Phylogenetic approaches for studying competition in mammals

Natalie Cooper

A thesis submitted for the degree of Doctor of Philosophy from the Division of Biology, Department of Life Sciences, Imperial College London.

Abstract

Interspecific competition is often proposed to shape mammalian evolution. Many studies use trait and distribution data on extant species, but this ignores temporal aspects of competition. Phylogeny provides a framework for integrating present-day data with clade histories.

Here, I use phylogenetic comparative methods and present-day data to investigate the role of competition in the evolution of four mammalian clades: New World leaf-nosed bats (Phyllostomidae), New World monkeys (Platyrrhini), Australasian possums (Phalangeriformes), and ground squirrels (Marmotini). I ask four specific questions: (1) Do community phylogenies, and/or the traits of community members, show patterns expected under competition? (2) Is there evidence of competition in the relationship among species' trait differences, phylogenetic differences and patterns of coexistence? (3) Does the intensity of competition affect rates of morphological evolution? (4) Are the tempo and/or mode of mammalian body size evolution influenced by competition?

I found evidence for competition in monkeys and squirrels, but not bats or possums. Competition did not influence rates of morphological evolution; instead body mass was the most important correlate across the groups. Across all mammals, the best-supported model of body size evolution corresponded to a scenario in which mammals experienced a relatively early burst of morphological evolution, followed by a slowdown in rate as competition for niches increased. In addition, around 60% of the variation in the tempo of body-mass evolution was explained by just a few predictors.

In conclusion, I find some support for competition shaping mammalian evolution. However, there is evidence that the importance of other processes may outweigh the effects of competition in some groups. Further study and methodological improvements are required to fully understand the relative role of competition in evolution. The methods developed in this thesis provide a useful starting point for such studies.

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Chapter 1: General introduction

1.1 Why use phylogenetic approaches for studying competition?

"The theory of natural selection is grounded on the belief that each new variety, and ultimately each new species, is produced and maintained by having some advantage over those with which it comes into competition…"

p.388, Darwin (1859).

Interspecific competition is the negative effect one species has upon another by consuming, or controlling access to, a resource that is limited in availability (Keddy 1989). Although primarily considered in an ecological context, Darwin recognised the critical role of competition in natural selection (see above; Darwin 1859). In fact, competition (or its absence) is invoked as the mechanism behind a variety of biological patterns and processes, including community assembly, adaptive radiations, mass extinctions, species' morphological differences, and variation in evolutionary rates (Brusatte et al. 2008; Dayan & Simberloff 2005; Harmon et al. 2003; Schluter 2000; Simpson 1944; Simpson 1953; Stanley 1973a). All of these ideas are based on the very simple theories of competitive exclusion and limiting similarity (Gause 1934; Hutchinson 1959). These theories state that a pair of coexisting species with similar traits will compete fiercely, resulting in either competitive exclusion of the inferior competitor (Gause 1934), or greater differences in the traits of the species than expected by chance (i.e. character displacement; Brown & Wilson 1956) .

Competition is expected to affect many present-day biodiversity patterns. For example, because of competition, species within a community are expected to have greater

variance in their traits than expected by chance. This could be the result of local extinction of intermediates caused by competitive exclusion, or character displacement among all the species within the community. In species rich systems, competition may also decrease rates of morphological evolution, because it prevents species from broadening their niches into the niche space of their competitors (de Mazancourt et al. 2008). Most studies of competition investigate these patterns using information on the traits or distributions of the species involved. These include experimental field or laboratory studies, where species are removed from, or introduced to, a community and the effects monitored (see review in Schoener 1983), investigations of character displacement (see review in Dayan & Simberloff 2005), and theoretical models (e.g. Meszena et al. 2006; Taper & Case 1992). However, these methods only use information on extant species and current species' distributions. In reality, the differences among species' traits, niches and distributions which are observed today are the result of interspecific competition throughout the clade's evolutionary history (i.e. they investigate the "ghost of competition past"; Connell 1980). Phylogeny provides a framework for the integration of present-day data with clade history. Thus, even in a group with a good fossil record, the best way of assessing the importance of competition to present-day diversity is to use explicitly phylogenetic approaches.

There are two reasons phylogenetic methods are useful for studying competition. The first reason concerns the underlying philosophy of the analyses. As Dobzhansky (1964) so elegantly stated, "nothing in biology makes sense except in the light of evolution". This is especially true for competition, as species only compete if they have similar resource-use traits, and close relatives tend to have more similar traits than distant relatives because they share a more recent common ancestor (Harvey & Pagel 1991).

This evolutionary dimension of competition was also recognised by Darwin (1859), who noted that species within the same genus generally compete more fiercely than species from different genera.

The second reason is a more practical one; the traditional field-based approach is time consuming (a recent field-based study of competition in corals has been running for 40 years; Connell et al. 2004), costly, and often only provides information on one particular system (e.g. Chihuahuan desert communities; Ernest et al. 2008). There are also limits on the size of an organism which can be easily removed or introduced, which may explain why most mammalian studies use rodents not larger species (Schoener 1983). Character displacement studies are less time consuming, but again often only analyse a few communities at a time (e.g. small cats of Israel; Dayan et al. 1990). Using phylogenetic approaches may provide a faster and more cost-effective way of gathering information on more general evolutionary patterns: even the most data and analysis heavy methods employed in this thesis could be done in the timeframe of a three-year research grant.

1.2 Phylogeny, community membership and competition

Some phylogenetic methods for studying competition already exist, particularly in the field of evolutionary community ecology (Webb et al. 2002). Competition has often been studied by community ecologists because competitive interactions are considered to be one of the factors which shape community assembly (Keddy 1989). For over a decade, biologists have been promoting the integration of community ecology and evolution with some success (Johnson & Stinchcombe 2007; Losos 1996; McPeek & Miller 1996; Webb et al. 2002), although the first studies combining the two were

carried out much earlier. Based on Darwin's (1859) suggestion that species within a genus tend to compete fiercely, these studies looked at species-to-genus ratios with the assumption that, if competition were structuring communities, there would be few species per genus within each community (Elton 1946; Jaccard 1922; Moreau 1948). Although early studies usually supported this hypothesis (see Elton 1946 for a review), species-to-genus ratios depend strongly on the number of species involved and, once this was taken into account, many later studies revealed more species per genus than expected within each community (Jarvinen 1982).

With the increasing availability of phylogenies, it became possible to use phylogeny rather than taxonomy to determine whether competition was shaping community structure. Webb (2000) proposed a simple way of doing this using two metrics he termed the net relatedness index (NRI) and the nearest-taxon index (NTI). In brief (these metrics are described in more detail in Chapter 3), these measures compare the phylogenetic distances between species in a community, to the phylogenetic distances between species in pseudo-communities randomly drawn from the species pool. If competition is structuring a community, species within the community should be, on average, less closely-related than the species within the randomly drawn pseudo-communities. Webb (2000; Webb et al. 2002) called this pattern "phylogenetic overdispersion". These approaches have collectively become known as "community phylogenetics" methods (Webb et al. 2002), and have been used widely in the last few years: a recent review article cites 23 examples from a range of taxa (Emerson & Gillespie 2008). Although 11 of these examples use metrics other than NRI and NTI, only NRI and NTI are used widely, i.e. by more than three studies. This is probably due

to their simplicity, and because they require only relatively simple data: a phylogeny and species lists.

Despite their advantages, there are some problems associated with community phylogenetics methods. Firstly, the power of the methods to detect competition increases as the spatial scale of the species pool decreases (Kraft et al. 2007; Swenson et al. 2006); thus a variety of pool sizes should be tested in each analysis (e.g. Cardillo et al. 2008; Cavender-Bares et al. 2006; Cooper et al. 2008). Taxonomic scale, i.e. whether the community is defined as just the species within a genus, or includes all the species within a higher taxonomic unit, is also important where the study community has a broad taxonomic definition, e.g. all Floridian plants (Cavender-Bares et al. 2006). As taxonomic scale decreases, the likelihood of competition occurring increases, since the species are, on average, more similar than when broader taxonomic scales are used (Swenson et al. 2006). The results also depend on whether the resource-use traits of the species are phylogenetically conserved, i.e. more similar in close relatives than distant relatives (Cavender-Bares et al. 2004; Kraft et al. 2007; Webb et al. 2002). Phylogenetic overdispersion is interpreted as evidence for competition structuring the community, based on the idea that the traits of the species in the community are also overdispersed. If the traits are not conserved then this assumption is untrue and other processes must account for the pattern (Webb et al. 2002). Information on species' traits is therefore essential for the correct interpretation of the results, yet only 12 of the 23 studies mentioned above considered the traits of the species within the communities in addition to their phylogenetic patterns (see Emerson & Gillespie 2008). There is however, a growing consensus that both resource-use traits and phylogeny need to be considered in these kinds of analyses (Kraft et al. 2007).

As well as being important in community ecology, competition is also a key component of certain models and theories of evolution, for example, the theory of adaptive radiation, the density dependent (or "niche-filling") model of cladogenesis, logistic models of diversification, and the early burst, or acceleration-deceleration (ACDC), model of evolution (Blomberg et al. 2003; Harmon et al. in review; Rabosky & Lovette 2008a; Schluter 2000; Sepkoski 1998; Valentine 1980; Walker & Valentine 1984). All of these models are based on the observation that clades often experience rapid diversification early in their history, followed by a slowdown in diversification rate towards the present. The suggested mechanism is that ecological opportunity is highest early in a clade's history when there are more empty niches, fewer predators and fewer competitors, and that the subsequent reduction in diversification rate reflects the increased levels of competition for niches as they fill up. Although the only way this can be tested directly is by using field or laboratory experiments on species with short lifespans (e.g. *Pseudomonas fluorescens* colonies; Meyer & Kassen 2007), many studies instead investigate the pattern indirectly and propose that competition is part of the explanation.

The simplest methods for investigating the relationship between diversification rate and clade age involve looking at the accumulation of species, or lineages, through time using the fossil record. If competition for niches is important in evolution as suggested above, such diversity-through-time plots should be logistic curves, i.e. high initial rates of species/lineage accumulation followed by decreasing rates towards the present. This is a common method in palaeontology but, although logistic curves are found in some marine groups (e.g. families of marine invertebrates; Sepkoski 1998), the overall pattern

in the terrestrial fossil record appears to be of species diversity increasing exponentially through time with no slowdown (Benton 1995; Benton & Emerson 2007).

Rather than straightforward graphical analyses, diversification rates can also be examined using present-day species and modelling approaches that use extensions of simple birth-death models (Nee et al. 1994; Rabosky & Lovette 2008a), since diversification is, by one definition, the rate of speciation minus the rate of extinction. These modelling approaches have also been extended to detect whether the differences in diversification rate through time are due to variations in the speciation rate with time, or if the diversification rate decrease after the initial high rate is actually the result of increased extinction over time (Rabosky & Lovette 2008b).

The diversification rate modelling methods described above are easy to apply and require only a phylogeny (albeit a comprehensive, fully-resolved, dated species-level phylogeny). However, they do not consider the traits of the species which are relevant to the strength of competition. They also often lack a spatial angle, unless the analyses are spatially-restricted to, for example, an island or island system. Consequently, these methods offer little mechanistic insight into the effects of competition on diversification history. Other methods, which explicitly consider traits and phylogeny simultaneously, are therefore better for assessing the importance of competition. Most of these methods involve fitting mathematical models of trait evolution across a phylogeny and then using the model parameter estimates to describe the mode of evolution (e.g. Blomberg et al. 2003; Harmon et al. in review). For example, the early burst model of trait evolution uses maximum-likelihood approaches to estimate a parameter, *r*, which describes the changes in anagenetic rate through time (Harmon et al. in review). In more

comprehensive studies, a number of evolutionary models are tested and their fit to the data is compared using some kind of model selection criterion (e.g. Harmon et al. in review).

The phylogenetic methods I have described for studying competition generally use phylogeny and one of either patterns of species' coexistence, or species' traits. However, data on the phylogeny, coexistence and traits are all needed in order to study competition. It would also be advantageous if the methods were relatively quick to carry out and easily generalised to a range of systems or communities. These are the kinds of methods I aim to develop in this thesis.

In order to do this I have chosen to use present-day mammals as my study group; and in particular four mammalian clades: New World leaf-nosed bats (Phyllostomidae); New World monkeys (Platyrrhini); Australasian possums (Phalangeriformes); ground squirrels (Marmotini). I chose mammals because the evolutionary history and ecology of the group is very well-known: there is an almost complete species-level mammalian phylogeny and ecological and life-history data are available for many species (Bininda-Emonds et al. 2007; 2008; Jones et al. in press). In addition, many classical evolutionary studies use mammalian examples (e.g. Simpson 1944; Stanley 1973a) so comparisons between my work and earlier studies will be possible. This makes mammals an excellent clade on which to further investigate the links between competition and evolution.

1.3 Thesis aims and outline

The overall aim of this thesis is to determine how important competition has been in shaping mammalian evolution, using novel, explicitly phylogenetic, comparative

methods and present-day data, rather than the more established non-phylogenetic approaches. To help do this, I ask the following research questions:

1. Do community phylogenies and/or the traits of species within a community show patterns consistent with competition?
2. Do models of the relationship among species' trait differences, phylogenetic differences and patterns of coexistence, provide evidence of competition?
3. Does the intensity of competition influence rates of morphological evolution? Is competition more or less important than other factors that shape rates of morphological evolution?
4. How does mammalian body size evolve? Do the tempo and/or mode of body size evolution have any connection to competition?
5. How important has competition been in shaping mammalian evolution?

Obviously such an undertaking requires a lot of data, including species-level ecological and life-history data, high quality specimen-level morphometric data, information on the distributions of the species, and reliable phylogenies (for my study groups). Chapter 2 deals with how these data were gathered and is referred to in the methods sections of the following chapters. It also introduces my four study clades in more detail. The subsequent four chapters are empirical analyses of the first four questions above.

CHAPTER 3: Do community phylogenies and/or the traits of species within a community show patterns consistent with competition?

In Chapter 3, I investigate whether community phylogenies support the prediction that competition is a powerful structuring force in mammalian communities. I first use the

community phylogenetics metrics of Webb et al. (2000; 2002) described briefly above, along with my own modifications, to investigate whether the assemblages show phylogenetic overdispersion; where species within a community are less closely-related than expected by chance. Since species which share a common ancestor tend to be similar, and competition is most fierce between similar species, phylogenetic overdispersion is expected in communities which are structured by competition. I find that overdispersion is commonplace in the communities, which suggests an important role for competition in mammalian community assembly. I then try to confirm these findings by testing for overdispersion in the traits of the species in the communities, using an analogous approach to community phylogenetics methods. I expect the traits of species within a community to be less similar than expected by chance, due to competition. I find overdispersion in the traits of one of my study groups and conclude that competition is probably responsible for these patterns in this group, but processes other than competition must affect the others.

CHAPTER 4: Do models of the relationship between species' trait differences, phylogenetic differences and patterns of coexistence, provide evidence of competition?

Chapter 3 used either species' coexistence patterns (i.e. whether or not a species was within a particular community) and phylogeny, or coexistence patterns and traits, to investigate competition. However, phylogeny, traits and coexistence all need to be combined if we are to fully understand how competition influences evolution. In Chapter 4, therefore, I include species' traits, phylogeny and coexistence patterns to investigate competition in my study groups. Using a matrix-based approach, I model the difference between the morphological traits of a pair of species as a function of their

phylogenetic difference and the degree to which their present-day geographic ranges overlap. If competition is important then (when I control for phylogeny), as species' geographic range overlap increases, species' trait differences should also increase through character displacement. I find the opposite of my expectations in two study groups (and no pattern in the other two): as geographic range overlap increases, trait differences decrease. This suggests that factors other than competition may be influencing evolution in my study groups.

CHAPTER 5: Does the intensity of competition influence rates of morphological evolution? Is competition more or less important than other factors that shape rates of morphological evolution?

The results of Chapters 3 and 4 throw uncertainty on the hypothesised role of competition in the evolution of my study groups. One reason for these results may be that other factors influence evolution, and these may be more important for regulating the trait differences I observe than competition. Therefore in Chapter 5 I investigate a broad range of correlates of the rate of morphological evolution in my four study groups, to determine which variables correlate with rate, and whether they are more important than competition in shaping morphological evolution in my study groups. I derive a measure of the relative rate of morphological evolution for each species using a novel methodology, and then use phylogenetic comparative analyses to investigate correlates of the rate of evolution. Putative correlates include body size, environmental variables e.g. temperature, geographic range size, life-history variables e.g. basal metabolic rate, as well as a measure of the intensity of competition. I find that the most important correlate of the rate of morphological evolution across all the groups is body size, and the intensity of competition does not feature in any of the best models.

CHAPTER 6: How does mammalian body size evolve? Do the tempo and/or mode of body size evolution have any connection to competition?

Since Chapter 5 showed that body size was the most important correlate of the rate of morphological evolution in my study groups, I decided to study body size evolution in more detail. In Chapter 6 I therefore investigate the tempo and mode of body size evolution in all extant mammals. Using three evolutionary models commonly used to characterise trait evolution, I first investigate which of these models best fits body-mass evolution across all mammals, and when mammals are split taxonomically and spatially. I find that across all mammals, the best model of body size evolution is where mammals experienced a burst of morphological evolution relatively early in their evolutionary history, followed by a slowdown in the rate of evolution, perhaps as available niches began to be filled and competition for niches became more intense. The best model of evolution varies when mammals are split taxonomically and spatially, however, the rate of body-mass evolution also varies spatially. I map this, then model the spatial variation in the rate of body size evolution using various predictors including environmental variables e.g. AET, geographical variables e.g. whether or not the area was an island, and variables pertaining to the species composition of the area e.g. species richness. I find that around 60% of the variation in the rate of evolution can be explained by just a few of these predictors, but that the remaining 40% is probably due to ecological factors, possibly including competition.

CHAPTER 7: How important has competition been in shaping mammalian evolution?

Finally, in Chapter 7, I draw the results of the previous chapters together in order to summarise my results and discuss whether, together, they suggest a dominant role for competition in mammalian evolution. I also discuss whether studying competition using phylogenetic approaches is useful and sufficient, and suggest areas for future study.

Chapter 2: Data collection

2.1 Introduction

The analyses in Chapters 3, 4 and 5 use a database I compiled which contains morphometric, ecological and locality data for 2456 museum specimens. This methods chapter deals with how this data was collected and checked for errors, and also describes other data sources used in this thesis, e.g. assemblage lists, life-history data and phylogenies. This information will be referred to in later chapters but described in detail only here. Other methods specific to particular chapters can be found in the methods sections of those chapters.

2.2 Study groups

I selected clades to study on the basis of four criteria. The clades needed to (1) contain enough species for reasonable replication, but not so many that it would be unfeasible to measure them all in the time available (between 50 and 200); (2) have a phylogeny with a resolution of at least 70% in the recent supertree of Bininda-Emonds et al. (Bininda-Emonds et al. 2007; 2008), with the dates of at least 70% of the nodes being estimated from molecular sequence or fossil data; (3) be well-represented in museum collections; and (4) represent novel research. The clades I selected were; (A) New World leaf-nosed bats (Phyllostomidae); (B) New World monkeys (Platyrrhini); (C) Australasian possums (Phalangeriformes); and (D) ground squirrels (Sciuridae: Xerinae: Marmotini) which I describe in more detail below.

New World leaf-nosed bats (Phyllostomidae): This clade contains 160 species which are grouped into 55 genera and eight subfamilies (Wilson & Reeder 2005). The family

ranges from the south-western United States and the West Indies, south to northern Argentina and Central Chile. Within this area they occupy a wide variety of habitats from tropical forests to deserts (Nowak 1999). Phyllostomids are particularly interesting since they are the most ecologically diverse bat family, containing sanguivorous, carnivorous, frugivorous, nectarivorous and insectivorous members. The phyllostomid section of the Bininda-Emonds et al. (2007; 2008) mammal supertree is well-resolved (84%).

New World monkeys (Platyrrhini): This clade contains 128 species, grouped into 16 genera and four families (Atelidae; Aotidae; Cebidae, including callitrichids; and Pitheciidae: Wilson & Reeder 2005). New World monkeys are found in forests from north-eastern Mexico to northern Argentina (Nowak 1999). Most species (except for the almost entirely folivorous genus *Alouatta*) are omnivorous, but the degree to which they rely on fruit, flowers, seeds and insects varies among genera (Nowak 1999). The supertree for this group is 87% resolved (Bininda-Emonds et al. 2007; 2008)

Australasian possums (Phalangeriformes): The 63 species of this clade are grouped into 20 genera and six families (Acrobatidae; Burramyidae; Petauridae; Phalangeridae; Pseudocheiridae and Tarsipedidae; Wilson & Reeder 2005). I excluded Tarsipedidae from my dataset since finding a complete specimen of its only member (*Tarsipes rostratus*) was not possible and it is also probably too small to compete with any of the other possums. Therefore, where I refer to Phalangeriformes throughout this thesis I mean only the families Acrobatidae, Burramyidae, Petauridae, Phalangeridae and Pseudocheiridae. Phalangeriformes are found in Australia, Tasmania and New Guinea as well as on islands from Sulawesi to the Solomons (Nowak 1999). They are, for the

most part, restricted to forested areas, and can be nectarivores, gumivores, folivores, frugivores or insectivores (Flannery 1995). The possum section of the mammal supertree is highly-resolved (92%; Bininda-Emonds et al. 2007; 2008).

Ground squirrels (Marmotini): This tribe contains 65 North American and 27 Eurasian species grouped into seven genera (Wilson & Reeder 2005). Note that, since the North American and Eurasian species will be unable to compete, I use only North American species in analyses where competition is predicted to cause the patterns observed (Chapters 3 and 4). Ground squirrels are found in a range of habitats from dense forests and shrubland to open grassland and desert. They are all, to some extent, omnivorous, although grassland species tend to be more herbivorous than their forest counterparts (Nowak 1999). The sciurid supertree is well-resolved (93%; Bininda-Emonds et al. 2007; 2008), especially for the North American species.

2.3 Morphometric traits

Morphometric traits were chosen to be ecologically relevant (see below). Only cranial traits were chosen because postcranial material is much less available in museum collections. The morphometric measurements I took were as follows (see Figure 2.1): (1) condylobasal length (CBL); (2) maximum zygomatic width (MZW); (3) tooth row length (excluding canines) (TR); (4) incisor row length (IR); (5) canine height (except squirrels) (CH); (6) canine diameter (except squirrels) (CD); (7) coronoid process height (CP); (8) mandibular condyle height (MC); (9) P_1 (premolar one) height (possums only) (P1); (10) P_3 height (possums only) (P3); (11) diastema length (squirrels only) (DL).

All of these traits have easily recognisable landmarks so they are repeatable, eight are present in at least three of the four study clades, and all have functional significance in

feeding (except CBL which was measured as an indication of skull size) as follows. The zygomatic arch (MZW) forms an attachment point for several muscles including the temporalis and masseter muscles. Species with wider zygomatic arches have increased masseter and temporalis muscle area which results in higher bite strength and allows increased usage of canines (Bogdanowicz et al. 1999; Freeman 1984). Larger temporalis muscles also help prevent jaw dislocation in species that use their incisors to rip at hard materials such as bark (Ball & Roth 1995). Both of these features are also associated with increasing carnivory and the hardness of food items that can be taken. The length of the two tooth rows (TR, IR), canine size (CH, CD) and diastema length (DL) are also related to diet. For example, nectarivorous species tend to have longer tooth rows than gumivores or frugivores (Dumont 1997) and, among carnivorous species, species with larger canines are more carnivorous and consume larger and/or harder prey than those with smaller canines (Bogdanowicz et al. 1999; Dayan & Simberloff 1994; Freeman 1984). For the possum families I also measured the height of the first and third premolar (P_1, P_3), because variation within these teeth is a good indicator of diet in these species. For example, species feeding on hard food items tend to have a large blade-like P_3, whereas nectar feeding species have small peg-like premolars (Flannery 1995). Low mandibular condyle height (MC) is associated with increasing gape allowing species to consume larger food items (Dumont 1997), whereas elevated mandibular condyle (and overall mandible) height is associated with an increase in masseter size, and hence bite strength, allowing harder food items to be consumed (Freeman 1979; Nogueira et al. 2005). Similarly, coronoid process height (CP) is related to masseter volume and attachment strength. Short coronoid processes are a feature of nectarivorous species which require little masticatory musculature to consume their liquid food source (Dumont 1997).

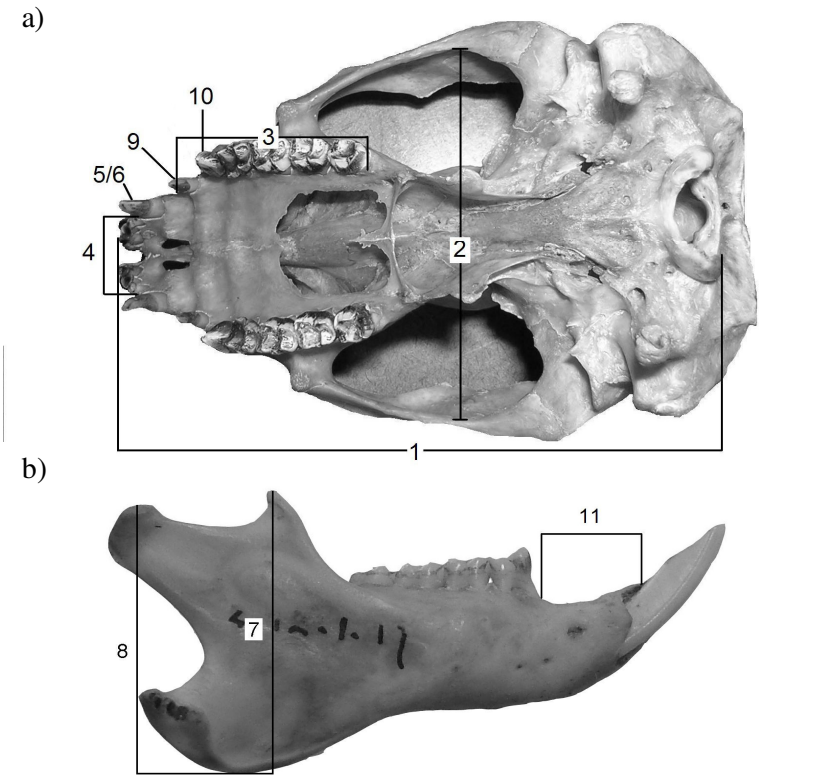


Figure 2.1: (a) Ventral view of a possum skull and (b) side view of a squirrel mandible showing morphometric measurements taken. 1 = CBL, 2 = MZW, 3 = tooth row length (TR), 4 = incisor row length (IR), 5 = canine height (except squirrels) (CH), 6 = canine diameter (except squirrels) (CD), 7 = coronoid process height (CP), 8 = mandibular condyle height (MC), 9 = P_1 height (possums only) (P1), 10 = P_3 height (possums only) (P3), 11 = diastema length (DL).

2.4 Data collection

Overall, I measured 2405 specimens (803 bats, 574 monkeys, 382 possums, 646 squirrels) from four museums (American Museum of Natural History, New York (AMNH), Harrison Zoological Museum, Sevenoaks (HZM), Natural History Museum, London (NHM), and Smithsonian Institute, Washington D.C. (SI)) over a period of 12 weeks which equates to around 450 hours. Jack Lighten (J.L.) measured 51 additional callitrichid specimens from the NHM as part of his MSc project. For each specimen, all of the following data were entered into a Microsoft Access database.

Morphometric measurements

Only data from female specimens from which it was possible to take every measurement were collected. I used only females to avoid any problems caused by sexual dimorphism which can lead to the two sexes forming separate morphospecies (e.g. Dayan et al. 1989; Dayan & Simberloff 1994). In the monkeys, possums and squirrels, males tend to be larger than females, but in bats, females tend to be larger than males (Lindenfors et al. 2007). The reasoning behind measuring only one sex applies regardless of whether males or females are the larger sex. Using females also removes the need to factor out differences caused by sexual selection on traits such as canine size in the males of some species. Where possible I used only adult specimens (defined as those with fully-erupted permanent dentition and completely-fused skull bones), so developmental differences were not an issue. However, in certain clades (most notably in Primates and rodents), complete skull fusion takes a long time (in humans complete spheno-occipital fusion does not occur until the age of fifteen or sixteen; Madeline & Elster 1995). To increase sample sizes I measured some intermediate specimens (bats: 1%; monkeys: 86%; possums: 6%; squirrels: 42%), defined as those with fully erupted permanent dentition and closed, but unfused, skull bones. These are likely to be adult in all respects apart from their unfused skull bones and should not affect the analyses since, at worst, size should be the only difference between adults and intermediates and CBL can be used to factor this out of the analyses. To test this I performed paired t-tests to determine whether the second and third principal components of measurements from adult and intermediate specimens differed. I ignored the first principal component as this reflects differences in trait size. PC2 and PC3 from adult and intermediate specimens were not significantly different from one another (PC2: $t_{55} = -0.48$, $p = 0.63$;

PC3: $t_{55} = 1.31$, $p = 0.19$). Thus using intermediate specimens should not be problematic.

Each measurement was taken to the nearest 0.1 mm using 150 mm digital callipers (Mitutoyo™). In order to assess measurement repeatability I took each measurement three times (cycling through all the measurements once, then repeating, rather than taking one measurement three times in a row in order to avoid autocorrelation). I repeated the bat measurements five times to account for the increased relative error introduced by their small size.

Label data

I recorded all the data on the specimen label including, where appropriate, notes made by curators and/or previous visitors. Label data included specimen number, genus, species, collection location and date, collector, details of associated material from the specimen in the collection (e.g. skin, postcranial skeleton), and any field measurements taken. I also recorded the age (adult or intermediate as defined above) of each specimen.

Georeferencing

Using mainly atlases and online geographic databases (see Appendices A1 and A2), I found locality data for each specimen. Specimen label locality data ranged in quality from precise coordinates to geographic regions (e.g. countries or continents), so the rationale for each choice was also recorded, as well as an ordinal representation of the accuracy of the locality data. I refer to this value as the accuracy rank of a locality and I defined this as follows: (1) Latitude and longitude given on label. This is the greatest level of accuracy possible for this kind of data; (2) Latitude and longitude of nearest town/city that could be uniquely identified; (3) Latitude and longitude of nearest

town/city that could not be uniquely identified. The coordinates assigned to these data are either an average of the towns or cities sharing a name if they are close together, or (where a choice can be justified) belongs to just one of the towns or cities; (4) Latitude and longitude of either (a) a nearby town or city where this is the second place listed on the specimen label, or (b) a geographical feature (including small islands), or (c) the midpoint of a small sub-national unit (e.g. US counties). Geographical features were not given an accuracy rank of (2) because they cover a much larger area than a town or city, thus are less accurate locality representations; (5) Latitude and longitude of the midpoint of a larger sub-national unit (e.g. US states); (6) Latitude and longitude of the midpoint of a country; (7) No label locality, or indecipherable label locality.

Over 90% of the specimens have accuracy ranks of between 1 and 4; 56% have accuracy ranks of between 1 and 3 and 48% have accuracy ranks of 1 or 2. Only 22 (0.86%) specimens have no locality data at all (accuracy rank 7). Less precise localities were omitted for analyses in which geographic distribution is important (Chapter 3).

Taxonomy

I recorded the genus, species and, where applicable, the subgenus, subfamily and family of each specimen and then, since the alpha taxonomy of museum specimens is often outdated due to curation lag, I converted them to the taxonomy of Wilson and Reeder (1993). I used this version of taxonomy rather than the updated 2005 taxonomy (Wilson & Reeder 2005) because initially the assemblage lists, species geographic range maps and phylogeny (see below) used the taxonomy of Wilson and Reeder (1993). Some of these have recently been updated (range maps: Jones et al. in press; phylogeny: Fritz et al. in press) but, since the taxonomy of the four clades did not change substantially between the two editions (see below), I have continued to use the 1993 taxonomy

throughout. Squirrel taxonomy did not change at all between 1993 and 2005, but within the bats, 13 new species were defined (10 through splitting of existing species and three new discoveries), eight changed genus, and two were lumped together. In the monkeys 18 new species were defined (10 through splitting of existing species and eight new discoveries), one changed genus, one changed its name and three species were lumped together. Finally, within the possums measured, five new species were defined (two through splitting of existing species and three new discoveries) and five moved genus.

Macroniche and Diet

Eisenberg (1981) used a matrix containing eight categories of substrate use and 16 categories of dietary specialisation to partition mammalian species into macroniches (see Table 2.1). Only five categories of substrate use (semi-fossorial, volant, terrestrial, scansorial and arboreal) and 12 categories of dietary specialisation (nectarivore, gumivore, gumivore/omnivore, aerial insectivore, foliage gleaning insectivore, insectivore/omnivore, frugivore/omnivore, frugivore/granivore, frugivore/herbivore, herbivore/browser, herbivore/grazer and sanguivore) are relevant for this study. Macroniches are equivalent to guilds (s*ensu* Root 1967) in that species in a macroniche consume the same sorts of resource in the same way. I will use macroniches to define potential competitors in Chapters 4 and 5 as the paucity of species-level dietary information prevents any more accurate definition of guild.

Table 2.1: Macroniches (*sensu* Eisenberg 1981 with some modifications) of the four study clades. bats = Phyllostomidae; monkeys = Platyrrhini; possums = Phalangeriformes; squirrels = Marmotini.

clade	macroniches	
	substrate	**dietary specialisation**
bats	Volant	Carnivore
		Carnivore/Insectivore
		Carnivore/Omnivore
		Frugivore
		Frugivore/Insectivore
		Frugivore/Omnivore
		Insectivore
		Insectivore/Frugivore
		Nectarivore/Omnivore
		Omnivore
		Sanguivore
monkeys	Arboreal	Folivore/Frugivore
		Frugivore/Omnivore
		Gumivore/Omnivore
possums	Arboreal	Frugivore/Herbivore
		Gumivore
		Herbivore/Browser
		Insectivore/Omnivore
		Nectarivore
	Scansorial	Frugivore/Herbivore
squirrels	Terrestrial/Semifossorial	Herbivore/Grazer
		Omnivore
	Terrestrial/Scansorial	Omnivore

Using PanTHERIA (Jones et al. in press) and other sources, including field guides and species accounts (Appendix A2), I recorded all food items eaten, which items made up the bulk of the diet, and the manner in which food resources were exploited, for each species in my dataset. This information was used in association with Eisenberg's (1981) matrix to define the macroniche of each genus. I used slightly different dietary specialisation categories from Eisenberg (1981) to better represent the diets of the study species (Table 2.1). I was unable to define species-level macroniches in some less well-known groups because only genus-level information was available. Where accurate dietary information was available for each species within a genus (e.g. bats: *Glossophaga*; monkeys: *Cebus*; possums: *Phalanger*; squirrels: *Marmota*), macroniche was conserved within genera, indicating that using genus-level macroniche designations is acceptable.

2.5 Error checking[1]

Morphometric datasets are prone to error, and although in many analyses error merely adds noise, some of my analyses are very susceptible to bias from measurement error. For example, some species are poorly-represented in museum collections; hence some of the species averages will be calculated using only a few specimens. If these have a lot of measurement error, the species-level analyses (e.g. Chapters 3, 4 and 5) could be biased. Accuracy and precision in data are also particularly important in phylogenetic analyses where measurement error combined with short branch lengths can appear to be signal. Therefore, before the analyses I thoroughly checked my data for errors. I identified four possible types of error in my dataset: (1) Typographical errors i.e.

[1] [1] These error checking protocols have been published as an appendix to Cooper, N. and Purvis, A. (In press). What factors shape rates of phenotypic evolution? A comparative study of cranial morphology of four mammalian clades. *Journal of Evolutionary Biology*.

mistakes in spelling, typing or data entry; (2) Measurement error i.e. where the three (or five for bats) repeated measurements of a trait from a particular specimen are not the same. This could reflect either the limits of the precision of the callipers (0.1mm) or discrepant measurements; (3) Curation error, e.g. specimens labelled with the wrong species binomial; (4) Measurer error, i.e. differences in the way different people took the measurements.

In my opinion, error checking was essential to the reliability of the data. However, most morphometric studies rarely correct for anything other than typographical errors and, to my knowledge, none correct for potential curation errors. This is the first time the methods below have been used for this purpose. In total I excluded data from 154 specimens as described below.

Typographical errors

For each specimen I calculated the standard deviation of every trait measured. Where this was greater than unity I checked the measurements of the trait for typographical errors. In most cases these were easily remedied by the movement of a line of data or the insertion of a decimal point. Where there was an obvious typographical error but no clear solution to the problem, I excluded the specimen from all later analyses.

Measurement errors

To explore the error structure of the data, I calculated the coefficient of variation (standard deviation/mean * 100) for every trait of each specimen measured. However, for the analyses I needed an average value for each trait of each specimen. Since the distribution of the three (or five) repeated measures for each trait was often skewed due to an outlier (leading to a large coefficient of variation), the trait mean was not a good

measure of central tendency. Instead, I chose to use the median for each trait. Using the median also removes the need to deal with single measurements having large errors, provided that the other two (or four) measurements are close together. If all three (or five) measurements are evenly spread there is no way to tell if the median is a truly representative measure of central tendency. Therefore, I devised a method for determining the "spread" of the repeated measurements. For monkeys, possums and squirrels, the differences between each pair of the three measurements were first calculated. The smaller difference between two measurements was defined as *a* and the larger difference as *d* (see Figure 2.2). Percentage spread was then calculated as $a/d * 100$. A small value indicates that two of the repeated measures are very similar and the third measurement is an outlier. A value near 50% indicates evenly-spaced measurements. For bats, the differences between the neighbouring measurements were calculated and labelled (from smallest to largest) as *a*, *b*, *c* and *d*. I then defined the difference between the smaller and larger measurement as *e* (Figure 2.2). Percentage spread was then calculated as $(a/e + b/e + c/e) * 100$. A value < 50% indicates that four of the measurements are within one half of the measurement range, with the fifth measurement being an outlier.

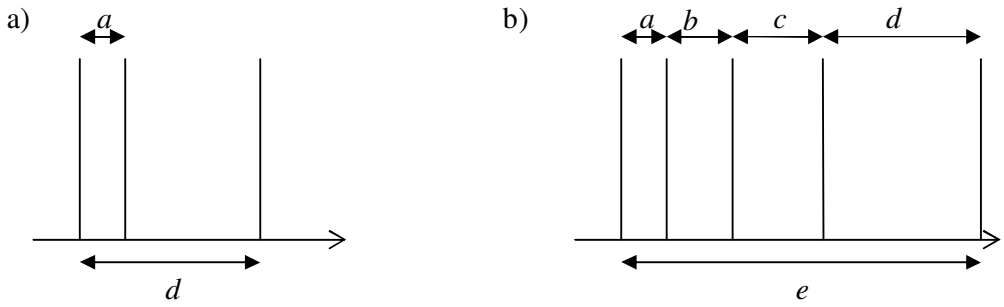


Figure 2.2: Diagram showing how percentage spread was calculated for a) specimens with three repeated measurements per trait, and b) specimens with five repeated measurements per trait. Each horizontal line represents a measurement. Note that the outlying measurement could also occur at the left-hand side of the distribution, and in b) *a*, *b*, *c* and *d* will not necessarily be in that order on the trait axis.

Curation errors

If a specimen were labelled with the wrong species name then it would tend to be more dissimilar to its proposed congeners than expected. In order to deal with this potential source of error I first assigned each specimen a vector (x_i, y_i, z_i) which consisted of the first three principal components obtained from a principal components analysis using the residuals from regressions of each trait median on condylobasal length (CBL). I used residuals instead of absolute values because this removes size from the analysis leaving shape, which should vary less between specimens of different ages and geographical origin (Bookstein 1991). I then used these specimen vectors to calculate an average value for each species (the species centroid: x, y, z) by using the mean specimen values for each species. Finally, I calculated the distance squared ($(x - x_i)^2$, $(y - y_i)^2$, $(z - z_i)^2$) between each specimen and its species centroid (Figure 2.3). Specimens with measurement errors (as defined above) were omitted from this analysis so they could not influence the results.

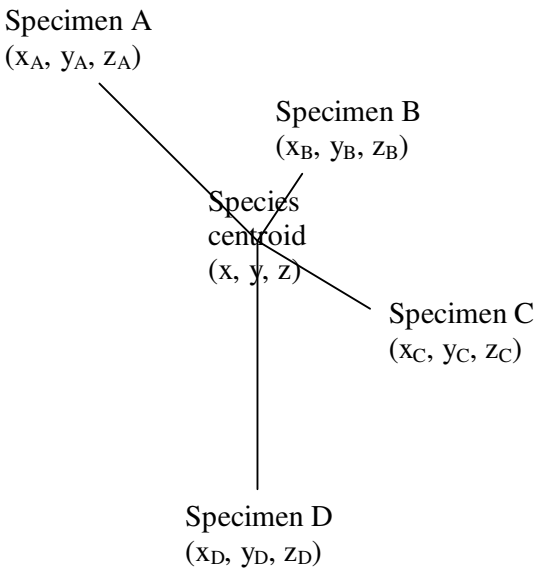


Figure 2.3: Diagram showing how specimen distances from species centroids were calculated in order to identify potential labelling errors.

Several specimens had a much greater distance from their species centroid than the other specimens (i.e. > 10 units greater). These specimens (which are disjunct from the rest of the distribution in Figure 2.4) were potentially mislabelled so I omitted them from all later analyses. When I removed these mislabelled specimens the distributions of the squared distances from species centroids were continuous for all clades, thus I determined that no further specimens needed to be omitted (Figure 2.4). Choosing this fairly lenient criterion for omission is arbitrary, as would be any criterion I selected. I chose this method because individuals within a species often vary substantially, thus choosing a more rigorous method may have led to the deletion of good data.

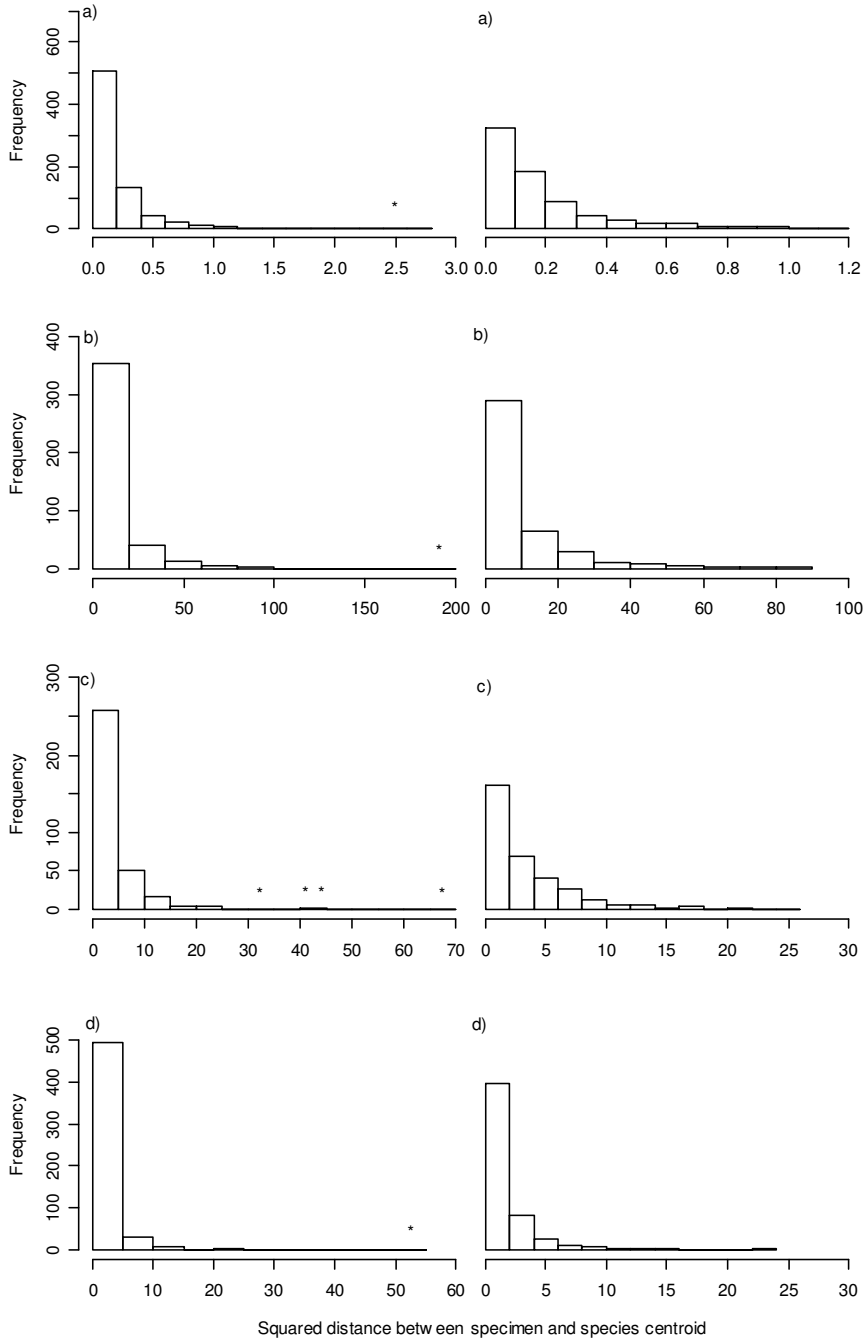


Figure 2.4: Histograms showing the distribution of squared distances between specimens and their species centroid. a) bats (Phyllostomidae), b) monkeys (Platyrrhini), c) possums (Phalangeriformes), and d) squirrels (Marmotini). *represents specimens with a squared distance from their species centroid that is disjunct from the rest of the distribution. Histograms on the right have been redrawn omitting the disjunct (potentially mislabelled) specimens; note that the scale of the x-axes on the right and left are different. Specimens with measurement errors have been omitted.

Measurer errors

Before using data collected by J.L., I needed to check that he had interpreted the landmarks in the way I intended, so that the analyses would not be biased by who measured the specimen. To do this I measured two specimens at random from the set of specimens used by J.L. I then calculated the median trait values for each specimen using first my measurements and then his measurements, and compared these two sets of median values using paired t-tests. The measurements were not significantly different, even when they were natural-log transformed prior to analysis, which suggests that measurer error was negligible (N.C. versus J.L.: untransformed values: $t_{15} = 0.48$, $p = 0.63$, mean difference = 0.04 mm; natural-log transformed values: $t_{15} = 1.43$, $p = 0.18$, mean difference = 0.02 mm).

Error checking summary

In total, 154 specimens (79 bats, 18 monkeys, 47 possums and 10 squirrels), or 6.403% of the total number of specimens, were omitted from the analyses during error checking. Table 2.2 shows the mean coefficient of variation for the four clades before and after the removal of specimens as detailed above.

Table 2.2: Measurement error information. *represents values after removal of typographical errors. bats = Phyllostomidae; monkeys = Platyrrhini; possums = Phalangeriformes; squirrels = Marmotini.

	before error checking*		after error checking	
clade	**mean coefficient of variation**	**standard deviation**	**mean coefficient of variation**	**standard deviation**
bats	1.49	1.96	1.39	1.80
monkeys	0.80	1.34	0.78	1.30
possums	1.77	2.47	1.60	2.03
squirrels	0.71	0.89	0.70	0.87

The amount of measurement error in the final dataset varied between clades and traits (Figure 2.5; Table 2.3), increasing slightly as the size of the trait decreased (regression: $t_{17972} = -47.20$, $p < 0.001$, slope = -0.030, $r^2 = 0.110$). Mandibular condyle height had greater error than expected given its size, probably due to difficulty in locating the landmarks of this trait. The amount of error also varied significantly with clade (ANOVA: $F_{3,17970} = 328.1$, $p < 0.001$). Bats had significantly higher measurement error than squirrels and monkeys. The measurement error of the possums was significantly higher than that of the smaller bats (and the other three clades), probably because of the high error associated with the small premolar traits which were only measured in the possum clade. Squirrels had the least measurement error, probably because no small tooth measurements were taken from them.

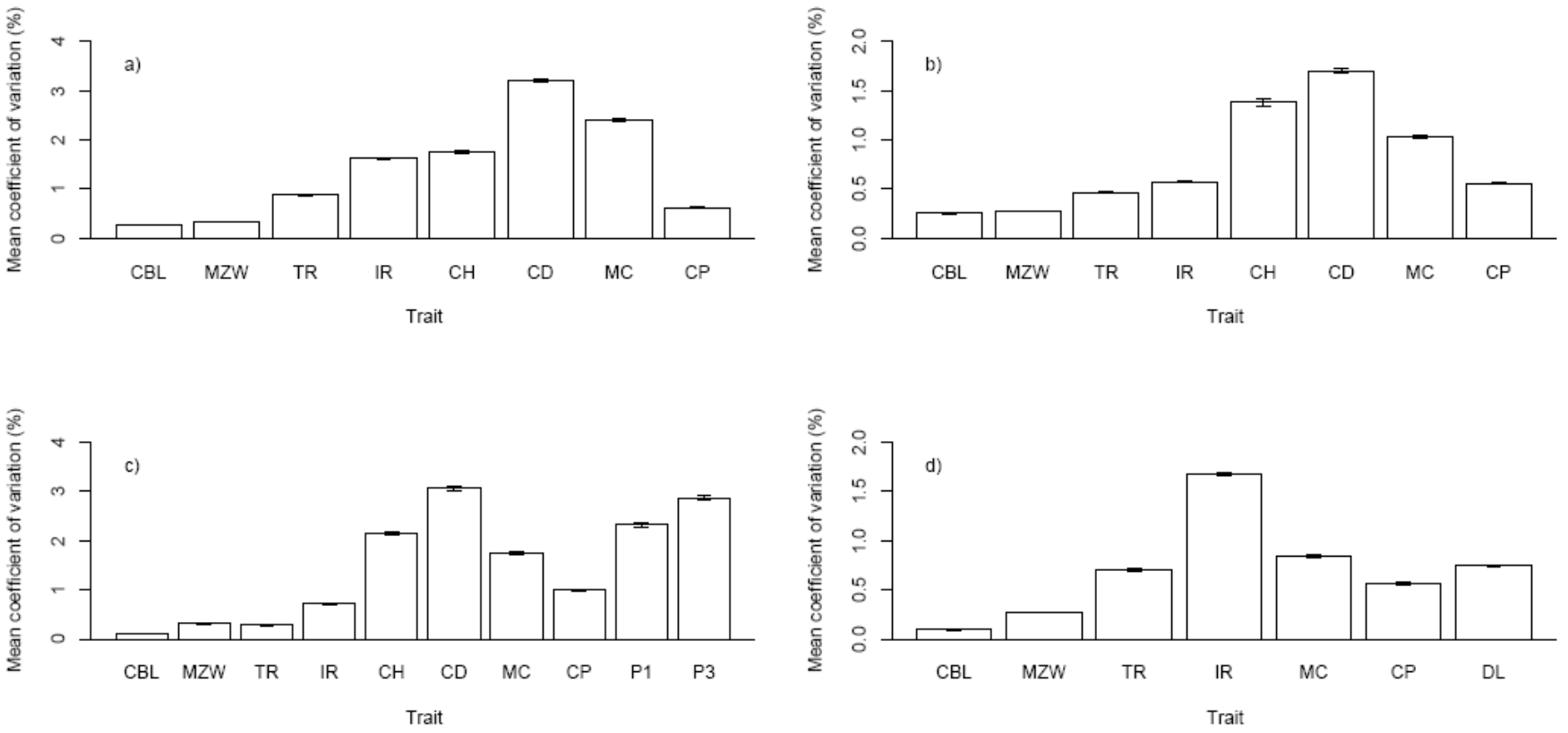


Figure 2.5: Mean coefficient of variation for different trait measurements in the a) bats (Phyllostomidae), b) monkeys (Platyrrhini) c) possums (Phalangeriformes), and d) squirrels (Marmotini). Error bars are ± standard error. CBL = condylobasal length, MZW = maximum zygomatic width, TR = tooth row length, IR = incisor row length, CH = canine height, CD = canine diameter, MC = mandibular condyle height, CP = coronoid process height, P1 = P_1 height, P3 = P_3 height, DL = diastema length.

2.6 Dataset coverage

The taxonomic and geographic coverage of the error-checked dataset are displayed in Table 2.3 and Figure 2.6.

Table 2.3: The taxonomic coverage of the dataset (after specimens with errors were removed) using the taxonomy of Wilson and Reeder (1993). bats = Phyllostomidae; monkeys = Platyrrhini; possums = Phalangeriformes; squirrels = Marmotini. Singletons are species or genera represented by only one specimen. Numbers in brackets represent the percentages of the total number of genera/species in each of the clades.

	number of genera measured		number of species measured		
clade	**total**	**singletons**	**total**	**singletons**	**total number of specimens**
bats	36 (77%)	1	104 (69%)	8	724
monkeys	15 (100%)	0	73 (87%)	8	607
possums	14 (70%)	0	36 (60%)	3	335
squirrels	5 (71%)	0	78 (85%)	0	636

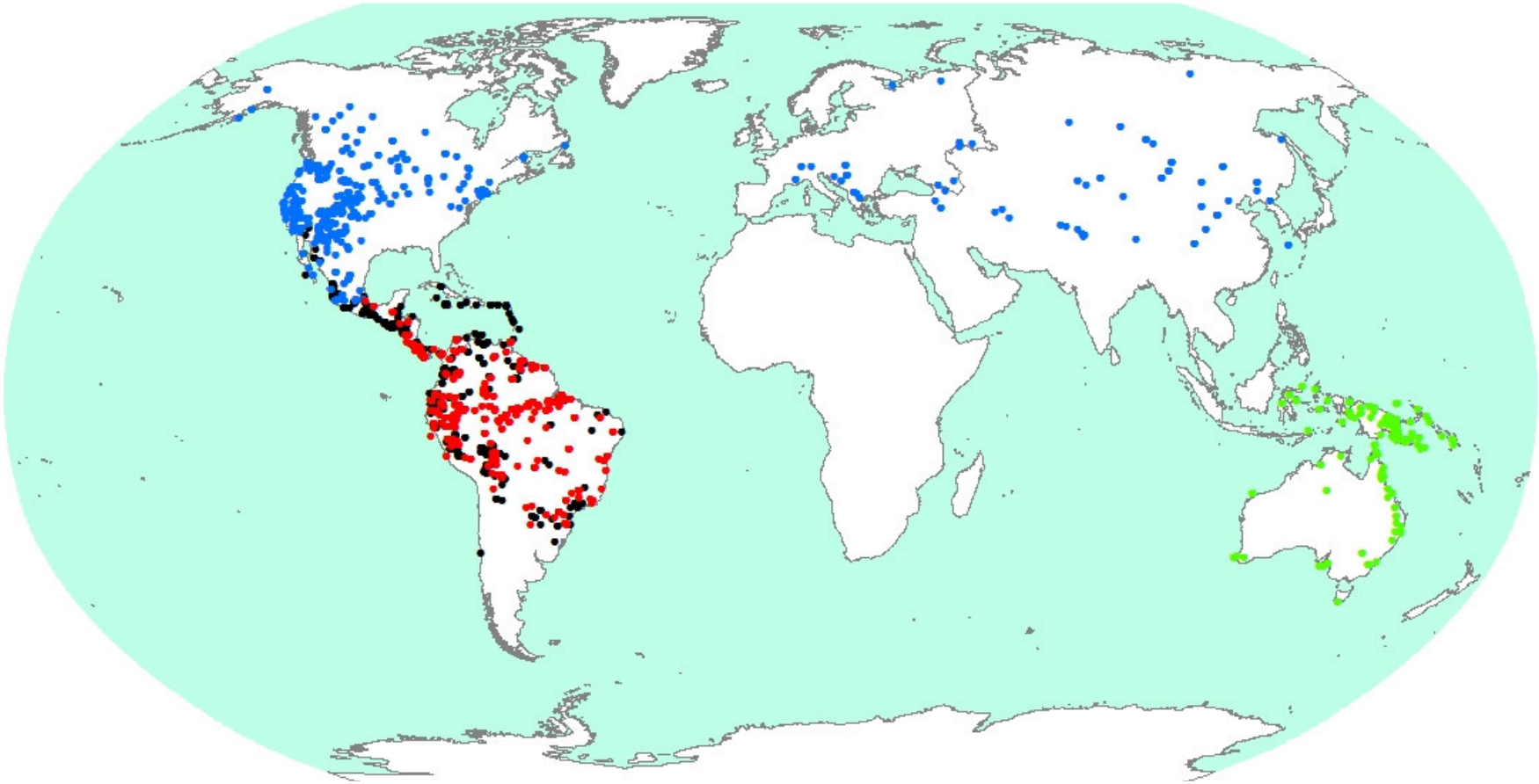


Figure 2.6: Point localities of bat (Phyllostomidae; black points), monkey (Platyrrhini; red points), possum (Phalangeriformes; green points) and squirrel (Marmotini; blue points) specimens.

2.7 Assemblage lists

There are many definitions of the term "community"; most are very general (e.g. "an assemblage of species populations that occur together" Begon et al. 1996) with unclear or arbitrary boundaries (Underwood 1986). Although efforts have been made to clarify community definition these have been criticised for being too restrictive (Looijen & van Andel 1999; Parker 2004). This confusion has led to the abandonment of the term "community" by some authors to be replaced by the term "local assemblage", defined as the "co-occurring species in a given habitat at a specific time and place" (Underwood & Pertraitis 1993). Strictly speaking I am using local assemblages where I use the term community in my thesis.

Assemblage membership was determined using mammal species checklists for a particular area compiled by J.Rodríguez. These checklists were selected from a database of mammal assemblages including 376 georeferenced localities varying in size from 10 to 440,000 km^2 and distributed worldwide. The lists were obtained from several published sources reporting inventories of species observed to exist inside these areas. Only localities with inventories considered to be "complete" by the original source, or that may be assumed to be complete from the information provided therein, were included in the database. Exotic species were excluded and taxonomy was standardised following Wilson and Reeder (1993). Other examples of the application of this database may be seen in Hortal et al. (2008), Rodríguez (1999), Rodríguez (2006) and Rodríguez et al.(2006). In total I obtained data for 34 monkey, 13 possum and 95 squirrel assemblages, sources and details of which can be found in the online supplementary material associated with Cooper et al. (2008).

2.8 PanTHERIA database

PanTHERIA (Jones et al. in press) includes taxonomic, life-history, geographic range and ecological data on almost every species of mammal (as defined by Wilson & Reeder 1993 and 2005), although not every species has entries for every trait. This database is the result of wide-ranging literature searches and rigorous error checking procedures over several years, thus it is a suitable source of data for the analyses. A complete description of the database can be found in Jones et al. (in press).

I will use a number of PanTHERIA traits during the analyses. For analyses of correlates of morphological evolution (Chapter 5) I will use traits such as gestation length, basal metabolic rate, longevity, population size, geographic range size and adult body-mass. I will also use adult body-mass in analyses of body size evolution across all mammals (Chapter 6). Many analyses (Chapters 3, 4, 5 and 6) also use the species' geographic range polygons.

The trait I will rely on the most in the analyses (Chapters 5 and 6) is adult body-mass, for which PanTHERIA has data on all but 20 of my study species. To test the reliability of these data, I regressed each species' body-mass against species' mean CBL, which should strongly correlate with adult body-mass in all my study clades. The results are shown in Figure 2.7. CBL and body-mass are strongly correlated across all four clades (all clades: $t_{254} = 58.4$, $r^2 = 0.93$, $p < 0.001$) and in three clades separately (monkeys: $t_{69} = 48.2$, $r^2 = 0.97$, $p < 0.001$, possums: $t_{31} = 19.9$, $r^2 = 0.93$, $p < 0.001$, squirrels: $t_{56} = 26.3$, $r^2 = 0.93$, $p < 0.001$). In the bats, CBL and body size are less strongly correlated ($t_{92} = 38.7$, $r^2 = 0.56$, $p < 0.001$) due to the presence of several outliers (see Figure 2.7) which have a much higher body-mass than expected given their skull length (*Ametrida*

centurio, Centurio senex, Macrophyllum macrophyllum, Phyllostomus latifolius, Sphaeronycteris toxophyllum, Vampyressa bidens and *Vampyressa nymphaea*). These species have flattened faces as an adaptation to feeding on fruit: when I omitted these species from the analysis the correlation became much stronger ($t_{84} = 16.3$, $r^2 = 0.76$, $p < 0.001$).

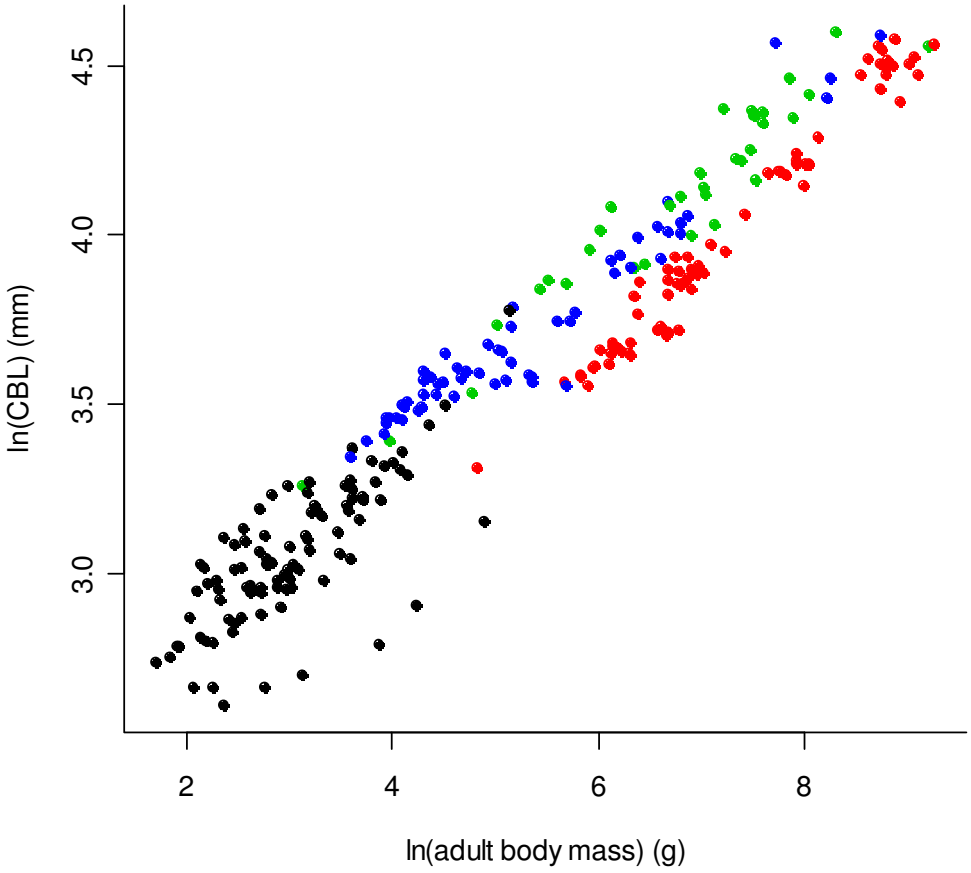


Figure 2.7: Mean species' condylobasal length (CBL) regressed against adult body-mass for bats (Phyllostomidae; black points), monkeys (Platyrrhini; red points), possums (Phalangeriformes; green points) and squirrels (Marmotini; blue points).

2.9 Phylogeny

Initially, I intended to use the mammal supertree (Bininda-Emonds et al. 2007, with corrected dates from Bininda-Emonds et al. 2008) for all analyses. However, although the supertree is generally well-resolved among genera, it is not well-resolved within

some genera (e.g., the monkey genus *Aotus* is represented as a single polytomy). Since some analyses are deleteriously affected by polytomies (e.g. analyses of character evolution), I modified the supertree as follows. There has been a lot of recent work on the molecular systematics of the Phyllostomidae (the supertree only used trees from sources published up to the end of 2000), which has altered understanding of the intergeneric relationships within the family. Therefore I built a new supertree for this group following the protocol described below. All phylogenetic topologies are shown in Appendix B.

Bats

The phylogeny of the phyllostomid bats has undergone various revisions since the publication of the Jones et al. (2002) supertree used in Bininda-Emonds et al. (2007). Since generic relationships have changed, I needed to construct a new supertree taking account of the current literature. Jones et al.(2002) used phylogenies published between 1970 and 2000. I collected all of the source trees they used and also searched for trees published between 2000 and the end of March 2007. I performed Web of Knowledge and Google Scholar searches on the word phyllostomid* with phenogram*, cladogram*, cladistic*, system*, taxonom*, or phylogen* and collected all the trees I could find (Appendix A3). I then subjected all the trees to the supertree protocols of Bininda-Emonds et al. (2004) as follows:

Tree selection: (1) *Validity and data quality***.** All of the source trees I selected represented valid analyses (*sensu* Bininda-Emonds et al. 2004). However, determining data quality was more difficult. Where I had the choice (i.e. multiple trees within a paper) I preferred strict consensus trees to majority rule consensus trees, bootstrapped trees to non-bootstrapped trees and avoided trees with very low node support values

where better-supported trees were available. (2) *Independence*. Only trees with non-overlapping datasets (character data and taxon-set) should be entered into a supertree analysis so that data duplication does not lead to spurious signal enhancement (Bininda-Emonds et al. 2004). If the taxon-set of a pair of trees did not overlap then I considered them as independent. If the taxon-set of a pair of trees did overlap then they were only considered independent if based on different data, i.e. different genes, different combinations of genes, different morphological characters, different combinations of morphological characters, or different combinations of molecular and morphological characters. This held unless one dataset was completely contained within another, e.g., regions within a gene or a subset of morphological characters from a large morphological dataset. For example, the phylogeny based on nectar-feeding attributes from the more complete morphological dataset in Carstens and Bryan (2002) is not independent of the phylogeny based on the complete dataset. Where the criteria for independence are not met there are a number of options. Where nonindependence occurred between studies, I used the most recent or most comprehensive (in terms of the number of taxa) study available. Where no obvious single choice existed (e.g. not all of the taxa were represented in any one study), I collected all the trees and created a "mini-supertree" of these using the methods described below. This "mini-supertree" was then entered into the supertree analysis as one source tree. Bininda-Emonds et al. (2004) suggest other solutions to this problem but they recommend the "mini-supertree" approach due to its ease of application. Where nonindependence occurred within studies (often where the authors analysed the same dataset by a number of methods e.g. Bayesian, maximum likelihood, parsimony), I used either the most comprehensive study (in number of taxa or characters) or, if this was not possible, I used the phylogenetic hypothesis explicitly preferred by the authors. If neither of these approaches worked, I

created a strict consensus tree of all the available trees and used this instead. (3) *Terminal taxa*. I standardised the taxonomy of all terminal taxa using Wilson and Reeder (1993). Where trees showed only intergeneric relationships I used the species of the genera which had been analysed in order to get the tree. Where this was not stated I used the type species for that genus as defined in Wilson and Reeder (1993).

Supertree construction: Once I had selected the source trees, I converted each into a MRP (matrix representation using parsimony) matrix using perl scripts written by Olaf Bininda-Emonds (O.B.E). In a standard MRP matrix, each character column is equivalent to a node in the phylogeny. The value in the matrix for a particular species is 1 if the species is present in the branches subtending from that node, and 0 if it is not. Each tree was also given an outgroup (MRP outgroup). More details on the MRP method can be found in Baum and Ragan (2004). The MRP matrices for each tree were then combined to make a "super matrix" containing each node of each source tree as a character, and each species of bat. If a species was not present in a given source tree its value for that character was "?" (i.e. missing data). I then performed a heuristic search on this super MRP matrix with the parsimony ratchet in PAUP*4.0 (Swofford 2002) using perl scripts written by O.B.E. The final supertree was a strict consensus tree of all the most parsimonious trees found during these searches.

For analyses in which soft polytomies are expected to bias the results (Chapters 3, 4 and 5), 15 species were removed in order to completely resolve the supertree. The species chosen were those represented by the fewest specimens as follows: *Artibeus amplus, Artibeus fraterculus, Artibeus jamaicensis, Artibeus lituratus, Lonchorhina aurita, Lonchorhina orinocensis, Platyrrhinus aurarius, Platyrrhinus brachycephalus,*

Platyrrhinus helleri, Platyrrhinus recifinus, Sturnira magna, Tonatia schulzi, Tonatia bidens, Uroderma bilobatum and *Uroderma magnirostrum.*

Monkeys

Most of the lack of resolution within the monkey phylogeny is within genera (but see below). Therefore I used the primate supertree of Vos (2006) to resolve the genera *Aotus* and *Alouatta*, and to place *Saimiri ustus, Saguinus inustus*, and *Callicebus personatus* within the phylogeny. I was unable to use this approach to resolve the genus *Pithecia* because of the conflict between this supertree and the mammal supertree (Bininda-Emonds et al. 2007; 2008). To resolve this genus I instead deleted one of the species involved (*Pithecia aequatorialis*, one specimen).

The mammal supertree represents the subfamilies Callitrichinae, Cebinae and the family Aotidae as a polytomy. Since the Callitrichinae and Cebinae are part of the same family (Cebidae; Wilson & Reeder 2005) I resolved this polytomy by making them sister clades following Purvis (1995).

Possums

The mammal supertree (Bininda-Emonds et al. 2007; 2008) is well-resolved for most possum genera, particularly when only the species I have data for are included. There are three problematic polytomies: within the genera *Dactylopsila*, *Petaurus* and *Pseudocheirus*. Both involve only three species (requiring the omission of only one species to remove the polytomy). Since no recent phylogenies or taxonomies resolve these genera, I omitted one species from each polytomy in analyses which require a completely resolved tree. The species omitted were *Dactylopsila tatei*, *Petaurus*

australis and *Pseudocheirus canescens*, as these were represented by the fewest specimens.

Squirrels

The mammal supertree (Bininda-Emonds et al. 2007; 2008) is well resolved for squirrels. Within the genera there are several problematic polytomies within *Ammospermophilus* and within *Spermophilus*. I used suggested sister species or subgeneric taxonomy from Wilson and Reeder (1993; 2005) to resolve these polytomies as follows: *Ammospermophilus harrisii, A. interpres, A. nelsoni* and *A. leucurus* are represented as a polytomy in Bininda-Emonds et al. (2007; 2008). *A. interpres* is considered to be a primitive sister to the other species of *Ammospermophilus* (Wilson & Reeder 2005), so I placed it as the outgroup to the rest of the genus. *A. harrisii* and *A. insularis* are considered to be sister species so I made them sister species in the phylogeny. This resolved the polytomy. Within *Spermophilus* (for more details compare the topology of Bininda-Emonds et al. 2007 to the squirrel phylogenies in Appendix B), I first moved *S. atricapillus* to make it the sister species of *S. beecheyi* as indicated by Wilson and Reeder (2005). Secondly, I placed *S. pygmaeus* and *S. relictus* as the outgroup to the group including *S. suslicus, S. beldingi, S. adocetus* and *S. mollis*. Finally, I resolved the polytomies in the *S. washingtoni* clade, using sub-generic taxonomy of Wilson & Reeder (2005): *S. parryi*, *S. undulatus* and *S. columbianus* are from the subgenus *Urocitellus* and *S. armatus*, *S. richardsonii* and *S. washingtoni* are from the subgenus *Spermophilus*. Making these groups sister species resolves the polytomies. Even with these amendments, there are still two polytomies in the squirrel tree but these are rectified by removing *S. adocetus*, *S. fulvus* and *S. citellus* in analyses where polytomies may affect the results (Chapters 3, 4 and 5).

In the mammal supertree (Bininda-Emonds et al. 2007; 2008) the genera *Marmota*, *Cynomys* and *Spermophilus* form a polytomy. No consensus exists in the literature as to how to resolve this polytomy so I resolved it in all of the three possible ways resulting in three phylogenies. I used all three phylogenies in each analysis which should indicate whether the analyses are sensitive to the phylogeny used (Chapters 3, 4 and 5).

Dating the phylogenies

All of the modified phylogenies described above were dated by Olaf Bininda-Emonds (O.B.E) using a procedure similar to that used to date the mammal supertree (Bininda-Emonds et al. 2007). First, two outgroups were added to each tree (bats: *Homo sapiens* and *Canis lupus*; monkeys: *Canis lupus* and *Rattus norvegicus*; squirrels: *Homo sapiens* and *Rattus norvegicus*) to root the phylogenies and to enable the divergence time of the ingroup node in each to be estimated using sequence data. Next, sequence data for each taxon were obtained from the dataset used to date the mammal supertree (Bininda-Emonds et al. 2007), with allowances being made for any changes in taxonomy for those trees based on the Wilson and Reeder (1993) taxonomy. The sequence data for each gene were then fitted to the respective tree under a maximum likelihood (ML) criterion using PAUP* version 4.0b10 (Swofford 2002) after determining the optimal model of evolution using ModelTEST version 3.6 (Posada & Crandall 1998). Initial divergence dates were obtained using relDate version 2.3 to determine the relative branch lengths and calibrate them against either fossil information (bats only) and/or information from the mammal supertree (Bininda-Emonds et al. 2007). These dates were then corrected for any potential negative branch lengths using chronoGrapher version 1.4 to obtain the final sets of divergence times. In addition, chronoGrapher was used to interpolate divergence dates for nodes missing such estimates based on the pure-

birth model of Purvis (1995) and applied in Bininda-Emonds et al. (2007). The degree of interpolation varied between the different trees. For each of the squirrel trees, only 5 of the 84 dates were based on interpolation. The amount of interpolation increased for the bat tree (24 of 94 nodes) and for the primate tree in particular (30 of 83 nodes). More detailed information about the dating procedure can be found in Bininda-Emonds et al. (2007).

Chapter 3: Are mammalian assemblages non-randomly assembled with respect to phylogeny and/or traits?[2]

3.1 Abstract

Interspecific competition has long been proposed as an important force in structuring mammalian communities. Although early work recognised that competition has a phylogenetic dimension, only with recent increases in the availability of phylogenies have truly phylogenetic investigations of mammalian community structure become possible. I test whether the phylogenetic structure of 142 assemblages from three mammalian clades (New World monkeys, North American ground squirrels and Australasian possums[3]) shows the imprint of competition. Across all assemblages there is a highly significant tendency for members to be more distantly related than expected by chance (phylogenetic overdispersion); this overdispersion is also significant within two of the clades (monkeys and squirrels) separately. This is the first demonstration of widespread overdispersion in mammal assemblages and implies an important role for either competition between close relatives where traits are conserved, habitat filtering where distant relatives share convergent traits, or both. Investigations of the species' cranial skeletal traits show greater trait variances within assemblages than expected by chance, supporting competition as the mechanism behind this phylogenetic overdispersion.

[2] Many of the analyses in this chapter have been published in Cooper, N., Rodriguez, J. and Purvis, A. 2008. A common tendency for phylogenetic overdispersion in mammalian assemblages. *Proceedings of the Royal Society B: Biological Sciences*, **275**: 2031–2037. doi: 10.1098/rspb.2008.0420. N.C. wrote the manuscript and performed all analyses, J.R. provided assemblage lists, A.P. supervised.

[3] Phyllostomid bats, included in other chapters, were not included in this chapter as there were no assemblage lists available in J.R's database.

3.2 Introduction

"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 [for existence] will generally be more severe between species of the same genus, when they come into competition with one another, than between species of distinct genera."

Charles Darwin (1859)

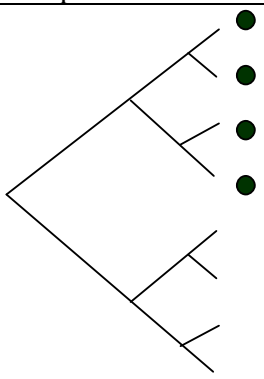
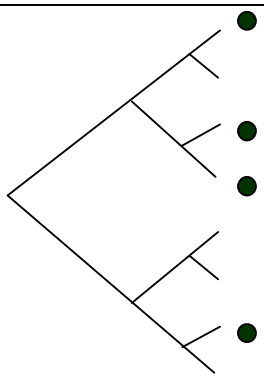
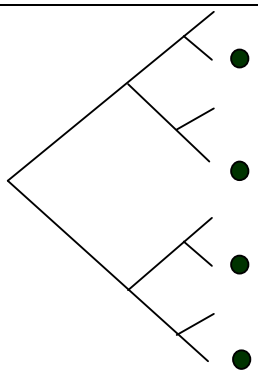
Interspecific competition has been shown to occur frequently in nature (Connell 1983; Schoener 1983) and has long been suggested as an important force in structuring mammalian communities. This theory assumes that species which are "too similar" in terms of their ecology will be unable to coexist due to competitive exclusion of the inferior competitor (Hutchinson 1959), so communities should contain only species which are sufficiently different to coexist. Because ecological similarity is often highest among closely-related species which share traits from a recent common ancestor (Harvey & Pagel 1991), competition must have a phylogenetic dimension. This has long been recognised: Darwin (1859) proposed that species in the same genus would be more likely to compete than those in different genera. However, without access to phylogenies, early work on mammalian community structure could only use taxonomy as a surrogate for phylogeny by, for instance, looking at species-to-genus ratios (Elton 1946).

If competition is important in structuring mammalian communities, few species per genus are expected to coexist in each community (Elton 1946; Table 3.1). Early studies often found such a pattern; however, these ratios depend strongly on the number of species involved and, once this was taken into account, later work revealed that many

communities contained more species per genus than expected (Jarvinen 1982). This result suggests that other factors, such as habitat filtering, where only ecologically similar species that share traits enabling them to survive in a locality can coexist, may also be shaping community assembly. Such factors will also have a phylogenetic dimension (Harvey & Pagel 1991).

With recent increases in the availability of phylogenies we can now use phylogeny, rather than taxonomy, to look at community structure. Table 3.1 outlines the taxonomic and phylogenetic patterns expected under different assembly rules. If competition affects community membership, then species in a community will be more distantly related than expected by chance (phylogenetic overdispersion: Webb et al. 2002). Conversely, if community membership is determined by habitat filtering, the species within a community will be more closely-related than expected by chance (phylogenetic clustering: Webb et al. 2002). Finally, if community assembly is not strongly influenced by phylogeny, or if multiple factors oppose and nullify each other, community lists will be randomly assembled with respect to phylogeny (Helmus et al. 2007).

Table 3.1: Schematic demonstrating how habitat filtering and competition affect patterns in the distribution of community members across phylogenies (black dots), species-to-genus ratios and the phylogenetic structure of communities. NRI = net relatedness index; NTI = nearest-taxon index.

Process	Habitat filtering: species share traits which allow them to exist in a particular environment	Random: neither process strongly effects community assembly or multiple factors working in opposing directions.	Competition: only species which are not too ecologically similar are able to coexist
Traits	Conserved. If traits are convergent the patterns are similar to those shown for competition.	Either conserved or convergent.	Conserved. If traits are convergent the patterns are similar to those shown for random communities.
Distribution of community species on phylogeny			
Species: Genus ratio	More species per genus than expected by chance	No more or less species per genus than expected by chance	Fewer species per genus than expected by chance
Phylogenetic structure	Phylogenetic clustering (positive NRI and NTI scores – see text)	Random phylogenetic structure (NRI and NTI scores not significantly different from zero – see text)	Phylogenetic overdispersion (negative NRI and NTI scores – see text)

"Community phylogenetic" methods (Webb et al. 2002), which compare the phylogenetic position of community members with those of non-members from a regional source pool, have been developed to test these ideas. Unfortunately the patterns are not always easy to interpret: phylogenetic overdispersion may also result from convergence of distantly related species (where traits are convergent rather than conserved; Cavender-Bares et al. 2004; Kraft et al. 2007). Likewise, phylogenetic clustering may also be due to historical or biogeographical factors, *in situ* speciation, or

limits on species dispersal that prevent species from leaving their ancestral ranges. Some of these alternatives can be investigated if there is available data on the traits mediating competition and resource use. For example, if a pattern of phylogenetic overdispersion is observed, whether this pattern is due to competition or another factor is ambiguous. If however, we also have data on the traits of the species within that assemblage, we can determine whether the traits also show a pattern of overdispersion, i.e. greater trait variance among the members of an assemblage than expected by chance. If so this suggests that competition, rather than habitat filtering, is determining community structure. If, on the other hand, the traits of the species within the assemblage are more similar than expected by chance, this suggest that trait evolution in the group must be convergent rather than conserved, hence the pattern of phylogenetic overdispersion is probably not due to competition.

Here I aim to determine whether community phylogenies support the prediction that competition is a powerful and widespread force in structuring mammalian communities. Previous studies of the phylogenetic structure of communities have focussed on plants and microbes (e.g. Cavender-Bares et al. 2004; Horner-Devine & Bohannon 2006; Webb 2000), but to my knowledge only one other study has looked at mammalian communities. Cardillo et al. (2008) performed a global-scale analysis of the phylogenetic structure of island mammal assemblages over broad taxonomic groupings. Here, I instead investigate patterns in three geographically restricted and moderately diverse mammalian clades: New World monkeys (Platyrrhini), Australasian possums (Phalangeriformes) and North American ground squirrels (Marmotini). This is the first time this question has been approached in this clade-based way, and this narrower phylogenetic focus should increase the likelihood of competition among the species

(Darwin 1859) as they should require more similar resources. In addition, the clades exhibit a range of life histories and live in a variety of habitats so I can test the generality of any patterns observed. Since competition and habitat filtering can both lead to phylogenetic overdispersion I also look at patterns of trait variances amongst communities to determine which of the two mechanisms is more likely.

I use two measures of assemblage phylogenetic structure: Webb's (2000; Webb et al. 2002) net relatedness index (NRI) and nearest-taxon index (NTI), to investigate the phylogenetic structure of multiple assemblages for each clade and focus on general patterns rather than on those of individual assemblages (as done in most previous studies). In order to help with interpreting the results, I then use an analogous method to calculate the standardised trait variances across multiple assemblages for each clade, again focussing on general patterns.

3.3 Materials and Methods

DATA

Species assemblages and species pools

Assemblage membership was determined using mammal species checklists for a particular area compiled by J.R. as described in Chapter 2: section 2.7. In total I obtained data for 34 monkey, 13 possum and 95 squirrel assemblages, more details of which can be found in the online supplementary material of Cooper et al. (2008).

The species pool for each assemblage was calculated by overlaying polygon geographic range maps in ArcGIS from Jones et al. (in press) and extracting all species occurring within the assemblage locality and up to a threshold distance of 500 km outside the

locality boundary. Community phylogenetic studies can be strongly dependent on the spatial scale of the species pool (Swenson et al. 2006), so I repeated the analyses using threshold distances of 100 km, 250 km and 1000 km when defining species pools. Assemblage phylogenetic structure is calculated relative to that of the species pool so it cannot be calculated if the assemblage constitutes the entire species pool. This happens more frequently with smaller thresholds: of the 142 assemblages, 67 represented the complete species pool when 100 km pools were used, 45 when 250 km pools were used, 29 when 500 km pools were used and 26 when 1000 km pools were used. Since the 1000 km pool analyses contained only three extra assemblages, and at this scale it is likely that some of the species included in the pool could not feasibly be members of the assemblage due to the geographic distances involved, I focus on results from the 500 km species pool analyses. However, pool size made no qualitative difference to the results (Table 3.4)

Phylogeny

The phylogenies used are described in Chapter 2: section 2.9 and each was completely resolved. In the Bininda-Emonds et al. (2007; 2008) supertree, the relationship among the genera *Cynomys*, *Marmota* and *Spermophilus* is unresolved. I created three new phylogenies, one for each possible resolution of the polytomy, and analysed each in turn. The topology used had no qualitative influence on the results (Table 3.3), so I only discuss results for the *Cynomys* outgroup tree.

Morphological traits

Traits were collected and error checked as described in Chapter 2: sections 2.3-2.5. I extracted the species means of each trait for each species before natural-log transforming them to normalise their distributions. All the morphological traits I used have some functional significance in resource use (see Chapter 2: section 2.3).

ANALYSES

All data analysis was carried out using R version 2.5.1 (R Development Core Team 2008) and I analysed the three mammalian clades separately i.e. I analysed the squirrels in an assemblage separately to the monkeys where there was overlap.

Measuring phylogenetic assemblage structure

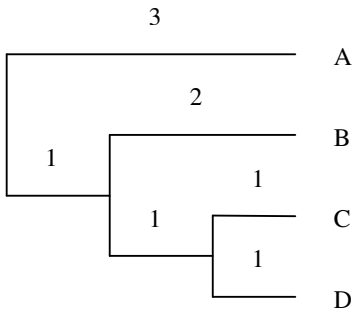
I determined NRI (net relatedness index) and NTI (nearest-taxon index) values (Webb 2000; Webb et al. 2002; see Figure 3.1 for example calculations) for each assemblage that had more than one species and did not constitute the complete source pool (110 assemblages in total using the 500 km species pools). NRI and NTI are both measures of the phylogenetic distance between taxa in an assemblage, where phylogenetic distance is defined as the sum of all intervening branch lengths between two taxa. However, they reflect phylogenetic structure in different parts of the phylogeny. NRI is based on the mean phylogenetic distance (MPD) of an assemblage, i.e. the mean phylogenetic distance between all possible pairs of taxa within the assemblage ($\overline{MPD}_{obs}$), and significant values reflect clustering or overdispersion across the whole of the pool phylogeny. NTI, on the other hand, is based on the mean nearest neighbour distance (MNND), i.e. the mean distance between each of *n* taxa (where *n* is the number of taxa in the assemblage) within the assemblage and its nearest neighbour in the assemblage phylogeny ($\overline{MNND}_{obs}$). NTI is therefore most sensitive to clustering or

overdispersion near the tips of the pool phylogeny. To allow comparisons between multiple assemblages, these MPD and MNND values are then standardised by (i) subtracting the mean MPD/MNND expected for *n* taxa drawn at random from the species pool using 10,000 iterations ($\overline{MPD}_n / \overline{MNND}_n$), and then (ii) dividing by the standard deviation of the MPD/MNND from these 10,000 randomly-drawn pseudo-assemblages ($s(MPD_n) / s(MNND_n)$). Both values are then multiplied by -1 so that clustered NRI and NTI values are positive and overdispersed values are negative, which is more intuitive than the reverse. Thus NRI and NTI are calculated as follows:

$$\text{NRI} = -\left(\frac{\overline{MPD}_{obs} - \overline{MPD}_n}{s(MPD_n)}\right) \quad (1)$$

$$\text{NTI} = -\left(\frac{\overline{MNND}_{obs} - \overline{MNND}_n}{s(MNND_n)}\right) \quad (2)$$

This procedure should mean NTI and NRI are approximately normally distributed; however, previous studies have shown that NRI is generally biased towards detecting overdispersion because of the branching structure of phylogenies (Kembel & Hubbell 2006; Swenson et al. 2006). Therefore, to test whether an individual assemblage was significantly clustered or overdispersed I compared MPD and MNND values for the real assemblage with those from the 10,000 randomly-generated pseudo-assemblages (with *n* species drawn at random from the assemblage's species pool) used to calculate NRI and NTI. A particular assemblage was considered significantly clustered if less than 250 (2.5%) of these random assemblages had a larger MPD/MNND value than that of the assemblage, or overdispersed if less than 250 (2.5%) had a lower MPD/MNND value than that of the assemblage.



Assemblage ABC		Assemblage BCD	
MEAN PHYLOGENETIC DISTANCE (MPD)			
Species pairs	**PD**	**Species pairs**	**PD**
A and B	3 + 1 + 2 = 6	B and C	2 + 1 + 1 = 4
A and C	3 + 1 + 1 + 1 = 6	B and D	2 + 1 + 1 = 4
B and C	2 + 1 + 1 = 4	C and D	1 + 1 = 2
MPD = (6 + 6 + 4)/3 = 5.333		***MPD = (4 + 2 + 2)/3 = 3.333***	
MEAN NEAREST NEIGHBOUR DISTANCE (MNND)			
Nearest neighbours	**Distance to nearest neighbour**	**Nearest neighbours**	**Distance to nearest neighbour**
A = B	3 + 1 + 2 = 6	B = C	2 + 1 + 1 = 4
B = C	2 + 1 + 1 = 4	C = D	1 + 1 = 2
C = B	2 + 1 + 1 = 4	D = C	1 + 1 = 2
MPD = (6 + 6 + 4)/3 = 5.333		***MPD = (4 + 2 + 2)/3 = 3.333***	

Figure 3.1: Example calculations of mean phylogenetic distance (MPD) and mean nearest neighbour distance (MNND)

Pooled NRI/NTI analyses

Null model choice is vital to interpreting the results of all analyses including those using NRI and NTI (Kembel & Hubbell 2006). I was therefore unable to test for trends across all assemblages using raw NRI values as these values tend to be negatively skewed, making the null expectation of any test uncertain. Therefore, I devised a novel and simple non-parametric method to analyse the pooled data.

For each assemblage I first calculated NRI for 10,000 randomly-generated pseudo-assemblages (with *n* species drawn at random from the assemblage's species pool). I then determined the centile of the observed NRI (which I term NRI%) within this distribution; if the observed value was tied with multiple random assemblages, the centile of the median of these tied values was used. If assemblage members are random picks from the source pool, the expected centile is 50 (i.e., the median of the null distribution). Thus, the expected median of the NRI% values, across the set of assemblages, was also 50. I therefore tested whether the median NRI% differed from 50 using Wilcoxon tests. Since this result used assemblages from all three clades, I also used Kruskal-Wallis rank sum tests to determine whether the different clades had significantly different NRI% values from each other.

NTI is expected to be approximately normally distributed with a mean of zero so I used t-tests to determine whether the mean of the distribution differed from zero, demonstrating a general trend towards either clustering or overdispersion. I then used analysis of variance (ANOVA) to determine whether the different clades had significantly different NTI values from each other.

Methodological bias

As mentioned in Chapter 2: section 2.7, the assemblage localities ranged in size from 10 to 440,000 km^2 and also contained different numbers of species. If NRI% or NTI values are affected by these factors they may bias the results. I therefore used Spearman's rank correlation tests to determine whether NRI% or NTI values were correlated with the natural-log transformed area of the assemblage locality (km^2), natural-log transformed assemblage species richness, natural-log transformed species pool species richness, or

assemblage:pool species richness ratio (calculated as assemblage species richness/species pool species richness).

Trait analyses

If competition is determining assemblage structure then the variance of traits which limit species coexistence should be greater among the members of an assemblage than expected by chance. In order to investigate this in my assemblages, I first calculated the variance for each trait in each assemblage ($trait\ \mathrm{var}$). Next, to allow comparisons between multiple assemblages, I standardised these trait variances by (i) subtracting the mean variance expected for n taxa drawn at random from the species pool using 10,000 iterations ($\overline{trait\ \mathrm{var}_n}$), and (ii) dividing by the standard deviation of the trait variance from these 10,000 randomly-drawn pseudo-assemblages ($s(trait\ \mathrm{var}_n)$). Finally I multiplied the value by -1 so that values were positive where trait variance was lower than expected by chance and negative where trait variance was higher than expected by chance. This meant both the calculation and results were analogous to the NRI/NTI analyses. Standardised trait variances were therefore calculated as follows:

$$\text{Standardised trait variance} = \frac{trait\ \mathrm{var} - (\overline{trait\ \mathrm{var}_n})}{s(trait\ \mathrm{var}_n)} \qquad (3)$$

Pooled trait analyses

Standardised trait variance is expected to be approximately normally distributed with a mean of zero, so I used t-tests to determine whether the mean of the distribution differed from zero demonstrating a general trend towards either lower or higher trait variance than expected by chance. I then used analysis of variance (ANOVA) to determine

whether the different clades had significantly different standardised trait variance values from each other.

3.4 Results

NRI/NTI

The Wilcoxon tests showed that the median NRI% (net relatedness index centiles) differed significantly from 50 for all assemblages combined (< 50, $p = 0.004$) and for monkeys (< 50, $p = 0.001$) but not for possums ($p = 0.999$) or squirrels ($p = 0.082$; Figure 3.2, Table 3.2). The results did not differ qualitatively when differently-sized species pools were used (Table 3.4).

The t-tests showed that the mean NTI (nearest-taxon index) values differed significantly from zero for all assemblages combined (< 0, $p = 0.002$), for monkeys (< 0, $p = 0.002$), for squirrels (< 0, $p = 0.043$), but not for possums ($p = 0.837$; Figure 3.2, Table 3.2). The NRI% and NTI values for possums were closer to the null expectation but there were no significant differences among clades in either NRI% or NTI (NRI%: Kruskal-Wallis $\chi^2 = 2.910$, d.f. = 2, $p = 0.233$; NTI: $F_{2, 110} = 0.729$, $p = 0.485$). The results did not differ qualitatively when differently sized species pools were used (Table 3.4).

Table 3.2: Results of Wilcoxon tests investigating whether the distribution of NRI% values have medians significantly different from 50, and of t-tests investigating whether the distribution of NTI values have means significantly different from zero, for all clades and each clade separately. monkeys = Platyrrhini; possums = Phalangeriformes; squirrels = North American Marmotini. n = number of communities. *p < 0.05; **p < 0.01.

clade	n	median NRI% (1st quartile, 3rd quartile)	V	mean NTI ± s.e.	t
monkeys	28	31.18 (19.58, 46.93)	67.00**	-0.401 ± 0.118	-3.397**
possums	10	49.45 (20.51, 73.12)	27.00	-0.055 ± 0.261	-0.212
squirrels	75	37.09 (24.95, 64.00)	1095	-0.222 ± 0.108	-2.060*
all	113	36.06 (20.80, 63.85)	2201**	-0.251 ± 0.081	-3.122**

Table 3.3: Results of Wilcoxon tests showing that values of NRI% and NTI did not differ significantly when phylogenies with different squirrel genera as outgroups were used. These analyses used a 500 km species pool

		NRI%		NTI	
outgroup one	outgroup two	W	p	W	p
Cynomys	*Marmota*	6225	0.746	6461	0.877
Cynomys	*Spermophilus*	6230	0.754	6337	0.924
Marmota	*Spermophilus*	6725	0.490	6362	0.964

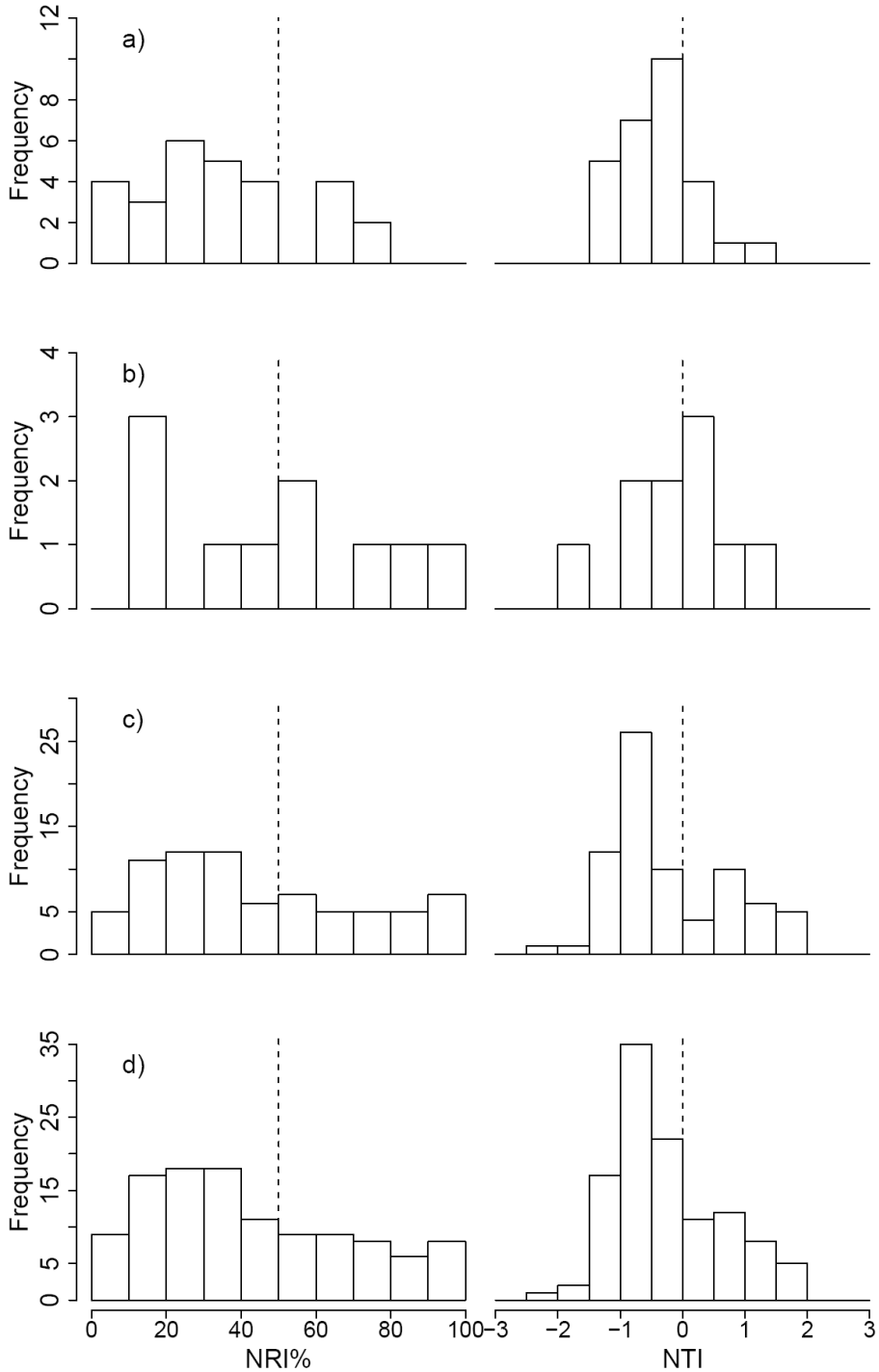


Figure 3.2: Distributions of NRI% values (left hand plots) and NTI values (right hand plots) for each clade separately and all clades combined. a) Platyrrhini; b) Phalangeriformes; c) North American Marmotini; d) all clades combined. In the NRI% plots the dashed line represents the 50th centile (median). In the NTI plots the dashed line is where NTI equals zero.

Table 3.4: Results for three different species pool sizes of Wilcoxon tests investigating whether the distribution of NRI% values have medians significantly different from 50, and of t-tests investigating whether the distribution of NTI values have means significantly different from zero, for all clades and each clade separately. m = Platyrrhini; p = Phalangeriformes; s = North American Marmotini. n = number of communities. *p < 0.05; **p < 0.01; ***p < 0.001.

pool size (km)	clade	n	median NRI% (1st quartile, 3rd quartile)	V	mean NTI ± s.e.	t
100	m	11	33.44 (19.42, 40.08)	13.00	-0.373 ± 0.297	-1.255
	p	7	37.66 (16.73, 78.01)	15.00	-0.285 ± 0.411	-0.693
	s	57	42.03 (25.38, 67.08)	653.0	-0.172 ± 0.134	-1.268
	all	75	37.27 (24.38, 66.01)	1058	-0.212 ± 0.116	-1.818
250	m	22	34.12 (23.11, 58.52)	71.00	-0.186 ± 0.180	-1.035
	p	9	43.86 (16.82, 77.70)	16.00	-0.162 ± 0.299	-0.541
	s	66	35.27 (24.73, 65.84)	803.5	-0.296 ± 0.131	-2.254*
	all	97	34.71 (22.10, 64.22)	1669*	-0.259 ± 0.101	-2.552*
1000	m	28	27.84 (10.62, 39.07)	40.00***	-0.594 ± 0.130	-4.567***
	p	10	50.67 (36.91, 77.27)	32.00	0.068 ± 0.230	0.297
	s	78	44.83 (23.76, 68.62)	1253	-0.214 ± 0.105	-2.041*
	all	116	39.67 (18.51, 65.78)	2321*	-0.281 ± 0.081	-3.466**

When the assemblages were considered individually, only six squirrel assemblages out of 75 (Coram Biosphere Reserve, MT: overdispersion: NRI = -1.707, p = 0.006; Dinosaur, NM: overdispersion: NTI = -1.666, p = 0.046; Guadalupe Mountains: overdispersion: NTI = -1.390, p = 0.04; Yellowstone NP: overdispersion: NRI = -1.099, p = 0.037; Zion: overdispersion: NRI = -1.230, p = 0.006, NTI = -2.056, p = 0.010) showed significant overdispersion. None of the individual monkey or possum assemblages were significantly overdispersed. No individual assemblages were significantly clustered. NRI and NTI values for individual localities can be found in the online supplementary material of Cooper et al. (2008).

Methodological bias

NRI% was not correlated with the area of the assemblage locality, the assemblage species richness or pool species richness, but was significantly correlated with the assemblage:pool species richness ratio (Table 3.5). NTI was not significantly correlated with the area of the assemblage locality, assemblage species richness or the assemblage:pool species richness ratio but was significantly correlated with species pool species richness (Table 3.5).

Table 3.5: Results of Spearman's rank correlation tests to determine whether NRI% or NTI values are associated with various predictor variables which may bias the results. Assemblage:pool species richness ratio = assemblage species richness/species pool species richness. ρ (rho) = Spearman's rank correlation coefficient. n = 113. *p < 0.05.

	NRI%		NTI	
predictor variable	**ρ**	**p**	**ρ**	**p**
Assemblage locality area (km^2)	0.048	0.612	0.127	0.181
Assemblage species richness	-0.025	0.791	0.109	0.250
Species pool species richness	0.151	0.111	0.222	0.018*
Assemblage: pool species richness ratio	-0.207	0.028*	-0.114	0.228

Trait variances

As detailed in Table 3.6, the t-tests showed that the mean standardised trait variance differed significantly from zero for all traits using all assemblages combined (all traits: $p < 0.001$), and for squirrels (all traits: $p < 0.001$), but for no traits in monkeys (These results are also displayed in Figure 3.3). There were significant differences among clades in mean standardised trait variance, with monkeys having significantly lower standardised trait variance than squirrels for all shared traits (CBL: $F_{2,107} = 9.246$, $p < 0.001$; MZW: $F_{2,107} = 6.841$, $p < 0.001$; TR: $F_{2,107} = 6.686$, $p < 0.001$; IR: $F_{2,107} = 7.472$, $p < 0.001$; MC: $F_{2,107} = 5.309$, $p < 0.001$; CP: $F_{2,107} = 8.058$, $p < 0.001$).

Table 3.6: Results of t-tests investigating whether the distributions of standardised trait variances have means significantly different from zero, for all clades combined and each clade separately. monkeys = Platyrrhini; possums = Phalangeriformes; squirrels = North American Marmotini. n = number of communities. CBL = condylobasal length; MZW = maximum zygomatic width; TR = tooth row length; IR = incisor row length; CH = canine height; CD = canine diameter; MC = mandibular condyle height; CP = coronoid process; P1 = P_1 height; P3 = P_3 height; DL = diastema length. ***p < 0.001

	monkeys (n = 28)		possums (n = 8)		squirrels (n = 74)		all (n = 110)	
trait	mean standardised trait variance ± s.e.	t	mean standardised trait variance ± s.e.	t	mean standardised trait variance ± s.e.	t	mean standardised trait variance ± s.e.	t
CBL	0.178 ± 0.170	1.045	-0.253 ± 0.344	-0.737	-0.636 ± 0.097	-6.583***	-0.401 ± 0.088	-4.564***
MZW	0.197 ± 0.165	1.191	-0.235 ± 0.318	-0.741	-0.618 ± 0.099	-6.237***	-0.383 ± 0.088	-4.346***
TR	0.175 ± 0.169	1.038	-0.202 ± 0.340	-0.595	-0.627 ± 0.103	-6.111***	-0.392 ± 0.091	-4.326***
IR	0.210 ± 0.202	1.037	-0.264 ± 0.329	-0.803	-0.644 ± 0.096	-6.701***	-0.399 ± 0.092	-4.331***
CH	0.322 ± 0.164	1.959	0.056 ± 0.309	0.181	-	-	-	-
CD	0.242 ± 0.171	1.414	-0.133 ± 0.376	-0.354	-	-	-	-
MC	0.076 ± 0.144	0.527	-0.144 ± 0.317	-0.456	-0.462 ± 0.086	-5.365***	-0.302 ± 0.075	-4.025***
CP	0.144 ± 0.161	0.898	-0.321 ± 0.327	-0.981	-0.569 ± 0.089	-5.365***	-0.369 ± 0.081	-4.547***
P1	-	-	0.040 ± 0.345	0.115	-	-	-	-
P3	-	-	-0.176 ± 0.467	-0.378	-	-	-	-
DL	-	-	-	-	-0.656 ± 0.091	-7.239***	-	-

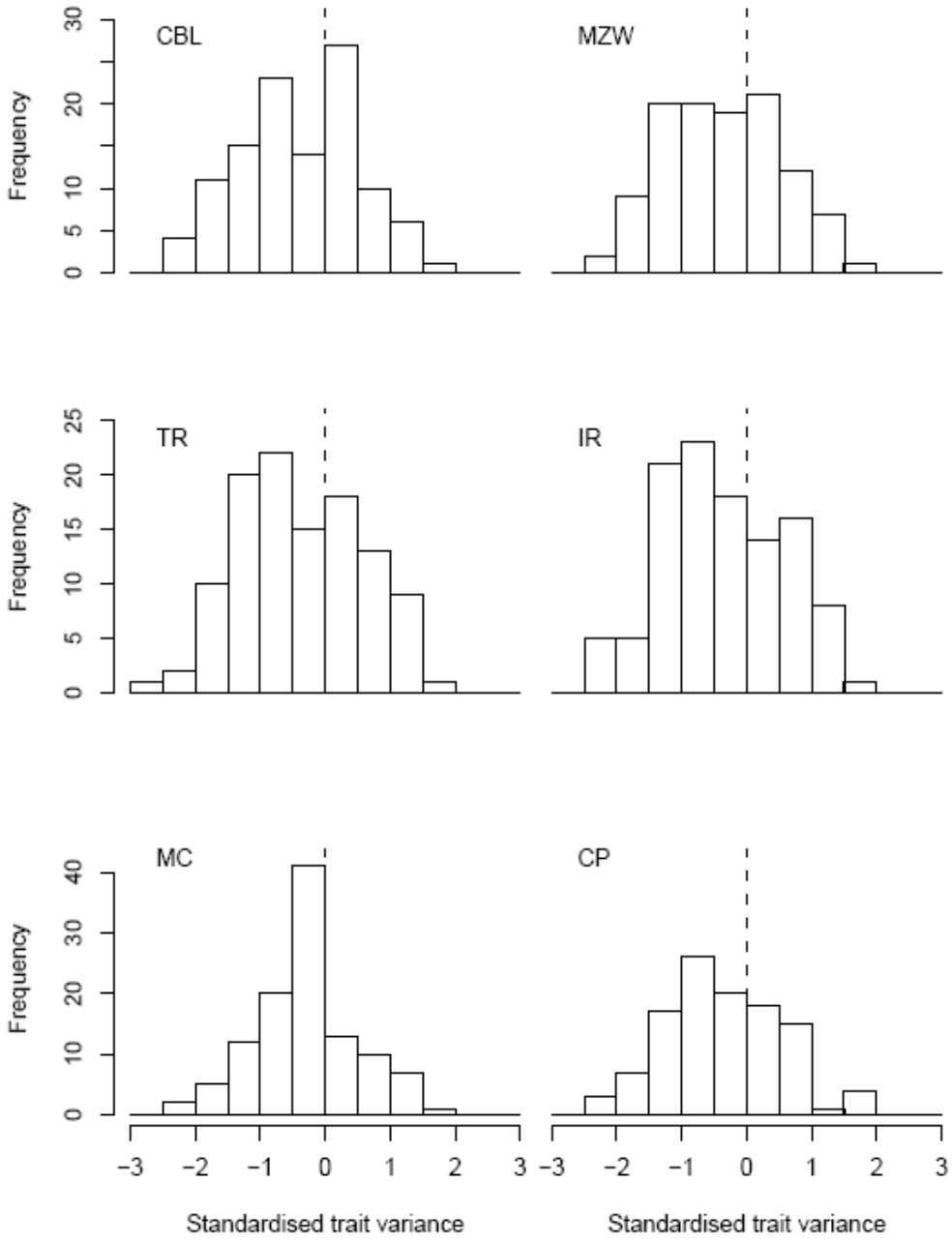


Figure 3.3: Distributions of standardised trait variances for all clades combined. CBL = condylobasal length; MZW = maximum zygomatic width; TR = tooth row length; IR = incisor row length; MC = mandibular condyle height; CP = coronoid process. The dashed line is where standardised trait variance is equal to zero.

3.5 Discussion

My results suggest a consistent tendency for mammalian assemblages to be more phylogenetically overdispersed than expected by chance, and that this tendency is only detectable by pooling many assemblages. This pattern is seen both across the whole phylogeny (net relatedness index/NRI results) and at the tips (nearest-taxon index/NTI results). Additionally, the three clades analysed do not have significantly different NRI% or NTI values suggesting that this could be a general, rather than a clade-specific, mammalian pattern.

The traditional interpretation of phylogenetic overdispersion is that competition among ecologically similar close relatives has led to exclusion of the inferior competitors and hence an assemblage with more distantly related species than expected. However, if traits allowing a species to exist in an area have evolved convergently in more distant relatives, then habitat filtering could also cause overdispersion (Cavender-Bares et al. 2004; Kraft et al. 2007). Determining whether competition or habitat filtering is more likely requires an analysis integrating data on the traits mediating competition and resource use. My analyses of traits in all clades provide support for competition being the mechanism behind the phylogenetic overdispersion, since every trait shows greater variance within assemblages than expected by chance. This fits with the predictions of earlier non-phylogenetic studies looking at how competition structures mammalian communities (Elton 1946), the results of Houle (1997), who found that primates that were phylogenetically "too close" did not coexist, and many previous studies which found similarly overdispersed trait values in other mammalian groups (see Dayan & Simberloff 2005 for a review).

When the clades were considered separately only the squirrels showed significant trait overdispersion. This suggests that closely-related squirrels (which will have similar trait values) do not coexist due to competition; instead squirrel assemblages are made up of species which are different enough to coexist. This has been seen on a smaller scale with other rodent species (Heske et al. 1994; Yom-Tov 1991). Monkey assemblage trait variances did not tend to depart from null expectations, although they were phylogenetically overdispersed. There are several possible explanations for this: firstly it is possible that the measured traits were not the ones which were most important for resource competition in monkeys. Thus there may be trait overdispersion which I could not detect with my morphological data. Secondly, different monkey genera are known to forage at different canopy levels (Fleagle 1999), and also vary the degree to which they include other items such as insects and sap in their diets (Nowak 1999). Perhaps these behavioural differences remove the need for morphological character displacement. Alternatively, it could be a taxonomic artefact: monkey species are often split into new species by taxonomists, and on these occasions their geographic ranges are split in two so there is no range overlap between sister species. Possum assemblages may generally be assembled at random with respect to phylogeny, perhaps because the traits involved in habitat filtering and competition in this group are independent of phylogeny, or because both mechanisms are acting and have cancelled each other out (e.g. Helmus et al. 2007). However, these results are based on only ten assemblages, so may not permit any robust conclusions.

Interestingly, few individual assemblages had significantly overdispersed NRI or NTI values. This could be due to low statistical power, since both the assemblages and species pools tended to be small. Also most assemblages were either too small or too

large with respect to the pool for maximum power (Kraft et al. 2007). In addition, competition does not always lead to competitive exclusion. Some species may be temporally or spatially segregated within the same habitat. Other species show behavioural plasticity which allows similar species to coexist (Houle 1997; Lovette & Hochachka 2006), or rapidly evolve different ecotypes (Harmon et al. 2003). Finally, the results focus on how competition between close relatives may limit species distributions in some mammalian clades. However, other factors also influence where species occur, such as geographical boundaries, limits on dispersal, differential extinction (human-mediated or otherwise), the distribution of resources (e.g. food and shelter), and interactions with species from different clades (e.g. predation). Although the narrow taxonomic focus of my approach should increase the likelihood of detecting competition in the clades (Darwin 1859), distant relatives may also compete. For example, in the Neotropics, frugivorous bats compete with birds (Palmeirim 1989) and potentially with monkeys as well.

My assemblage lists come from species checklists which may be incomplete. This incompleteness could only undermine the results if, for some reason, the omissions caused the species on the lists to appear phylogenetically overdispersed. An alternative approach would be to use species' range map overlap to determine assemblage membership (e.g. Davies et al. 2007). However, that approach is also problematic as maps tend to overestimate species' ranges and hence species' overlap (Hurlbert & Jetz 2007). Species checklists, whilst imperfect, are much more likely to capture sets of interacting species. Here I use range maps only to delimit source pools, so any errors will affect only the pools; and I show that varying the threshold for inclusion in the source pool has no qualitative impact on the results. My NRI results also appear to be

influenced by the size of the species pool and the NTI results by the ratio of the number of species in the assemblage to the number of species in the pool (Table 3.5). Since where NRI was affected by these factors, NTI was not, and vice versa, I believe the general pattern of overdispersion in the assemblages was not merely due to methodological bias. However, these factors should be considered in future studies.

My results suggest that species distributions, and perhaps trait values, are influenced by those of other, closely-related species. Since species' geographic range maps do not reflect the local heterogeneity in distributions that may be caused by such interactions, our knowledge of where species actually occur may be unreliable. Previous authors have recognised this and its implications for biodiversity research and conservation (Hurlbert & Jetz 2007). Likewise, the current trend for mapping how geographic ranges will shift under particular climate change scenarios may underestimate how species will be affected if these among-species interactions are ignored. Such interactions may make it much harder to predict how species will respond to their rapidly-changing environment.

Chapter 4: Competition and the evolution of mammalian morphological traits: a phylogenetic comparative study

4.1 Abstract

Traditional studies of competition tend to focus on the link between species' traits and coexistence. More recent studies have investigated the relationship between phylogeny and coexistence. However, few studies have so far considered the links between species' traits, phylogeny and coexistence simultaneously. Here I propose a model which uses all three variables to investigate the effects of competition on morphological evolution. I use partial Mantel tests to investigate the association between species' trait differences and geographic range overlap whilst controlling for phylogeny, in four mammalian clades. If competition has been important in the morphological evolution of the clades, I expect species' traits to become increasingly different as the degree of geographic range overlap between the species increases, all other things being equal. I find no significant pattern across the clades as a whole. However, when I only consider species within the same macroniche to be competitors, I find a significant result for monkeys and squirrels but in the opposite direction to my expectations: coexisting species tend to have more similar traits than expected by chance. There are no significant patterns in the bats or possums. This suggests that habitat filtering, and/or convergent evolution, may be more important than competition in determining the species' morphological traits, or that competition in these groups is reduced by different, perhaps behavioural, mechanisms.

4.2 Introduction

Although studied primarily by ecologists, competition between species has been suggested to drive differences in evolutionary rates (Stanley 1973a) and is therefore of interest to evolutionary biologists. Despite this, traditional studies of competition have focussed on the link between traits and coexistence without explicitly considering evolution (e.g. Dayan & Simberloff 1994). In such studies, ecological theory states that co-occurring species with similar traits (and therefore niches) will compete fiercely, and those which are "too similar" will be unable to coexist due to competitive exclusion of the inferior competitor (Gause 1934; Hutchinson 1959). Thus species that compete and coexist should have greater differences in their trait values than expected by chance, i.e. their traits should show character displacement (Brown & Wilson 1956). However, the evolutionary component of competition is also important, since competition only occurs between species with similar niches/traits and which coexist (Keddy 1989), and the niche/traits of a species are, at least partly, determined by the species' evolutionary history (Harvey & Pagel 1991). Therefore, in order to fully understand the influence of competition on evolution, we need to understand the links between species' traits, evolutionary history (i.e. phylogeny) and coexistence.

The evolutionary history of a species influences its traits in several ways. Firstly, close relatives tend to have similar traits because they share a common ancestor and hence a common starting point for their trait evolution (Harvey & Pagel 1991). In addition, the degree of adaptation to a given environment is dependent on physiological constraints which also have phylogenetic pattern; e.g. marine mammals possess a suite of adaptations to living in water but still need to breathe air because their mammalian ancestors had lungs not gills (Eisenberg 1981). Finally, historical environmental

conditions will have contributed to the trait evolution of species in the past, and hence may also influence their descendants. However, there are also striking examples of convergent evolution, where distantly related species with similar niches have evolved similar adaptations. For example, all subterranean mammals have reduced appendages to aid movement underground (Nevo 1979), so trait similarity is not necessarily connected to phylogenetic similarity.

Species coexistence and phylogeny are also linked, though indirectly through their effects on species' traits. Since species with similar traits are expected to compete, and close relatives have more similar traits than distant relatives (Harvey & Pagel 1991), patterns of species coexistence are expected to be phylogenetically structured. This idea has been used to develop "community phylogenetic" methods (Webb et al. 2002 and Chapter 3) which compare the phylogenetic position of community members with those of non-members from a regional source pool, to determine whether species within a community are more or less closely related than expected by chance. If competition affects community membership, then species in a community will be more distantly related than expected by chance (phylogenetic overdispersion: Webb et al. 2002). Conversely, species within a community could be more closely-related than expected by chance (phylogenetic clustering: Webb et al. 2002). The latter case would suggest that species within the community require similar traits in order to survive in the area, and that avoiding competition is a secondary concern. This is commonly called habitat filtering. Many examples of both phylogenetic overdispersion and clustering can be found in the literature (see Emerson & Gillespie 2008 for a recent list). Unfortunately, the interpretation of phylogenetic overdispersion and clustering is not always straightforward: for example, if species have undergone convergent evolution,

phylogenetic overdispersion may actually be the result of habitat filtering selecting species with similar traits, rather than competition selecting species with different traits (Webb et al. 2002). Therefore, although most studies of this kind use only phylogeny and ignore species' traits, there is a growing consensus that both traits and phylogeny need to be considered (Kraft et al. 2007).

My aim in this chapter is to determine whether species' traits are influenced by competition, whilst controlling for the effects of phylogeny. Since competition is difficult to demonstrate and quantify without extensive field work, I instead use species' coexistence (the degree of geographic range overlap) as a proxy for the potential intensity of competition between two species. Here I propose that the influence of competition on species' morphological traits can be investigated using the following model:

Trait differences = f(phylogenetic difference, coexistence difference) (4)

The important feature of this model is whether the coefficient for the coexistence term is negative or positive when controlling for phylogeny. If competition is important, this coefficient should be negative, so that as overlap with an ecologically similar species increases, trait differences also increase in order to reduce competition. Conversely, if habitat filtering is important, the coexistence coefficient will be positive so that as overlap with an ecologically similar species increases, trait differences decrease.

This method is similar to one recently proposed by Freckleton and Jetz (2009). They modelled how species' traits depended on both phylogeny and the geographical distances between species, with the prediction that as species become more closely-related and/or closer together in space, phylogenetic niche conservatism and spatial

autocorrelation would ensure that their traits would also become more similar. At the fairly large (regional to global) spatial scales in which they are interested, their model (which does not consider interactions among species) is not contradicted by the method I propose here. However, the model suggests that, at the spatial scale of communities, interactions among species may oppose their model's predictions: species in close proximity, both spatially and phylogenetically, will be more likely to compete and hence will be more different than expected by the method of Freckleton and Jetz (2009).

Here I test the model using four mammalian study clades: New World monkeys, Australasian possums, North American ground squirrels and New World leaf-nosed bats (see Chapter 2: section 2.2). The first three of these clades have been suggested to exhibit competition using methods that consider their traits only (all clades combined and squirrels; Chapter 3) and their phylogeny only (all clades combined, monkeys and squirrels; Chapter 3 and Cooper et al. 2008). They therefore provide a useful test of this new method, which accounts for both traits and phylogeny.

4.3 Materials and Methods

DATA

Morphological distance matrices

I collected the trait data and error-checked it as described in Chapter 2: sections 2.3-2.5. I then created Euclidean distance matrices for each clade using the natural-log transformed species' means of all the traits. These are the morphological distance matrices referred to throughout.

Phylogenetic distance matrices

The phylogenies used are described in Chapter 2: section 2.9 and each was completely resolved. In the Bininda-Emonds et al. (2007; 2008) supertree, the relationship among the genera *Cynomys*, *Marmota* and *Spermophilus* is unresolved. I therefore created three phylogenies, one for each possible resolution of the polytomy, and analysed each in turn. The topology used made no qualitative difference to the results, but I report the results from each below.

Since the amount of phylogenetic signal in a trait can vary substantially, I transformed each phylogeny using λ before performing any analyses. λ is a multiplier of the off-diagonal elements of a phylogenetic variance covariance matrix that best fits the data, and varies between λ = 1, where the data are structured according to a Brownian motion model of trait evolution, and λ = 0, where the data have no phylogenetic structure (Pagel 1999). I obtained the maximum likelihood (ML) estimate of λ using natural-log transformed condylobasal length (CBL) measurements for each species, with GEIGER (Harmon et al. 2008). I then transformed each phylogeny by the appropriate ML estimate of λ and these λ-transformed phylogenies were used to produce phylogenetic distance matrices (i.e. cophenetic rather than variance-covariance matrices which are phylogenetic similarity matrices) for each clade.

Species co-occurrence matrices

In order for a pair of species to compete and influence each others' morphology, their geographic ranges must overlap. However, simply noting whether ranges overlap or not, is not a good indicator of species interaction strengths, since a species that is found across the entire range of another should have greater influence on it than a species

found in only a small part of its geographic range. Therefore, rather than using this naïve approach, I calculated the number of 1° grid cells the species pairs shared, and then divided this by the total number of 1° grid cells occupied by the first species, to get the proportion of shared cells (see Figure 4.1). Note that the resulting matrices were not symmetrical. Since the models required difference and not similarity matrices, I then subtracted these values from unity to create a coexistence difference matrix. An example of how these values were calculated is shown in Figure 4.1: species A and B share one 1° grid cell, species A occupies 12 1° grid cells, and species B occupies one 1° grid cell. Thus the value in the species' coexistence matrix for species A with B is 1 - (1/12) = 0.917, and for species B with A it is 1 - (1/1) = 0 (i.e. zero difference). Species which overlap spatially do not necessarily compete. Thus I created another set of species coexistence matrices which only counted two species as sharing grid cells if the two species were in the same macroniche (Chapter 2: section 2.4; Eisenberg 1981). Using macroniches increases the likelihood that the species are actually competing because they are equivalent to ecological guilds (Chapter 2: section 2.4; Eisenberg 1981). In the example (Figure 4.1), if A was a volant frugivore and B was a volant carnivore, the values in the species' coexistence matrices would be 1 for both (i.e. completely different). I performed the analyses using both types of species coexistence matrix.

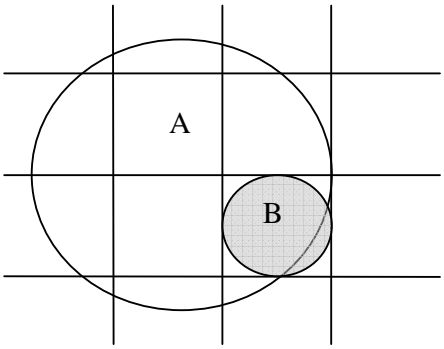


Figure 4.1: Example calculation for species' coexistence matrices. Species A and B share one 1º grid cell, species A occupies 12 1º grid cells, and species B occupies one 1º grid cell. The value in the species' coexistence matrix for species A with B is 1 - (1/12) = 0.917, and for species B with A it is 1 - (1/1) = 0.

ANALYSES

For each of the four clades, I performed partial Mantel tests (Manly 1997) controlling for the phylogenetic distance between the species, to determine whether there was any association between species' coexistence and species' morphological differences, independent of phylogeny. Since the elements of the matrices were not independent, significance testing was performed using 10,000 permutations (equivalent to $\alpha = 0.001$; Manly 1997) of the columns and rows of the morphological distance matrix to determine whether the association was higher than that expected by chance (one-tailed test).

All data analysis was carried out using R version 2.6.2 (R Development Core Team 2008), and partial Mantel tests used the package vegan (Oksanen et al. 2008).

4.4 Results

Results of the partial Mantel tests are shown in Table 4.1. When all species are included in the species' coexistence matrix there is a non-significant negative association between species' coexistence and species' morphological differences in all four clades.

However, when only species within the same macroniche are considered, the association is positive in all clades except possums, and significantly positive in monkeys and squirrels. The topology of the squirrel phylogeny I used had no qualitative effect on the results.

Table 4.1: Results of partial Mantel tests looking for an association between species' morphological differences and species' coexistence whilst controlling for phylogeny. "all species" analyses use the complete species' coexistence matrices; "same macroniche" analyses count species' range overlaps only if the two species are in the same macroniche. r = correlation coefficient; C = *Cynomys* outgroup squirrel topology; M = *Marmota* outgroup squirrel topology; S = *Spermophilus* outgroup squirrel topology.

			all species		same macroniche	
clade	**n**	**λ**	**r**	**p**	**r**	**p**
bats	87	1.000	-0.119	0.988	0.043	0.107
monkeys	69	0.984	-0.030	0.844	0.057	0.029
possums	30	1.000	-0.149	0.962	-0.016	0.602
squirrels C	61	0.990	-0.046	0.818	0.131	< 0.001
squirrels M	61	0.986	-0.047	0.824	0.137	< 0.001
squirrels S	61	0.988	-0.046	0.816	0.131	< 0.001

4.5 Discussion

When phylogeny is taken into account, monkey and squirrel species tend to be more similar than expected by chance as the overlap between their geographic ranges increases. This result is the opposite of my expectations, i.e. that coexisting species would be less similar than expected by chance due to competition. This suggests that, for monkeys and squirrels, there is some evidence that habitat filtering or convergence to similar morphologies are more important than competition in determining their morphological traits. This result is also consistent with the model of Freckleton and Jetz

(2009), which suggests that species in close proximity will be similar due to spatial autocorrelation, and this may also be the result of habitat filtering.

All of the monkeys (except for species in the genera *Alouatta*: howler monkeys and *Brachyteles*: woolly spider monkeys) are arboreal frugivore/omnivores and are therefore probably feeding on similar foods in similar areas. This may account for the similarity in the traits of the coexisting species, but does not necessarily mean that competition is unimportant in this group. The different genera are known to forage at different canopy levels (Fleagle 1999), and also vary the degree to which they include other items such as insects and sap in their diets (Nowak 1999). Perhaps these behavioural differences remove the need for morphological character displacement. Species may also reduce competition by taking differently-sized fruits, or by foraging at different times of the day (e.g. the genus *Aotus*, owl monkeys, are nocturnal; Nowak 1999). The other possible mechanism behind this result is that, rather than similar *in situ* adaptations to similar foods, habitat filtering has occurred, i.e. the species present in the area are there because they all have traits which enable them to survive there. It is likely that both convergent evolution and habitat filtering are involved in this pattern. Previous work (Chapter 3 and Cooper et al. 2008) proposed that habitat filtering combined with convergent trait evolution explains both the presence of phylogenetic overdispersion, and the absence of trait overdispersion in this group, and the results here seem to support this explanation.

Evidence for habitat filtering in squirrels directly contradicts the results of earlier phylogenetic- and trait- based studies (Chapter 3 and Cooper et al. 2008), which both found convincing evidence for the influence of interspecific competition in the clade

outweighing that of habitat filtering. One mechanism for this difference could lie in the methods used. The models used in this chapter differ from those used by Cooper et al. (2008) and in Chapter 3 in several respects. Firstly, the previous models considered species within a community, rather than species pairs within the same macroniche, and assumed that they all had the same degree of influence on each other. In squirrels, species within the genera *Marmota* and *Cynomys* (marmots and prairie dogs respectively) are members of the terrestrial/semifossorial herbivore/grazer macroniche, species within the genera *Ammospermophilus* and *Spermophilus* (antelope ground squirrels and ground squirrels respectively) are in the terrestrial/semifossorial omnivore macroniche, and species within the genus *Tamias* (chipmunks) are in the terrestrial/scansorial omnivore macroniche. Thus, since only species within the same macroniche were expected to compete strongly, this method only considers either marmots and prairie dogs, or antelope ground squirrels and ground squirrels, or chipmunk species, as competitors. Conversely, the previous analyses assumed that species from all five genera would compete with one another. This explanation fits with the analyses of Davis (2005) which showed habitat filtering, but only within the genus *Marmota*.

Together, the results of this method and those of my previous studies suggest that morphology is highly conserved within macroniches: i.e. the marmot and prairie dog species, ground squirrel species, and chipmunk species all have very similar adaptations to their niches. However, within a whole community, one generally finds overdispersion in both the species' phylogeny and traits, because communities tend to contain a small number of species from each of the three macroniches (see community lists; online supplementary materials in Cooper et al. 2008). This suggests that the macroniches

exist, extrinsic to the taxa. It also suggests a future modelling approach, with low rates of morphological change within macroniches and high rates of morphological change where species move from one macroniche to another.

Another factor that could explain the differences in the results are the different spatial and taxonomic scales of the two methods: Chapter 3 and Cooper et al. (2008) use broader geographic and taxonomic scales than the method described here (areas of assemblage localities versus 1° grid cells, and whole communities versus pairs of species within the same macroniche, which tends to be conserved within genera). However, using finer spatial and taxonomic scales should increase the likelihood of detecting overdispersion and competition (Swenson et al. 2006), whereas the opposite appears to be the case.

The models described above are necessarily simplified versions of how evolution has actually taken place. Each entry in the matrices compares just one species to another species, and thus assumes any trait differences between the two are the result of their pairwise phylogenetic and geographic differences alone. In reality, each species' traits are likely to be affected by a number of other species and reflect the combined effects of competing with all these species. In addition, I assumed that the geographic ranges of the species have remained constant throughout their evolutionary history. This is certainly not true and hence my method may infer competition where there is none, and miss historical competition due to more recent species range shifts. Additionally, factors other than evolutionary history and geographic range overlap are likely to influence morphological trait evolution and may confound the results. For example, environmental conditions can affect species' traits via selection over relatively short

time-scales, e.g. woodrats (*Neotoma cinerea*) have decreased their body-mass in response to climatic warming in only 25,000 years (Smith et al. 1995).

In conclusion, species within the monkey and squirrel clades tend to be more similar than expected by chance, as the overlap between their geographic ranges increases. This suggests that habitat filtering or convergence to similar morphologies is more important than competition in determining their morphological traits, or that competition in these groups is reduced by different, perhaps behavioural, methods.

Chapter 5: What factors shape rates of morphological evolution in mammals?[4]

5.1 Abstract

Understanding why rates of morphological evolution vary is a major goal in evolutionary biology. Classical work suggests that body size, interspecific competition, geographic range size and specialisation may all be important factors and each may increase or decrease rates of evolution. Many phylogenetic comparative methods, however, assume a constant rate of evolution of quantitative characters, which are logarithmically transformed prior to analysis so that rates of proportional change are studied. Here I investigate correlates of proportional evolutionary rates in New World leaf-nosed bats, New World monkeys, Australasian possums and ground squirrels, using phylogenetic comparative methods. I find variation in rates of morphological evolution both among, and within, the study groups. I also find that the most important correlate of the rate of evolution across all the groups is body size. Although large species evolve fastest in all four clades, and there is a non-linear relationship in monkeys and possums, with slowest evolution in species of intermediate size. I also find significant increases in rate with high environmental temperature in bats, and low mass-specific metabolic rate in squirrels. The mechanisms underlying these correlations are uncertain and appear to be size-specific. I conclude that there is significant variation in rates of evolution, but its meaning is not yet clear.

[4] Many of the analyses in this chapter have been published as Cooper, N. and Purvis, A. (in press). What factors shape rates of phenotypic evolution? A comparative study of cranial morphology of four mammalian clades. *Journal of Evolutionary Biology*. N.C. collected the data, performed all the analyses and wrote the manuscript. A.P. supervised.

5.2 Introduction

"It is abundantly evident that rates of evolution vary. They vary greatly from group to group, and even among closely related lineages there may be strikingly different rates. Differences in rates of evolution […] are among the reasons for the great diversity of organisms on the earth."

George Gaylord Simpson (1953)

Rates of morphological evolution vary at all taxonomic levels: mammals have evolved faster than molluscs (Stanley 1973a); within mammals, carnivores have evolved faster than primates (rates of body-mass evolution; Mattila & Bokma 2008); and within primates, Strepsirrhines have evolved faster than Platyrrhines (rates of body-mass evolution; Purvis et al. 2003). Much work has focussed on quantifying rates of evolution (see review in Roopnarine 2003), but our understanding of *why* rates vary is far from complete. There are many longstanding hypotheses regarding the causes of rate variation, including life-history variables (e.g. body size), interactions with other species (e.g. competition), and environmental factors (Darwin 1859; Simpson 1953; Stanley 1973a; 1979). However, these hypotheses were generally based on observational data and most have yet to be investigated in a modern quantitative framework. Here I aim to test some of these classical predictions about rate variation, and the interconnections between the variables involved, in order to improve understanding of evolutionary rates.

In the classical evolutionary literature there are four main hypothesised correlates of morphological evolution: body size, interspecific competition, geographic range size and ecological specialisation (Figure 5.1). Note that where I refer to the "rate of

morphological evolution", I mean the rate of proportional change in morphology, i.e. the rate of change in log-transformed values. Body size is expected to affect rates of morphological evolution because it correlates with almost every aspect of a species' biology (Calder 1984; Figure 5.1). However the direction of this relationship is disputed: Stanley (1979) and Simpson (1953) argued that large species evolve more quickly, possibly because their low population sizes and low fecundity restrict gene flow (Stanley 1979). However, smaller species tend to have faster life-histories, i.e. shorter generation times and shorter lifespans, which are predicted to increase the rate of evolution (Simpson 1953), although he notes that the correlations between evolutionary rates and generation time are often unpredictable.

Each of the other three variables may also, theoretically, either increase or decrease rates of evolution. Competition can cause increased evolution away from the morphology and niche space of a competitor (i.e. character displacement; Dayan & Simberloff 2005). Alternatively it may inhibit the rate of evolution by preventing evolution into very different, already occupied niches, and instead cause species to evolve into niches that are very similar to their original niche, through the increased packing of niche space (de Mazancourt et al. 2008). Stanley (1979) believed species with large geographic ranges would show low rates of evolution, as the opposing forces of gene flow, which he believed would decrease rates, and local selection pressures, which he believed would increase rates, would cancel each other out. Darwin (1859), on the other hand, suggested that morphological evolutionary rates would be higher in widespread species since they would experience differing selection pressures (e.g. different environmental conditions, competitors and predators) across their range. Finally, ecological specialisation may increase rates of morphological evolution into

specialised niches (e.g. in adaptive radiations; Schluter 2000), whereas broadly adapted species may evolve more slowly due to selection for a more generalised morphology (Simpson 1953).

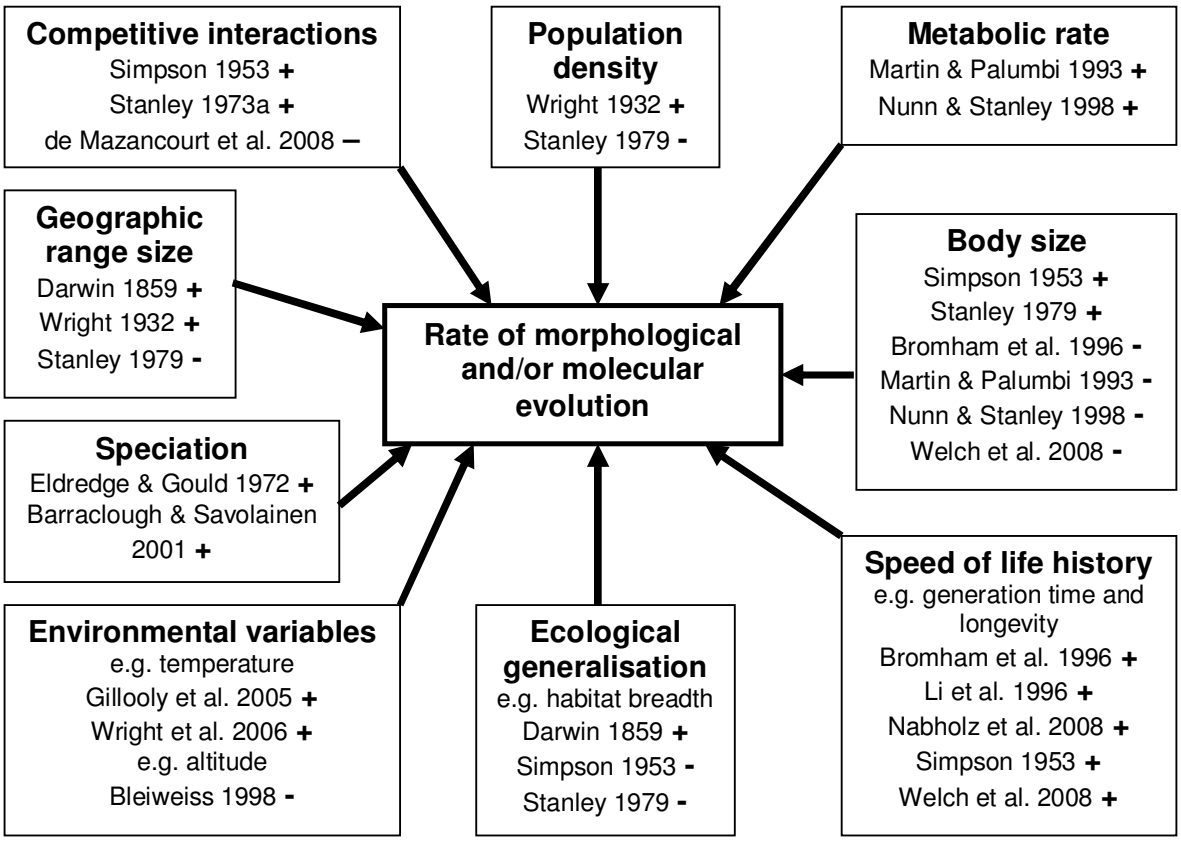


Figure 5.1: Diagram showing the variables which are hypothesised to affect rates of morphological and/or molecular evolution along with selected references for the hypotheses. + = hypothesised positive relationship between the variable and evolutionary rate; - = hypothesised negative relationship between the variable and evolutionary rate. Note that these variables are themselves often interconnected, directly or indirectly, but the relationships between them have been omitted to increase clarity.

All of these variables may interact with one another, and may be jointly influenced by other variables (not shown on Figure 5.1 for clarity). For example, body size is influenced by competitive interactions, predation, sexual selection and environmental variables such as temperature (e.g. Peters 1983; Rodríguez et al. 2008). Body size itself

is a surrogate for, or perhaps a result of, traits which have been hypothesised to influence evolutionary rates, e.g. population density, basal metabolic rate and speed of life-history (Charnov 1993; Kozlowski & Weiner 1997). Some of these variables are also affected by factors which influence body size, e.g. environmental temperature (Gillooly et al. 2001). Geographic range size is influenced by body size, competition and the ecological flexibility of the species involved (Gaston & Blackburn 2000). Species with larger geographic ranges are likely to share their range with more competitors and predators, and are more likely to be habitat (and dietary) generalists, whereas specialists tend to have restricted ranges (Brown 1995). This complexity needs to be considered in analyses of evolutionary rates. In addition to these factors, speciation may also increase rates of morphological evolution if it occurs in a punctuated, rather than a gradual, manner (Eldredge & Gould 1972). However, to investigate whether speciation has an important influence on the rate of morphological evolution it is first necessary to distinguish the evolutionary mode of traits (either punctuated or gradual). Unfortunately it is difficult to distinguish evolutionary mode using present-day data (Bokma 2002), so I do not investigate speciation here.

Recently there has been a growing body of literature on correlates of rates of molecular evolution. Rates of molecular evolution are also known to vary among lineages (Welch et al. 2008), the most famous examples being “slow” primates (especially hominoids) and “fast” rodents (Li et al. 1996). Many explanations for this rate heterogeneity have been proposed (see Figure 5.1 for a summary), and these overlap with the morphological rate correlates discussed above, although the predictions are not always the same (see below and Figure 5.1). Again, small body size is predicted to increase rates of evolution, since smaller species have shorter generation times, higher mass-

specific metabolic rates (BMR) and shorter lifespans. Each of these factors is thought to increase mutation rates and hence evolutionary rates (Bromham et al. 1996; Li et al. 1996; Martin & Palumbi 1993; Nabholz et al. 2008). In the molecular literature, high environmental temperatures are also expected to increase rates of molecular evolution since they may (though not necessarily in endotherms) increase individual growth rates, shorten generation times and increase BMR (Bromham & Cardillo 2003; Gillooly et al. 2001; Wright et al. 2006). Rates of molecular evolution are also correlated with rates of diversification (Barraclough & Savolainen 2001). Since all morphological traits must have some genetic underpinning, it follows that there must be some, albeit very complex, connection between rates of morphological and molecular evolution (even though molecular and morphological rates are rarely directly correlated; Bromham et al. 2002; Davies & Savolainen 2006). Therefore, I can test hypotheses in this study of rates of morphological evolution from both the recent molecular and classical morphological literature.

Here I disentangle some of these predictions about why rates of evolution vary and investigate how the factors discussed above and shown in Figure 5.1 are interconnected. I investigate whether body size (and, where the data are available, the variables which are predicted to explain the effects of body size, e.g. BMR, population density, generation time and longevity), ecological generalisation, interspecific competition, geographic range size and environmental temperature, are correlated with rates of morphological evolution in mammals. I analyse each predictor's effect individually, and in multiple regressions with the other variables, using phylogenetic generalised linear models (PGLM; Freckleton et al. 2002) to control for the effects of phylogeny. Mammals are an ideal clade on which to test these hypotheses because I have life-

history, ecological and geographic range data for many extant species (see Chapter 2) and an almost complete species-level phylogeny (Bininda-Emonds et al. 2007; 2008). In addition, most of the literature discussed above used mammals as a study group. This kind of analysis requires a well-resolved phylogeny and high quality, specimen-level morphometric data on species' morphological traits with dense taxon-sampling. My four study clades (New World leaf-nosed bats: Phyllostomidae; New World monkeys: Platyrrhini; Australasian possums: Phalangeriformes; and ground squirrels: Marmotini) meet all these criteria and are, therefore, ideal groups to work on.

5.3 Methods

DATA

Morphological traits

Traits were collected and checked for errors as described in Chapter 2: sections 2.3-2.5. I extracted the species' means of each trait for each species then natural-log transformed them to normalise their distributions and to fit with the idea that growth is multiplicative. The null model used throughout is the Brownian motion model of character evolution, fitted to log-transformed data; this model is also referred to as "log-Brownian".

Phylogeny

The phylogenies used are described in Chapter 2: section 2.9 and each was completely resolved. In the Bininda-Emonds et al. (2007; 2008) supertree, the relationship among the genera *Cynomys*, *Marmota* and *Spermophilus* is unresolved. I created three new phylogenies, one for each possible resolution of the polytomy, and analysed each in turn. The topology used had no qualitative influence on the results (Tables 5.5-5.7 and

Table 5.9), so I focus on results for the *Cynomys* outgroup tree although all results are presented for comparison.

Relative rates of evolution

In order to calculate a measure of the relative rate of evolution, I first created Euclidean distance matrices for each clade using the species' means of all the traits (see Chapter 2: section 2.3). I used all traits combined so that the correlates I obtained would represent more general patterns of evolution in the groups, rather than correlates of just one specific trait. The Euclidean distance matrices for each clade were then used to provide morphological branch lengths for the phylogenies described above, by setting the phylogenetic topology as a constraint tree and optimising the distance matrix along it using minimum evolution in PAUP*4.0 (Swofford 2002). This resulted in a non-ultrametric tree for each study clade. We define the relative rate of morphological evolution for a particular species within a clade as the root-to-tip distance for that species using these optimised phylogenies. The morphological distance between two species is the result of the time they have been evolving, and differences in their rate of evolution. Since all the species within a study clade are extant and share a common ancestor, they have all had the same amount of time to evolve. Therefore, time is a constant in these analyses, and any differences between the root-to-tip distances of the species within a clade represent differences in the rate of change in morphology of the species.

Other traits

Adult body-mass (g), mass-specific basal metabolic rate ($mLO_2hr^{-1}g^{-1}$), gestation length (days), maximum longevity (months), population density (individuals per km^2), geographic range size (km^2) and mean annual temperature across the geographic range

(ºC) were taken from PanTHERIA (Jones et al. in press). I filled gaps using some other sources (Appendix A4). As a proxy for the intensity of competition, I calculated the mean number of potential competitors (defined as species within the same macroniche; Chapter 2: section 2.4 and Eisenberg 1981) per 1º grid cell across the species' geographic range. I also created an index of ecological generalisation/specialisation, defined as the habitat breadth of the species multiplied by its diet breadth. Habitat breadth was the number of WWF biomes (Olson et al. 2001) within which the species occurred, and diet breadth was the number of different food types eaten (from vertebrates/invertebrates/fruit/flowers, nectar and pollen/seeds/grass/leaves, branches and bark/roots and tubers: Jones et al. in press). An increase in either value represents increasing generalisation. Unfortunately data on every variable were not available for each clade. Table 5.1 shows the number of species with values for each variable within the four clades.

ANALYSES

All analyses were carried out in R version 2.6.2 (R Development Core Team 2008). Most variables were natural-log transformed to normalise their distributions and improve model diagnostics, with the following exceptions where I used different transformations which improved model diagnostics more than natural-log transforms: inverse transformed relative rate of evolution^{-1} (bats and possums), inverse transformed gestation length (bats), inverse transformed longevity (bats and monkeys), square root transformed geographic range size (bats), square root transformed number of competitors (bats and possums), untransformed number of competitors (monkeys and squirrels), square root transformed generalisation index (squirrels).

Table 5.1: Number of species with records for given variables for each clade. bats = Phyllostomidae; monkeys = Platyrrhini; possums = Phalangeriformes; squirrels = Marmotini. BMR = mass-specific basal metabolic rate; Competition = average number of competitors per 1º grid cell across the specie's range; Generalisation = habitat breadth*diet breadth.

	bats	**monkeys**	**possums**	**squirrels**
Total clade size	88	72	30	73
Body-mass	88	71	28	65
BMR	25	8	8	23
Population density	0	51	12	32
Gestation length	15	42	4	46
Longevity	11	49	12	24
Temperature	85	69	29	64
Competition	87	69	29	73
Geographic range	87	69	29	73
Generalisation	87	69	29	73

Correlates of relative rates of evolution

I performed all analyses using phylogenetic generalised linear models (PGLM; Freckleton et al. 2002) using the R package CAIC (available at https://r-forge.r-project.org/projects/caic) to account for the non-independence introduced because close relatives tend to be similar due to shared common ancestry (Harvey & Pagel 1991). The PGLM method is equivalent to the phylogenetic generalised least-squares (PGLS) approach and is based on the usual generalised least-squares (GLS) model except that the phylogenetic dependence of the data is incorporated into structure of the error term (Freckleton et al. 2002; Pagel 1999; Rohlf 2001). This error term consists of a matrix of expected trait covariances calculated using the maximum-likelihood (ML) estimate of λ. λ is a multiplier of the off-diagonal elements of a phylogenetic variance-covariance matrix that best fits the data, and varies between $\lambda = 1$, where the data are structured

according to a Brownian motion model of trait evolution, and $\lambda = 0$, where the data have no phylogenetic structure (Pagel 1999). For each regression, the ML estimate of λ is calculated along with the other regression parameters, thus the regressions are carried out whilst controlling for the actual degree of phylogenetic non-independence that is present (rather than assuming complete phylogenetic dependence, as in independent contrasts, or phylogenetic independence, as in non-phylogenetic regressions).

I first used single predictor PGLM regressions to investigate the effects of body-mass, gestation length, BMR, longevity, geographic range size, environmental temperature, degree of generalisation and number of competitors, on the relative rate of morphological evolution. I also looked for non-linear relationships by including the square of each variable. I only carried out regressions where I had ten or more degrees of freedom (see Table 5.1).

PGLM is a generalisation of the independent contrasts method (Rohlf 2006), and its performance is therefore likely to be reduced if the pattern of trait variation among species departs strongly from the assumed random-walk model. This can result in points with very high leverage that could affect the parameter estimates and increase the error rates of the regressions. To avoid this heteroscedasticity (Diaz-Uriarte & Garland 1996), I therefore repeated the regressions after removing any highly influential points (i.e. those with a studentised residual exceeding ±3; Jones & Purvis 1997). Deletion of points did not make a qualitative difference to any of the results, so I only report results after deletion to improve the clarity of the tables.

Before building multivariate models I checked the predictors for collinearity (following the method of Belsey et al. 1980) because it can lead to unreliable model parameter estimates. I found collinearity (i.e. variance inflation factors greater than 3) among the following variables. In bats, temperature was collinear with geographic range size; in possums, temperature, geographic range size, and generalisation were all collinear with one another, and in monkeys, body-mass was collinear with mass-specific metabolic rate. These combinations of variables were therefore not entered into the best model analyses (see below). All other combinations of variables had variance inflation factors below three and condition indices below nine (Belsey et al. 1980).

Since I had too few degrees of freedom (see Table 5.1) to fit minimum adequate models, I instead fit every possible model for each clade given the following rules: (1) none of the variables could be collinear; (2) there were at least ten data points per parameter; and (3) any influential observations (see above) were removed. The most complex models contained three variables and all possible interaction terms. Since missing values prevented the use of AIC values in model selection, I instead defined the best model as the model with the highest adjusted-r^2, where all predictors and interaction terms were significant ($p < 0.05$).

Node density effect

The node density effect (NDE) is an artefact of the way trees are constructed which can lead to greater root-to-tip lengths in clades with more terminal taxa (Fitch & Bruschi 1987; Venditti et al. 2006). This occurs because when branch lengths are calculated during tree building, it is likely that multiple DNA sequence changes along a long unbroken branch will remain undetected, but might be revealed if the branch is subdivided by increasing the number of species, and hence nodes, which subtend from

the branch. This may affect the analyses since I use root-to-tip distances to calculate the relative rate of morphological evolution. If the NDE is problematic in this study, there will be a significant positive curvilinear relationship between the number of nodes crossed and the root-to-tip length. I tested each of my trees for such a curvilinear relationship using the "delta" test of Venditti et al. (2006), as implemented online at www.evolution.reading.ac.uk (Venditti et al. 2008). The NDE is indicated if the strength of the relationship (β) is significantly greater than zero, and the curvature of the relationship (δ) is significantly greater than unity.

5.4 Results

Correlates of relative rates of evolution

Differences in the relative rates of evolution (i.e. root-to-tip distances) among the subgroups within each clade are shown in Figures 5.3. There appears to be marked variation within the groups.

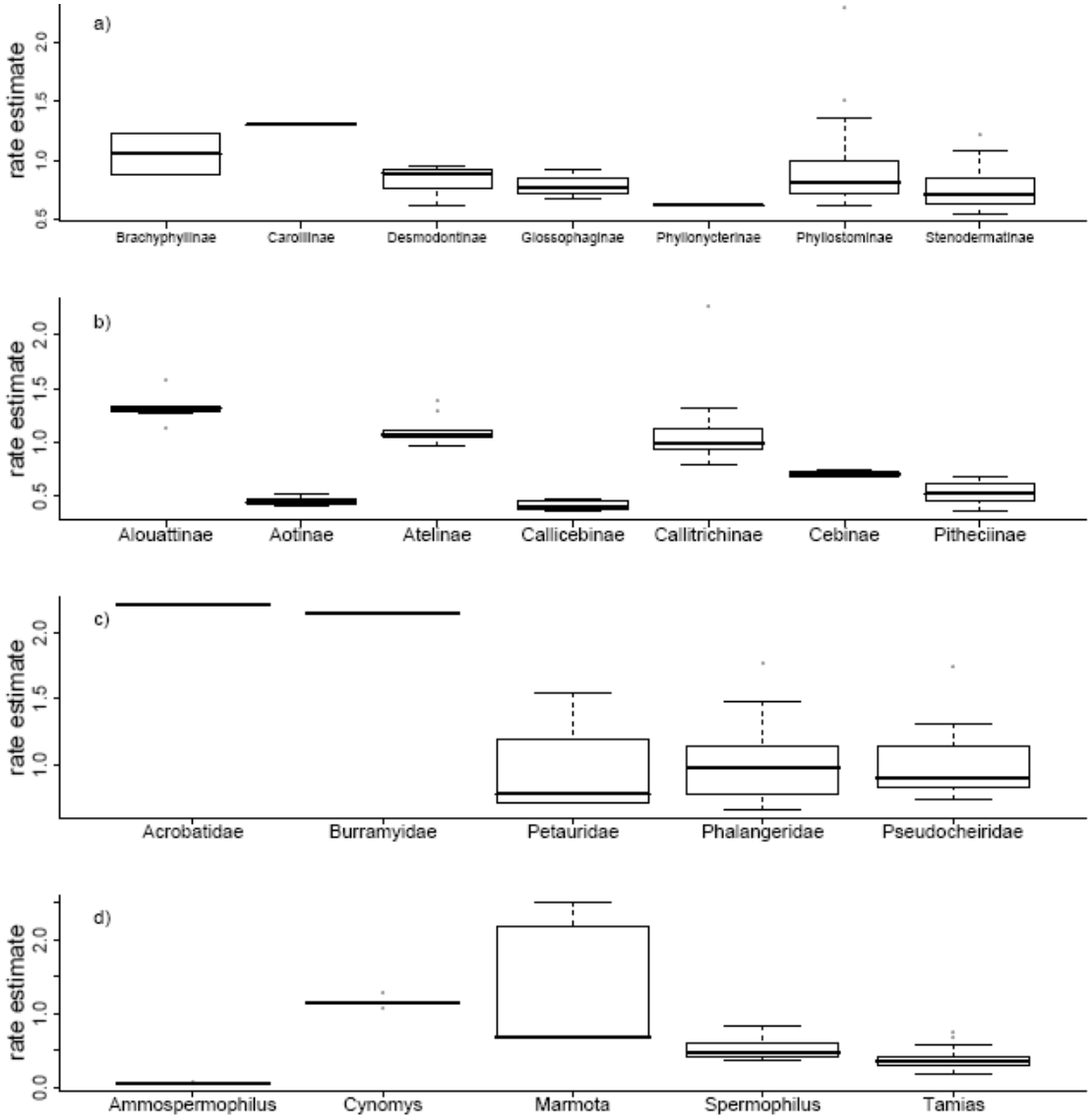


Figure 5.2: Box and whisker plots showing how relative rates of evolution vary among and within: (a) bat (Phyllostomidae) subfamilies; (b) monkey (Platyrrhini) subfamilies; (c) possum (Phalangeriformes) families; and (d) squirrel (Marmotini) genera. Bold line = median; box = interquartile range; whiskers = 1.5*interquartile range; points = outliers.

Results of single predictor phylogenetic generalised linear models (PGLM) predicting differences in rates of evolution are shown in Tables 5.2-5.7. All four clades showed significant correlations between rate and body-mass either linearly, such that large species evolved fastest (bats: $r^2 = 0.087$; squirrels: $r^2 = 0.211$), or non-linearly, such that small and large species evolved fastest (bats: $r^2 = 0.270$; monkeys: $r^2 = 0.440$; possums:

$r^2 = 0.451$). Rates in both bats and squirrels were also correlated with BMR (bats: non-linearly with high rates at low and high BMR: $r^2 = 0.248$; squirrels: negatively, $r^2 = 0.379$; and non-linearly with high rates at low and high BMR, $r^2 = 0.509$). Other variables were significant predictors in only one clade, e.g. environmental temperature (bats; non-linearly with highest rates at mid-range temperatures, $r^2 = 0.095$); number of competitors (monkeys; non-linearly with highest rates for either many or few competitors, $r^2 = 0.078$), geographic range size (monkeys; positively, $r^2 = 0.217$), and gestation length (squirrels; non-linearly with highest rates at mid-range gestation lengths, $r^2 = 0.087$). The squirrel phylogeny used made very slight qualitative or quantitative difference to the results (Tables 5.5-5.7): there were no significant non-linear relationships between rate and gestation length, but there were significant negative correlations between rate and temperature.

The best models for predicting each clade's relative rate of evolution are shown in Tables 5.8 and 5.9. Body size is a significant correlate in each clade, either linearly (squirrels: positive correlation, $r^2 = 0.467$) or non-linearly (bats: positive correlation, $r^2 = 0.341$; monkeys and possums: highest rates in the smallest and largest species, $r^2 = 0.440$ and $r^2 = 0.451$). In bats, high relative rates of evolution are also associated with high environmental temperatures and there is a significant negative interaction between body-mass and environmental temperature. In squirrels, high rates were also correlated with low BMR. The squirrel phylogeny used made no qualitative, and very little quantitative, difference to the results (Table 5.9). The value of λ for the four best models varied between 0.495 in bats and 0.768 in possums, to $\lambda > 0.950$ in monkeys and squirrels.

Table 5.2: Results from PGLM regressions of various predictors on the rate of morphological evolution in bats (Phyllostomidae). BMR = mass-specific basal metabolic rate; GestationL = gestation length; Competition = average number of competitors per grid cell across the specie's range; GR = geographic range size; Generalisation = habitat breadth*diet breadth. *p < 0.05, **p < 0.01, ***p < 0.001.

predictor	λ	slope ± se	d.f.	t	r^2
Body-mass	0.636	0.126 ± 0.044	85	2.838**	0.087
Body-mass &	0.561	-1.115 ± 0.258 &	76	-4.324*** &	0.270
Body-mass^2		0.190 ± 0.040		4.759***	
BMR	< 0.001	-0.227 ± 0.163	23	-1.394	0.078
BMR	< 0.001	-1.093 ± 0.417 &	22	-2.623* &	0.248
BMR^2		0.980 ± 0.439		2.229*	
GestationL	< 0.001	19.30 ± 41.88	13	0.461	0.016
GestationL	< 0.001	-47.88 ± 425.8 &	12	-0.112 &	0.018
GestationL^2		-4945 ± 31180		-0.159	
Temperature	0.746	-0.283 ± 0.353	80	-0.802	0.008
Temperature &	0.766	123.8 ± 45.36 &	80	2.730** &	
Temperature^2		-11.49 ± 4.196		-2.737**	0.095
Competition	0.593	-0.038 ± 0.032	82	-1.175	0.017
Competition &	0.715	-0.117 ± 0.115 &	84	-1.015 &	0.014
Competition^2		0.020 ± 0.023		0.854	
GR	0.684	< 0.001 ± < 0.001	79	1.425	0.025
GR &	0.703	< 0.001 ± < 0.001 &	78	0.130 &	0.034
GR^2		< 0.001 ± < 0.001		0.289	
Generalisation	0.702	0.003 ± 0.058	81	0.060	< 0.001
Generalisation &	0.768	0.226 ± 0.273 &	83	0.829 &	0.008
Generalisation^2		-0.050 ± 0.061		-0.820	

Table 5.3: Results from PGLM regressions of various predictors on the rate of morphological evolution in monkeys (Platyrrhini). BMR = mass-specific basal metabolic rate; PopDensity = population density; GestationL = gestation length; Competition = average number of competitors per grid cell across the specie's range; GR = geographic range size; Generalisation = habitat breadth*diet breadth. *p < 0.05, ***p < 0.001. †Longevity & Longevity^2 result is not shown as the solution is computationally singular.

predictor	λ	slope ± se	d.f	t	r^2
Body-mass	1.000	0.046 ± 0.062	69	0.733	0.008
Body-mass &	0.968	-2.546 ± 0.359 &	69	-7.097*** &	0.440
Body-mass^2		0.182 ± 0.025		7.264***	
PopDensity	1.000	0.003 ± 0.024	49	0.138	< 0.001
PopDensity &	1.000	0.081 ± 0.101 &	48	0.800 &	0.013
PopDensity^2		-0.012 ± 0.016		-0.790	
GestationL	1.000	0.093 ± 0.266	40	0.351	0.003
GestationL &	1.000	-13.26 ± 16.03 &	39	-0.827 &	0.021
GestationL^2		1.307 ± 1.569		0.833	
Longevity†	1.000	-15.94 ± 30.302	47	-0.526	0.006
Temperature	1.000	-0.170 ± 0.288	65	-0.590	0.005
Temperature &	0.988	1.403 ± 15.11 &	65	0.093 &	0.046
Temperature^2		-0.171 ± 1.388		-0.123	
Competition	0.975	-0.003 ± 0.006	66	-0.540	0.004
Competition &	0.971	-0.048 ± 0.020 &	66	-2.360* &	0.078
Competition^2		0.003 ± 0.001		2.286*	
GR	1.000	0.019 ± 0.004	66	4.279***	0.217
GR &	1.000	0.019 ± 0.119 &	64	0.156 &	0.010
GR^2		< 0.001 ± 0.005		-0.097	
Generalisation	1.000	0.003 ± 0.023	65	0.131	< 0.001
Generalisation &	0.982	< 0.001 ± 0.111 &	65	-0.004 &	0.014
Generalisation^2		0.005 ± 0.026		0.203	

Table 5.4: Results from PGLM regressions of various predictors on the rate of morphological evolution in possums (Phalangeriformes). BMR = mass-specific basal metabolic rate; PopDensity = population density; Competition = average number of competitors per grid cell across the specie's range; GR = geographic range size; Generalisation = habitat breadth*diet breadth. ***p < 0.001.

predictor	λ	slope ± se	d.f.	t	r^2
Body-mass	0.695	-0.098 ± 0.050	26	-1.950	0.128
Body-mass &	0.768	-1.118 ± 0.267 &	25	-4.182*** &	0.451
Body-mass^2		0.084 ± 0.022		3.858***	
PopDensity	< 0.001	0.011 ± 0.055	10	0.206	0.004
PopDensity &	< 0.001	0.296 ± 0.260 &	9	1.140 &	0.126
PopDensity^2		-0.033 ± 0.029		-1.121	
Longevity	< 0.001	-0.215 ± 0.132	10	-1.635	0.211
Longevity &	< 0.001	-3.034 ± 2.100 &	9	-1.445 &	0.343
Longevity^2		0.327 ± 0.243		1.345	
Temperature	0.693	-0.236 ± 0.362	27	-0.652	0.015
Temperature &	< 0.001	20.86 ± 22.08 &	26	0.945 &	0.041
Temperature^2		-1.980 ± 2.077		-0.954	
Competition	0.701	0.012 ± 0.067	28	0.180	0.001
Competition &	0.660	-0.136 ± 0.226 &	27	-0.601 &	0.018
Competition^2		0.059 ± 0.087		0.680	
GR	0.786	0.026 ± 0.028	28	0.929	0.030
GR &	0.818	0.005 ± 0.244 &	27	0.022 &	0.031
GR^2		0.001 ± 0.011		0.088	
Generalisation	0.825	0.066 ± 0.048	28	1.385	0.064
Generalisation &	0.825	0.049 ± 0.151 &	27	0.326 &	0.065
Generalisation^2		0.005 ± 0.042		0.118	

Table 5.5: Results from PGLM regressions of various predictors on the rate of morphological evolution in squirrels (Marmotini) using the *Cynomys* outgroup phylogeny. BMR = mass-specific basal metabolic rate; PopDensity = population density; GestationL = gestation length; Competition = average number of competitors per grid cell across the specie's range; GR = geographic range size; Generalisation = habitat breadth*diet breadth. *p < 0.05, **p < 0.01, ***p < 0.001. †Longevity & Longevity^2 result is not shown as the solution is computationally singular.

predictor	λ	slope ± se	d.f	t	r^2
Body-mass	0.994	0.301 ± 0.073	63	4.100***	0.211
Body-mass &	0.980	0.700 ± 0.397 &	62	1.763 &	0.192
Body-mass^2		-0.033 ± 0.029		-1.143	
BMR	1.000	-1.093 ± 0.305	21	-3.582**	0.379
BMR	1.000	0.031 ± 0.562 &	20	0.056 &	0.509
BMR^2		0.940 ± 0.408		2.302*	
PopDensity	1.000	-0.041 ± 0.055	30	-0.740	0.018
PopDensity &	1.000	-0.123 ± 0.239 &	29	-0.515 &	0.022
PopDensity^2		0.007 ± 0.020		0.354	
GestationL	1.000	0.011 ± 0.650	44	0.017	< 0.001
GestationL &	1.000	34.63 ± 17.14 &	43	2.020* &	0.087
GestationL^2		-5.032 ± 2.491		-2.020*	
Longevity†	1.000	0.430 ± 0.390	22	1.103	0.052
Temperature	1.000	-0.124 ± 0.063	57	-1.959	0.063
Temperature &	1.000	0.001 ± 0.454 &	56	0.003 &	0.064
Temperature^2		-0.015 ± 0.055		-0.280	
Competition	0.999	-0.048 ± 0.035	67	-1.365	0.027
Competition &	1.000	0.007 ± 0.113 &	66	0.061 &	0.009
Competition^2		-0.008 ± 0.026		-0.309	
GR	1.000	0.015 ± 0.010	68	1.447	0.030
GR &	1.000	-0.086 ± 0.115 &	65	-0.749 &	0.023
GR^2		0.004 ± 0.005		0.836	
Generalisation	1.000	0.016 ± 0.037	68	0.419	0.003
Generalisation &	1.000	-0.287 ± 0.335 &	69	-0.858 &	0.015
Generalisation^2		0.061 ± 0.067		0.915	

Table 5.6: Results from PGLM regressions of various predictors on the rate of morphological evolution in squirrels (Marmotini) using the *Marmota* outgroup phylogeny. BMR = mass-specific basal metabolic rate; PopDensity = population density; GestationL = gestation length; Competition = average number of competitors per grid cell across the specie's range; GR = geographic range size; Generalisation = habitat breadth*diet breadth. *p < 0.05, **p < 0.01, ***p < 0.001. †Longevity & Longevity^2 result is not shown as the solution is computationally singular.

predictor	λ	slope ± se	d.f	t	r^2
Body-mass	0.975	0.329 ± 0.077	61	4.256***	0.229
Body-mass &	0.989	0.759 ± 0.456 &	57	1.663 &	0.217
Body-mass^2		-0.035 ± 0.034		-1.040	
BMR	1.000	-1.119 ± 0.306	21	-3.650**	0.388
BMR	1.000	-0.023 ± 0.569 &	20	-0.040 &	0.509
BMR^2		0.911 ± 0.411		2.214*	
PopDensity	1.000	-0.039 ± 0.058	30	-0.679	0.015
PopDensity &	1.000	-0.113 ± 0.243 &	29	-0.466 &	0.018
PopDensity^2		0.006 ± 0.020		0.315	
GestationL	1.000	0.023 ± 0.658	44	0.035	< 0.001
GestationL &	1.000	33.71 ± 17.62 &	43	1.913 &	0.078
GestationL^2		-4.894 ± 2.558		-1.913	
Longevity†	1.000	0.408 ± 0.415	22	0.982	0.042
Temperature	1.000	-0.154 ± 0.060	58	-2.547*	0.101
Temperature &	1.000	0.216 ± 0.382 &	57	0.564 &	0.116
Temperature^2		-0.044 ± 0.045		-0.979	
Competition	0.993	-0.033 ± 0.038	68	-0.863	0.011
Competition &	0.989	-0.048 ± 0.131 &	63	-0.364 &	0.014
Competition^2		0.002 ± 0.029		0.067	
GR	0.999	0.021 ± 0.010	67	2.027	0.058
GR &	0.999	-0.100 ± 0.122 &	66	-0.820 &	0.066
GR^2		0.005 ± 0.006		0.988	
Generalisation	1.000	0.048 ± 0.032	71	1.484	0.030
Generalisation &	1.000	-0.275 ± 0.324 &	70	-0.849 &	0.044
Generalisation^2		0.064 ± 0.064		1.003	

Table 5.7: Results from PGLM regressions of various predictors on the rate of morphological evolution in squirrels (Marmotini) using the *Spermophilus* outgroup phylogeny. BMR = mass-specific basal metabolic rate; PopDensity = population density; GestationL = gestation length; Competition = average number of competitors per grid cell across the specie's range; GR = geographic range size; Generalisation = habitat breadth*diet breadth. *p < 0.05, **p < 0.01, ***p < 0.001. †Longevity & Longevity^2 result is not shown as the solution is computationally singular.

predictor	λ	slope ± se	d.f	t	r^2
Body-mass	0.981	0.293 ± 0.075	61	3.901***	0.200
Body-mass &	0.996	0.714 ± 0.395 &	59	1.810 &	0.181
Body-mass^2		-0.035 ± 0.029		-1.233	
BMR	1.000	-1.088 ± 0.306	21	-3.549**	0.375
BMR	1.000	0.015 ± 0.563 &	20	0.027 &	0.502
BMR^2		0.919 ± 0.029		2.257*	
PopDensity	1.000	-0.041 ± 0.055	30	-0.752	0.019
PopDensity &	1.000	-0.125 ± 0.234	29	-0.537 &	0.023
PopDensity^2		0.007 ± 0.019		0.371	
GestationL	1.000	-0.033 ± 0.642	44	-0.052	< 0.001
GestationL &	1.000	34.27 ± 17.32 &	43	1.979 &	0.084
GestationL^2		-4.982 ± 2.513		-1.982	
Longevity†	1.000	0.446 ± 0.387	22	1.154	0.057
Temperature	1.000	-0.122 ± 0.058	62	-2.105*	0.067
Temperature &	1.000	0.119 ± 0.372 &	61	0.319 &	0.073
Temperature^2		-0.030 ± 0.046		-0.654	
Competition	0.998	-0.029 ± 0.035	71	-0.843	0.010
Competition &	1.000	0.020 ± 0.108 &	69	0.186 &	0.011
Competition^2		-0.011 ± 0.024		-0.455	
GR	1.000	0.020 ± 0.012	68	1.761	0.044
GR &	1.000	-0.090 ± 0.110 &	70	-0.815 &	0.048
GR^2		0.005 ± 0.005		0.960	
Generalisation	1.000	0.025 ± 0.043	68	0.575	0.005
Generalisation &	1.000	-0.200 ± 0.326 &	67	-0.613 &	0.012
Generalisation^2		0.045 ± 0.065		0.695	

Table 5.8: Best models from a set of all possible models (see text) predicting the relative rate of morphological evolution in four clades. bats = Phyllostomidae; monkeys = Platyrrhini; possums = Phalangeriformes; BM = body-mass; Temp = temperature. *p < 0.05, **p < 0.01, ***p < 0.001.

	bats		**monkeys**		**possums**	
	d.f.	80	**d.f.**	69	**d.f.**	25
	λ	0.495	**λ**	0.968	**λ**	0.768
	adjusted r^2	0.341	**adjusted r^2**	0.440	**adjusted r^2**	0.451
	log likelihood	7.736	**log likelihood**	27.00	**log likelihood**	-3.157
predictor	**slope ± se**	**t**	**slope ± se**	**t**	**slope ± se**	**t**
BM	7.367 ± 3.173	2.322*	-2.546 ± 0.359	-7.097***	-1.118 ± 0.267	-4.182***
BM^2	0.192 ± 0.039	4.964***	0.182 ± 0.025	7.264***	0.084 ± 0.022	3.858***
Temp	4.239 ± 1.749	2.423*	-	-	-	-
BM:Temp	-1.552 ± 0.582	-2.668**	-	-	-	-

Table 5.9: Best models from a set of all possible models (see text) predicting the relative rate of morphological evolution in squirrels (Marmotini) using three different phylogenetic topologies. BM = body-mass; BMR = mass-specific basal metabolic rate. *p < 0.05.

	***Cynomys* outgroup**		***Marmota* outgroup**		***Spermophilus* outgroup**	
	d.f.	20	**d.f.**	20	**d.f.**	20
	λ	1.000	**λ**	1.000	**λ**	1.000
	r^2	0.467	**r^2**	0.472	**r^2**	0.455
	log likelihood	-16.29	**log likelihood**	-16.64	**log likelihood**	-16.47
predictor	**slope ± se**	**t**	**slope ± se**	**t**	**slope ± se**	**t**
BM	0.265 ± 0.112	2.369*	0.275 ± 0.117	2.345*	0.262 ± 0.115	2.284*
BMR	-0.817 ± 0.300	-2.723*	-0.829 ± 0.304	-2.722*	-0.825 ± 0.302	-2.727*

Node density effect

There was no evidence of the node density effect (NDE) in any of the four study clades (all clades: β significantly < 0; all clades: δ significantly < 1.000)

5.5 Discussion

Rates of morphological evolution vary both within and among the four study clades, even within the more taxonomically-restricted squirrels. For each clade, 34-47% of the variation in rate can be explained by just a few predictors, one of which is always body size. High environmental temperatures in bats, and low mass-specific basal metabolic rates (BMR) in squirrels, are also associated with high rates of morphological evolution in the best models.

Body size is the most commonly-hypothesised correlate of rate variation in the literature, but the proposed direction of this relationship differs between morphological (positive) and molecular (negative) studies, e.g. Simpson (1953) versus Bromham et al. (1996). My results suggest that both may be correct: in the best models, two of the clades (monkeys and possums) show a strong non-linear relationship between the rate of morphological evolution and body size, with the highest rates in large and small species. The other two clades show faster evolution in larger species (bats and squirrels). The different patterns in the four clades are not due to differences in the body-mass range of each clade since, although the bats are smaller than the other three clades, the squirrels have a similar body-mass range to that of the monkeys and possums which show a non-linear relationship between body-mass and rate. This indicates that body size, or one of its correlates, is very important in determining rates of morphological evolution, but that the mechanism behind the relationship between body-mass and the rate of morphological evolution is probably different for the different clades.

Large body size is predicted to increase rates of morphological evolution because large species should have low population densities and hence reduced gene flow compared to smaller species (Stanley 1979). In squirrels, the large species also live in burrows and are highly philopatric (Solomon 2003) which may further reduce gene flow (see below). However, population density was not a significant correlate of rate in any clade, though present-day abundance may be a very poor reflection of abundance through evolutionary history. In addition, although larger species have lower population sizes, they are also better dispersers (Van Vuren 1998) which could ameliorate any reduction in gene flow caused by low abundance. Furthermore, although smaller populations are traditionally thought to evolve more quickly due to enhanced rates of fixation, in reality these rates are not much higher than those of large populations and, since large populations will have more mutations, morphological evolution should actually be faster in large, not small, populations (Price et al. 2009). If I do not accept the explanation of restricted gene flow (except perhaps in Marmotini; see below), why do large species evolve faster in the clades I studied? Since body size correlates with most species' traits (Calder 1984), its significance in the models may represent some other variable, either an ecological trait for which I had too little data, or variables I did not include. One possibility is that large species have larger home ranges than smaller species (Eisenberg 1981) which could result in individuals of larger species encountering more varied selection pressures (in terms of the environment, predators, competitors etc.) than those of smaller species. Such individual-based variation in selection pressures would not necessarily be picked up by the geographic range variable. Alternatively, this result may be related to speciation rates (if most evolution occurs at speciation events, i.e. is punctuated rather than gradual), since large mammals

may have slightly higher origination rates than small mammals (Liow et al. 2008), though this effect would be weak.

Understanding the mechanisms behind the correlation between rate and small body size is equally complex. Small species are predicted to evolve faster than large species because they have a faster speed of life-history, which increases the number of opportunities for mutation and selection (Bromham et al. 1996). However, apart from in the squirrels, none of the life-history speed variables (BMR, longevity, and gestation length) appeared in the best models. This could be because the small number of species in some models reduced the power of the analyses, or perhaps reflects a missing variable, for example, small species are worse dispersers than large species (Van Vuren 1998), and have smaller home ranges (Eisenberg 1981), which may restrict their gene flow enough to increase rates of morphological evolution.

Interestingly, the lowest rates of morphological evolution in each clade occur round the median body-mass for that clade. This suggests that there may be some kind of buffering effect of species diversity in all four clades (de Mazancourt et al. 2008). If one assumes that the body-mass of a species is a good indicator of its niche, this would mean that species close to the modal body-mass are unable to evolve a very different body-mass/niche because their niche space is restricted by competition with the many other species with similar body-masses/niches. Larger species (and also smaller species in monkeys and possums) may be less restricted as there are fewer species with the same body size to restrict their diversification, which would explain their higher rates of morphological evolution.

The bat model supports another prediction of the molecular literature: high rates of morphological evolution in bats are correlated with high environmental temperatures. There was also a negative interaction between environmental temperature and body size in the best bat model, such that, for a given environmental temperature, smaller bats evolve faster than larger ones. External temperatures are probably particularly important to bats, as the high metabolic costs of flight mean that thermoregulation is difficult. This result may also reflect the fact that at high latitudes bats tend to hibernate which slows their already slow life-history, and slow life-history characteristics are predicted to reduce rates of molecular evolution (Welch et al. 2008). In addition, environmental temperature is predicted to increase rates of molecular evolution by shortening generation-times and increasing BMR, even in endotherms (Gillooly et al. 2001), and since high BMR was quite strongly associated with high rates of morphological evolution ($r^2 = 0.248$) in the bat PGLM (though not in the best model for bats), this is a possible mechanism. However, this relationship was non-linear; low BMR was also correlated with high rates, perhaps because large species have low BMR.

In squirrels, the best model for predicting the rate of morphological evolution indicated that large species with low mass-specific BMR have the highest rates of evolution. Most previous studies have found a positive correlation between BMR and rate (e.g. Martin & Palumbi 1993), so this negative correlation in squirrels is interesting. It seems likely that some feature of the ecology of large, low BMR squirrels, i.e. marmots and prairie dogs, results in faster rates of morphological evolution. One candidate feature is that all of these species live in burrow systems. The transition to a burrowing lifestyle is thought to have resulted in adaptive radiations of several clades (Nevo 1979), and these burrowing squirrels tend to be highly philopatric (Solomon 2003) which will reduce

dispersal and hence gene flow, perhaps enough to increase the rate of morphological evolution.

Even in the "best" models, over 50% of the variation in rates of morphological evolution in all clades remained unexplained. This may have been due to missing variables. The variation in λ for the best models provides some suggestions as to the kind of variables I may have missed: in monkeys and squirrels, λ was close to unity, indicating that much of the lack-of-fit had a phylogenetic basis. This could be a missing life-history variable, or some aspect of the species' biogeography. The bat and possum models, on the other hand, had lower λ values suggesting that there may be missing ecological variables. Additionally, the power to detect relationships may have been low due the small number of species in some models, or perhaps correlates of morphological rates are highly idiosyncratic. This is likely since, in theory, all of the major correlates can both negatively and positively affect rates of morphological evolution. If these variations operate at the species-level then it is not surprising that I do not find many group-wide correlations. Another problem is the measure of rate, which reduces morphological differences in size and shape to one number. If size and shape have different evolutionary drivers I would find it hard to detect correlates with this method. Additionally, in studies of molecular rates, the significant correlates often depend on the gene used (Bromham et al. 1996); likewise in morphological studies the correlates may depend on the traits used. Mammalian cranial characters are generally thought to be under stabilising selection (Lynch 1990) and conserved phylogenetically, due to their functional complexity (Caumul & Polly 2005), which could account for the low number of correlations between the predictors and rate. However, factors such as dietary adaptations are known to influence skull shape and size in squirrels and monkeys

(Caumul & Polly 2005; Marroig & Cheverud 2001), suggesting that there is meaningful rate variation and it may be predictable, but I would need more predictors and/or data to understand it. More careful identification of the factors which shape morphological evolution in each group may provide a clearer understanding of why these rates vary. Finally, as in nearly all comparative analyses, I have used species' mean values for all the traits and thus ignored intraspecific variation. This was unavoidable due to data limitations and because it is difficult to handle such variation within the same framework (but see Felsenstein 2008, for recent developments). It is likely that neglecting this variation reduces the chance of detecting significant effects, especially of variables with high intraspecific variance such as population density. However, this only makes the method more conservative, so does not reduce my confidence in the significant correlations I discovered.

Body size appears to be the most important correlate of morphological evolution in the four mammalian study clades. This supports both classical and more recent predictions since the relationship is non-linear in both monkeys and possums, with highest rates in both small and large species. However, understanding the underlying mechanisms for these correlations is difficult, because variables predicted to underpin these body size correlations (e.g. low population density, fast speed of life-history) were not directly correlated with the rate of morphological evolution. In addition, it seems likely that the mechanisms behind rate variation may depend on the size of the species involved. I conclude therefore, that whilst there is significant variation in rates of morphological evolution, I do not yet know what it means. More study, and data, are needed to untangle the complex interactions among rates of morphological evolution, species' traits, ecology, interspecific interactions and the environment.

Chapter 6: Body size evolution in mammals[5]

6.1 Abstract

Since body size correlates with virtually every aspect of species' biology, investigation into the tempo and mode of body size evolution may provide many evolutionary insights. Here I use body-mass data from 3473 of 4510 extant mammalian species and an almost complete species-level phylogeny to determine the best model of body-mass evolution across all mammals, split taxonomically and spatially. I find that, of the three evolutionary models tested (the Brownian motion (BR) model, the Ornstein-Uhlenbeck (OU) model, and the early burst (EB) model), EB fits best across all mammals. However, within orders and ecoregions, it is generally not possible to differentiate among the three models (except for: Carnivora, Insectivora, Lagomorpha and 34 ecoregions = BR; Chiroptera and Peramelemorphia = OU; Primates and 96 ecoregions = EB). I conclude that mammals experienced a burst of morphological evolution relatively early in their history followed by a slowdown in rate, perhaps caused by adaptive radiation followed by the decreased availability of empty niches. The rate of body-mass evolution also varies spatially: spatial simultaneous autoregressive (SAR) models show that over 60% of the variation in rate can be explained by just a few predictors. High rates of body-mass evolution are associated with low environmental temperatures, low elevations, low species richness, high ordinal richness (i.e. body plan disparity), mainlands and ecoregions which did not suffer extensive megafaunal extinctions in the Quaternary. I conclude that mammalian body size is the result of complex interplay among geography, the species composition of the area and past anthropogenic impacts.

[5] Many of the analyses in this chapter will soon be submitted to *American Naturalist*. N.C. performed all the analyses and wrote the manuscript. A.P. supervised.

6.2 Introduction

Body size is possibly the most informative single trait of an organism, since it influences practically every aspect of a species' biology (Calder 1984). Consequently, body size can be a good predictor of a large number of ecological and physiological traits. In mammals, for example, large species have a slower speed of life-history (Charnov 1993; Kozlowski & Weiner 1997), lower mass-specific metabolic rates (Kleiber 1932), smaller population sizes, lower abundance (Damuth 1993), slower rates of molecular evolution (Welch et al. 2008), shorter durations in the fossil record (Liow et al. 2008), wider geographic ranges (Gaston & Blackburn 2000), larger home ranges (Eisenberg 1981), and higher prevalence of extinction risk (Cardillo et al. 2005) than small species. Each of these traits may affect the tempo and mode of evolution, thus greater understanding of body size evolution may provide a greater understanding of evolution in general.

Mammals are a good clade on which to investigate body size evolution in more detail. They differ greatly in their body sizes (ranging from < 2 grams to 10^5 kilograms; Jones et al. in press), I have body-mass data on most extant species (3473 of 4510) and an almost complete species-level phylogeny (Bininda-Emonds et al. 2007; 2008). In addition, variation has been reported in the rate of body-mass evolution among both clades (e.g. carnivores versus primates; Mattila & Bokma 2008; Webster & Purvis 2002) and regions (Rodríguez et al. 2008). Using this data I can ask a range of questions about the evolution of body-mass in mammals: for example, how has body-mass evolved in mammals? How and why do the tempo and mode of body-mass evolution vary, both taxonomically and spatially?

The three models of body-mass evolution I investigate here are as follows: (1) the Brownian motion (BR) model, also known as the log-Brownian model when fitted to logarithmically transformed data. This assumes gradual evolution of body-mass through the phylogeny, with body-mass variance slowly increasing with time (Felsenstein 1973). I included the BR model as it is assumed to be the underlying mode of evolution in many comparative studies (although this assumption is rarely tested; Freckleton & Harvey 2006) and hence acts as a null model of trait evolution. (2) The Ornstein-Uhlenbeck or "rubber-band" (OU) model. This is a modified BR model where body-mass values are constantly pulled back towards an optimum by some kind of ecophysiological constraint (Hansen 1997). I chose to test the OU model as Clauset and Erwin (2008) recently showed apparent taxon-specific lower limits of mammalian body size, indicating that OU may be an appropriate model for this clade. Also the idea that evolutionary trends are the result of diffuse evolution within certain physiological bounds is pervasive in the palaeontological literature (Jablonski 1997; McShea 1994; Stanley 1973b). (3) The early burst (EB) model (also known as the ACDC model; Blomberg et al. 2003). This predicts that most diversification in body-mass occurs early in a lineage, with rates of body-mass evolution decreasing towards the present, so that subclades tend to retain their differences through time (Blomberg et al. 2003; Harmon et al. in review). This model is consistent with adaptive radiations early in the history of a clade followed by a slowdown in diversification rate due to, for instance, niche-filling. Such a pattern is often seen in the fossil record (e.g. declines in origination rates for higher taxa in fossil groups; Sepkoski 1998) and has been reported in mammals (Foote 1997); thus I also chose to investigate this model.

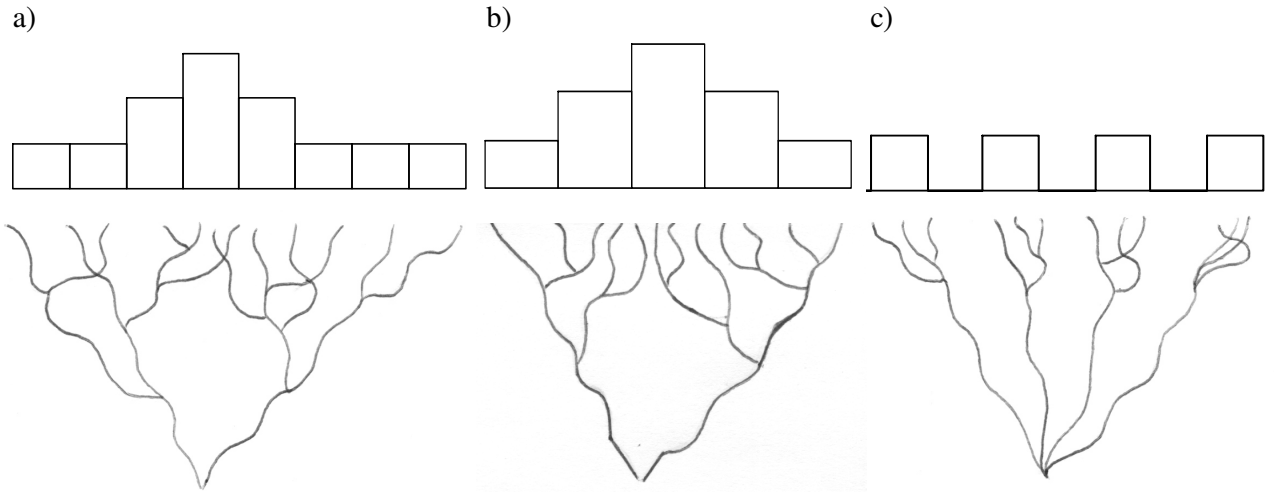


Figure 6.1: Graphical representation of the three models of body-mass evolution a) Brownian motion (BR); b) Ornstein-Uhlenbeck (OU); c) early burst (EB). The histograms show the kinds of body-mass distributions expected from each model, i.e. a) normal distribution of body-mass values; b) normal distribution of body-mass values but within set upper and lower bounds; c) similar body-masses within lineages.

Here I first aim to determine which of the three models best explains body-mass evolution within mammals overall. However, mammals are a diverse group, thus it seems unlikely that all mammalian clades will have the same model of body-mass evolution. Certainly there is no consensus in the literature on an evolutionary model for all mammals. For example, Cenozoic ungulates show an early burst of morphological evolution followed by slowdown (Foote 1997), whereas Primates fit a Brownian model (Gillman 2007). In addition, there may be spatial variation in the mode of evolution. For example, tropical species are predicted to evolve more quickly than temperate species (Wright et al. 2006), so may be more likely to show rapid bursts of evolution. Temperate species, on the other hand, are more constrained by the demands of

their environments than tropical species, so may be more likely to show OU-like patterns of body-mass evolution. To investigate this variation further, I therefore split mammals by Order (Wilson & Reeder 1993) and WWF ecoregion (Olson et al. 2001, see methods), to determine whether the models varied taxonomically and/or spatially. Rates of evolution are also predicted to vary spatially (e.g. fast rates in the tropics: Wright et al. 2006), so I also examined the spatial pattern of rate variation using within ecoregion rates of body-mass evolution.

Finally, I looked for correlates of the rate of body-mass evolution. I first looked at rates within orders to determine whether there was a relationship between the rate of evolution and clade age, species richness, median body-mass or median geographic range size of the species within each order. However, few orders contain enough species to test in this way, so degrees of freedom were low. Therefore, I instead focussed on predicting spatial variations in rate of body-mass evolution, again using ecoregions as the spatial unit of my study. I predict that many factors may influence rates of body-mass evolution within an ecoregion, including the ecoregion's location, species composition and extinction filters. The location of an ecoregion may influence rates of body-mass evolution in several ways. Firstly, difficulties in colonising, or surviving on, islands mean that island faunas contain few large species (Lomolino 2005), which may reduce apparent rates of evolution in island ecoregions. Additionally, the island rule predicts that body size evolution will be faster on mainlands than on islands, since island species are apparently evolving towards a body-mass optimum (Lomolino 2005; but see Meiri et al. 2005). Secondly, the location of an ecoregion often defines its climate and I predict that rates will be positively correlated with AET and environmental temperature, since high-energy environments such as the tropics are

often thought to have high rates of evolution (Rohde 1978; but see Pawar 2005). Tropical ecoregions should therefore, also have higher rates of evolution than non-tropical ecoregions. In addition, environmental variables may interact with elevation (which may also influence evolutionary rates; Bleiweiss 1998).

The species composition of an ecoregion is also likely to influence rates. For example, the average body size of the species within an ecoregion, as well as the average geographic range size of the species, is predicted to influence rates of evolution, although the direction of the correlation is disputed (see Chapter 5). Including these variables also helps control for the different body-mass and geographic range size distributions of species in the tropics compared to those at higher latitudes.

Much body-mass evolution probably occurred outside the focal ecoregion with species dispersing there later. This can have a big influence on apparent rates of body-mass evolution within an ecoregion, with high apparent rates where many different kinds of taxa dispersed into the area. To attempt to control for this, I include the degree of disparity in body plans (here indicated by the ordinal richness of an area; Foote 1997) as a predictor. I expect a positive correlation between the degree of disparity in body plans and the rate of body-mass evolution. This effect will be diluted as species richness increases.

Finally, extinction filters may shape rates of body-mass evolution, since areas which have been exploited by humans for a long time (e.g. South America and Western Europe) are likely to have lost their megafauna and hence should have lower apparent rates of body-mass evolution than areas which suffered less human impact (e.g. Africa).

One of the major historical human impacts on mammals was the late Quaternary megafaunal extinction, when most large (≥ 44 kg) mammals became extinct everywhere except in Sub-Saharan Africa (Koch & Barnosky 2006). I therefore use whether an ecoregion is within Sub-Saharan Africa or not as a proxy for the effect of extinction filters. It was not possible to find a more accurate proxy at a fine enough spatial scale to be useful.

I investigated both univariate and multivariate relationships between the rate of body-mass evolution and the AET, environmental temperature, elevation, area, species richness and ordinal richness of each ecoregion, as well as the median body-mass and geographic range size of the species within the ecoregion. I also investigated whether the within ecoregion rate of body-mass evolution was higher in non-tropical or tropical biomes, on islands, archipelagos or mainlands, and within or outside Sub-Saharan Africa.

6.3 Materials and methods

DATA

Body-mass and correlates data

Median body-mass (g) for 3473 species was taken from PanTHERIA (Jones et al. in press). For analyses investigating spatial variation in models and rates of body-mass evolution (see below), I chose to use WWF ecoregions (Olson et al. 2001), rather than grid cells, as spatial units for three reasons. Firstly, ecoregions are at a relatively small scale compared to the whole globe, but have sufficiently large sample sizes for modelling. Secondly, ecoregions represent more natural units than grid cells since they delimit biogeographical areas with distinctive flora and fauna (Olson et al. 2001).

Finally, the coarser scale of ecoregions may avoid some of the errors arising from converting imprecise species' geographic ranges to grid cell occurrence (Jetz et al. 2008). In addition, grid cells are often smaller than species geographic ranges so this would increase small-scale spatial autocorrelation which would then immediately be removed in the spatial models (see below). To determine which species occurred within each ecoregion, I overlaid ecoregion shapefiles (Olson et al. 2001) with the PanTHERIA mammal geographic ranges (Jones et al. in press) in ArcMap version 9.2. This information was used to extract median body-mass (g) and median geographic range size (km^2) within each WWF ecoregion. Ecoregion mean actual evapotranspiration (AET, mm; UNEP 1994), mean annual temperature (ºC; Hijmans et al. 2005), mean elevation (m; USGS EROS 1996), area (km^2), whether the ecoregion was an island, archipelago or mainland, and WWF biogeographic realm and biome, were extracted from GIS layers by S. Fritz (*pers.comm.*).

The species and ordinal richness within each ecoregion were calculated using the taxonomy of Wilson and Reeder (1993), because the phylogeny used (see below) uses this taxonomy. Ecoregions were defined as tropical if they were within the six entirely tropical/subtropical WWF biomes (tropical and subtropical coniferous forests; tropical and subtropical moist broadleaf forests; tropical and subtropical dry broadleaf forests; tropical and subtropical grasslands; savannas and shrublands; mangrove; and deserts and xeric shrublands) and non-tropical if they were within the remaining eight WWF biomes (tundra; boreal forests/taiga; temperate coniferous forests; temperate broadleaf and mixed forests; temperate grasslands; savannas and shrublands; Mediterranean forests; woodlands and shrub; montane grasslands and shrublands; flooded grasslands and savannas). As a proxy for the effect of extinction filters, ecoregions were classed as

being within Sub-Saharan Africa or not, since only Sub-Saharan Africa retained a large proportion of its megafauna after the Late Quaternary extinction (Koch & Barnosky 2006).

I used natural-log transformations of all continuous variables prior to analysis to normalise their distributions, except for environmental temperature and elevation variables which are sometimes negative. When I repeated the analyses using elevation deciles instead of raw values there was no qualitative change in the results (data not shown). Collinearity amongst predictor variables can lead to unreliability in model parameter estimates. Since I expect correlations among the variables, I checked the predictors for collinearity prior to model building (following the method of Belsey et al. 1980). For all predictors, variance inflation factors are lower than three and condition indices are lower than nine, which indicates that no undesirable levels of collinearity are present (Belsey et al. 1980).

Phylogeny

Initially I used the mammal supertree of Bininda-Emonds et al (2007; 2008). However, this supertree has many polytomies which can affect estimates of evolutionary rates and parameters (Webster & Purvis 2002). Therefore I removed polytomies, based on the reliability of the body-mass data for the species involved. Since it is more likely that the species' body-mass median will be unrepresentative of the species as a whole where it is based on only a few records, I defined the "data quality" of each species as the number of records (though note this is equivalent to the number of sources, not necessarily the number of specimens), used to produce its median body-mass. I then removed polytomies as follows: for polytomies at the tips, I kept the two species with the best

quality body-mass data, as defined above. Where there was a tie, two species were chosen at random from the set of species with the best quality data. For internal polytomies, I kept the two nodes which contained the greatest number of species. Where there was a tie, I kept the nodes which contained the set of species with the highest mean body-mass data quality. If there was still a tie, two nodes were chosen at random from the set of nodes with the highest species richness and mean body-mass data quality. Because selections were occasionally random, I repeated this process 100 times to get 100 fully-bifurcating trees. Each contained 1477 species in total and varied by 34-37 species. I repeated the analyses testing the evolutionary models for each order (see below) using all 100 trees, to account for differences that may arise due to the different species left in the analyses. The results were quantitatively similar, and the phylogeny used did not alter which model of evolution was selected (data not shown but will be available as an online appendix to the paper). In all other analyses I use just one of the resolved trees chosen at random (models of evolution for all species and orders use tree 10; models and correlates of rates of evolution within ecoregions use tree 48), since the analyses were too computationally intensive to repeat for all 100 trees.

ANALYSES

Models of body-mass evolution

The three models of body-mass evolution described in the introduction have the following parameters: (1) the Brownian motion (BR) model has two parameters, the most important of which for my purposes is σ^2, the Brownian rate parameter (Felsenstein 1973). This parameter is present in the other two models and I also used it as a measure of the relative rate of evolution (see below); (2) The Ornstein-Uhlenbeck

(OU) model is a modified BR model with an additional parameter, α, which describes the strength of the constraint force (Hansen 1997). Note that when α = 0, OU is equivalent to BR. (3) The early burst (EB) model also has three parameters. The r parameter describes how rates of evolution change over time: where r is negative, rates decrease through time, but when r = 0, EB is equivalent to BR (Blomberg et al. 2003; Harmon et al. in review).

I fitted BR, OU and EB models to all species combined, each order separately (where number of species in the order > 9: resolved phylogeny = 15 orders; unresolved tree = 16 orders), and each ecoregion (where number of species in the ecoregion > 9: unresolved tree = 722 ecoregions; unresolved tree = 734 ecoregions) using the R package GEIGER (Harmon et al. 2008). I then used the Bayesian information criterion (BIC) to determine the best model of body-mass evolution in each case. Note that I required the BIC of the best model to be at least 4 units smaller than that of the other two models in order to consider it a significantly better fit (Burnham & Anderson 2002). I used BIC rather than the Akaike information criterion (AIC), because AIC is often overly generous to models with more parameters (Burnham & Anderson 2002), which could lead to it favouring the three-parameter OU and EB models over the two-parameter BR model. AIC and AIC weights are also presented in tables to allow comparisons with other papers. In order to determine the effects of phylogeny resolution, I fitted each of these models using both a resolved tree (tree 10) and the unresolved tree.

Correlates of rates of body-mass evolution

I defined the relative rate of body-mass evolution for an order, or ecoregion, as the Brownian rate parameter, σ^2, obtained by fitting BR models of evolution for the species

within the order or ecoregion (using either the unresolved tree or, orders: resolved tree 10, ecoregions: resolved tree 48). I used σ^2 from the BR model, rather than the OU or EB models, as most of the orders and ecoregions did not strongly favour any of the three models (see Results) and BR is generally used as the null model of trait evolution.

I first calculated σ^2 for each of the orders with more than nine species (15 orders using resolved tree 10; 16 orders using the unresolved tree). I investigated the relationships between the rate of body-mass evolution within each order and the species richness, age, median body-mass and median geographic range size of the species within the order. I performed all of the regressions using independent contrasts (Felsenstein 1985), generated using the R package CAIC (available at https://r-forge.r-project.org/projects/caic), to account for the non-independence introduced because close relatives tend to be similar due to shared common ancestry (Harvey & Pagel 1991).

Next, I calculated σ^2 for each of the ecoregions with complete records for all the variables and greater than nine species within the ecoregion (711 ecoregions using resolved tree 48; 716 ecoregions using the unresolved tree). I aimed to investigate both univariate and multivariate relationships between σ^2 and the AET, environmental temperature, elevation, area, species richness and ordinal richness of each ecoregion, as well as the median body-mass and geographic range size of the species within each ecoregion. I also aimed to determine whether σ^2 was higher in non-tropical or tropical biomes, on islands, archipelagos or mainlands, and within or outside Sub-Saharan Africa. I repeated the island analyses omitting archipelagos, but this did not qualitatively affect the results (data not shown) so I left archipelagos in to increase degrees of freedom.

Spatial autocorrelation (SA) is likely to occur in these analyses since the values of a given variable will be more similar in nearby ecoregions than would be expected by chance (Legendre & Legendre 1998). Many methods for dealing with spatial autocorrelation exist. Here I use simultaneous autoregressive (SAR) models (Kissling & Carl 2008). These are linear regression models with an extra (autoregressive) term that describes the spatial autocorrelation structure of the dataset. This autoregressive term is a "spatial weights matrix" which identifies the neighbourhood of each ecoregion (i.e. which ecoregions are neighbours, defined by the great-circle distance between them) and the weight of each neighbour (so that, for example, closer neighbours have higher weighting than more distant ones). Neighbourhood definitions can be varied by changing the distance between ecoregions classed as neighbours and the weighting can be changed by altering the coding style for the spatial weights matrix.

The performance of SAR models is dependent on three factors: (1) the specified model type (SAR_{error}, SAR_{lag} or SAR_{mixed} models); (2) the coding style for the spatial weights matrix (either 'B' = binary, 'W' = row-standardised, or 'S' = variance-stabilising); and (3) the neighbourhood distance (i.e. how far apart two points can be and still be classed as neighbours). Kissling and Carl (2008) provide detailed descriptions of all the options. Here I use SAR_{error} models with row-standardised (type 'W') coding (see Kissling & Carl 2008 for details), as these performed best across their simulations. Neighbourhood distance is harder to define because the degree of SA varies among datasets, and thus the neighbourhood distance required cannot be determined *a priori*. For example, a variable that gradually increases from north to south will have higher SA than a variable which changes rapidly. In this instance, two points 1 km apart would have values of the

gradually changing variable that were more similar than those of the rapidly changing variable, thus the neighbourhood distance would need to be larger for the former than the latter. To solve this problem, Lichstein et al (2002) suggest using the maximum distance at which residuals from an ordinary least squares (OLS) model are spatially autocorrelated as the neighbourhood distance, since past this distance there is no SA. This maximum distance is where a Moran's *I* plot of the OLS model residuals first crosses the x-axis. Kissling and Carl (2008), however, recommend trying multiple distances and then using model selection criteria, e.g. AIC, to find the best neighbourhood distance. Here I develop this suggestion further: for each model I find the optimal neighbourhood distance (i.e. the one which gives the lowest AIC value in the SAR_{error} model) between 500 km and the maximum distance at which residuals from an OLS model are autocorrelated. The maximum distances were obtained by investigation of Moran's *I* plots of the OLS model residuals (Figure 6.2), and thus are different for each model.

I used the R package spdep (Bivand 2008) to fit spatial SAR_{error} models for each predictor against σ^2 (see details above). After fitting each model I examined Moran's *I* plots of the model residuals to ensure SA had been removed (Figure 6.2). I then calculated r^2 values for the models using the following formula:

$$r^2 = 1 - \exp(-2/n(\text{loglik}_{full} - \text{loglik}_{null}) \quad (5)$$

where n = sample size, loglik_{full} = log likelihood of the fitted model, loglik_{null} = likelihood of the null model (Nagelkerke 1991). The null model is a model containing the intercept and no autoregressive term (note: this can lead to very high r^2 values as they describe not only how fitting a slope improves the model fit, but also how accounting for SA improves the model fit).

Next, I fitted spatial SAR_{error} models, containing all variables and three interaction terms (median body-mass:median geographic range size; area:median geographic range size; environmental temperature:elevation), for predicting σ^2 across ecoregions. I report only the results of the full models because, with so many parameters, the huge number of models would have made an information-theoretic approach unfeasible. I did not use stepwise regression to obtain minimum adequate models (MAM) because these methods have a greatly inflated Type I error rate (around 40% for models with ten parameters; Mundry & Nunn 2009), although the results are qualititatively similar when I did use MAMs (data not shown). I assessed the contribution of each variable in the full models to the model fit with likelihood ratio tests following the method of Lichstein et al. (2002). I also carried out non-spatial models so I could compare the results to those of non-spatial studies.

Finally, I used ArcMap version 9.2 to create maps showing variations in the relative rate of body-mass evolution (σ^2) across ecoregions. I also presented this information per 1° grid cell to allow comparisons with any future studies that may use grid cells as their spatial units. I also mapped the squared-residuals and fitted values obtained from the full models in order to determine which parts of the world fit the models well and which fit the models poorly.

Except where otherwise stated, I used R version 2.6.2 in all analyses (R Development Core Team 2008).

6.4 Results

Models of body-mass evolution

Across all mammals, the best model of body-mass evolution was the early burst (EB) model (Table 6.1). However, within orders and ecoregions it was often impossible to choose among the three models, as their BIC values were not sufficiently different (i.e. < 4 units different; Burnham & Anderson 2002). The exceptions to this were as follows. In the resolved tree: Carnivora, Insectivora and Lagomorpha = BR; Chiroptera and Peramelemorphia = OU; Primates = EB; 34 ecoregions = BR; 96 ecoregions = EB (Table 6.2; Figure 6.3); unresolved tree: Chiroptera and Peramelemorphia = OU; Primates = EB; one ecoregion = OU; 363 ecoregions = EB (Table 6.3; Figure 6.3). The BR ecoregions are found in northern Africa, North America, central South America, north India and Papua New Guinea. The EB ecoregions are found in northern South America, Central America and east Africa. In the unresolved tree results, EB ecoregions are also found across much of central Asia, Eurasia and west North America and there is one OU ecoregion on the north-west coast of Australia.

Soft polytomies create terminal branches that are too long, and although removing supernumerary terminal branches reduces some of the problems associated with polytomies, it still leaves these long branches. The long branches will artificially reduce rates towards the present and thus increase relative rates deeper in both the unresolved and resolved trees. This therefore predicts EB in areas and clades where the resolution of the mammal supertree is low. Within orders, only Primates are defined as EB and the resolution of their phylogeny is higher (approximately 86%) than that of the other groups (around 82%). However, the polytomy bias may be an issue in the ecoregion analyses since ecoregions defined as EB were significantly less-resolved than non-EB

ecoregions (t-test with Welch's approximation for degrees of freedom: resolved tree: $t = 8.384$, d.f. = 122.2, $p < 0.001$; unresolved tree: $t = 7.773$, d.f. = 646.9, $p < 0.001$), suggesting the EB ecoregions result may be an artefact of the poor resolution of the tree in some places. This problem is less apparent in the resolved tree analyses, which only have 96 EB ecoregions, as opposed the 363 EB ecoregions in the unresolved tree analyses. Another feature to note is that a single unusual datum can drive large clade differences: e.g. Dasyuromorphia (marsupial carnivores) have an inferred rate of body-mass evolution which is ten times that of the other orders due to one very large species (*Sarcophilus laniarius*, Tasmanian devil).

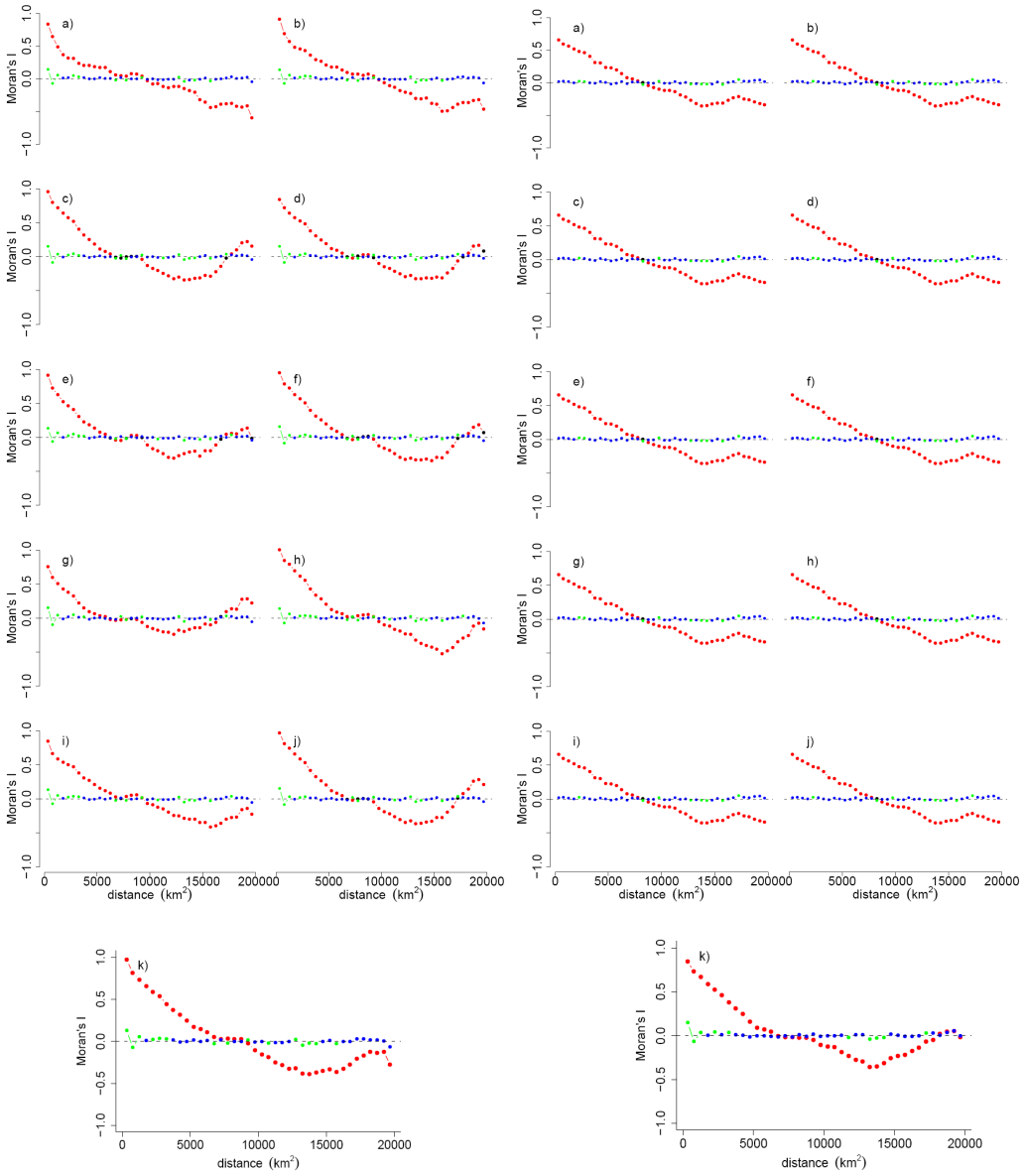


Figure 6.2: Moran's I plots for all continuous variables showing how the SAR_{error} models remove spatial autocorrelation (SA) from the OLS models. Left-hand plots used a resolved phylogeny (tree 48); right-hand plots used the unresolved tree. Red points = OLS model residuals with significant SA; green points = SAR_{error} model residuals with significant SA; blue points = SAR_{error} model residuals with no significant SA; a = AET; b = environmental temperature; c = elevation; d = species richness; e = ordinal richness; f = median body-mass; g = median geographic range size; h = tropical or non tropical; i = Sub-Saharan Africa or not Sub-Saharan Africa; k = island or mainlands.

Table 6.1: Results of fitting BR, OU and EB models of body-mass evolution on all species using either a fully-resolved phylogeny (tree 10) or the unresolved tree. n = number of species; σ^2 = Brownian rate parameter; α = OU constraint parameter; r = early burst parameter; AIC_w = AIC weight; best model = model with the lowest BIC.

resolved phylogeny (n = 1477)						
model	**σ^2**	**α**	**r**	**AIC**	**AIC_w**	**BIC**
BR	0.046	-	-	3648	< 0.001	3659
OU	0.047	<0.001	-	3650	< 0.001	3666
EB	0.224	-	-0.010	3621	1.000	3637
best model = EB						
unresolved phylogeny (n = 3473)						
model	**σ^2**	**α**	**r**	**AIC**	**AIC_w**	**BIC**
BR	0.038	-	-	7452	< 0.001	7464
OU	0.037	< 0.001	-	7455	< 0.001	7473
EB	0.159	-	-0.009	7410	1.000	7428
best model = EB						

Table 6.2: Results of fitting BR, OU and EB models of body-mass evolution within each order using a fully-resolved phylogeny (tree 10). n = number of species; σ^2 = Brownian rate parameter; α = OU constraint parameter; r = early burst parameter; best model = model with the lowest BIC (parameter values highlighted in bold). ? = BIC values which do not differ enough (< 4 units) for any model to be preferred over the others. *High rates of evolution in Dasyuromorphia are driven by a single large species: *Sarcophilus laniarius*.

		BR			OU				EB				
Order	**n**	**σ^2**	**AIC**	**BIC**	**σ^2**	**α**	**AIC**	**BIC**	**σ^2**	**r**	**AIC**	**BIC**	**best model**
Artiodactyla	105	0.058	268.2	273.5	0.066	0.009	269.1	277.0	0.058	0	270.2	278.2	?
Carnivora	195	**0.066**	**501.3**	**507.9**	0.066	< 0.001	503.3	513.1	0.066	0	503.3	513.1	**BR**
Cetacea	36	0.063	114.6	117.7	0.063	< 0.001	116.6	121.3	0.277	-0.042	111.5	116.3	?
Chiroptera	242	0.033	553.2	560.1	**0.044**	**0.018**	**542.5**	**553.0**	0.033	0	555.2	565.6	**OU**
Dasyuromorphia	50	0.101*	153.4	157.2	0.137	0.031*	153.7	159.4	0.101*	0	155.4	161.2	?
Didelphimorphia	29	0.020	71.84	74.57	0.020	< 0.001	73.84	77.94	0.045	-0.021	72.70	76.80	?
Diprotodontia	83	0.062	230.0	234.8	0.062	< 0.001	232.0	239.2	0.144	-0.019	230.1	237.4	?
Insectivora	80	**0.024**	**201.6**	**206.4**	0.024	< 0.001	203.6	210.8	0.025	0	203.6	210.8	**BR**
Lagomorpha	58	**0.017**	**71.22**	**75.34**	0.017	< 0.001	73.22	79.40	0.017	0	73.22	79.40	**BR**
Macroscelidea	11	0.017	24.36	25.16	0.017	< 0.001	26.36	27.56	0.058	-0.038	25.48	26.68	?
Peramelemorphia	10	0.049	29.86	30.47	**0.235**	**0.332**	**23.94**	**24.84**	0.049	0	31.86	32.77	**OU**
Perissodactyla	13	0.008	22.91	24.04	0.008	< 0.001	24.91	26.61	0.038	-0.043	22.75	24.44	?
Primates	163	0.020	212.5	218.7	0.020	< 0.001	214.5	223.8	**1.100**	**-0.054**	**193.6**	**202.8**	**EB**
Rodentia	293	0.048	704.8	712.2	0.053	0.006	704.7	715.8	0.048	0	706.8	717.8	?
Xenarthra	16	0.039	46.98	48.53	0.100	0.065	44.74	47.06	0.039	0	48.98	51.30	?

Table 6.3: Results of fitting BR, OU and EB models of body-mass evolution within each order using an unresolved tree. n = number of species; σ^2 = Brownian rate parameter; α = OU constraint parameter; r = early burst parameter; best model = model with the lowest BIC (parameter values highlighted in bold). ? = BIC values which do not differ enough (< 4 units) for any model to be preferred over the others.

		BR			OU				EB				
Order	**n**	**σ^2**	**AIC**	**BIC**	**σ^2**	**α**	**AIC**	**BIC**	**σ^2**	**r**	**AIC**	**BIC**	**best model**
Artiodactyla	211	0.063	497.5	504.2	0.064	0.001	499.5	504.2	0.063	0	499.5	509.6	?
Carnivora	261	0.062	638.7	645.4	0.062	< 0.001	640.7	645.4	0.062	0	640.7	650.7	?
Cetacea	76	0.055	228.4	235.1	0.055	< 0.001	230.4	235.1	0.131	-0.023	228.0	238.0	?
Chiroptera	668	0.030	1293	1299	**0.040**	**0.022**	**1260**	**1264**	0.030	0	1295	1305	**OU**
Dasyuromorphia	60	0.099	176.9	183.6	0.137	0.033	177.1	181.8	0.099	0	178.9	189.0	?
Didelphimorphia	62	0.020	144.0	150.7	0.020	< 0.001	146.0	150.7	0.071	-0.033	142.8	152.9	?
Diprotodontia	114	0.055	273.8	280.5	0.055	< 0.001	275.7	280.5	0.138	-0.021	273.2	283.2	?
Insectivora	233	0.029	515.1	521.8	0.030	< 0.001	517.1	521.8	0.029	0	517.1	527.2	?
Lagomorpha	60	0.019	77.80	84.50	0.019	0.002	79.75	84.45	0.019	0	79.80	89.85	?
Macroscelidea	14	0.013	26.12	32.83	0.013	< 0.001	28.12	32.83	0.061	-0.046	26.47	36.53	?
Peramelemorphia	19	0.055	46.92	53.62	**0.359**	**0.319**	**42.13**	**46.83**	0.055	0	48.92	58.97	**OU**
Perissodactyla	18	0.007	26.52	33.23	0.007	< 0.001	28.52	33.23	0.033	-0.041	26.26	36.32	?
Primates	230	0.016	249.2	255.9	0.016	< 0.001	251.2	255.9	**1.027**	**-0.056**	**221.6**	**231.7**	**EB**
Rodentia	1369	0.032	2653	2659	0.032	< 0.001	2655	2659	0.032	0	2655	2665	?
Scandentia	17	0.009	27.67	34.38	0.012	0.013	29.58	34.28	0.009	0	29.67	39.73	?
Xenarthra	29	0.048	88.94	95.64	0.051	0.003	90.89	95.59	0.048	0	90.94	101.0	?

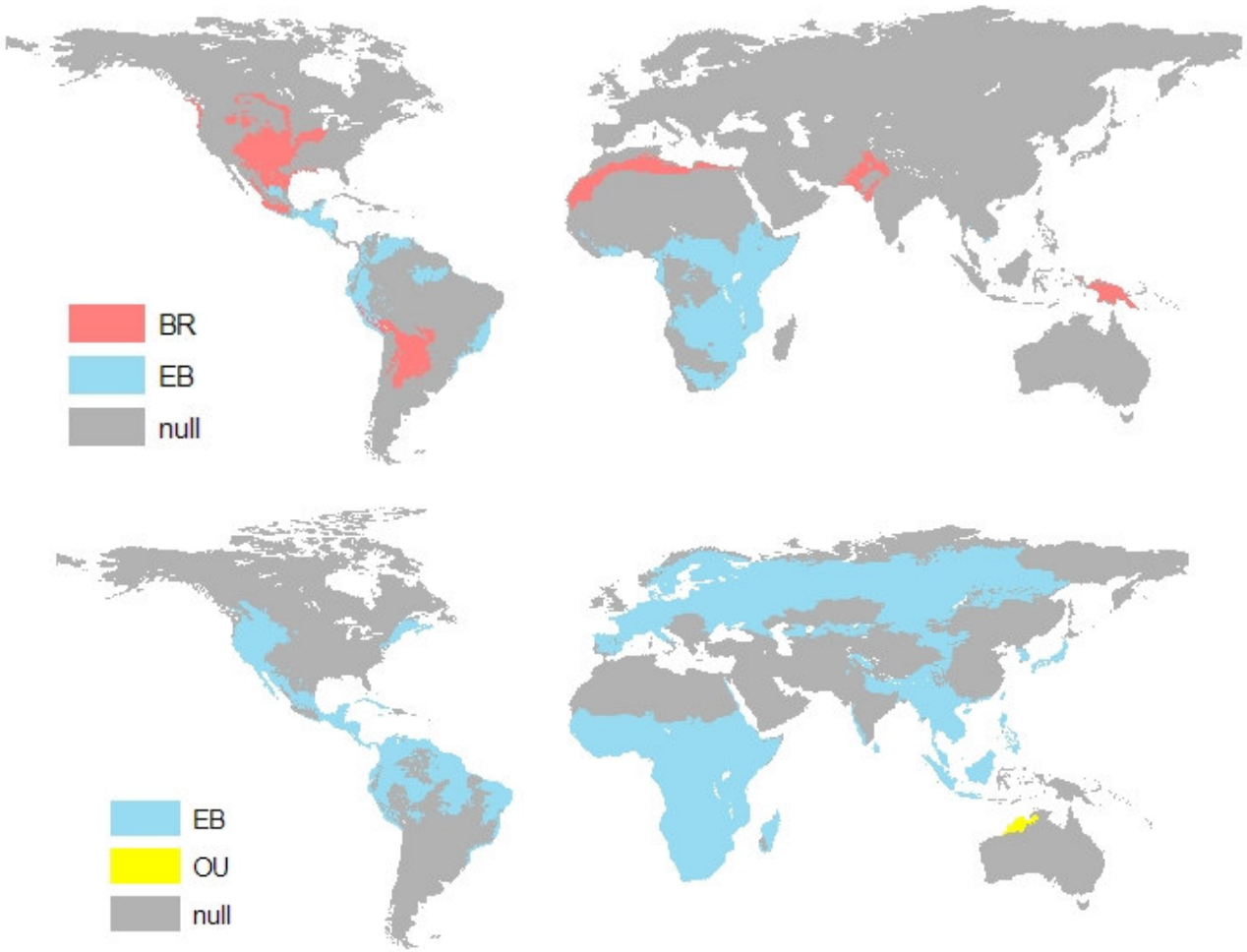


Figure 6.3: Best model of body size evolution within each ecoregion with > 9 species for a resolved phylogeny (top panel; tree 48) and an unresolved phylogeny (lower panel). Ecoregions in white were not evaluated (number of species in ecoregion ≤ 9 species). Ecoregions in grey have BIC values which were not different enough (< 4 units) for any model to be preferred over the others.

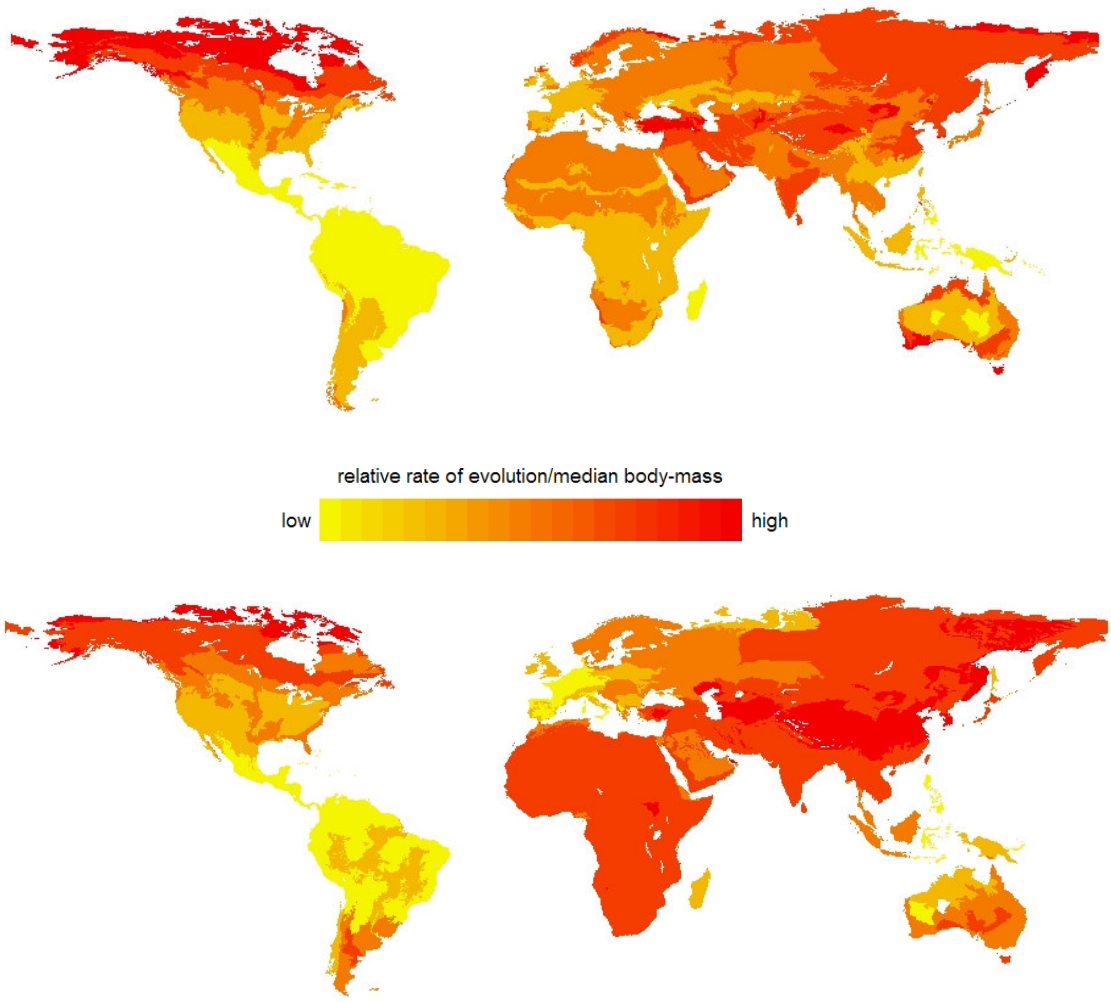


Figure 6.4: Relative rate of evolution (Brownian rate parameter σ^2; top panel) and median natural-log transformed body-mass (lower panel) within each ecoregion for ecoregions with > 9 species using a fully-resolved phylogeny (tree 48). Ecoregions in white were not evaluated (number of species in ecoregion ≤ 9 species).

Correlates of rates of body-mass evolution

Within orders, there are no significant relationships between σ^2 and the species richness ($t_{14} = 1.061$, $p = 0.306$, $r^2 = 0.074$), clade age ($t_{14} = -1.679$, $p = 0.115$, $r^2 = 0.168$), median body-mass ($t_{14} = 0.197$, $p = 0.847$, $r^2 = 0.003$) or median geographic range size ($t_{13} = 0.581$, $p = 0.571$, $r^2 = 0.025$) of the species within the order.

Variations in the relative rate of body-mass evolution (Brownian rate parameter, σ^2) within each ecoregion, along with the median body size of the species within each ecoregion, are shown in Figure 6.4 (resolved tree only). Rates are highest in northern North America and north-eastern Eurasia and lowest in South America. This pattern is similar for the unresolved phylogeny (not shown). In addition, high rates do not merely appear to be the result of either small or large body-mass of species within the ecoregions, because the body-mass median and σ^2 maps are far from identical. Figure 6.5 also shows the pattern of σ^2 variation within each 1° grid cell (resolved tree only). The general pattern is similar to that in Figure 6.4, however, much of North Africa is missing as the grid cells there have too few species for models to be fitted.

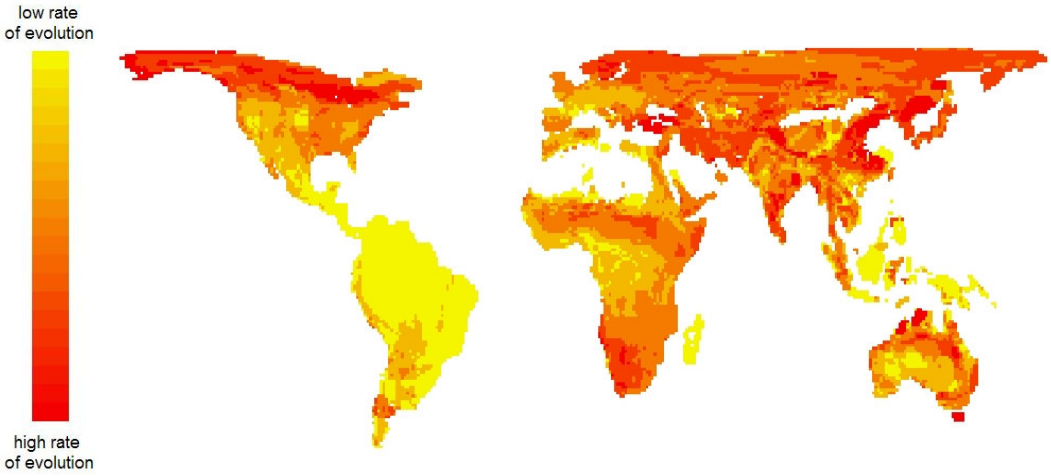


Figure 6.5: Relative rate of evolution (Brownian rate parameter σ^2) within each 1° grid cell, for grid cells with more than nine species, using a fully-resolved phylogeny (tree 48). Grid cells in white were not evaluated (number of species in grid cell ≤ 9 species).

Results from non-spatial and spatial models investigating correlates of the relative rate of evolution (σ^2) per ecoregion are shown in Tables 6.4-6.7. In single predictor spatial models, σ^2 increases with ordinal richness, median geographic range size and median body-mass; and decreases with increasing AET, environmental temperature, ecoregion

area and species richness. In the resolved tree analyses only, tropical species have a lower rate of body-mass evolution than non-tropical species and Sub-Saharan African species have a higher rate of body-mass evolution than non Sub-Saharan African species.

The full spatial models predicting the relative rate of body-mass evolution per ecoregion (Tables 6.6 and 6.7) show that ecoregions with a high rate of body-mass evolution tend to be characterised by low environmental temperature, elevation, species richness and AET (unresolved tree model only), high ordinal richness, and tend to be on mainlands and within Sub-Saharan Africa (resolved tree model only). The most important of these predictors were low species richness and high ordinal richness, followed by low environmental temperature and low elevation. Note that although this appears to be a description of the cold, low elevation, low diversity ecoregions of the North Temperate Zone (e.g. Canada), the same qualitative result was obtained when only the tropical ecoregions were considered (data not shown), so the result is not driven by these northern ecoregions. The spatial and non-spatial models have fairly similar parameter estimates. More variables are significant in the non-spatial models, presumably due to spatial autocorrelation.

Maps of fitted and squared residual σ^2values obtained from the spatial model (resolved tree 48) are shown in Figure 6.6. Model fit is fairly good across most of the globe, but underestimates σ^2 in some areas, e.g. Northern Africa, parts of Anatolia and Siberia. It also overestimates σ^2 in parts of Europe, Western and Southern Africa, Central Australia and parts of Siberia. Model fit in Australia is particularly poor.

Table 6.4: Results of single predictor non-spatial (OLS) and spatial (SAR_{error}) models predicting rate of body-mass evolution (σ^2) within each ecoregion using a resolved phylogeny (tree 48). nb dist = optimised neighbourhood distance (km); BM = body-mass; GR = geographic range size. *p < 0.05; **p < 0.01; ***p < 0.001.

	non-spatial					spatial SAR			
predictor	**slope ± se**	**t_{709}**	**r^2**	**AIC**	**nb dist**	**slope ± se**	**z_{707}**	**r^2**	**AIC**
AET	-0.019 ± 0.001	-19.30***	0.345	-3518	885.3	-0.005 ± 0.001	-4.517***	0.736	-4464
Temperature	< -0.001 ± < 0.001	-19.62***	0.352	-3526	882.4	< -0.001 ± < 0.001	-2.859**	0.729	-4453
Elevation	< 0.001 ± < 0.001	1.509	0.003	-3220	940.9	< -0.001 ± < 0.001	-0.129	0.821	-4442
Area of ecoregion	0.004 ± 0.001	6.550***	0.057	-3260	942.3	-0.001 ± < 0.001	-4290***	0.816	-4460
Species richness	-0.018 ± 0.001	-14.21***	0.222	-3396	853.1	-0.011 ± 0.001	-9.670***	0.795	-4522
Ordinal richness	-0.012 ± 0.003	-4.191***	0.024	-3235	977.9	0.005 ± 0.002	2.154*	0.817	-4442
Median BM	0.013 ± 0.001	16.79***	0.284	-3456	985.8	0.005 ± 0.001	6.782***	0.764	-4481
Median GR	0.008 ± 0.001	8.012***	0.083	-3280	881.5	0.005 ± 0.001	3.696***	0.810	-4459
Tropical	-0.024 ± 0.002	-13.88***	0.214	-3389	881.6	-0.003 ± 0.001	-2.654**	0.822	-4453
Africa	-0.004 ± 0.003	-1.529	0.003	-3220	979.1	0.016 ± 0.005	3.108**	0.777	-4447
Island	-0.010 ± 0.002	-6.043***	0.049	-3254	871.7	-0.001 ± 0.001	-1.071	0.813	-4442

Table 6.5: Results of single predictor non-spatial (OLS) and spatial (SAR_{error}) models predicting rate of body-mass evolution (σ^2) within each ecoregion using an unresolved tree. nb dist = optimised neighbourhood distance (km); BM = body-mass; GR = geographic range size. *p < 0.05; **p < 0.01; ***p < 0.001.

	non-spatial					spatial SAR			
predictor	**slope ± se**	**t_{714}**	**r^2**	**AIC**	**nb dist**	**slope ± se**	**z_{712}**	**r^2**	**AIC**
AET	-0.014 ± 0.001	-19.09***	0.338	-4011	924.9	-0.004 ± 0.001	-3.783***	0.681	-4828
Temperature	-0.001 ± <0.001	-23.51***	0.436	-4127	1040	<-0.001 ± <0.001	-1.967*	0.616	-4809
Elevation	<0.001 ± <0.001	1.292	0.002	-3718	956.2	<-0.001 ± <0.001	-0.656	0.782	-4805
Area of ecoregion	0.003 ± <0.001	6.225***	0.051	-3754	924.3	-0.001 ± <0.001	-6.718***	0.786	-4858
Species richness	-0.013 ± 0.001	-14.86***	0.236	-3909	852.7	-0.011 ± 0.001	-13.35***	0.760	-4929
Ordinal richness	-0.009 ± 0.002	-4.510***	0.028	-3736	1001	0.006 ± 0.002	3.342***	0.780	-4818
Median BM	0.011 ± <0.001	22.34***	0.412	-4096	991.3	0.007 ± <0.001	14.43***	0.713	-4988
Median GR	0.007 ± 0.001	10.08***	0.125	-3811	956.4	0.006 ± 0.001	5.695***	0.762	-4836
Tropical	-0.019 ± 0.001	-16.02***	0.265	-3936	1038	-0.001 ± 0.001	-1.728	0.705	-4809
Africa	-0.004 ± 0.002	-1.839	0.005	-3720	956.4	0.006 ± 0.004	1.336	0.781	-4806
Island	-0.006 ± 0.001	-5.615***	0.042	-3747	991.3	-0.001 ± 0.001	-1.241		-4809

Table 6.6: Results of multi-predictor non-spatial (OLS) and spatial (SAR_{error}) models predicting rate of body-mass evolution (σ^2) within each ecoregion using a resolved phylogeny (tree 48). nb dist = optimised neighbourhood distance (km); BM = body-mass; GR = geographic range size; Temp = temperature; Elev = elevation. $^{n.s.}$p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001.

	non-spatial			**spatial SAR** (nb dist = 960.1)		
	d.f. = 696	$\mathbf{r^2}$ = 664	**AIC** = -3966	**d.f.** = 694	$\mathbf{r^2}$ = 604	**AIC** = -4624
predictor	**slope$_{*1000}$ ± se**	**t**	**LR**	**slope$_{*1000}$ ± se**	**z**	**LR**
AET	-3.287 ± 1.197	-2.745**	7.658	0.379 ± 1.212	0.313 $^{n.s.}$	0.097
Temperature	-0.951 ± 0.113	-8.427***	69.07	-1.122 ± 0.159	-7.044***	42.93
Elevation	-0.006 ± 0.001	-5.770***	33.22	-0.006 ± 0.001	-6.438***	38.04
Area of ecoregion	-7.686 ± 7.048	-1.091 $^{n.s.}$	1.214	3.650 ± 4.109	0.889 $^{n.s.}$	0.788
Species richness	-23.42 ± 1.946	-12.03***	134.4	-15.40 ± 1.782	-8.643***	70.93
Ordinal richness	33.22 ± 3.290	10.10***	97.20	22.38 ± 2.786	8.032***	61.75
BM	5.924 ± 13.35	0.444 $^{n.s.}$	0.201	-12.31 ± 10.35	-1.189 $^{n.s.}$	1.411
GR	-8.379 ± 6.202	-1.351 $^{n.s.}$	1.862	-3.901 ± 4.426	-0.881 $^{n.s.}$	0.776
Tropical	-2.387 ± 1.683	-1.418 $^{n.s.}$	2.052	-1.294 ± 1.070	-1.210 $^{n.s.}$	1.462
Africa	-0.948 ± 1.864	-0.508 $^{n.s.}$	0.264	18.07 ± 4.523	3.995***	15.37
Island	-6.759 ± 1.378	-4.904***	24.15	-3.863 ± 1.150	-3.359**	11.18
BM*GR	0.017 ± 0.860	0.020 $^{n.s.}$	< 0.001	0.947 ± 0.663	1.427 $^{n.s.}$	2.032
area*GR	0.573 ± 0.458	1.250 $^{n.s.}$	1.596	-0.214 ± 0.267	-0.803 $^{n.s.}$	0.644
Temp*Elev	< 0.001 ± < 0.001	2.173*	4.809	< 0.001 ± < 0.001	2.885**	8.272

Table 6.7: Results of multi-predictor non-spatial (OLS) and spatial (SAR_{error}) models predicting rate of body-mass evolution (σ^2) within each ecoregion using an unresolved tree. nb dist = optimised neighbourhood distance (km); BM = body-mass; GR = geographic range size; Temp = temperature; Elev = elevation. $^{n.s.}$p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001.

	non-spatial			**spatial SAR** (nb dist = 1062)		
	d.f. = 701	**r^2 =** 782	**AIC =** -4779	**d.f. =** 699	**r^2 =** 433	**AIC =** -5184
predictor	**slope$_{*1000}$ ± se**	**t**	**LR**	**slope$_{*1000}$ ± se**	**z**	**LR**
AET	-0.658 ± 0.683	-0.964 $^{n.s.}$	0.948	2.297 ± 0.800	2.873**	8.105
Temperature	-0.796 ± 0.065	-12.28***	139.4	-0.910 ± 0.111	-8.234***	47.30
Elevation	-0.005 ± 0.001	-8.499***	70.22	-0.005 ± 0.001	-7.422***	43.98
Area of ecoregion	-9.182 ± 4.009	-2.290*	5.339	0.419 ± 2.891	0.145 $^{n.s.}$	0.021
Species richness	-13.47 ± 1.119	-12.03***	134.4	-13.43 ± 1.208	-11.123***	114.0
Ordinal richness	19.76 ± 1.880	10.51***	104.8	21.87 ± 1.884	11.607***	123.3
Median body-mass	-11.69 ± 7.472	-1.565 $^{n.s.}$	2.497	-11.96 ± 7.069	-1.692 $^{n.s.}$	2.857
Median GR	-12.22 ± 3.512	-3.480**	12.26	-4.861 ± 3.052	-1.593 $^{n.s.}$	2.532
Tropical	-1.534 ± 0.971	-1.580 $^{n.s.}$	2.546	0.059 ± 0.751	0.078 $^{n.s.}$	0.006
Africa	-1.438 ± 1.074	-1.339 $^{n.s.}$	1.829	5.062 ± 2.793	1.812 $^{n.s.}$	3.207
Island	-3.994 ± 0.782	-5.109***	26.17	-3.831 ± 0.770	-4.978***	24.31
BM*GR	1.168 ± 0.480	2.434*	6.027	1.064 ± 0.452	2.357*	5.533
area*GR	0.621 ± 0.260	2.383*	5.779	-0.026 ± -0.026	-0.138 $^{n.s.}$	0.019
Temp*Elev	< 0.001 ± < 0.001	1.803 $^{n.s.}$	3.313	< 0.001 ± < 0.001	2.366*	5.574

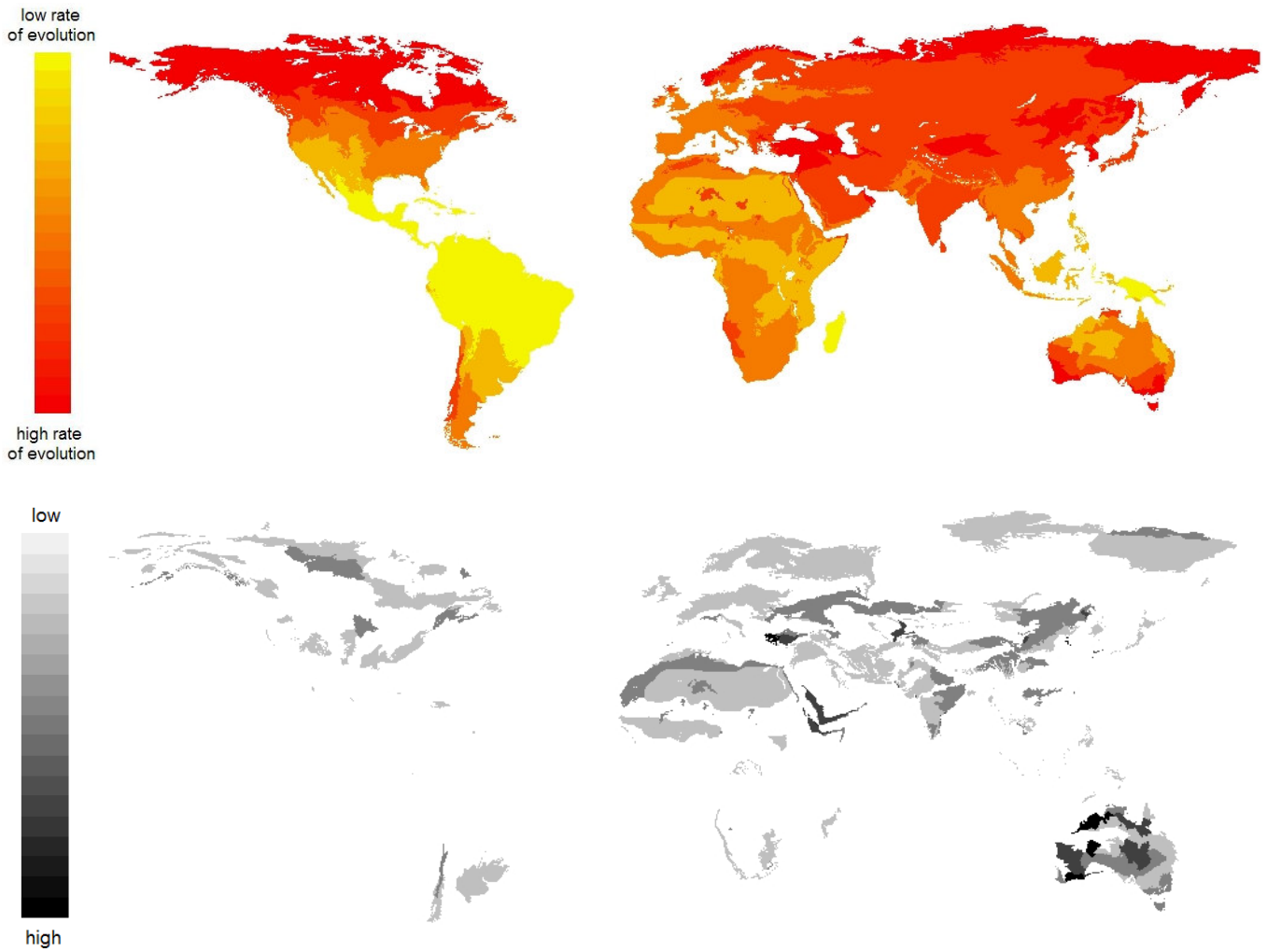


Figure 6.6: Fitted values (top panel) and squared residual values (lower panel) from spatial SAR_{error} models predicting the relative rate of evolution (σ^2) per ecoregion (for ecoregions with > 9 species and using a resolved phylogeny: tree 48).

6.5 Discussion

Models of body-mass evolution

Across all mammals, early burst (EB) is the best single model for explaining body-mass evolution. This suggests that mammals experienced a rapid burst of morphological diversification relatively early in their history, i.e. not necessarily in the Cretaceous, and their diversification rates subsequently slowed. The reasons for this pattern are probably ecological. Before mammals began to dominate the majority of global faunas, the species were able to diversify into many empty niches. This may have been due to colonisation of new areas (EB ecoregions coincide with areas supposed to have experienced major adaptive radiations of mammals, e.g. South America), rapid environmental changes (e.g. the Palaeocene-Eocene thermal maximum; Gingerich 2006), "key innovations", or competitive release following the K-T mass extinction event (Carroll 1997; but see Bininda-Emonds et al. 2007). As time went on, a higher proportion of the available niches became occupied and so the rate of morphological evolution slowed. This fits well with other phylogenetic studies on extant mammals (Bininda-Emonds et al. 2007), and also with palaeontological models and studies (assuming that increased higher taxon richness is correlated with increased morphological disparity; Foote 1997), which suggest that origination rates of higher taxa are faster near the start of a lineage and decrease through time (Sepkoski 1998; Valentine 1980). This pattern holds in Valentine's (1980) model even when extinction is included, a factor that is missing from my models.

Within orders and ecoregions it is generally impossible to differentiate among the three models of evolution. This may reflect a mixture of evolutionary modes within a clade,

or perhaps the masking of the true model by subsequent events, e.g. extinction. There are, however, exceptions where clades do favour a certain model: carnivores, insectivores and lagomorphs all favour the Brownian model of evolution, which is consistent with the results of Harmon et al. (in review). Interestingly, bats favour the OU model of evolution, indicating that their body-mass evolution has been constrained. One possible explanation for this is flight: many have recognised that, due to gravity and energy requirements, there are upper and lower bounds on the size at which flight is possible (Rayner 1996; Stanley 1973b), although the upper limit for bats may reflect other trophic or behavioural factors such as competition with birds, or the constraints imposed by their hanging roosting posture (Rayner 1996). Harmon et al (in review) find that birds also favour an OU model of body size evolution, which lends support to this conjecture. Peramelemorphia (bandicoots and bilbies) also favour the OU model, but are a clade of low-diversity: the ten members of the clade present in this study all have very similar body sizes, and hence apparent bounds on their body-mass range. The one OU ecoregion reflects the high species-richness of Peramelemorphia there.

Primates favour the early burst model of evolution. This suggests that relatively early in their evolution, the clades split into significantly differently-sized lineages (i.e. the large Old World monkeys, small New World species and the even smaller “primitive” species e.g. lemurs and galagos) but that body size was conserved within these lineages. This result is consistent with adaptive radiation in these groups as they colonised new areas (Schluter 2000), and is supported by significant differences among the body size distributions of Primate clades in different regions (Kappeler & Heymann 1996). However, this result may just reflect taxonomic inflation, i.e. the elevation of subspecies to the species level (Isaac et al. 2004), which would result in many similarly-sized

species towards the present with any body size differences being found deep within the tree. Unfortunately Primates are particularly prone to taxonomic inflation, as they are relatively large and charismatic (Isaac et al. 2004).

The lack of decisiveness among the three models has advantages for comparative biologists. Many comparative studies assume a model of Brownian motion evolution, but have been criticised for not confirming this assumption (Freckleton & Harvey 2006). This study shows that the Brownian motion model of evolution is probably an adequate model for most mammalian clades. Certainly the OU and EB models are often no better. This is also true of mammals in Harmon et al. (in review), although they find that within other clades, most notably fish, the OU model is consistently better than BR. In addition, this confirms that using the Brownian rate parameter for later analyses is sensible.

Correlates of rates of body-mass evolution

Within orders, rates of body-mass evolution cannot be explained by either the species richness or age of the order, nor by the median body-mass or median geographic range size of the species within the order. Instead, the variation among within order rates is probably idiosyncratic. For example, low rates in the Perissodactyla may reflect the severely reduced morphological disparity of the group, caused by extinction of many perissodactyls in the Quaternary and earlier (Koch & Barnosky 2006). The highest rates are seen in Artiodactyla and Carnivora, clades with broad geographic distributions, perhaps indicating that exposure to a wide variety of selection pressures increased their rates of evolution.

Around 60% of the variation in ecoregion rates of body-mass evolution can be explained by just a few predictors: high rates are associated with low temperature, low elevation, few species, many orders, whether the ecoregion was within Sub-Saharan Africa, and whether the ecoregion was on a mainland or archipelago rather than an island.

The finding that low elevations are associated with high rates of body-mass evolution is consistent with work on molecular rates of evolution in hummingbirds (Bleiweiss 1998). Topology is also known to influence mammalian body sizes in the Western hemisphere, with larger species found in lower areas (Rodríguez et al. 2008). However, the negative effect of temperature on rate of body-mass evolution is more surprising, since rates of molecular evolution in mammals are expected to increase with environmental temperature (Gillooly et al. 2001) and evolution is believed to be faster in high temperature areas, such as the tropics (Rohde 1978). Certainly species within colder climates are often larger than those in warmer areas (Rodríguez et al. 2008; Roy 2008), so perhaps this causes an increase in the rate of body-mass evolution towards large body size in these areas. However, an increase in the rate of evolution could equally be towards smaller body sizes. Another possibility is that the currently cold ecoregions have been more unstable (in terms of temperature and vegetation) over time than currently warmer ecoregions, and that this climatic instability has promoted faster rates of evolution in low temperature areas due to rapidly changing selection pressures (Stanley 1979). We can be fairly sure that the colder temperate zones have been more climatically variable than the tropics since the last glacial maximum 21,000 years ago (and possibly for hundreds of thousands of years previously; Jansson 2003), but whether these differences operate at a finer spatial scale is unknown. Finally, this pattern could

be due to the differences in the body-mass distributions of species at low and high latitudes. In the tropics, the majority of species are small to medium-sized, whereas in the temperate zone there are species from across the whole size spectrum (Rosenzweig 1995). This may account for the higher rates in colder places. I included the median body-mass of species within an ecoregion to attempt to control for this; however, the median may not completely capture the variation in body-mass distributions.

As the ordinal richness of an area increases, so do the number of body plans. Thus rates of body-mass evolution will increase unless the body sizes of the two orders are similar. This effect will be diluted as the species richness of the different orders increases. High rates therefore reflect low numbers of species within each order. This fits with recent work that showed species diversity can inhibit species evolution and increase niche conservatism (de Mazancourt et al. 2008).

I predicted higher apparent rates of body-mass evolution in Sub-Saharan Africa compared to the rest of the world, due to the Late Quaternary megafaunal extinctions which affected everywhere but Sub-Saharan Africa (Koch & Barnosky 2006): the apparently lower rates of evolution elsewhere are driven by the absence of species at the top end of the body-mass distribution. The model still overestimates rates of body-mass evolution in Europe, possibly due to more recent extinctions of large European mammals, or size-selective harvesting removing the largest individuals and reducing body-mass means (Roy 2008). I also found that island ecoregions had lower rates of body-mass evolution than mainland ecoregions. This is probably caused by differences in the body-mass distributions of island versus mainland mammals (i.e. both the largest and smallest species are absent from islands due to the difficulties of island

colonisation; Lomolino 2005) and would lead to lower apparent rates of body-mass evolution. In addition, large mammals may struggle to survive on small islands due to resource limitations, again removing species from the top-end of the body-mass distribution. The island rule also predicts a lower rate of evolution on islands, because island species are evolving towards a body-mass optimum (Lomolino 2005). However, I reject this explanation, as both the idea of an optimum body size for mammals and the island rule itself are probably unsound (Meiri et al. 2008; Meiri et al. 2005).

Although the model describes around 60% of the variation in rate of body-mass evolution, what of the remaining 40%? Model fit differed among realms, with the best fit in the Neotropics and the worst fit in Australia. These differences may be idiosyncratic, or may reflect environmental or other predictors I failed to include in the models. Recent evolution due to ecological factors may account for the higher apparent rates of evolution at the edges of the Afrotropical and Palaearctic, Palaearctic and Indomalayan, Indomalayan and Australasian, Palaearctic and Nearctic biomes. These are all faunal interchange zones, thus the higher rates may be apparent, i.e. due to an increase in the number of orders emigrating to these areas, or real increases in rate towards the present due to the evolution of body-mass character displacement within these changeable communities. The interchange zone between the Nearctic and Neotropics, however, does not have a high apparent rate of body-mass evolution, perhaps because the land bridge there has existed for longer (around 5.3-1.8 million years compared to the Bering Strait land bridge which was only formed 70,000 years ago) allowing the communities affected by mammalian migrations to reach some kind of body-mass distribution equilibrium.

Clearly, the models I describe above are oversimplifications of the way evolution happened. Most species will have undergone range shifts and most ecoregions will have experienced climatic shifts. Thus even if all the species within an ecoregion did evolve there, it was most likely under different conditions. Making inferences from present-day patterns is therefore difficult. However, although this may confound my attempts to find correlates, it mainly makes the analyses more conservative (following the logic of Davies et al. 2004). Significant correlates of evolutionary rates should reflect the most important variables and may expose ecological factors influencing body-mass evolution closer to the present. Extinction is also an issue; any non-random loss of species of a particular body size will affect rates of evolution. This is quite likely, since we know that rates of both historical and human-mediated extinctions have been higher in large mammals (Cardillo et al. 2005; Liow et al. 2008). Although the interpretation of these results is difficult, they do provide an interesting starting point for further study of body-mass evolution in mammals, particularly on the role of ecological interactions in more recent periods.

Mammalian body-mass evolution appears to be influenced by a complex combination of geography, climate, past human impacts and possibly climate history. This complexity is interesting and has implications for studies of this kind. Macroecologists analysing patterns of body-mass across the world consider geography and ecology, but rarely consider clade history. Conversely those working on body-mass evolution concentrate on historical factors but often ignore geography. My results show that combining both macroecological and macroevolutionary approaches is vital to improving our understanding of body-mass evolution and its associated effects on species' ecology.

Chapter 7: General Conclusions

7.1 How important has competition been in shaping mammalian evolution?

The overall aim of the preceding chapters was to determine how important competition has been in shaping mammalian evolution, using novel, phylogenetic comparative methods and present-day data. To do this I used four study groups: New World leaf-nosed bats (Phyllostomidae), New World monkeys (Platyrrhini), Australasian possums (Phalangeriformes) and ground squirrels (Marmotini). Here I first summarise the results for each of these groups (Table 7.1), then discuss some of the limitations of my methods and whether phylogenetic approaches, and present-day data, are useful and sufficient for this type of study.

Table 7.1: Summary table of results from preceding chapters. bats = Phyllostomidae; monkeys = Platyrrhini; possums = Phalangeriformes; squirrels = Marmotini. ✓ = evidence of competition found; × = evidence of competition not found.

	bats	monkeys	possums	squirrels
Chapter 3	NA	✓×	××	✓✓
Chapter 4	×	×	×	×
Chapter 5	×	✓	×	×
Chapter 6	×	✓	×	×

Bats

I found no significant relationship between bat trait differences and the degree of overlap with competitors when I controlled for phylogeny (Chapter 4). I also found no significant correlation between the relative rate of morphological evolution in bats and

the intensity of competition (Chapter 5). Finally, although Chiroptera as a whole favoured an OU model of body-mass evolution, I was unable to distinguish between the three models of trait evolution tested when only phyllostomid bats were considered (data not shown; Chapter 6). There were no assemblage lists for bats so they were not included in Chapter 3. From these results alone, I conclude that competition was not a dominant factor in the evolution of phyllostomid bats. Although previous studies have shown character displacement within bats (e.g. Gannon & Racz 2006), overdispersed trait patterns are apparently uncommon in bat assemblages (Patterson et al. 2003; Stevens & Willig 2000). This is thought to be because other factors, such as the high mobility of the species, environmental conditions, the physiological constraints of flight, or predation (Patterson et al. 2003; Rydell & Speakman 1995), have greater influence on bat evolution than interspecific competition.

Monkeys

Monkey assemblages showed significant phylogenetic overdispersion, i.e. the species within the assemblages were more distantly related than expected by chance. However, the traits of the species within the assemblages were not overdispersed, suggesting that some process other than competition had caused the pattern of phylogenetic overdispersion (Chapter 3). This result was supported by the fact that species' traits became more similar as overlap with competitors increased (Chapter 4). These results suggest that competition was not dominant in monkey evolution. However, this picture is complicated by results from later chapters which suggest that competition was important. For example, although not part of the best model, competition intensity was a significant correlate of the relative rate of morphological evolution in single predictor regressions (Chapter 5). In addition, the best model of evolution for Primates, and for

New World monkeys alone (data not shown), was the early burst model, which is designed to reflect increasing competition for niches with time (Chapter 6). The importance of competition in primate communities is supported by previous non-phylogenetic studies (e.g. Fleagle 1999; Houle 1997; Peres & Janson 1999), however, species' responses to competition may not be morphological (see below), which may explain why I do not always find evidence of competition.

Another explanation for these conflicting results is taxonomic inflation, i.e. the elevation of subspecies to the species-level (Isaac et al. 2004). Primates are particularly susceptible to taxonomic inflation as they are large, charismatic and studied by many taxonomists (Isaac et al. 2004). When primates are split into new species, the geographic ranges of the elevated subspecies are often just the geographic range of the original species divided in two. This means that sister-species pairs cannot have overlapping geographic ranges, and apparent phylogenetic overdispersion is therefore inevitable (Chapter 3). This also has implications for the analyses where I defined potential competitors as species with overlapping geographic ranges (Chapters 4 and 5), since sister species created in such a way will not have overlapping ranges and thus would not be classed as competitors.

Taxonomic inflation may also influence body size distributions across a phylogeny. Extra species near the present will result in many similarly-sized species at the tips of a phylogeny, and any significant body size differences would only be found deep within the tree. This is the same pattern predicted by the early burst model of trait evolution, the favoured model of body-mass evolution in monkeys. I realised taxonomic inflation might be a issue in primates but I believed that using the taxonomy of Wilson and

Reeder (1993) would reduce the problem compared to using newer taxonomies (e.g. Groves 2001; Wilson & Reeder 2005; see also Isaac et al. 2004).

Possums

The phylogenetic structure and traits of the possum assemblages did not differ from null expectations (Chapter 3). In addition, I found no significant relationship between the species' trait differences and the degree of overlap with competitors when I controlled for phylogeny (Chapter 4). Nor did I find any significant correlation between the relative rate of morphological evolution in possums and the intensity of competition (Chapter 5). Finally, I was unable to distinguish between the three models of body-mass evolution tested, when either Diprotodontia or just Phalangeriformes were considered (data not shown; Chapter 6). From these results alone, I conclude that competition was not dominant in the evolution of possums. It should be noted however, that the possum dataset is small (only 36 species), which may have decreased the power of the analyses to such an extent that significant effects of competition were not detectable. Compared to the other three clades, possums are not well-studied, but several earlier studies on marsupials have implicated competition in community assembly (Russell et al. 1989). However, these results remain controversial since much of the evidence is equivocal (Lee & Cockburn 1985; Russell et al. 1989).

Squirrels

The squirrel assemblages showed significant phylogenetic overdispersion, i.e. the species within the assemblages were more distantly related than expected by chance. The traits of the species within the assemblages were also overdispersed, suggesting that

competition had played an important role in determining the pattern of phylogenetic overdispersion (Chapter 3). However, analyses in subsequent chapters provided evidence to the contrary. For example, after controlling for phylogeny, species' traits became more similar as the amount of overlap with potential competitors increased (Chapter 4). In addition, I failed to find any correlation between the relative rate of morphological evolution in squirrels and the intensity of competition (Chapter 5). Finally, I was unable to distinguish between the three models of body-mass evolution tested. This was the case when either Rodentia or just the Marmotini (data not shown; Chapter 6) were considered. The results of previous studies are also unclear with regards to the importance of competition in squirrel evolution: habitat filtering, rather than competition, has been reported in marmots (Davis 2005), but there are many examples of character displacement in rodents more generally (Dayan & Simberloff 2005).

7.2 Some limitations of the current study

The results presented in this thesis suggest that competition has not been particularly important in shaping the evolution of bats or possums, but that it may have been important in monkeys and squirrels. Across all mammals however, the favoured model of body size evolution was the early burst model, which implies a role for competition in mammalian evolution (Chapter 6). In addition, few would disagree with the statement that mammals compete for resources. Why, then, do my methods not detect an unambiguous role for competition in the four study clades?

One explanation is that, throughout this thesis, the measure of competition was flawed. In Chapter 3, I assumed that species would compete if they currently coexisted and were

within the same clade. In Chapters 4 and 5, I defined potential competitors as species which coexisted, were in within the same clade and the same macroniche. In addition, I assumed that the response of species to competition would either be distributional (i.e. competing species would not coexist in an assemblage; Chapter 3), or morphological (i.e. competing species would exhibit trait differences; Chapters 3, 4 and 5). These measures ignore four key points. Firstly, they assume that the dominant competitive interactions are among closely-related species. Whilst close relatives are, on average, expected to compete most fiercely (Darwin 1859), distant relatives may also compete strongly, e.g. frugivorous birds and bats (Palmeirim 1989). Secondly, the measures assume that the present-day coexistence (in terms of geographic range overlap) of two similar species necessarily implies that the species interact. Heterogeneity of habitats may mean that, although two species' ranges overlap, the species never come into contact with one another. For example, rock squirrels (*Spermophilus variegatus*) and least chipmunks (*Tamias minimus*) have overlapping ranges, but rock squirrels live on rocky outcrops whereas the chipmunks live in forests or meadows (Kays & Wilson 2002). As knowledge of habitat preferences increases, it will be possible to incorporate it into the framework used here. Thirdly, by only looking at distributional and morphological responses to competition, these measures do not detect occasions where competition is reduced by other, perhaps behavioural, mechanisms. For example, different monkey genera are known to forage at different canopy levels (Fleagle 1999), and also vary the degree to which they include other items such as insects and sap in their diets (Nowak 1999). Species may also reduce competition by taking differently-sized food items, using different foraging methods (e.g. aerial versus foliage-gleaning insectivorous bats; Eisenberg 1981), or by foraging at different times of the day (e.g. the genus *Aotus*, owl monkeys, are nocturnal; Nowak 1999). Possums may also reduce

competition by having different altitudinal ranges (Flannery 1995). Finally, as in any analysis using present-day species' geographic ranges, these measures do not consider that species' ranges change through time due to habitat and climate changes. Therefore, a species' current distribution and trait values may be the result of historical competition with a competitor that is now absent (the "ghost of competition past"; Connell 1980).

It is possible that I find little evidence for competition shaping mammalian evolution because competition is truly of limited importance. Brusatte et al. (2008) recently showed that the radiation of the dinosaurs was not due to reduction in competition as previously thought. Other studies have suggested that the number of species has increased exponentially over time and has never reached its limit, which suggests that competitive interactions do not restrict species evolution (Benton & Emerson 2007). However, I think that, given the limitations of the data available to me, and the assumptions of the methods, finding even weak evidence for competition shaping mammalian evolution suggests that it must have some role. A more likely explanation for the weak effect is that the signal of competition has been confounded by the effects of other factors on evolution, such as predation, extinction, climate change or habitat change. These factors have been suggested to account for the weak effects of competition in other systems (Meyer & Kassen 2007; Patterson et al. 2003). All of these factors may also interact with competition to produce present-day patterns in mammals. Future studies should attempt to tease apart these potential drivers of evolutionary change.

7.3 Is studying competition using a phylogenetic approach useful and sufficient?

This thesis demonstrates both the good and bad points of a phylogenetic approach. The advantages were that it was possible to relatively easily, cheaply and quickly study competition in four different study groups and in mammals as a whole (Chapter 6). This made it possible to draw some general conclusions about mammalian evolution. Also, by explicitly considering phylogeny, the phylogenetic relationships between the species were controlled for rather than ignored.

There are, however, limitations to the phylogenetic approaches used here. The major problem was that without a good proxy to determine whether or not species compete, the results can be hard to interpret. For example, a null result could either reflect the absence of an effect of competition, or just that the measure of competition was flawed. It is clearly important that a more sophisticated proxy for the intensity of competition is found. The development of such a measure would require close collaboration between evolutionary biologists, field biologists and palaeoecologists, so that for a given community it would be possible to confirm current competition in the field, and to determine which species may have been interacting in the past. It would also be beneficial if future studies could analyse competition at a range of taxonomic scales. Here, I only considered species within a study clade as competitors, but a more realistic scenario would also include more distant relatives. For example, in tropical frugivores, mammals, birds and even insects should be included to get a true understanding of the role of competition in these systems. Some analyses have already considered competition among bats and birds (Palmeirim 1989; Rydell & Speakman 1995). In the shorter term, it would be interesting to try these methods on other mammalian clades,

and perhaps other groups such as birds, to determine whether the four study clades reflect general mammalian, or even general vertebrate, patterns of evolution.

7.4 Conclusion

In conclusion, I find some support for competition shaping mammalian evolution. However, there is evidence that the importance of other processes may outweigh the effects of competition in some groups. The factors which influence this balance between drivers of evolution remain poorly understood and further study and methodological improvements are required if we are to understand the relative role of competition in mammalian evolution. Generally phylogenetic comparative methods regard evolution in different lineages as independent, ignoring the effects of species interactions. The methods in this thesis present a first step towards including species' interactions in evolutionary studies.

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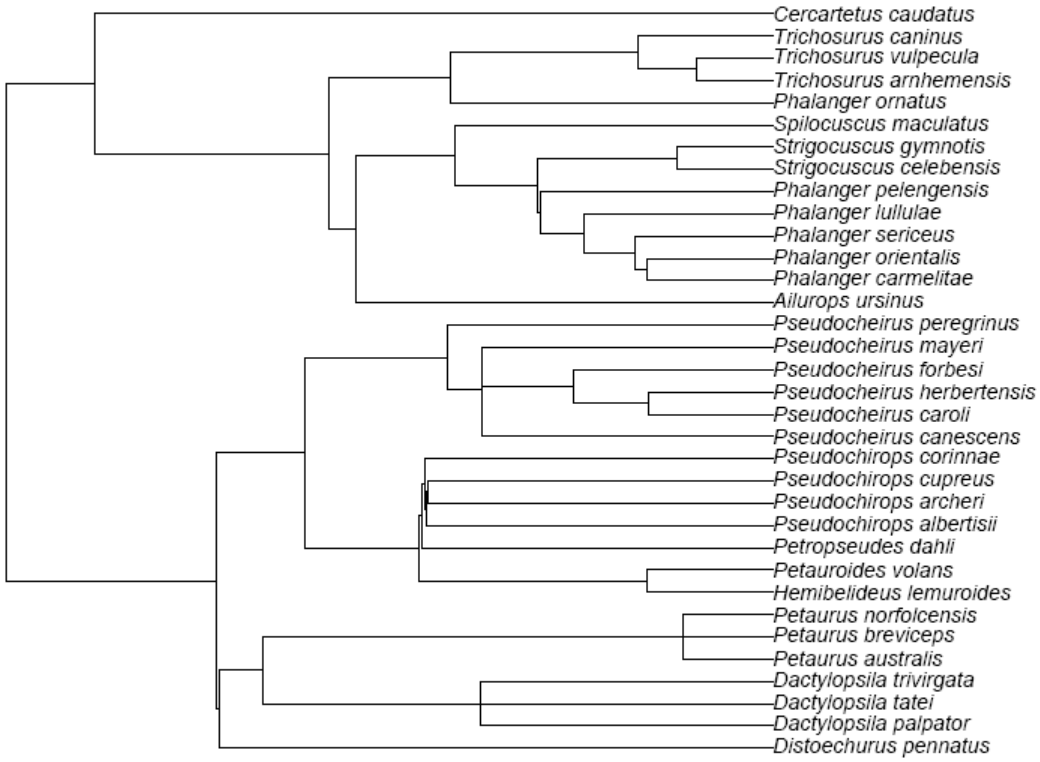
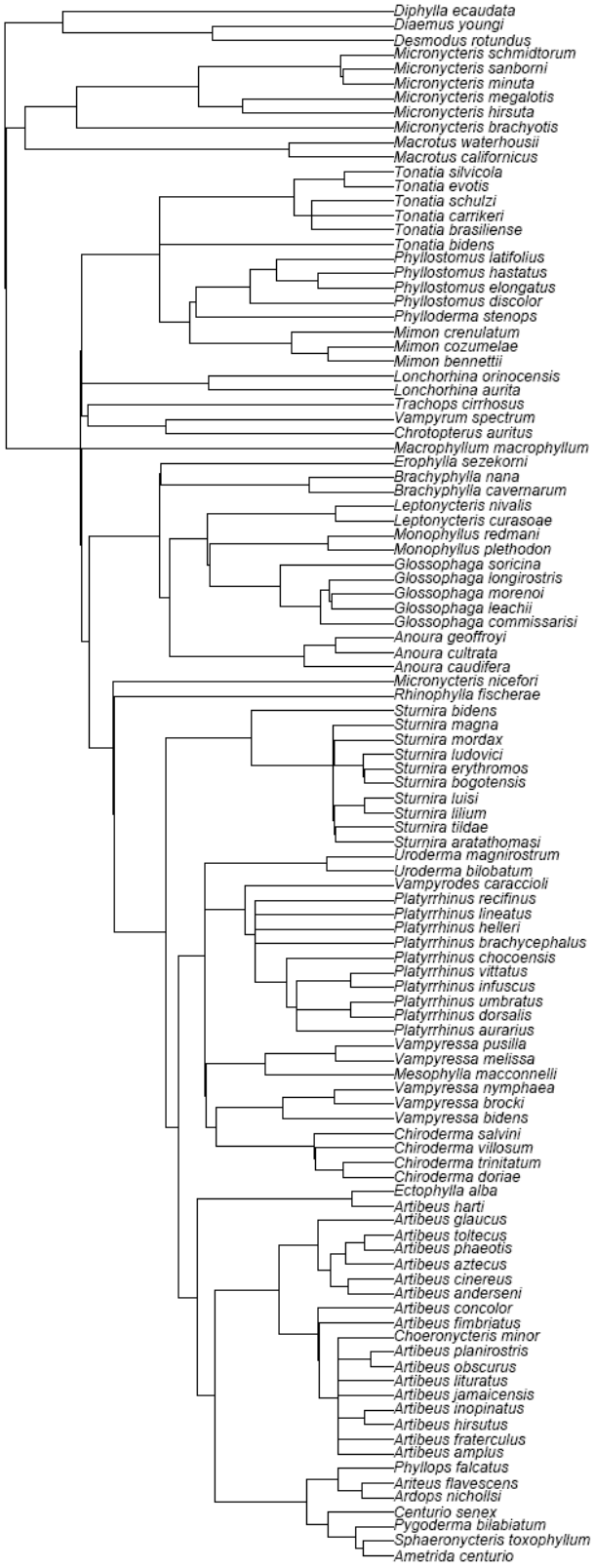
Appendix B: Phylogenetic topologies.

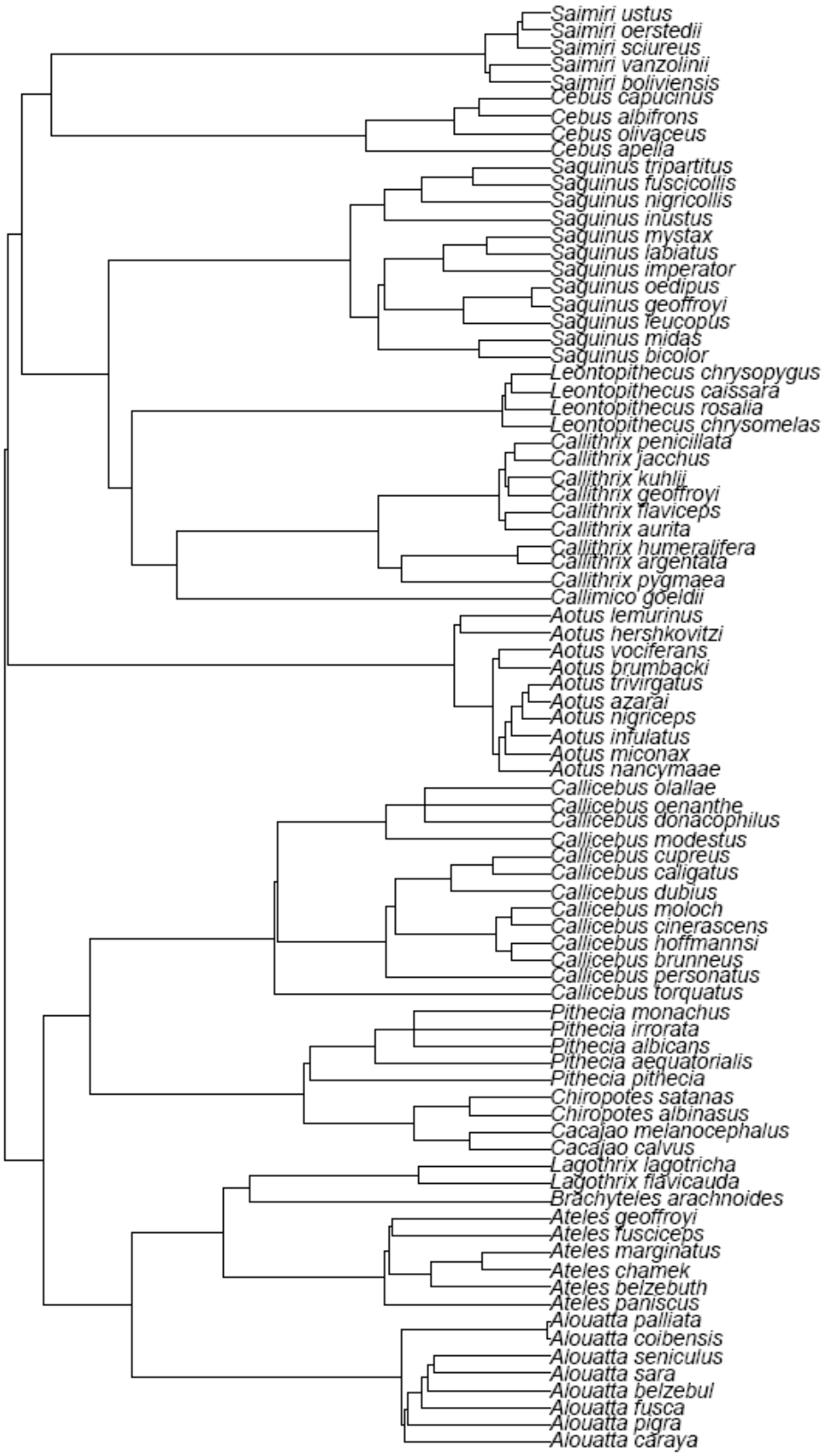
Australasian possums (Phalangeriformes).



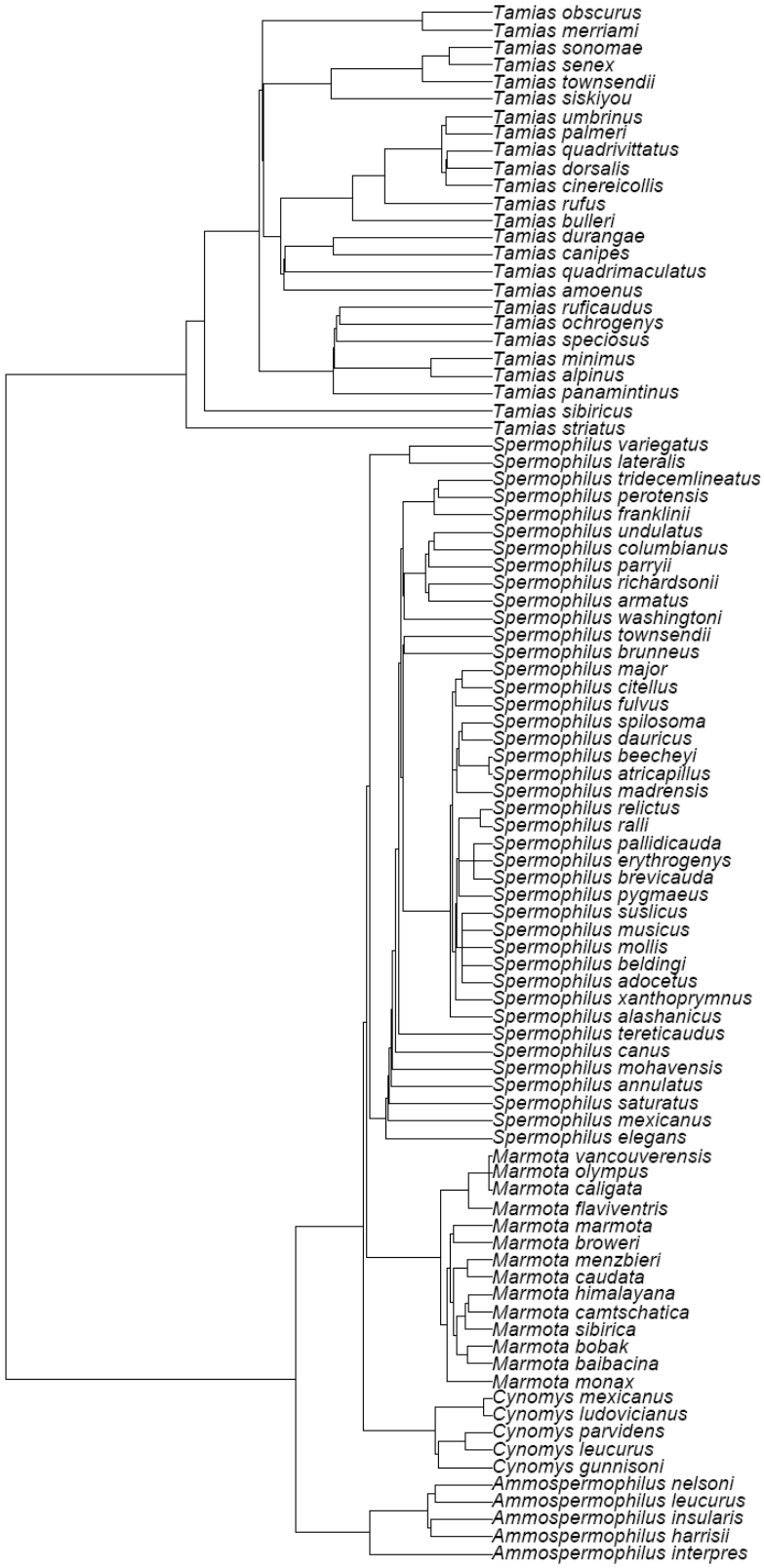
New World leaf-nosed bats (Phyllostomidae).



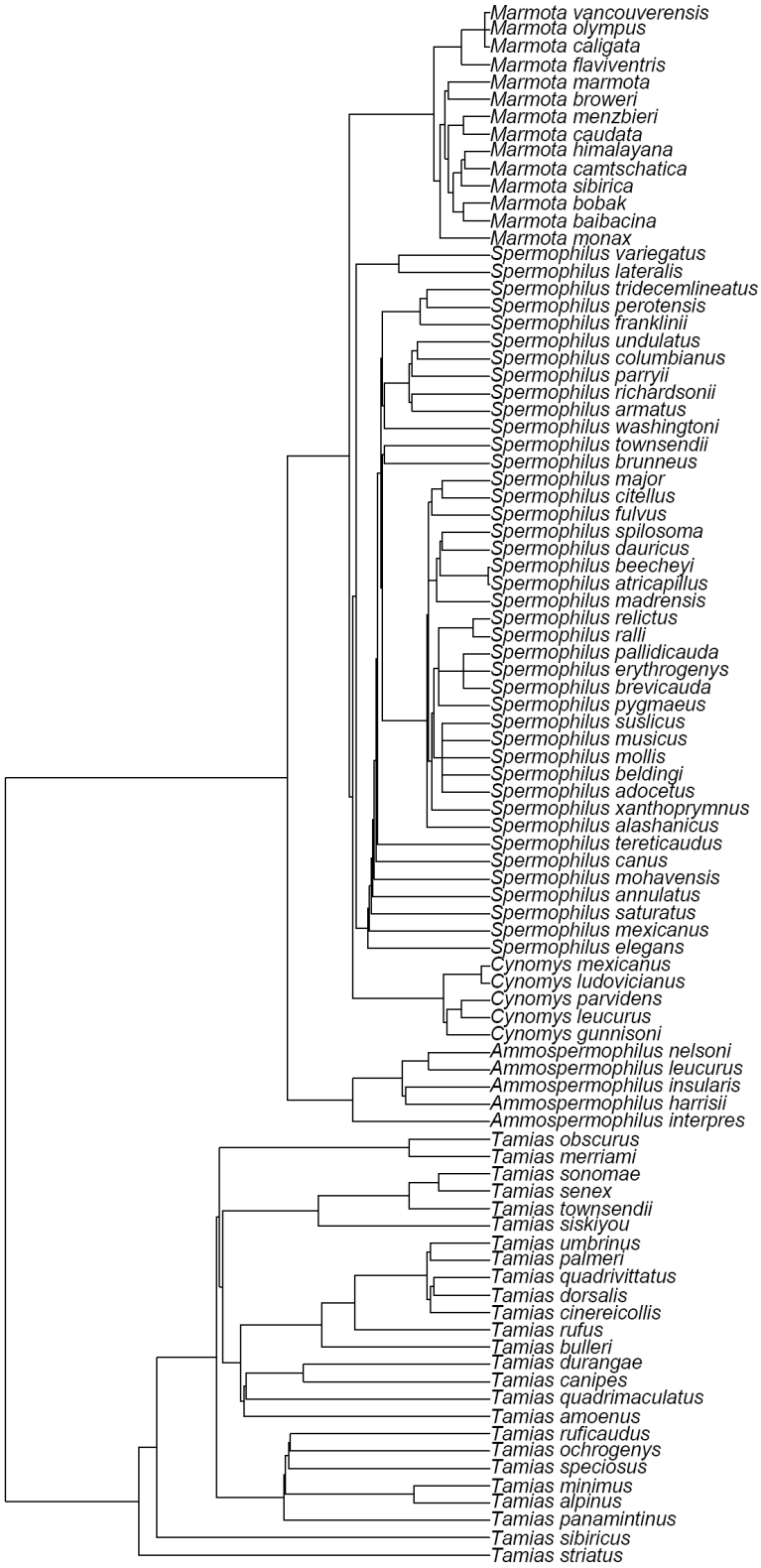
New World Monkeys (Platyrrhini).



Ground squirrels (Marmotini): a) *Cynomys* outgroup topology.



Ground squirrels (Marmotini): b) *Marmota* outgroup topology.



Ground squirrels (Marmotini): c) *Spermophilus* outgroup topology.