninae		
	Euclymene sp.	(Verrill, 1900)
	Praxiella sp.	(Verrill, 1881)
Order OPHELIIDA		
Family Opheliidae		
Subfamily Travisiinae		
	Travisia forbesii	(Johnston, 1840)
Subfamily Scalibregmatidae		
	Scalibregma inflatum	(Rathke, 1843)
Order TEREBELLIDAE		
	Terebellidae spp.	
Family Melinnindae		
	Melinna palmate	(Grube, 1869)
Family Ampharetinae		
	Ampharete lindstroemi	(Hessle, 1917)
Family Triobranchidae		
	Terebellides stroemi	(Sars, 1835)
Family Terebellidae		
Subfamily Amphitritinae		
	Axionice maculata	(Dalyell, 1853)
	Pista lornensis	(Pearson, 1969)
Subfamily Polycirrinae		
	Polycirrus norvegicus	(Wollebaek, 1912)
Order SANELLIDA		
Family Sabellidae		
	Sabellidae spp.	
Family Serpulidae		
Subfamily Serpulinae		
	Hydroides norvegica	Gunnerus, 1786
Order OLIGOCHAETA		
	Oligochaeta spp.	

Phylum CRUSTACEA
Class EUMALACOSTRACA
Subclass PERCARIDA
Order MYSIDACEA
Suborder MYSIDA
Family Mysidae
Mysidae spp.
Order AMPHIPODA
Suborder GAMMARIDEA
Superfamily OEDICEROTOIDEA
Family Oedicerotidae
Westwodilla caecula (Bate, 1856)
Superfamily LEUCOTHOIDEA
Family Leucothoidae
Leucothoe lilljeborgi (Boeck, 1861)
Superfamily AMPELISCOIDEA
Family Ampeliscidae
Ampelisca diadema (Costa, 1853)
Suborder CAPRELLIDEA
Infraorder CAPRELLIDA
Superfamily CAPRELLOIDEA
Family Caprellidae
Caprellidae spp.
Order CUMACEA
Cumacea spp.
Family Leuconiidae
Eudorella truncatula (Bate, 1856)
Subclass EUCARIDA
Order DECPODA
Suborder PLEOCYEMATA
Infraorder CARIDEA
Superfamily CRANGONOIDEA
Family Crangonidae
Crangon crangon (Linnaeus, 1758)
Infraorder THALASSINIDEA
Superfamily THALASSINOIDEA
Family Upogebiidae
Upogebia sp. (Leach, 1814)
Infraorder ANOMURA
Superfamily PAGUROIDEA
Family Paguirdae
Anapagurus laevis (Bell, 1845)

Phylum MOLLUSCA
Class GASTROPODA
Subclass PROSOBRANCHIA
Order HETEROSTROPHA
Superfamily PYRAMIDELLACEA
Family Pyramidellidae
Subfamily Odostomiinae
Odostomia sp. (Fleming, 1813)
Subclass OPHISTOBRANCHIA
Order CEPHALASPIDEA
Superfamily PHILINACEA
Family Cylichnidae
Cylichna (Cylichna) cylindracea (Pennant, 1777)
Family Philinidae
Philine (Philine) aperta (Linnaeus, 1767)

Class PELECYPODA
Order NUCULOIDEA
Superfamily NUCULACEA
Family Nuculidae
Subfamily Nuculinae
Nucula nitidosa (Winckworth, 1930)

Order MYTILOIDA
Superfamily MYTILACEA
Family Mytilidae
Subfamily Mytilinae
Mytilus edulis (Linnaeus, 1758)
Subfamily Modiolinae
Modiolus modiolus (Linnaeus, 1758)
Order VENEROIDA
Superfamily LUCINACEA
Family Lucinidae
Subfamily Myrteinae
Myrtea spinifera (Montagu, 1803)
Family Thyasiridae
Subfamily Thyasirinae
Thyasira flexuosa (Montagu, 1803)
Superfamily GALEOMMATACEA
Family Montacutinae
Subfamily Mysellinae
Mysella bidentata (Montagu, 1803)
Superfamily TELLINACEA
Family Semelidae
Abra alba (Wood, 1802)
Abra nitida (Müler, 1776)
Superfamily VENERACEA
Family Petricolidae
Mysia undata (Pannant, 1777)

Order MYOIDA
Suborder MYINA
Superfamily MYACEA
Family Corbulidae
Subfamily Corbulinae
Corbula gibba (Olivi, 1792)

Phylum ECHINODERMATA
Class OPHIUROIDEA
Order OPHIURA
Family Amphiuridae
Amphiura chiajei (Forbes, 1843)
Amphiura filiformis (Müler, 1776)

Chapter 6

The phylogenetic and trait structure of British bird and butterfly assemblages through time

6.1 Abstract

Species turnover in British bird and butterfly communities is widespread and well-documented, and is frequently linked to habitat degradation and climate change. Few studies have looked at how the phylogenetic and trait dispersion of assemblages change through time, but there is evidence to suggest that it decreases in the face of environmental damage. Using data from the British Trust for Ornithology's Breeding Birds Survey and UK Butterfly Monitoring Scheme, and a novel phylogeny of all resident butterflies in Britain, I assessed changes in phylogenetic and trait dispersion through time. Both datasets show strong underdispersion , apart from birds' abundances, which are phylogenetically overdispersed. However, the abundance-weighted mean of most butterfly traits has changed through time, indicating filtering mechanisms have changed through time. In addition, I find evidence of a phylogenetic bias to the species lost and

gained from assemblages. I argue that while there may have been a change in the drivers that structure British bird and butterfly assemblages, there has been little change in the magnitude of the effect of those drivers on assemblage structure.

6.2 Introduction

Most of Britain's birds and butterflies are considered to be in decline (Thomas *et al.*, 2004; Botham *et al.*, 2010; Eaton *et al.*, 2010). Although species' responses vary, there is a general consensus that specialist birds (Siriwardena *et al.*, 1998) and butterflies (Warren *et al.*, 2001) are declining the most, and that changes in farming practices have driven the particularly intense declines seen in many farmland birds (Robinson & Sutherland, 2002; Newton, 2004). Much of this work has focused on assessing species individually, but a growing number of studies have examined how assemblages as a whole respond to environmental change.

Such assemblage-based studies have found that increased land-use pressure tends to homogenise bird (e.g., Devictor *et al.*, 2008; Davey *et al.*, 2012) and butterfly (e.g., Eklöf *et al.*, 2012) communities, leading to an overall loss of diversity. As habitats become more degraded, specialist species are replaced by generalist species, reducing β diversity. Such changes can readily be assessed in a community phylogenetic context, asking whether assemblages become dominated by closely-related species with shared environmental tolerances (e.g., Warwick, 1995; Dinnage, 2009; Helmus *et al.*, 2010; Willis *et al.*, 2010). Similarly, if land use changes are selecting for particular kinds of species, functional trait data should help detect and describe those changes.

Despite the wealth of available data on their distributions, assemblage composition, and traits, no such study has yet been published for British birds or butterflies; the closest perhaps is Thomas' (2008) analysis of phylogenetic pattern in bird conservation concern. Indeed, there have been only a handful of cross-sectional (comparing different assemblages of different ages; Webb *et al.*, 2006; Letcher, 2009) and longitudinal (tracking particular assemblages through time; Cavender-Bares & Reich, 2012; Cadotte *et al.*, 2012) community phylogenetic studies in

any system, anywhere. Few studies have looked at the dispersion of functional traits, but variability has been reported in how the dispersion of species' traits responds to environmental change (e.g., Pakeman, 2011; Ding *et al.*, 2012; Gerisch *et al.*, 2012). Further, there is an ongoing debate as to whether functional trait and phylogenetic dispersion data do (Kraft & Ackerly, 2010) or do not (Swenson *et al.*, 2012) exhibit similar patterns.

To address these issues, I examined the phylogenetic and functional trait dispersion of the British Trust for Ornithology's Breeding Birds Survey (BTO's BBS; `http://www.bto.org/volunteer-surveys/bbs`) and UK Butterfly Monitoring Scheme (UKBMS) (`http://www.ukbms.org`), using a new phylogeny that contains all resident British butterfly species. Both are extremely detailed datasets that should permit the detection of even small changes in assemblage composition because they span so many years and species. With the exception of birds' abundances, both datasets show evidence of underdispersion, which suggests habitat filtering. Dispersion varies among sites, but there is little evidence of any change in assemblage structure through time. I also find evidence of phylogenetic pattern to species that are lost from, or join, assemblages. Combined with evidence showing that the traits of species within assemblages have changed, I argue there has been a change in the type of filtering processes operating in Britain without a change in the magnitude of that filtering.

6.3 Methods

Below I describe how the bird and butterfly ecological and environmental variable data were collected, the source of the phylogenies, the measures of dispersion used, and finally how the data were statistically analysed. All statistical analyses apart from those used to construct the phylogeny were conducted in `R` (v. 2.15.1; R Core Team, 2012), and so all named software outside the 'phylogenetic data' section are `R` packages.

Bird data

Data were taken from the BTO's BBS. In brief, volunteers biannually (first in early-April/mid-May, second in mid-May/late June) conduct surveys in randomly selected 1km x 1km squares across the UK. The abundance, species, and approximate distance of birds from the transect are recorded, along with basic weather information. Not all sites have been surveyed since the start of the scheme, so I worked with only those sites surveyed every year from 1994 to 2011 (excluding one site where 1510 crows (*Corvus frugilerus*) were seen in one visit), leaving a total of 161 sites. Detection probabilities vary among species, but this can be corrected for using distance sampling to estimate species' detectability (Buckland *et al.*, 2004a,b). For each species in each site and each year, I took the greatest observed abundance within 100m of each transect, and divided this by the species detectability scores calculated by Davey *et al.* (2012). This meant fifty-two very rare species (less than 0.001% of total sightings) were excluded from the analysis. I calculated Pagel's λ (using `pgls` in `caper`; Orme *et al.*, 2011) values for six bird traits taken from the BTO, to test for phylogenetic conservatism (supplementary materials, figure 6.12a). However, these traits are insufficient to cover the broad range of life history categories of birds, and so I undertook no further analysis of the bird trait data.

Land cover data were taken from Fuller *et al.* (2002), which records the percentage cover of thirteen land use categories ('sea/estuary', 'inland water', 'coastal', 'bog', 'dwarf shrub heath', 'montane', 'broad-leaved woodland', 'coniferous woodland', 'grassland', 'bracken', 'arable crops/horticulture', 'urban', and 'bare ground') in each of the Ordnance Survey's 10km x 10km grid squares of Britain. I extracted land cover data for only those squares in my subset of the bird dataset, square-rooted and then arc-sin transformed these data, and took the first two components of a scaled principal components analysis (loadings, variance, and component choice described in table 6.1a and its legend). I recorded which land use type was the most common in each grid cell, and subsequently collapsed three land use categories ('broad-leaved woodland', 'dwarf shrub heath', and 'montane') into one category ('other') because there were so few sites with these designations. I calculated mean temperature and rainfall data from the Met Office

(UKCP09 dataset; http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/) across each year's the breeding season (April-July). Finally, I fitted a generalised linear model with a Poisson error family and a log link function, with separate slopes and intercepts for each site, to the total abundance of all birds at each site, and used the residuals from this regression as a measure of the relative overall abundance of birds in each site.

Butterfly data

Data were taken from the UKBMS, a scheme where volunteers collect weekly butterfly abundance data across hundreds of sites in the UK, which has been in operation since 1976. The UKBMS produces yearly overall abundance estimates for each species in each site (using a log-linear Poisson regression model; ter Braak *et al.*, 1994). I analysed only the 48 sites where confident estimates of abundance for more than 95% of species could be made for over twenty years. Trait data were taken from Dennis *et al.* (2004; described in table 6.2), and these were also tested for phylogenetic conservatism using Pagel's λ (supplementary materials, figure 6.12b).

The same land cover data were used for both the bird and butterfly datasets, although for the butterflies the principal components analysis was restricted to those grid cells within the butterfly dataset. The two principal components used are described in table 6.1b. The modal land-use type was not included as an explanatory variable, as the UKBMS provides a brief description of each site, from which I categorised each site as 'grassland', 'woodland', or 'other'. Weather data were taken from the CRU TS 2.1 (Mitchell & Jones, 2005), and the first two principal components from a principal components analysis for that year recorded (table 6.1c). While these data have the same spatial resolution as those used for the birds (10km x 10km grid cells), they do not cover as many years (I have data only until 2000). However, they do include variables known to affect butterfly community structure, and their use makes these results more directly comparable with previous assemblage-based analyses of the UKBMS dataset (e.g., Menéndez *et al.*, 2007). Finally, I used the same regression approach to generate relative

overall abundance estimates for the butterflies as I did for the bird data.

Phylogenetic data

I used Thomas' (2008) phylogeny of UK birds, and resolved taxonomic conflicts between it and the BBS data manually. The seven birds in the BTO dataset missing from the phylogeny were excluded from the analysis, representing 3% of all birds counted when detectability is accounted for. A phylogeny of all resident British butterflies was assembled using *cytochrome c oxidase subunit I* sequences taken from `GenBank` (Benson *et al.*, 2009). Several nodes were constrained using information from recently published phylogenies that are based on more loci (see figure 6.1 for both the finished phylogeny and constraint information). The sequences were aligned in `Geneious` (v.5.3; `http://www.geneious.com/`), and a two-codon (1&2, 3) GTR+γ+I (with four rate categories) substitution model was used for five separate analyses using `BEAST` (Drummond *et al.*, 2006; Drummond & Rambaut, 2007; Drummond *et al.*, 2012). To choose the DNA substitution model, I performed one `BEAST` run with all possible combinations of GTR models with γ and invariant site models, no, two, and three separate codon positions, and the SDR model (Shapiro *et al.*, 2006). I then compared the posterior likelihood of these runs according to Bayes factors as calculated in `Tracer` (Rambaut & Drummond, 2012) using Suchard *et al.*'s (2001) method. All `BEAST` analyses used a different random starting tree, a relaxed lognormal clock, ran for five million generations, and were sampled every 2000 generations. The runs were checked for convergence and mixing, and to make sure that all parameters had an estimated sample size greater than 300 using `Tracer` (Rambaut & Drummond, 2012). The five runs from the optimal DNA substitution model were combined with a 10% burn-in, and then their maximum clade credibility tree used for all further analyses.

	PC 1	PC 2
Sea/estuary	0.04	**-0.34**
Inland water	**0.26**	0.17
Coastal	-0.05	**-0.41**
Bog	**0.29**	-0.08
Dwarf shrub heath	**0.46**	-0.04
Montane	**0.34**	-0.12
Broad-leaved woodland	-0.15	**0.43**
Coniferous woodland	**0.37**	0.08
Grassland	0.12	**0.33**
Bracken	**0.37**	-0.03
Arable	**-0.35**	-0.25
Urban	-0.26	**0.37**
Bare ground	0.11	**0.40**
Variance explained	32.2%	19.4%

(a) Bird land cover

	PC 1	PC 2
Sea/estuary	-0.27	**0.38**
Inland water	**0.20**	-0.19
Coastal	**-0.32**	0.20
Bog	**0.19**	0.15
Dwarf shrub heath	0.30	**0.47**
Montane	0.17	**0.25**
Broad-leaved woodland	0.28	**-0.38**
Coniferous woodland	**0.41**	0.11
Grassland	**0.38**	-0.01
Bracken	0.26	**0.36**
Arable	-0.23	**-0.28**
Urban	-0.01	**-0.17**
Bare ground	**0.35**	-0.28
Variance explained	25.9%	20.8%

(b) Butterfly land cover

	PC 1	PC 2
Warmest month	**-0.41**	0.19
Coldest month	-0.14	**0.53**
Growing days	-0.37	**0.43**
Possible sun	-0.06	**0.44**
Summer rain	**0.45**	0.18
Winter rain	0.33	**0.39**
Total rain	**0.43**	0.35
Transpiration	**0.40**	-0.05
Variance explained	44.7%	25.2%

(c) Butterfly weather

Table 6.1: Principal component loadings and variance explained for the explanatory variables used in the bird and butterfly analyses. (a) describes the land cover data for the bird analyses, (b) the land cover for the butterfly analyses, and (c) the weather data for the butterfly analyses. The axis that each variable loads onto the most (in absolute terms) is emboldened. In each case, the first two principal components were chosen with reference to a scree plot, which is usually a conservative way to choose how many principal components to use in an analysis (Jackson, 1993).

Trait	Range/units
Competitive strategy	-2—+2
Stress-tolerator strategy	-2—+2
Ruderal strategy	-2—+2
Wetland biotopes	1—5
Skeletal biotopes	1—5
Arable biotopes	1—5
Pasture biotopes	1—5
Spoil biotopes	1—5
Wasteland biotopes	1—5
Woodland biotopes	1—5
Garden biotopes	1—5
Ellenberg light values	1—9
Ellenberg moisture values	1—9
Ellenberg pH values	1—9
Ellenberg nitogen values	1—9
Specific leaf area	area/mass
Leaf dry matter content	dry/fresh wt (%)
N foliar	(predicted)

(a) Host plant

Trait	Range/units
Wing expanse	mm
Proboscis length	mm
Oviposition behaviour	1—9
Egg load	mean number developed eggs
Egg load	mean total egg production
Egg size	length × breadth (mm)
Relative egg size	ES / WL
Larval growth rate	1—9
Larval duration period	days
Development duration of early stadia	days
Adult lifespan	days, summer brood
Adult lifespan	days, inc. hibernation
Hibernation stage	egg /larval /pupal /adult
Adult hardiness	1—9
Mobility score	sum of 9 ranked variables

(b) Morphology and life history

Trait	Range/units
Number of biotopes occupied	count
Number of host plants	count
Phagy score	1—4
Host-plant phenology	binary; annuals
Host-plant phenology	binary; biennials
Host-plant phenology	binary; short-lived perennials
Host-plant phenology	binary; long-lived perennials
Utility resource use	count of non-consumable resources

(c) Habitat

Table 6.2: Description of butterfly trait data. All data and descriptions are adapted from Dennis *et al.* (2004).

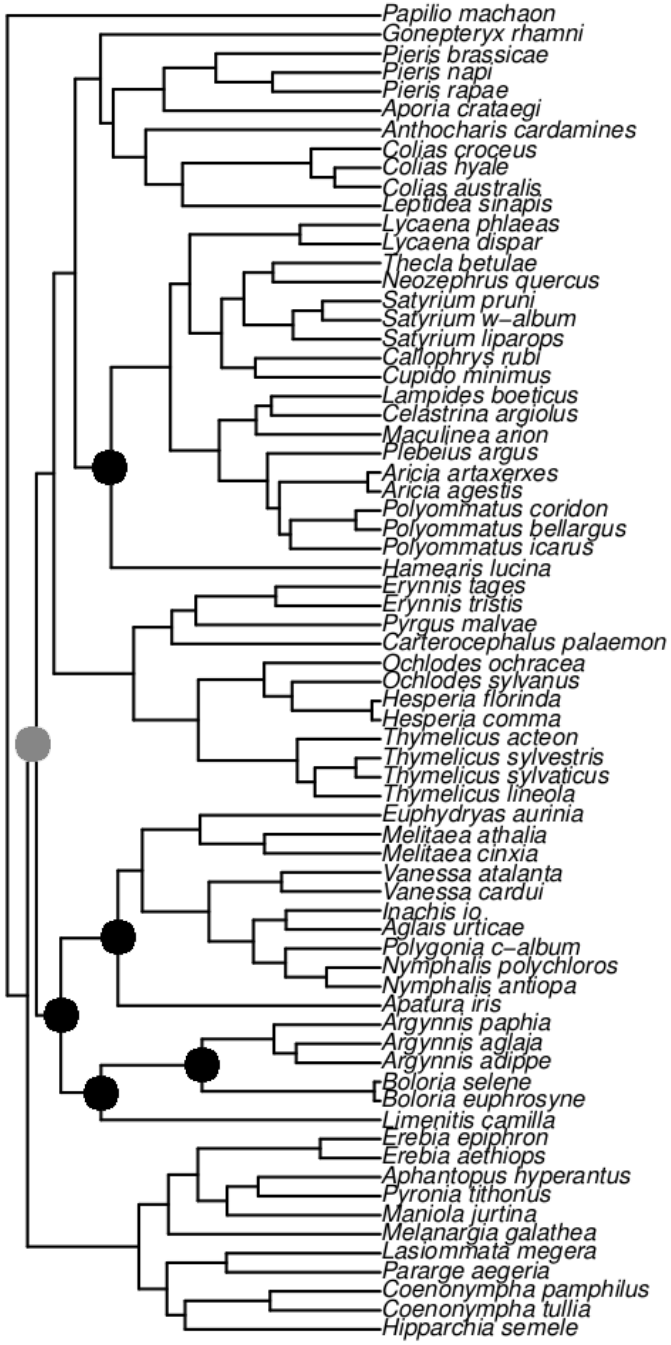


Figure 6.1: Butterfly phylogeny. Created as described in text. Coloured circles at nodes indicate clades that were constrained to be monophyletic based on recent multi-locus higher-level Lepidoptera phylogenies; circles in black come from Wahlberg *et al.* (2009), while the grey circle is based on Mutanen *et al.* (2010). *Papilo machaon* was defined as the out-group for all `BEAST` analyses.

Measures of assemblage structure

To assess phylogenetic dispersion, I calculated D (using presence/absence of species; Fritz & Purvis, 2010) with a source pool of all UK species, and D_C (using species' abundances; previous chapter) with a source pool of only those species within each assemblage. To look at the phylogenetic structure of species turnover, the D_C value of each year's species' abundances subtracted from the previous year's was also calculated (D'_C); species only recorded in the previous year were included in these calculations. As in the previous chapter, a D'_C value significantly less than one would indicate phylogenetically clustered turnover, perhaps because whole clades were increasing/decreasing *en masse*, while a value greater than one would indicate overdispersion of turnover.

There are a large number of measures that quantify functional traits, but comparatively few that investigate their dispersion. *FDis* (Legendre *et al.*, 2010) is the mean distance of species in an assemblage from their centroid in multidimensional trait space, and is modified from Anderson *et al.*'s (2006) multivariate dispersion by weighting each species according to its abundance. Throughout, I refer to *FDis* when I have weighted species' distances according to their abundances, and *FDand* when I have not weighted according to abundance; thus D is analogous to *FDand*, and D_C is analogous to *FDis*. I did not transform species' traits (following Legendre *et al.*, 2010). To assess the statistical significance of *FDand*, I randomly shuffled species' presences/absences within each sample (a year within a site) one thousand times, and compared the observed and randomised samples' *FDand* values. I did the same, but restricted to only those species present within an assemblage, to assess the significance of *FDis*.

Analogously to D'_C, I related species turnover to species' traits according to equation 6.1, which is described below. I scaled all 36 numerical traits so that they had a standard deviation of one, and took the absolute value of these scaled trait data (where $trait_i$ is the trait value for species i) multiplied by the turnover data used to calculate D'_C (where $turnover_{ij}$ is the change in abundance for species i in site/year j). I summed these trait differences across each species in the assemblage and divided this sum by the total number of species in that site/year (n_{ij}).

I then summed these trait totals and divided them by the number of traits (n_k; 36) to get a single 'trait turnover' value for each site in each year. A trait turnover value of zero would indicate there had been no overall change in the trait composition of an assemblage, while a value greater than one would indicate that there was no like-for-like replacement of species' traits. I assessed the statistical significance of these trait turnover values by randomly permuting turnover within each assemblage 1000 times, and comparing observed and randomised assemblages' trait turnover values.

$$trait\ turnover_j = \frac{\sum_k \frac{\sum_i |turnover_{ij} \cdot trait_i|}{n_{ij}}}{n_k} \tag{6.1}$$

I calculated the abundance-weighted mean of each trait for each butterfly assemblage in each year, and recorded the slopes of regressions of mean trait values against time (with a separate intercept and slope fitted for each site) separately for each trait. If these slopes significantly deviate from zero, it would suggest assemblage-level shifts in mean trait value through time, and thus that the trait composition of assemblages was changing.

Statistical analysis

Drivers of dispersion

Since the data are temporally autocorrelated, I fitted Generalised Least Squares (GLS) models (using `gls` in `lme4`; Pinheiro *et al.*, 2011) with autoregressive autocorrelation models (of one order) for each site to each of the dispersion measures. I took a model averaging approach (following Burnham & Anderson, 2002), using functions from `MuMIn` (Bartoń, 2012) to fit all the possible sub-models of the maximal models described below. Model-averaged estimates were taken from those models with a δAIC_c of four or less, and the 'importance' of each explanatory variables assessed by summing the Akaike weights of models containing that variable. Parameter estimates were averaged over only those models containing that parameter, and their standard errors were calculated according to equation 4 in

Burnham & Anderson (2004). Butterfly and bird data from years where weather information was unavailable were not included in these models, but preliminary analyses of all the data without the weather data yielded qualitatively identical results (not shown).

Two different maximal models were fitted for each dispersion measure. In the first (the 'site' models), the interaction between site and year was fitted, and overall relative abundance and weather variables fitted as additive terms. In the second (the 'habitat' models), the maximal model incorporated all environmental variables and their interactions with habitat-type. The site models should be more sensitive to overall change, as in the extreme they fit separate slopes and intercepts for each site. However, fitting a separate intercept for each site makes robust estimation of site-level environmental effects difficult, and so only the habitat models allow comparison of the importance of environmental drivers. A few butterfly records with unusual species compositions (e.g., 4142 meadow browns (*Maniola jurtina*) in one site in 1997) caused usually large or small dispersion values, and so values beyond the 1^{st} and 99^{th} quantiles were excluded in the butterfly analyses; this did not qualitatively affect these results (not shown). Following Grueber *et al.*'s 2011 advice for model averaging studies, all continuous explanatory variables were scaled to have a mean of zero and a standard deviation of 0.5.

To test for a spatial pattern in assemblages' dispersion, I calculated *Moran's I* of site models' estimates of site and site-year interaction coefficients (when those estimates were supported in models with a δAIC_c of four or less). I did so using `moran.test` in `spdep` (Bivand *et al.*, 2012b), and a spatial weights matrix based on each site's eight nearest neighbours.

Pattern in lost and gained species

After exploratory analyses, I defined a species as 'lost' from a site if it had an abundance greater than 5 in at least five years of the data, and had not been seen for at least five years by the end of the dataset. Similarly, a species was 'gained' if it had been absent for at least the first five years of the dataset, and had at

least five years where its abundance was greater than 5.

For each lost species, I recorded its least phylogenetic distance (LPD) from other species in its most abundant year in each site, and (for the butterflies) its distance from the centroid of its assemblage in the multidimensional trait space used to calculate *FDand* (trait distance; TD). For each gained species, I recorded its LPD and TD in the first year of the dataset. I also recorded the median LPD and TD of all other species in an assemblage in the same year that I recorded gained or lost species' LPD and TD values. The choice of year is conservative; if phylogeny or traits have predictive power over species' turnover, they should have predictive power when we would be least likely (*a priori*) to predict that species would enter or leave an assemblage.

I plotted the LPD and TD of the lost and gained species against the medians of the other species in each assemblage, and counted how many lost/gained species' LPD/TD values were greater or lesser than the medians of the other species in each assemblage. I used χ^2 tests to see whether these counts differed among lost and gained species. Where there was no significant difference, I grouped lost and gained species together, and calculated the likelihood of observing that many changing species with greater or lesser LPD/TD values than median LPD/TD values if both outcomes were equally likely under a Bernoulli distribution.

6.4 Results

Measures of assemblage structure

There is no relationship between D and D_C, and while there is a correlation between *FDis* and *FDand*, the relationship is very weak (figure 6.2). This implies a disconnect between the processes determining which species are present in an assemblage and the processes determining species' abundances within assemblages. Examples of bird (figure 6.14) and butterfly (figure 6.15) assemblage phylogenetic structure through time are shown in the supplementary materials.

Birds

Overall, bird D values are phylogenetically clustered (mean value significantly less than 1; $t = 172_{2663}$ $p < 0.0001$), while the mean of D_C values is overdispersed (significantly greater than 1; $t_{2663} = 16.6$, $p < 0.0001$). D'_C values indicate phylogenetically random species turnover (no significant difference from a mean of 1; $t_{2506} = -1.79$, $p = 0.074$). There is little obvious change in D, D_C, and D'_C through time (figure 6.3), and all variables related to year have extremely small coefficients in the site and habitat models (figure 6.4). Site-level variation dominates the site models, and while variables involving land use categories have large coefficients in the habitat models, the overall explanatory power of habitat models is very low. D decreases with overall relative abundance, while D_C increases, in both site and habitat models (figures 6.3 and 6.5). Site estimates of D showed significant spatial autocorrelation (*Moran's* $I = 0.22$, $p < 0.0001$), but D_C did not (*Moran's* $I = 0.034$, $p = 0.13$); D'_C did not show significant variation in overall mean among sites (figure 6.4) and so no autcorrelation estimates were calculated for D'_C.

Butterflies

Overall, butterfly mean values of D (significantly less than 1; $t = 55.7_{1239}$ $p < 0.0001$), D_C (significantly less than 0; $t_{1239} = -9.15$, $p < 0.0001$), and D'_C (indistinguishable from 0; $t_{1184} = 1.21$, $p = 0.22$) show phylogenetic clustering. In the trait measures, *FDand* was essentially as expected at random (only 8% and 0.7% of observed values were significantly under- or over-dispersed respectively), though most (50%) *FDis* values were significantly under-dispersed, all at the 5% significance level. The overwhelming majority of trait turnover values (98.9%) were more under-dispersed than expected at random at the 5% significance level.

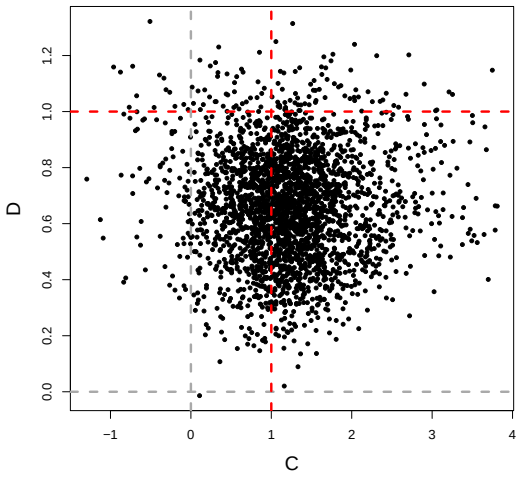
There is little obvious change in any butterfly dispersion measure through time (figures 6.3 and 6.6); although some models support the inclusion of year terms (figures 6.7 and 6.8), the slope estimates are either small, or (in the case of site-year interactions) do not significantly deviate from an overall mean of zero

(though note the skewed distribution of *FDand*; figure 6.9). While trait turnover has a coefficient that indicates increase through time, its low importance (25%) in the site models (which also have very low predictive power) indicate this increase is not of biological significance. In general, model fit was extremely poor for the habitat models, and the site models emphasise site-level variation (figures 6.7 and 6.8). However, many abundance-weighted mean trait values did significantly change through time (figure 6.10). Trait turnover's year parameter was not important (present in only two of the eight models with a δAIC_c of four or less), and its standard errors overlap with zero; thus trait turnover did not reliably change over time.

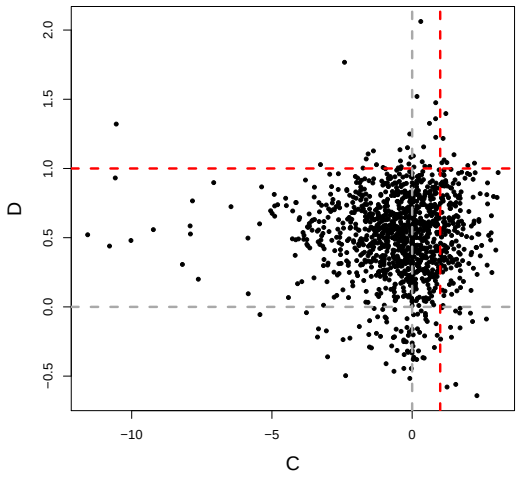
Site estimates of D showed significant spatial autocorrelation (*Moran's* $I = 0.15$, $p = 0.0016$), but neither site nor site-year interaction estimates of D_C did (both *Moran's* $I < 0.035$, both $p > 0.15$). D'_C showed significant spatial autocorrelation of site estimates (*Moran's* $I = 0.10$, $p = 0.19$), but not of site-year interaction estimates (*Moran's* $I = -0.055$, $p = 0.77$). No measures of trait dispersion exhibited spatial autocorrelation (all *Moran's* $I < 0.03$, all $p > 0.15$).

Pattern in lost and gained species

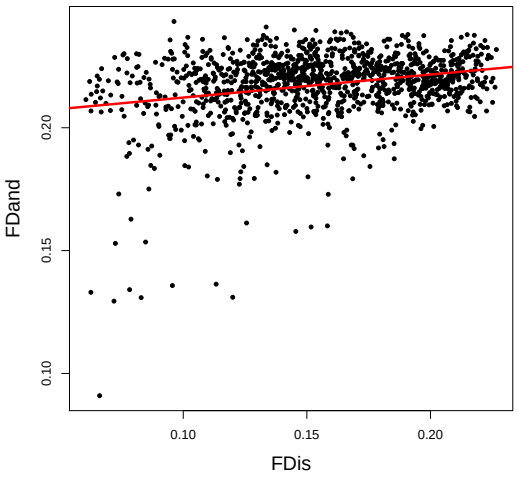
Birds lost from assemblages tended to be closely-related to other species in their assemblages, while birds joining assemblages were more distantly-related (figure 6.11a). However, in butterflies, species that were either lost or gained from assemblages tended to be distantly-related to the other species in their assemblages (figure 6.11b), and there was no pattern to species' loss or gain in terms of traits (figure 6.11c).



(a) Birds (phylogenetic)



(b) Butterflies (phylogenetic)



(c) Butterflies (traits)

Figure 6.2: Comparisons of presence/absence and abundance-based dispersion measures. Neither the birds' (a; $r = -0.0052$, $t_{2679} = -0.2692$, $p = 0.79$) nor the butterflies' (b; $r = -0.023$, $t_{1238} = -0.80$, $p = 0.42$) D and D_C values are correlated with one another. However, the butterflies' *FDand* and *FDis* measures are correlated with one another (c; $r = 0.27$, $t_{1224} = 9.64$, $p < 0.0001$). The grey and red dashed lines in (a) and (b) mark values of zero and one respectively on each axis, while the red line in (c) is a linear regression through *FDand* and *FDis* ($intercept = 0.20$, $slope = 0.094$, $F_{1,1224} = 92.96$, $r^2 = 0.071$, $p < 0.0001$).

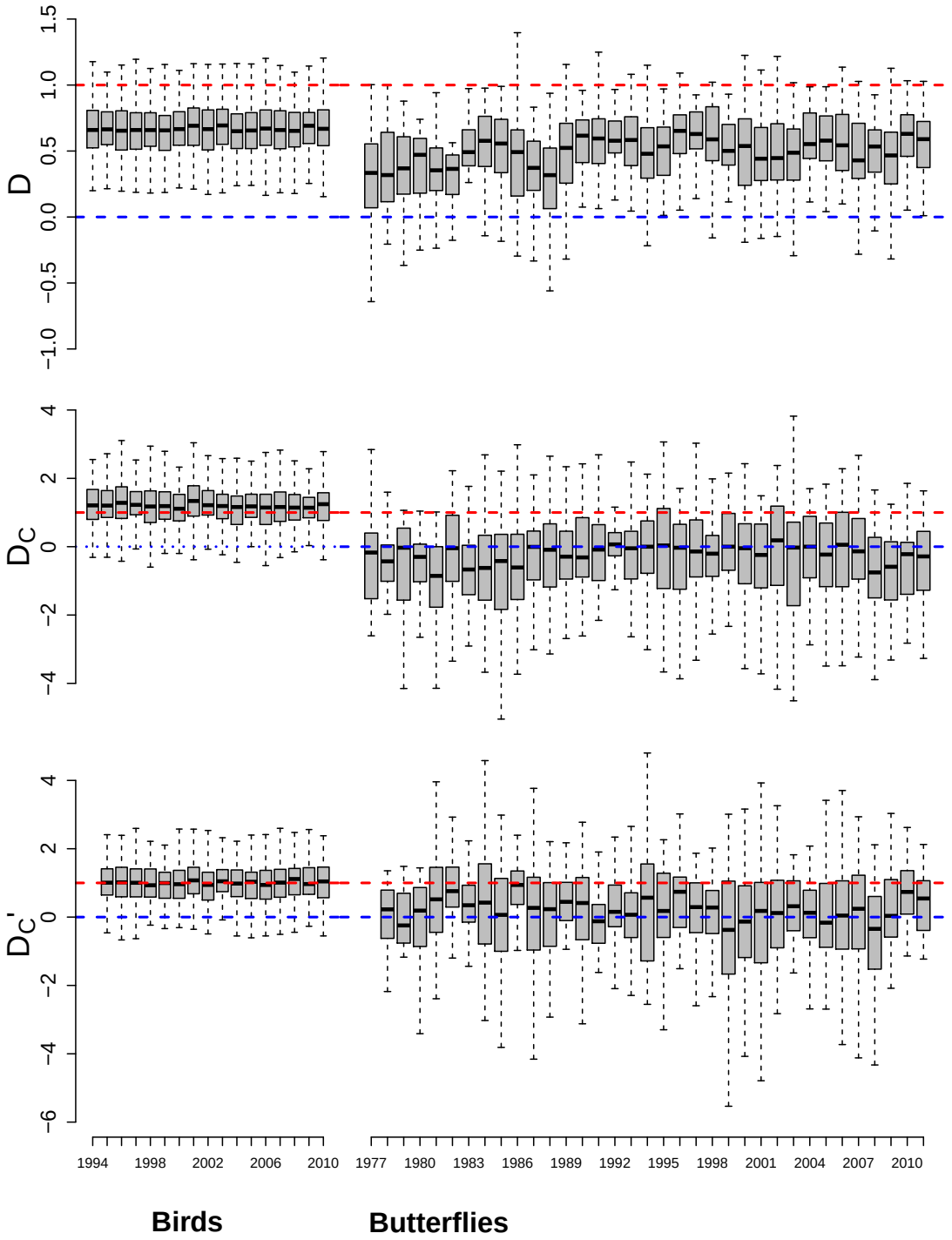


Figure 6.3: Phylogenetic structure of bird and butterfly assemblages over time. Each box indicates the median and inter-quartile range of dispersion measures' values in each site in a particular year. The 'whiskers' of each plot extend to the most extreme data point or 1.5 × the interquartile range from the box, whichever is lesser. Birds recorded after 2006, and butterflies recorded after 2000, are shown, but were not statistically modelled (as described in the text).

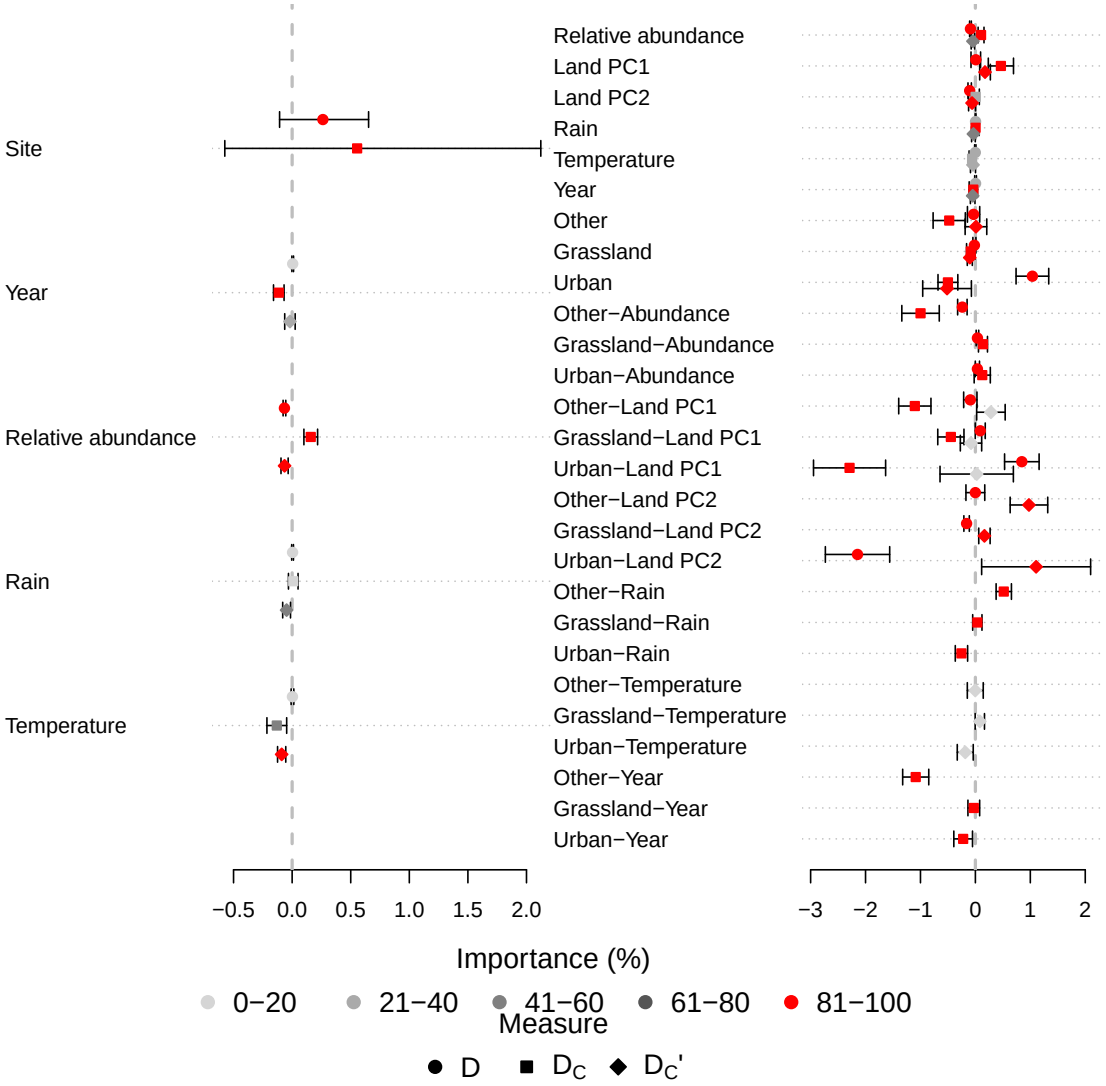
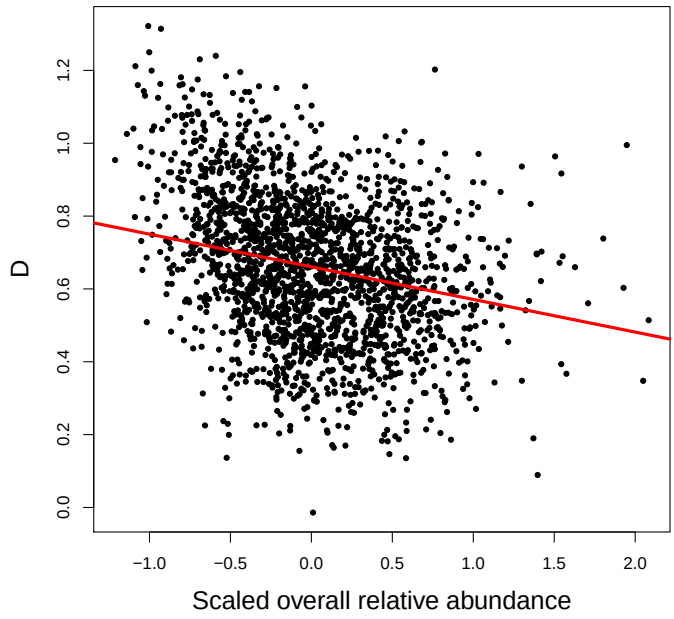
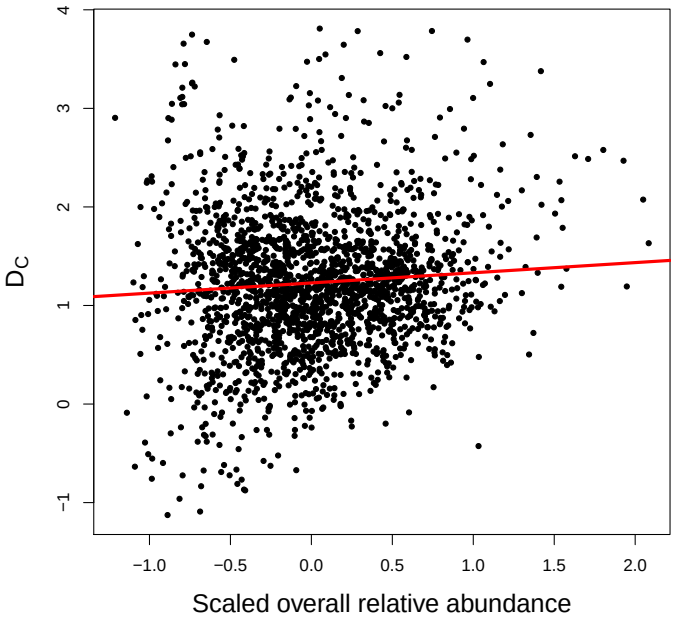


Figure 6.4: Model-averaged coefficients of bird models. The left-hand panel describes the coefficients of the site models, while the right-hand panel describes the habitat models. The legend is described at the bottom of the figure; plotting symbol indicates which phylogenetic dispersion measure is shown, and the bars indicate the standard errors of those estimates (with the exception of 'site', where they indicate the range of estimates for each site). The colour of the symbols describes the importance of each coefficient. For the site models (a), r^2 of 0.69, 0.31, and 0.0083, from 5, 5, and 6 models, were found for the D, D_C, and D'_C models respectively. For the habitat models (b), r^2 of 0.24, 0.06, and 0.02, from 7, 4, and 28 models, were found for the D, D_C, and D'_C models respectively. Note that 'year' is an important parameter in the site models of D_C, but that the magnitude of this effect is very small; since all continuous variables were scaled to have a mean of zero and standard deviation of 0.5, a slope of 0.1 indicates a change of 0.16 throughout the entire dataset.



(a) D



(b) D_C

Figure 6.5: Plots of birds' phylogenetic dispersion against relative overall abundance. (a) and (b) show plots of relative overall abundance against D and D_C respectively. The red lines pass through the means of D and D_C, and their slopes are taken from the model-averaged coefficients of the site models.

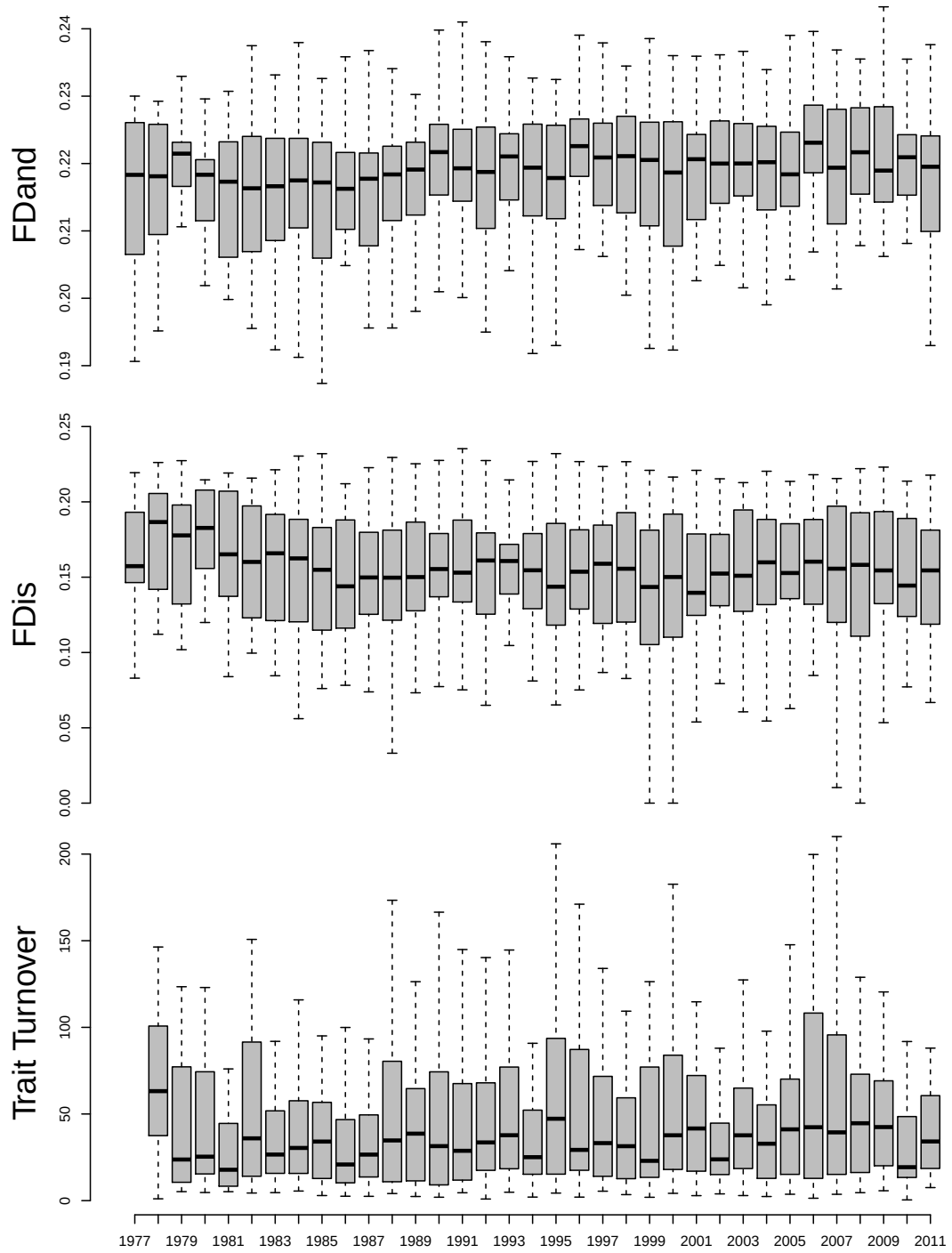


Figure 6.6: Trait structure of butterfly assemblages over time. Each box indicates the median and inter-quartile range of dispersion measures' values in each site in a particular year. The 'whiskers' of each plot extend to the most extreme data point or 1.5 × the interquartile range from the box, whichever is lesser. While records from after 2000 are shown, these were not statistically modelled (as described in the text).

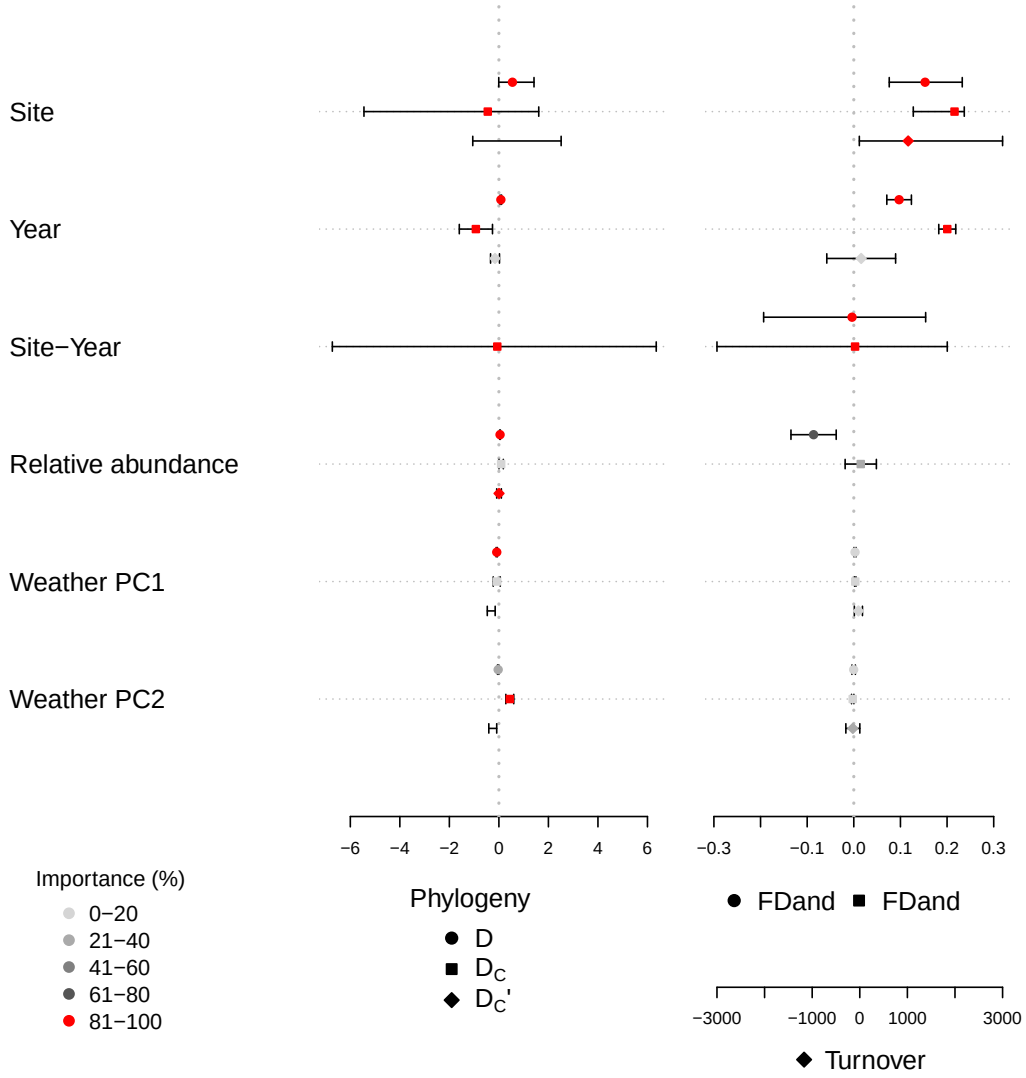


Figure 6.7: Model-averaged coefficients of the butterfly site models. The left-hand panel describes the coefficients of the phylogenetic dispersion models, while the right-hand panel describes the trait models. Note that the scale of the axes vary for the trait dispersion measures. The legend is described at the bottom of the figure; plotting symbol indicates which phylogenetic dispersion measure is shown, and the bars indicate the standard errors of those estimates (with the exception of 'site' and 'site-year', where they indicate the range of estimates for each site and site-year interaction). The colour of the symbols describes the importance of each coefficient. In the phylogenetic models r^2s of 0.60, 0.52, and 0.18, from 13, 31, and 45 models, were found for the D, D_C, and D'_C models respectively. In the trait models, r^2s of 0.54, 0.41, and 0.16, from 6, 5, and 8 models, were found for the *FDand*, *FDis*, and trait turnover models respectively.

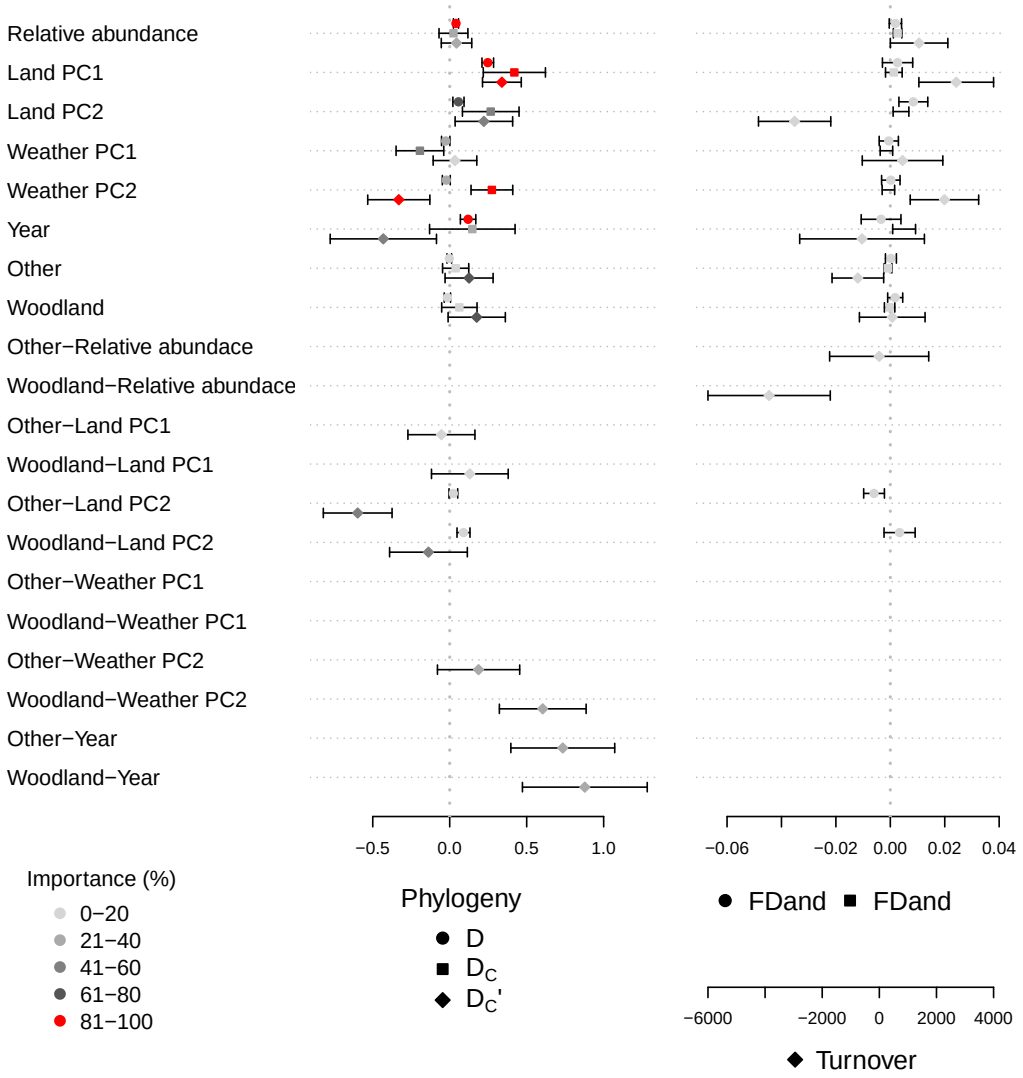
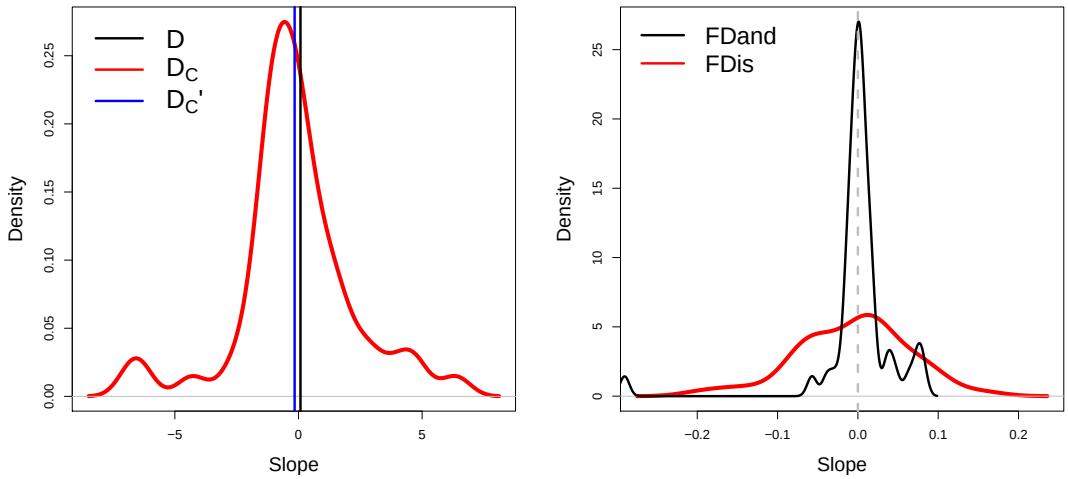


Figure 6.8: Model-averaged coefficients of the butterfly habitat models. The left-hand panel describes the coefficients of the phylogenetic dispersion models, while the right-hand panel describes the trait models. Note that the scale of the axes vary for the trait dispersion measures. The legend is described at the bottom of the figure; the symbol indicates which phylogenetic dispersion measure is shown, and the bars indicate the standard errors of those estimates (with the exception of 'site', where they indicate the range of estimates for each site). The colour of the symbols describes the importance of each coefficient. In the habitat models, r^2s of 0.18, 0.02, and 0.03, from 13, 31, and 45 models, were found for the D, D_C, and D'_C models respectively. In the habitat models, r^2s of 0.0070, 0.01, and 0.0044, from 28, 39, and 25 models were found for the *FDand*, *FDis*, and trait turnover models respectively.



(a) Phylogenetic (b) Trait

Figure 6.9: Slopes of dispersion measures in butterfly site models. While the site models suggest there are changes in dispersion through time, these plots make it clear that these changes are not of a large magnitude. Note that all continuous variables were scaled to have a mean of zero and standard deviation of 0.5, so a slope of 0.05 indicates a change of 0.081 throughout the entire dataset. In (a), which shows the phylogenetic measures' coefficients, D and D'_C are extremely close to zero, while D_C's estimates (which support an interaction with site) have a mean not significantly different from zero ($mean = -0.094$, $t_{47} = -0.27$, $p = 0.79$). Similarly in (b), which shows the trait measures' coefficients, neither *FDand* ($mean = 0.001$, $t_{46} = 0.14$, $p = 0.89$) nor *FDis* ($mean = -0.006$, $t_{46} = -0.61$, $p = 0.54$) have overall means significantly different from zero.

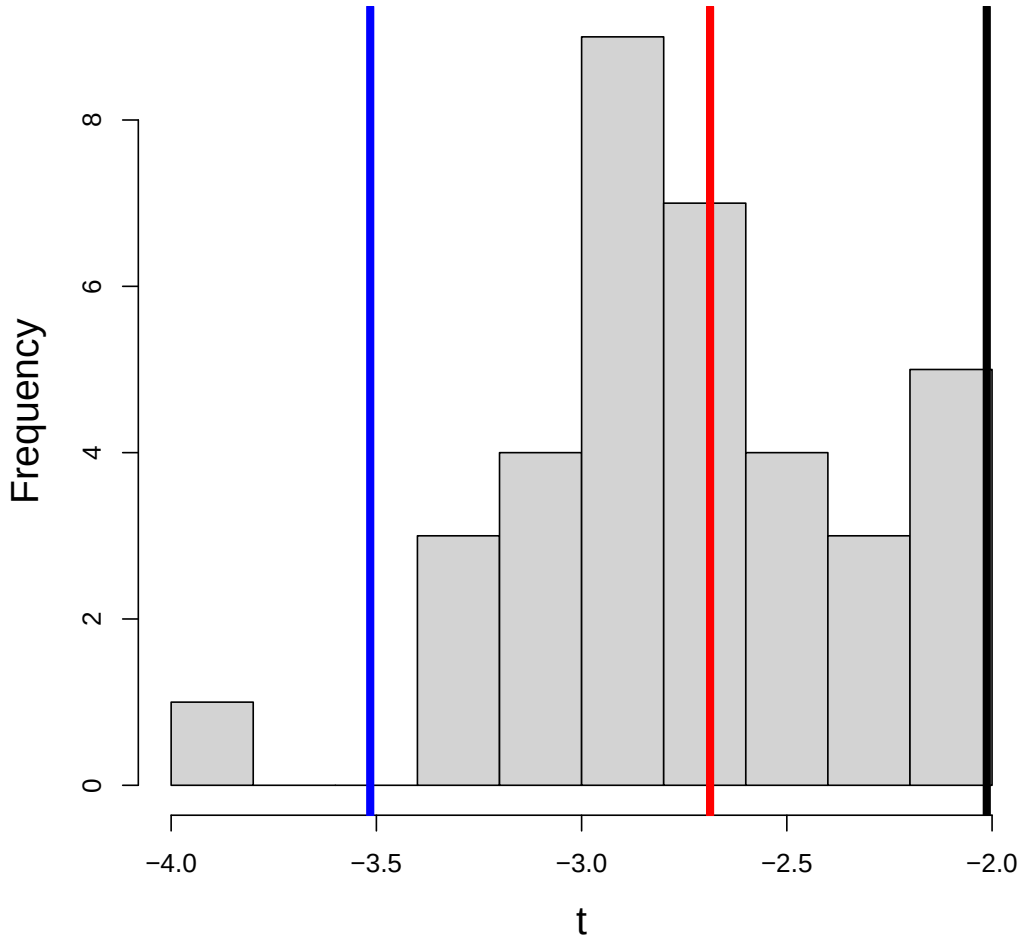
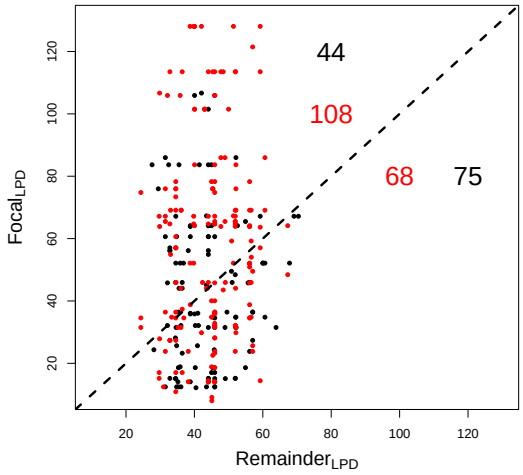
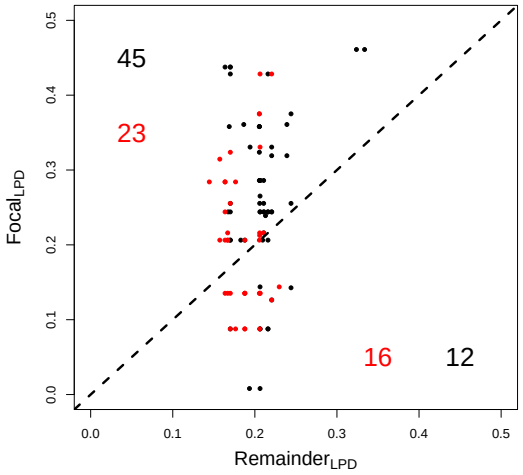


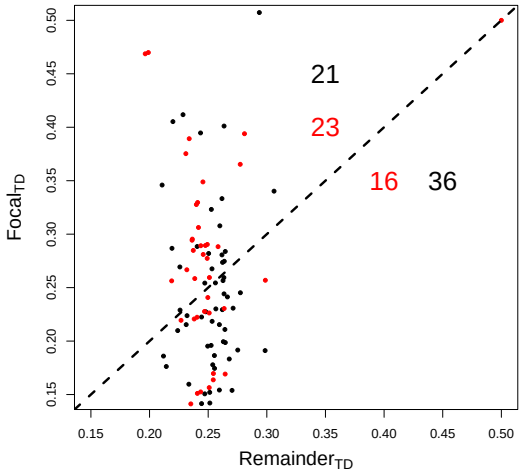
Figure 6.10: T-statistics of change in mean trait values through time. Histogram of t-test statistics from tests of whether the mean of each trait's slope of change through time differ from zero are shown, with black, red, and blue lines indicating two-tailed significance at the 5%, 1%, and 0.1% levels respectively.



(a) Birds (phylogenetic)



(b) Butterflies (phylogenetic)



(c) Butterflies (traits)

Figure 6.11: Phylogenetic and trait pattern to lost and gained species. Lost (black) and gained (red) species' LPD and TD are plotted vertically against the median LPD and TD values for the rest of their assemblage. A black dotted line indicates where lost/gained (focal) species' LPD or TD is equal to other species (the remainder's) LPD or TD. In (a), there is a tendency for lost species to be closely related to the other members of an assemblage, and the opposite pattern for gained species ($\chi^2_1 = 15.9$, $p < 0.0001$). Lost and gained butterfly species do not differ according to phylogeny (b; $\chi^2_1 = 3.56$, $p = 0.059$; $p_{Bernoulli} < 0.0001$), but there is a significant tendency for lost and gained species to have greater LPD and TD values than the rest of the assemblage (b; $p_{Bernoulli} < 0.0001$). There is no significant pattern to species loss or gain according to traits in the butterfly data (c; $\chi^2_1 = 3.72$, $p = 0.054$; $p_{Bernoulli} = 0.18$).

6.5 Discussion

I have presented evidence that the phylogenetic and functional trait structures of British birds and butterflies have remained constant over time. While bird assemblage composition (D) was phylogenetically clustered, species' abundances (D_C) were overdispersed. This contrasts with butterflies, where all measures of dispersion bar the trait measure *FDand* were consistent with under-dispersion. Most bird and butterfly traits show strong phylogenetic signal (supplementary materials; figure 6.12), suggesting it is reasonable to assume niche conservatism (reviewed in Wiens *et al.*, 2010) when interpreting phylogenetic dispersion. A potential caveat to the butterfly results is the absence of any data on detectability, although the UKBMS abundance estimates assessed by Isaac *et al.* (2011) compared favourably to estimates derived from distance sampling.

General patterns

The difference in birds' D and D_C values could reflect clade-level habitat filtering, within the context of which competition is detectable. Nee *et al.* (1991) found that bird clades with large body masses have relatively low abundances, but that within clades species with greater body masses are more abundant, presumably because of a competitive advantage. Bird body weight shows phylogenetic signal (supplementary materials; figure 6.12a), and so these results extend Nee *et al.*'s findings. Note that bird abundances' overdispersion is undetectable with the widely-used *PSE* measure (Helmus *et al.*, 2007) (supplementary materials, figure 6.13). Every measured aspect of butterfly assemblage structure was phylogenetically clustered, suggesting butterfly assemblage composition is mostly determined by habitat filtering.

D and D_C seem to detect more structure than *FDand* and *FDis*, possibly because the traits used in the butterfly analysis do not capture broad habitat-preference (which phylogeny appears to, see figure 6.16 in the supplementary materials). However, the trait turnover data are strongly under-dispersed, indicating these traits capture change within-assemblages quite well. That D and D_C should

not be correlated with one another in either dataset (figure 6.2) implies that different processes are operating at different spatial scales in the two datasets. The correlation between *FDand* and *FDis* is likely spurious, and so different processes are evident in these data too; the fit of the relationship is extremely poor, and more reflects the relative invariance of *FDand* and the influence of extremely low-scoring outlier assemblages than a relationship between the two measures. In general, D'_C and trait turnover are poorly predicted by the site and habitat models; neither dataset can guarantee constant sample effort through time, and butterflies and birds are highly mobile species, so this may reflect the limitations of the BBS and UKBMS data.

Site-level variation

There was great variation in the coefficients for site-level means in the butterfly models (figure 6.7), and, to a lesser extent, the bird models (figure 6.4), but the habitat models have very low explanatory power (as judged by r^2; figures 6.4 and 6.8) and so this variation is idiosyncratic with respect to the environmental variables in this study. Indeed, while there is no *overall* trend to the butterfly data, a small number of sites are undergoing quite severe changes in phylogenetic dispersion through time (figure 6.9). Butterflies are small animals that exploit variations in microclimate (e.g., Ravenscroft, 1994; Batary *et al.*, 2007), and it would be difficult to comparably measure such variation across the hundreds of UKBMS sites. Moreover, butterfly population dynamics are known to be synchronised through space (Powney *et al.*, 2010, 2011); these dispersion estimates show some spatial autocorrelation, hinting that interactions among assemblages may be important.

Both site and habitat models (figures 6.4) indicate that bird species' presences are more phylogenetically clustered (lesser D) when overall relative abundance is greater, while abundances are more overdispersed (greater D_C). This apparent inconsistency could be explained by poorly-adapted, opportunist species being driven from a site in the face of extreme competition, leaving only those (closely-related) species best-adapted to that environment, and thus decreasing

D. Scarcity of resources could bring the remaining species into increased competition, causing an increase in the phylogenetic dispersion of species' abundances when only those species present in the assemblage are considered.

No change in dispersion over time

Parameter estimates for changes in phylogenetic and trait dispersion through time were either very small, or showed no systematic departure from zero, in both datasets. That sites should vary in their slope is to be expected, and as the centre of the distribution of those slopes is zero there is evidence only of variation, not of trend. A possible exception is butterfly *FDis*, whose right-skew suggests some assemblages were being more strongly filtered according to traits as time went on. Indeed, there is an inflection of *FDis* early in time in figure 6.6, but drawing strong inferences from the beginning of any time series, particularly one gathered by volunteer recorders likely to be initially unfamiliar with recording techniques, is unwise.

UKBMS sites tend to be located in sites rich in butterflies, so these results could be biased. However, these butterfly data have revealed changes in assemblage composition (González-Megías *et al.*, 2008), and I found variation in sites' dispersion values, suggesting these data would be capable of detecting a marked shift in dispersion if one had taken place. I therefore think that, although the drivers of British bird and butterfly assemblages may have changed (and the significant change in mean trait values suggests they have), the magnitude of these new drivers' impact is as intense as previous drivers. Despite turnover in composition, the overall number of birds (page 5; Eaton *et al.*, 2010) and butterflies (figure 3; Botham *et al.*, 2010) has changed very little in the past few decades, and so the overall carrying capacity of Britain may not have reduced—if these sites are representative—despite shifts in land use. Thus there is no reason to suppose the limitations imposed by novel filters are any stronger than those of the past.

The decline of farmland birds in the face of habitat changes does not mean that structural processes are changing; as traditional farmland is removed, so the birds

in the habitat that replaces it are filtered according to a different set of constraints that may leave similar kinds of structural signatures. Moreover, the reported increase in generalist British birds is actually quite slight: one measure of community specialisation changed at most only 4% between 1994 and 2006 (figure 2b; Davey *et al.*, 2012). However, the modest changes Davey *et al.* (2012) and this study detect could be because these data do not cover the rapid intensification of farming during the 1980s (Eglington & Pearce-Higgins, 2012). British butterflies are designated as specialists or generalists according to Pollard & Yates (1993), who warn "*this division into 'matrix'* [generalist] *and 'island'* [specialist] *butterflies is not always clear-cut and a species may occur in the general matrix in one part of the country and be more restricted in another*" (page two). Generalist and specialist species may be emergent properties of the way in which assemblages are structured, in which case changes in individual species' abundances do not reflect a change in the way in which structuring processes operate. Generalist butterflies are phylogenetically clustered, and habitat preferences in butterflies shows phylogenetic pattern (supplementary materials, figure 6.16). Thus while butterfly habitat degradation may change butterfly assemblage composition, the magnitude of phylogenetic dispersion in assemblages need not change.

Species turnover

Species lost from bird assemblages are more closely related to other members of that assemblage, and the converse is true of species gained (as found in other taxa; Jiang *et al.*, 2010; Schaefer *et al.*, 2011). The lack of phylogenetic signal to bird turnover (D'_C) either reflects an averaging of these two processes, or (perhaps more likely) the difficulty of estimating turnover of species that typically live longer than a year with yearly data. Species losses and gains are likely to be relatively-rare events that reflect ecological processes particular to those species, since otherwise phylogenetic dispersion in bird assemblages would have changed through time.

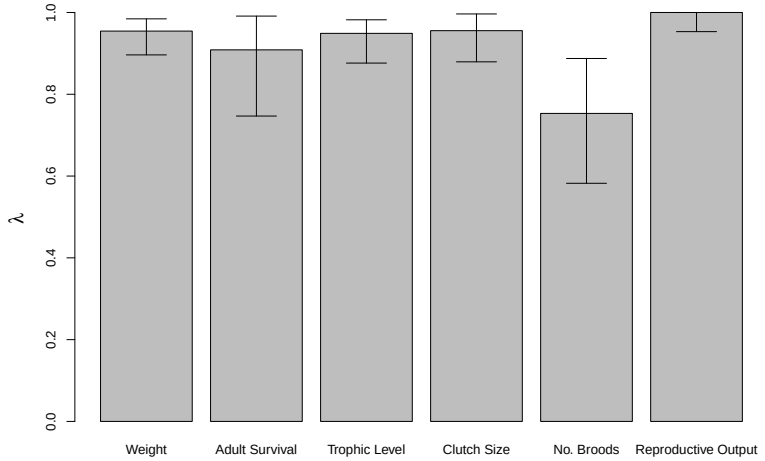
Butterflies breed and die in a single year—they cannot vary their reproductive effort across years as birds can (reviewed in Lack, 1968)—and the strong phylo-

genetic signal to butterflies' turnover could reflect their consequent sensitivity to environmental conditions. Phylogeny seems a better predictor of species lost or gained from an assemblage; unlike the birds, both species lost and gained from an assemblage are more distantly related to the other members of that assemblage. As with the bird results, the processes by which species are lost or gained from assemblages must be different to those that govern their general structure, since otherwise butterfly assemblages would have become more phylogenetically overdispersed through time.

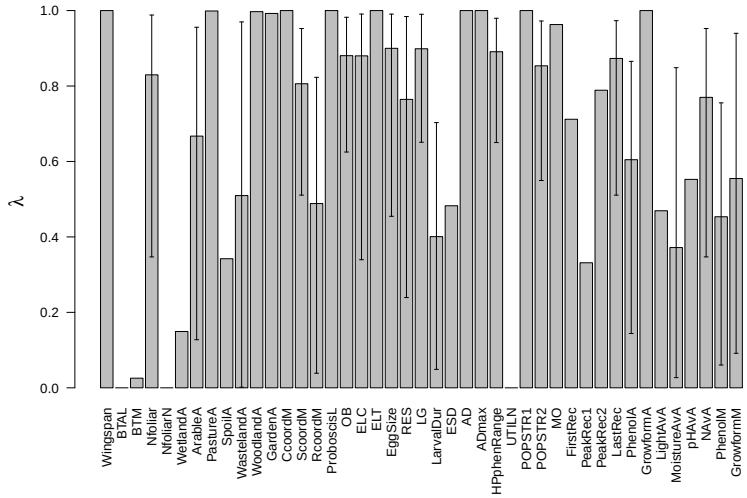
6.6 Conclusion

I have presented evidence of relatively unchanged phylogenetic and functional trait dispersion through time in the face of well-documented species turnover. The overwhelming majority of sites show evidence of habitat filtering, indicating that species' interactions with their environment is the dominant driver of assemblage structure, although there is evidence of the influence of competition in the bird data. That the forces structuring assemblages have remained so constant offers hope that no 'point-of-no-return' has yet been reached, and that species' declines can be reversed if environmental change is stopped or, better still, reversed.

6.7 Supplementary materials



(a) Birds



(b) Butterflies

Figure 6.12: Phylogenetic conservatism of bird (a) and butterfly (b) traits. Each bar represents the trait's maximum likelihood estimate of its optimal Pagel's λ (Pagel, 1999; Freckleton *et al.*, 2002) value, and its error bars indicate the 95% confidence intervals of that estimate. Butterfly trait codes are as defined in Dennis *et al.* (2004).

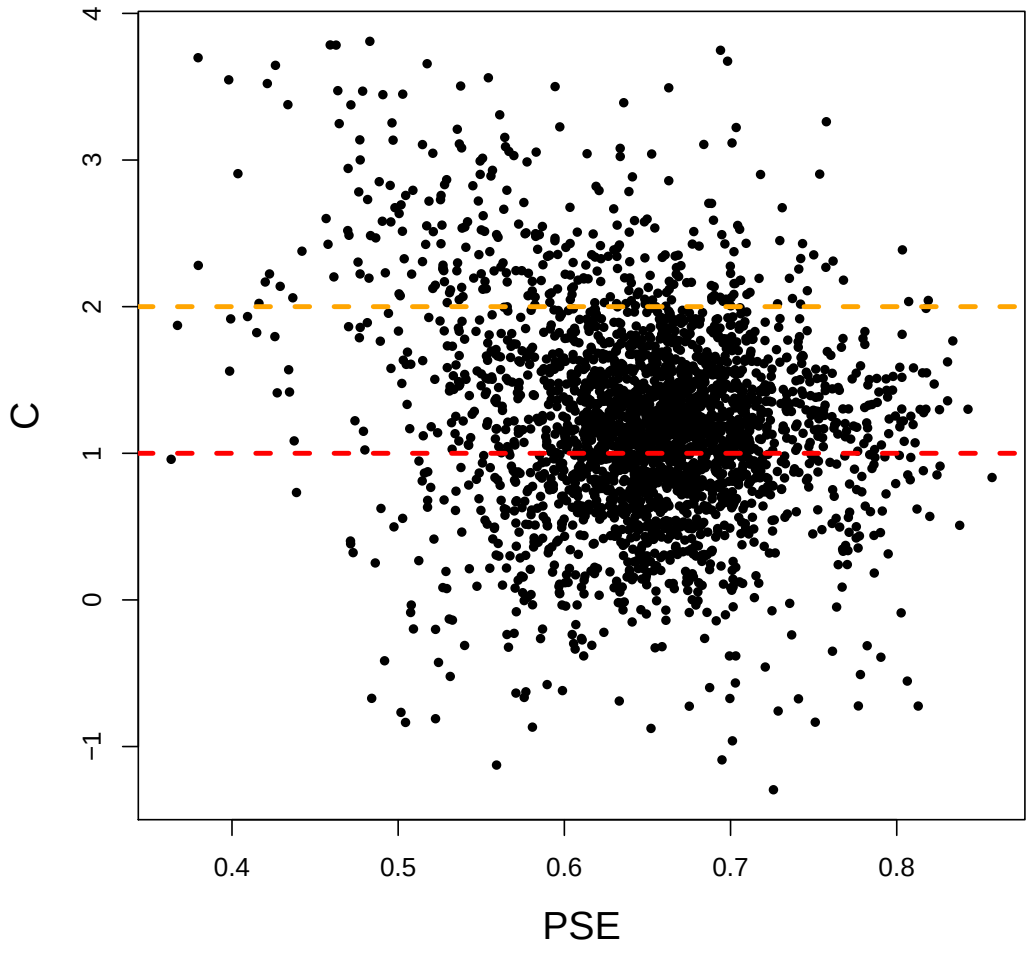


Figure 6.13: Comparison of *PSE* and D_C values for the bird data. *PSE* values were calculated using the function `pse` in `picante` (Kembel *et al.*, 2010) with the same data used to calculate D_C. As discussed in chapter two, *PSE* cannot measure overdispersion of species' abundances. If anything, *PSE* decreases with greater D_C values, which might otherwise be taken as evidence of phylogenetic clustering.

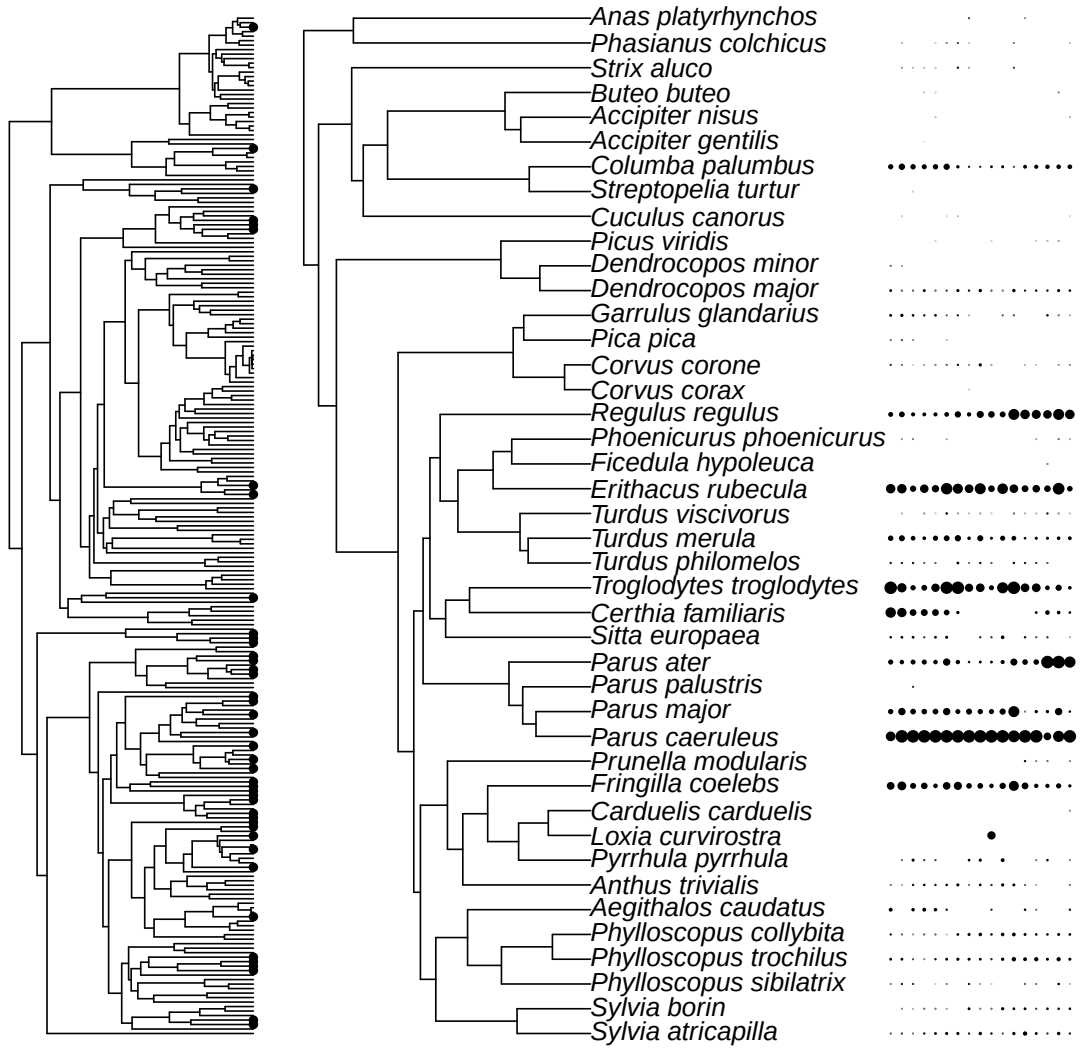


Figure 6.14: Example of bird assemblage phylogenetic structure. The left-hand phylogeny is the complete UK bird phylogeny, with species present in the assemblage marked with black circles. The right-hand phylogeny shows only those species present in the assemblage, with black circles (whose size represent species' abundances relative to overall assemblage abundance) for each year of recording, starting with 1994 at the left, and moving through to 2011 at the right. The assemblage is in UK grid cell SO7475, and is approximately 20 miles South-West of Birmginham. The site models' estimate mean D and D_C values of -0.11 and -0.23 respectively in this site. Note that there is variation in species' abundances through time, yet the phylogenetic structure of abundances appears relatively stable through time.

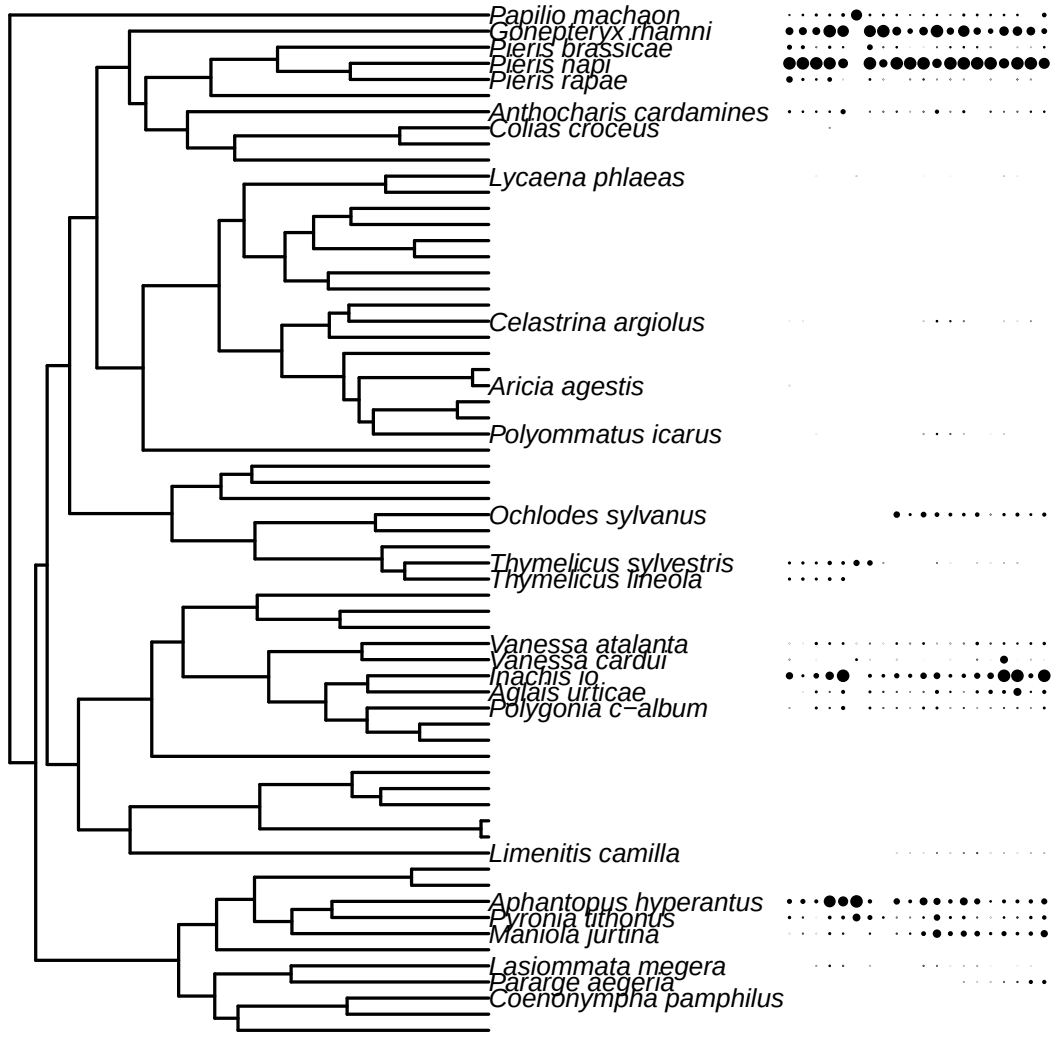


Figure 6.15: Example of butterfly assemblage phylogenetic structure. Species present in the assemblage at any point in time are named, and species abundances are represented by the size of the black circles (relative to overall assemblage abundance) moving left-to-right from 1981–2000. The assemblage is inside UK grid cell TG31, and is approximately 5 miles East of Norwich. The site models' estimate mean D and D_C values of -0.23 and -1.30 respectively. Note that there is variation in species' abundances through time, yet the phylogenetic structure of abundances appears relatively stable through time.

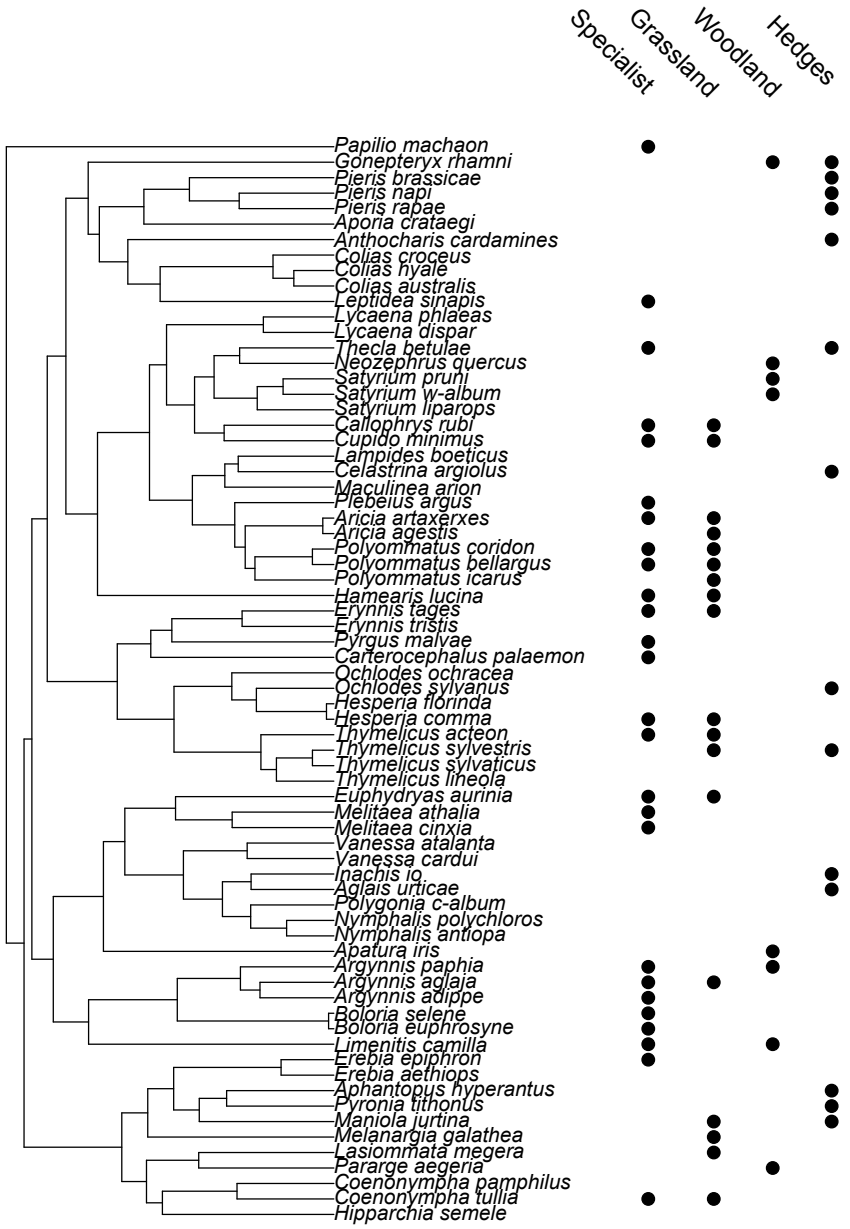


Figure 6.16: Phylogenetic structure of butterfly habitat preferences. Specialist butterflies (according to Pollard & Yates, 1993), and butterflies characteristic (according to Asher *et al.*, 2001) of chalk grassland, mature broad-leaved woodland, and hedges and arable field margins, are marked on the phylogeny. D values of habitat preference are 0.034, 0.46, 0.12, and 0.23 for specialism, grassland, woodland, and hedge habitats respectively; all preferences are significantly more phylogenetically clustered than would be expected at random ($p < 0.02$ for all).

Chapter 7

Beyond the *EDGE*: prioritising British plant species according to evolutionary distinctiveness, and accuracy and magnitude of decline, using *EDAM*

7.1 Abstract

Conservation biologists do not have infinite resources, and so must prioritise some species over others. The *EDGE*-listing approach ranks species according to their evolutionary distinctiveness and degree of threat, but ignores the uncertainty about both threat and evolutionary distinctiveness. I develop a new family of measures, which I name *EDAM*, that incorporates species' evolutionary distinctiveness, the magnitude of their decline, and the accuracy with which their decline can be predicted. Further, I show how the method can be extended to explore phyogenetic uncertainty. Using the vascular plants of Britain as a case study, I find that the various *EDAM* measures prioritise different species and parts

of Britain, and that phylogenetic uncertainty can strongly affect some species' scores.

7.2 Introduction

Global biodiversity is declining (Millennium Ecosystem Assessment, 2005; Butchart *et al.*, 2010), forcing conservation biologists to prioritise their finite conservation budgets in order to save as many species as possible (the 'Noah's Ark problem'; Weitzman, 1998). The *EDGE* approach (Isaac *et al.*, 2007) prioritises species according to how evolutionary distinctive ('*ED*') and globally endangered ('*GE*') they are. *EDGE* listing is a popular approach (cited over 90 times on `Web of Knowledge`), and has been applied to mammals (Isaac *et al.*, 2007) and amphibians (Isaac *et al.*, 2012), while a similar method has been used for birds (Redding & Mooers, 2006).

EDGE listing is a powerful tool, but its components are not optimised for country-level prioritisation. Red Listing status (the *GE* component) is a global hierarchy, as its maintainer (IUCN) acknowledges by funding the 'National Red List' project (`http://www.nationalredlist.org/`). Similarly, calculating evolutionary distinctiveness with a global phylogeny will understate the national importance of species whose close relatives live only in other countries. Such clades might be distinctive and important local components of many ecosystems, but would paradoxically be prioritised in none of them.

More fundamentally, it is unclear how an *EDGE* list distinguishes between the magnitude of a threat, and the accuracy with which we can predict that threat. Unexplained or unexpected declines may be of more concern because we may not know how to reverse them. It is often forgotten that, in the Red Lists, "*threatened categorization does not necessarily indicate conservation actions are required*" (Mace *et al.*, 2008). Distinguishing among the finer points of species' declines is impractical when dealing with the thousands of species in the global Red Lists, but individual countries have fewer species and often have more detailed, comparable data on those species.

I propose a family of prioritisation strategies ('*EDAM*') that borrows heavily from the *EDGE* system, incorporating species' evolutionary distinctiveness, the magnitude of their decline, and the accuracy with which we can predict their declines. Each of these components is transformed to be on a common numerical scale, making their implicit tradeoff in *EDGE* explicit in *EDAM*. Using a novel genus-level phylogeny for the majority of vascular plant species in the UK, I report the species and parts of Britain that *EDAM* and *EDGE* prioritise.

7.3 *EDAM* framework

EDGE consists of two components: evolutionary distinctiveness ('*ED*'; the phylogenetic diversity of a clade split equally among its members), and how globally endangered ('*GE*') a species is according to the IUCN Red List. I propose a general family of prioritisation indices ('*EDAM*'), which incorporate *ED*, the accuracy with which decline (or threat) can be predicted ('*A*'), and the magnitude of that decline (or threat) ('*M*'). There are many ways of assessing the latter two of these components; throughout this manuscript I will use subscripts to indicate which are being used. *EDAM* indices, like *EDGE*, are the sum of their components, but under *EDAM* each of these components are scaled such that their mean is zero and their standard deviation one. Thus each component contributes equally to the measure, and subjective judgements about which components are more important can readily be made explicit by multiplying components by a weighting factor.

An *EDAM* measure need not contain all three terms. For instance, EDM_{rl} incorporates only evolutionary distinctiveness and Red Listing status, and differs from *EDGE* only in that its components are scaled. However, EDM_{-rl} incorporates evolutionary distinctiveness and the *negation* of Red Listings status—this would prioritise species that are evolutionarily distinct and not threatened. Prioritising such species would be unhelpful, but if applied to data on species' range change (as with $EDA_{prec}M_{-rc}$ in the case study below), this might be used to identify potentially damaging invasive species. If components are to be multiplied by scal-

ing factors, I suggest they are represented in the subscripts of the measures; for example, $EDM_{2 \cdot rl}$ would weight Red Listing status as twice as important as evolutionary distinctiveness, and vice-versa for ED_2M_{rl}. There are also *precautionary* measures (*pEDAM* measures), where evolutionary distinctiveness is added to the greatest of the accuracy and magnitude measures, emphasising species that are either declining very rapidly, or whose declines we understand very poorly. Such a measure would not be possible if both accuracy and magnitude had not been transformed to be directly comparable.

Weighting conservation actions according to the credibility of a clade would be perverse, but it is useful to know the effect that phylogenetic uncertainty has on prioritisation. Most methods of phylogeny construction produce a set of credible, but not optimal, trees, and repeating analyses across this subset gives an estimate of the impact of phylogenetic uncertainty. Estimates could be weighted by the likelihood of the tree across which each measure was calculated if desired.

7.4 Case study: British vascular plants

Calculating *EDAM* measures requires three components: evolutionary distinctiveness, accuracy of decline, and magnitude of decline. Below I describe how each of these components were generated, and then the particular *EDAM* measures calculated with them. For comparison, *EDGE* scores were also calculated. Note that these *EDAM* results are based on decline, not threat, although the approach would be similar if data on the uncertainty of threat were available.

Phylogeny building (evolutionary distinctiveness)

Samples were collected from natural British populations of one species in each of 548 different plant genera. Total DNA was extracted from silica-dried material using a CTAB method (Doyle & Doyle, 1987). DNA was purified using CsCl/ethidum bromide (1.55mg/ml) density gradients in a Discovery 90 ultraspeed centrifuge (Sorvall). The ethidium bromide was removed from the DNA

suspension with an equal volume of butan-1-ol (stored with x1 SSC) and dialysed once with Synthesis™ double distilled water (Milli-Q) for 4 hours, and then twice with x1 TE buffer (4 hours each time). Double stranded PCR amplification of *rbcL* was performed in an ABI thermal cycler, using pre-made 2.5mM $MgCl_2$ PCR Mastermix (ABgene), 14μM of forward and reverse primer, 1.0μl BSA (0.4% w/v), and between 50-100ng of total DNA, in 50μl reaction volumes. Thermal cycler conditions were (1) 96°C, 1min; (2) 96°C, 1min, (3) 48°C, 30sec, (4) 72°C, 1min; cycle (2)-(4) was repeated for 28 cycles, (5) 72°C, 7min; (6) 4°C. Products were cleaned using QIAquick PCR Purification Kit (Qiagen).

An additional 97 *rbcL* sequences were downloaded from `GenBank` (Benson *et al.*, 2009), representing 91% of native genera in Britain (according to *PLANTATT*; Hill *et al.*, 2004). Using Stace (2010) to assign genera to families, and the Angiosperm Phylogeny Group III (APG; 2009) constraint tree included in the latest version of `Phylomatic` (Webb & Donoghue, 2005), I constructed a family-level constraint tree based on the APG III classification.

I aligned the sequences using `MAFFT` (Katoh *et al.*, 2005; Katoh & Toh, 2008), and chose the phylogeny with the greatest likelihood (under a *GTR-*γ DNA substitution model) from two separate `RAxML` (Stamatakis, 2006) runs. Each run partitioned the alignment into three codon positions, used the '*GTR-PSR*' (previously called '*GTR-CAT*') DNA substitution model, and was constrained using the constraint tree described above. The first run used 500 random starting trees (the best tree's log likelihood was −93656.22), and the second was an integrated rapid bootstrap search with 2000 random bootstrap searches and 400 subsequent thorough maximum likelihood searches (the best tree's log likelihood was −93669.50). Since the best-scoring tree was found in the first search, I annotated that tree with the 2000 rapid bootstrap trees from the second search, and rate smoothed it using `PATHd8` (Britton *et al.*, 2007), setting the root age to 1.

Genera in the phylogeny containing more than one species were replaced with a polytomy containing all the species listed in *PLANTATT* in that genus, with the polytomy placed either half-way along the branch that led to that genus' representative in the phylogeny, or at the 80$^{\text{th}}$ quantile of genus age in the phylogeny, whichever was smallest. This reduces bias introduced by particularly isolated sis-

ter species; many of the gymnosperm genera are distantly related to one another, and excessively long branches within genera are likely to bias results. Evolutionary distinctiveness values are relatively unaffected by the particular quantile at which this cut is made (figure 7.1).

Evolutionary distinctiveness was calculated across the phylogeny using the `ed.calc` function in `caper` (Orme *et al.*, 2011) with the `Isaac` correction for polytomies. The natural logarithm of these *ED* values was used to calculate *EDGE*, and the same data were scaled to have a mean of zero and standard deviation of one for use in the *EDAM* measures. In the original *EDGE* list one was added to the *ED* values before taking their logarithm to normalise them (Isaac *et al.*, 2007); doing so was not necessary in this case, and actually made the data extremely non-normally distributed. The entire rate smoothing, species addition, and *ED* calculation procedure was performed not just on the best-scoring phylogeny, but also on the 2000 bootstrap replicates.

Range change (magnitude of decline) and Red List status

I used the relative change index of Telfer *et al.* (2002) to measure species decline. Briefly, this was defined for each species as the residuals from a regression of the logit-transformed proportion of occupied cells in 1987–1999 (taken from Preston *et al.*, 2002) against the logit-transformed proportion of occupied cells in 1930–1969 (taken from an update to Perring & Walters, 1962). This is not an absolute measure of decline; the observed decline is relative to the other species in the dataset, but for the purpose of prioritisation this distinction is unimportant. Range change values were reversed so that greater numbers indicate a greater decline, and scaled to have a mean of zero and standard deviation of one. When calculating *EDGE*, Red List category (taken from the 2011 update of Cheffings & Farrell, 2005) was treated as a continuous variable (Least Concern=0, Near Threatened and Conservation Dependent=1, Vulnerable=2, Endangered=3, Critically Endangered=4; as in Isaac *et al.*, 2007).

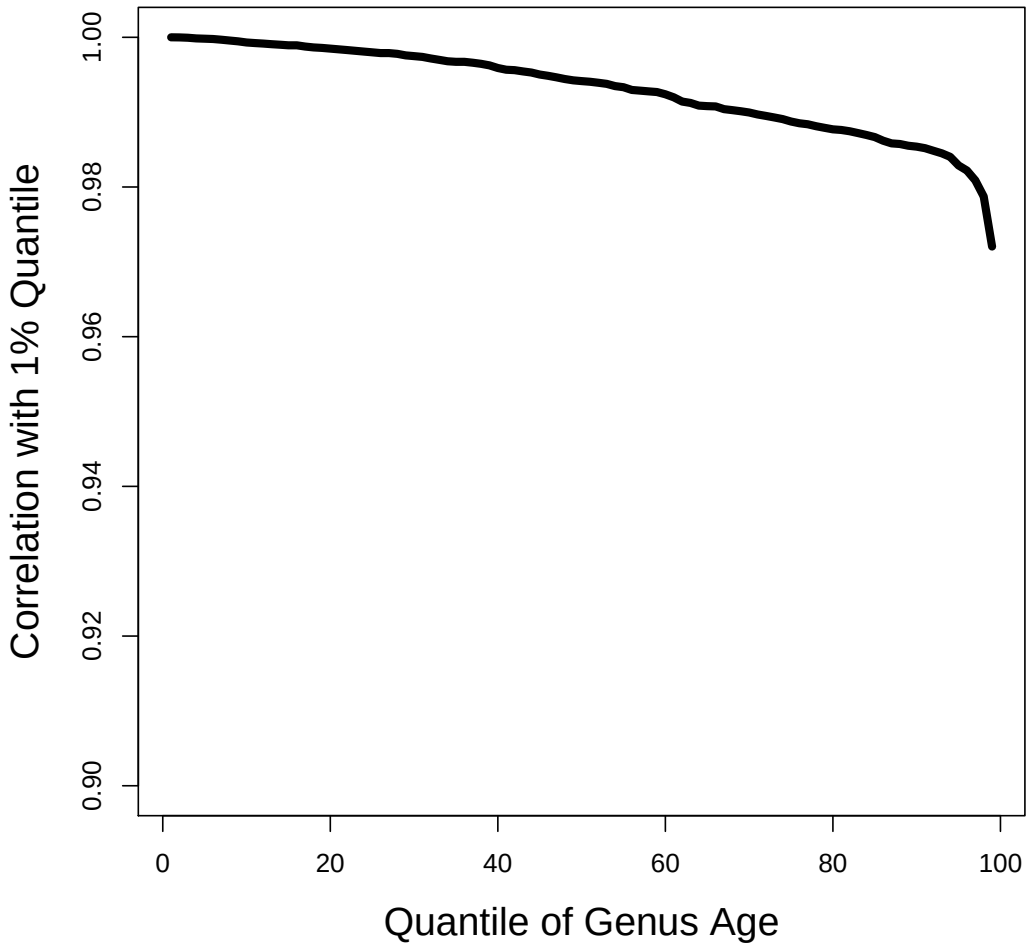


Figure 7.1: Evolutionary distinctiveness is relatively unaffected by the maximum age of genera. Genera were cut into the best-scoring phylogeny as described in the text, but at each integer quantile of genus age, and the evolutionary distinctiveness scores of all species correlated with the scores when the genera were cut at the 1st quantile. In the figure, the correlation coefficients are plotted against quantile at which the cuts were made.

Predictive accuracy (accuracy of decline)

Species distribution models predict where species are likely to be found, and so their accuracy provides a good measure of the accuracy with which species' declines can be predicted. Species distribution models (generalised boosted models) were produced using the same underlying data and method as Rapacciuolo *et al.* (2012); each was calculated using 10km x 10km grid cells and incorporate the same environmental data as Rapacciuolo *et al.* (2012) and additional land use data from Fuller *et al.* (2002), but do not account for biotic interactions. Cells containing less than 10% land were excluded from further analysis, since they are relatively uninformative when assessing model fit.

An occupancy model's accuracy can be assessed by calculating the area under its receiver operating curve (AUC approaches), but comparing AUC values among species is controversial (see Lobo *et al.*, 2008). Instead, we use one of three new measures of predictive accuracy—Rapacciuolo *et al.*'s '*precision*' (in prep.). Briefly, the method is based on the POC approach of Phillips & Elith (2010), where the modelled probability of a species being lost or gained is plotted on the horizontal axis, and on the vertical the average fraction of sites (calculated using a moving window) where that species is lost or gained. Ideally, summing each pair (lost/gained) of points would yield a curve that passed through the origin with a slope of one, and *precision* sums the absolute deviation from this line across all points (see equation 7.1). Species' precision estimates were scaled to have a mean of zero and a standard deviation of one.

$$precision = 1 - \frac{\sum(observed - ideal)}{n} \tag{7.1}$$

Calculating the measures

I calculated the measures listed in table 7.1 using the range change and predictive accuracy data described above, and the best-scoring phylogeny's evolutionary distinctiveness values. I compared $EDGE$ and EDM_{rc} by regressing them against each other and their components. Additionally, I calculated the $EDAM$ mea-

sures across all 2000 rapid bootstrap trees, to assess the impact of phylogenetic uncertainty on their values.

While the various measures may rank species' importance differently, the spatial arrangement of species might be such that these differences are unimportant. To see whether the indices prioritised different parts of Britain, I calculated the mean of each index of the species within each grid cell of the Preston *et al.* (2002) distribution data. Using the *classIntervals* function in the R package *classInt* (Bivand *et al.*, 2012a), these mean index values were split into twenty 'Jenks' quantiles and plotted.

7.5 Results

Phylogeny

The phylogeny (in Newick format, annotated with bootstrap values) is available from the author on request, as is a `OneZoom` (Rosindell & Harmon, 2012) file that allows the phylogeny to be interactively explored. The genus-level phylogeny is shown in figure 7.2, but due to space constraints species' labels are not printed.

Comparing *EDGE* and EDM_{rc}

EDGE and EDM_{rc} were strongly correlated, but many more species were tied for *EDGE* values (figure 7.3), suggesting *EDGE* was less precise. Both measures were significantly correlated with their components, but *EDGE* was more correlated with *ED* than Red Listing status (figures 7.4a and 7.4b), suggesting *EDGE* is driven by *ED* in this dataset. EDM_{rc} was correlated almost equally with *ED* and range change (figures 7.4c and 7.4d), suggesting it equally reflects its two components.

The *EDAM* values were stable across the bootstrapped phylogenies, and when correlated with the optimal phylogeny's values all bootstraps' values had correlation coefficients greater than 0.92. However, figure 7.5a reveals some species'

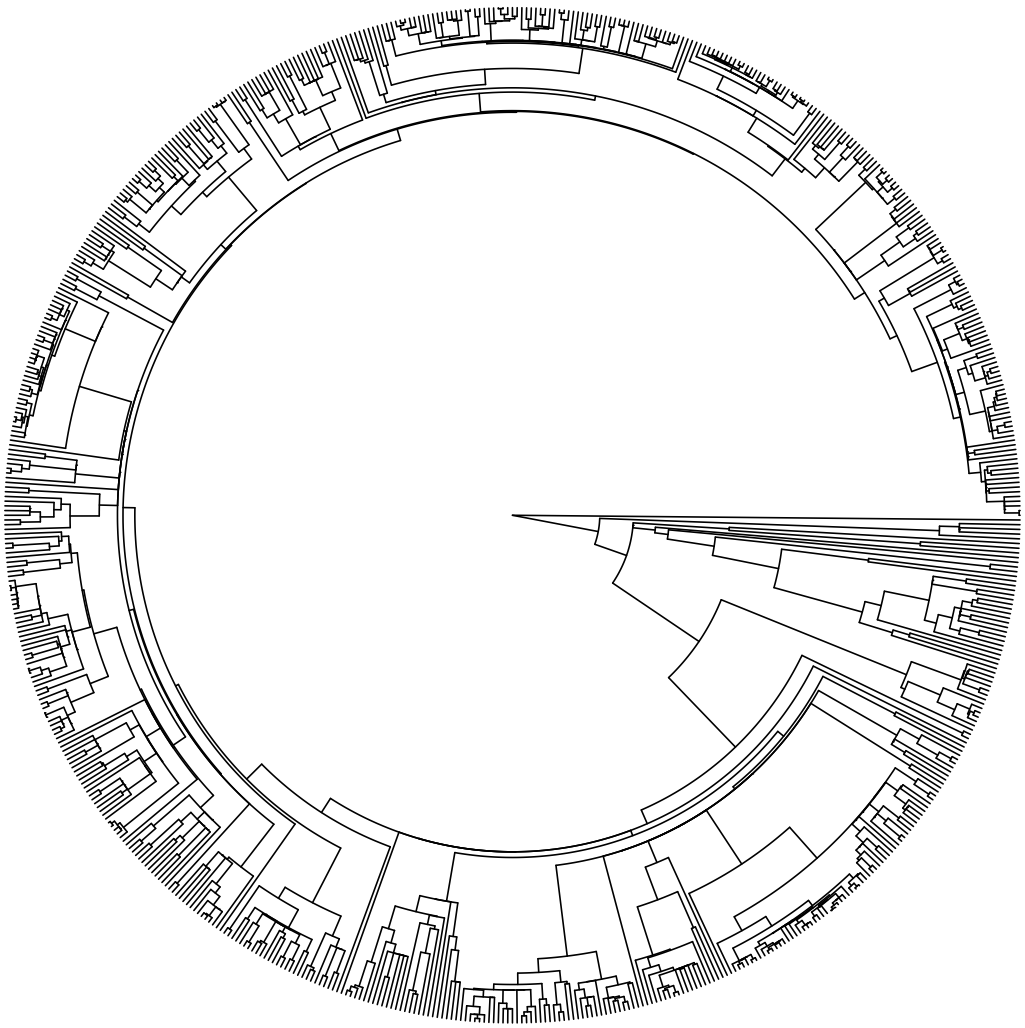


Figure 7.2: Genus-level phylogeny. Branch lengths are proportional to divergence time. Species' names are not plotted due to space limitations.

EDM_{rc} estimates vary considerably across the bootstraps. The species with the greatest standard deviation of bootstrapped EDM_{rc} is shown in figure 7.5b, where three distinct groupings of EDM_{rc} values can be seen.

Conservation priorities

Each measure's highest ranking twenty species are listed in table 7.2. While species' EDM_{rc}, $EDA_{prec}M_{rc}$, and $pEDA_{prec}M_{rc}$ scores are correlated with one another, $EDA_{prec}M_{-rc}$ is less strongly correlated to the others, implying it is highlighting a different set of species (figure 7.6).

Maps of cells' mean scores are shown in figure 7.7. Both *EDGE* and EDM_{rc} prioritise Scotland, although *EDGE* has relatively few high-ranking grid cells. Upland areas of Northern England (including the Yorkshire Dales and the Lake District) and Wales (including the Brecon Beacons and Snowdonia National Park) seem to have many evolutionarily distinct species that are unpredictably declining ($EDA_{prec}M_{rc}$). The South West of England and Wales, and parts of Isle of Lewis, are highlighted by $EDA_{prec}M_{-rc}$ as having unpredictably spreading evolutionary distinct species. The precautionary measure ($pEDA_{prec}M_{rc}$) highlights grid cells throughout Britain, but mostly in England and Wales.

7.6 Discussion

Peformance of *EDAM*

EDM_{rc} was more precise than *EDGE*, and gives equal weight to both evolutionary distinctiveness and decline, suggesting EDM_{rc} is a better way to prioritise British conservation. However, the data required for the *EDAM* approach means it is unlikely to supplant *EDGE* as a global prioritisation scheme. Predictive accuracy is difficult to quantify, and species distribution models, while tractable and relatively quick to produce, typically ignore biotic interactions and assume

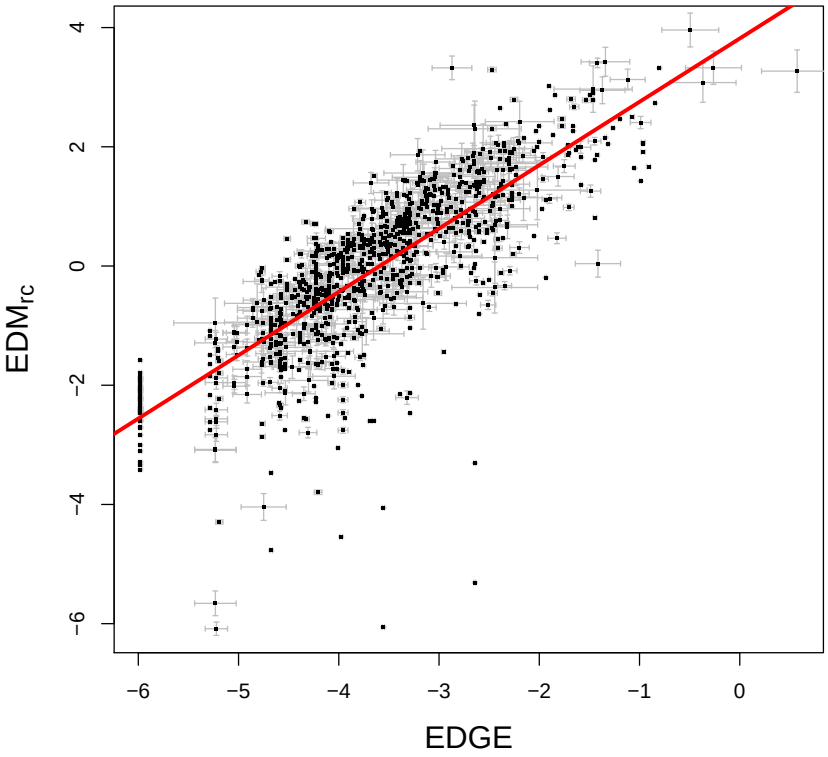
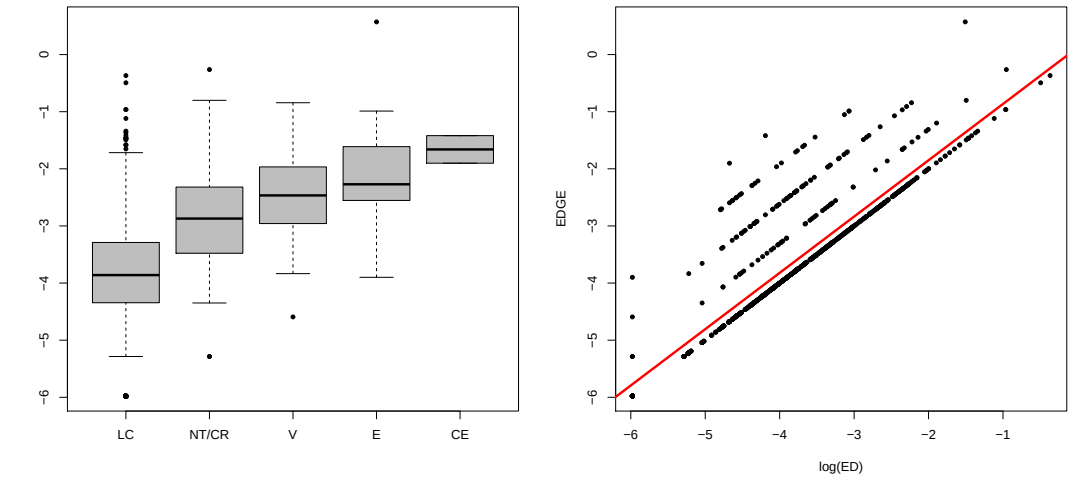
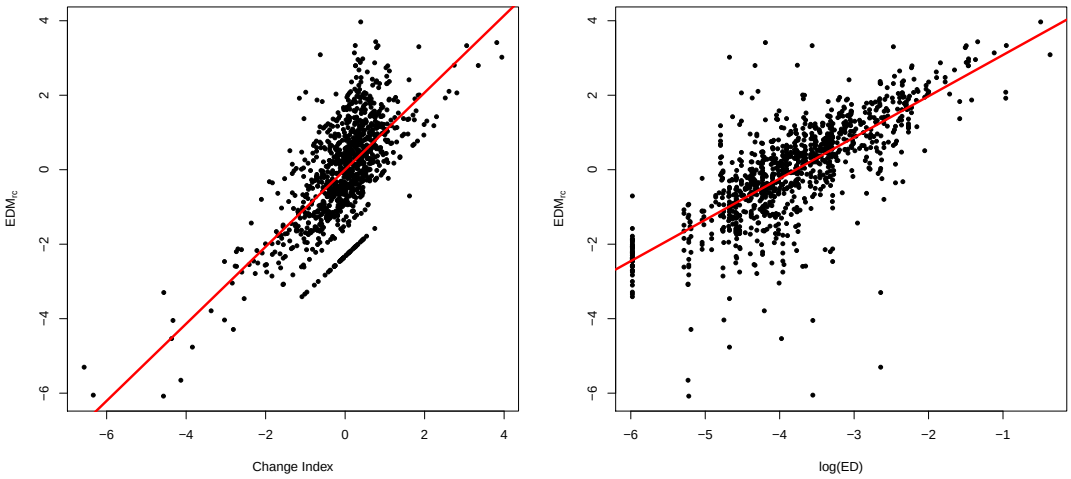


Figure 7.3: Plot of *EDGE* scores against EDM$_{rc}$, showing they are strongly correlated (red regression line; $F_{1,1051} = 1846$, $r^2 = 0.64$, $p < 0.0001$). The standard deviations of the EDM_{rc} and *EDGE* values' bootstrapped estimates are shown as grey whiskers around each point; these were not incorporated in the regression quoted above. There are 553 tied *EDGE* scores, and no tied EDM$_{rc}$ scores; a line of tied *EDGE* species can be seen at the left of the plot. A greater number of tied species indicates a lack of precision.



(a) *EDGE* vs. Red List category

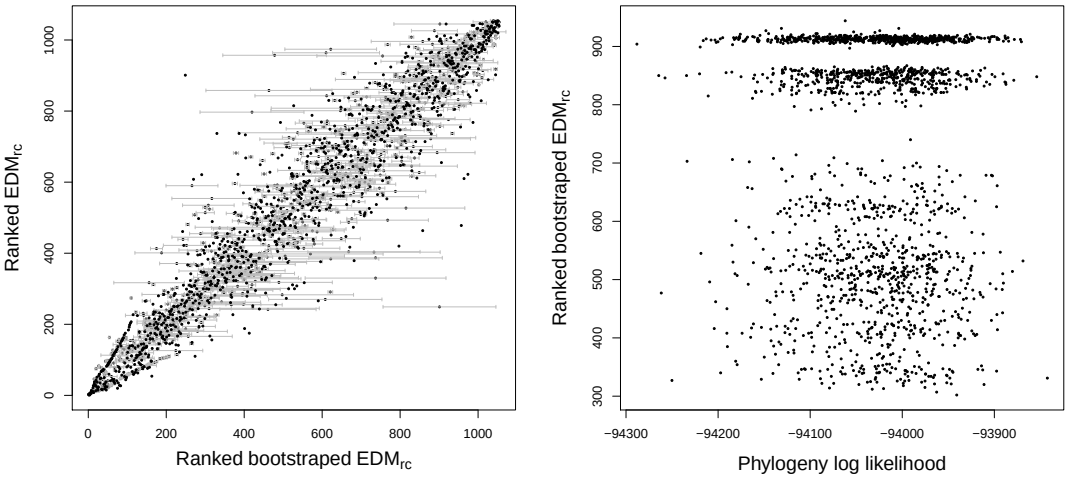
(b) *EDGE* vs. log(ED)



(c) EDM_{rc} vs. range change

(d) EDM_{rc} vs. log(ED)

Figure 7.4: *EDGE* and EDM_{rc} plotted against their components. In (a) and (b), *EDGE* is plotted against Red List category (increasing in threat level from left-to-right; $r^2 = 0.20$) and the logarithm of evolutionary distinctiveness ($r^2 = 0.78$) respectively. The larger r^2 when regressed against log(ED) suggests *EDGE* is more strongly related to *ED* than *GE*. (c) and (d) show EDM_{rc} against change index ($r^2 = 0.47$) and the logarithm of evolutionary distinctiveness ($r^2 = 0.56$) respectively. EDM_{rc} is related almost equally strongly to its components, and so is less biased than EDGE. All models above were statistically significant ($p < 0.0001$) and were linear regressions, with the exception of comparison of *EDGE* and Red Lists status, which was an ANOVA. Note that EDM_{rc} is calculated with scaled values, but is not regressed against them above.



(a) Ranks of EDM_{rc} versus bootstrapped EDM_{rc}

(b) Exemplar species' EDM_{rc} ranks

Figure 7.5: Variability of EDM_{rc} values across bootstrapped phylogenies. In (a), the ranks of the best phylogeny's EDM_{rc} values are plotted against the median ranks across all the bootstrapped phylogenies, with grey whiskers showing the standard deviations of those ranks. (b) plots the rank of *Wahlenbergia hederacea*'s EDM_{rc} in each bootstrapped phylogeny against that phylogeny's log. likelihood. *Wahlenbergia hederacea* is the species with the largest standard deviation in (a). Three distinct groupings of EDM_{rc} values can be seen in (b), likely reflecting equally likely islands in treespace (see discussion).

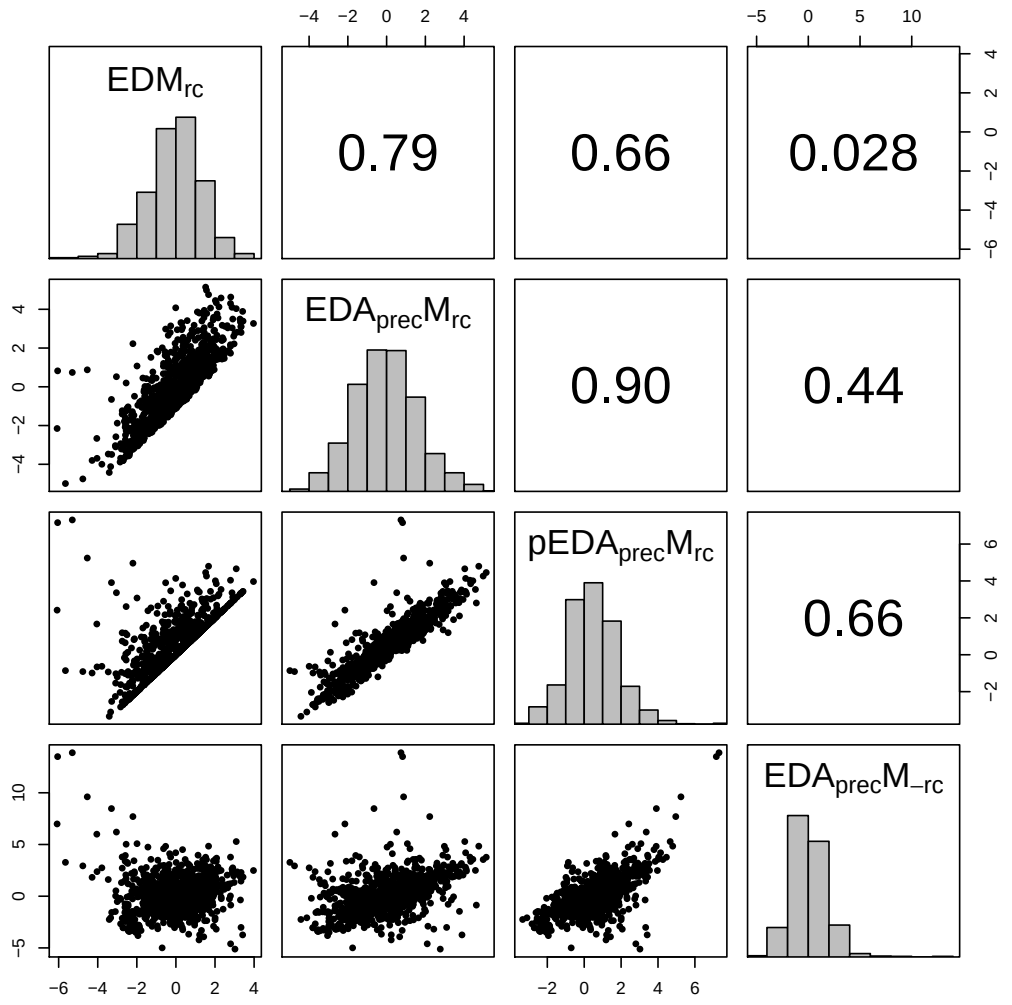
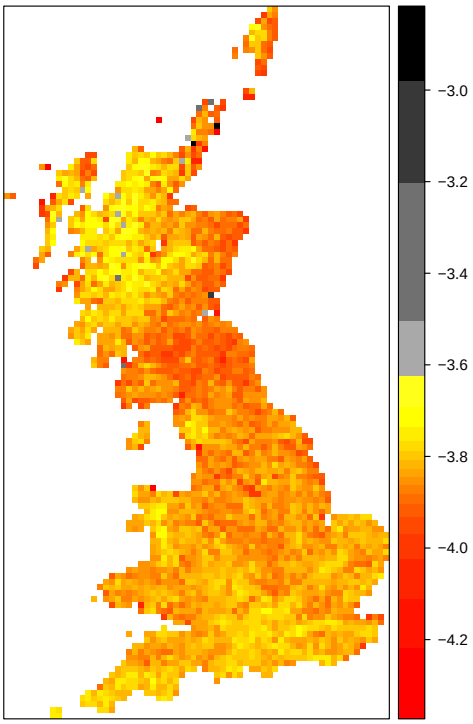
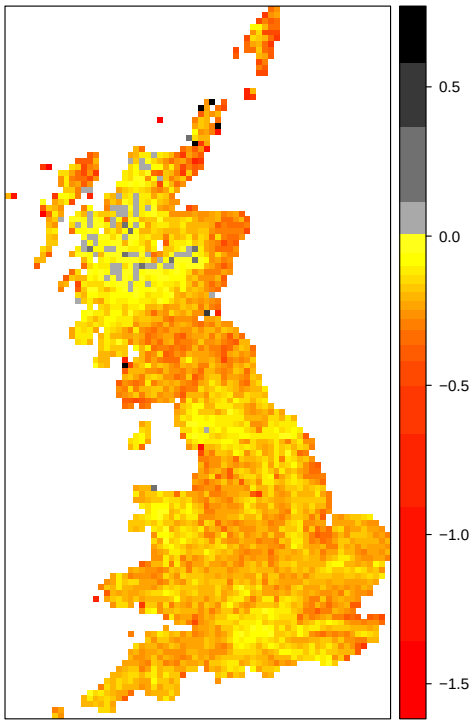


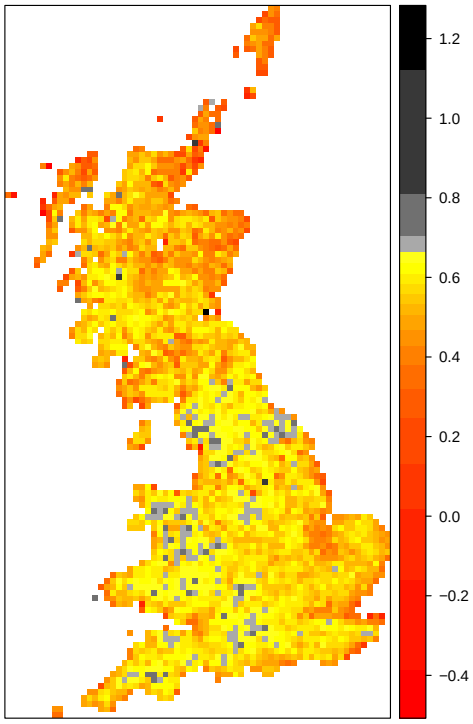
Figure 7.6: Scatter plots of the *EDAM* measures against one another (lower panels), histograms of their distributions (along the diagonal), and correlation coefficients of the measures (upper panels). Note the poor correlation between $EDA_{prec}M_{-rc}$ and EDM_{rc}.



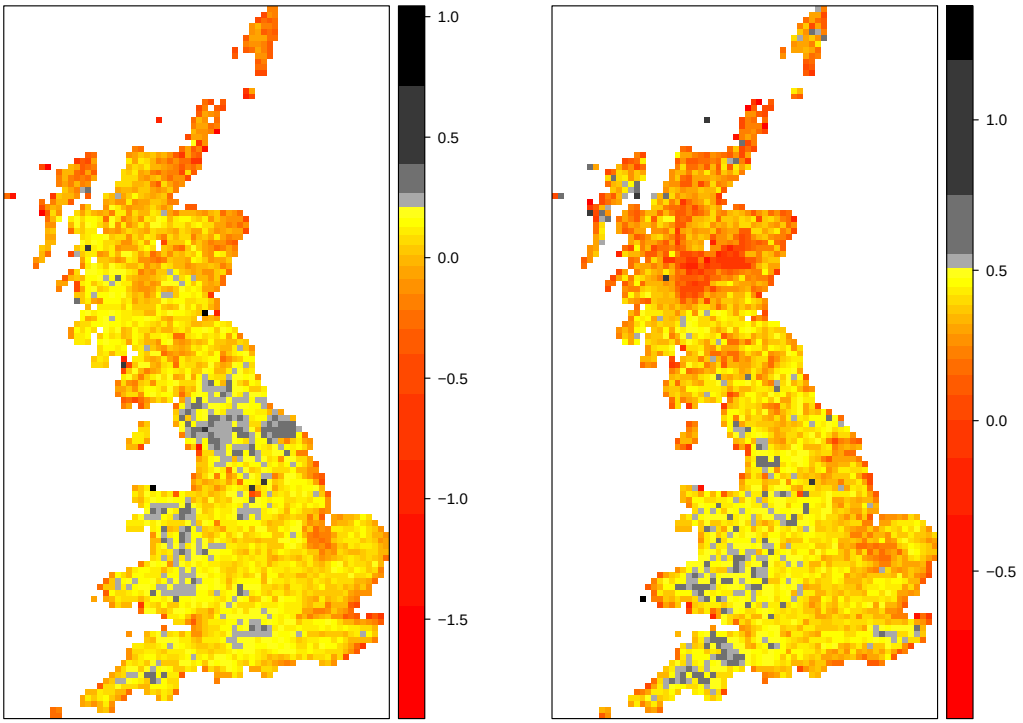
(a) *EDGE*



(b) EDM_{rc}



(c) $pEDA_{prec}\mathrm{M}_{rc}$



(d) $EDA_{prec}\mathrm{M}_{rc}$ (e) $EDA_{prec}\mathrm{M}_{-rc}$

Figure 7.7: Mean of prioritisation measures for species in grid cells across Britain. Each map has a legend to the right hand size, splitting the values into twenty 'Jenks' quantiles (see text). The greatest four quantiles have been coloured differently, to emphasise the high-priority sites. Note that the distributions of all five measures have extremely long tails (as shown by the size of the quantiles in the legends).

stationarity of species' distributions. Other methods of assessing predictive accuracy, such as literature reviews and community-based models, can be prohibitively time-consuming and difficult to directly compare among taxa.

Some species' ranked EDM_{rc} values vary greatly among the bootstrapped phylogenies, which is concerning in species where there is no obvious relationship between EDM_{rc} rank and the likelihood of the phylogeny across which it was calculated (figure 7.5). In particular, the three distinct groupings in figure 7.5b suggests that three islands in treespace were sampled (discussed in Sanderson *et al.*, 2011); since each island seems equally likely, there may be no correct score for this species. Accurately prioritising species that are difficult to place in a phylogeny ('rogue taxa'; see Aberer *et al.*, 2012) without more sequence data may not be possible. However, rogue taxa are the exception, not the rule, and on the whole the bootstrap replicates were congruent with the best phylogeny's rankings. Rogue taxa pose no problem for a prioritisation system as long as they are identified, but testing prioritisation lists by randomly altering phylogenies (as in Isaac *et al.*, 2012) will not detect them.

Prioritisation

At first glance, the number of common species in the lists of prioritised species (e.g., *Pteridium aquilinum*—bracken; table 7.2) might be surprising. These surprises reflect how evolutionarily distinct British non-angiosperm plants are, but the measures also prioritise several severely declining species (e.g., *Galeopsis angustifolia*). Limiting the lists to angiosperms or down-weighting evolutionary distinctiveness would alter the rankings if desired, and I consider it a strength of the *EDAM* approach that we can make our decisions explicit in this way. More importantly, the purpose of a quantitative prioritisation exercise is not necessarily to produce a single, definitive list for conservation, but to help us consider how we prioritise nature. For example, *Selaginella selaginoides* is fairly uncharismatic (even for a clubmoss), yet it has the highest EDM_{rc} score. *S. selaginoides* is declining in Britain, and gives its name to an entire (declining) species group in Braithwaite *et al.* (2006), yet is not a UK Biodiversity Action Plan (BAP; 2007)

species. It is likely that *S. selaginoides* is not a priority because it is widespread throughout Europe; highlighting it in the EDM_{rc} rankings re-opens the question of whether distinct, declining components of our flora should be conserved regardless of their status elsewhere.

EDGE and EDM_{rc} prioritise similar parts of the UK, although EDM_{rc} highlights large areas of the Scottish highlands *EDGE* does not. Interestingly, those measures that incorporate accuracy highlight upland areas of England and Wales, and large parts of Cornwall in the case of $EDA_{prec}M_{-rc}$. The difficulty predicting these areas may reflect their relatively high elevation, and that many of them (such as Dartmoor) are particularly wet. Many of these areas are national parks; if parks are placed in areas of unusual natural beauty, it is perhaps little surprise that the species there are atypical and so have distributions that are difficult to accurately predict. The precautionary $pEDA_{prec}M_{rc}$ measure seems intermediate between the EDM_{rc} and $EDA_{prec}M_{rc}$, which is perhaps to be expected since it is a sort of compound measure.

Wider conservation issues

There is some evidence that species distantly related to an assemblage are more likely to invade (van Wilgen & Richardson, 2012), and more damaging when they do (Strauss *et al.*, 2006), though there are counter-examples (Tingley *et al.*, 2011). More work is needed, but it is reasonable to highlight evolutionarily distinct species whose ranges are expanding as potential future problems, particularly given that distantly related species tend to be ecologically dissimilar (reviewed in Wiens *et al.*, 2010). Although precise ecological data on invasive species is often missing, invasives are often taxonomically defined, and so can usually be placed in a phylogeny. Thus an *EDAM* approach could help identify potential problems, particularly in concert with information on the phylogenetic structure of protected areas. The UK has excellent data on the species composition of most protected areas, and this study's *rbcL* phylogeny could be used for such analyses.

Prioritising species on the basis that their declines are poorly-understood might seem strange for two reasons. Firstly, such species might be more difficult to

save, although this might make them of greater academic interest and investigating them might uncover new conservation techniques. Secondly, it might seem better to weight species' declines according to our confidence in that decline, rather than treat magnitude and accuracy as distinct. However, that would not necessarily be precautionary (see Myers, 1993), and could lead us to prioritise species on the basis of sampling effort. Accuracy of prediction (ideally) relates to our understanding of the drivers of range change, and, if desired, we could choose to prioritise species whose declines we understand well enough to reverse.

Conservationists can rarely achieve all their goals simultaneously, and instead different components (e.g., evolutionary distinctiveness, species diversity, and ecosystem services) must be traded off against one another. By scaling the components of *EDAM* so that each is comparable, we have a starting point from which we can explore the implications of prioritising different aspects of our biota, and make our subjective decisions more explicit. The *EDAM* lists presented here are designed for very different purposes, and it is unlikely that a single list of species to prioritise will ever suffice for British plants, let alone other threatened taxa. However, I feel that the success of the *EDGE* program demonstrates that incorporating evolutionary distinctiveness into conservation strategies strikes a chord with the majority of biologists, and that explicitly incorporating uncertainty into the system can only be for the better.

Measure	Formula	Prioritises
EDGE (EDM_{rl})	unscaled log(ED) + Red List	Global threat
EDM_{rc}	ln(ED) + range change	British threat
$EDA_{prec}\mathrm{M}_{rc}$	log(ED) + range change + precision of decrease	Range change and low precision of decrease
$EDA_{prec}\mathrm{M}_{-rc}$	log(ED) + reversed range change + precision of increase	Range change and low precision of increase
$EDA_{prec}\mathrm{M}_{rc}$	log(ED) + max(range change, AUC)	Greatest of threat and accuracy of prediction

Table 7.1: Summary of measures. Note that all measures prioritise evolutionary distinctiveness ('ED' above), and that all components are scaled such that their means are zero and standard deviations one unless stated. As discussed in the text, in the *EDAM* framework *EDGE* values could be called EDM_{rl}, although *EDGE* components are not scaled.

EDM_{rc}	EDGE
Selaginella selaginoides	*Lycopodiella inundata*
Pteridium aquilinum	*Pilularia globulifera*
Galeopsis angustifolia	*Osmunda regalis*
Pilularia globulifera	*Selaginella selaginoides*
Himantoglossum hircinum	*Hymenophyllum wilsonii*
Hymenophyllum wilsonii	*Daphne mezereum*
Sinapis arvensis	*Wolffia arrhiza*
Lycopodiella inundata	*Isoetes echinospora*
Botrychium lunaria	*Isoetes lacustris*
Osmunda regalis	*Zostera noltei*
Ranunculus arvensis	*Adonis annua*
Cryptogramma crispa	*Spartina maritima*
Huperzia selago	*Astragalus danicus*
Tamus communis	*Cuscuta epithymum*
Hymenophyllum tunbrigense	*Botrychium lunaria*
Oxalis acetosella	*Frankenia laevis*
Scleranthus annuus	*Myriophyllum verticillatum*
Mentha pulegium	*Colchicum autumnale*
Narthecium ossifragum	*Ruppia cirrhosa*
Tofieldia pusilla	*Pteridium aquilinum*

$EDA_{prec}M_{rc}$	$EDA_{prec}M_{-rc}$	$pEDA_{prec}M_{rc}$
Myrica gale	*Polypodium vulgare*	*Polypodium vulgare*
Cruciata laevipes	*Tripleurospermum inodorum*	*Tripleurospermum inodorum*
Adoxa moschatellina	*Polygonum arenastrum*	*Polygonum arenastrum*
Scleranthus annuus	*Polypodium interjectum*	*Sedum album*
Jasione montana	*Sedum album*	*Adoxa moschatellina*
Drosera intermedia	*Poa humilis*	*Osmunda regalis*
Drosera rotundifolia	*Papaver somniferum*	*Myrica gale*
Narthecium ossifragum	*Tripleurospermum maritimum*	*Cruciata laevipes*
Radiola linoides	*Osmunda regalis*	*Geranium pratense*
Oxalis acetosella	*Glyceria declinata*	*Narthecium ossifragum*
Geranium pratense	*Prunus domestica*	*Drosera intermedia*
Mercurialis perennis	*Adoxa moschatellina*	*Selaginella selaginoides*
Osmunda regalis	*Meconopsis cambrica*	*Polypodium interjectum*
Sanicula europaea	*Tilia platyphyllos*	*Meconopsis cambrica*
Galeopsis angustifolia	*Polystichum setiferum*	*Drosera rotundifolia*
Circaea lutetiana	*Polystichum aculeatum*	*Polystichum aculeatum*
Linum catharticum	*Geranium pratense*	*Jasione montana*
Pinguicula lusitanica	*Pinus sylvestris*	*Circaea lutetiana*
Gnaphalium sylvaticum	*Equisetum telmateia*	*Allium ursinum*
Erica tetralix	*Euphorbia lathyris*	*Mercurialis perennis*

Table 7.2: Highest-ranked twenty species according to each measure. The highest ranking species is listed first.

Chapter 8

Conclusion

In this thesis, I have attempted to answer a wide range of questions using a broad range of taxa, since I feel one of the major strengths of a community phylogenetic approach is it allows comparisons to be drawn across otherwise incomparable systems. The first half of the thesis (chapters 1–4) focuses on what phylogenetic structure is and how it should be measured, laying the groundwork for the latter chapters (5–7), where I examined ecological communities under change.

I started by outlining some of the major areas in which community phylogenetic methods have advanced our understanding of ecology (chapter one), and then reviewed how assemblage phylogenetic structure is measured (chapter two). In chapter three, I re-analysed the plants of the 50ha study site at Barro Colorado Island, and found shifts in assemblage structure over extremely fine spatial scales. However, my demonstration of increased phylogenetic clustering in younger clades was noticeable only in finely-resolved phylogenies, which the *de facto* tool for producing assemblage phylogenies (`Phylomatic`; Webb & Donoghue, 2005) is unable to produce. So, in chapter four, I presented `phyloGenerator`, an automated phylogeny generation program for ecologists that uses existing DNA data to produce detailed phylogenies.

Using this tool, I attempted to explain spatial and temporal variation in an ecosystem function (bioturbation) in benthic invertebrates (chapter five). While these invertebrate assemblages are phylogenetically structured, I found little evidence

that either traits or phylogeny predicted bioturbation, and instead suggested that environmental conditions and species richness were the dominant drivers. However, with more detailed trait data and longer time series, I found strong evidence of habitat filtering in British butterfly assemblages, and contrasting evidence of habitat filtering and competition in bird assemblages (chapter six). Perhaps most interestingly, I found that phylogenetic and trait-based measures of bird and butterfly assemblage structure has remained relatively constant through time, despite considerable change in species abundances.

If Britain's biota is phylogenetically structured, it might be useful to incorporate that information into conservation planning, and my final analysis chapter (seven) attempts to do this for British plants. It describes an extension to the *EDGE* conservation prioritisation framework (Isaac *et al.*, 2007), *EDAM*, that incorporates uncertainty in species' phylogeny and future distributions.

8.1 Future directions

Invasive species

Attempts to quantify how invasive species affect phylogenetic community structure have been hampered by the difficulty of specifying the source pool of potential invading aliens. A pleasing solution was found by Strauss *et al.* (2006), who demonstrated a phylogenetic signal to severity of invasiveness, altogether avoiding the problem of estimating the pool of potential invaders. This approach provides hope that community phylogenetics might allow for a predictive approach to invasive species (*sensu* Lavergne *et al.*, 2010), whereby possible invasive species are predicted on the basis of phylogeny alone. Indeed, chapter six suggests that species' phylogenetic distance from members of an assemblage could be used to predict their likelihood of invasion.

Interaction networks

There has been relatively little work on the phylogenetic structure of interaction networks. The four most relevant papers (Ives & Godfray, 2006; Rezende *et al.*, 2007; Eklöf *et al.*, 2012; Naisbit *et al.*, 2012) find evidence of phylogenetic (or taxonomic) conservatism of function or structure, implying that closely-related species perform similar roles. However, it is still unclear whether there is a relationship between the degree of specialisation and the phylogenetic dispersion of the group of species with which an organism interacts. If phylogeny can be used to predict interaction networks (*sensu* Ives & Godfray, 2006), it could be particularly important for species distribution modelling, where even modest improvements in the prediction of biotic interactions could be of great use.

Metaphor

The intersections between similar fields are often interesting by virtue of metaphor: if two fields interpret a problem differently, combining their approaches can yield new insight. One example is the parallels between modelling turnover in ecological assemblages and base substitution in DNA sequences. We could model species turnover with a transition matrix, where the likelihood of a species entering a community can be predicted by the identity of the species they replace. The problem would then be analogous to parameterising a substitution model when building a phylogeny. Simplifying the transition matrix in the same way we search for the optimal DNA (or protein) substitution model could help identify interacting species. Simplifying this matrix would be difficult, but could be aided by pre-existing data on species' traits and phylogenetic relatedness. Habitat types where these transition probabilities are different, and the effect of history, could be handled similarly to partitions in a DNA sequence. An initial attempt to do this, which I carried out with the aid of the developers of the phylogenetics program `RAxML` (Stamatakis, 2006), is outlined in the appendix.

8.2 Concluding remarks

There will never be one perfect definition of an ecological assemblage, and so there will never be one perfect way of describing one. It is no surprise that some researchers expressed misgivings about the incursion of phylogenetic structure into ecology; initial attempts to incorporate phylogenies into comparative analysis were met with criticism, and many feared implicit assumptions of the approach were ignored (e.g., Westoby *et al.*, 1995). Such initial skepticism is healthy—there is always a danger that a new framework will be applied simply because it can be, without any critical evaluation of its implications.

The incorporation of phylogenetic structure into ecology is not without its pitfalls. Invoking niche conservatism when interpreting phylogenetic dispersion is contentious (e.g., Mayfield & Levine, 2010), and explaining phylogenetic structure solely in terms of traits can relegate phylogeny to a stand-in for trait data yet to be collected. By measuring phylogenetic structure we are acknowledging that species are not separate, identically-distinct units, and that they share a common evolutionary history. Phylogenetic structure is an attempt to link the ecology of species with the way in which those species came to be, and condemning the entire field on the basis that some of its measures are difficult to interpret misses this.

It is too soon to say whether the measurement of phylogenetic assemblage structure will become an established part of mainstream ecology. However, ecologists and evolutionary biologists have been exchanging ideas for almost as long as the two fields have existed, and I can see no reason they should, or would, want to stop. The current approach to community phylogenetics may well become defunct, but ecology and evolutionary biology are too tightly-linked for them to be studied in complete isolation. Species' evolutionary history was shaped by their ecology, and it seems natural to see what the shape of their evolutionary history can reveal about their present-day ecology.

Appendix: Modelling ecological communities as if they were DNA sequences

Abstract

Ecologists are interested in understanding and predicting how ecological communities change through time. While it might seem natural to measure this through changes in species' abundances, practical limitations often mean this is not possible. I present an approach inspired by DNA substitution models that attempts to estimate historic interactions between species, and thus estimate rates of turnover in ecological communities. As an example with simulated data shows, the method is not yet complete, but another example using UK butterfly community data shows the method may have promise.

Introduction

Many ecologists recognise broad habitat types and sub-types, grouping communities they define as similar in structure. A good example is the British National

Vegetation Classification system (Rodwell, 1991), which hierarchically classifies all plant communities with the UK. Ecologists also recognise a wide variety of variability within these categories, and the recent interest in Neutral Theory (Hubbell, 2001) and stochastic variation at all spatial scales (reviewed in Vellend, 2010) suggests ecologists want to model this variation. However, models that allow for interspecific differences are often over-parameterised, and summary statistics of structure do not necessary help us make future predictions about species composition.

One way round this problem has been to model a community as proceeding through a series of states, each with their own associated species compositions and abundances. The probability of moving among these states can be modelled using Markov chains, and predictions about future ecological composition can be made (reviewed in Logofet & Lesnaya, 2000). This seems a natural way to model the habitat types that were discussed above, but it cannot model variation within states, assumes the history of a community is unimportant, and requires that a system reaches a final, stable state. Moreover, such methods require *a priori* definitions of states, and as such cannot be driven by the data themselves.

My alternative is to model species turnover as a transition matrix, where the likelihood of a species entering a community can be predicted by the identity of the species they replace, creating a model with species-level parameters and predictions. The problem of over-parameterisation can be solved by simplification of this matrix, in much the same way that a DNA or protein substitution matrix is often simplified by allowing certain bases or amino acids to share parameters. However, this method has the major drawback of requiring an accurate way of determining the history of species interactions in a community, which is rarely known.

Methods

Overview and description of problem

I modelled the fate of each individual in a community over a number of discrete time-steps, and attempted to estimate parameters of interest for each species in a community based on what each individual did. I assumed an individual could do one of only four things in each time-step:

- Reproduction. That individual dies, and is replaced by another of the same species, or that individual survives to the next time-step.
- Replacement. That individual dies, and is replaced by another of a different species.
- Death. That individual dies, but is not replaced by another of any species.
- Addition. That individual enters the community, but does not replace any other individual. This allows communities to increase in overall abundance.

Although this model is fairly simple, it is difficult to estimate the parameters involved (the rate of reproduction, loss, death and addition) for each species because the history of the community is not clear from the identities of the species in it. Taking table 1 as an example, it is difficult to tell what happened between the first and second measurements of that community that led to species A increasing in number and species B become less abundant. Any attempt to infer what events were most likely to have happened requires an estimate of the relative likelihoods of those events taking place, creating a circularity.

Description of method

The method assumes the community composition of a certain number of communities, each with a number of repeated measurements taken at the same, regular time intervals, are known perfectly. It then generates a null *transition matrix* (ta-

Species	Abundance
A	10
B	20
C	20

(a) First Community

Species	Abundance
A	20
B	10
C	20

(b) Second Community

Table 1: The problem of estimating species turnover. What happened in the time between the first measurement of this community (a) and the second (b)? Did ten individuals of species B become replaced by ten of species A? Did ten individuals of species B die out without leaving descendants, and ten members of species A come from outside the community? Did ten individuals of species C become replaced by ten of species A, and another ten came in from outside the community? There are an infinite number of possible transitions between the two communities, and no obvious way to determine what happened without already having a model of the likelihood of all the possible transitions.

	A	B	C	Death	Addition
A	reproduction	replacement	replacement	death	addition
B	replacement	reproduction	replacement	death	addition
C	replacement	replacement	replacement	death	addition

Table 2: Example *transition matrix*. Each species is a represented by letter ('A', 'B', and 'C'), and each element represents a parameter of the model, as described in the text.

ble 2), which contains the relative rates of reproduction, replacement, death, and addition for each species. Note that within each row all bar the last column must sum to one (since each individual must do *something* in each time step), while in the last column all the rows must sum to one since every time an individual enters the community it must be of *a* species.

Then, in random order, each individual recorded in a community at a given time has its most likely source (be it a reproduction, replacement or addition event) calculated given the number of individuals in that community's previous time step that haven't already been assigned to another event. If a community has fewer individuals than the previous time step, the most likely species to have died is calculated and an individual of that species assigned to that event in much the same way. This creates an *event matrix*, of the same dimensions as the *transition*

matrix, with counts of the number of times each possible event in the *transition matrix* took place.

Each parameter in the *transition matrix* (in a random order) is estimated, each time re-calculating the *event matrix* and scaling the other parameters so that in each row all elements bar the last sum to one, and in the last column all the elements sum to one. This process of recalculating the entire *transition matrix* can be iterated as many times as is required, and while at present only one null matrix can be used as a starting position, there is no reason more matrices could not be used as starting points.

A program, written in `C++`, that carries out this method is available online (`lottery`; `http://www.github.com/willpearse/lottery`).

Example with simulated data

I present an example of this method with ten random communities, each with ten years of data, starting with 100 individuals and having ten individuals added at each time-step. I used `lottery` to simulate these data, and then make one attempt (with five iterations) to estimate *transition* and *event* matrices. Tables 3 and 4 show the *transition* and *event* matrices used to simulate the data and that were estimate by the program, along with the null *transition matrix* used to start the search.

It is clear that the method has flaws. Although species with higher reproduction rates have higher estimated rates these estimates are inflated, the method is poor at detecting death events, and underestimates rates of addition. I think these problems reflect the fact that all transition and death rates for a species are identical, as are all species' addition rates. There likely exist a number of equally-likely ways of explaining these results, and I feel the model has got caught in a local optimum, something that repeated searches from different locations might help detect. In particular, note that the death parameter for most species is quite close to 0.1 — given there are ten additions at each time step, and the

	a	b	c	d	e	Death	Addition
a	**0.46**	0.11	0.11	0.11	0.11	0.11	0.20
b	0.07	**0.66**	0.07	0.07	0.07	0.07	0.20
c	0.02	0.02	**0.88**	0.02	0.02	0.02	0.20
d	0.03	0.03	0.03	**0.85**	0.03	0.03	0.20
e	0.09	0.09	0.09	0.09	**0.53**	0.09	0.20

(a) Real

	a	b	c	d	e	Death	Addition
a	**0.20**	0.16	0.16	0.16	0.16	0.16	0.20
b	0.16	**0.20**	0.16	0.16	0.16	0.16	0.20
c	0.16	0.16	**0.20**	0.16	0.16	0.16	0.20
d	0.16	0.16	0.16	**0.20**	0.16	0.16	0.20
e	0.16	0.16	0.16	0.16	**0.20**	0.16	0.20

(b) Null

	a	b	c	d	e	Death	Addition
a	**0.65**	0.01	0.12	0.11	0.02	0.01	0.23
b	0.03	**0.84**	0.06	0.05	0.01	0.01	0.16
c	0.00	0.01	**0.96**	0.01	0.00	0.01	0.2771
d	0.01	0.01	0.01	**0.95**	0.01	0.01	0.01
e	0.01	0.06	0.04	0.052	**0.82**	0.01	0.32

(c) Estimated

Table 3: Values of the *transition matrix* used to generate the data (a), as the null to start the search procedure (b), and given as the estimated result (c). Reproduction parameters have been highlighted. This example shows a general tendency of the program to under-estimate death, and to over-estimate the likelihood of an individual to reproduce.

communities start with 100 individuals, the rates of death and immigration are so close for most species it may be difficult for the program to detect what is going on. Indeed, note that the species with the lowest rate of death when the data were simulated ('c') also has the highest estimated addition rate.

	a	b	c	d	e	Death	Addition
a	**566**	121	148	150	131	136	169
b	125	**1234**	123	111	124	122	195
c	88	92	**2785**	79	80	63	173
d	108	93	92	**2447**	82	85	166
e	126	130	137	143	**786**	120	197

(a) Real

	a	b	c	d	e	Death	Addition
a	**896**	12	96	93	57	8	45
b	84	**1627**	78	24	26	0	63
c	11	34	**3104**	27	10	1	116
d	22	28	33	**2785**	38	1	106
e	34	101	31	61	**1215**	0	54

(b) Estimated

Table 4: Values of the *event matrix* used to generate the data (a), and estimated at the end of the run (b). Reproduction parameters have been highlighted. This example shows a general tendency of the program to under-estimate death, and to over-estimate the likelihood of an individual to reproduce.

Example with ecological data

I used the butterfly community data and phylogeny from chapter six as a test case. I took the best-recorded site's yearly abundances of five groups of butterflies (the 'skippers', 'whites', 'hairstreaks, coppers and blues', 'fritillaries and nymphalids', and 'browns' as defined in Asher *et al.*, 2001) as input for the program. While grouping the butterflies in this way is not ideal, it reduces the complexity of the problem, and is not unreasonable given the phylogenetic signal to species' traits shown in chapter six. The results, after only one search with five iterations, are shown in table 5.

Clearly it is not appropriate to make strong claims about the validity of these results, but a general point can be made. These matrices are much more variable in terms of parameters that those estimated from the simulated data. This suggests that, even though the fitting process is unlikely to have yet been perfected, there appears to be some signal in this data, probably reflecting the biology of

	Whites	Blues	Skippers	Fritillaries	Browns	Death	Addition
Whites	**0.38**	0.01	0.02	0.01	0.01	0.57	0.04
Blues	0.30	**0.22**	0.04	0.01	0.07	0.35	0.03
Skippers	0.00	0.00	**0.99**	0.00	0.00	0.00	0.01
Fritillaries	0.15	0.01	0.08	**0.15**	0.15	0.45	0.68
Browns	0.01	0.00	0.01	0.00	**0.95**	0.01	0.24

(a) *Transition Matrix*

	Whites	Blues	Skippers	Fritillaries	Browns	Death	Addition
Whites	**16016**	590	76	64	1052	3556	2408
Blues	497	**2208**	237	153	481	119	443
Skippers	380	61	**863**	6	188	107	242
Fritillaries	168	30	71	**358**	73	40	78
Browns	2039	386	83	98	**6495**	930	1759

(b) *Event Matrix*

Table 5: Values of the *transition* and *event* matrices when the method was applied to real data. For ease of reading, the names of two of the groups are abbreviated to 'blues' and 'fritillaries' from 'hairstreaks, coppers and blues' and 'fritillaries and nymphalids', respectively. See text for further discussion, but note that these parameters do not resemble those of the simulated data, in particular having large 'death' parameter estimates.

the system. Few of the clades seem to be interacting with other clades, in that their replacement parameters are often quite low, which is consistent with the phylogenetically conserved turnover found in chapter six. An interesting exception to this is that the blues appear to be being replaced by the whites, although it would be unwise to draw strong conclusions from a relatively untested method that is being applied to a single site.

Further work

The simulated example shows the problems remaining with the method, and makes it clear that more work is needed. The butterfly data may still be a good test case for the method once it has been refined, since few butterflies have overlapping generations and, in its current form, the method assumes there is no generational overlap.

Although the order in which individual events are assigned to the *event matrix* is randomised in each iteration of the program, the assignment of events according to whichever is the most likely is rather deterministic. This is another possible explanation for the inaccurate estimation of rates in the simulated data, and so more explicitly incorporating stochastic processes is an important next step.

Currently, the method cannot be used with more than a handful of species or it takes too long to parameterise the *event matrix*, although speeding this part of the program up may not be too difficult. However, allowing the user to specify a number of candidate simplified *transition matrices* that share parameters across species would not just allow more species to be analysed, but also allow explicit ecological hypotheses to be tested.

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