THE DISTRIBUTION OF PHYLOGENETIC DIVERSITY OF MAMMALS IN MEXICO AND ITS IMPLICATIONS FOR CONSERVATION

by

ENA EDITH MATA ZAYAS

A thesis submitted to the University of Plymouth

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences

Faculty of Science

2007

Abstract

The current rate of biodiversity loss has stimulated studies aimed at identifying areas of concentration of biodiversity where conservation efforts can be targeted. Phylogeny has become an important element in conservation either to preserve areas of high phylogenetic diversity (and therefore evolutionary history) or to identify species attributes that make them prone to become endangered or at risk of extinction. This dissertation dealt with the quantification of phylogenetic diversity of Mexican mammals, its geographic distribution, and its correlation with both the life history attributes of the species and selected characteristics of the environment. In order to do this, I had to construct a complete and reasonably well-resolved phylogeny of the 416 species of terrestrial mammals. This has allowed assessing the benefits and limitations, as well as the similarities and differences, of the two indices of phylogenetic information currently in use: Faith's index of phylogenetic diversity (*PD*) and Clarke & Warwick's index of taxonomic distinctiveness (*TD*). This has also allowing to evaluate the degree of correspondence between the distribution of these indices and the distribution of the natural protected areas of Mexico and to identify the minimum number of reserves (and their location) that would be required to protect all 416 species. Although these indices show a high degree of correlation, by emphasising slightly different aspects of the topology of the classification, they sometimes differ in their identification of priority areas. The results show that the value of either *PD* or *TD* is determined primarily by species-richness (*S*) and secondarily by the topology of the phylogeny. In general, areas of high phylogenetic complexity (HPA, those made up of distantly-related taxa, independent of their number) are found mainly in regions traditionally recognised as worthy of conservation, such as the Transvolcanic Belt and the tropical South-East region. Comparative analysis employing the method of independent contrasts showed the correlation between different life history attributes of the species, as well as the correlation between these life history attributes and some characteristics of the environment (such as latitudinal range, average temperature and average precipitation in the distribution of each species). This permitted exploration of the benefits and limitations of life histories as subjects for conservation.

List of Contents

List of Tables

List of Figures

List of Equations

List of Abbreviations/Acronyms

CONABIO: National Commission for Biodiversity, Mexico

SNIB: National System of Biodiversity Information, Mexico

PST: Placental Supertree (by Bininda-Edmonds *et al.* 2007)

NPA: Natural Protected Area

CONANP: National Council of Natural Protected Areas, Mexico

SINANP: National System of Protected Natural Areas, Mexico

TVB: Transvolcanic Belt

HPA: High priority areas for conservation (based mostly, buy not exclusively on phylogenetic diversity)

Acknowledgements

First and foremost, I would like to express my gratitude to Dr Miguel Franco for all his support, enthusiasm and encouragement through out this research. Thanks to his valuable guidance, interest and ever friendly attitude I was able to complete my research.

I would also like to thank the other members of my supervisory team, Dr P. Ramsay and Dr D. Bilton for their advice and encouragement through out the course of my studies.

I would like to thank The Mexican Council of Science and Technology (CONACYT) for funding my PhD and research project. I am grateful to the National Commission for Biodiversity (CONABIO, Mexico) for allowing me the use of its biodiversity databases.

My special thanks to Pauline Framingham from the School of Geography for introducing me to the world of GIS and for all her help. I thank Dr Paul Williams of the Natural History Museum, London, for allowing me the use of his WorldMap programme and his early advice on the use of diversity indices. Many thanks to Dr Stephen Heard for his help and time spent teaching me the use of his SkewMatic programme.

Many thanks to the people who made my life in the School of Biological Sciences such a pleasant experience.

To my parents, my deepest gratitude for their continuous support, encouragement and faith.

My warmest gratitude to my husband, Cesar, for his support and always cheerful disposition.

Finally, I wish to thank all my friends and colleagues for making my life in Plymouth so enjoyable. Thank you all very much.

Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

This study was financed by a studentship from the National Council of Science and Technology (Consejo Nacional de Ciencia y Tecnologia), Mexico.

Relevant scientific seminars and conferences were attended at which work was sometimes presented; and several papers are being prepared for publication.

Presentation and Conferences attended:

- Mata Zayas, Ena E. *The distribution of mammal diversity in Mexico.* Internal seminar of the Terrestrial Ecology Research Group (TERG). School of Biological Sciences, May 2006. University of Plymouth.
- Mata-Zayas, Ena E. and Miguel Franco. *The distribution of mammal diversity in Mexico: implications for conservation. VC*'s Research and Innovation Conference. Collaboration in research and innovation: opportunities and benefits. Wednesday 4th April 2007. University of Plymouth. Poster Presentation.
- Mata-Zayas, Ena E. and Miguel Franco. *The distribution of phylogenetic Diversity of Mexican Mammals and its implications for conservation.* XXI Annual Meeting of the Society of Conservation Biology. Nelson Mandela Metropolitan University. Port Elizabeth, South Africa. 1-5 July, 2007. Poster Presentation.

Attended Courses:

- Biological Diversity. School of Biological Sciences. (University of Plymouth).

- Techniques in Botanical Conservation. School of Biological Sciences. (University of Plymouth).
- Gilbert White and Recording: Past, Present and Future (University of Southampton).
- Geographic Information Systems and Spatial Analysis (University of Plymouth).
- Introduction to ArcGIS, ESRI-UK (Exeter).
- GTA Course: Learning, Teaching and Assessment. Theory and Practice (University of Plymouth).
- Systematic conservation planning and the role of software: from data to implementation and management (Nelson Mandela Metropolitan University, South Africa).
- A variety of courses (computing, bibliographic databases, reference manager, personal development, etc) of the Skills Development Programme for research students provided by the Graduate School.

External Contacts:

Dr Paul Williams, The Natural History Museum, London, UK

Dr Stephen Heard. University of New Brunswick, Canada

Word count of main body of thesis: 35,572 words.

Signed .....

Date 14.12.07

CHAPTER 1. GENERAL INTRODUCTION

The world's biological diversity is being eroded rapidly. Loss and fragmentation of habitats, global climate change, as well as overexploitation, invasive species and diseases constitute serious threats to biodiversity (Magurran 1988, Perlman and Adelson 1997, Gaston and Spicer 1998, Margules and Pressey 2000, Ricklefs 2004). The conservation of biodiversity, including the conservation of essential ecological and evolutionary processes, is one of the most important issues in current biological research (Ferson and Burgman 2000, Mace *et al.* 2000, Pullin 2002, Balmford *et al.* 2005). In order to set long-term conservation priorities, it is necessary to develop appropriate concepts and methodology, as well as to collect the relevant data.

Recent research on the quantification of biological diversity attempts to incorporate the degree of differentiation of organisms in a community or sample by taking into account their taxonomic or phylogenetic relatedness. In so doing it attempts to gauge the more difficult to quantify component of genetic diversity (Humphries *et al.* 1995). These measures of taxonomic and phylogenetic diversity, combined with other attributes such as rarity, endemism and vulnerability of individual taxa, have been used either in isolation or in various combinations in conservation studies (Walker and Faith 1994, Freitag *et al.* 1997, Polasky *et al.* 2001, Posadas *et al.* 2001, Rodrigues and Gaston 2002a, Keith *et al.* 2005, Davies *et al.* 2007, Vamosi and Vamosi 2007). Despite their recent popularity, these measures have not had sufficient impact on conservation planning, and their

application faces limitations due to incomplete phylogenetic information. This, however, is changing as more detailed phylogenetic information becomes available for many taxa.

The quantification of the phylogenetic biodiversity of mammals in Mexico and its distribution, and the identification of areas of conservation value are the fundamental problems that this dissertation attempts to tackle.

1.1 BACKGROUND

Species richness is the most commonly used measure of biodiversity (Purvis and Hector, 2000). There is, however, no reason to single out species, as richness can also be calculated at any taxonomic level.

Darwin's conceptual framework included two components (Darwin 1859): 1) all organisms are connected by common ancestry (the phylogeny) and 2) the forms and function of organisms are closely tied to the environments where they live (they must therefore be characterised by specific spatial patterns of distribution). Because there is a continuum of relatedness among all organisms (this was a crucial corollary of Darwin's work), taking this degree of relatedness into account comes closer to estimate the more difficult to measure level of genetic diversity. Indices that take phylogenetic information (genetic distance between species) into account are known as measures of phylogenetic diversity.

I will make use of phylogenetic information in the account of the geographic distribution of mammal diversity, employing the mammals of Mexico as a case

study, in the understanding that biodiversity has a historical and evolutionary component. This task will involve:

1. Construction of a phylogenetic tree from the published systematic information of the group.
2. Measuring phylogenetic diversity on a country-wide scale.
3. Evaluating the effect that incomplete phylogenetic information has on perceived patterns of biodiversity.

Mammals are a taxonomic group that has been intensively studied all over the world, and Mexico is no exception. Their geographic patterns are well known and studied from different points of view and employing different tools (Arita *et al.* 1997, Fa and Morales 1998, Arita and Figueroa 1999, Ceballos *et al.* 2002a, Escalante *et al.* 2003, Vazquez and Gaston 2004, Sanchez-Cordero *et al.* 2005). Mammals are present in all habitats and occupy a variety of positions in the food chain. Their presence in an area reflects both the adaptations that enable them to thrive there and the general wellbeing of the habitat. In addition to this, the phylogenetic relationships within the mammals are fairly well documented.

1.2 STRUCTURE OF THE THESIS

This thesis has two main aims. Firstly, to quantify phylogenetic diversity of Mexican mammals, and secondly, to explore its distribution in order to identify priority areas for conservation. Specifically, the thesis is divided into chapters, each of which tackles the following issues:

Chapter 2, Current Priorities in the Conservation of Biodiversity. This chapter describes what the main tendencies in conservation planning are, and how phylogeny has become an important tool in biological conservation.

Chapter 3, CONABIOs Biodiversity Databases, discusses the use of databases on biodiversity research, and uses the data of the Mexican National Commission of Biodiversity to illustrate the advantages and limitations of databases compiled from a variety of sources.

Chapter 4, The taxonomy and phylogeny of Mexican mammals, presents two contrasting, systematic classifications: 1) a straightforward Linnaean taxonomy and 2) a hypothetical phylogenetic supertree constructed from information in the literature.

Chapter 5, The phylogenetic diversity of Mexican mammals, employs several indices proposed to measure phylogenetic diversity and tree shape to quantify the diversity of Mexican mammals.

Chapter 6, The geographic distribution of phylogenetic diversity, looks at the geographic distribution of the diversity measures calculated in the previous chapter and investigates their relationship with geographic and environmental traits.

Chapter 7, Life history, distribution and risk, examines whether some ecological and evolutionary characteristics are associated with diverse taxa while others are associated with rare, endemic and threatened ones

Finally, **Chapter 8**, General discussion, addresses the general issue of the role that phylogeny has in identifying priority areas for conservation.

CHAPTER 2. CURRENT PRIORITIES IN THE CONSERVATION OF BIODIVERSITY

2.1 INTRODUCTION

Life has existed on Earth for about four thousand million years. During this time, and despite major catastrophic events, the variety of life has gradually increased (Perlman and Adelson 1997). The current term for this richness and diversity of life is *Biodiversity*. Global patterns of the distribution of biodiversity are the result of a variety of ecological and evolutionary processes, historical events and geographical circumstances (Gaston 2000). How is biodiversity distributed across the surface of the Earth? The answer to this question is not only of academic interest, but is also important to address the urgent need to conserve biodiversity from degradation and extinction (Williams *et al.* 1997). Before we can even begin to address this question, we must start by agreeing on a definition of biodiversity and how to measure it.

2.1.1 DEFINITION OF BIODIVERSITY

The term biodiversity was coined during the National Forum on Biological Diversity by E. O. Wilson (1988). The most accepted definition of Biological Diversity is the one agreed during the Meeting of the Commission on Biological Diversity in 1992 (CBD 1996). This refers to the variety of life on Earth; it includes terrestrial and aquatic ecosystems, ecological processes and the diversity of

species and individuals within each species. Biodiversity can be conveniently measured at three levels of biological complexity: ecosystems, species and genes. The biodiversity of a geographic area is reflected in the different types of ecosystems that it contains, the number of species, the changes in species richness from one region to another, the number of endemics, subspecies, varieties or races, as well as in the genetic variability between and within species (Heywood *et al.* 1995, Gaston 1996a, Gaston and Spicer 1998, Neyra and Durand 1998, Purvis and Hector 2000).

The Earth is currently experiencing an unprecedented decline in biological diversity (Maurer 1994). Given the rate at which this decline is occurring, it is generally accepted that conservation efforts must be addressed in the understanding that only a small fraction of species can be protected (Cabeza and Moilanen 2001). In order to set priorities for conservation, it is necessary to define operational measures of biodiversity that would allow us to identify, as objectively as possible, those areas whose protection would result in the conservation of the maximum amount of biodiversity.

2.1.2 Biodiversity Measures for Conservation

Measures of biodiversity are used in a variety of ecological and conservation studies (Magurran 1988, Perlman and Adelson 1997). The more commonly employed measures are:

- **Species Richness (*S*)**: This is a direct measure of diversity; it is defined as the total number of species present in an area. It does not take into account their relative abundances or their distribution.
- **Simpson Index (*D*)**: This takes into account both the richness and the proportion of each species from a sample within a particular area. The index assumes that the proportion of individuals in an area is a measure of their importance.
- **Shannon index (*H*)**: Similar to the Simpson's index, this measurement takes into account species richness and proportion of each species within an area. The index comes from information theory and is a measure of the likelihood of correctly guessing a species in the sample. Thus, it measures the information content of this sample.

Although biodiversity can be measured at other taxonomic levels (Sogin and Hinkle 1997), the species level represents an identifiable, objective and convenient level of study.

- **Higher taxa richness**

  Richness can be also calculated as the number of genera, families, orders, classes, etc in a given area. Higher taxon richness has been suggested to be a useful surrogate for species richness and a better surrogate than species for gene and phylogenetic diversity. Indeed, several studies support the relationship between the number of higher taxa, such as families, and the number of species among different areas (Roy *et al.* 1996, Williams *et al.* 1997, Balmford *et al.* 2000, Viveiros 2002, Villaseñor *et al.*

2005). However, because the equivalence of taxonomic categories above the species level is unwarranted, the species level is still arguably the most objective genetic and geographic unit.

Traditional diversity indices (such as *S*, *D* and *H*) do not depend on taxonomic relations between species and implicitly assume that all species are equal and should count the same. Currently, however, it is accepted that not all taxa need to be treated equally when priorities for conservation are being set (Vane-Wright *et al.* 1991, Vazquez and Gittleman 1998, Barker 2002). This is because species are not equivalent in terms of the amount of unique evolutionary history that they represent. Some authors have proposed giving different weight to species because some species are more distinctive and genetically isolated than others and would represent a more significant loss if they became extinct (May 1990, Crozier 1997, Nee and May 1997). For instance, one species of apomictic *Taraxacum* (Class Magnoliopsida) may not deserve the same attention as *Welwitschia mirabilis*, a gymnosperm that is the single representative of order Welwitschiales (Class Gnetopsida; von Willert 1994). Another classical example of species that represent disproportionate amounts of evolutionary history are the tuataras (*Sphenodon punctatus and S. gunther*i), which are the sole survivors of Order Sphenodontia (Class Reptiles; Daugherty *et al.* 1990). Thus, a new kind of diversity measures that take the degree of relatedness of the species in an area into account has been developed to incorporate evolutionary processes in systematic conservation planning (Bininda-Emonds *et al.* 2000, Purvis *et al.* 2005b).

2.2 PHYLOGENY AND CONSERVATION

The concept of biodiversity is based on the differences that naturally exist among organisms. Biologists have argued that the value of biodiversity is associated with the variety of genes that can be expressed by organisms as potentially useful phenotypic traits or characters (morphological features, behaviour, biochemistry, etc). In the absence of detailed genetic information for every organism on the planet, an informed phylogenetic tree (hypothesis) represents the best approximation to quantifying the degree of relatedness of organisms in a community. The utility of a phylogenetic classification lies in aiming at protecting areas that not only have many species, but species that are clearly different. This is because any difference between two species begins by those differences being expressed through their genes (Williams *et al.* 1994, Humphries *et al.* 1995). Therefore, phylogenetic diversity acts as a surrogate of the more difficult to quantify genetic diversity.

It is conceivable that two communities may be identical in terms of richness and evenness, but they are likely to differ in the degree of taxonomic/phylogenetic relatedness of their constituent species. Most published studies on conservation and reserve design apply methods that maximise species diversity as a surrogate for the broader biological/genetic diversity that ought to be protected. However, species richness may not be an ideal measure of biodiversity, as it assumes that all species have the same value as conservation units (Vane-Wright *et al.* 1991, Balmford *et al.* 1996, Clarke and Warwick 1998, Rodrigues and Gaston 2002a). Pielou (1975) was one of the first authors to suggest that diversity would be higher in a community in which species were divided amongst many genera as opposed

to one where the majority of species belong to the same genus. This point of view has been supported and expanded in the last decade (May 1990, Vane-Wright *et al.* 1991, Faith 1996, Williams *et al.* 1996b, Mace *et al.* 2003).

On the other hand, speciation and extinction have an important phylogenetic component (Nee and May 1997, Heard and Mooers 2000). Thus, the extinction of species not closely related to any other living ones would represent a disproportionate loss of evolutionary history and genetic diversity, much greater than the extinction of individual species which have many close relatives (Faith 1994, Purvis and Hector 2000, Polasky *et al.* 2001, Rodrigues and Gaston 2002a). These different species, and the places where they live, should therefore, have priority for conservation (Vazquez and Gittleman 1998, Barker 2002). A measure of biological diversity that considered the taxonomic/phylogenetic relationships among species, and therefore their evolutionary history, ought to be preferred over a simple measure of species richness when selecting areas for conservation (Caley and Schulter 1997, Reyers and van Jaarsveld 2000, Pullin 2002).

Indices based on taxonomic/phylogenetic information attempt to measure this evolutionary component of biodiversity. Assemblages with the highest taxonomic/phylogenetic diversity will be those that contain species which differentiated earlier in their evolutionary history and, therefore, show a larger taxonomic/phylogenetic differentiation. Methods that employ measures of taxonomic/phylogenetic diversity for setting up conservation priorities are focused on maximizing the variety, rather than just the number of species (the twigs of the tree). If extinction (i.e., pruning of the evolutionary tree) is inevitable, it is preferable to keep twigs surviving in as many branches as possible, rather than in

a single branch in what may be an "awkward position" in the tree. Pushing the analogy further, and although this would obviously take a long time, while the former would eventually reconstitute the general shape of the tree, the latter will inevitably bend it in a particular direction.

Several measures have been proposed to quantify the degree of differentiation of species in an assemblage (Crozier 1997, Bininda-Emonds *et al.* 2000, Crozier *et al.* 2006). These measures include:

- Genetic Diversity (GD) based on genetic-distance methods (Crozier 1992, 1997),
- Phylogenetic Diversity (PD; Faith 1992) and Taxonomic Distinctness TD (Clarke and Warwick 1998), which are measures of total and average distance, respectively, along the phylogenetic tree,
- Taxonomic Endemicity Standardized Weight Index, which attempts to combine taxonomic differentiation of the taxa with their endemicity (Posadas *et al.* 2001),
- The fraction of evolutionary history preserved after an extinction event (Nee and May 1997), and, more recently,
- Indices of phylogenetic variability, richness and eveness (Helmus *et al.* (2007).

Among all these measures, two general measures of phylogenetic diversity with clear conceptual significance and wide applicability will be considered in this study. These are the Phylogenetic Diversity Index and the Taxonomic Distinctness (or Distinctiveness) Index.

2.2.1 PHYLOGENETIC DIVERSITY

The index of phylogenetic diversity (*PD*) measures how closely related the species in an assemblage are (Faith 1994). It is based on known branch lengths of the phylogenetic tree of a taxon in an area: *PD* is the cumulative branch length of the full tree. In general, patterns of differences among species are most likely to be congruent with the pattern of their genealogical relationships through genetic inheritance. The level of *PD* thus tends to capture not only the degree of relationships, but also the degree of difference in the biological characteristics of the taxa under consideration (Vane-Wright *et al.* 1991, Faith 1994, 1996). However, because *PD* is a measure of total diversity, as new species are added to the list *PD* always increases. This is said to make *PD* highly dependent on species richness and thus, sampling effort, i.e., the completeness of the species record in the area of study (Clarke and Warwick 2001).

2.2.2 TAXONOMIC DISTINCTIVENESS

Clarke and Warwick (1998) defined an index of phylogenetic dissimilarity which they termed Taxonomic Distinctiveness (*TD*). As with *PD*, *TD* could be calculated for a particular taxon in a particular biological community. However, unlike *PD* which is a measure of total branch length of the phylogenetic classification, taxonomic distinctiveness is a measure of average length. It measures the average distance between a pair of species in the community sample. Although originally Clark and Warwick employed a taxonomic classification (hence the name of their index), taxonomic distinctiveness can be

calculated employing either a standard Linnaean taxonomy or a phylogenetic tree connecting all the species in the dataset. The same is true of *PD*. This makes the choice of names rather unfortunate. Nonetheless, because of historical precedence, we will employ to these names. However, to avoid continuous reference to these misnomers, we will make use of their acronyms. What the reader must remember is that they are indices of taxonomic/phylogenetic dissimilarity.

Both *PD* and *TD* provide some advantages over simple species richness and traditional species diversity indices. Like the latter, they could also be weighted by the abundance of species in the dataset. In practice, however, this information is not usually available in records of species richness in a locality. On the plus side, it means *PD* and *TD* can be calculated from simple species presence-absence data. In recent years there has been some discussion over the relative merits of *PD* and *TD* (Bininda-Emonds *et al.* 2000, Magurran 2004, Rodrigues *et al.* 2005). For example Clarke and Warwick argue that *TD* is preferable over *PD* because: 1) It is independent of the total number of species in the sample, i.e. it is robust against variation in sampling effort; 2) It can be compared across studies and sites; and 3) It appears to be more sensitive to measure the consequences of environmental degradation than richness estimates, which show initial increases as generalist species move in (von Euler and Svensson 2001, Pullin 2002, Magurran 2004). The truth of the matter is that, although arriving at their estimated values employing different algorithms, *PD* and *TD* measure essentially the same property of the sample. Thus, although *PD* is a measure of total branch length of the tree, the average *PD* can easily be

calculated by dividing *PD* by the number of species in the sample. By the same token, multiplying *TD* by the number of species provides an analogue of *PD*.

As mentioned above, a similar confusion arises from their names. Both *PD* and *TD* can be calculated employing either a taxonomic or a phylogenetic classification. The choice is not a matter of taste but of availability of information. It seems obvious that, if a phylogenetic classification exists, this should be preferred over a taxonomic one. Nonetheless, in order to compare their performance when the nature and quality of the classification varies, in this dissertation we employ both a taxonomic and a phylogenetic classification of the organisms under study.

To simplify matters, in this dissertation we will redefine *PD* and *TD* as measures of total diversity. Their corresponding average measures will be denoted *AvePD* and *AveTD*. When referring to any of these measures, we will indistinctly employ the generic denominations of either "taxonomic diversity" or "phylogenetic diversity", with the added qualification total or average.

2.2.3 Conservation

To plan conservation strategies that minimize the loss of evolutionary history, we must understand how this loss is related to phylogenetic patterns in current extinction risks and past speciation rates (Nee and May 1997). The use of phylogenetic-based information indices could help to assist decisions concerning conservation priorities because they consider the evolutionary component of biodiversity and allow identification of those areas that will ensure the preservation

of the evolutionary potential implicit in phylogenetically diverse communities (Brooks *et al.* 1992). In order to test the performance of both *PD* and *TD*, we will explore the patterns of geographic distribution of both their total and average measures applied to information from Mexico. These measures of diversity can be used in conjunction with species richness, rarity and threatened status in setting conservation priorities (Virolainen *et al.* 1999).

Brooks and McLennan (1991) suggest that historical ecological methods, such as phylogenetic and macroecological investigations, can provide information that will complement current conservation/management practices. To discover generalities, it is important to consider the influence of linage-specific traits (Harvey and Pagel 1991). Unfortunately, shared phylogenetic history means species are not statistically independent entities. Therefore, direct analyses using standard statistical tests are inappropriate (Harvey and Pagel 1991). This non-independence of the characteristics of species invalidates many statistical tests used in examining the co-evolution of traits in comparative analyses (Felsenstein 1985, Harvey and Pagel 1991, Garland et al. 1992, Jones and Purvis 1997, Jones et al. 2003a). In recent years, there has been a surge of methods specifically designed to deal with this limitation. In particular, the use of independent contrasts (Felsenstein 1985, Purvis and Rambaut 1995) has allowed robust testing of the presumed correlated evolution of individual traits. In the context of the present investigation, this allows us to investigate the relationship between life history traits and both measures of the environment and measures of the degree of threat that individual species are subject to.

2.3 THE DISTRIBUTION OF BIODIVERSITY

Biodiversity is unevenly distributed; its variation is explained by different ecological and historical factors. A large proportion of the diversity of organisms can be explained in terms of their geographic patterns, e.g., range size, endemicity and gradients of biodiversity in latitude and altitude (Gaston and Williams 1996, Caley and Schulter 1997). In addition, it is recognized that many ecological processes at the local community level are influenced by processes occurring at much larger scales than the local plots traditionally studied to elucidate them would suggest (Maurer 1994, Caley and Schulter 1997, Ricklefs 2004).

The most widely cited example of a direct gradient in overall taxonomic diversity is latitude. Overall, taxonomic diversity is high towards the tropics and decreases towards the poles. Diversity is also generally observed to be higher in low to middle elevations and in forests; and to be lower at higher altitudes and in arid regions. Nevertheless there are some groups that do not present these patterns, like some butterflies and birds (Prendergast *et al.* 1993, Gaston and Williams 1996), or whole plant families whose primary adaptation is to some limiting physical condition, such as cacti (Tellez-Valdes and DiVila-Aranda 2003, Ortega-Baes *et al.* 2006).

Another aspect related to spatial pattern is endemicity. Endemism occurs when a species or other taxonomic group is restricted to a particular geographic region, due to factors such as isolation or response to ecological or climatic conditions. Thus, a taxon is said to be endemic to a particular region. The size of the region will usually depend on the level of the taxon under consideration: other

things being equal, it is expected that a family will be endemic to a much larger area than a species. High levels of endemism mean that a high proportion of species are found in this location and nowhere else. Endemism can also be viewed as a form of range-size rarity (Gaston and Williams 1996). Some studies suggest that aggregates of endemic species are often located in areas immediately adjacent to areas with dense human populations, possibly because traditional human settlements relied on ecoclimatic conditions which also determined the peaks of endemism (Fjeldsa 2000). Levels of endemism show some common patterns of variation with area, latitude and species richness (Gaston and Spicer 2004). Taxa endemics to a region tend to rise as the area size increases. When considering the latitude, the number of endemics tends to increase towards the equator. Levels of endemism and of species richness tend to be positively correlated, often approximating a power function (Brummitt and Lughadha 2003, Fa and Funk 2007).

A high proportion of the variation in species richness can also be explained in terms of environmental variables such as temperature, precipitation, productivity and topography, as well as their interactions and co-variation (Gaston and Williams 1996, Vazquez and Gaston 2004). These relationships are useful to understand how the environmental conditions affect rates of speciation and extinction, the resources available for species, and the interactions with the physiological attributes of species (Vazquez and Gaston 2004).

Researchers typically want to know if one area is more diverse than another. Assuming the community is a natural unit (Harper and Hawksworth 1995), ecologists recognize that species form a characteristic grouping, which is

also associated with particular geographic localities (Magurran 2004). For this reason, maps of large-scale biodiversity are a useful tool to guide conservation efforts (Williams *et al.* 1997, Williams *et al.* 2002a). But, not effective at regional or local levels.

2.3.1 Megadiverse Countries and Mexico

Seventeen countries in the world are catalogued as megadiverse. Together, these countries contain ~75 % of the total biodiversity of the planet (Mittermeier *et al.* 1997). Their high diversity is measured in terms of the number of vascular plants and vertebrate species as well as the number of endemics. Most of these countries are located in the tropics (Fig. 2.1). Mexico is one of those countries; it occupies the fourth place in the world in terms of biological diversity (Mittermeier *et al.* 1997). Together with Brazil, Colombia and Indonesia, it has one of the highest number of species in the world (Table 2.1).

Figure 2.1 Megadiverse countries (in black) according to Mittermeir *et al.* (1997).

Mexico holds ~10% of the terrestrial diversity of the planet (Mittermeier *et al.* 1997). A variety of factors accounts for this diversity. These include the various climates and geomorphological features which result in a variety of vegetation types; similarly, the complex topography presumably allows, first, geographic and, then, genetic isolation of populations. Finally, the particular biogeographic history of the region, which allowed the mixing of Nearctic and Neotropical taxa and produced an incredibly varied flora and fauna (Fa and Morales 1998, Neyra and Durand 1998) .

Table 2.1 Megadiverse countries in terms of vascular plants and vertebrates (Mittermeier and Goettsch Mittermeier, 1997).

Taxon	Country (number of species)				
Vascular Plants	Brazil (53,000)	Colombia (48,000)	Indonesia (35,000)	China (28,000)	**Mexico (26,000)**
Amphibians	Colombia (583)	Brazil (517)	Ecuador (402)	**Mexico (284)**	China (247)
Reptiles	Australia (755)	**Mexico (717)**	Colombia (520)	Indonesia (511)	Brazil (468)
Birds	Colombia (1,815)	Peru (1,703)	Brazil (1,622)	Ecuador (1,559)	Indonesia (1,531)
Mammals	Brazil (524)	**Mexico (522)**	Indonesia (515)	China (499)	Colombia (456)

2.4 PRACTICAL APPROACHES TO PROTECTED AREA DESIGNATION

It is generally assumed, that the most effective way of preserving biodiversity is by maintaining populations of native species in their natural ecosystems through the establishment of natural reserves (Margules and Pressey 2000, Cabeza and Moilanen 2001, Posadas *et al.* 2001). Ecologists and conservation biologists are often responsible for the design of nature reserves or protected areas which provide different habitats to support a variety of species. Because it is not always possible to sample intensively enough to produce even a rough estimate of species number, ecologist have searched for alternative means of identifying relevant areas for conservation (Pullin 2002).The establishment of a reserve system can be summed up in two essential steps (Margules and Pressey 2000, Cabeza and Moilanen 2001, Cabeza 2003):

1. The definition of explicit conservation goals for the planning region; i.e, the selected criteria for measuring conservation value.
2. The application of optimization methods (or algorithms) to select those sites that meet the criteria in the most efficient way.

Optimal selection of reserves depends on the understanding of regional biodiversity patterns (Kerr 1997). However, in some circumstances, there is not enough information on the distribution of biodiversity attributes, such as endemicity, rarity, etc. It has been suggested that no single measure is adequate for a complete evaluation of biodiversity, so it would seem more adequate to integrate different approaches to produce a broad perspective on conservation

priorities (Prendergast *et al.* 1993, Kerr 1997, Posadas *et al.* 2001, Bonn *et al.* 2002, Justus and Sarkar 2002). Surrogacy approaches are becoming increasingly popular and can in some instances successfully map richness gradients (Williams *et al.* 2002b). Therefore, it is important to explore surrogates or indicators that can be used for reserve selection and, it is also recommended, include macroecological analysis of patterns and processes affecting occurrence, richness, and persistence of biodiversity at different temporal and spatial scales (Blackburn and Gaston 1998).

Some common criteria for evaluating conservation value that could be incorporated into the selection procedure are listed in Table 2.2 (Gaston and Williams 1996, Kerr 1997, Maddock and Benn 2000, Margules and Pressey 2000, Myers *et al.* 2000, Justus and Sarkar 2002, Coppolillo *et al.* 2004, for a more detailed list see Redford *et al* 2003). Redford *et al.* (2003) emphasize that, before collaboration can take place in conservation, participants must understand the different approaches and priorities.

An important aim of a reserve system is to represent the largest possible variety of biodiversity and to assure the long term persistence of species, habitats and natural processes characteristic of a certain region (Pressey *et al.* 1996, Margules and Pressey 2000, Possingham *et al.* 2000, Rodrigues and Gaston 2002b). The method normally used to select protected areas is described in Table 2.3 (Margules and Pressey 2000, Pullin 2002):

Table 2.2 Criteria for evaluating conservation value

Criterion	Description
Species richness	The diversity of species of a local ecological community. The number of species in an area.
Endemism	A taxon is endemic to an area if it occurs there and nowhere else. The area of endemism can be large or small, and the proportion of taxa in an area that are endemic to it tends to be an increasing function of the size of the area.
Rarity	Classic rare species are those of small distribution and narrow habitat specificity. However, rarity should be evaluated at three levels: geographic range, habitat specificity and population size.
Complementarity	Property of two sites that occurs when some of the natural features in a site differ from the features of the other. When sites are highly complementary they contain (almost) non-overlapping representation of natural features.
Irreplaceability	A measure of the likelihood that the site will be required as part of a reserve network that satisfies a specific conservation goal. A site is highly irreplaceable when it includes unique or rare natural features.
Threatened species	Taxa in danger of extinction and whose survival is unlikely if the causal factors continue operating.
Functional diversity	The conservation of functional diversity attempts to preserve not only species but also natural ecosystem processes.
Umbrella and flagship species	Conservation of a single or a restricted number of speciesin the hope that protection of overall diversity will follow naturally.
Vulnerability	Risk of a site being transformed, such that some natural features are lost.
Hotspots	Hotspots are areas of extreme taxonomic richness, high number of endemics and high degree of threat.

Table 2.3 Reserve design method (taken from Margules and Pressey, 2000).

Stages	Description
1 Compile data on the biodiversity of the planning region.	Carry out preliminary classification of biodiversity.
2 Identify conservation goals for the planning region.	Select criteria for measuring conservation value.
3 Review existing conservation areas	Examine the existing system of protected areas and other land use systems.
4 Selected additional conservation areas	Fill the gaps in the protected area system where elements of biodiversity are not adequately protected
5 Implement conservation actions	Set priorities for action to fill gaps.
6 Maintain the required values of conservation areas	Progress is reviewed periodically and priorities revised if necessary.

Present reserves may be insufficient to represent and maintain total of biodiversity (Margules and Pressey 2000), among other things because most current reserves were not chosen to meet specific biodiversity objectives (Pressey *et al.* 1996, Possingham *et al.* 2000). Hence, the national systems of protected areas need to be carefully designed if large gaps in biodiversity protection are to be avoided (Kerr, 1997). Finally, the availability of suitable software for statistical modelling, database management, geographic information systems (GIS) and remote sensing have enabled ecologists to analise data on species distribution and conservation (Savitsky and Lacher Jr. 1998, Gaston 2000, Lehmann *et al.* 2002).

2.5 SUMMARY

In order to set priorities for conservation, it is necessary to define operational measures of biodiversity. Species richness is the simplest, most

universal parameter employed to quantify biodiversity and is useful when selecting areas for conservation (Margules *et al.* 2002). However, this simple measure assumes that all species have the same value, independently of their endemism, rarity, distinctiveness, etc (Faith 1994, Magurran 2004). This limitation of species richness has motivated the development of indices of diversity that take phylogeny into account. Phylogeny has become an important tool for conservation and to understand both the processes that have generated the current diversity and the processes that threaten it (Rodrigues and Gaston 2002a, Purvis *et al.* 2005b). Two indices of phylogenetic diversity stand out: Phylogenetic Diversity (Faith 1992) and Taxonomic Distinctiveness (Clarke & Warwick 1998). Both indices require detailed taxonomic or phylogenetic information. The latter, in particular, has recently been calculated for a few taxa. Similarly, the existence of large databases of geographically referenced specimen records was only possible in recent years. Together with powerful computer programs, large distribution databases and taxonomic/phylogenetic information of the taxa contained in these databases are the most powerful informational tools with which biodiversity will be analysed and measured in the near future (Webb *et al.* 2002).

The existence of biodiversity data resources from different fields of knowledge (e.g. systematics, biogeography, ecology) and the strong demand to integrate, synthesize, and visualize this information from different perspectives have resulted in the creation of the field of Biodiversity Informatics (Canhos *et al.* 2004, Soberon and Peterson 2004). This new area of research entails the use and management of biodiversity information employing practical measures of biodiversity, such as the indices mentioned above, and computerised methods to

represent their geographic distribution and environmental correlates. It is urgent to evaluate and, if informative, apply this methodology to plan the conservation of highly biodiverse countries, such as Mexico. This is the task we set ourselves in this dissertation.

CHAPTER 3. CONABIO'S BIODIVERSITY DATABASES

3.1. INTRODUCTION

The growing interest in biological diversity and its conservation has motivated the development of multidisciplinary methods. These include use of null models, improved phylogenetic information, and handling of large databases containing information on the distribution and other attributes of collected specimens (Webb *et al.* 2002, Magurran 2004). Museum specimens contain collection and location information, such as date of collection, collector's name, collection method, site characteristics, geographic coordinates, and names of localities and political units (Colwell 1996). Most of this information is deposited in scientific collections in museums and universities worldwide (Khrishtalka and Humphrey 2000). A biodiversity database is an organised set of such data, which is stored in a computer and can be used to address a variety of questions (Colwell 1996, Peterson *et al.* 1998, Khrishtalka and Humphrey 2000, Bottu and Van Ranst 2003, Graham *et al.* 2004). The information contained in these databases has been used for studies of systematics, ecology, evolution, genetics, biogeography, biodiversity and conservation research and planning (Navarro-Siguenza *et al.* 2002), as well as in agriculture and health surveys. In biodiversity studies, databases constitute an invaluable resource (Parker *et al.* 1998).

The interest in surveying the biological wealth of a country has increased significantly in the last 30 years. Australia has been a leading country in this field.

Since the 1970's, Australian herbaria have been digitising their data cooperatively (Canhos *et al.* 2004). The Environmental Resources Information Network (ERIN) was established in 1989 to provide geographically-related environmental information for planning and decision-making (ERIN 1999). This initiative was considered by other countries, such as Costa Rica with INBio, Brazil with BDT, England with the National Biodiversity Network and Mexico with CONABIO (Khrishtalka and Humphrey 2000, Canhos *et al.* 2004, Soberon and Peterson 2004). Today more and more countries have attempted to create their own programmes to systematise their biological information.

The demand to integrate, synthesize, and visualize the information contained in these databases for a variety of purposes has led to the development of Biodiversity Informatics (Knyazhnitskiy *et al.* 2000, Canhos *et al.* 2004, Soberon and Peterson 2004). Biodiversity Informatics employs computers to examine massive data files (primary data) in a critical synthesis (Knyazhnitskiy *et al.* 2000, Soberon *et al.* 2007). Moreover, rapid advances in communication via the internet have allowed large data sets to be readily compiled and distributed (Khrishtalka and Humphrey 2000) such as with the Global Biodiversity Information Facility (GBIF), Species 2000 and NatureServe services. At the same time, sophisticated computational methods have been developed to identify sets of nature reserves that maximise the representation of regional diversity such as Lifemapper, WorldMap, DIVA-GIS, Desktop GARP, BAT, C-Plan, MARXAN, MARXENT and others (Williams *et al.* 1997, Williams 1999, Peterson *et al.* 2000, Possingham *et al.* 2000, Bonn *et al.* 2002, Cowling *et al.* 2003, Hijmans *et al.* 2004).

The accurate mapping of the geographic distribution of biodiversity and its environmental correlates using primary biodiversity data depends on reliable systematics to reduce bias such as synonymy, misidentification and outdated classifications, as well as incorrect spatial referencing (Crisp *et al.* 2001, NBN 2004, Soberon and Peterson 2004, Soberon *et al.* 2007). Those potential biases are associated with the use of specimen data (Crisp *et al.* 2001). When transferring the specimen's information into a computerised database, errors in taxonomic identification and geographic position are rarely checked. If we add errors in the transcription process itself, the quality of the information contained in a database may vary a great deal. Errors are common and should be expected, but cannot be ignored (Golubov and Soberon 2003, Canhos *et al.* 2004, Graham *et al.* 2004, Soberon and Peterson 2004). These errors are mainly due to the heterogeneous origin of the distributed biodiversity databases (Soberon and Peterson 2004). In this chapter, the process of validation of the information contained in CONABIO's databases is described. Errors were common and would restrict confidence in the results obtained from them.

3.2. METHODS

CONABIO'S DATABASE: A CASE STUDY

For this study, the datasets of a number of seed plant families and the complete dataset of the mammals of Mexico was requested from the Mexican National Commission for Biodiversity (CONABIO). CONABIO is the Inter-Ministerial Commission dedicated to develop, maintain and update the National

System of Biodiversity Information (SNIB). CONABIO holds electronically the specimen-based collection from Mexico and several overseas institutions. It shares its information on biological diversity both by direct requesting and by Internet (CONABIO 2005). The information for seed plants (gymnosperms and a selection of angiosperm families) and mammals was obtained in January 2004. The dataset includes information on taxonomy, locality, geographic coordinates, collector's name, collection's data, vegetation type and degree of endemism.

The gymnosperms database was the smallest with 9,806 records. It included five classes: Ginkgopsida, Cycadopsida, Gnetopsida, Pinopsida and Taxopsida. Cycadopsida contained two families: Cycadaceae and Zamiaceae. Class Pinopsida included six families: Araucariaceae, Cupressaceae, Pinaceae, Podocarpaceae, and Taxodiaceae. The remaining classes contained one family each. The total number of genera and species were 28 and 221, respectively. The most diverse family was Pinaceae with 42% of the species, followed by Cupressaceae and Zamiaceae with about 20% each (Table 3.1). The taxonomic sources are specified in Appendix A. The distribution was corroborated employing other sources such as The Cycads Pages (Hill *et al.* 2004) and The Gymnosperms Database Web Page (Earle 1997) .

Due to the fact that angiosperms are a very large group, only 11 families were considered. We chose those that were either the most diverse in Mexico or contained a significant proportion of endemics. These families were: Agavaceae, Arecaceae, Commelinaceae, Orchidaceae, Poaceae, Acanthaceae, Asteraceae, Cactaceae, Fabaceae, Fagaceae and Rubiaceae. The total number of genera and species was 1,294 and10,449, respectively. The total number of records for

angiosperms was 225,802 (Table 3.2). The most numerous families were Fabaceae, Poaceae and Asteraceae; together they represent nearly 70% of records, 60% of genera and 64% of species in this database. The taxonomic sources are provided in Appendix A. Corroboration was sought from electronic databases such as Flora Mesoamericana, W3TROPICOS, eFloras, Delta Database, etc. Distribution was corroborated by comparing coordinates against available maps. Although for certain taxa their distribution may be well known, for other groups a deeper evaluation was required and often accurate, sufficiently reliable information was not available.

The mammals' dataset comprised 10 orders, 35 families, 154 genera, and 432 species contained in 129,074 records. Rodentia was the biggest order containing almost 60% of all records, followed by Chiroptera with 30% (Table 3.3). An updated taxonomic list of Mexican mammals was elaborated based primarily on McKenna and Bell (1997), Villa and Cervantes (2003) and Ramirez-Pulido *et al.* (2005). Species exclusively insular or marine were excluded. The data analysed incorporated all major taxonomic changes up to 2005. Distribution of each mammal species was corroborated comparing published maps with their geographic coordinates given by CONABIO's database. The maps were taken from Villa and Cervantes (2003), Arita and Rodrigues, (2004) and InfoNatura Webpage (2004). The MaNis server (Stein and Wieczoreck 2004) was also consulted for records of Mexican Mammals; however, their output was the same as CONABIO's Database.

The varied origin of records held by CONABIO made it necessary to control for reliability. Despite CONABIO's process of manual georeferencing and

taxonomic validation, some errors still persisted in the database. These errors can be grouped into three categories: 1) Incomplete or incorrect taxonomic information (e.g. misspelled names); 2) Lack of taxonomic validation (e.g., synonymy and outdated taxonomy), and 3) Inaccurate georeferencing. Correcting these errors represented a tremendous effort. Incomplete taxonomic information was common in all the groups. The databases contained some records or data points without information on their scientific names. For instance, those records whose genus was described as ND (no determined or non available) were removed. On the contrary, records with specific name defined as ND, blanks or *sp.* were considered as *sp.* With the exception of those recovered employing the procedure described next, these records had to be excluded from the analyses. We were able to determine a few of these incomplete records in cases where genera were known to contain only one species. Thus, for example, *Centurio* sp. or *Centurio* (blank) corresponded to *C. senex*; *Taxus* sp. or *Taxus* (blank) corresponded to *T. globosa*. Another method used to find out a specific name was through knowledge of the distribution of the genus; e.g., reviewing the distribution maps of the implicated genera. This, however, required confidence in the geographic information, which is good for some organisms (e.g., mammals), but may be poor in others.

Misspelling was a very frequent error. There were some specimens listed with two, three or even four misspelled specific names (e.g., *Quercus ocotaefolia*, *Q. ocoteafolia* or *Q. ocoteifolia*). Because this artificially inflated the number of species, a substantial effort was required to find out and then correct these names.

Incorrect taxonomic names (synonymy) were also common. In other words, the validated generic and/or specific name was different from the name given in

the database. For instance *Commelina serrulata*, *Tradescantia serrulata* and *Tripogandra serrulata*, are the same species but just one was the currently accepted name (*Tripogandra serrulata*). Often, there were more than two synonyms, e.g., *Agave americana* is the accepted name for *A. vivipara, A. dominencis, A. coccinea*, and *A. laurentiana.* Other specimens showed inconsistent taxonomic identification, for example, when their nomenclature was no longer valid. To address these problems, decisions had to be made as to which classification, nomenclature and taxonomic authority would be employed at a variety of taxonomic levels. The nomenclature used in each biological group of seed plants is provided in Appendix A. In order to obtain satisfactory species lists, an exhaustive review was carried out for each taxonomic group. In the, fortunately, few instances where scientific name validation was not possible (e.g., because the given name had not been mentioned, accepted or rejected in specialised sources, we took these records as valid. Although incorrect determination could potentially also occur, this was beyond our ability to detect it.

Some specimens may have inaccurate or insufficient georeferencing and a thorough re-evaluation had to be conducted. It was also necessary to check if the records from CONABIO belonged to native or introduced organisms. This is because some naturalised or alien species were included in the database (usually, but not always labelled as "introduced species" for seed plants). These data were therefore corrected as far as it was realistically feasible. Nonetheless, it is important to emphasise that for some taxonomic groups, particularly among some angiosperms families, a thorough depuration was impossible to achieve. Among

the reasons for this are the lack of available information and lack of consensus among experts.

3.3. RESULTS

The results are presented separately for each of the three taxonomic groups: gymnosperms, angiosperms and mammals. The validation process for gymnosperms and mammals is explained in detail. Due to the enormous amount of information in the angiosperm dataset, only aspects of the reviewing process considered of particular relevance are mentioned.

3.3.1 GYMNOSPERMS

The reviewed database included three orders: Cycadales, Gnetales and Coniferales. These are integrated into 6 families, 14 genera and 150 species. There were 9,233 records in total, which represented 94.3% of the original data set (Table 3.1).

Cycads in Mexico belonged to three genera of Zamiaceae: *Ceratozamia*, *Dioon* and *Zamia*. Once the data were corroborated in both nomenclature and georeferencing, the number of species was 32. Data points from cycads were concentrated in dry and tropical vegetation types.

Order Gnetales contained only one family and one genus, Ephedraceae and *Ephedra*, respectively. It included five species from temperate regions.

Table 3.1 Gymnosperms data from CONABIO's database showing both original and reviewed information.

	Original Data			Reviewed Data		
Family	Genera	Species	Records	Genera	Species	Records
Ginkgoaceae	1	1	3	-	-	-
Cycadaceae	1	4	36	-	-	-
Zamiaceae	6	43	781	3	32	662
Ephedraceae	1	10	106	1	5	90
Araucariaceae	1	4	17	-	-	-
Cupressaceae	7	49	1700	4	25	1823
Pinaceae	4	94	6552	4	67	6376
Podocarpaceae	1	7	253	1	3	212
Taxodiaceae	5	7	285	-	-	-
Taxaceae	1	2	69	1	1	70
Totals	**28**	**221**	**9806**	**14**	**133**	**9233**

The conifers were represented by four families: Cupressaceae, Pinaceae, Podocarpaceae and Taxaceae. These families together contained 10 genera and 113 species. Pinaceae showed the highest species number with 88, followed by Cupressaceae with 25. Family Pinaceae included four genera: *Abies*, *Picea*, *Pseudotsuga* and *Pinus*; the latter with 50 species representing 52 % of all conifers. The updated list from family Cupressaceae resulted in four genera: *Calocedrus*, *Cupressus*, *Juniperus* and *Taxodium*; *Juniperus* was the genus with more species, 17. The remaining two families only had a few species; Podocarpaceae resulted in a single genus, *Podocarpus*, with three species whereas Taxaceae was a monospecific family. In general, conifers were abundant in temperate regions, particularly in the mountains.

3.3.2 ANGIOSPERMS

The resulting database from angiosperms comprised 11 orders, 12 families, 1058 genera and 7721 species (Table 3.2). There were a total of 211,334 records for angiosperms, which represented 93.59% of the original data set.

Table 3.2 Angiosperm data from CONABIO's database showing both original and reviewed information.

	Original Data			Reviewed Data		
Family	Genera	Species	Records	Genera	Species	Records
Liliopsida						
Agavaceae	18	252	4406	12	186	3502
Nolinaceae	-	-	-	4	39	622
Poaceae	207	1452	53658	186	1047	51523
Commelinaceae	20	141	3499	12	84	3091
Arecaceae	102	266	3015	23	84	2639
Orchidaceae	158	1145	15779	128	697	14432
Magnoliopsida						
Acanthaceae	52	372	5649	33	343	5117
Asteraceae	382	2990	44363	376	2437	41426
Fabaceae	175	2286	58109	140	1459	54565
Cactaceae	77	631	10069	60	484	9422
Fagaceae	4	233	11489	2	218	10463
Rubiaceae	99	643	15766	82	643	14532
Totals	**1294**	**10411**	**225802**	**1058**	**7721**	**211334**

Former family Agavaceae was separated into Agavaceae and Nolinacea. Families Fabaceae, Poaceae and Asteraceae were the largest groups and together they comprised 79% of records. Asteraceae and Fabaceae contained the largest number of species, 2437 and 1459 respectively, followed by Poaceae with

1047 species. Families Agavaceae, Nolinaceae, Commelinaceae, Arecaceae and Acanthaceae represented together 9.83% of species and 7% of records. These data show both the contrasting diversity of families and their varied representation in CONABIO's database. For the most diverse and taxonomically complex families (Asteraceae, Fabaceae and Poaceae) an exhaustive review proved impossible.

3.3.3 MAMMALS

The mammal records from the updated CONABIO's Database summed 128,114 in 14 orders, 35 families, 159 genera and 434 species (Table 3.3), 416 when excluding marine and insular mammals. These data represented 99.26% of the original records. Within this database, many records were wrongly georeferenced and it was common to find species allocated outside the species' known distribution.

Orders Rodentia and Chiroptera were the most diverse and the most widely distributed groups across the country. Rodentia held about 49% of the species in the database, while Chiroptera contained 31%. Orders with intermediate species numbers were Carnivora and Insectivora with 7 and 5%, respectively. The smallest order was Perissodactyla, with one single species (0.23%). The taxonomic classification of mammals is presented in Chapter 4.

Although most of the taxonomic and distribution updating was made for the order Rodentia, there were some important modifications in Artiodactyla, and Chiroptera. For the former, a new species of deer is now accepted, and for the latter, two new genera of Vespertillionidae family have been recognised. The

states with the highest number of species were Oaxaca, Chiapas, Veracruz and Guerrero.

Table 3.3 Mammal data from CONABIO's database showing both original and reviewed information.

	Original data			Reviewed data		
Order	Genera	Species	Records	Genera	Species	Records
Artiodactyla	7	8	1520	7	9	1520
Carnivora	21	31	6166	21	31	6160
Chiroptera	59	133	37771	63	133	37349
Didelphimorphia	5	7	2137	6	7	2128
Insectivora	6	22	1938	-	-	-
Soricomorpha	-	-	-	4	20	1930
Erinaceamorpha	-	-	-	2	2	3
Lagomorpha	3	13	3987	3	13	3978
Perissodactyla	1	1	85	1	1	85
Primates	2	3	565	2	3	565
Rodentia	46	210	74381	46	211	73879
Xenarthra	4	4	519	-	-	-
Pilosa	-	-	-	2	2	328
Cingulata	-	-	-	2	2	189
Total	**154**	**432**	**129069**	**159**	**434**	**128114**

3.4. DISCUSSION

Data validation (correct name and distribution) was unevenly achieved because of the differences in reliable and available information for the three biological groups. In spite of this, some specimen data errors were common in the three groups: wrong spelling of the taxon; synonymy, so a single species may

appear more than once with different names; misidentification of the specimen and errors in geo-referencing. Whereas there were some groups which were well known taxonomically, such as the gymnosperms and mammals, for some angiosperm families the information was incomplete and not easily accessible. It would therefore take a substantial amount of ground work to correct all the errors, a task that was beyond our abilities.

The gymnosperm data contained many errors (Fig. 3.1). Only three classes of extant gymnosperms are found in Mexico: Cycadopsida, Gnetopsida and Pinopsida (Judd *et al.* 2002). Therefore, records from class Ginkgopsida, native to Asia, were removed from the database. On the other hand, class Taxopsida has been reclassified as a family of Pinopsida. Thus, records from the former were moved to the latter. Records not belonging to these three classes were eliminated.

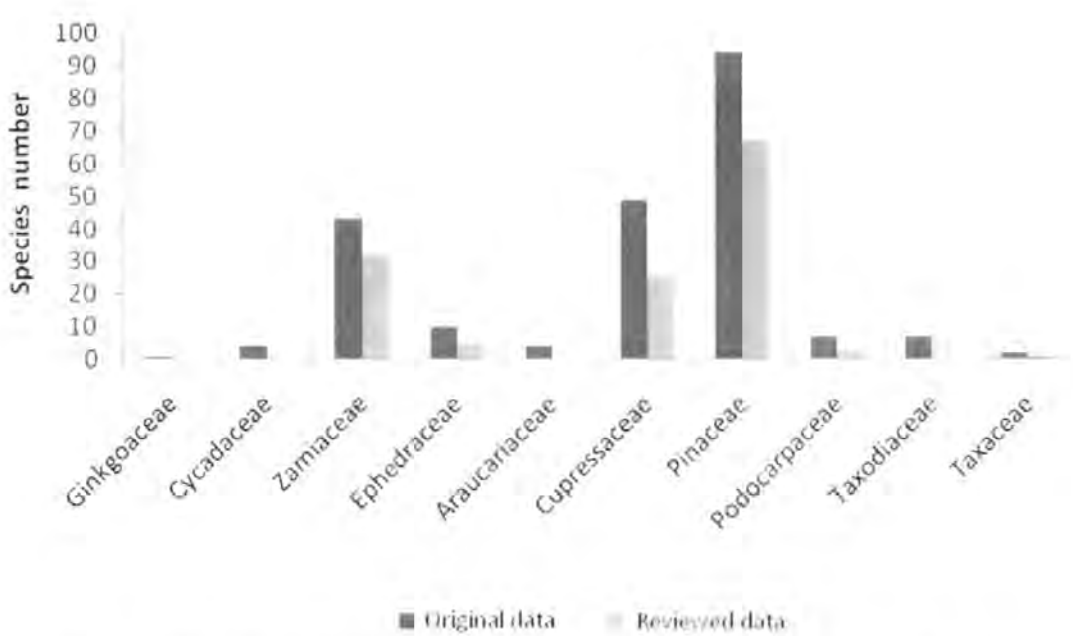


Figure 3.1 Number of gymnosperm species in the database before and after the examination process.

Extant cycads are limited to the tropical and subtropical regions of the world. There are around 200 described species separated into two families, Cycadaceae and Zamiaceae (Hill *et al.* 2004). Mexico has the second largest cycad diversity with 42 recognised species. The cycads of Mexico are represented by three distinctive genera from family Zamiaceae: *Ceratozamia*, *Dioon* and *Zamia* (Hendricks 1998, Vovides 1998). Consequently, all records from family Cycadaceae in the database were deleted. The total number of cycad species represented in CONABIO's database after examining their nomenclature and distribution was 32. Most of these species are documented as narrow endemics and threatened (Vovides 1998, Hill *et al.* 2004).

Family Ephedraceae was represented by one genus: *Ephedra* (Rzedowski 1998). After examination, the number of species was reduced from ten to five, mainly due to synonymy.

The Class Pinopsida, order Coniferales was the most diverse, with 10 genera and 113 species. The original data included six families: Araucariaceae, Cupressaceae, Pinaceae, Podocarpaceae, Taxaceae and Taxodiaceae. However, after reviewing, only four families remained. This is because Araucariaceae, a southern hemisphere family, is alien to Mexico and Taxodiaceae has been incorporated into Cupressaceae (Earle 1997).

Although seven genera are listed in the Cupressaceae (*Calocedrus*, *Chamaecyparis*, *Cupressus*, *Juniperus*, *Libocedrus*, *Platycladus* and *Thuja*), *Chamaecyparis* and *Platycladus* were removed because they are native to Asia. *Libocedrus* has been moved to *Calocedrus*. The five genera formerly in family

Taxodiaceae have been moved to Cupressaceae and only genus *Taxodium* was taken into account because the other four were not native to Mexico. Finally, five genera were acknowledged in family Cupressaceae: *Calocedrus, Cupressus, Juniperus*, *Thuja* and *Taxodium* (Watson and Eckenwalder 1993, Earle 1997). Mexico is the most diverse country in *Pinus* species (Styles 1998) and their secondary centre of diversification (Mirov 1967). There are 48 recognised species of *Pinus* in Mexico, 50% of which are endemic to the country. These 48 species correspond to 48% of the total number of pine species in the world. In the database, the genus *Pinus* originally reported 79 species. After reviewing them, this number was reduced to 50. This difference in the number of species was due to the occurrence of two specific names that were not possible to corroborate. The remaining two families of Coniferales only had a few, non problematic species.

Among the angiosperms, families Fabaceae, Poaceae and Asteraceae were the largest groups (Fig. 3.2). Together they made up 79% of records. These were followed by Orchidaceae and Rubiaceae (13.7 % together). According to Rzedowski (1998), most species of Mexican angiosperms belong to these five families plus Cactaceae (Fig. 3.3). Considering the completeness of CONABIO's database for all the other families, it seems that the Cactaceae are under-represented in CONABIO's database (Fig. 3.2 and Fig. 3.3). Because family Nolinaceae is now classified as a separate family from Agavaceae, the number of families increased from 11 to 12. Families Agavaceae, Nolinaceae, Commelinaceae, Arecaceae and Acanthaceae represented 9.83% of species and 7% of records.

Family Asteraceae, Poaceae and Cactaceae were better represented in north and central Mexico, while Orchidaceae and Rubiaceae were more diverse in the south, and Fabaceae was abundant in temperate regions. These data showed the contrasting diversity within families, their varied distribution and their different representation in the database. Due perhaps to having the highest

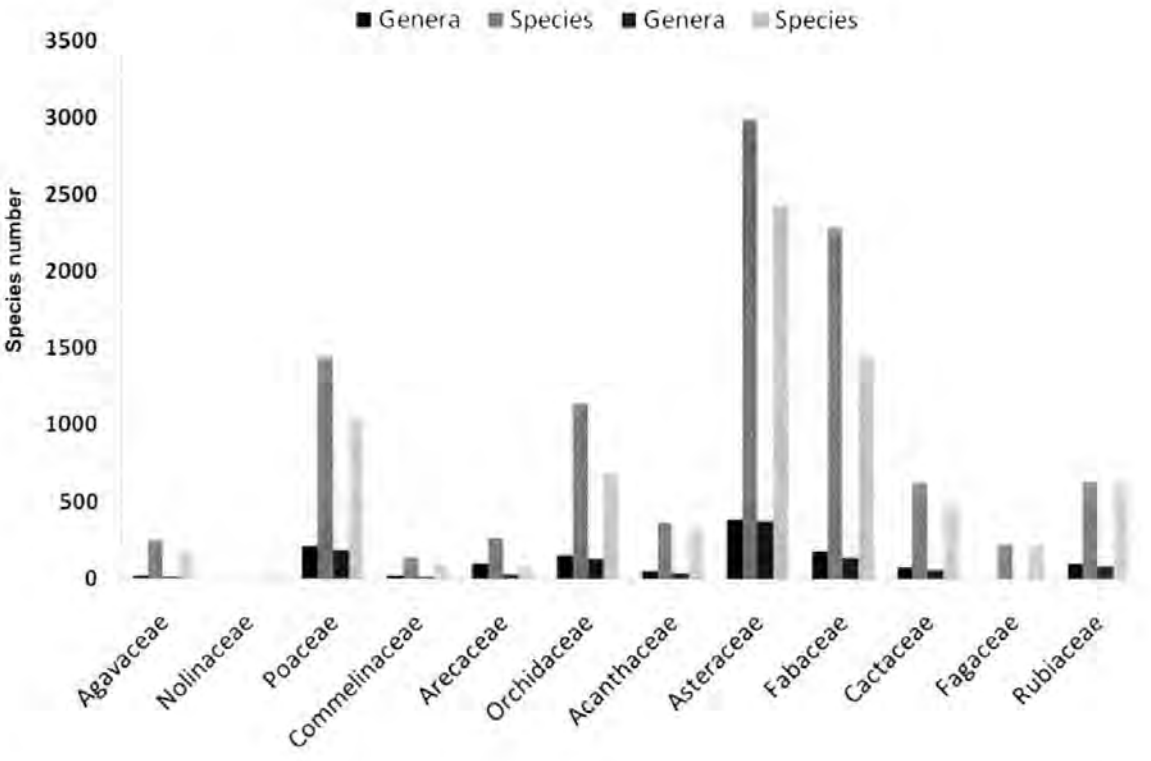


Figure 3.2 Number of angiosperm genera and species in the database before (first and second bars, respectively) and after (third and fourth bars) the examination process

diversity of the three groups studied (gymnosperms, angiosperms and mammals), the angiosperms were the most difficult taxon, containing the three problems: 1) incorrect taxonomic information, 2) lack of taxonomic validation, and 3) inaccurate georeferencing. Nonetheless, and despite the difficulty of unequivocally confirm the revised 211,334 records, the CONABIO database suggest that, with the

exception of Cactaceae and Agavaceae, previous estimates of angiosperm diversity underestimate the true figures for these families (Fig. 3.3).

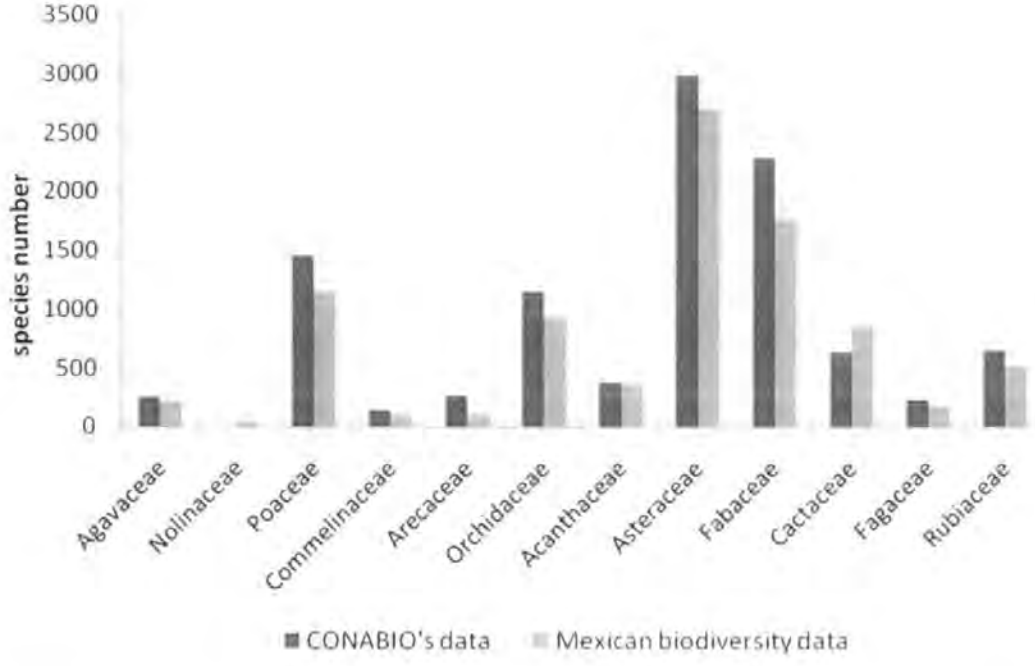


Figure 3.3 Comparison of the diversity of angiosperm families reported in CONABIO database and from the taxonomic literature (from Neyra and Duran, 1998).

Mexico occupies the second place in the world in mammal species richness (Ceballos *et al.* 2002a). Mammals are a well-known biological group and, consequently, their records did not exhibit significant changes (Fig. 3.4). Although there were some data points with inaccurate georeferencing and distribution information, this database was the most trustworthy. Nonetheless, and similar to the other datasets, there were gaps in the information and some areas of Mexico were poorly represented. The contrasting diversity of orders was evident in this group. Whereas orders Rodentia and Chiroptera were the most diverse and the most widely distributed taxa across the country, there were others, such as Primates and Perissodactyla, with three or fewer species, usually restricted to the southeast of Mexico.

The states with the higher number of species were Veracruz, Guerrero, Oaxaca and Chiapas. The distribution of the different orders coincided with that reported in the literature (Fa and Morales 1998, Ceballos *et al.* 2002a, Villa R. and Cervantes 2003). Primates, xenarthras and perissodactyls were restricted to the tropical zones of the Yucatan Peninsula and the tropical coastal zones. Lagomorphs, insectivores and chiropters were more diverse in the central part of the country, particularly along the Transvolcanic Belt. Rodents were abundant in the central plateau, from the north plains to the highlands of Chiapas (Ceballos *et al.* 1998, Fa and Morales 1998).

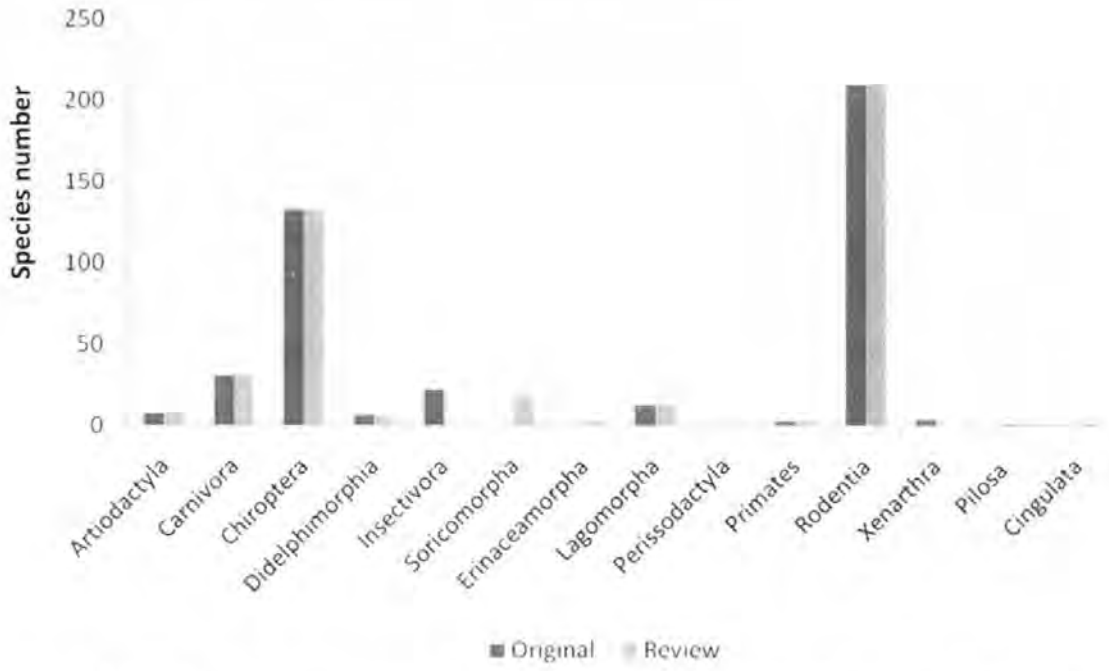


Figure 3.4 Number of mammal species by order in the database before and after the review process

Databases such as CONABIO's are becoming increasingly important in the study of the distribution of biodiversity (Webb *et al.* 2002, Magurran 2004). Their usefulness as tools for conservation, however, depends on the reliability of their information. Therefore, careful consideration to taxonomic and geographic

accuracy is paramount (Golubov and Soberon 2003, Isaac *et al.* 2004). The heterogeneous origin of these databases makes quality control even more important (Canhos *et al.* 2004, Soberon and Peterson 2004). A good understanding of errors and error propagation can lead to effective quality control.

Taxonomy is the tool by which the components of biological diversity are identified, enumerated and arranged in classifications that reflect patterns of relationships (Novacek 1992). It provides the fundamental information on which to base our efforts to conserve biological diversity (CBD 1996). The problem of inaccurate information is not exclusive of or even particularly unusual in CONABIO's databases. It occurs as a natural consequence of the variety of sources and degrees of taxonomic expertise of the people involved in the different stages of its compilation. It is, however, precisely because of this heterogeneity of sources, expertise and the sheer number of people involved in the process that users of biodiversity database information must guarantee some degree of quality control.

One of the objectives of the recently formed international Union of Biological Sciences' Taxonomic Database Working Group (TDWG) is to work on a standard called "Access to Biological Collection Data (ABCD)". TDGW was formed to establish international collaboration among biological databases projects, to promote standard and guidelines for the recording and exchange of data about organisms (http://www.tdwg.org). Web-based tools for validating georeferences, taxonomic identifications, and collection dates (or at least flagging records with high probabilities of error), such as The SpeciesLink and ORNIS projects, are developing a number of data cleaning tools which are currently being tested and

evaluated (Canhos *et al.* 2004, Soberon and Peterson 2004, Stein and Wieczoreck 2004). It would be interesting to investigate the performance of these new tools compared to a careful, "manual" cleaning process such as the one done here.

Another aspect which has been highlighted by this study is the representativeness of the collections. Wide gaps were found, where significant areas of Mexico are still poorly represented in the collections (records). Both the geographic and the ecological coverage of the study taxa were uneven. In general, specimen data has rarely been gathered in a systematic way across a broad region. These may be because: 1) individual collections specialize on particular regions and often no single collection contains sufficient geographic or taxonomic representation (Navarro-Siguenza *et al.* 2002), or 2) difficulty of access to certain areas or restrictions in time available for collecting specimens in the field. For example, specimens are often collected close to roads ("the roadmap effect"), in areas known to yield good results, and in areas closer to population centres and research institutions (Crisp et al 2001). Systematic inventories and analyses of geographic, ecological, taxonomic and genetic diversity are needed to avoid this problem.

The geographical representation of where museum specimens were collected is a first step in the investigation of the historical and ecological reasons for the distribution of particular taxonomic groups. However, when using these databases, it is possible to combine different data layers, looking for particular combinations of unexplored ecological features. Alternative methods that allow predictions of distributions based on incomplete knowledge, such as GARP, may

be required (Colwell 1996, Peterson *et al.* 1998, Bottu and Van Ranst 2003, Graham *et al.* 2004). However, one must also be aware of the uncertainties of predictive distribution modelling (Barry and Elith 2006). It is also possible that data from the literature may also be used to provide complementary data and further details.

Despite their imperfections, biodiversity databases (such as CONABIO's), are important and useful tool to determine the distribution of species and its possible causes. They have proved effective to record information on the complex interactions that determine biodiversity, the effects of disease, pollution, agriculture, etc. (Knyazhnitskiy *et al.* 2000), as well as documenting species decline (Shaffer *et al.* 1998). Undoubtedly, information from museum specimens is invaluable in all aspects of the study and conservation of biological diversity (Parker *et al.* 1998, Golubov and Soberon 2003).

CHAPTER 4. THE TAXONOMY AND PHYLOGENY OF MEXICAN MAMMALS

4.1 INTRODUCTION

The first step to calculate biodivesity indices is to generate a species list, particularly a taxonomic species list which provides the fundamental information on which to base our efforts to conserve biological diversity (CBD 1996, Mace 2004). However, special attention should be paid when taxonomic lists are used in studies of conservation (Mace *et al.* 2003, Agapow *et al.* 2004, Isaac *et al.* 2004, Mace 2004) to avoid taxonomic inflation. Thus, a valid taxonomy against which candidates for listing, protection and management can be tested is essential (Isaac *et al.* 2004, Mace 2004).

On the other hand, in order to quantify the biodiversity of an area in terms of the path length of their phylogeny (as it has been proposed in this dissertation), a phylogenetic tree representing the relatedness of individual species with a fully resolved cladogram would be required (Williams *et al.* 1994, Warwick and Clarke 2001). Detailed information of the systematics of the group under study is necessary. Unfortunately, the information required to build a reliable cladogram is not available for every mammalian order. For this reason, in order to evaluate the effect that incomplete phylogenetic information has on perceived patterns of biodiversity, a comparison of the results obtained employing taxonomy *vs.* phylogeny would be useful.

Most studies on mammalian diversity use the taxonomic classification proposed by Wilson and Reeder (1993) in their "Mammals of the World" species list (although a new list published on 2005 is available). However, major changes to the mammals' nomenclature were recently proposed by McKenna and Bell (1997). Wilson and Reeder (1993) is the standard reference for mammals in Mexico, and recent changes of nomenclature have been accepted at or below the species level (Ramírez-Pulido *et al.* 1996, Arita and Ceballos 1997, Ceballos *et al.* 2002b, Villa R. and Cervantes 2003). Ramirez-Pulido *et al.* (2005) recently compiled a new taxonomic list incorporating all changes.

Mexico occupies the second place in the world in terms of the number of mammal species (Ceballos *et al.* 2002a). Mammals are represented by a total of 522 species (terrestrial and marine). Terrestrial mammals are contained in 35 families, 165 genera and 448 species (Ceballos *et al.* 2002a, Villa R. and Cervantes 2003). Rodents and bats are the most diverse orders (Fig. 4.1). Small mammals such as rodents, bats and shrews comprise very diverse genera (Table 4.1). Four genera of order Rodentia (*Peromyscus*, *Chaetodipus, Neotoma* and *Reithrodontomys)* represent 20.98% of all mammal diversity in Mexico.

Table 4.1 Mammalian most diverse genera in Mexico

Order	Genus	Number of species
Rodentia	*Peromyscus*	46
	Chaetodipus	18
	Neotoma	17
	Reithrodontomys	13
Chiroptera	*Myotis*	19
Soricomorpha	*Cryptotis*	13
	Sorex	12

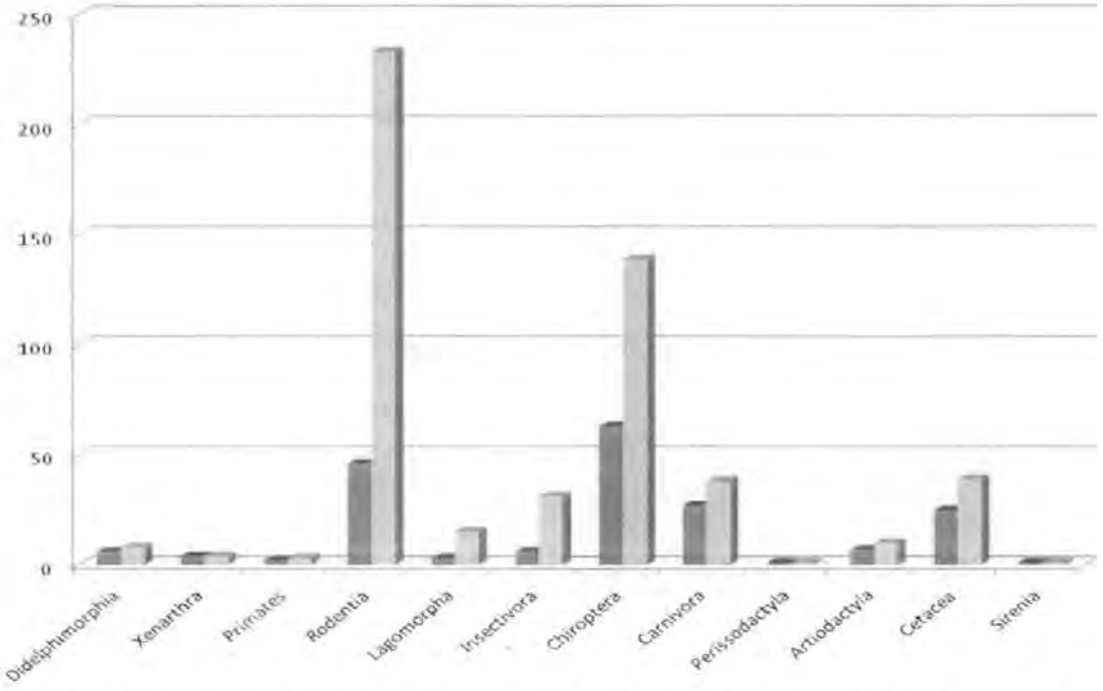


Figure 4.1 Number of genera (dark bar) and species (light bar) for the 12 orders of Mammals of Mexico (Villa R. and Cervantes 2003).

Methods used to assemble phylogenies of whole, usually large, taxonomic groups (supertrees) are based on combining tree topologies instead of primary character data. Overall, trees used to build supertrees can be originated by four different data sources: a) morphological traits, b) molecular markers, c) a combination of both, and d) taxonomical information. Among the methods to build these supertrees, two are the most popular: 1) the "traditional" approach consists of overlapping trees with respect to the terminal taxa they contain, and 2) the matrix representation with parsimony method (or MPR) defined as the process whereby a tree structure is converted into the form of a matrix using a coding method (e.g. additive binary coding). The tree structure and its matrix representation have a one-to-one correspondence and are equivalent structures (Sanderson *et al.* 1998, Bininda-Emonds 2004). Due to the difficulty of

standardising the criteria employed to assign the codes, the traditional approach was employed in this dissertation to produce the supertree of Mexican mammals.

In this chapter, in order to estimate the effect the resolution of the classification would have on the results, two contrasting, achievable classifications were elaborated: 1) a Linnaean taxonomy and 2) a hypothetical phylogenetic supertree constructed from information in the literature.

4.2 METHODS

4.2.1 TAXONOMIC CLASSIFICATION

An updated taxonomic list of Mexican mammals was produced based on classifications by McKenna and Bell (1997), Villa and Cervantes (2003) and Ramirez-Pulido *et al.* (2005). Insular or marine species were excluded. The final continental species list incorporated all taxonomic changes up to 2005 (from subclass to species level) in 14 hierarchical taxonomic categories.

4.2.2 PHYLOGENETIC TREE

Published phylogenetic trees from each mammalian order were compiled and used to elaborate a more informed hypothesis of the phylogenetic relationships of all species in the study. The information was gathered from a wide range of different systematic studies. The full sources of the cladograms employed are listed in Appendix B. In cases where more than one possible phylogeny was given in the source, the consensus tree was chosen. Trees estimated from

molecular data were favoured over those that employed morphological information. In some cases, trees had been estimated employing both types of data.

Tree assemblage followed a hierarchical sequence from order, following the topology of orders within class Mammalia determined by Murphy *et al.* (2001), to species level. Supertrees were readily available for the orders Lagomorpha (Stoner *et al.* 2003), Insectivora= Lipotyphla, now divided into orders Soricomorpha and Erinaceamorpha (Grenyer and Purvis 2003b), Chiroptera (Jones *et al.* 2002) and Carnivora (Bininda-Emonds *et al.* 1999). Initially, these supertrees were employed as starting points for their respective order. However, once they were corroborated with alternative phylogenetic sources, additional changes were made. Although rather complete, those supertrees did not contain all the species that occur in Mexico. Therefore, an exhaustive search for the phylogenies of these groups and those of the remaining orders was carried out. For those species whose phylogenetic information was not available, taxonomic information was employed (Crozier *et al.* 2005).

Each tree source was saved as an image file and captured by the TreeTHIEF v1.0 program (Rambaut 1999). This file was then converted into a Nexus format using the TreeVIEW program (Page 1996). Trees in Nexus files were loaded and edited in McCLADE 4.0 (Madisson and Madisson 2003). Species not included in the mammals database (Chapter 3) were removed. Because of the variety of methods that have been employed to investigate the phylogenetic relationships of different taxonomic groups (Maximum likehood, Bayesian and/or Maximum Parsimony), employing a variety of genes (cit b, nuclear, etc.), branch

lengths were assumed to be constant. The resulting ordinal trees were displayed graphically using McCLADE 4.0 (Maddison and Maddison 2003). Although only taxa represented in our dataset were included in the final supertree, a comprehensive review of phylogenies for the 12 orders of mammals that occur in Mexico was undertaken. The graphical representation of the full supertree was elaborated in FigTree v1.0 (Rambaut 2006).

A new phylogeny of placental mammals was proposed by Bininda-Edmonds *et al.* (2007). This placental supertree (PST) was, however, not considered for the phylogenetic diversity analyses presented here (Chapter 5). Firstly, because it was published after these analyses had been conducted and therefore too late to consider the new supertree and rerun the analyses. And secondly because, although PST contains 4,510 species (99% of the world's extant species), for the 416 native species that are considered in this dissertation (9.18% of the world extant mammals), the use of more specific phylogenetic sources carried out by experts of smaller groups employing molecular methods was still necessary. Nonetheless, differences in the relationships between PST and the composite phylogeny used here are briefly discussed when those differences occur.

4.3 RESULTS AND DISCUSSION

4.3.1 THE TAXONOMY OF MEXICAN MAMMALS (*T*)

The total number of continental species was 416, which represent 93.08% of Mexican mammal diversity (terrestrial species). The taxonomic classification is

given in Table 4.2; their endemicity is also presented (to be used in Chapter 6).The mammals of Mexico belong to two subclasses: Marsupialia and Placentalia, and 12 orders.

Table 4.2 Taxonomic classification (*t*) of the continental mammals included in this study. *Endemic taxa

Subclass Marsupialia
Magnorder Ameridelphia
Order Didelphimorphia
Family Didelphidae
Subfamily Caluromyinae
Caluromys
Caluromys derbianus
Subfamily Didelphinae
Tribe Didelphini
Chironectes
Chironectes minimus
Didelphis
Didelphis marsupialis
Didelphis virginiana
Philander
Philander opossum
Tribe Monodelphinae
Subtribe Monodelphina
Marmosa
Marmosa mexicana
Tlacuatzin
*Tlacuatzin canescens**

Subclass Placentalia
Magnorder Epitheria
Superorder Preptotheria
Grandorder Anagalida
Mirorder Duplicidentata
Order Lagomorpha
Family Leporidae
Subfamily Leporinae
Lepus
Lepus alleni
Lepus californicus

Lepus callotis
*Lepus flavigularis**
Romerolagus
*Romerolagus diazi**
Sylvilagus
Sylvilagus audubonii
Sylvilagus bachmani
Sylvilagus brasiliensis
*Sylvilagus cunicularius**
Sylvilagus floridanus
*Sylvilagus insonus**

Mirorder Simplicidentata
Order Rodentia
Suborder Hystricognatha
Infraorder Hystricognathi
Superfamily Cavioidea
Family Agoutidae
Subfamily Agoutinae
Agouti
Agouti paca
Subfamily Dasyproctinae
Dasyprocta
*Dasyprocta mexicana**
Dasyprocta punctata
Family Erethizontidae
Subfamily Erethizontinae
Coendou
Coendou mexicanus
Erethizon
Erethizon dorsatum
Suborder Myomorpha
Infraorder Myodonta
Superfamily Muroidea
Family Muridae
Subfamily Arvicolinae
Superfamily Arvicolini
Microtus
Microtus californicus
Microtus guatemalensis
Microtus mexicanus
*Microtus oaxacensis**
Microtus pennsylvanicus
*Microtus quasiater**

*Microtus umbrosus**

Tribe Ondatrini

Ondatra

Ondatra zibethicus

Subfamily Sigmodontinae

Tribe Baiomyni

Baiomys

Baiomys musculus

Baiomys taylori

Scotinomys

Scotinomys teguina

Tribe Ichthyomyni

Rheomys

*Rheomys mexicanus**

Rheomys thomasi

Tribe Neotomini

Hodomys

*Hodomys alleni**

Nelsonia

*Nelsonia goldmani**

*Nelsonia neotomodon**

Neotoma

Neotoma albigula

*Neotoma angustapalata**

Neotoma fuscipes

*Neotoma goldmani**

Neotoma lepida

Neotoma mexicana

Neotoma micropus

*Neotoma nelsoni**

*Neotoma palatina**

*Neotoma phenax**

Xenomys

*Xenomys nelsoni**

Tribe Oryzomyni

Oligoryzomys

Oligoryzomys fulvescens

Oryzomys

Oryzomys alfaroi

*Oryzomys caudatus**

Oryzomys couesi

*Oryzomys melanotis**

Tribe Peromyscini

Habromys

*Habromys chinanteco**
*Habromys lepturus**
Habromys lophurus
*Habromys simulatus**

Megadontomys

*Megadontomys cryophilus**
*Megadontomys nelsoni**
*Megadontomys thomasi**

Neotomodon

*Neotomodon alstoni**

Onychomys

Onychomys arenicola
Onychomys leucogaster
Onychomys torridus

Osgoodomys

*Osgoodomys banderanus**

Peromyscus

Peromyscus aztecus
*Peromyscus beatae**
Peromyscus boylii
*Peromyscus bullatus**
Peromyscus californicus
Peromyscus crinitus
*Peromyscus difficilis**
Peromyscus eremicus
*Peromyscus eva**
*Peromyscus furvus**
Peromyscus gratus
Peromyscus guatemalensis
Peromyscus gymnotis
*Peromyscus hooperi**
Peromyscus leucopus
Peromyscus levipes
Peromyscus maniculatus
*Peromyscus megalops**
*Peromyscus mekisturus**
*Peromyscus melanocarpus**
*Peromyscus melanophrys**
Peromyscus melanotis
*Peromyscus melanurus**
Peromyscus merriami
Peromyscus mexicanus
Peromyscus nasutus
*Peromyscus ochraventer**

Peromyscus pectoralis
*Peromyscus perfulvus**
*Peromyscus polius**
*Peromyscus spicilegus**
Peromyscus truei
*Peromyscus winkelmanni**
*Peromyscus yucatanicus**
*Peromyscus zarhynchus**
Reithrodontomys
*Reithrodontomys burti**
*Reithrodontomys chrysopsis**
Reithrodontomys fulvescens
Reithrodontomys gracilis
*Reithrodontomys hirsutus**
Reithrodontomys megalotis
Reithrodontomys mexicanus
Reithrodontomys microdon
Reithrodontomys montanus
Reithrodontomys sumichrasti
Reithrodontomys tenuirostris
*Reithrodontomys zacatecae**
Tribe Sigmodontini
Sigmodon
*Sigmodon alleni**
Sigmodon arizonae
Sigmodon fulviventer
Sigmodon hispidus
*Sigmodon leucotis**
*Sigmodon mascotensis**
Sigmodon ochrognathus
Tribe Tylomyni
Nyctomys
Nyctomys sumichrasti
Otonyctomys
Otonyctomys hatti
Ototylomys
Ototylomys phyllotis
Tylomys
*Tylomys bullaris**
Tylomys nudicaudus
Tylomys tumbalensis
Suborder Sciuromorpha
Infraorder Castorimorpha
Family Castoridae

Subfamily Castorinae
Tribe Castorini
Subtribe Castorina
Castor
Castor canadensis
Infraorder Geomorpha
Superfamily Geomyoideae
Family Geomyidae
Subfamily Geomyinae
Tribe Geomyini
Cratogeomys
Cratogeomys castanops
*Cratogeomys fumosus**
*Cratogeomys goldmani**
*Cratogeomys gymnurus**
*Cratogeomys merriami**
*Cratogeomys neglectus**
*Cratogeomys tylorhinus**
*Cratogeomys zinseri**
Geomys
Geomys arenarius
*Geomys tropicalis**
Orthogeomys
*Orthogeomys cuniculus**
Orthogeomys grandis
Orthogeomys hispidus
*Orthogeomys lanius**
Pappogeomys
*Pappogeomys alcorni**
*Pappogeomys bulleri**
Zygogeomys
*Zygogeomys trichopus**
Tribe Thomomyini
Thomomys
Thomomys bottae
Thomomys umbrinus
Subfamily Heteromyinae
Tribe Dipodomyini
Dipodomys
Dipodomys deserti
*Dipodomys gravipes**
Dipodomys merriami
*Dipodomys nelsoni**
Dipodomys ordii

*Dipodomys phillipsii**
Dipodomys simulans
Dipodomys spectabilis
Tribe Heteromyini
Heteromys
Heteromys desmarestianus
Heteromys gaumeri
*Heteromys nelsoni**
Liomys
Liomys irroratus
Liomys pictus
Liomys salvini
*Liomys spectabilis**
Tribe Perognathini
Chaetodipus
*Chaetodipus arenarius**
*Chaetodipus artus**
Chaetodipus baileyi
Chaetodipus californicus
Chaetodipus eremicus
Chaetodipus fallax
Chaetodipus formosus
*Chaetodipus goldmani**
Chaetodipus hispidus
Chaetodipus intermedius
*Chaetodipus lineatus**
Chaetodipus nelsoni
Chaetodipus penicillatus
*Chaetodipus pernix**
Chaetodipus spinatus
Perognathus
Perognathus amplus
Perognathus flavescens
Perognathus flavus
Perognathus longimembris
Perognathus merriami
Infraorder Sciurida
Family Sciuridae
Subfamily Petauristinae
Glaucomys
Glaucomys volans
Subfamily Sciurinae
Tribe Marmotini
Subtribe Spermophilina

Ammospermophilus

Ammospermophilus harrisii

Ammospermophilus interpres

Ammospermophilus leucurus

Cynomys

Cynomys ludovicianus

*Cynomys mexicanus**

Spermophilus

*Spermophilus adocetus**

*Spermophilus annulatus**

*Spermophilus atricapillus**

Spermophilus beecheyi

*Spermophilus madrensis**

Spermophilus mexicanus

*Spermophilus perotensis**

Spermophilus spilosoma

Spermophilus tereticaudus

Spermophilus variegatus

Tribe Sciurini

Subtribe Sciurina

Sciurus

Sciurus aberti

*Sciurus alleni**

Sciurus arizonensis

Sciurus aureogaster

*Sciurus colliaei**

Sciurus deppei

Sciurus griseus

Sciurus nayaritensis

Sciurus niger

*Sciurus oculatus**

Sciurus variegatoides

Sciurus yucatanensis

Tribe Tamiasciurini

Tamiasciurus

*Tamiasciurus mearnsi**

Tribe Tamiini

Tamias

*Tamias bulleri**

Tamias dorsalis

*Tamias durangae**

Tamias merriami

Magnorder Archonta

Order Chiroptera

Suborder Microchiroptera

Infraorder Yangochiroptera

Superfamily Molossoidea

Family Molossidae

Subfamily Molossinae

Eumops

Eumops auripendulus

Eumops bonariensis

Eumops glaucinus

Eumops hansae

Eumops perotis

Eumops underwoodi

Molossops

Molossops greenhalli

Molossus

Molossus aztecus

Molossus coibensis

Molossus molossus

Molossus rufus

Molossus sinaloae

Promops

Promops centralis

Subfamily Tadarinae

Nyctinomops

Nyctinomops aurispinosus

Nyctinomops femorosaccus

Nyctinomops laticaudatus

Nyctinomops macrotis

Tadarida

Tadarida brasiliensis

Superfamily Nataloidea

Family Natalidae

Natalus

Natalus stramineus

Family Thyropteridae

Thyroptera

Thyroptera tricolor

Superfamily Noctilinoidea

Family Mormoopidae

Mormoops

Mormoops megalophylla

Pteronotus

Pteronotus davyi
Pteronotus gymnonotus
Pteronotus parnellii
Pteronotus personatus

Family Noctilionidae

Noctilio
Noctilio albiventris
Noctilio leporinus

Family Phyllostomidae

Subfamily Carollinae

Carollia
Carollia brevicauda
Carollia perspicillata
Carollia subrufa

Subfamily Desmodontinae

Tribe Desmodontini

Desmodus
Desmodus rotundus

Diaemus
Diaemus youngi

Tribe Diphyllini

Diphylla
Diphylla ecaudata

Subfamily Glosophaginae

Tribe Choeronycterini

Subtribe Anourina

Anoura
Anoura geoffroyi

Tribe Glossophagini

Subtribe Choeronycterina

Choeroniscus
Choeroniscus godmani

Choeronycteris
Choeronycteris mexicana

Hylonycteris
Hylonycteris underwoodi

Lichonycteris
Lichonycteris obscura

Musonycteris
*Musonycteris harrisoni**

Glossophaga
Glossophaga commissarisi
Glossophaga leachii
*Glossophaga morenoi**

Glossophaga soricina

Leptonycteris

Leptonycteris curasoae

Leptonycteris nivalis

Subfamily Macrotinae

Macrotus

Macrotus californicus

Macrotus waterhousii

Subfamily Micronycterinae

Micronycteris

Micronycteris brachyotis

Micronycteris megalotis

Micronycteris schmidtorum

Micronycteris sylvestris

Subfamily Phyllostominae

Tribe Lonchorhinini

Lonchorhina

Lonchorhina aurita

Tribe Macrophyllini

Macrophyllum

Macrophyllum macrophyllum

Trachops

Trachops cirrhosus

Tribe Phyllotomini

Mimon

Mimon benettii

Mimon crenulatum

Phylloderma

Phylloderma stenops

Phyllostomus

Phyllostomus discolor

Tonatia

Tonatia brasiliense

Tonatia evotis

Subfamily Vampyrinae

Chrotopterus

Chrotopterus auritus

Vampyrum

Vampyrum spectrum

Subfamily Stenodermatinae

Tribe Mesostenodermatini

Subtribe Enchisthenina

Enchisthenes

Enchisthenes hartii

Tribe Stenodermatini
Subtribe Artibeina
Artibeus
*Artibeus hirsutus**
Artibeus intermedius
Artibeus jamaicensis
Artibeus lituratus
Dermanura
Dermanura azteca
Dermanura phaeotis
Dermanura tolteca
Dermanura watsoni
Subtribe Stenodermatina
Centurio
Centurio senex
Subtribe Vampyressina
Chiroderma
Chiroderma salvini
Chiroderma villosum
Platyrrhinus
Platyrrhinus helleri
Uroderma
Uroderma bilobatum
Uroderma magnirostrum
Vampyressa
Vampyressa pusilla
Vampyrodes
Vampyrodes caraccioli
Tribe Sturniri
Sturnira
Sturnira lilium
Sturnira ludovici
Superfamily Vespertilionoidea
Family Vespertilionidae
Subfamily Myotiinae
Myotis
Myotis albescens
Myotis auriculacea
Myotis californica
Myotis carteri
Myotis ciliolabrum
Myotis elegans
Myotis evotis
Myotis fortidens

Myotis keaysi
Myotis lucifuga
Myotis nigricans
*Myotis peninsularis**
*Myotis planiceps**
Myotis thysanodes
Myotis velifera
*Myotis vivesi**
Myotis volans
Myotis yumanensis

Subfamily Vespertilioninae
Tribe Antrozoini
Antrozous
Antrozous pallidus
Bauerus
Bauerus dubiaquercus
Baeodon
*Baedon alleni**
Rhogeessa
*Rhogeessa aeneus**
Rhogeessa genowaysi
Rhogeessa gracilis
Rhogeessa mira
Rhogeessa parvula
Rhogeessa tumida
Tribe Lasiurini
Lasiurus
Lasiurus blossevillii
Lasiurus borealis
Lasiurus cinereus
Lasiurus ega
Lasiurus intermedius
Lasiurus xanthinus
Tribe Nycticeini
Eptesicus
Eptesicus brasiliensis
Eptesicus furinalis
Eptesicus fuscus
Nycticeius
Nycticeius humeralis
Tribe Plecotini
Corynorhinus
*Corynorhinus mexicanus**
Corynorhinus townsendii

Euderma

Euderma maculatum

Idionycteris

Idionycteris phyllotis

Tribe Vespertilioni

Parastrellus

Pipistrellus hesperus

Perimyotis

Pipistrellus subflavus

Suoerfamily Emballonuroidea

Family Emballonuridae

Subfamily Emballonurinae

Tribe Diclidurini

Balantiopteryx

Balantiopteryx io

Balantiopteryx plicata

Centronycteris

Centronycteris maximiliani

Diclidurus

Diclidurus albus

Peropteryx

Peropteryx kappleri

Peropteryx macrotis

Rhynchonycteris

Rhynchonycteris naso

Saccopteryx

Saccopteryx bilineata

Saccopteryx leptura

Order Primates

Family Cebidae

Subfamily Atelinae

Ateles

Ateles geoffroyi

Subfamily Mycetinae

Alouatta

Alouatta palliata

Alouatta pigra

Grandorder Ferae

Order Carnivora

Suborder Caniformia

Infraorder Arctoidea
Superfamily Ursoidea
Family Ursidae
Subfamily Ursinae
Ursus
Ursus americanus
Ursus arctos
Infraorder Cynoidea
Family Canidae
Subfamily Caninae
Tribe Canini
Canis
Canis latrans
Canis lupus
Tribe Vulpini
Urocyon
Urocyon cinereoargenteus
Vulpes
Vulpes velox
Infraorder Mustelida
Family Mustelidae
Superfamily Lutrinae
Tribe Lutrini
Lontra
Lontra longicaudis
Subfamily Mephitinae
Conepatus
Conepatus leuconotus
Conepatus mesoleucus
Conepatus semistriatus
Mephitis
Mephitis macroura
Mephitis mephitis
Spilogale
Spilogale putorius
*Spilogale pygmaea**
Subfamily Mustelinae
Eira
Eira barbara
Galictis
Galictis vittata
Mustela
Mustela frenata
Subfamily Taxidiinae

Taxidea

Taxidea taxus

Family Procyonidae

Bassariscine

Bassariscus

Bassariscus astutus

Bassariscus sumichrasti

Potos

Potos flavus

Procyoninae

Nasua

Nasua narica

Procyon

Procyon lotor

Suborder Feliformia

Family Felidae

Subfamily Felinae

Herpailurus

Herpailurus yagouaroundi

Leopardus

Leopardus pardalis

Leopardus wiedii

Lynx

Lynx rufus

Puma

Puma concolor

Subfamily Pantherinae

Panthera

Panthera onca

Grandorder Lipotyphla

Order Erinaceamorpha

Superfamily Talpoidea

Family Talpidae

Subfamily Talpinae

Scalopina

Scalopus

Scalopus aquaticus

Scapanus

Scapanus latimanus

Order Soricomorpha

Superfamily Soricoidea

Family Soricidae

Subfamily Soricinae
Tribe Blarini
Cryptotis
Cryptotis goldmani
Cryptotis goodwini
*Cryptotis magna**
Cryptotis mayensis
Cryptotis merriami
*Cryptotis mexicana**
Cryptotis parva
Tribe Nectogalini
Megasorex
*Megasorex gigas**
Notiosorex
Notiosorex crawfordi
Tribe Soricini
Sorex
*Sorex emarginatus**
*Sorex macrodon**
*Sorex milleri**
Sorex monticolus
*Sorex oreopolus**
Sorex ornatus
Sorex saussurei
*Sorex sclateri**
*Sorex stizodon**
*Sorex ventralis**
*Sorex veraepacis**

Grandorder Ungulata
Mirorder Altungulata
Order Perissodactyla
Suborder Ceratomorpha
Infraorder Tapiromorpha
Superfamily Tapiroidea
Family Tapiridae
Tapirus
Tapirus bairdii

Mirorder Eparctocyona
Order Artiodactyla
Suborder Rumiantia
Superfamily Bovoidae
Family Ovidae

Subfamily Bovinae
Tribe Bovini
Subtribe Bovina
Bos
Bos bison
Subfamily Ovinae
Tribe Ovini
Subtribe Ovina
Ovis
Ovis canadensis
Superfamily Cervoidea
Order Antilocapridae
Subfamily Antilocaprinae
Antilocapra
Antilocapra americana
Family Cervidae
Subfamily Odocoileinae
Tribe Odocoileini
Mazama
Mazama americana
*Mazama pandora**
Odocoileus
Odocoileus hemionus
Odocoileus virginianus
Suborder Suiformes
Superfamily Suoidea
Family Tayassuidae
Subfamily Tayassuinae
Pecari
Pecari tajacu
Tayassu
Tayassu pecari

Magnorder Xenarthra
Order Cingulata
Dasypodoidea
Family Dasypodidae
Dasypodinae
Dasypodini
Dasypus
Dasypus novemcinctus
Tolypeutinae
Priodontini
Cabassous

Cabassous centralis

Order Pilosa

Vermilingua

Family Myrmecophagidae

Cyclopes

Cyclopes didactylus

Tamandua

Tamandua mexicana

4.3.2 A PHYLOGENETIC SUPERTREE OF MEXICAN MAMMALS (*P*)

Marsupialia is represented in Mexico only by Order Didelphimorphia, and its position in the tree is placed near its base. For subclass Placentalia, the position of every order in the full tree followed the topology for placental Mammals of Murphy *et al.* (2001). This topology is compatible with recent studies, dividing placentals into the southern hemisphere clades Afrotheria (not present in America) and Xenarthra, and a monophyletic northern hemisphere clade (Boreoeutheria) composed of Euarchontoglires and Laurasiatheria (Waddell et al. 2001, Delsuc et al. 2002, Hudelot et al. 2003, Waddell and Shelley 2003, Springer et al. 2004a). Three superordinal clades are recognised: I) Xenarthra – which includes Orders Cingulata and Pilosa, II) Euarchontoglires – which includes Orders Primates, Lagomorpha and Rodentia, and III) Laurasiatheria – which includes Orders Soricomorpha, Erinaceamorpha, Chiroptera, Carnivora, Artiodactyla and Perissodactyla (Fig. 4.2). The resulting full species-level composite phylogenetic tree is shown in Figure 4.3. A detailed discussion of the relationships described by this tree is beyond the scope of this chapter. Nonetheless, some general observations on each mammalian order are made below.

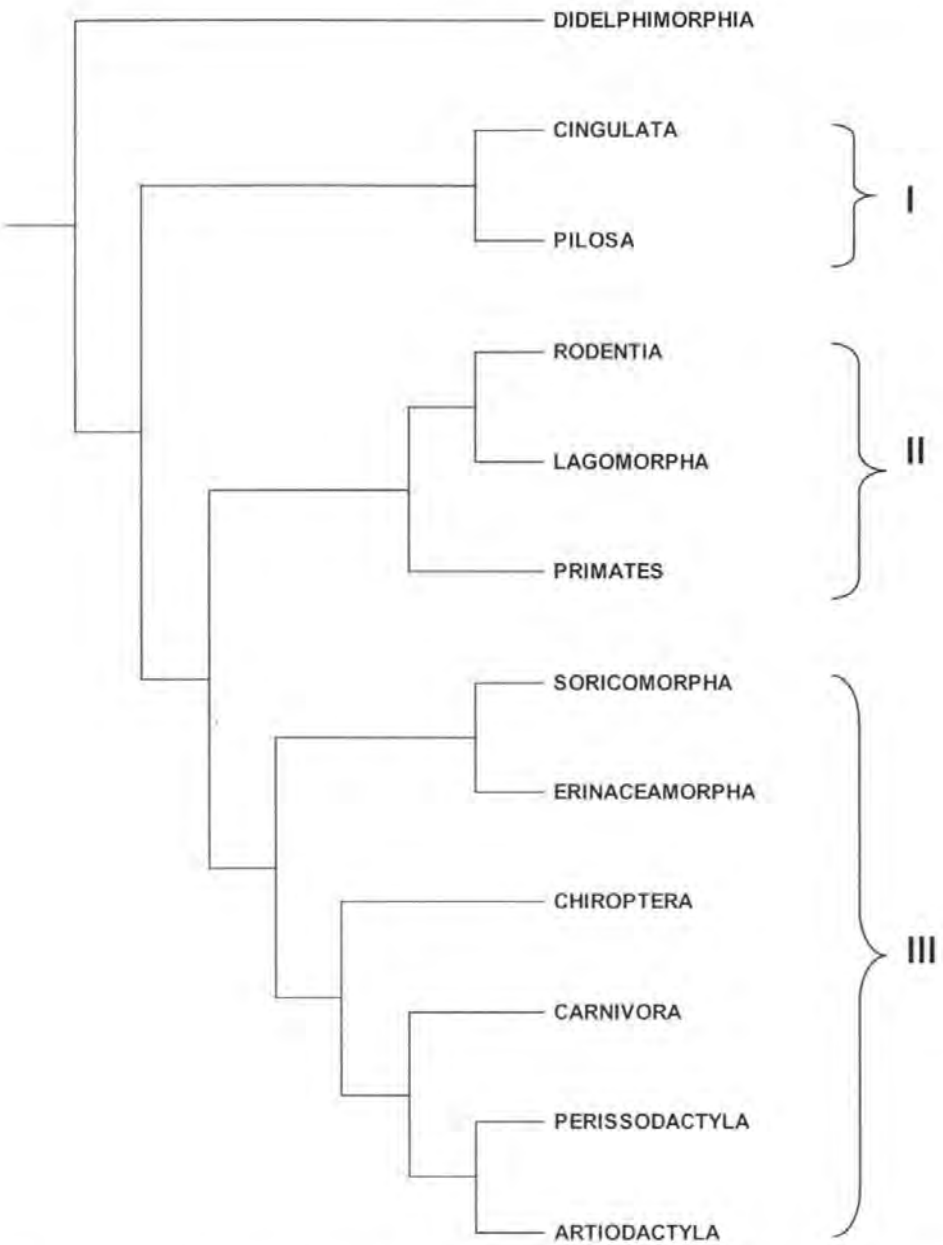


Figure 4.2 The ordinal phylogenetic tree of the mammals studied. The numbers on the right refer to the major clades to which the orders belong: I) Xenarthra, II) Euarchontoglires and III) Laurasiatheria.

Figure 4.3 Next page, hypothetical species-level phylogenetic tree of the 416 Mexican mammals included in this study. Notice that the tree is dominated by two major clades: Euarchontoglires (in blue) and Laurasiatheria (in red). This diagram is only intended to show the overall topology of the tree. For details of the position of each species consult the individual order-level trees in the figures below.

Order Didelphimorphia

This order includes only the family Didelphidae; the relationships for the species considered in this research are fully resolved (Fig. 4.4, Voss and Jansa 2003). Two main clades are distinguished, which are taxonomically named as subfamily Caluromyinae (one species) and Subfamily Didelphinae (four genera, six species).

Order Cingulata and Order Pilosa

Former Order **Xenarthra** is now taxonomically recognized as Magnorder Xenarthra (McKenna and Bell 1997) and divided into two different orders: Order Cingulata (armadillos, here represented by *Dasypus novemcinctus* and *Cabassus centralis*) and Order Pilosa (anteaters and sloths, here represented by *Cyclopes didactylus* and *Tamandua mexicana*; Figure 4.4). These two groups are strongly supported by molecular systematic analysis (Delsuc *et al.* 2001, Delsuc *et al.* 2002).

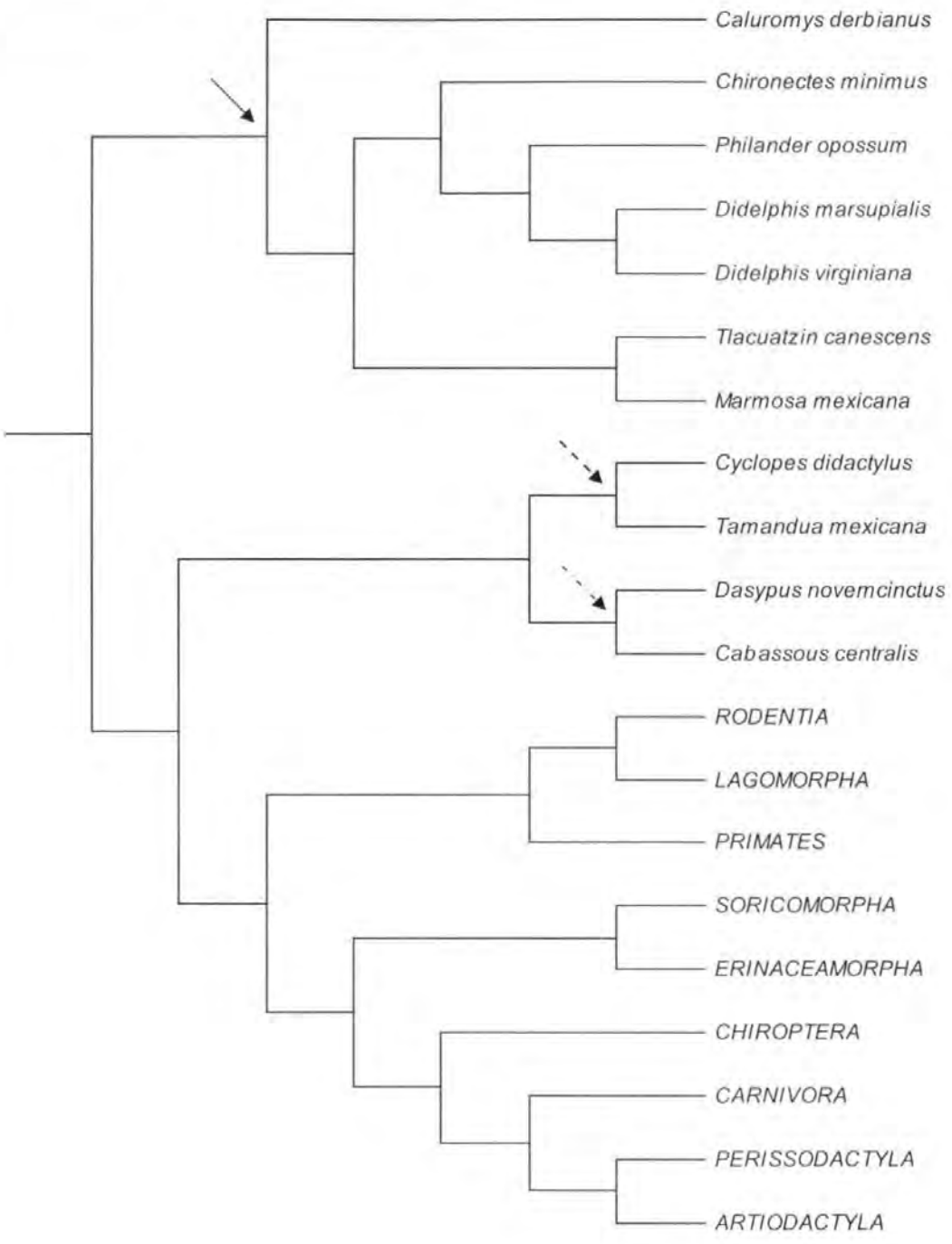


Figure 4.4 Phylogenetic relationships among species of Order **Didelphimorphia** (full arrow); and Orders **Cingulata** (bold dashed arrow) and **Pilosa** (dashed arrow); all of them rooted to the full mammalian tree.

ORDER RODENTIA

The current taxonomy uses the shape of the lower jaw (sciurognath or hystricognath) as the primary character. This is the most commonly used approach for dividing the order into suborders. According to this taxonomy, the orders occurring in Mexico are: Sciuromorpha, Castorimorpha (Castorioidae, Geomyioidea) and Myomorpha. On the other hand, several molecular phylogenetic studies have used gene sequences to determine the relationships among rodents, but these studies are yet to produce a single consistent and well-supported taxonomy. Despite this, some clades seem consistent, and the three major clades (Fig. 4.7) recognised by Hunchon *et al.* (2002), Adkins *et al.* (2003) and DeBry (2003) are: a) Myodonta, the mouse–related clade, here represented by species in the families Muridae (this is the most species-rich family), Geomyidae and Heteromyidae, and Castoridae, b) the group of squirrels and chipmunks, here represented by family Sciuridae, and c) the Hystricognathi group (pacas and porcupines)

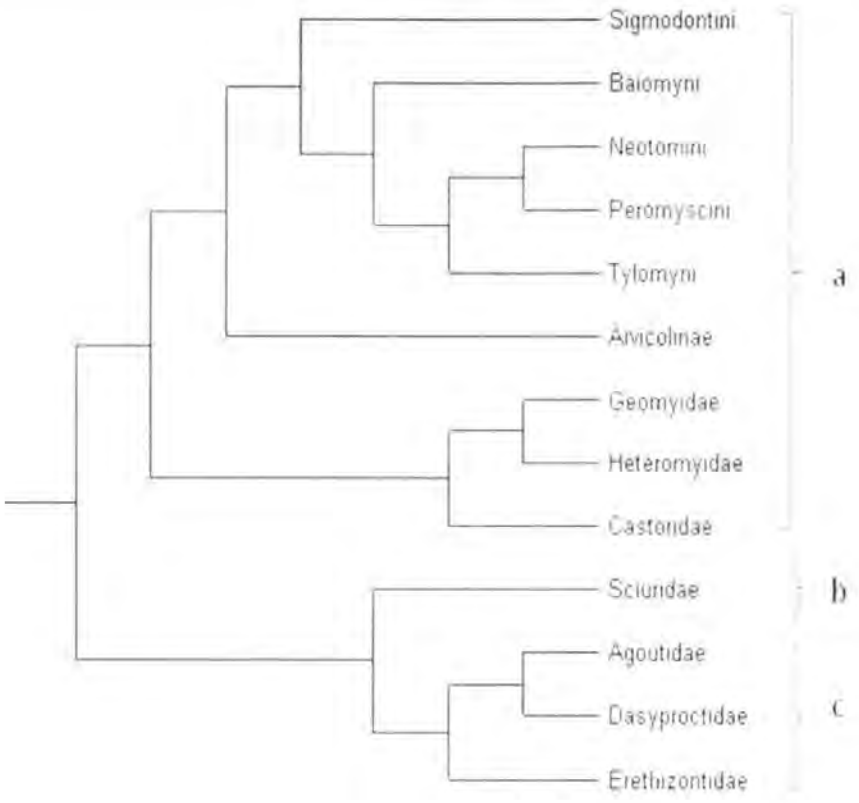


Figure 4.5 Phylogenetic tree of infraorder relationships in Rodents. In addition, subfamilies of Muridae are also presented: Sigmodontinae (represented by tribes Sigmodontini, Baiomyni, Neotomini, Peromyscini and Tylomyni) and Arvicolinae. For nomenclature of groups a, b and c see text.

The phylogenetic tree of rodent species is shown in Figures 4.6, 4.7 and 4.8. It was not possible to find phylogenetic information for all the species in this group. The relationships among the North American members of Family Muridae have not been resolved to species level, particularly for the genera *Peromyscus* and *Reithrodontomys*. Therefore, taxonomic information and their hypothetical politomies (Purvis and Garland 1993, Crozier *et al.* 2005) were employed.

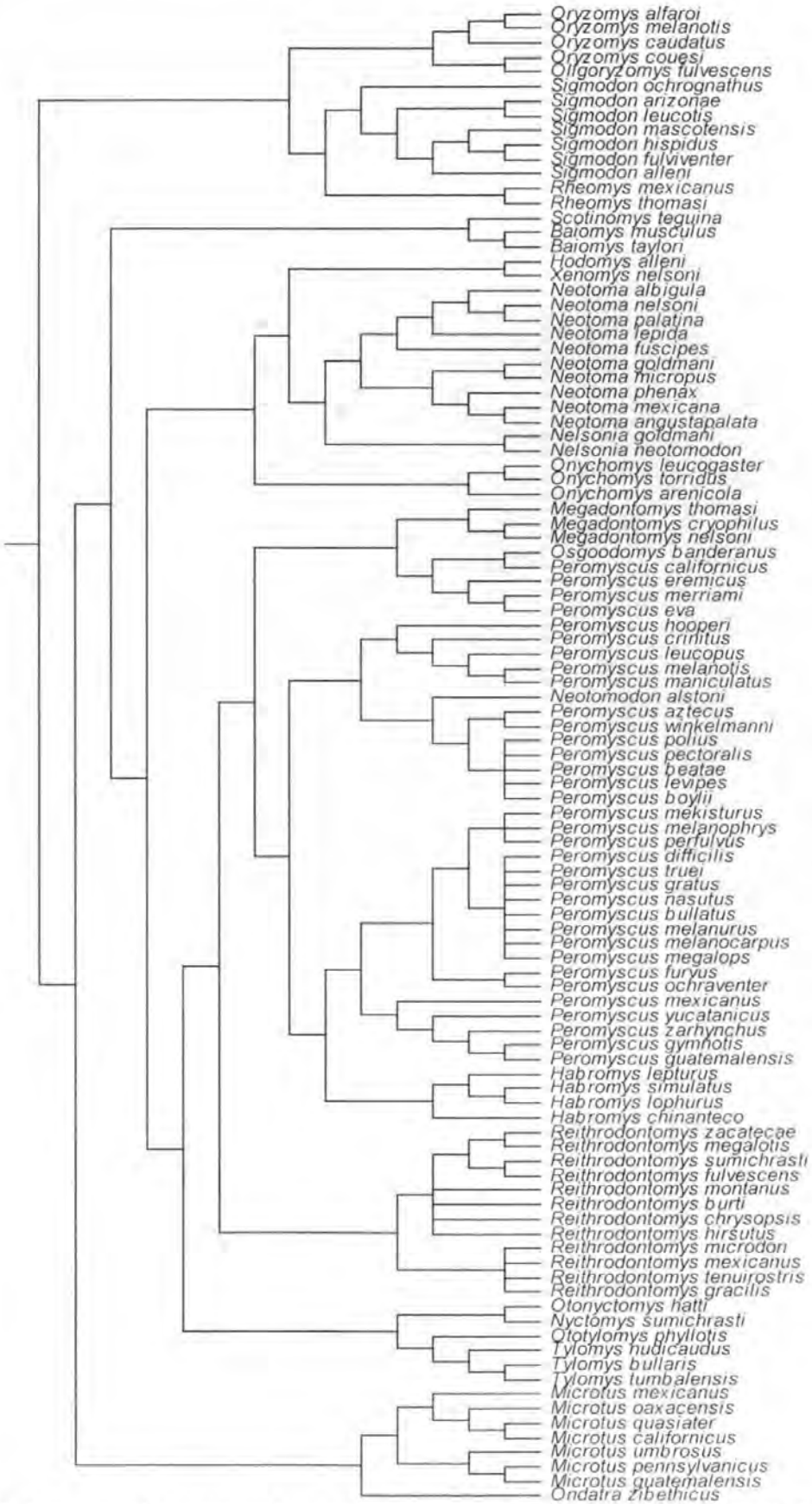


Figure 4.6 Phylogenetic relationships among species of Order **Rodentia** (Family Muridae, subfamilies Sigmodontinae and Arvicolinae).

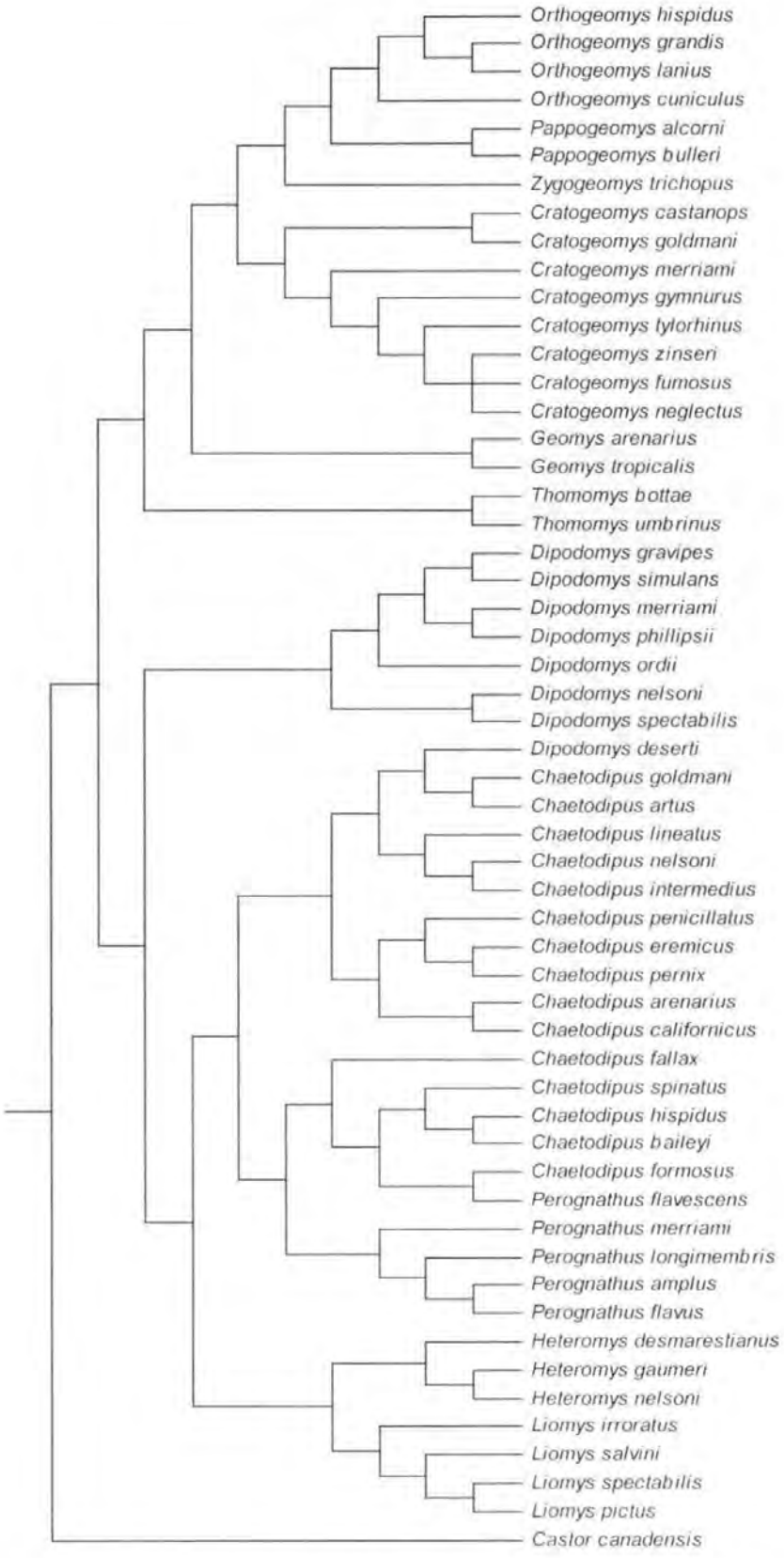


Figure 4.7 Phylogenetic relationships among species of Order **Rodentia** (continuation) Families Geomyidae and Heteromyidae (Geomoyidea) and Family Castoridae (*Castor canadensis*).

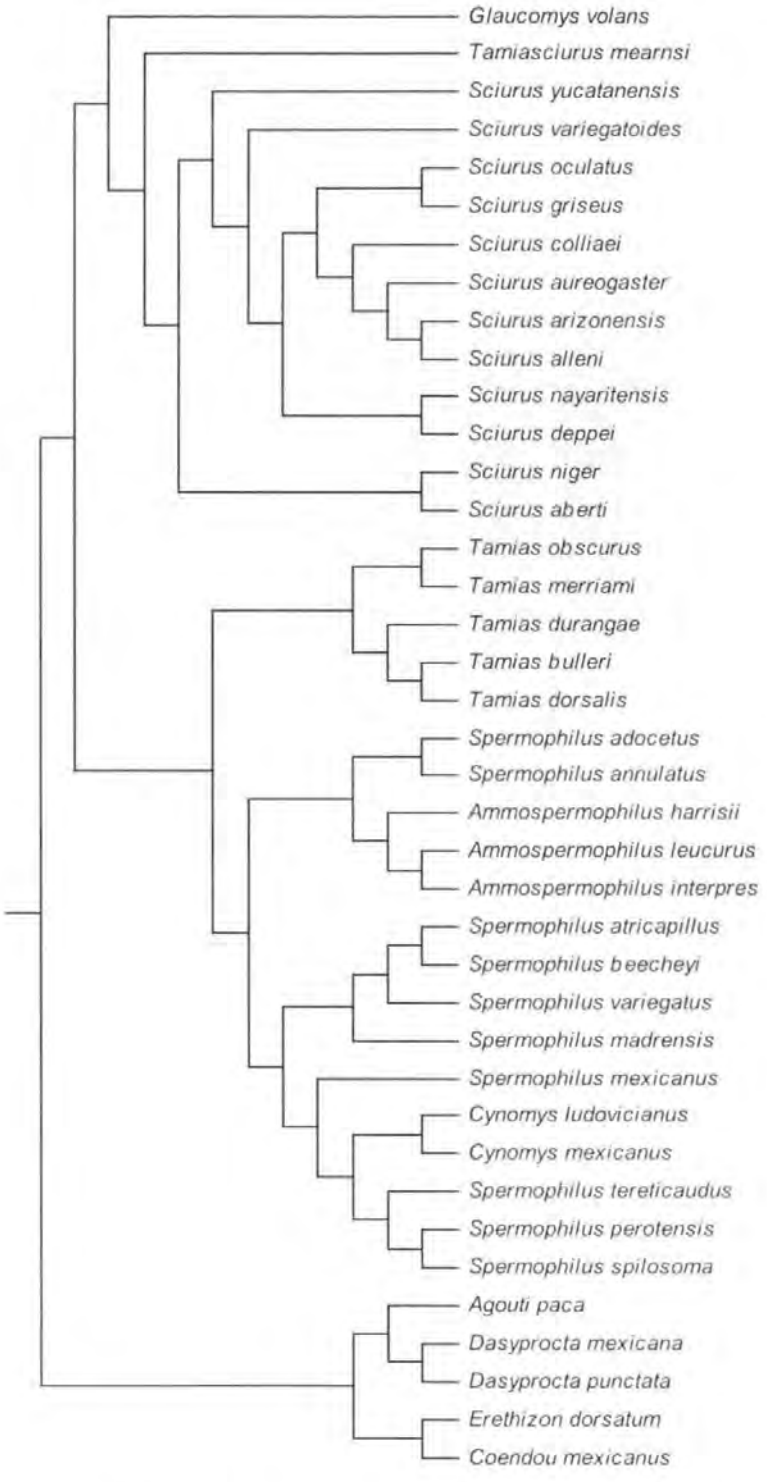


Figure 4.8 Phylogenetic relationships among species of Order **Rodentia** (continuation). Family Sciuridae and the Hystricognathi (pacas and porcupines).

Order Primates

The group of monkeys in Mexico is not particularly diverse. It is represented by two genera and three species (Fig. 4.5). Their position on the tree is as a sister clade of Glires (Rodentia and Lagomorpha), grouped in Euarchontoglires.

Order Lagomorpha

Lagomorphs comprised three well differentiated genera: the monotypic genus *Romerolagus* and the two polytipic genera *Sylvilagus* and *Lepus* (Fig. 4.5). A phylogenetic supertree constructed from taxonomic and phylogenetic studies is available for this order (Stoner *et al.* 2003). This was taken as the starting point, but modified by the work of Robinson and Matthee (2005).

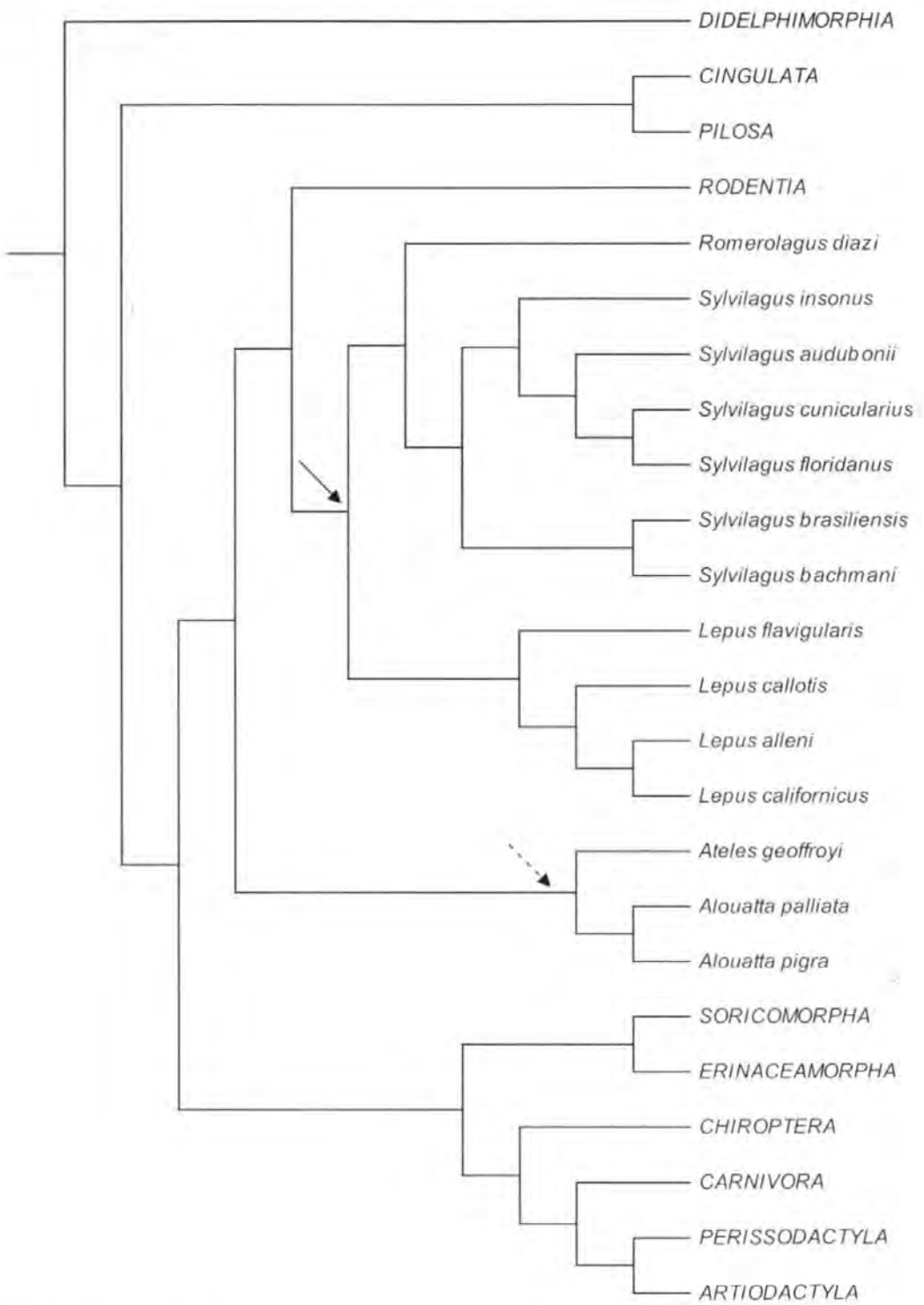


Figure 4.9 Phylogenetic relationships among species of Orders **Lagomorpha** (full arrow) and Order **Primates** (dashed arrow) rooted to the full mammalian tree.

Order Soricomorpha and Order Erinaceamorpha

Order Insectivora has now been recognized as Grandorder Lipotyphla and has been split into three separate Orders, two of them present in Mexico. These are Soricomorpha (the shrews: *Sorex, Cryptotis, Notiosorex* and *Megasorex*) and Erinaceomorpha (moles: *Scalopus* and *Scapanus;* Fig. 4.10). The relationships among shrew species are not fully resolved for genera *Sorex* and *Cryptotis* (Grenyer and Purvis 2003b). These high levels of politomy are also evident in the PST.

Order Chiroptera

All the members of this group that occur in Mexico belong to the suborder Yangochiroptera. The Bat's family-level tree followed the one proposed by Teeling *et al.* (2005). Three well differentiated groups are present in Mexico. These are the Superfamilies Emballonuroidea, Noctillionoidea (both represented in Fig. 4.11) and Vespertillionoidea (Fig. 4.12). The position of species in each family followed, mostly, the topology determined on the MRP supertree of Jones et al (2002). However, that supertree does not incorporate all chiropteran species present in the database; therefore other sources were employed to determine their position on the tree. The topology of this tree shows more politomies than any of the other groups considered in this dissertation.

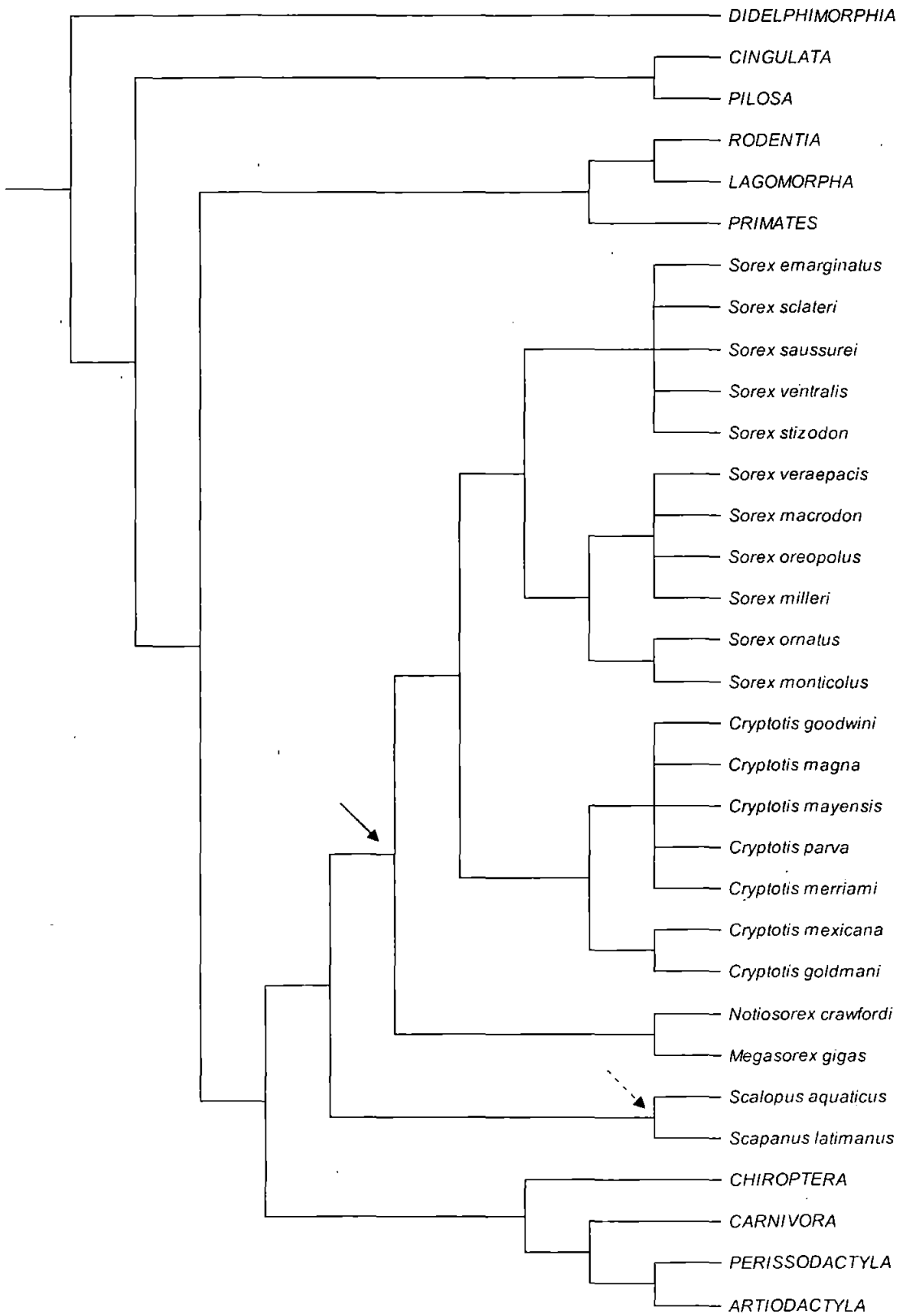


Figure 4.10 Phylogenetic relationships among species of Order **Soricomorpha** (full arrow) and **Erinaceamorpha** (dashed arrow) rooting to the full mammalian tree.

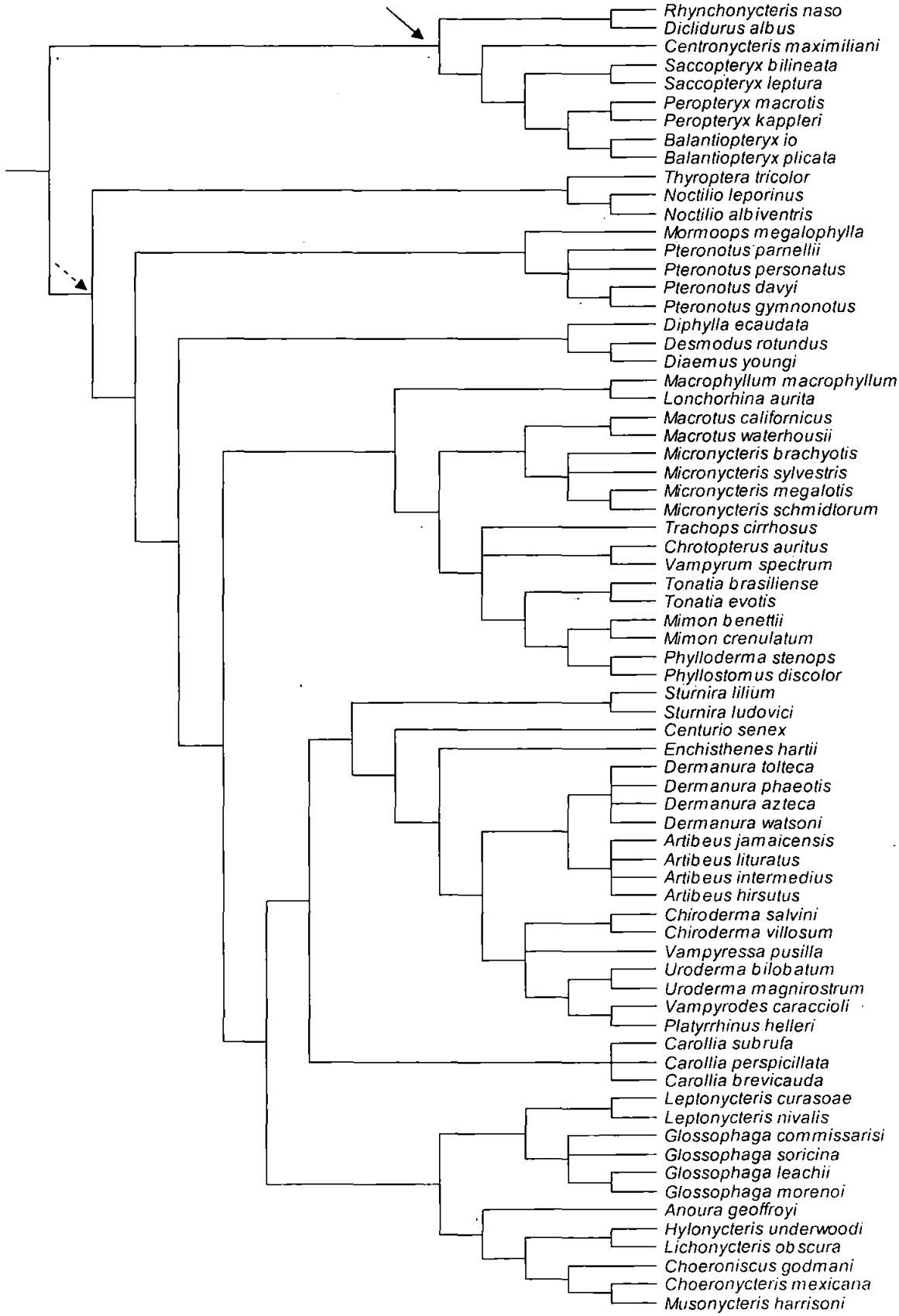


Figure 4.11 Phylogenetic relationships among species of the Order **Chiroptera**; Superfamilies Emballonuroidea (full arrow) and Noctillionoidea (dashed arrow).

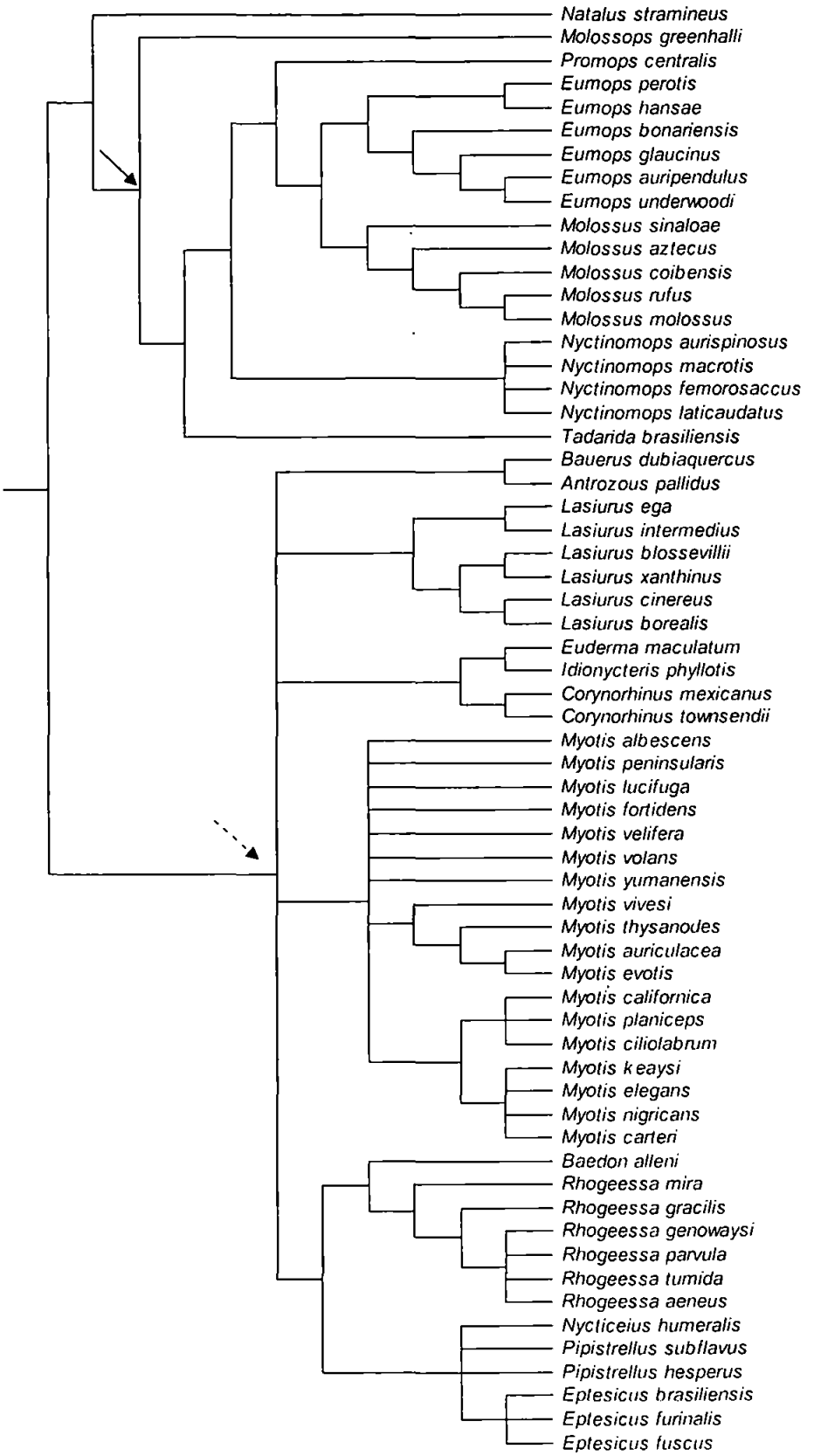


Figure 4.12 Phylogenetic relationships among species of Order **Chiroptera;** Superfamily Vespertillionoidea (families Natalidae (*Natalus stramineus*), Molossidae (full arrow) and Vespertillionidae (dashed arrow)).

ORDER CARNIVORA

The relationships within this order have long been recognized. Carnivora diverged into two monophyletic clades, the Caniformia and the Feliformia. This has been robustly supported by morphological, molecular, and MPR phylogenies (Flynn and Nedbal 1998, Bininda-Emonds *et al.* 1999, Koepfli and Wayne 2003) . Among Canimorphia, the monophyly of the suprafamilial Arctoidea (here represented by family Ursidae, and superfamily Musteloidea) has been well supported too (Fig. 5.14). The phylogenetic relationships at family level followed the topology of the molecular phylogeny proposed by Flinn *et al.* (2005).

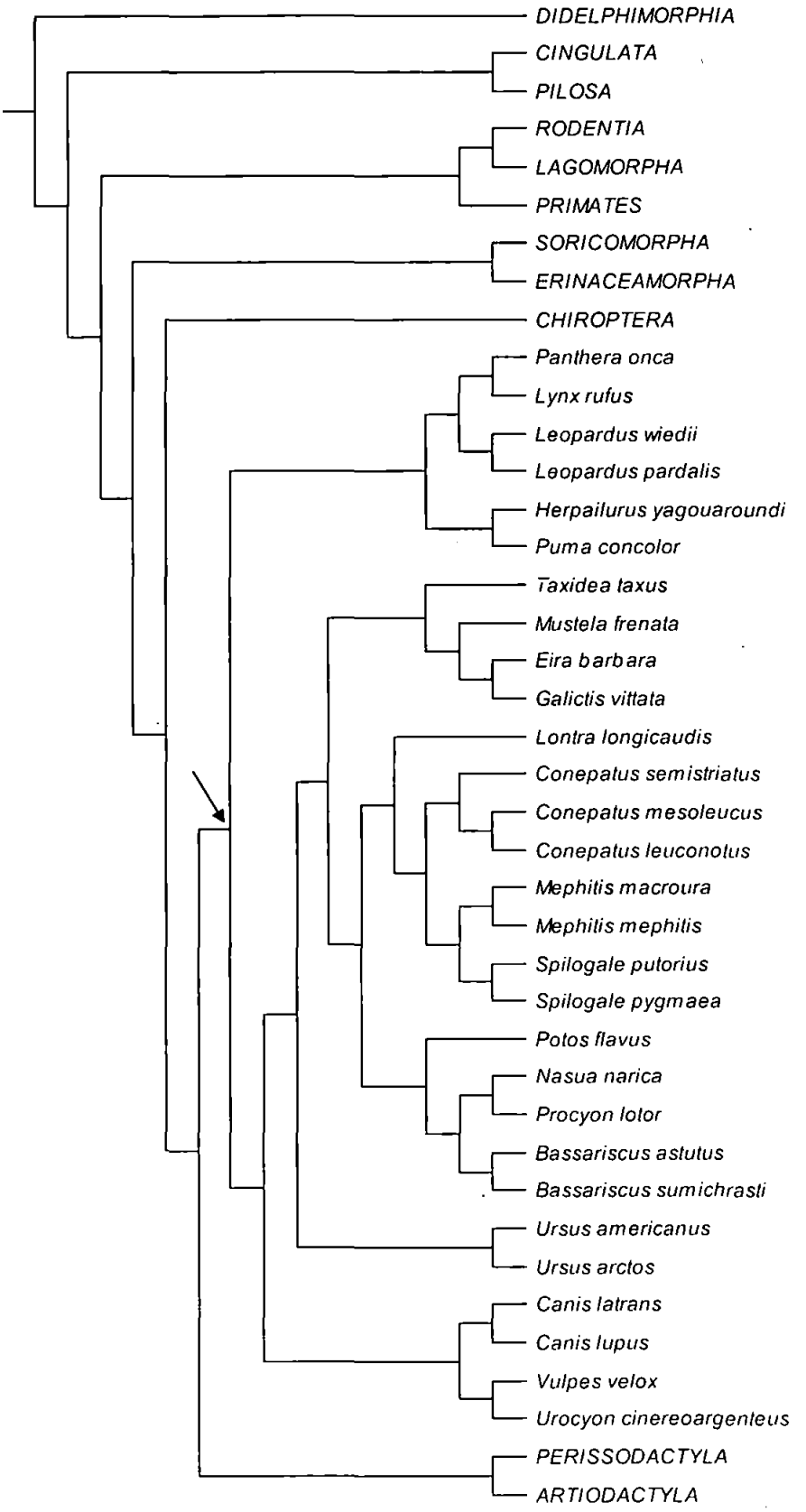


Figure 4.13 Phylogenetic relationships among species of Order **Carnivora** (arrow) rooting to the full mammalian tree.

ORDER PERISSODACTYLA AND ORDER ARTIODACTYLA

Baird's tapir (*Tapirus bairdii*) is the only species of Perissodactyla represented in Mexico. This order and Artiodactyla are sister clades. Within Artiodactyla, two main subdivisions are evident; these are traditionally recognised as suborder Suiformes (pecaries) and suborder Rumiantia. Their relationships and those at species level are supported by both morphological and molecular data (Geisler 2001, Hassanin and Douzery 2003) and coincide with the topology produced by supertree analysis (Price *et al.* 2005). The Perissodactyla and Artiodactyla relationships are displayed in Figure 4.15

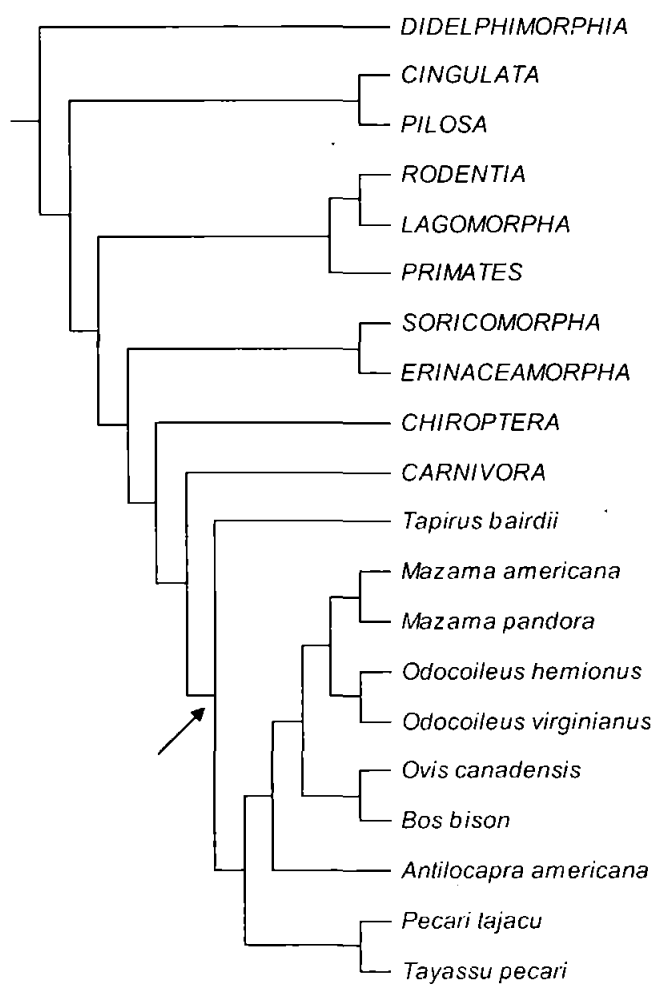


Figure 4.14 Phylogenetic relationships among species of Orders **Perissodactyla** (*Tapirus bairdii*) and **Artiodactyla** rooting to the full mammalian tree (see arrow).

Because of the availability of systematics studies is uneven represented across the mammalian orders, due perhaps to the complexity of each taxa, the resulting phylogeny was hard to construct but resulted in a sufficiently resolved classification. As supertrees become more widely employed in comparative and macroevolutionary studies (Mooers and Heard 1997, Heard and Mooers 2000, Agapow and Purvis 2002, Mace *et al.* 2003, Cardillo *et al.* 2006), this first phylogeny of Mexican mammals represents an important piece of essential information.

CHAPTER 5. THE PHYLOGENETIC DIVERSITY OF MEXICAN MAMMALS

5.1.INTRODUCTION

It is generally agreed that conservation must be addressed in the understanding that we might only be able to protect a small fraction of the current species (Cabeza and Moilanen 2001). Species richness (*S*), the most common measure of biodiversity used in conservation, is a direct measure of diversity; it is defined as the total number of species present in an area. Although more informative than species richness, traditional diversity indices, such as the Simpson Index (*D*) and the Shannon index (*H*), weight all species equally. However, taxa need to be valued differently when priorities for conservation are being set (Vane-Wright *et al.* 1991, Vazquez and Gittleman 1998, Barker 2002). Employing objective weightings, i.e., avoiding the extreme of allocating weights to species in terms of some perceived, subjective value, the diversity of an area can be valued in inverse proportion to the degree of relatedness of the species present in it. As explained before, two indices that take into account taxonomic/phylogenetic relatedness to assess diversity, and may thus help us set conservation priorities, are Phylogenetic Diversity (Faith 1992) and Taxonomic Distinctness (Clarke and Warwick 1998). In addition, Diversity Skewness can also provide important information regarding the shape of the phylogenetic tree, as this shape could have implications on the direction of the evolutionary potential of the taxonomic group under study.

5.1.1 Measures of Diversity Based on Relatedness of Species

Pielou (1975) was one of the first authors to suggest that diversity should be considered higher in a community in which species are divided amongst many genera as opposed to one where the majority of species belong to the same genus. This point of view has been further developed to produce quantitative measures of this phylogenetic component. In turn, these measures have had important consequences in setting conservation priorities in the last decade (Vane-Wright *et al.* 1991, Faith 1996, Williams *et al.* 1996b).

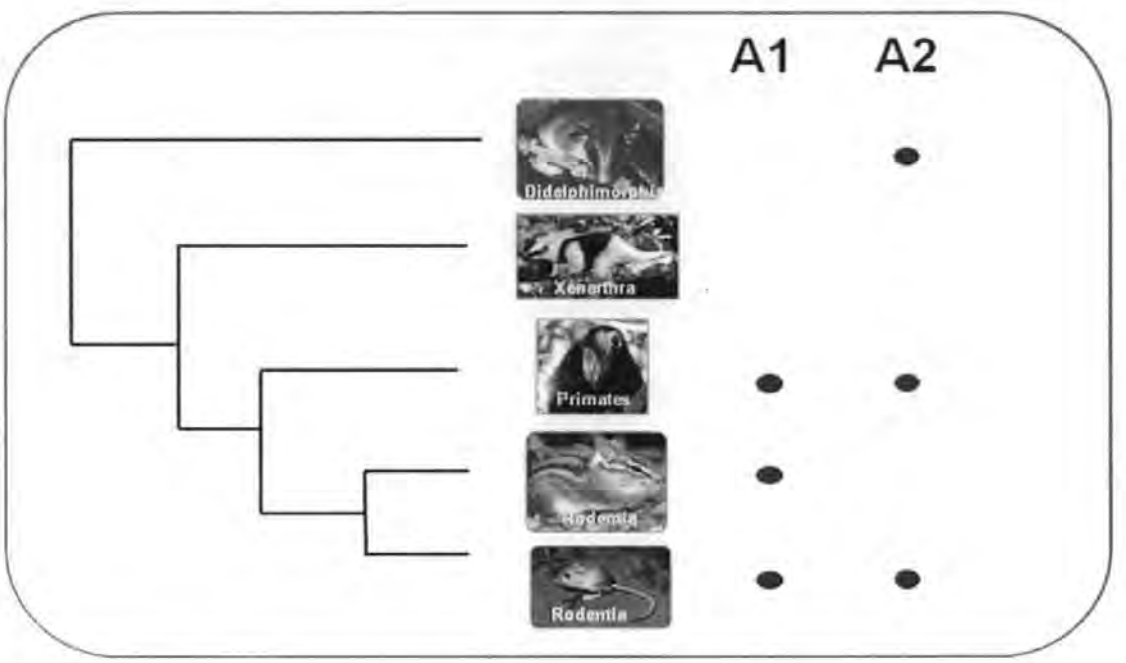


Figure 5.1 Representation of a hypothetical phylogenetic tree of four species of mammals included in three different Orders and that occur in two different areas (A1 and A2).

Indices based on phylogenetic information attempt to measure the evolutionary component of biodiversity. Assemblages with the highest phylogenetic values will be those that contain species which differentiated earlier in their evolutionary history and, therefore, show a larger taxonomic range. When

choices have to be made, these assemblages merit conservation over less differentiated ones (Vane-Wright *et al.* 1991). In the example above (Fig. 5.1), both area 1 (A1) and area 2 (A2) contain three species. Species in area 1 are more closely related to each other than species in area 2. That is, the length of the tree connecting species in A2 is longer than that connecting species in A1. Area 2 thus has higher phylogenetic diversity and ought to be conserved first.

Phylogenetic Diversity Index (PD)

The index of phylogenetic diversity (*PD*) measures how closely related the species in an assemblage are (Faith 1994). It is based on known branch lengths: *PD* is the cumulative branch length of the full tree. In general, patterns of difference among species are most likely to be congruent with the pattern of their genealogical relationship through genetic inheritance. The numerical value of *PD* thus tends to capture not only the degree of relationship, but also the degree of difference in the biological characteristics of the taxa under consideration (Vane-Wright *et al.* 1991, Faith 1994, 1996). The *PD* Index is calculated as:

$$PD = \sum_{k} b_k \qquad \text{Equation 1}$$

where b_k is the length of each of the k branches in the phylogeny. *PD* includes, but is not restricted to, branch lengths based on time (Faith 2003). Because *PD* is a measure of total diversity, it increases as new species are added to the list. According to Clarke and Warwick (2001), this makes *PD* highly dependent on species richness and, thus, the sampling effort required to determine it. It is,

however, obvious that the ratio between *PD* and species number (*S*) measures the average phylogenetic distance in the sample (*AvePD*):

$$AvePD = PD / S \qquad \text{Equation 2}$$

Thus, given a statistically representative sample of species in a community or area, this mean distance should yield similar numerical values in independent, but equally representative samples.

Taxonomic distinctness index (TD)

Average TD (AveTD)

Clarke and Warwick (1998) defined what they intended to be an alternative index of diversity that, unlike *PD*, would be independent of sampling effort. They termed this index taxonomic distinctiveness. This index measures not the total branch length, but the average distance between all pairs of species in a community sample. This distance is defined as the path length through a standard Linnean taxonomy or, if the information exists, through the phylogenetic tree connecting the species in the sample (the number of taxonomic steps back to a common ancestor). This index is calculated as:

$$AveTD = \left[\sum\sum_{i<j} \omega_{ij}\right] / \left[S(S-1)/2\right] \qquad \text{Equation 3}$$

where *S* is the number of species present, ω_{ij} is the 'distinctness weight' (or taxonomic distance) given to the path length linking species *i* and *j* in the classification, and the double summations are over all pairs of species *i* and *j*.

It has been argued that because taxonomic distinctiveness can be calculated from simple species presence-absence data, it has a number of advantages over the simpler species richness measure and over classic species diversity indices (von Euler and Svensson 2001, Pullin 2002, Magurran 2004) such as Shanon's, Margalef's and Pielou's. The benefits that supporters of *TD* cite are: 1) it is independent on sampling effort, i.e., it is said to be robust against variation in sampling effort, 2) it can be compared across studies and sites, and 3) it appears to be more sensitive to measure the consequences of environmental degradation than species richness estimates. However, because the number of species in the sample is known, the product of *AveTD* and the number of species in the sample provides a measure of total path length or total "taxonomic distinctness" (*TD*). That is:

$$TD = AveTD \cdot S \qquad \text{Equation 4}$$

Given the fact that both *PD* and *TD* (as well as *AvePD* and *AveTD*) calculate the same property of the phylogenetic tree (albeit from different starting points), they must be correlated. In consequence, the discussion regarding their relative merits is unwarranted. We will return to this issue in the discussion. Finally, given the confusing names given to these indices, but in order not to confuse things further, in this study we use the term Taxonomic Diversity as synonymous of Taxonomic Distinctness (or distinctiveness) and, just as *PD* and *AvePD* refer to total and average Phylogenetic Diversity, *TD* and *AveTD* will refer to measures of total and average Taxonomic Diversity, respectively.

VARIATION IN TD (VARTD)

Clarke and Warwick (2001) suggested that under anthropogenic disturbance the species that tend to disappear first are those belonging to taxa that are relatively species poor. The remaining species are then from a smaller number of groups that tend to be relatively more species-rich. It is possible that species removal does not affect *AveTD*, although it will affect the "evenness" of the distribution of taxa across the classification. Thus, Variation in Taxonomic Distinctness (*VarTD*) was defined as the variance of the taxonomic distances in the tree (Clarke and Warwick 2001). This measure reflects the unevenness of the distribution of taxa across the classification. It can be thought of as an index of the complexity of the hierarchical tree (high *VarTD* = high taxonomic complexity and uneven distribution of species in the classification). This distribution can go from a completely uniform distribution (when all path lengths between species are equal, such as with a diverse genus that dominates a community) to an uneven distribution where the path lengths are very different (e.g., some speciose clades and some poorly represented ones). Such a difference in the (usually hierarchical taxonomic) clasification is reflected in variability of the full set of pairwise distinctness weights that produce *AveTD* (Warwick *et al.* 2002). Variation in taxonomic distinctness is defined as:

$$VarTD = \left[\sum_{i<j}\sum(\omega ij - AveTD)2\right]/\left[S(S-1)/2\right] \qquad \text{Equation 5}$$

As with *AveTD*, Clarke and Warwick maintain that, with the exception of rather small samples where *VarTD* has a slight negative bias, *VarTD* is independent of sample size. Other authors concur with Clarke and Warwick that

the advantage of *AveTD* over *PD* is its ability to produce a measure that is independent of sample-size (Clarke and Warwick 1998, Price *et al.* 1999, Bhat and Magurran 2006). This, however, lacks fundament, as both *PD* and *TD* can be expressed as either averages or totals. The only advantage of *TD* is that, given the algorithm to calculate it, it also provides a measure of variability. On the other hand, because the tree topology is known, other indices of tree shape can be calculated. In particular, Colless index of skewness (Heard 1992) was also calculated.

5.1.2 Diversity Skewness (*DS*)

The presence of asymmetry within phylogenies, where some groups are markedly more speciose than their sister clades, has been of immense interest in studies of evolution and conservation. This is because asymmetry is the result of a series of evolutionary processes that had produced either high diversification (speciation) or depauperation (extinction) within particular clades. Heard and Cox (2007) have indeed remarked the "astonishing unevenness in biodiversity among major clades". Currently, as more phylogenetic information is becoming available, diversity skewness can be quantified using the topology of the phylogenetic trees (Heard 1992, Mooers and Heard 1997). Diversity skewness (*DS*) is low when all lineages have had similar diversification and the phylogeny is balanced (Fig. 5.2a). On the contrary, *DS* is high when some lineages have diversified more than others or some lineages have lost a disproportionate number of species resulting in an unbalanced phylogeny (Fig. 5.2b).

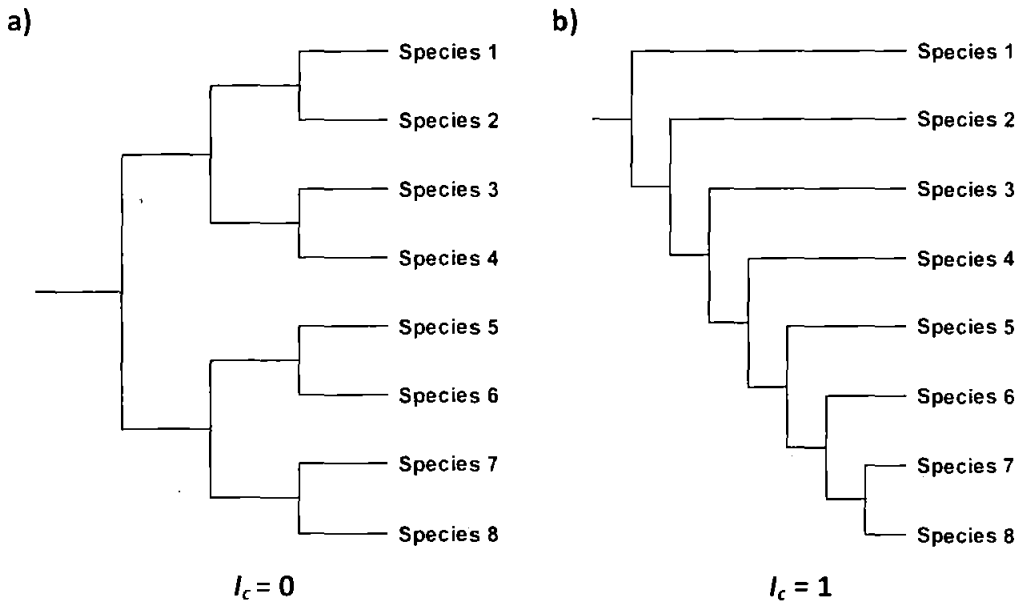


Figure 5.2 The extremes of phylogenetic tree balance. a) Perfectly balanced tree. b) Perfectly unbalanced tree.

COLLESS'S INDEX OF PHYLOGENETIC TREE IMBALANCE (I_C)

There are several measures for assessing tree topology and asymmetry. Among them, Colless's index of phylogenetic tree imbalance, (I_C) is commonly used because it is simple, intuitive, and powerful (Heard 1992, Agapow and Purvis 2002, Stam 2002, Blum and Francois 2006, Heard and Cox 2007). Colless's index takes values from 0, for a perfectly balanced phylogeny (low skewness; Figure 5.2a) to 1, for a perfectly imbalanced phylogeny (high skewness; Figure 5.2b). I_c is defined as the normalised sum of the difference in species richness between the two subclades defined at each internal node of the phylogenetic tree:

$$I_c = \frac{2}{(n-1)(n-2)} \sum_{nodes} \left| S_R - S_L \right| \qquad \text{Equation 6}$$

where there are n species in the tree and the right and left branches at a node define subclades of S_R and S_L number of species.

Some studies suggest that high diversity skewness is the norm in most taxa and at all phylogenetic scales (Mooers and Heard 1997, von Euler 2001, Purvis and Agapow 2002). It is assumed that this phylogenetic tree imbalance is originated by differences in evolutionary rates within trees. However, other sources of imbalance have been identified, such as tree incompleteness and low quality of the data (Mooers 1995, Stam 2002). Due to the fact that most of the studies that have quantified tree imbalance have considered entire global classifications, Heard and Cox (2007) suggest that spatial patterns in skewness should be analysed at a variety of scales (from global clades to regional and local scales).

The objective of this chapter was to quantify the phylogenetic diversity of Mexican mammals employing the indices of (phylogenetic/taxonomic) diversity defined above, including measures of tree variability and tree imbalance.

5.2. METHODS

5.2.1 DATA SET

As already explained in Chapter 3, information on the geographic distribution of mammals was obtained from CONABIO. This information consisted of records from museum specimens detailing their identity and geographic location (data recorded up to 2004). Insular and marine mammals were excluded. The mammal database consisted of 128,114 records (or occurrences) for 416 continental species in 12 orders.

All mammal records were re-projected from latitude and longitude coordinates into the Lambert conic projection, in ArcInfo 9.2 (ESRI 2004). This projection was used so distances and areas were approximately equal across the country. The species records were aggregated to a regular grid of square cells, 30' × 30' (size area of 2,835.77 km^2 approximately). Some researchers suggest that grid cells of this size reduce the effect of bias in sampling effort, for example along roads and near settlements, common to herbarium and museum data (Margules *et al.* 1994, Crisp *et al.* 2001, Chapman 2005), while still representing the mesoscale variability of the phenomenon studied (Arita *et al.* 1997, Bickford *et al.* 2004). A distributional matrix of 749 cells by 416 species was constructed, recording the presence (1) or absence (0) of each species in each cell.

In order to evaluate the effect that sampling intensity (completeness of data) would have on the results, a cell size of 10'×10' was also employed. in this case, the information was entered into WORLDMAP, a Geographic Information System developed by Paul Williams at the Natural History Museum, London, to explore geographical patterns of diversity (Williams 1999, Williams *et al.* 2002a). WORLDMAP uses a system of either equal-area or nearly equal area grid cells. In this case, the distributional matrix consisted of 416 species by 3, 318 cells.

To differentiate these two scales, the 30'×30' grid cell system will be referred to as S30', and the 10'×10' grid system will be denoted S10'. Using these two scales allowed us to investigate the possible loss of resolution that aggregation of data would produce (Freitag and Van Jaarsveld 1998, Stockwell and Peterson 2003). Alternatively, it allowed us to test the effect that smaller sampling effort (fewer records per cell) would produce at a higher resolution.

5.2.2 Diversity Analyses

In addition to Species Richness (*S*, the number of species in each grid-cell) we employed the more recently developed biodiversity measures mentioned in the introduction to this chapter, which describe the taxonomic spread of species (Bininda-Emonds *et al.* 2000, Clarke and Warwick 2001, Faith and Baker 2006). These indices, calculated for each grid cell (area), were the originally proposed (total) Phylogenetic Diversity, *PD* (Faith 1994), Average Taxonomic Distinctness, *AveTD* (Clarke and Warwick 1998), and Variation of Taxonomic Distinctness, *VarTD* (Clarke and Warwick 2001). In addition to these, and because analogous indices can be calculated from each of *PD* and *AveTD*, Average *PD* (*AvePD*) and Total *TD* (*TD*) were also computed (Table 5.1).

The taxonomic and phylogenetic classifications employed were described in Chapter 4. As it was mentioned there, these two classifications were employed in order to gauge the effect that contrasting resolutions of the classification would have on the results. The Linnaean taxonomy will be referred to as ***t*** (Table 4.2). The phylogenetic tree will be referred to as ***p*** (Fig. 4.3). The encoding process of the phylogenetic tree is presented in Appendix C.

Because of the variety of methods that have been employed to investigate the phylogenetic relationships of different taxonomic groups and because these have also used diverse genes, branch lengths were assumed to be constant. This is also recommended by Faith (1992). Therefore, *PD* calculated for the species assemblage in each grid cell counts the total number of branch segments joining them.

Table 5.1 Measures of diversity based on relatedness of species.

INDEX NAME	FORMULA
Total Phylogenetic Diversity	$PD = \sum_k b_k$
Average Phylogenetic Diversity	$AvePD = PD/S$
Total Taxonomic Distinctness	$TD = AveTD * S$
Average Taxonomic Distinctness	$AveTD = \left[\sum\sum_{i<j} \omega_{ij}\right] / \left[S(S-1)/2\right]$
Variation of Taxonomic Distinctness	$VarTD = \left[\sum_{i<j} \sum (\omega ij - AveTD)2\right] / \left[S(S-1)/2\right]$

b_k= length of each of the k branches of the phylogeny; S = number of species; ω_{ij} = distinctness weight (taxonomic distance) along the path length linking species i and j in the taxonomic/phylogenetic tree. The double summations are over all species pairs (i and j) over all S species.

It is unfortunate that these biodiversity indices, which make use of information on the classification of the taxa under consideration, were named taxonomic distinctness (*TD*) and phylogenetic diversity (*PD*). This gives the impression that they employ different classification methods. This, however, is not necessarily the case. As has been explained already, each of these two indices can be expressed as either a total or an average measure. Also, each of them can be calculated employing either a taxonomic or a phylogenetic classification. In order to compare the information that each index and classification provides, this study employs four combinations of indices and classifications: (i) *TD* employing taxonomy, generically labelled *TD(t)*, (ii) *TD* employing phylogeny *TD(p)*, (iii) *PD* employing taxonomy *PD(t)*, and (iv) *PD* employing phylogeny *PD(p)*. In addition, indices may represent either totals (*PD* or *TD*) or averages (*AvePD* or *AveTD*). Finally, in the case of *TD*, there is also a measure of variability (*VarTD*). These indices were calculated in PRIMER-E v5 using the DIVERSE routine (Clarke and Gorley 2001).

The statistical analysis of the results was carried out in STATISTICA 6 (StatSoft-Inc 2003). Statistical test of associations between variables were carried out by means of regression and correlation analyses (Sokal and Rohlf 1995).

In addition, It is also possible to simulate the distribution of both *AveTD* and *VarTD* from random subsets of species from the inventory in an "Expected Distinctness' Test" (Clarke and Warwick 1998, Clarke and Gorley 2001, Clarke and Warwick 2001). From these simulations, it is possible to calculate their 95% confidence interval. The departure of individual samples (map cells) from the expected mean value and its position relative to the 95% confidence interval can then be evaluated. These simulations were carried out in PRIMER 5 using the routine TAXTDTEST.

Finally, Colless's index of phylogenetic tree imbalance (I_c) was calculated using the programme SkewMatic 2.01 (Heard and Cox 2007). This programme runs with "reasonable well resolved" phylogenies, i.e., the tree must not have politomies with more than 4 ramifications. In consequence, some modifications had to be made to the phylogeny for those clades where this situation was present. This was achieved by deliberately bifurcating those branches employing taxonomic information, if possible, or, in a few cases, arbitrarialy.The modifications were required in some rodent genera (*Peromyscus* and *Reithrodontomys;* Figure 4.6*)*; insectivores (*Cryptotis* and *Sorex,* Figure 4.10*)*, and one genus of Chiroptera (*Miotys*, Figure 4.12*)*. This analysis was only computed for scale S30'.

5.3. RESULTS

5.3.1. TOTAL DIVERSITY MEASURES

Total diversity indices for Mexican mammals were highly positively correlated with species richness (Table 5.2; Figs. 5.3 and 5.4) and positively correlated with each other (Fig. 5.5); although not necessarily following linear relationships. Also, because they are positively related to species richness, the value of these indices increased with cell size (i.e., from S10' to S30'). This is because there is a larger number of species per sample unit (grid cell) in S30' than in S10'. results showed that the classification employed *(*either *t* or *p)* had little effect on the relationship between either *PD* or *TD* and *S* (Figs. 5.3 and 5.4). Both *PD* and *TD* increased faster at S30' than at S10'. *TD* showed linear relationships with *S* while *PD* approximated power relationships with *S*, regardless of the classification employed. Both *PD* and *TD* showed wider dispersion when using a taxonomic classification than when employing a phylogenetic classification, at both scales.

Table 5.2 Correlation coefficients between *S* and Total Biodiversity Indices. All correlations are significant at p<0.01. (657 < *n*(S30') < 690; 2571 < *n*(S10') < 3318).

	S10'				S30'			
	S	*TD (t)*	*PD (t)*	*TD (p)*	*S*	*TD (t)*	*PD (t)*	*TD (p)*
S								
TD (t)	0.97				0.95			
PD (t)	0.97	0.93			0.98	.96		
TD (p)	0.98	0.92	0.96		0.99	.95	.97	
PD (p)	0.93	0.88	0.94	0.96	0.96	.92	.96	.98

Since both *PD* and *TD* are correlated with S, *PD* and *TD* are correlated with each other (Fig. 5.5). Although with a slight curvature, the relationship between *PD* and *TD* at S10' was close to linear for both types of classification. On the other hand, the relationship between *PD* and *TD* at S30' (employing either *t* or *p;* Fig 5.5b and 5.5d, respectively), approximated a power function. Variation around these trends was higher when employing a taxonomic, as opposed to a phylogenetic classification. As with measures of total diversity, scale S30' yielded higher values than scale S10' as *S* increases with cell size.

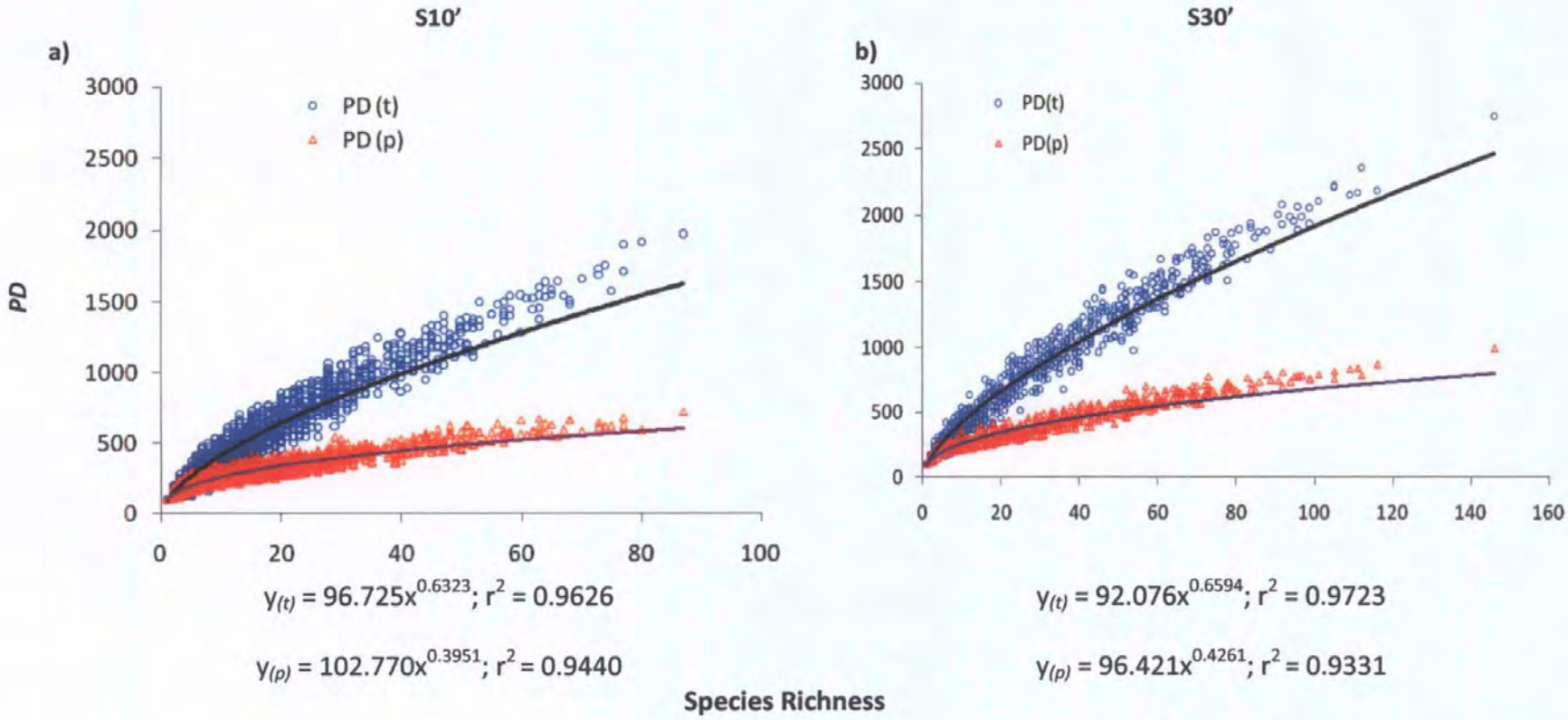


Figure 5.3 The relationships between Total Phylogenetic Diversity (*PD*) and Species Richness using two different scales (S10' and S30') and either a taxonomic *(t)* or a phylogenetic *(p)* classification. The line of best fit and the correlation coefficients are shown.

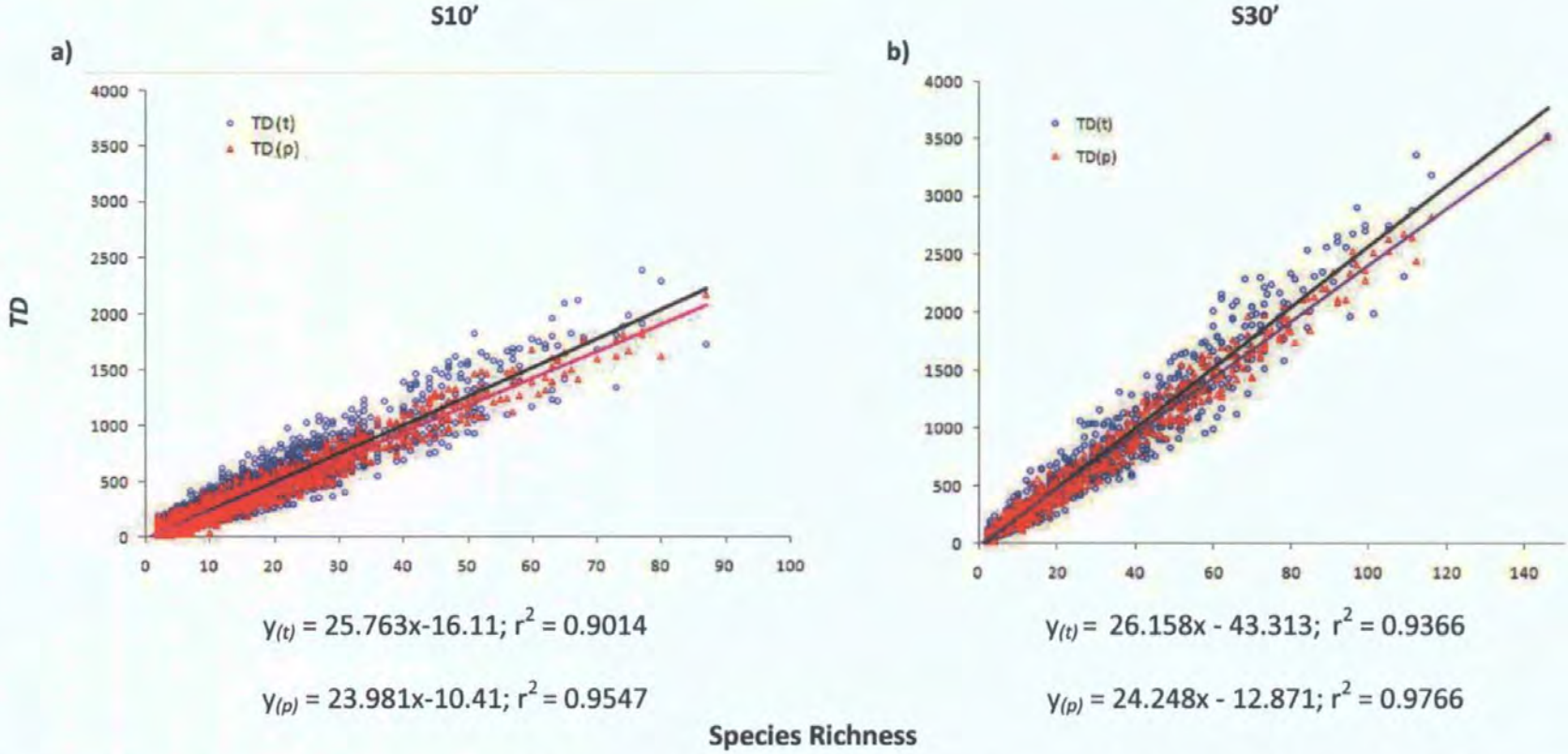


Figure 5.4 The relationships between Total Taxonomic Diversity (*TD*) and Species Richness, using two different scales (S10' and S30') and either a taxonomic *(t)* or a phylogenetic *(p)* classification. The line of best fit and the correlation coefficients are shown.

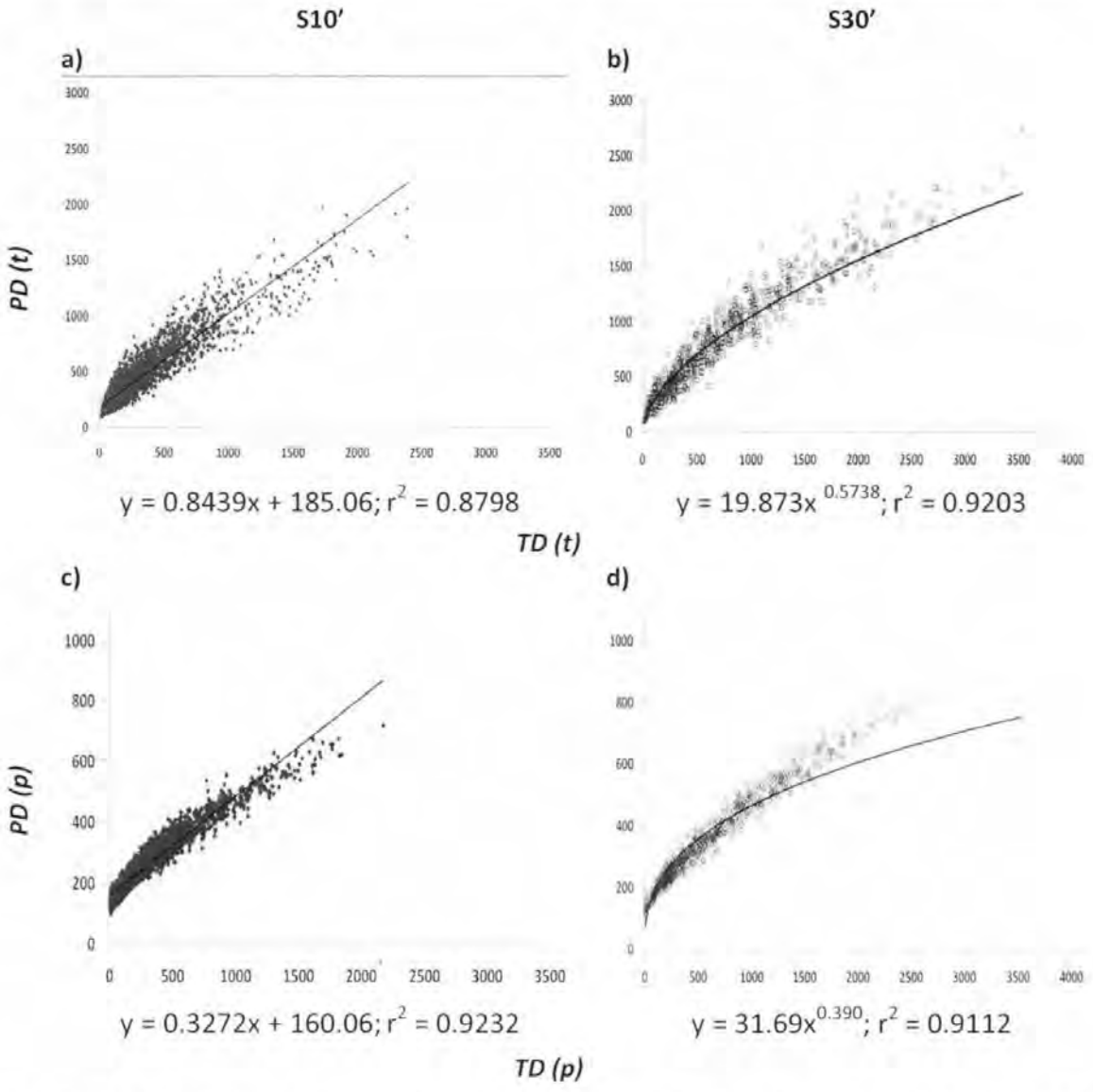


Figure 5.5 Relationship between Taxonomic diversity (*TD*) and Phylogenetic diversity (*PD*) using two different scales (10' and 30') and either a taxonomic *(t)* or a phylogenetic *(p)* classification.

5.3.2. Average Diversity Measures

Scatterplots of *AveTD* followed the expected funnel shape (Clarke and Warwick 1998), closing or "stabilising" as *S* increases (Fig. 5.6a and Fig. 5.6b). Once again, the phylogenetic classification *(p)* produced less variation than the taxonomic one at both scales. Unlike *AveTD*, which is calculated from the

distances of every pair of species in each sample (cell), *AvePD* showed a declining value with increasing *S* because *AvePD=PD/S* obviously decreases as *S* increases. It decreased faster and had lower variability when employing a phylogenetic classification than when employing a taxonomic one (Fig. 5.6c and Fig. 5.6d).

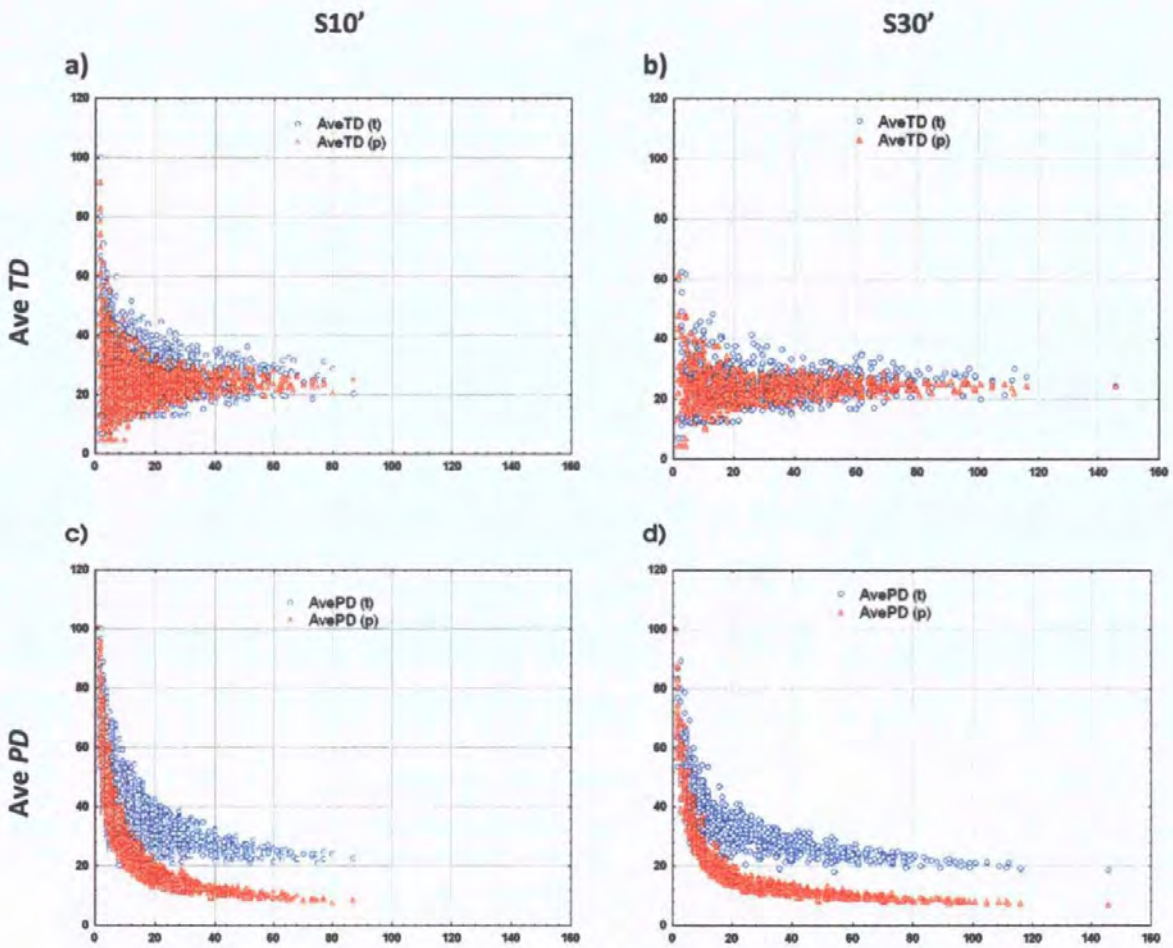


Figure 5.6 Relationship between Average Taxonomic Diversity (*AveTD*) and Species Richness (*S*), and between Average Phylogenetic Diversity (*AvePD*) and *S* using two different scales (S10' and S30') and either a taxonomic (*t*) or a phylogenetic *(p)* classification.

5.3.3. Variation of Taxonomic Distinctness

All four combinations of scale and classification followed the expected funnel shape for *VarTD*. As was the case for *TD* and *AveTD* (but also for *PD* and Ave*PD*), the phylogenetic classification produced less variation and lower values of *VarTD* than the taxonomic one. For both scales, *VarTD* employing a phylogenetic classification exhibited a more symmetrical shape than that calculated employing a taxonomic classification (Fig. 5.7).

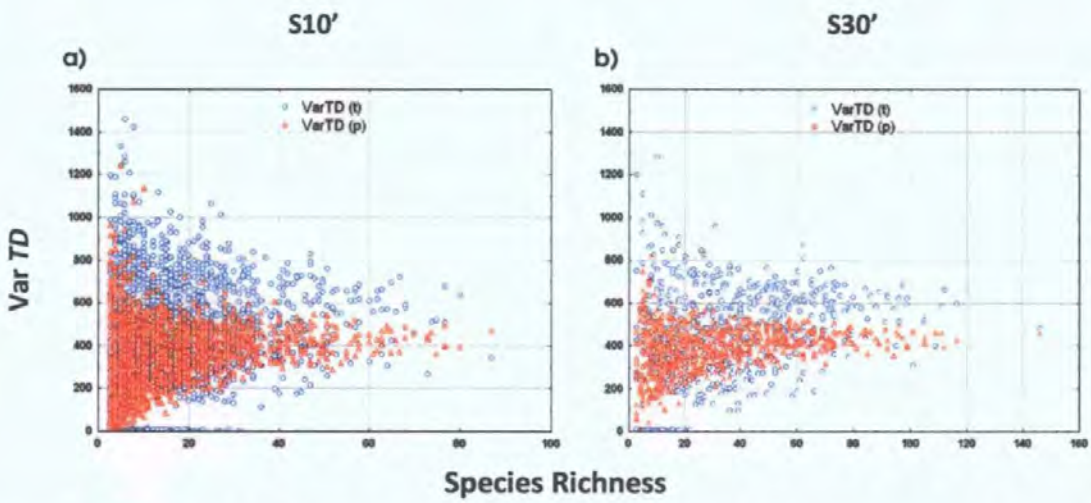


Figure 5.7 Relationship between *VarTD* and *S* employing either taxonomy or phylogeny at two spatial scales.

5.3.4. Expected Taxonomic Distinctness Analysis

AveTD

Results of the simulated 95% probability funnel plots yielded an expected mean *AveTD* which was close to the observed means for this statistic (Table 5.3). Nevertheless, the pattern that each combination of scale and classification type displayed was different from each other. Employing scale S10', 69.97% of areas fell within the probability funnel for *AveTD(t)*, whereas for *AveTD(p)* the figure was

74.86% (Fig. 5.8). *AveTD(t)* showed that areas that fall above the upper limit (9.74% from the total) occur more distantly than those which fall below the lower limit (20.29%; Fig. 5.8a). On the other hand, when phylogenetic information was used (*AveTD(p)*), the probability funnel was more symmetrical than that obtained employing a taxonomic classification: 11.49% of areas fell above the upper limit and 13.66% fell below the lower limit. With this classification, values of cells outside the confidence intervals were closer to these limits, and departure from these limits increased as the number of species decreased (Fig. 5.8b).

Table 5.3 Observed and expected values of mean *AveTD* and *VarTD* for Mexican mammals.

Measure	S10'		S30'	
	Observed	Expected	Observed	Expected
$AveTD\ (t)_{mean}$	23.60	23.45	23.63	23.61
$AveTD\ (p)_{mean}$	22.76	22.84	23.55	23.58
$VarTD\ (t)_{mean}$	403.06	303.26	435.24	404.05
$VarTD\ (p)_{mean}$	339.53	279.68	388.60	373.85

For some cells, values of *AveTD(t)* and *AveTD(p)* seemed to present a very similar position in the respective funnel. However, for some other cells this position was strikingly different. In other words, cells that fall within the "taxonomic" limits can fall outside the "phylogenetic" limits and *vice versa*. Moreover, some cells that fell above the upper limit when employing one classification fell below the lower limit when the other classification was used. Using the bigger S30' scale, most cells fell within the simulated 95% confidence limit (funnel). For *AveTD* the figures were 84.47% using taxonomy and 89.02% using phylogeny (Fig. 5.9). When this distribution was calculated using phylogenetic data (Fig. 5.9b) it displayed a more

symmetrical shape than when using taxonomy (Fig. 5.9a). 5.22% of the cels fell above the upper limit and 5.76 % fell below the lower one. When using taxonomic information, there was an unbalanced funnel with 4.28% of cells having values of *AveTD* that were higher than expected and 11.25% lower than expected (i.e., a significantly reduced *AveTD*). At this scale, *AveTD* yields closer values for the area with the maximum number of species in this study employing either classification. In this case, both figures occurred slightly below the mean. However, for some other cells *AveTD* differed considerably from one classification to another (Table 5.3). The main conclusion to draw from this is that, although the numerical patterns look the same, making conservation decisions on individual areas (cells) is risky because it depends on the accuracy of the classification employed and the geographic scale used to quantify diversity. The latter means that sampling effort is relevant in the estimation of *AveTD* and, consequently, (total) *TD*. Both *PD* and *TD* are subject to error due to sampling effort/incompletness of the survey.

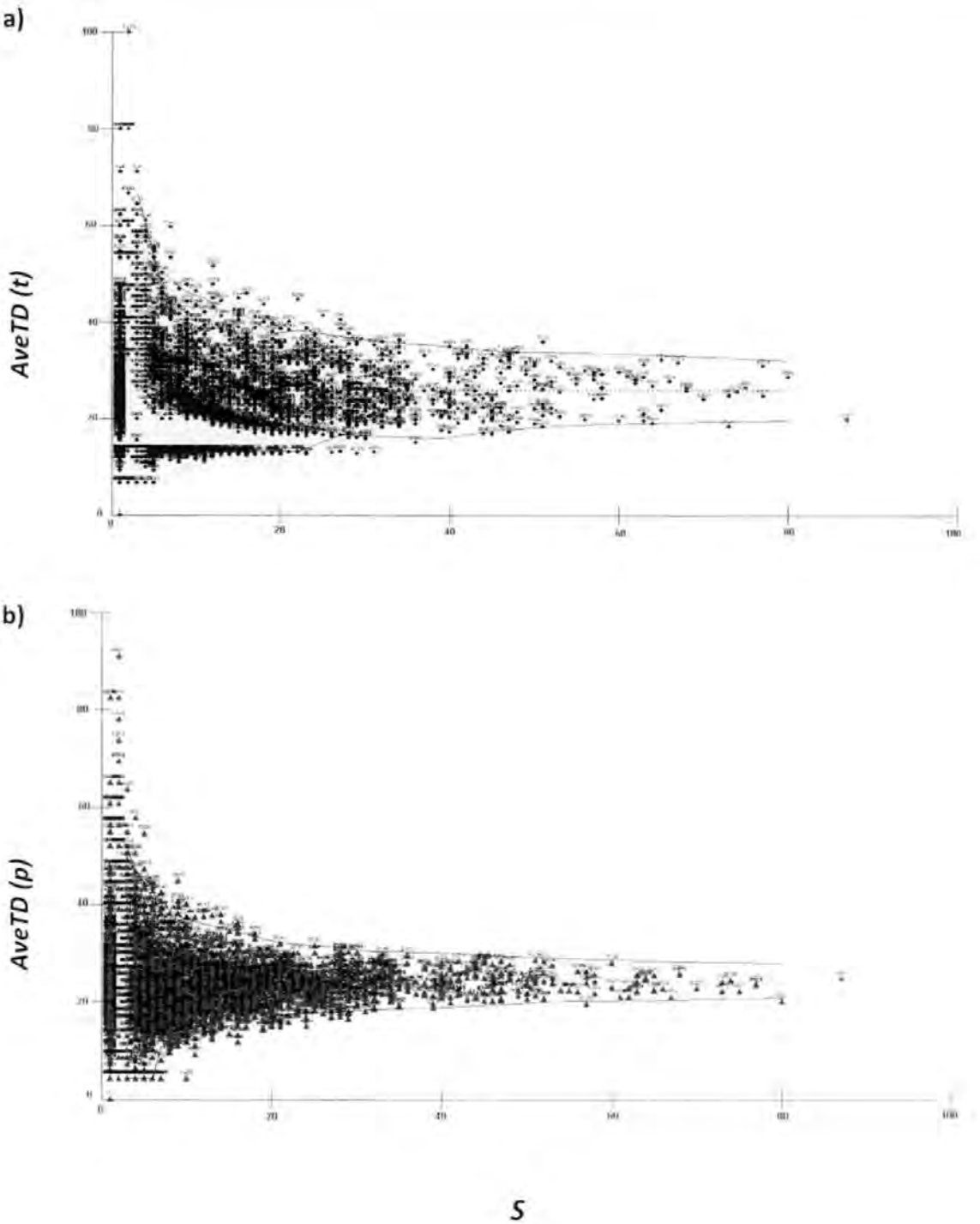


Figure 5.8 Simulated mean of *AveTD* (dashed line), 95% probability funnel and observed index values for Mexican mammals in 3,318 10' grid areas (cells), employing (a) a taxonomic classification, and (b) a phylogenetic classification.

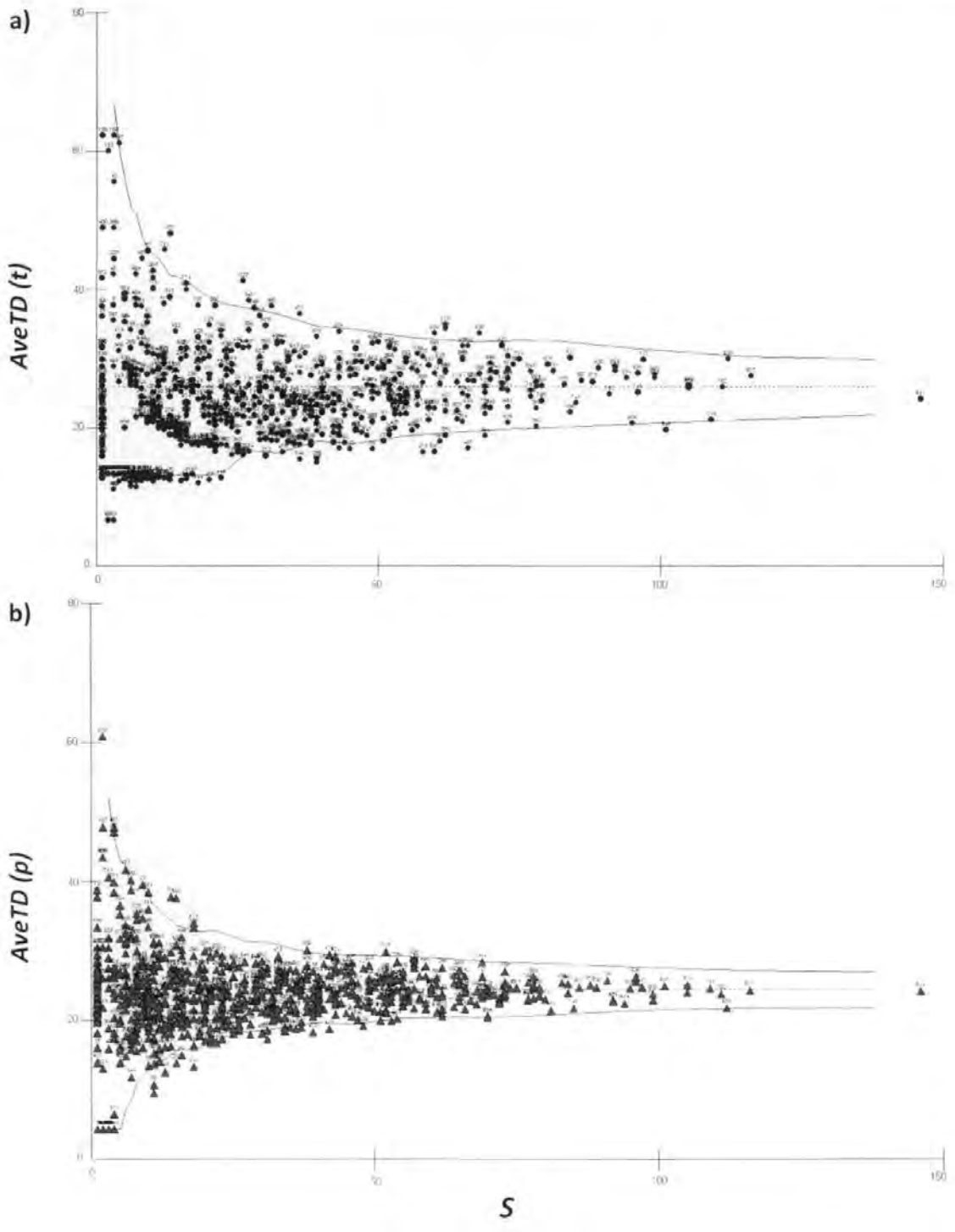


Figure 5.9 Simulated mean of *AveTD* (dashed line), 95% probability funnel and observed index values for Mexican mammals in 749 30' grid areas (cells), employing (a) a taxonomic classification, and (b) a phylogenetic classification.

VarTD

Contrary to what happened with *AveTD*, when measuring the variability of *TD*, the expected means were different from those observed at both scales and classifications (Table 5.3). The observed mean of *VarTD(t)* was notably higher than the expected one for the cells with few species; whereas in that for *VarTD(p)* this difference was smaller. The expected means of *VarTD* for S30' cells differ from the observed values as well. However, these differences were less marked for *VarTD(p)* than for *VarTD(t)* (Fig. 5.10).

The 95% probability funnel of *VarTD* reveals a different shape depending on the type of classification used, but not on the scale. The simulated funnels employing the taxonomic classification follow a very similar asymmetrical pattern at both scales (Figs. 5.10a and 5.11a respectively). For both scales, the lower limit dropped drastically to 0 as the number of species decreased. On the contrary, the simulation's probability envelope for *VarTD* employing the phylogenetic classification exhibited a symmetrical funnel shape for both scales (Figs. 5.10b and 5.11b), and tended to stabilise faster that its taxonomic equivalent as species number increased. At small values of *S*, both *AveTD* and *VarTD* depart from the expectation.

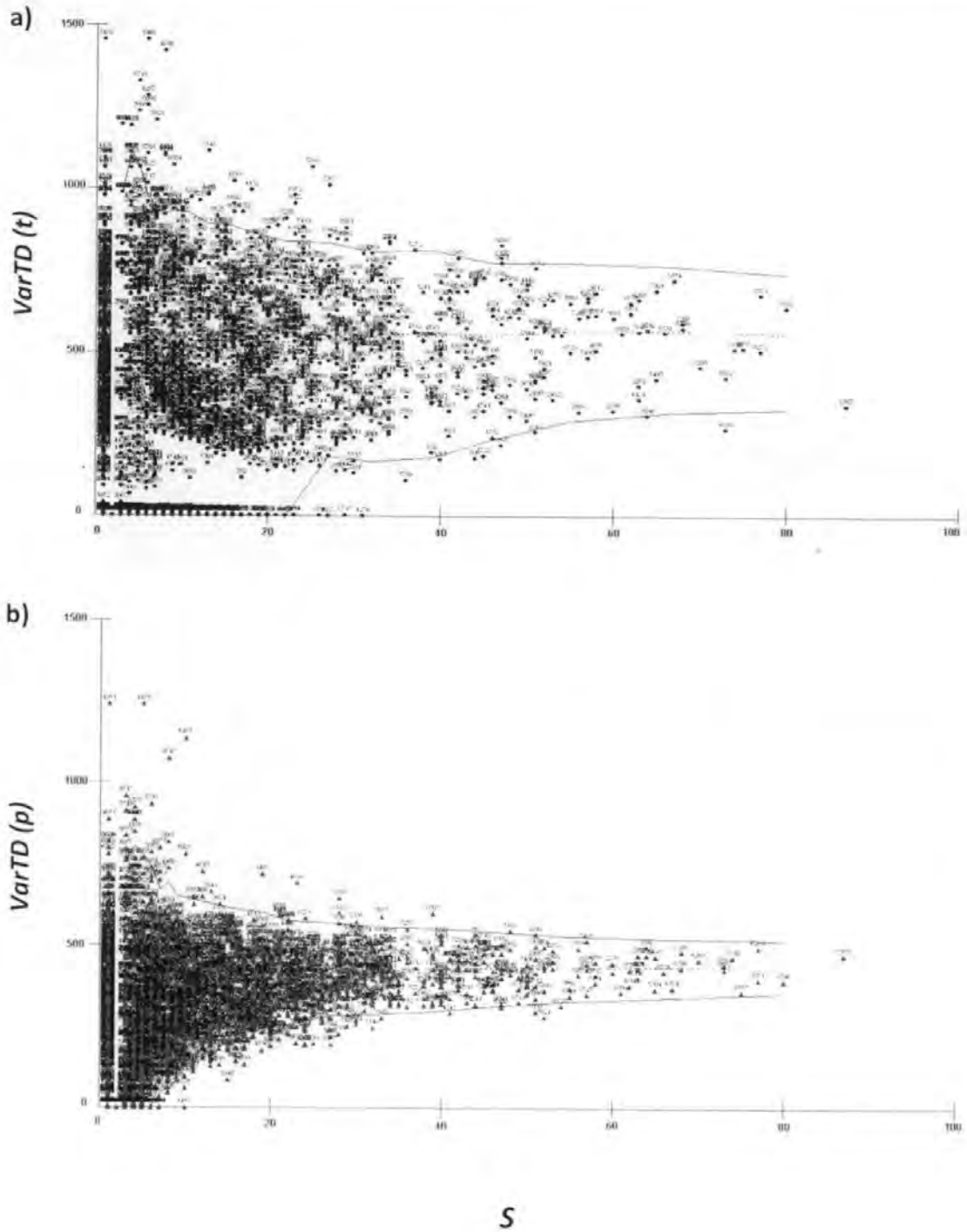


Figure 5.10 Simulated mean of *VarTD* (dashed line), 95% probability funnel and observed index values for Mexican mammals in 3,318 10' grid areas (cells), employing (a) a taxonomic classification, and (b) a phylogenetic classification.

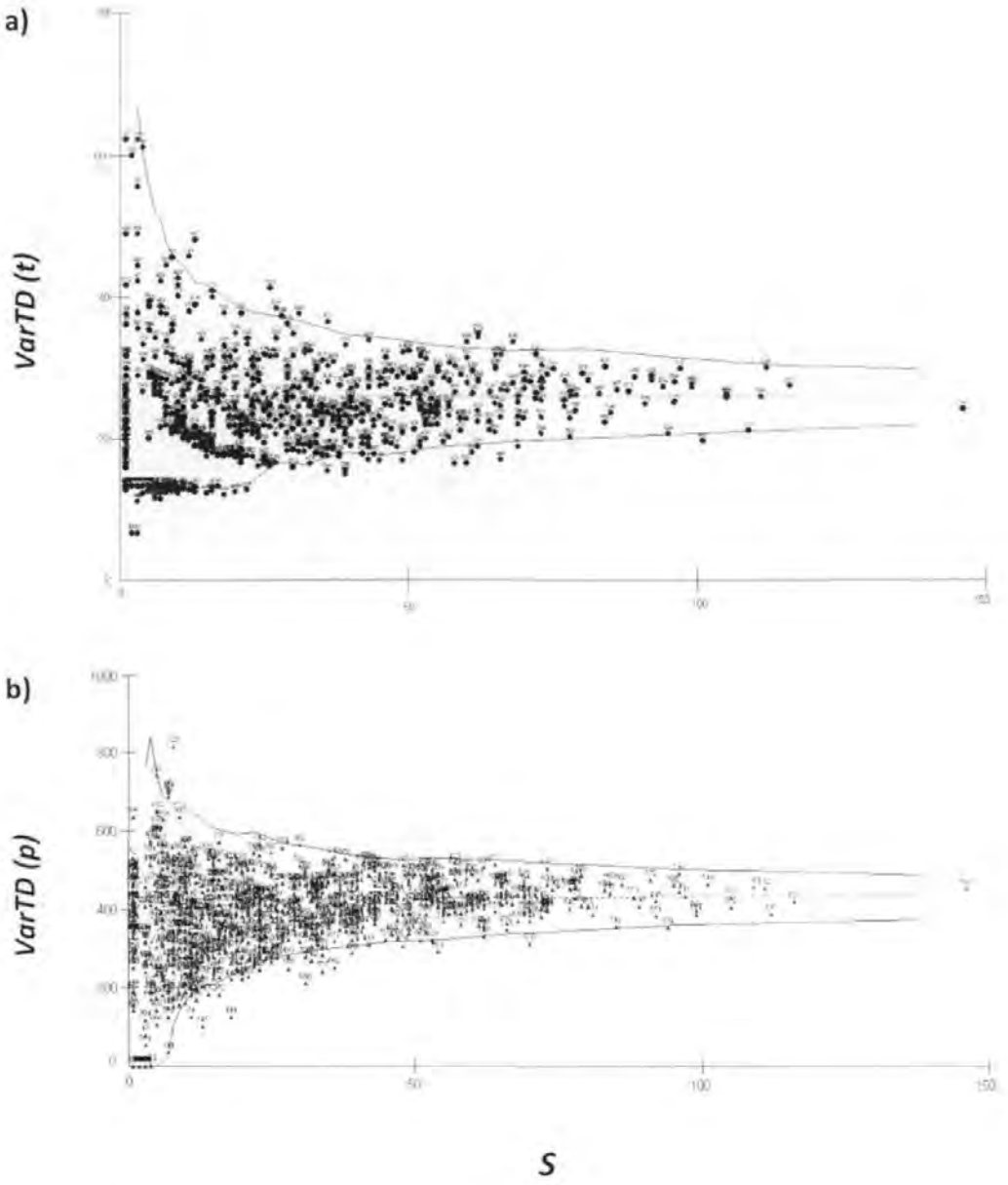


Figure 5.11 Simulated mean of *VarTD* (dashed line), 95% probability funnel and observed *index values* for Mexican mammals in 749 30' grid areas (cells), employing (a)a taxonomic classification, and (b) a phylogenetic classification.

5.3.5. Phylogenetic Tree Imbalance

Local phylogenies for the species assemblages in each grid cell range from perfectly balanced (I_c=0) to perfectly imbalanced (I_c=1). At low species richness

there was more variation in tree shape. We can probably ignore values of I_c=1 and I_c=0 as they only occur at very low species numbers. As the number of species increases, trees tend to be more symmetric and less variable (Fig. 5.12a). I_c followed a similar relationship with *PD* as it did with *S*. That is, tree shape becomes more balanced and less variable as *PD* increases (Fig. 5.12b).The value of I_c for the the whole phylogeny was also very well balanced (I_c = 0.039).

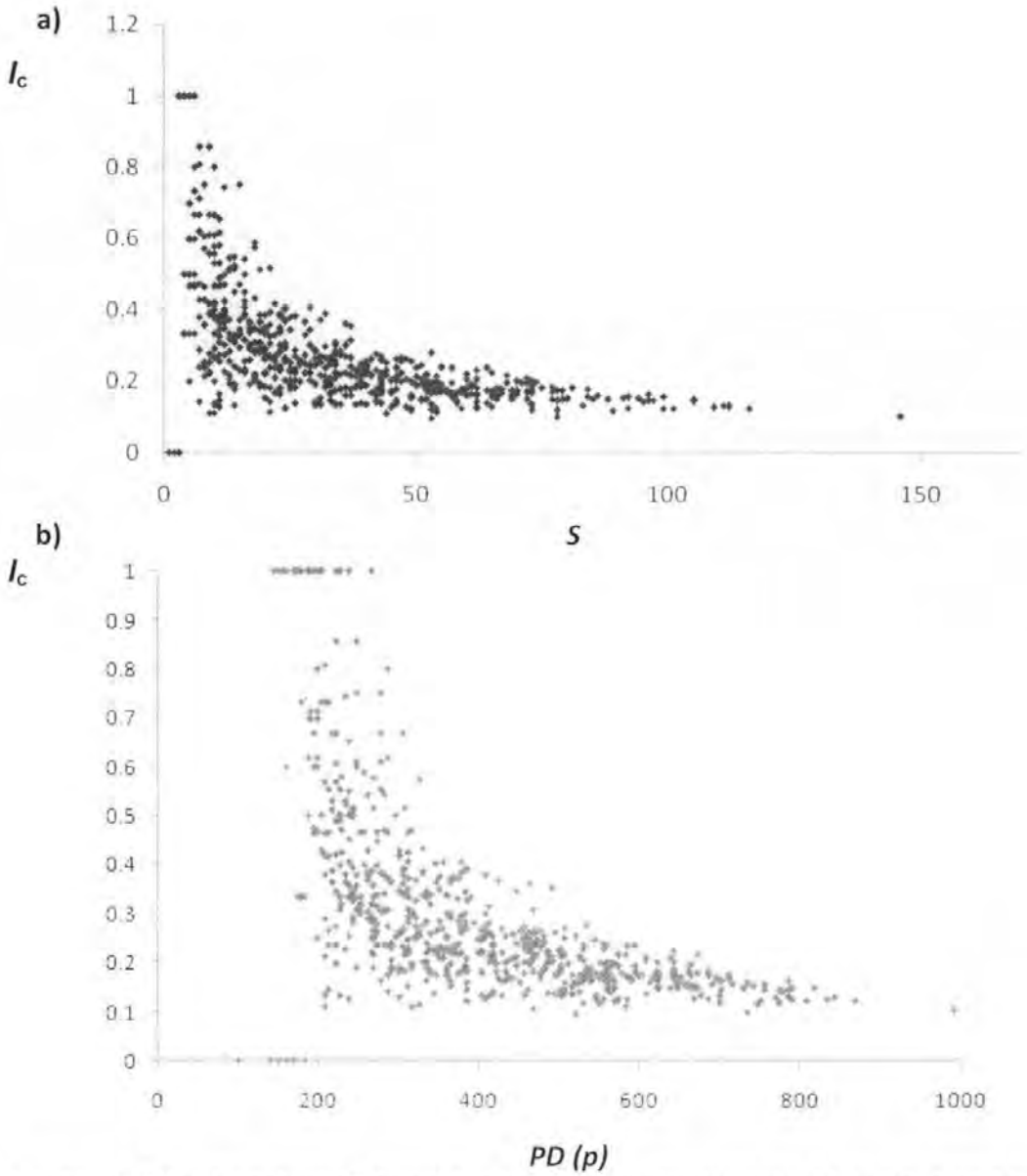


Figure 5.12 Relationships of Diversity Skewness (Colless' Index, I_c) and a) *S* and b) *PD(p)* using *S30'*.

5.4.DISCUSSION

5.4.1. DIVERSITY MEASURES

Measures of biodiversity based on relatedness of species employing presence/absence data were successfully calculated for the mammals of Mexico at two levels of resolution. The use of two different scales showed that the variability of the estimations increases as the scale decreases. This has two causes: the first, more interesting one, is the heterogeneity among sample units (an ecological effect); the second factor, however, is an obvious consequence of the decrease in sample size as the necessarily finite sample is divided into smaller units (a statistical effect). Despite the large number of records in the database (128,114 records), finer detail will always require more intense sampling. This is difficult to achieve in any collection of specimens. Because of the difficulty to separate these two effects, care should be taken in the interpretation of results at lower resolutions.

Total Biodiversity Indices for Mexican mammals were highly correlated with Species Richness. This is because measures of total diversity tend to follow species richness rather closely (Warwick and Clarke 2001). However, *PD* provides more information on the relatedness of the species making up an assemblage. The relationship between *PD* and *S* departs from linearity and the reason for this seems obvious: as species accumulate, the probability of adding a new order/family/ genus decreases because the likelihood of that genus/family/order already being in the sample increases. Thus, adding new species decreases their relative contribution to *PD* as species number increases.

Values of *TD* for both scales and both types of classification tend to overlap, whereas the *PD(t)* curve differs from the *PD(p)* one at both scales. Employing a taxonomic classification (*TD(t)* and *PD(t)*) produces more dispersion and higher values than *PD(p)* at both scales. Thus, the use of a phylogenetic classification is preferable over the use of a taxonomic one.

Although algorithmically similar, their direct (*PD*) and indirect (*TD*) methods of calculation yield different results. Thus, although qualitatively similar, care must be taken in the use and interpretation of these two indices: they are not interchangeable. Finally, and although closely correlated, *TD* and *PD* are preferable over the simpler species-richness index.

Because total biodiversity indices (*PD* and *TD*) are correlated with Species Richness, they cannot possibly be independent of sampling effort. Unless completeness of records can be guaranteed (and this is unlikely ever to be the case) intermediate scales that balance ecological detail (spatial heterogeneity) with sampling effort (number of records) are preferable over large or small ones (Arita *et al.* 1997, Crisp *et al.* 2001, Bickford *et al.* 2004). A grid cell of 30' × 30' (S30'~2,835.77 km^2) worked reasonably well in this case. A larger one would lose ecological detail. A smaller one would suffer from small sample size per cell.

This dependency on sample size is true for both total and average measures (*PD*, *TD*, *AvePD* and *AveTD*). Authors are therefore mistaken when they say that *AveTD* is insensitive to sampling effort and should be preferred over (total) *PD* (Warwick and Clarke 2001, Magurran 2004). Both indices contain essentially the same information: one can work "downwards" from (total) *PD* to

AvePD or "upwards" from *AveTD* to (total) *TD*. Provided we compare like with like (*PD* with *TD*, *AveTD* with Ave *PD*), these indices quantify, albeit with different algorithms, essentially the same thing: the distance between species in the tree of life.

AveTD is not an indicator of diversity in the general sense. It is a measure of heterogeneity of taxonomic or phylogenetic relatedness. On the other hand, because of the way it is calculated, *AvePD* decreases as the number of species increases. It would therefore be incorrect to compare their values across studies with different levels of sampling effort. On the other hand, the results of the simulated 95% probability funnel plots of *AveTD* show that these are close to their observed means. The mean values of *AveTD* index for both scales and both classifications were indeed independent of sample size and the number of species, but were not independent of the type of aggregation data (i.e., taxonomic or phylogenetic). *AveTD*'s independence from sample size and number of species suggests that, unlike *AvePD*, it can more confidently be compared across studies with differing and uncontrolled degrees of sampling effort (Warwick *et al.* 2002). It also confirms that *AveTD* is not a surrogate of species richness.

The variability of *TD* (*VarTD*) is a consequence of the complexity of the phylogenetic or taxonomic tree. However, because museum records are always incomplete, it is difficult to separate the effect of phylogenetic complexity from the effect of the error produced by the incompleteness of the records. Alternative measures of variability may help shed light on the relative contribution of these two effects.

5.4.2. TREE IMBALANCE

Local phylogenies for the species assembles (grid cells) varied from perfectly balanced (diversity skewness=0) to perfectly imbalanced (diversity skewness=1). Tree shape became more balanced as *S* (or *PD*) increased (Fig. 5.11). The low Diversity Skewness found for richer local assemblages (those with high *S* and/or *PD*) may be due to the pervasiveness of rodent (the dominant Euarchontoglires order) and bat species (the dominant Laurasiatheria order). That is, areas with high *S*/*PD* will tend to be rich in rodents and bats and, given that these two groups balance the tree, I_c will tend to be low. This pattern is the opposite of what other studies of global phylogenies have documented, where skewness increases with diversity at different phylogenetic scales (Mooers and Heard 1997, von Euler 2001, Purvis and Agapow 2002). Phylogenetic tree imbalance is thus assumed to be originated by differences in evolutionary rates of different branches of the phylogenetic tree. One cannot discount, however, the possibility that tree incompleteness and low quality of data are the sources of this imbalance (Mooers 1995, Stam 2002). A finer analysis of how phylogenetic diversity is determined or changes at different taxonomic levels is necessary before generalisations from individual studies can be justified.

Having quantified phylogenetic diversity (in its wider sense), the next chapter investigates its geographic distribution.

CHAPTER 6. THE GEOGRAPHIC DISTRIBUTION OF PHYLOGENETIC DIVERSITY AND ITS CONSERVATION

6.1 INTRODUCTION

In prioritising areas for conservation at a national scale, a multicriteria approach is commonly considered. This approach focuses mainly on species richness, endemic species and threatened species (Prendergast *et al.* 1993, Kerr 1997, Posadas *et al.* 2001, Justus and Sarkar 2002). In this chapter, we explore the correlation between traditional biodiversity surrogates (species richness, endemic species and threatened species) and phylogenetic diversity.

It is well known that the distribution of biodiversity across the planet is complex and unevenly distributed. This heterogeneity is related to how species abundance varies across geographic and environmental gradients. This is why a large proportion of the diversity of organisms can be explained in terms of the geographic patterns of individual species, e.g., range size, endemicity and latitudinal, altitudinal and depth gradients of the physical variables of the environment, as well as additional complications, e.g., their variation across peninsulas and bays (Rosenzweig 1995, Gaston and Williams 1996, Caley and Schulter 1997, Gaston and Spicer 2004, Morrone 2004). In addition, the dominance of particular environmental variables, such as temperature, precipitation, productivity and topography, over large areas, determines the patchy distribution of groups of species, or communities (Gaston and Williams 1996). These relationships are useful to understand how the environmental conditions affect rates of speciation and extinction, the resources available for species, and

the interactions with the physiological attributes of species (Vazquez and Gaston 2004).

The biodiversity measures calculated in Chapter 5, can be interpreted in the context of their spatial patterns at different spatial scales, just as previous authors have employed the simpler Species Richness measure. Because the current trend is to focus conservation efforts at wider, ideally global, scales (Heywood *et al.* 1995, Gaston 2000, Canhos *et al.* 2004, Rodrigues *et al.* 2004, Balmford *et al.* 2005, Brooks *et al.* 2006, Cardillo *et al.* 2006, Grenyer *et al.* 2006), focussing at the national scale of a megadiverse country combines elements that operate at different scales, from local to global.

6.1.1 The Biogeographic Context

Mexico (Latitude: 14.53 to 32.72 N; Longitude: -118.37 to -86.71W) covers an area of 1,953,162 km^2, with an estimated coastline of 11,208 km. It is nearly equally distributed above and below the Tropic of Cancer. It occupies the transition zone between two biogeographic realms, the Nearctic and the Neotropical (see small map on Fig. 6.1); however, Neotropical elements have been able to spread further north along the coasts, whereas Nearctic elements dominate the mountains and central plateau. The Transvolcanic Belt (TVB) represents a sharp boundary, a barrier to the movement of organisms with different ecological requirements, between the temperate north (of Nearctic origin) and the tropical south (of Neotropical origin).It is therefore the present limit between these two biogeographic realms. The TVB traverses the country in an east-west direction from the Veracruz state along the Gulf of Mexico to the Colima and Jalisco states

on the Pacific coast. Dating back from the middle and late Cenozoic (i.e., from ~40 million years ago;(Ferrusquia-Villafranca 1998), the TVB became the important barrier we recognise today at the end of the Miocene, approximately 6 million years ago, when the emergence of Central America brought together the floras and faunas of North and South America. Together with another important historical element, the severe climatological changes that took place during the Pleistocene, the resulting isolation of tropical biotas resulted in speciation and endemism. In many cases, these species were able to extend their areas of distribution after temperatures increased and glaciers receded along the mountain ranges (Neyra and Durand 1998, Ramamoorthy *et al.* 1998).

Other important physiographical features of Mexico are the Baja California Peninsula in the north, the Central Plateau (which comprises several central and northern states), several important mountain ranges which dominate the landscape of southern and southeastern Mexico, and the Yucatan Peninsula and Chiapas lowlands.

Figure 6.1 Biogeographic provinces in Mexico (map from CONABIO). The small map shows the separation between the Nearctic and Neotropical regions (Neyra and Durand, 1998).

The Sierra Madres, which run north to south along the Pacific and Gulf of Mexico coasts, together with the TVB, enclose the Central Plateau. The Sierra Madre Occidental averages 2,250m in elevation, with some peaks >3,000m. The median elevation of the Sierra Madre Oriental is 2,200 meters, also with some peaks >3,000m. The TVB is distinguished by considerable seismic activity and contains Mexico's highest volcanic mountains (>4,000m). These factors create an enormous number of environmental variants. The changes in altitude produce climatic variations in the intensity of solar radiation, atmospheric humidity, diurnal oscillation of temperature and amount of available oxygen (Neyra and Durand 1998, CONABIO 2005).

Water availability is unevenly distributed throughout the country. The mountainous terrain and dissected topography of Mexico result in remarkable climatic variability over short spatial distances, with variations corresponding as much to altitude as to latitude. Other permanent controls influencing the climate include land-sea distributions, the influence of offshore ocean currents, and the incidence of tropical storms. Despite all these variations, the climate of Mexico can be divided into three broad categories: 1) The wet, tropical climates that are generally found in southern Mexico and along the Pacific and Gulf coasts, south of latitude 24°N; 2) the temperate, seasonally moist climates typical of the mountainous areas and central plains; and 3) the dry climates generally found in the northern part of the country, including the Baja California Peninsula and the Pacific coastal plains of the north (Neyra and Durand 1998, Ramamoorthy *et al.* 1998, Cantu *et al.* 2004).

Table 6.1 Vegetation types and their land cover in Mexico.

Vegetation type	%
Xeric Scrubland	37.62
Coniferous and Oak Forest	19.35
Deciduous Tropical Forest	13.77
Evergreen Tropical Forest	9.95
Grassland	8.17
Thorn Forest	5.80
Subdeciduous Tropical Forest	3.24
Aquatic and Subaquatic Vegetation	1.18
Cloud Forest	0.92

A general classification of vegetation types in Mexico was proposed by Rzedowski (Table 6.1). The main types are grouped according to geophysical features, climates and soils (Neyra and Durand 1998, Rzedowski 1998). The most widespread vegetation types are Xeric Scrubland (38% of the country's land area), followed by Coniferous and Oak Forest (20%) and Deciduous Tropical Forest (13.77%).

6.1.2 Distribution (Endemism and Rarity)

Endemic species have often been targeted to set conservation priorities (Myers *et al.* 2000). Because of their small geographic ranges and, usually, their small population numbers, they are generally considered more prone to extinction than widespread species (Leigh 1981, Rabinowitz 1981, Gaston 1996b). The distribution of endemism reveals some common patterns of variation with area, latitude and species richness. For instance, the number of taxa endemic to a region tends to increase as the size of the area increases; similarly, the number of endemics tends to rise towards lower latitudes (Gaston and Spicer 2004), and

levels of endemism tend to approximate a power function with species richness (Brummitt and Lughadha 2003, Fa and Funk 2007). Most endemic species have relatively restricted geographic ranges, and those species are more prone to extinction than widespread species (Gaston 1996b). Classic rare species are those of restricted distribution and narrow habitat specificity.

In Mexico, there are 169 (~30%) endemic species and 13 (7.9%) endemic genera (Table 6.2; Ceballos *et al.* 2002a, Escalante *et al.* 2003). Most of those endemic taxa are rodents. The TVB, the forests along the Pacific coast and the islands in the Gulf of California are areas particularly rich in endemic mammals (Arita *et al.* 1997).

Table 6.2 Genera of mammals endemic to Mexico

Order	Genera
Didelphimorphia	*Tlacuatzin*
Insectivora	*Megasorex*
Chiroptera	*Musonycteris, Baeodon*
Leporidae	*Romerolagus*
Rodentia	*Pappogeomys, Zygogeomys* *Osgoodomys, Megadontomys* *Nelsonia, Neotomodon* *Xenomys, Hodomys*

6.1.3 Threatened Species

The pattern of occurrence of threatened species is another element used in conservation. Threatened species are already at risk of loss in the near future and, therefore, they require urgent protection (Bonn *et al.* 2002, Brooks *et al.* 2002). The World Conservation Union (IUCN) is the international organism that compiles the Red List of Threatened Species (http://www.iucnredlist.org). This list provides

taxonomic information, conservation status and distribution data on taxa that have been deemed under threat employing the IUCN Red List Categories and Criteria. Taxa that are facing a higher risk of global extinction are listed as Critically Endangered (CR), Endangered (EN) and Vulnerable (VU). The list also includes information on taxa that are already considered Extinct (EX) or Extinct in the Wild (EW), and on taxa categorised as Near Threatened (NT) because they are close to meeting the threatened thresholds. Those taxa that cannot be evaluated because of insufficient information are determined as Data Deficient (DD). The remaining, non listed species are classified as at Lower Risk (LR) (IUCN 2001). Thirty eight terrestrial mammals' species from Mexico are listed under some risk category in the IUCN Red List: CR (6 species), EN (15) and VU (17).

On the other hand, the Mexican government, through the Ministry of Natural Resources' National Institute of Ecology (INE), has developed a risk evaluation system to assess the conservation status of native taxa (SEMARNAT 2002). The INE list represents a comprehensive analysis to evaluate the conservation status of Mexican mammals (Sanchez-Cordero *et al.* 2005), and includes information at species and subspecies level. The INE categories are: Endangered (E), Threatened (T), Protected (P) and Extinct or Extirpated from Mexico (Ex). A total of 82 continental species are classified as at risk or extinct/extirpated: E (31 species), T (51), P (62) and Ex (12). Although the classification of individual species in these two lists tends to be similar, there are some exceptions. For instance, *Heteromys nelsoni* is considered as P in the INE list and as CR in that produced by IUCN; these represent a measure of conservation action and a category of conservation status, respectively.

The mammals of Mexico face severe threats, the greatest of which is habitat loss. Much of their former habitat has been destroyed to create farmland to feed a growing human population (Ceballos *et al.* 2002a). At least eight species have already been eradicated or become extinct, and 229 species (44%, including both marine and terrestrial species) are thought to be facing serious conservation problems (Ceballos *et al.* 1998, Ceballos *et al.* 2002a).

6.1.4 THE MEXICAN NATIONAL RESERVE NETWORK (SINANP)

The current natural reserves in Mexico belong to the National System of Protected Natural Areas (SINANP, "Sistema Nacional de Areas Naturales Protegidas"). The organisation overseeing these protected natural areas (ANPs, "Areas Naturales Protegidas"; hereafter NPAs) is the National Council of Natural Protected Areas (CONANP) which administers 167 reserves in six categories (Table 6.3). Nine regions are recognised (Fig. 6.2): Baja California Peninsula and North Pacific (1), Northwest and Gulf of California (2), North and Sierra Madre Occidental (3), Northwest and Sierra Madre Oriental (4), Gulf of Mexico and Costal Plateau (5), West and Central Pacific (6), Central Plateau and Transvolcanic Belt (7), South Border and South Pacific (8), and Yucatan Peninsula and Mexican Caribbean (9).

Although the SINANP was created with the intention to include those areas that by their biodiversity and ecological characteristics are considered of special relevance, the Natural Protected Areas of Mexico were established over many years, often unrelated to the protection of biodiversity (Cantu *et al.* 2004). It

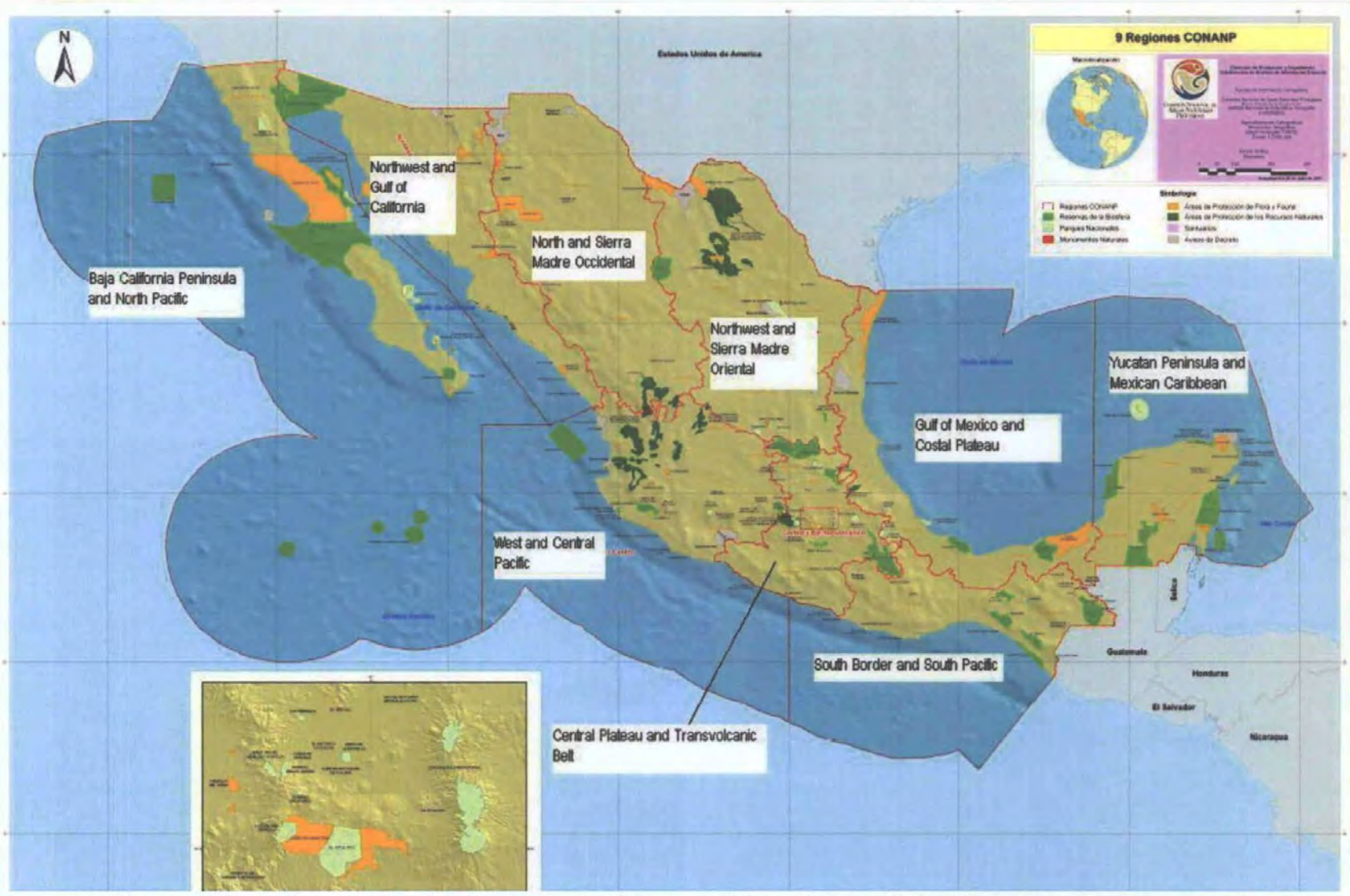


Figure 6.2 Regions of the National System of Natural Protected Areas (CONANP, 2004). See text for an explanation.

is,therefore, important to identify valuable sites for conservation of biodiversity employing current criteria and methods (Perez-Lozada and Crandall 2003). Ideally, this would entail developing measures of biodiversity which integrate ecological considerations, endemicity and geographic distribution with the evolutionary history of taxa.

Table 6.3 Categories of Protected Natural Areas in Mexico (CONANP, 2004)

Category	Number	Surface (ha)
Biosphere Reserves	35	10,479,534
National Parks	66	1,397,163
Natural Monuments	4	14,093
Natural Resources Protection Area	2	39,724
Flora and Fauna Protection Area	30	5,371,930
Sanctuary	28	689
Other categories	2*	553,094
Total	167	17,856,227

*Areas in the process of being classified/decreed

A total of 82% of the mammal species of Mexico are represented in its reserve network (Ceballos *et al.* 2002a, Ceballos 2007). There is therefore some mismatch between the distribution of mammals and the distribution of Protected Areas (Ceballos 2007). The evaluation of this situation by Ceballos and collaborators has been based on measures of species richness and it would be interesting to investigate the degree of protection of mammals in this reserve network employing the current measures of phylogenetic diversity described in this investigation. It would also be interesting to investigate the correlation between measures of the environment and phylogenetic diversity, between endemism and phylogenetic diversity, and between risk (as estimated from the published

classifications of threatened species) and phylogenetic diversity. The objective ofthis chapter is, therefore, to examine these relationships taking into account the current distribution of Natural Protected Areas.

6.2 METHODS

The scale used for the analyses presented in this chapter was S30' (0.5° x 0.5°). This coarser scale was preferred over S10' because of its greater accuracy to measure biodiversity (previous chapter) due to smaller sampling error. Likewise, phylogeny (*p*) was preferred over taxonomy (*t*) because it provides a more realistic picture of the genealogical relationships among the studied species.

6.2.1 CHARACTERIZATION OF THE PHYSICAL ENVIRONMENT

Information on temperature, precipitation and elevation produced by INEGI (National Institute of Geography and Informatics) was obtained from maps available at CONABIO's website (http://www.conabio.gob.mx/informacion/geo_espanol/doctos/cart_linea.html). The maps employed were: 1) Average Mean Temperature, 2) Average Mean Precipitation, and 3) Altitude. Because the information in these maps is given in ranks, the average values of these variables were calculated for each grid cell (Tables and Maps are shown in Appendix D). All environmental attribute data were transformed to raster (grid) format, with pixels of 0.5° × 0.5°. The map of current natural reserves in Mexico was downloaded from http://www.conanp.gob.mx/. This

characterization of each grid cell allowed exploration of the correlation between different measures of diversity described in the previous chapter and attributes of the environment.

6.2.2 Distribution of Diversity (*S*, *PD*, *TD* and *DS*)

The diversity indices computed in Chapter 5 were plotted over a map of Mexico to identify areas of high diversity. The diversity distribution maps were overlaid onto both the environmental maps and the map of natural reserves (Fig 6.2, CONANP 2004). This allowed us to assess whether the geographic distribution of taxonomic and phylogenetic diversity matched the distribution of existing reserves. The term area was used as synonymous of grid cell; whereas NPA was the term used to refer to a natural reserve included in the National Reserve Network (SINANP).

Indices of phylogenetic diversity showed a high degree of correlation. However, by emphasising slightly different aspects of the topology of the classification they sometimes differed in the identification of areas of high diversity.The regressions between either *PD* or *TD* and *S* described in the previous chapter (Fig. 5.3) showed that the values of *PD* and *TD* are determined by (mostly) species-richness and (then) the topology of the phylogeny. To separate these two effects, the residuals from the power model fitted to the relationship of *PD vs. S* and *TD vs. S* were computed. It was expected that these residuals would measure the degree of relatedness of species in a sample (grid cell) independently of sampling effort (number of species). Thus, distantly related

species would produce a high value of residuals, and closely related species would yield low residuals. This method should therefore also aid in identifying areas of exceptionally high diversity.

6.2.3 Distribution of Endemic and Rare Species

Endemic species were those with a distribution exclusive to Mexico. Mammal species described as endemics were taken from Ceballos (1998), Escalante (2003) and Sanchez-Cordero *et al.* (2005) (Table 4.2). The number of endemic species ("Endemic Species Richness"= *ESR*) was quantified for each grid cell.

Rare species can be defined in terms of the distribution and number of individuals. Here, the term is referred to those species with a narrow range size. The number of cells that each species occupy was counted and rare species were defined as those whose occurrence was less than 9 cells (~ 25,400 km^2).

6.2.4 Threatened Species

The conservation status of Mexican mammals according to INE classification (SEMARNAT 2002) were recorded. The categories were: threatened, endangered, protected, and extinct (or extirpated from Mexico). The total number of listed species was counted on each grid cell.

6.2.5 COMPLEMENTARITY ANALYSIS

In order to quantify the increase in biodiversity over the whole country as sample size (number of grid cells) increases, the expected species accumulation curve (Mao's tau; Colwell 2005, Xuan Mao *et al.* 2005) was estimated employing the program EstimateS 8.0 (Colwell 2005). This estimated the expected number of species as sample size (number of areas or grid cells) increases. In a second step, the cumulative number of species was calculated employing the areas with the highest values of *PD* ranked in decreasing order.

On the other hand, a complementarity analysis was employed to identify the smallest area (number of grid cells) needed to capture all mammal species in the dataset. Complementarity between each pair of areas is used to estimate the shared species between areas from those with no species in common to those containing exactly the same species. This type of analysis is usually employed in studies of optimal reserve selection (Csuti *et al.* 1997). The algorithm described by Rebelo (Rebelo and Sigfried 1992, Rebelo 1994) implemented in DIVA-GIS 5.2 software (Hijmans and Spooner 2001, Hijmans *et al.* 2005) was used. Rebelo's algorithm selects grid cells so as to identify the minimum set of cells that captures the maximum amount of species. The algorithm selects the cell with most species in it and then, step by step, selects cells that contain the highest number of additional (not previously included) species. In the case of cells having the same number of additional species, a random cell is selected from such cells. Selecting these complementary cells is a nonlinear optimization problem for which Rebelo's (1994) algorithm finds a near-optimal solution. The minimum number of grid cells

needed to include all species was determined and then, the location of these grid cells was identified and mapped.

6.3 RESULTS

6.3.1 GEOGRAPHICAL AND ENVIRONMENTAL FACTORS

The results of the study of the relations between diversity (*PD*, *TD* and *DS*, along with *S* and *ESR* for comparisons) and the attributes of the environment are shown in Appendix E. In general, both *PD* and *TD* tend to increase from the North to the South; i.e, they are higher towards lower latitudes. Higher diversity is found between latitude 15° to 27°N. Mammal diversity has a tendency to increase from West to East, being more diverse between longitudes 106° and 92°W. Correlation coefficients of geographical gradients are very similar for both diversity indices (Table 6.4). There was no significant correlation between diversity and elevation and between diversity and temperature (Table 6.4). On the other hand, diversity was positively correlated with precipitation. Finally, Diversity Skewness (I_c) did not show correlation with environmental variables except longitude.

Table 6.4. Correlation coefficients among biodiversity measures and geographic and environmental attributes. * Correlations are significant at p<0.01.

	Latitude	Longitude	Altitude	Temperature	Precipitation
S	-0.60*	0.59*	-0.09	0.10	0.56*
PD	-0.57*	0.56*	-0.01	0.04	0.49*
TD	-0.55*	0.56*	-0.08	0.08	0.52*
I_c	0.17	-0.18*	-0.03	-0.01	-0.13
ESR	-0.48*	0.20*	0.13	-0.09	0.22*

6.3.2 Areas of High Diversity

As shown, the diversity of mammals (as measured by *S*, *PD*, and *TD*) increases towards lower latitudes (Figs. 6.3, 6.4 and 6.5, respectively). The distribution of *TD* (Fig. 6.5), but not that of *PD* (Fig. 6.4), tracks the distribution of *S* (Fig. 6.3). In other words, areas with higher values of *PD* do not necessarily coincide with those areas with the largest number of species. For the purpose of this study, grid cells of *PD*>660 (Fig. 6.4) were defined as areas of high (phylogenetic) diversity; *S* for these areas ranked from 52 to 146 species. The number of cells with *PD*>660 was 50, 28 of them are likely to be included in the reserve network in 40 NPAs (Table 6.7).

Most high values of the residuals of the relationship between *PD* and *S* (i.e., representing communities of more distantly related species) are found along the TVB, the Sierra Madre Oriental and the states of Oaxaca and Chiapas (Fig. 6.6, orange and red cells). The distribution of high *PD* residuals matches the distribution of 29 out of 50 cells with high *PD*. *TD* on the other hand, shows high residual values dispersed across the country (Fig. 6.7). The distribution of Diversity Skewness (Fig. 6.8) indicates that those areas with high *PD* (Fig. 6.4) have more balanced, symmetrical local phylogenies. The opposite, however, is not true: not all balanced phylogenies show high *PD*. The reason for this is simple, as balanced phylogenies may contain few or many species.

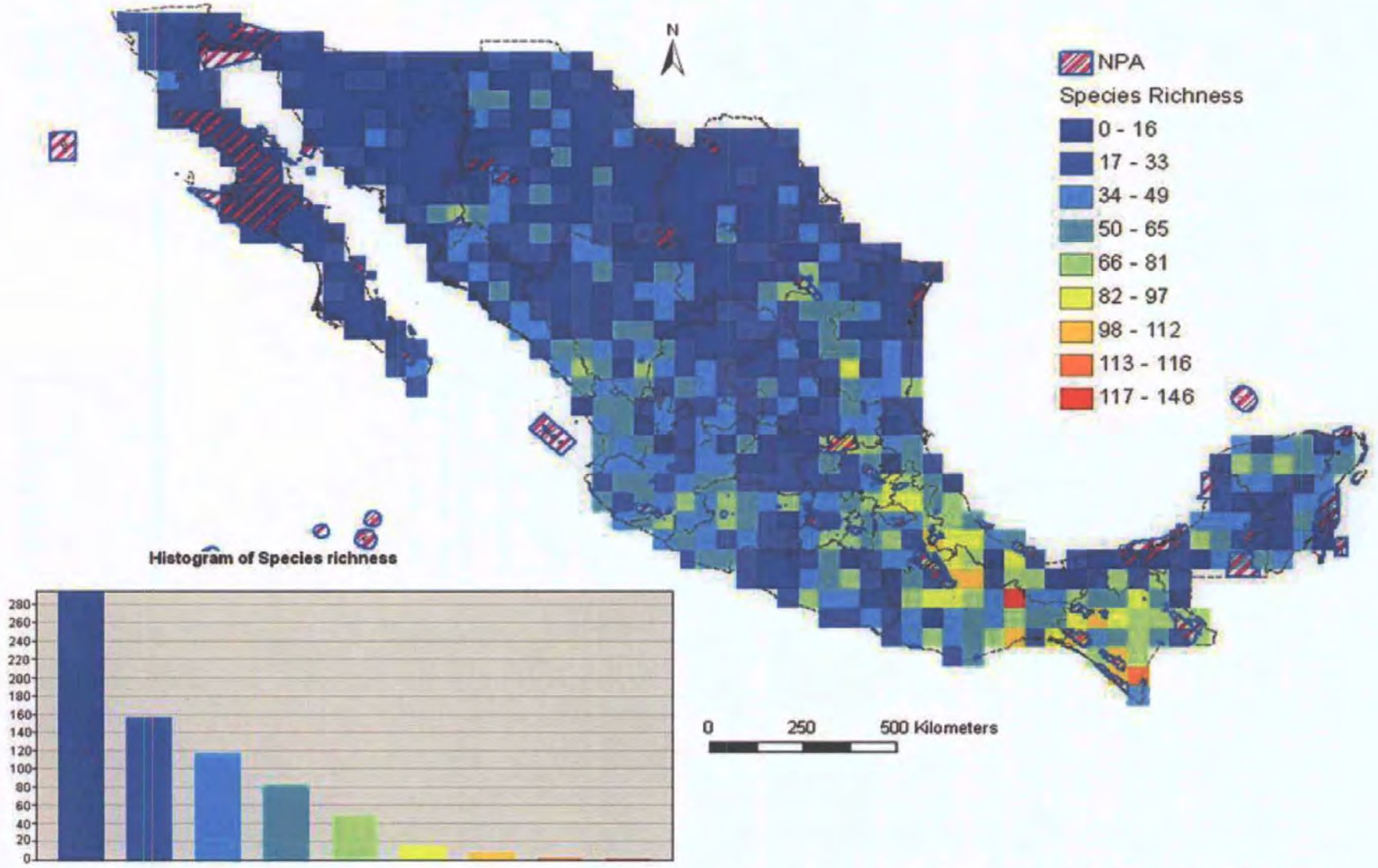


Figure 6.3 Occurrence (species richness) of Mexican mammal species represented in ArcInfo at a scale of 30'×30' (S30'). Hatched pink and blue areas represent NPAs. The frequency distribution of *S* employing the same scale on the right is shown.

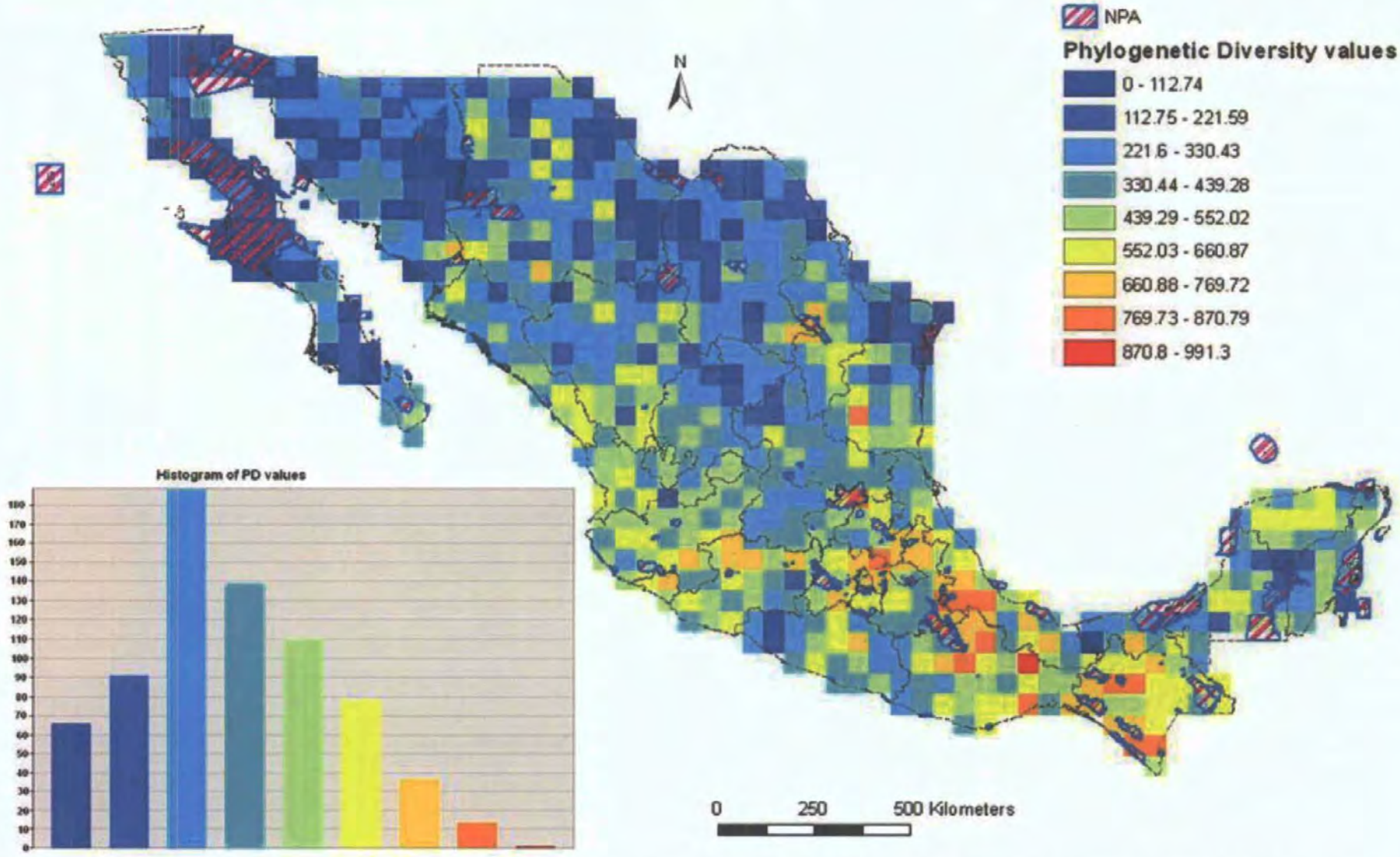


Figure 6.4 Geographical representation of *PD(p)* values at S30' superimposed on a map of the Mexican Natural Protected Areas (NPAs). The frequency distribution of *S* employing the same scale on the right is shown.

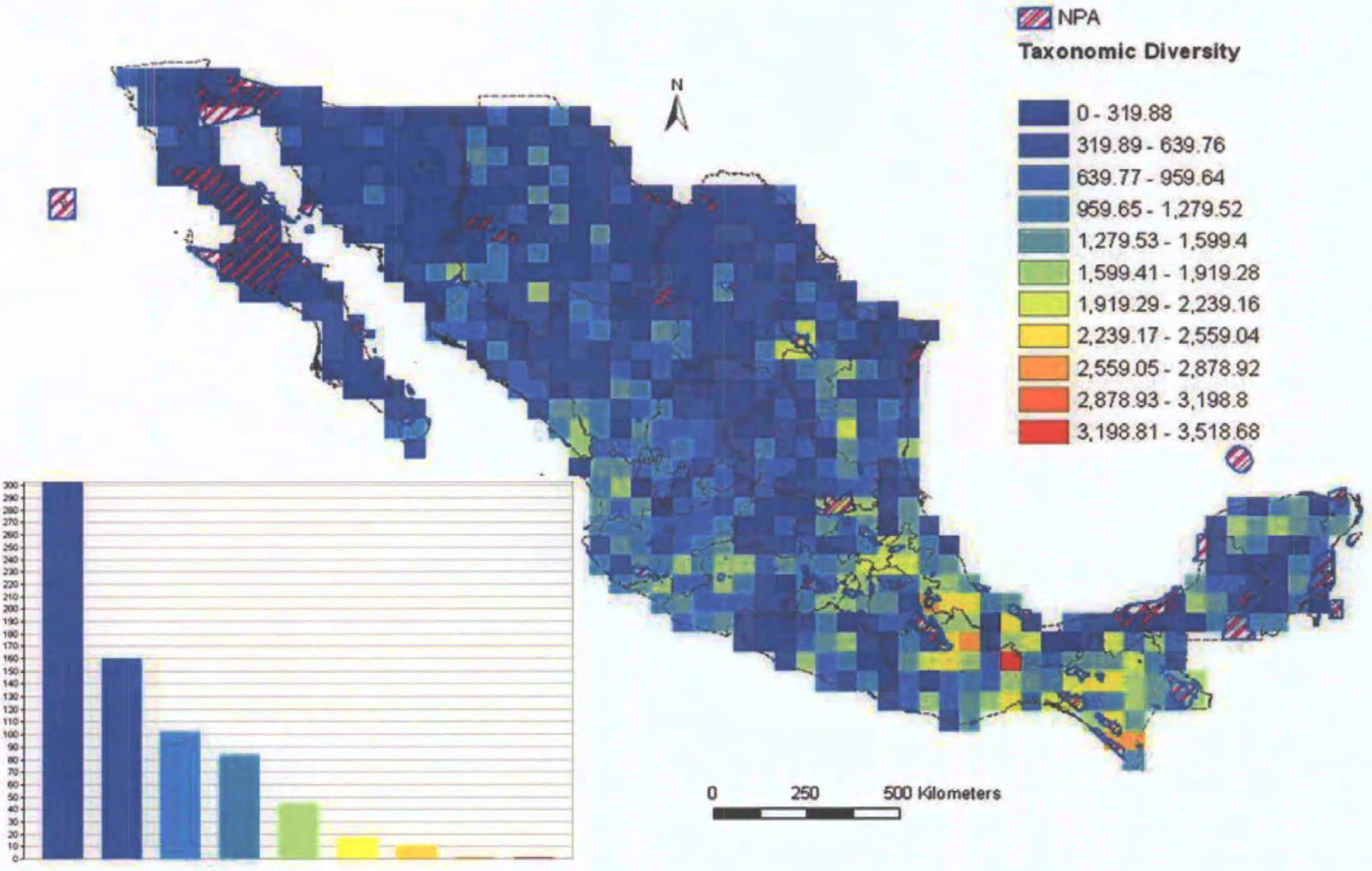


Figure 6.5 Geographical representation of *TD(p)* values at S30' superimposed on a map of the Mexican Natural Protected Areas (NPAs). The frequency distribution of *S* employing the same scale on the right is shown.

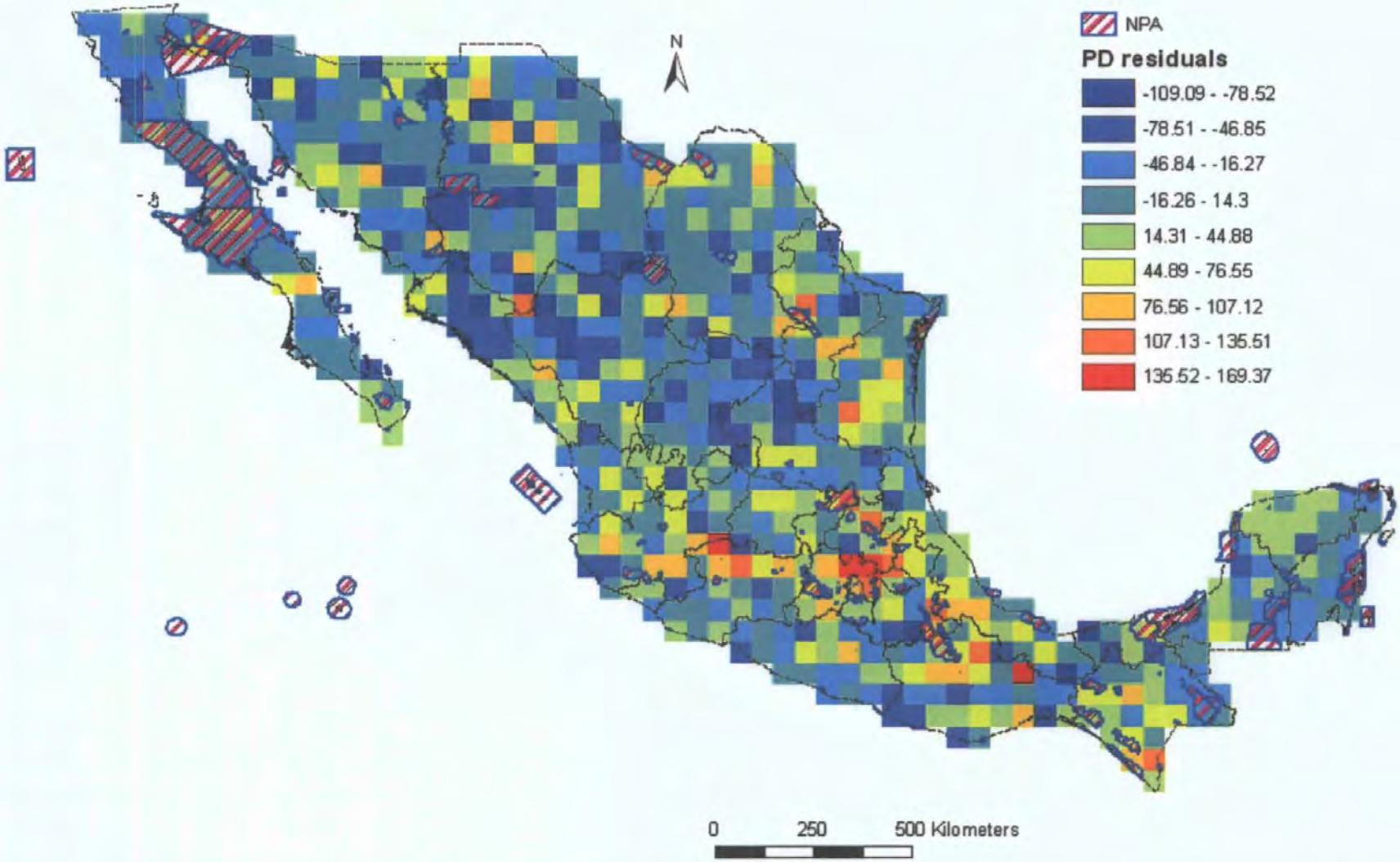


Figure 6.6 Geographical representation of the residuals of the correlation between *PD(p)* and *S* at S30', superimposed onto a map of the Mexican Natural Protected Areas (NPAs).

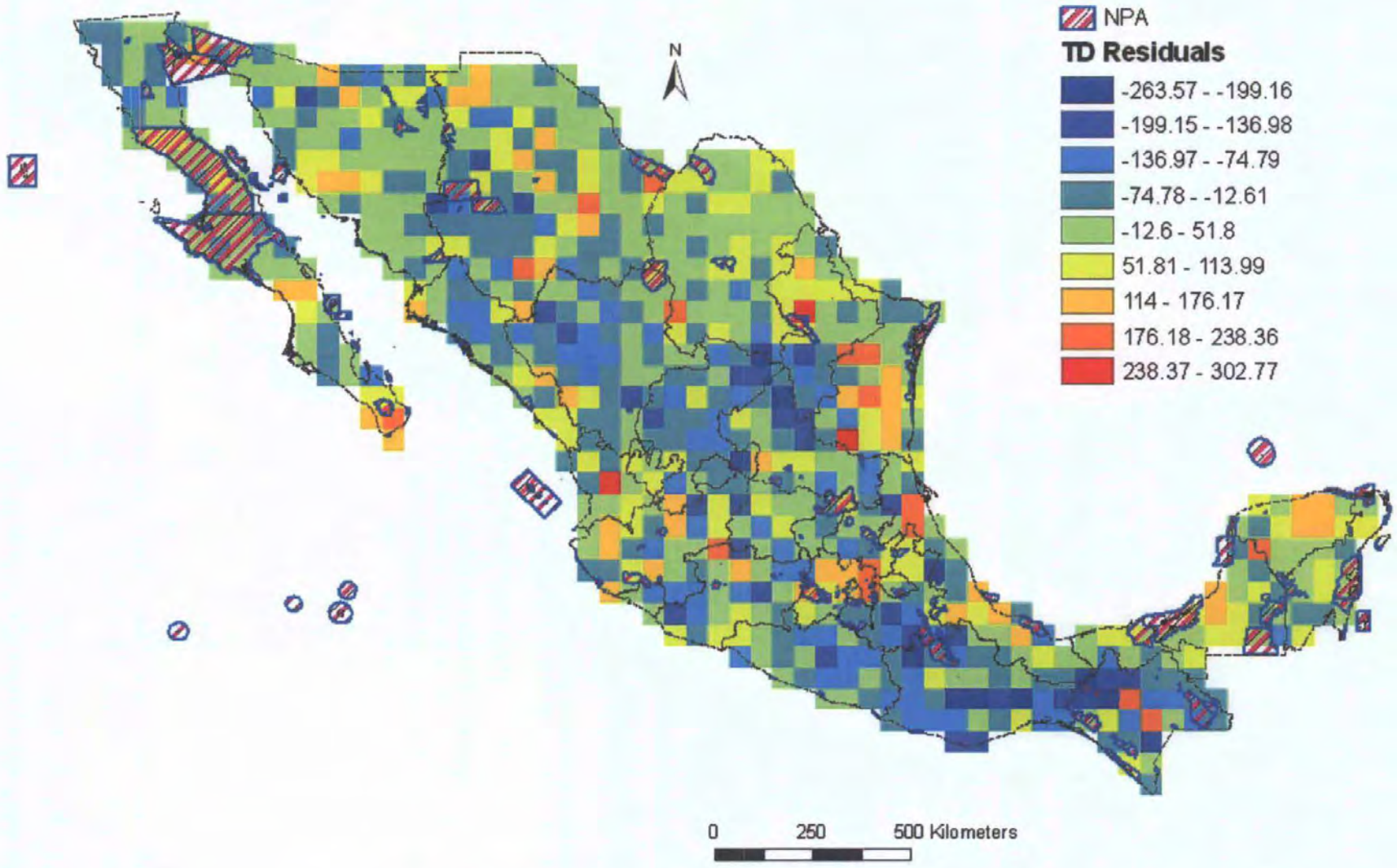


Figure 6.7 Geographical representation of the residuals of the correlation between *TD(p)* and S at S30', superimposed on a map of the Mexican Natural Protected Areas.

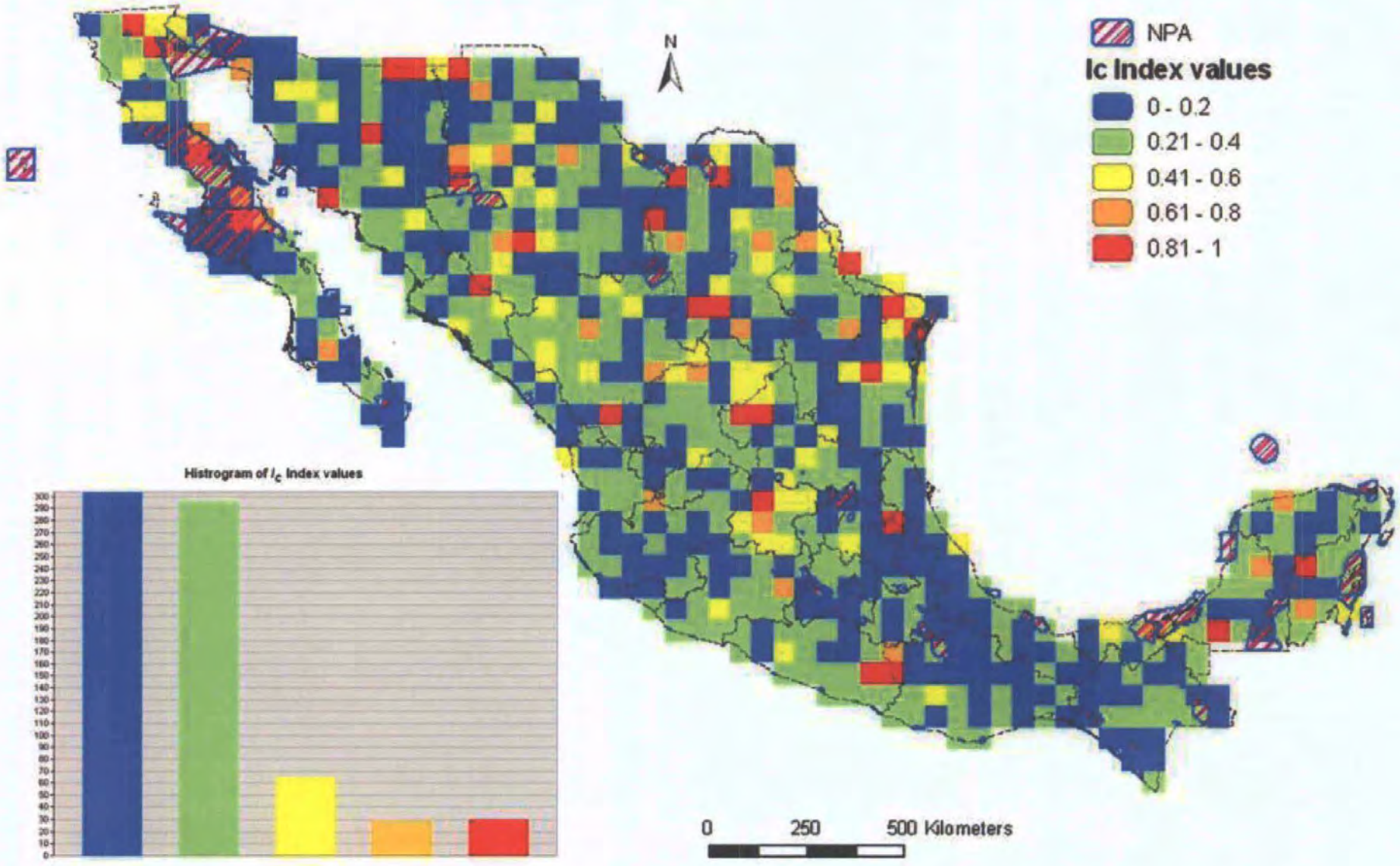


Figure 6.8 Geographical representation of Diversity Skewness (tree imbalance index, I_c) and its frequency distribution.

6.3.3 Endemic and Rare Species

The number of endemic species in the database was 117 (27.99%). Orders Rodentia and Chiroptera are the richest in endemic species (Table 6.5).There are 110 species (26.32%) with narrow range size; these are mainly small mammals such as rodents, bats, shrews and moles (Table 6.5). Levels of endemism were positively correlated with *S*, as well as with *PD* (Table 6.6). The number of endemics increases towards lower latitudes (Table 6.4). Most rare species were distributed in the North of the Baja California Peninsula and in the South region of the country (particularly in the States of Oaxaca and Chiapas). Areas with higher number of endemics (*ESR*≥10) tend to have balanced local phylogenies (Table 6.6).

Table 6.5 The threat status of continental mammals in Mexico.

Order	Species	Endemics	Rare	Risk*	Protected
Didelphimorphia	7	1	1	1	1
Cingulata	2	0	1	1	0
Pilosa	2	0	0	2	0
Primates	3	0	0	3	0
Lagomorpha	11	4	3	3	0
Rodentia	198	86	73	35	26
Soricomorpha	20	10	9	4	12
Erinaceamorpha	2	0	2	2	0
Chiroptera	133	14	21	18	18
Carnivora	29	1	0	10	4
Perissodactyla	1	0	0	1	1
Artiodactyla	9	1	0	2	1
Total	**416**	**117**	**110**	**82**	**63**

* Endangered and threatened species

Table 6.6 Correlation coefficients among Biodiversity Measures. All correlations are significant at $p<0.01$.

	S	*ESR*	Threaten	Rare	I_c	*TD*
S						
ESR	0.53					
Threaten	0.81	0.30				
Rare	0.40	0.04	0.56			
I_c	-0.59	-0.33	-0.44	-0.18		
TD	0.99	0.50	0.79	0.37	-0.60	
PD	0.96	0.56	0.72	0.31	-0.62	0.98

6.3.4 Threatened Species Hotspots

There are 82 species allocated to some of the risk categories (Table 6.5); rodents represent the group with more threatened species (8.37%), followed by bats (4.31%) and carnivors (2.87%). Most of the protected species are rodents (6.22%), bats (4.31%) and shrews (2.87%). The cells with more threatened species were found in the north of the Baja California Peninsula, and in the central-east and south-east states.

As expected, species in the different risk categories overlap; some endemic and/or threatened species are also rare, and some threatened species are also endemic and/or rare.

6.3.5 Natural protected areas (NPAs)

Using the species accumulation curve (Mao's tau) calculated by EstimateS (Colwell *et al.* 2004), the expected number of grid cells that would protect 90% of *S* is 169 (Fig. 6.9). However, this is a projection based on random sampling of

cells with replacement, not the actual cells. Targeting those known cells containing the highest values of *PD* (whose *S* ranks from 52 to146), showed that the 53 cells with the highest values of *PD* would host a total of 350 species (84.17% of the sample; Fig. 6.10).

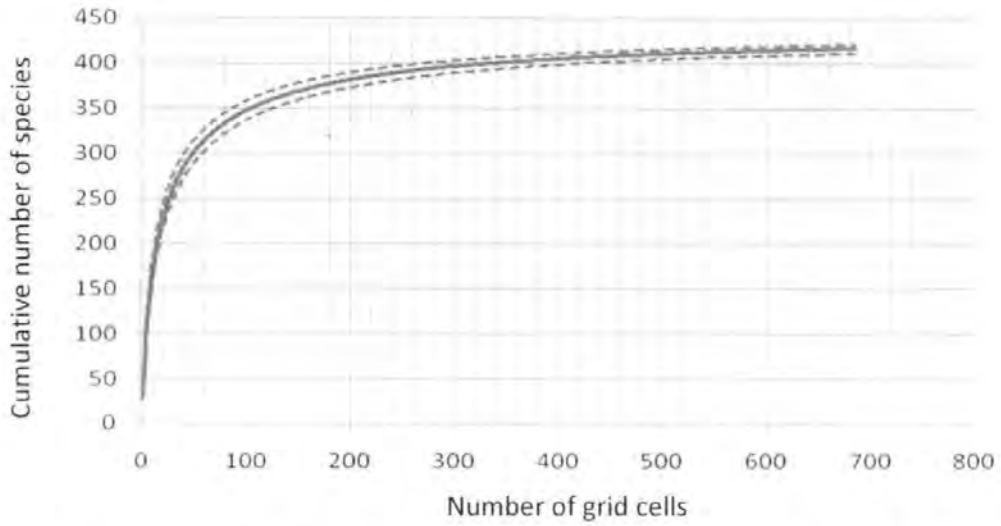


Figure 6.9 The predicted species accumulation curve (Mao's tau) for the mammals of Mexico employing the program EstimateS 8.0.

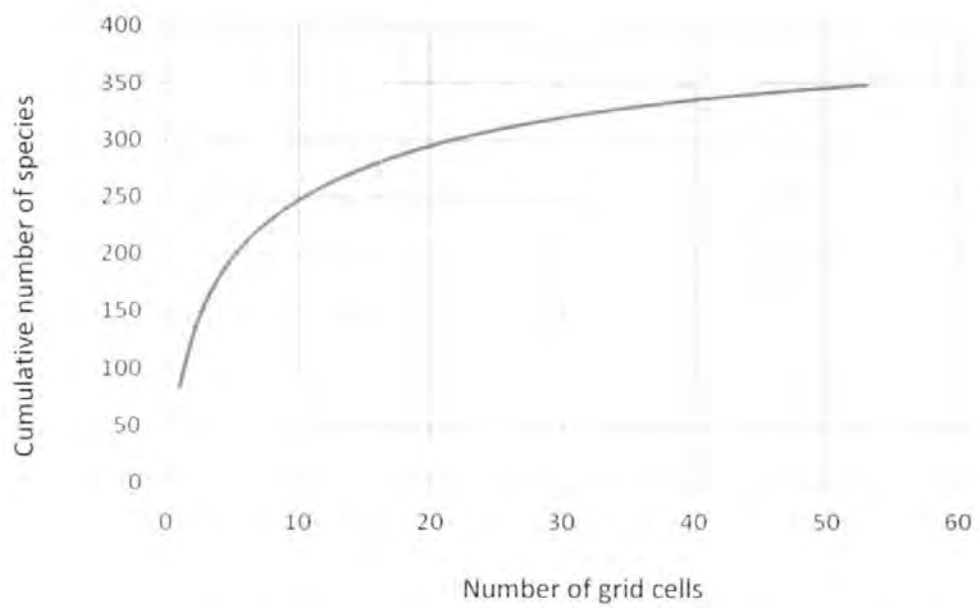


Figure 6.10 Number of species represented by the 53 cells with the highest values of *PD*. These 53 cells would represent 350 species.

On the other hand, targeting specifically complementary areas (i.e., skipping areas that do not add new species to the cumulative sample), the minimum number of grid cells needed to include all 416 species was 51 (Fig. 6.11). The distribution of 18 (out of 51) complementary cells match the distribution of some NPA; on the other hand, the position of 17 complementary cells coincide with areas of high diversity. Endemic and rare species are fully represented in the complementary area system in 45 and 48 cells, respectively.

The geographical position of 28 of the most diverse *PD* areas overlaps with the distribution of 40 NPA in the reserve network, and also with 17 complementary areas. The 40 NPAs referred above are mainly located on the Centre and Transvolcanic Belt CONANP region, and most of them are National Parks (Table 6.7; Fig 6.2).

Table 6.7 CONANP Regions with high *PD* values and Complementary cells

CONANP Region	Number of NPA	Complementary cells
Centre and Transvolcanic Belt	22	3
South Frontier, Isthmus and South Pacific	10	6
Gulf of Mexico and Costal Plateau	6	2
Northwest and Gulf of California	2	1
Northest and Sierra Madre Oriental	3	1
West and Pacific Centre	3	3
North and Sierra Madre Occidental	1	1

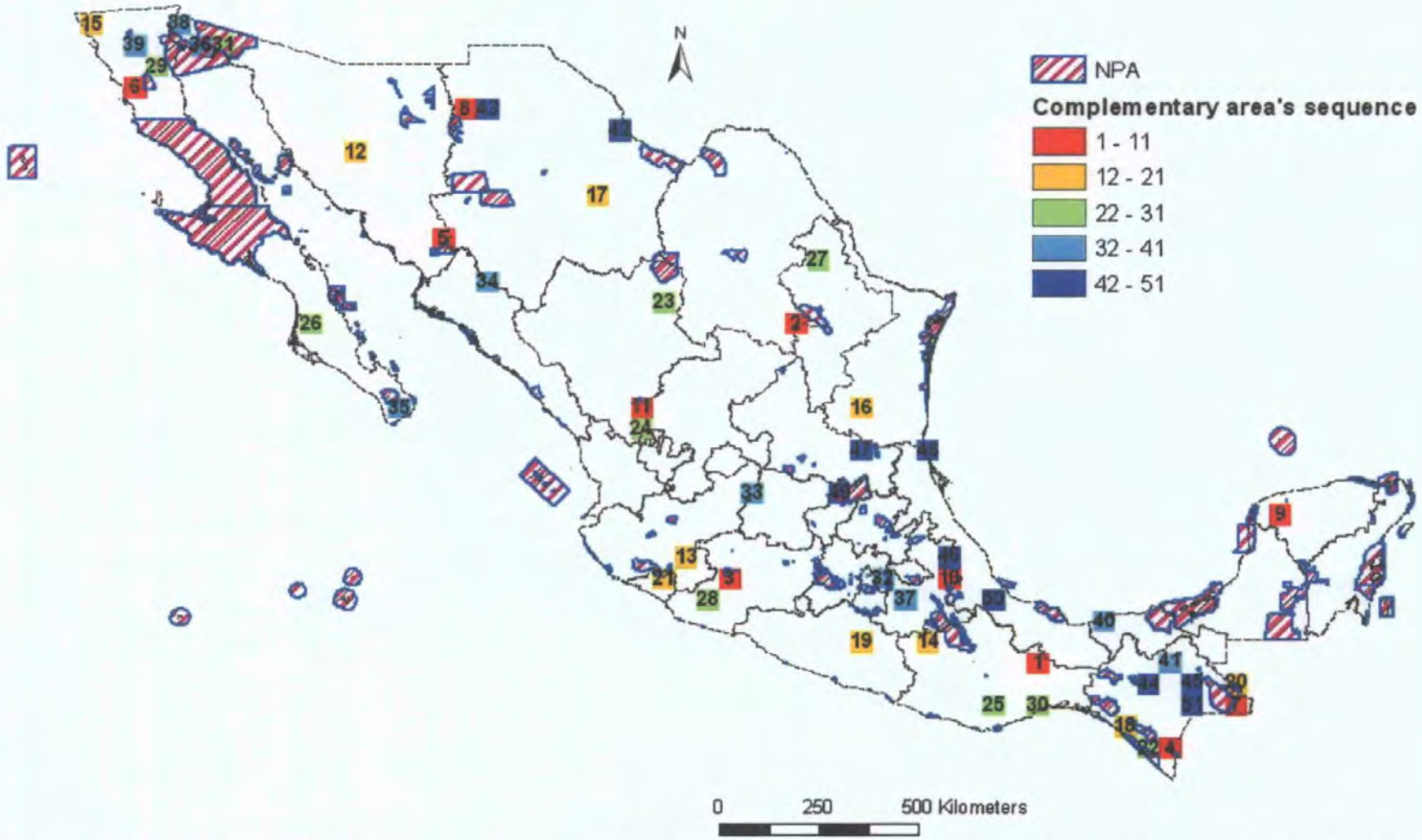


Figure 6.11 Complementarity areas at S30' (calculated in DIVA-GIS software) representing all 416 species of terrestrial mammals. The scale in this case represents the sequence of species richness, thus 1 is the richest cell (with 146 species) and 51 is the "poorest" of the 51 richest areas (with 60 species).

Figure 6.12 illustrates 85 high diversity areas as measured by: 1) *PD* and *PD* residuals, red cells; 2) complementary area system, green numbered cells, notice that red numbered cells are those complementary cells that also match the distribution of high *PD*; 3) *ESR*≥10, dark green cells, most of them either match the distribution of *PD* or are incorporated in the Complementarity system; 4) threatened species≥16, areas that do not correspond to any of the three previous measures are shown in pink. Rare species hotspots are included in the complementarity cells, particularly in the Baja California Peninsula. These 85 areas have been identified as high priority areas for conservation (HPA) in this study. Detailed information of each HPA is given in Appendix F.

Figure 6.12 Geographical representation of high priority conservation areas (HPA; see text for explanation) superimposed on the map of Mexican Natural Protected Areas.

6.4 DISCUSSION

6.4.1 DIVERSITY, GEOGRAPHIC AND ENVIRONMENTAL CORRELATIONS

Measures of diversity, such as *PD*, *TD* and *DS*, showed different degrees of correlation with variables of the environment (See Table 6.4 and Appendix E). In general, both *PD* and *TD* tend to increase towards lower latitudes, being higher in the tropical East part of the country. Although *PD*, *TD*, *S* and *ESR*, tended to be higher in low and middle elevations, there was not a clear monotonic relationship between them. There was no apparent relationship with temperature, either. Diversity, however, increased with precipitation. With the exception of its relationship with precipitation, Diversity Skewness (I_c) did not show significant correlation with biogeographic/environmental variables . Thus, it seems that local phylogenies tend to be more balanced when precipitation ranks from 2300 to 3300mm. Finally, although there was not a clear relationship between *DS* and altitude, when the map of I_c was superimposed on the elevation map, balanced phylogenies were mainly situated over the Neotropical mountain ranges (Sierra Madre del Sur and Sierra Mixe) and, further north, over the Sierra Madre Oriental.

6.4.2 THE DISTRIBUTION OF DIVERSITY

The diversity of mammals measured by *S*, *PD*, *TD* and *ESR* increases from the north to the south. Areas of high *TD* are (mostly) correspondent with areas of high *S*, whereas, areas with higher values of *PD* do not necessarily match those areas with the larger number of species. Although with some coincidences, the distribution of *S* and *TD*, on the one hand, and *PD*, on the other, showed different

patterns. Although algorithmically similar, their "bottom-up" (*PD*) and "top-down" (*TD*) methods of calculation yield different results. Thus, care must be taken in the use and interpretation of these two indices. To identify areas of high diversity in this study *PD* and *PD* residuals were chosen. High diversity grid cells (53) hold 350 species from the total sample of 416 species. The distribution of high *PD* residuals (when regressed against *S*) matched the distribution of the 58% higher *PD* areas; these grid cells were identified as high-priority areas for conservation.

Cells of high *PD* values and high *PD* residual values were found across the TVB as well as in the Tropical region, predominantly in the States of Hidalgo, Puebla, Veracruz, Oaxaca and Chiapas. The area of highest *PD* (and also *S*) is found in the State of Oaxaca, on the boundaries between The Sierra Madre del Sur and The Gulf of Mexico Plateau. The main explanation of such distribution of *PD* is related with the geographical pattern that each mammal order displays in the country. Because biogeographic features have influenced the geographical distribution on mammals in Mexico, regional affinities are often found (Fig. 6.13;(Arita and Ceballos 1997, Fa and Morales 1998). For instace, Lagomorpha, Soricomorpha and Erinaceamorpha are more diverse in both the Central Plateau and TVB; and they are more related with the North-American and Mexican faunas. Members of order Rodentia (the one with the larger number of species) are abundant on the Central Plateau, spreading from the north to the highlands of Chiapas, and share affinities with North-American and Mexican faunas. Orders Cinculata, Pilosa, Primates, Chiroptera and Perissodactyla share affinities with South-American fauna, and therefore, are mostly restricted to the tropical zones of

the Yucatan Peninsula and the tropical coastal zones. Members of order Chiroptera are also diverse on the central part of the country and the TVB.

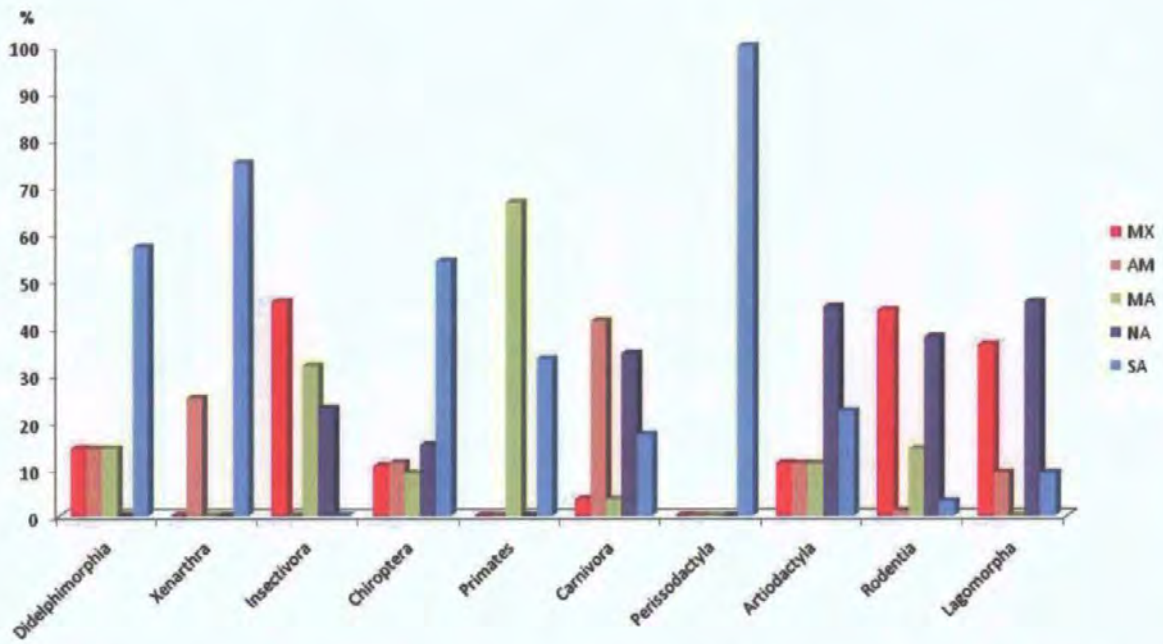


Figure 6.13 Regional affinities of mammalian Orders of Mexico (in percentage): MX= Mexico (endemics); AM=America; MA=Mesoamerica; NA=North America and SA=South America (modified from Arita and Ceballos, 1997).

Levels of endemism were positively correlated with species richness, as well as with *PD*, and with decreasing latitude. Most rare species were distributed in the north of the California Peninsula and in the south region of the country (mostly in the States of Oaxaca and Chiapas).

From our sample, 27.99% are endemic species (predominantly rodents), 18.8% are narrow endemics and 21.37% are threatened. There were 23 endemic species inhabiting the TVB, nine of them belonging to six endemic genera (*Musonycterys, Baedon, Romerolagus, Nelsonia, Neotomodon* and *Pappogeomys*). The total number of species with narrow range size was 110 (26.32%); these are mainly small mammals (Table 6.5). Regional affinities of rare

species are with Mexico (endemics: 57), with North America (25), with South America (16) and with Mesoamerica (12). As with endemics, most rare species are distributed in the North of the California Peninsula and in the South region of the country (mostly in the States of Oaxaca and Chiapas). In addition, 64.54% rare species are listed in some risk category. Threatened species were concentrated in the tropical regions of the country; most of them were endemic, too.

6.4.3 Priority Areas for Conservation

A multi-criteria approach is commonly considered in prioritising areas for conservation at national scales. This approach focuses mainly on species richness, endemic species and threatened species (Prendergast *et al.* 1993, Kerr 1997, Posadas *et al.* 2001, Justus and Sarkar 2002). In this study, however, phylogenetic diversity was favoured in the first instance over the other criteria to identify high priority areas. Phylogenetic diversity is the degree with which species differ from one another; its usefulness at prioritising areas is to seek those areas that not only have many species, but species that are particularly different. These different species, and the places where they live, should have priority for conservation (Vazquez and Gittleman 1998, Barker 2002).

Additionally, complementarity analysis to choose the least non-overlapping representation of species was also employed. The minimum number of grid cells needed to include all 416 species was 51. Endemic and rare species would be fully represented in this complementary area system. Complementary cells are

spread across the country; 33.33% of them overlap with the distribution of high diversity areas and 17 complementary cells match the distribution of some NPAs.

The number of areas identified as high priority areas (HPA) was 85 as measured firstly in terms of high *PD* and complementarity and secondly, on the number of endemic, rare and threatened species. Distributions of sites of high values of species at risk overlap with areas of either high diversity or complementarity or both, predominantly in the tropical states. However, some rare species hotspots are included in complementarity cells in the Baja California Peninsula. The map of HPA is shown in Figure 6.12.

The position of 28 HPA coincides with the distribution of 40 NPA in the reserve network. Those 40 NPAs are mainly located in CONANP's region Centre and Transvolcanic Belt, and most of them are National Parks (Table 6.7; Fig 6.2). The results showed that there were several NPA in the reserve system that did not match the distribution of any area rich in *PD, S,* or some other biodiversity measure, nor did they match the distribution of any complementary area (except in northern Baja California). Those reserves are concentrated in the northern states. On the other hand, more protected areas are needed in the states of Michoacan, Mexico, Puebla, Oaxaca, Veracruz and Tabasco, where the long term persistence of high diversity is not assured.

An assessment of the effectiveness of SINANP in conserving mammal species richness,showed that there is a mismatch between the distribution of mammals and the distribution of Protected Areas in Mexico (Ceballos 2007) . Similarly, this study shows that SINANP does not yet cover a representative

proportion of valuable, highly diverse areas. Therefore, additional reserves are needed in areas identified as HPAs here. It is important to bear in mind that the establishment of a reserve is only the first step to ensure the long term persistence of species. After a reserve has been created,it is necessary to understand the ecological and biological factors that maintain their populations. For this reason, studies using occurrence data must then be complemented with other approaches, such as population viability analysis, predictive habitat modelling, and more detailed inventories that provide information on the abundance and health of populations.

A point that needs to be stressed is that the identification of HPAs employing collection records is that there is no guarantee that the high diversity identified in some areas represents the current situation. These areas may have already suffered severe habitat transformation. Although most records from CONABIO's database (~90%) are from specimens collected after 1950 some specimens date from before 1900. An analysis that took into account the temporal component of diversity would be ideal, but no collection would have the level of temporal detail that would be required. Prospecting the HPAs identified by this study is simple and economical. This task is also urgent.

CHAPTER 7. LIFE HISTORY, DISTRIBUTION AND RISK

7.1 INTRODUCTION

Biodiversity is being lost at an alarming rate and at least one-third of mammals are threatened with extinction by anthropogenic activities (http://www.iucnredlist.org). Population declines and species extinctions are known to be associated with extrinsic human pressures, environmental modifications, and the biological traits characteristic of individual species (Purvis *et al.* 2000, Cardillo *et al.* 2004). Because species do not respond equally to human impacts, such as habitat loss or hunting, some species are far more likely to become threatened with extinction than others (Cardillo *et al.* 2005). There are significant interactions among external variables, as well as among biological traits that characterise the most threatened species (Jones et al. 2003b, Cardillo *et al.* 2005).

Recently, comparative analyses have been applied in conservation studies. These have attempted to: 1) identify general ecological principles underlying mechanisms that cause conservation problems (such as invasions and over-harvesting); 2) provide a basis for prioritising conservation actions or further research (because there is not enough time to conduct studies of population dynamics of every species), and 3) predict which species will experience conservation problems (Fisher and Owens 2004, Purvis *et al.* 2005a). Several studies have investigated whether rare species are randomly distributed across taxa (Bennett and Owens 1997, Purvis *et al.* 2000, Pilgrim *et al.* 2004). There is

evidence to suggest that rare species are clustered within certain groups. This suggests that a predisposition to rarity, as well as to extinction risk, is perhaps determined by inherited characteristics. For this reason, recent studies have attempted to predict species predisposition to rarity by analyzing species traits across phylogenies (Pilgrim *et al.* 2004).

Comparative life-history studies indicate that mammalian populations can be placed along a fast-slow continuum. The "fast end" of this continuum is occupied by species that mature early and have large reproductive output and short generation times, whereas those species with the opposite set of traits occupy the "slow end" (Read and Harvey 1989, Oli 2004, Bielby *et al.* 2007). Life history deals primarily with the interactions between reproductive rates (age at maturity, litter size, frequency of reproduction) and survival (Millar and Hickling 1991). Body size is one of the most fundamental ecological parameters, correlating with many life history attributes (Fa and Purvis 1997, Pyron 1999, Murray and Dickman 2000, Orme *et al.* 2002, Lovegrove and Haines 2004, Isaac *et al.* 2005). It is therefore of interest to investigate the possible association between these attributes and extinction risk, and between them and measures of rarity.

7.1.1 Correlates of Body Size, Range size and Latitude with Extinction Risk

It has been documented that some life history characteristics are associated with diverse and widespread taxa while others are associated with rare, endemic ones (Gittleman and Purvis 1998, Agapow and Isaac 2002, Purvis *et al.* 2005a); in particular, body size and range size are predicted to be related to rarity. Similarly, there is a range of life history and ecological predictors of risk, which arise from the way that species traits are associated with vulnerability. Traits such as small geographic range size, large body mass and slow life history (low reproductive rate) characterise the most threatened species (Taylor and Gotelli 1994, Purvis *et al.* 2000, Bennett and Owens 2002, Cardillo *et al.* 2004, Cardillo *et al.* 2006).

Other common relationship is that small-sized species tend to have smaller geographical ranges than large-sized species (Gaston 1996b). However, the relationship more often tends to be of triangular form, i.e., at large geographic ranges species of all sizes may occur, with the upper limit determined by the size of the study area, while at smaller ranges there is more evidence of a positive relationship between range size and body size (Kent 2005). One explanation for this is that larger-bodied species with small geographical ranges will have a higher probability of extinction (Diniz-Filho 2004). Cardillo *et al.* (2006) proposed the term "latent extinction risk" as the discrepancy between a species' currrent extinction risk and the risk predicted from its biological traits. In Cardillo *et al.*'s study, Mexico does not appear as one of their "Latent Extinction Risk Hotspots" for mammals at a global scale. This may be either because the mammals of Mexico do not face

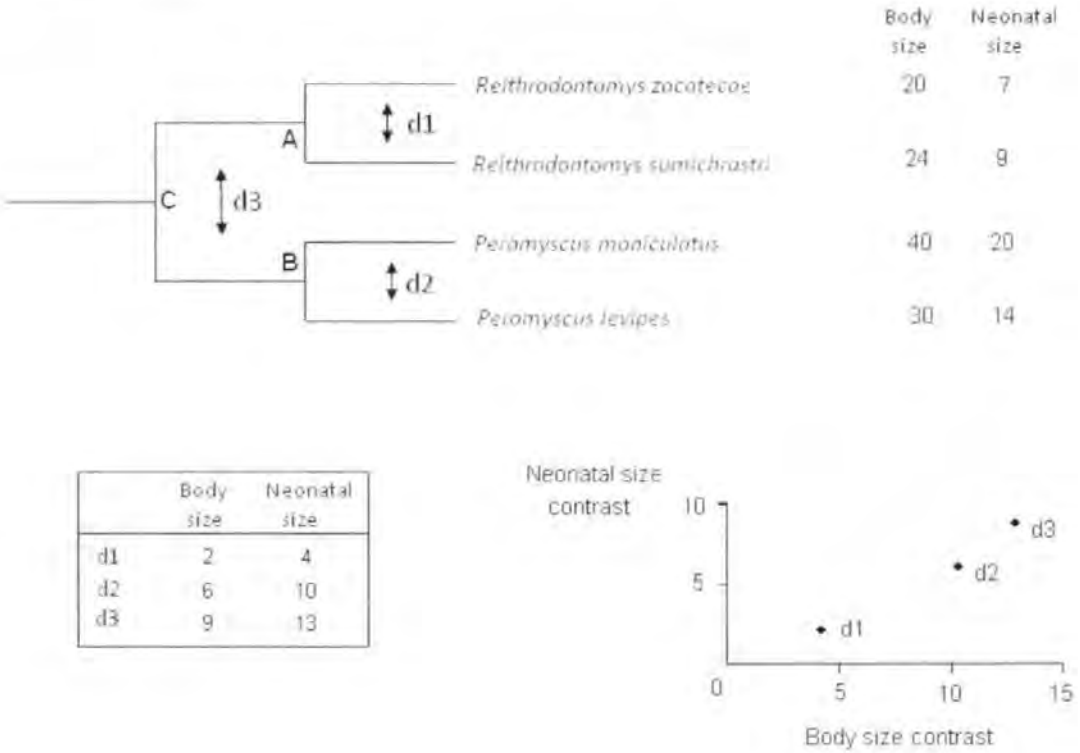
latent extinction risks or because of limited information. Since it is thought that some of these species are indeed at risk, particularly because of habitat loss; this mismatch may be due to the use of different red lists to categorize species at risk.

7.1.2 THE COMPARATIVE METHOD

Identifying correlations between life history traits and ecological or evolutionary characteristics, such as climate or extinction risk, requires consideration of the degree of relatedness of species in the dataset. The fact that species share phylogenetic history means that their characteristics are not statistically independent entities. This non-independence of species' characteristics invalidates statistical tests used to examine the co-evolution of traits in comparative analyses (Felsenstein 1985, Harvey and Pagel 1991, Garland *et al.* 1992, Jones and Purvis 1997, Jones *et al.* 2003a). This lack of independence is in essence what is meant when authors refer to "phylogenetic constraits", "phylogenetic inertia" or "phylogenetic effects". Phylogenetic comparative methods are statistical methods that test for correlations between variables, taking into account this phylogenetic non-independence between species. A family of methods to compare the characteristics of species has been developed in recent years. Among these methods, the comparative analysis by independent contrasts is a powerful technique to study characteristics that can be assumed to vary in a continuous way. In fact, it is also possible to investigate how a continuous variable changes in relation to a categorical (usually dichotomous) variable. Thus, one could investigate not only how, for example, reproductive output is related to body size, but also how any of these two characteristics is

related to, say, parity, the ability to reproduce once or many times over the course of life.

The analysis by independent contrasts is ideally suited to investigate if life history characteristics are associated with endemicity, rarity or extinction risk. It has been found that the geographic range size of mammals is correlated with phylogenetic history (Jones *et al.* 2005b). Thus, in this chapter the comparative method of Phylogenetically Independent Contrasts (PICs) proposed by Felsenstein (1985) and implemented by Purvis and Rambaut (1995) will be employed to investigate the possible relationship between the life history traits of Mexican mammals and both attributes of the environment where they live and biodiversity surrogates (endemicity, rarity and extinction risk). The method is based on comparisons (i.e., differences) between pairs of species in a completely resolved (i.e., dichotomous) phylogeny (Fig. 7.1). Character values are subtracted from one another for each terminal species pair to yield a measure of difference or contrast in each particular character. The procedure is carried "backward" along the phylogenetic tree to compare the mean for each ancestral node until the root of the tree is reached. In the case of incompletely resolved phylogenies, polytomies can be resolved arbitrarily to give only one contrast (Pagel 1992). Pairs of contrasts can then be used in correlations and regressions forced through the origin (Garland *et al.* 1992). PIC's are necessary because of the pseudoreplication and elevated Type 1 error rates that result from treating species as independent sample units when the relevant variables evidently have a phylogenetic component (Garland *et al.* 1992, Gittleman and Purvis 1998).



	Body size	Neonatal size
d1	2	4
d2	6	10
d3	9	13

Figure 7.1 The Phylogenetically Independent Contrasts Method. The values of two life-history traits, body size (x) and neonatal size (y) for 4 mammals' species are shown. *Reithrodontomys zacatecae* and *R. sumuchrastri* diverge at node *A*, so any trait differences between them, d1, must have evolved since then. Similarly, the differences between *Peromyscus maniculatus* and *P. levipes*, d2, must have arisen since those lineages split at *B*. These two sets of differences are statistically independent. At node *C*, the difference, d3, between the average trait values at A and B generate a third independent contrast. In this example, body size and neonatal sizes contrasts are positively correlated with each other. Independent contrasts can be calculated for each life-history variable and the relationship between the changes in those variables can then be investigated using standard statistical techniques (Adapted from Pagel and Harvey, 1991).

Felsenstein's method has some technical limitations: it requires a known phylogeny and branch lengths, and it assumes a Brownian motion model of evolution (see Purvis and Rambaut 1995). Nonetheless, the method has proven robust in a number of studies and simulations, and has been used to test or suggested new hypotheses in the fields of ecology and evolution (e.g.(Franco and

Silvertown 1996, Gittleman and Purvis 1998, Purvis *et al.* 2000, Orme *et al.* 2002, Brashares 2003, Jones *et al.* 2003b, Stuart-Fox and Owens 2003).

A comparative phylogenetic approach reveals that threatened lineages have particular biological characteristics that may predispose them to higher risk of extinction (Purvis *et al.* 2005b). Latitudinal variation among species in life-history traits is often suggested to contribute to high tropical species richness. However traditional methods of analyzing such variation rarely control for phylogeny because authors treat each species as an independent data point. In the same way that closely related species are likely to be more similar in their biology than more distantly related species (due to more recent common ancestry), they are more likely to inhabit the same geographical region (Cardillo 2002). For example, it has been found that geographical variation in body size among butterfly species can be attributed mostly to the changing representation of different families at different altitudes (Cardillo 1999, 2002).

This chapter attempts to examine the relationships among life history attributes, geographical range size, distribution (endemicity and rarity) and environmental preferences within a phylogenetic framework in Mexican mammals. It also investigates the possible association between those traits and extinction risk.

7.2 METHODS

7.2.1 DATABASE

Data for 416 species was considered. The information used for this analysis is classified in four types (Table 7.1): life-history (9 traits), environment (3 variables), geographic distribution (4 variables) and conservation status (=risk category). Mammal biological trait values were obtained from published data and online databases; the sources are given in Appendix G. Information about endemism and extinction risk category was obtained from the literature (see Chapter 6). Environmental variables and range size were calculated from data included in Chapter 6.

The life history traits considered were: body size, neonate size, gestation length, age at first reproduction (AFR), litter size, litters per year, age at weaning and maximum life span. Body size was measured in grams as the mean of males and females combined. Where data for only one sex was available, or where sex was not specified, this value was used. Where more than one value was available, the mean value was used. Gestation length does not include the period of delayed implantation. Where a range of litter sizes was given, the mean value was used. The environmental variables of the habitat where each species occurs were estimated from the cartographic information. Thus, average values were calculated from the ranges where the species were present. The variables employed were average temperature, average precipitation and altitude. Occurrence, the number of grid cells occupied by a species, was used as an estimator of range size (Gaston 1996b, IUCN 2001); occurrence and range size are therefore synonyms. The average latitude from the species' range was

Table 7.1 Variables used in this study, units are shown in parenthesis.

Data type	Name	Var	Sample size
Life History trait	Body size (g)	bsize	298
	Neonate weight (g)	nwsize	158
	Weaning size(g)	wsize	89
	Gestation length (mo)	gest	175
	Weaning age (mo)	wean	161
	Age at first reproduction (mo)	AFR	142
	Maximum life span (mo)	mxlife	146
	Litter size	litsize	248
	Litters per year	lityr	186
Environmental variable	Average Temperature (°C)	temp	416
	Average Precipitation (mm)	pp	416
	Average Altitude (m)	alt	416
Geographic distribution	Mean Latitude	latitude	416
	Range size	occur	416
	Endemicity	endemic	117 (endemic) 299 (nonendemic)
	Rarity	rare	39 (rare) 377 (widespread)
Conservation status	Risk	risk	56 (listed) 360 (not listed)

calculated and used to test if it was correlated with life history traits, as well as with occurrence (Stuart-Fox and Owens 2003). This calculation has the limitation that it assumes all 416 species are either restricted to or centred in Mexico. The variables above were continuous (Table 7.1). Species were also classified as either endemic (coded as 1) or non endemic (0) and rare (1) or widespread (0).

Similarly, conservation status was recorded as either listed (1) or not (0) in INE's threatened species classification (SEMARNAT 2002). The latter three variables (endemicity, rarity and threat) were obviously categorical (Table 7.1).

7.2.2 Comparative Analyses

The comparative method of Phylogenetically Independent Contrasts (PICs) proposed by Felsenstein (1985) and implemented by the CAIC programme (Purvis and Rambaut 1995) was used. Statistical test of associations between variables were carried out by regression or correlation analyses (Sokal and Rohlf 1995). To examine the relationship between variables, least squares regressions through the origin were used. Correlation analyses were used to investigate the degree of association between variables. The analyses examine relationships between life-history variables and body size, occurrence (as a measure of range size), environment and latitude. All variables were logarithmically transformed before analyses because allometric relationships generally follow power rules.

The CRUNCH algorithm of CAIC was used to investigate the association between continuous variables. At any node, a positive contrast in any of the regressed variables means that they are varying in the same direction as the predictor variable. Conversely a negative contrast means that, among the taxa being contrasted, the variables of interest are varying in the opposite direction of the predictor variable. On the other hand, the BRUNCH algorithm was used to investigate association when categorical variables were considered. For contrasts with categorical variables if there is a significant bias towards negative scores or a

mean significantly below zero, then a smaller continuous response variable evolves with (coded) higher values of the discrete, usually dichotomous, predictor variable. Under the null hypothesis that evolution in the continuous (dependent) variable has not been linked in any way to the evolution of the categorical trait, we should expect half the contrasts in the dependent variable to be positive and half negative, and the mean value of the contrasts to be zero. To test this null hypothesis, a two-tailed sign test of the contrasts was used (Purvis and Rambaut 1995). A significant bias towards positive scores, or a mean significantly greater than zero, indicates that the evolution of the higher coded value of the dichotomous variable is correlated with the evolution of a larger response variable, while a significant excess of negative scores, or a mean significantly below zero, would indicate that smaller values of the dichotomous variable would be correlated with the evolution of higher values of the response variable (Purvis and Rambaut 1995, Jones and Purvis 1997, Jones *et al.* 2003b).

The composite phylogenetic tree of the mammals of Mexico build in Chapter 4 was used (Fig 4.3). Branches were assumed to be of equal length (Bennett and Owens 1997, Jones *et al.* 2003b, Stuart-Fox and Owens 2003) . Violation of this assumption would lead to heteroscedasticity in the contrasts (Garland *et al.* 1992). Despite this, simulation studies have shown that, in the absence of independent branch length information, setting branches to equal lengths yields acceptable Type I error rates for large sample sizes (Freckleton *et al.* 2002), and performs better than branch lengths estimated using alternative methods (e.g. algorithms based on tree topology;(Ackerly 2000). Regression and correlation analyses were carried out in Statistica (StatSoft-Inc 2003).

7.3 RESULTS

7.3.1 Relationship Between Body Size-Life History Traits and Body Size-Environmental Attributes

Species-body size distributions were heavily right-skewed, and remained markedly so after body size was logarithmically transformed, i.e., most species were small. Overall, body size and life-history variables were significant correlated (Table 7.2). Positive relationships were found between body size and newborn size, wean size, gestation length, weaning age, age at first reproduction and maximum life span (Table 7.2, Figure 7.2). In contrast, negative associations were found between body size and litter size and between body size and number of litters per year. Consequently, large-sized species have fewer, larger and less frequent neonates than small-sized species. Occurrence (as a measure of range size), mean latitude and characteristics of the physical environment (temperature, precipitation and altitude) were not correlated with body size (Table 7.2, Fig 7.2).

Table 7.2 Predictor Variable: Body Size (n=contrasts; * p<0.01)

	R^2	Slope	F-ratio	n
Life-History traits				
Gestation length	0.135	0.141	45.6347*	167
Newborn size	0.665	0.795	520.1512*	149
Weaning age	0.163	0.191	55.1419*	
Wean size	0.788	0.843	605.9291*	85
Age at first reproduction	0.121	0.179	35.81	136
Max Life span	0.078	0.162	19.4798*	134
Litter size	0.023	-0.057	9.9775*	228
Litters per year	0.079	-0.079	14.5368*	174
Environmental Variables				
Ave Temperature	0.003	0.006	0.1768	262
Ave Precipitation	0.006	-0.042	3.54	262
Ave Altitude	0	0.012	0.65	262
Distribution				
Latitude (mid)	0.003	0.008	1.0271	355
Occurrence	0.005	-0.038	0.1182	262

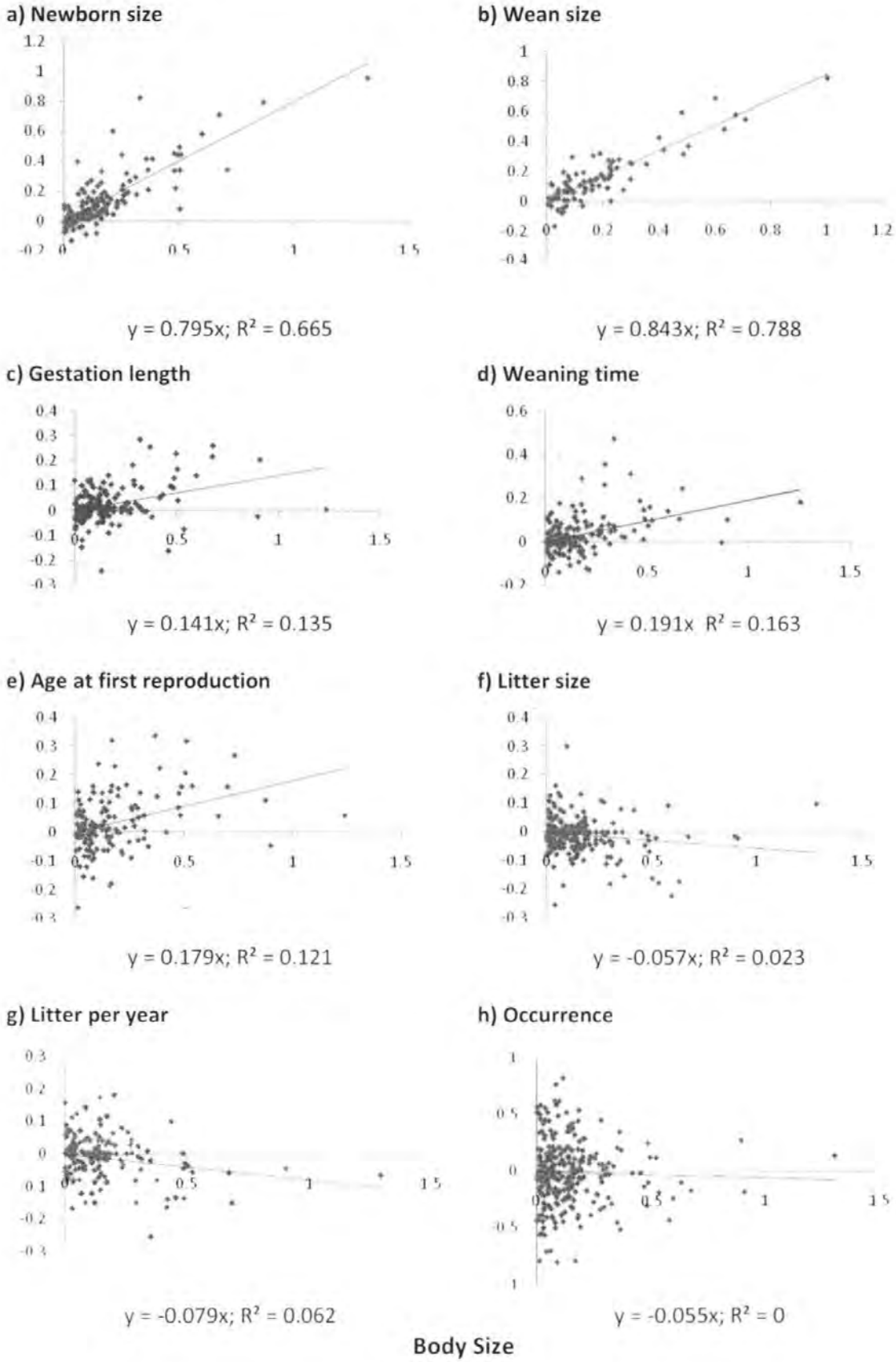


Figure 7.2 Correlations between body size and life-history traits (a-g) and occurrence (h)

7.3.2 Correlation Between Range Size and Life History Traits

Because life history deal primarily with the interactions between reproductive rates (age at maturity, litter size, frequency of reproduction) and survival (Millar and Hickling 1991), the remaining biological traits (neonate size, wean size and age at weaning) were not tested in this analysis. Range size was not significantly correlated with any life history attribute except age at first reproduction (Table 7.3). It was, however, correlated with the environmental variables temperature and altitude, but not with precipitation.

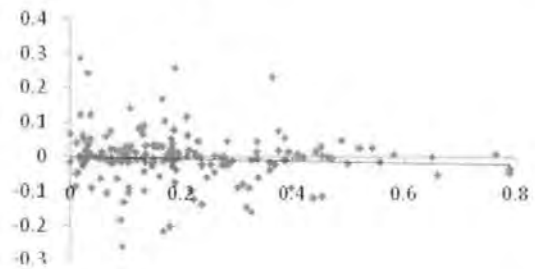
Table 7.3 Predictor Variable: Occurrence (n=contrasts; * p<0.01

	R^2	Slope	F-ratio	n
Life-History traits				
Gestation length	0.008	-0.029	1.8969	168
Age at first reproduction	0.035	-0.087	7.7989*	168
Max Life span	-0.00	0.032	0.2284	140
Litter size	0.005	0.023	2.5804	136
Litters per year	0.013	0.046	6.332	173
Ecological Variable				
Ave Temperature	0.013	-0.003	4.9027*	355
Ave Precipitation	0.000	0.020	0.7842	355
Ave Altitude	0.070	0.105	26.6725*	355
Distribution				
Latitude	0.022	0.021	7.9456*	355

The relationship between range size and latitude was positive, i.e., species that present a large geographic range size tend to have the midpoint of their distribution at higher latitudes (Figure 7.4). There was a significant correlation between latitude and occurrence (Table 7.3). It must be highlighted that the

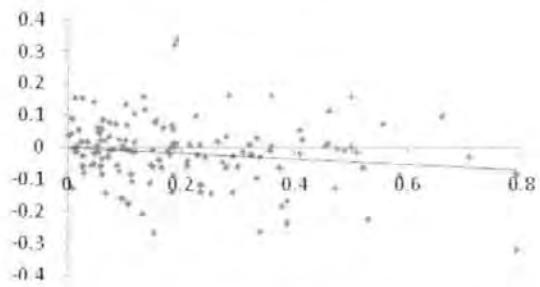
significant correlations explained only a very small amount of the variation in the data.

a) Gestation length



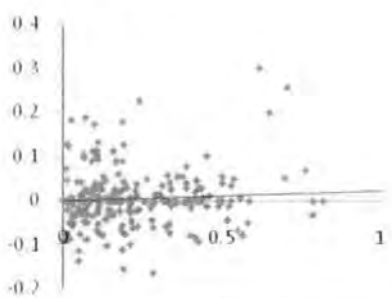
y = -0.029x; R^2 = 0.008

b) Age at first reproduction



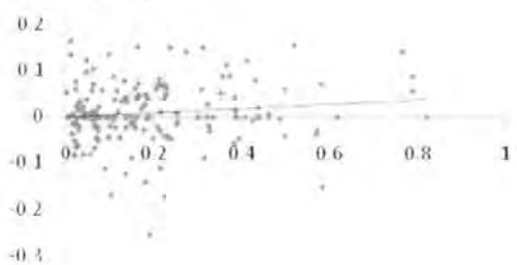
y = -0.087x; R^2 = 0.035

c) Litter size



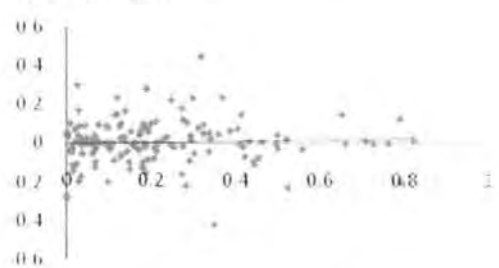
y = 0.023x; R^2 = 0.005

d) Litter per year



y = 0.046; R^2 = 0.013

e) Max life span



y = 0.032x; R^2 = -0.00

Occurrence

Figure 7.3 Relationships between occurrence and life-history traits

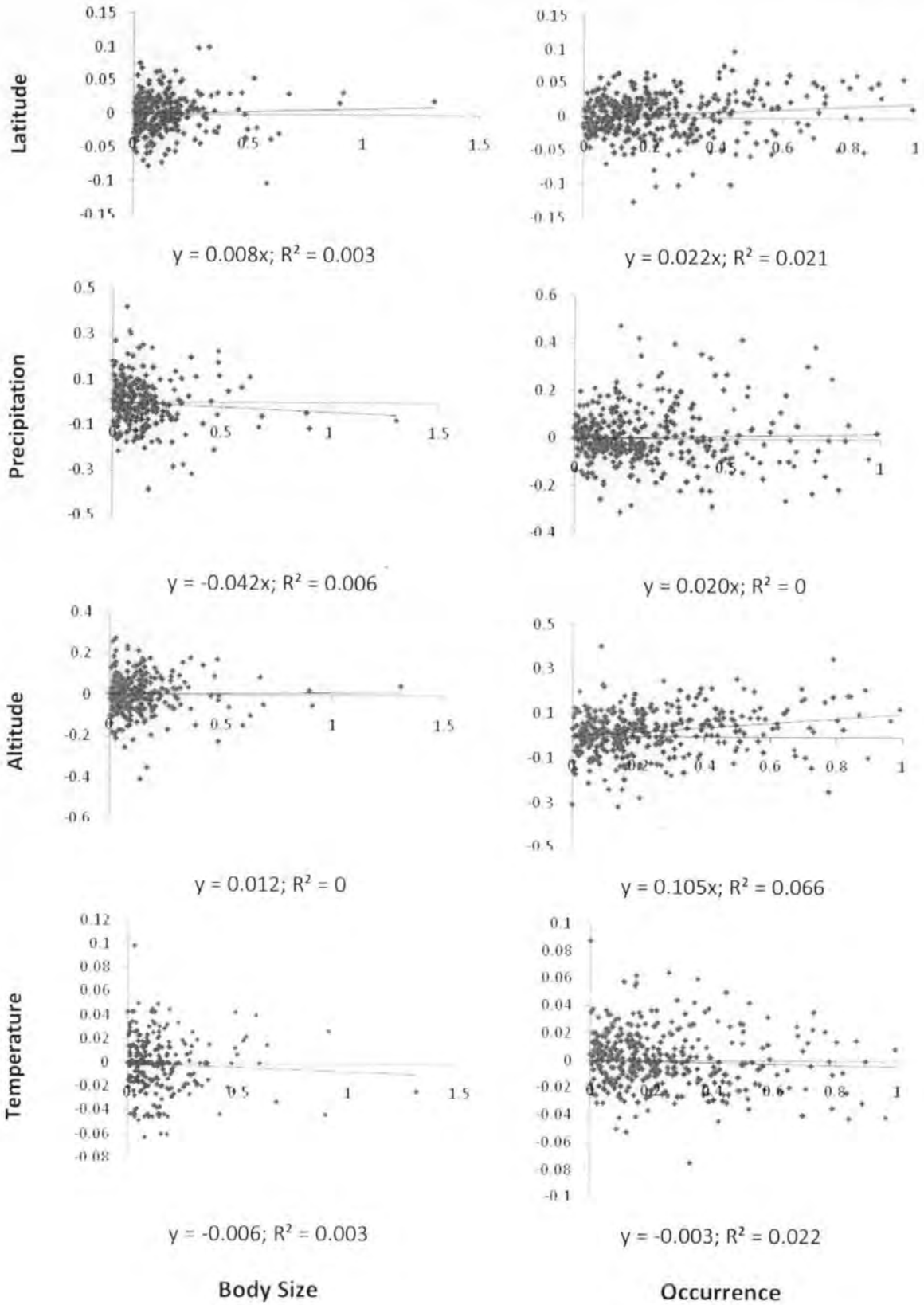


Figure 7.4 Relationships between environmental variables and body size (left-hand side) and occurrence (right-hand side)

7.3.3 The Relationship Between Life History Traits and Latitude.

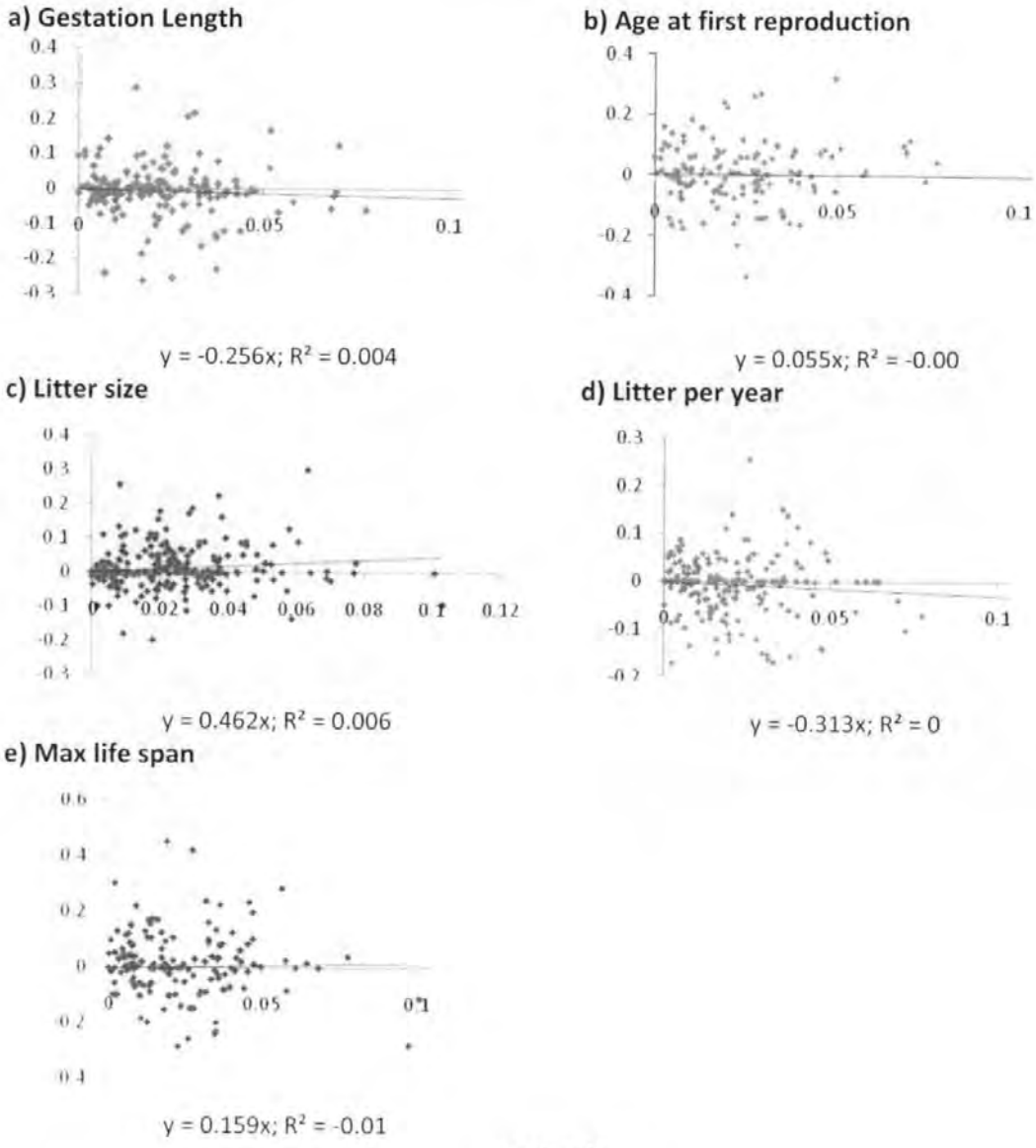


Figure 7.5 Relationships between latitude and life-history traits

No significant correlation was found between the distribution of life-history traits and latitude (Table 7.4, Fig. 7.5).

Table 7.4 Correlations between latitude (midpoint) and life-history traits.

Life-History traits	R^2	Slope	n
Gestation length	0.004	-0.256	135
Age at first reproduction	0.000	0.055	135
Max Life span	0.012	0.159	140
Litter size	0.006	0.462	228
Litters per year	0.0052	-0.313	173

7.3.4 Endemicity, Rarity, and Extinction Risk

Endemicity, rarity and risk were significantly associated with body size, range size and latitudinal distribution (Table 7.5). Large bodied species tended to have wider distributions (low endemicity and rarity), but higher extinction risk (i.e., were classified in INE's list) than small bodied ones. Not surprisingly, endemicity, rarity and the perception of a higher extinction risk were common in species with small range sizes (occurrence). Interestingly, species whose distribution is shifted towards the north (higher latitudes) tended to be endemic, rare and have higher extinction risk.

Table 7.5 Test for correlations between body size, occurrence and latitude with endemicity, rarity and extinction risk. *p < 0.001, employing a t test

Predictor/ variable	mean	t	df
Body size			
Endemicity	-0.01676	-0.4205*	28
Rarity	-0.01631	-0.4834*	25
Risk	0.0571	1.6133*	57
Occurrence			
Endemicity	-0.24771	-7.0843*	74
Rarity	-0.28131	-6.1613*	52
Risk	-0.28885	-8.7918*	91
Latitude			
Endemicity	0.018909	4.9361*	74
Rarity	0.017017	3.9597*	52
Risk	0.012323	3.7666*	91

7.4 DISCUSSION

Recently, comparative analyses have been used in conservation studies to prioritise conservation actions and to predict which species are more likely to experience conservation problems (Fisher and Owens 2004). These studies indicate that there is a correlation between the life-history of the organisms and ecological predictors of elevated risk. In turn, because life history has a strong phylogenetic component, extinction risk also has a phylogenetic bias (Doughty 1996, Bennett and Owens 1997, Martins 2000, Pilgrim *et al.* 2004, Cardillo *et al.* 2005).

7.4.1 Relationship Between Body Size, Life History Traits and Environmental Attributes

Body size was positively correlated with other biological traits related to weight (newborn size and wean size) or developmental time (gestation length, weaning age, age at first reproduction and maximum life span). On the contrary, negative correlations were found between body size and variables where energy is spent in offspring (litter size and number of litters per year). This means that large-sized species mature later, have fewer, bigger neonates, wean them later, and have few, smaller litters per year than small-sized species. Similarly, low reproductive rates and long life expectancy are associated with large size, while high reproductive rates and short lives are associated with small size. These patterns are well established in the literature on world mammals (Read and Harvey 1989, Millar and Hickling 1991). Although these correlations were all significant in the Mexican dataset (Table 7.2), considerable variation was evident.

7.4.2 Correlates Between Body Size (and Life History Traits) and Range Size

The relationship between body size and geographical range size is quite variable. This relationship has been identified as positive in several animal groups, using either cross-species or phylogenetically independent contrasts analysis, over areas embracing the complete ranges of most, if not all, study species. On the other hand, smaller-scale studies tend to reveal both positive and negative relationships with equal frequency (Brown and Maurer 1987, Taylor and Gotelli 1994, Gaston and Blackburn 1996a, Pyron 1999). In this study, however, the

relationship between body size and occurrence (as a measure of range size) was not significant (Fig 7.2h). Similar no significant results have been obtained for Australian marsupials (Murray and Dickman 2000), as well as in previous analysis of Mexican mammals (Arita 1993). There is no indication of a correlation between occurrence and life history attributes, but occurrence had a significant correlation with environment (temperature, altitude, latitude) (Table 7.3). Studies of the physiological requirements and constraints of Mexican mammals would help predict their potential ranges. This is particularly relevant under a global climate change scenario.

The relationship found here between range size and latitude is interesting because it confirms the observation made in other studies of a decreasing latitudinal range size towards the equator (Rapoport's Rule). This has the consequence of increasing species richness towards the tropics (Stevens 1989).

The results presented here also confirm the common finding that small body size species tend to have more restricted geographic ranges than larger ones (Brown and Maurer 1987, Taylor and Gotelli 1994, Olifiers *et al.* 2004). Nevertheless, it has been documented that the distribution of body mass shows a great variation when examined at different geographic scales (Gaston and Blackburn 1996b). Positive interspecific relationships between body size and geographical range size have been found over areas holding the complete ranges of most, if not all, study species; whereas smaller-scale studies tend to reveal both positive and negative relationships with equal frequency (Gaston and Blackburn 1996b). Because the present study was carried out at a national scale ($\sim 1.9 \times 10^6 km^2$), the results suggest that Mexican mammals do not fit this

generalisation for body size-range size relationships. We must bear in mind, however, that restricting calculation of the range size of mammals with larger continental distributions to the area they cover in Mexico underestimates their range size.

Others explanations for this lack of relationship are restricted data, the method of analysis employed, and the reduction of range size that many species have experienced as a consequence of anthropogenic activities (Gaston 2003). Species considered to be facing risk of extinction typically fall close to the lower limit of their "minimum viable geographical range size" (i.e. the minimum geographic range necessary to their long-term persistence; (Diniz-Filho *et al.* 2005).

Population declines and species extinctions are known to be associated with extrinsic human pressures, environmental conditions, and the biological traits characteristic of individual species (Cardillo *et al.* 2005, Cardillo *et al.* 2006). However traditional methods of analyzing such relationships rarely control for phylogeny because authors treat each species as independent data points. However, comparative phylogenetic approaches reveal that threatened lineages share particular biological characteristics that may predispose them to higher risk of extinction. Specifically, larger body mass, low reproductive rate and small geographic range size characterise the most threatened species. These characteristics vary considerably, and species respond to various human pressures and threats differently. Apparently, the lineages for which larger body mass is associated with greater threat status are more vulnerable to human persecution or introduced predators, whereas breeding specialisations are more

influenced by habitat loss (Cardillo *et al.* 2005). There is also evidence in the literature that ecological flexibility in diet and litter size may allow some species with risk traits such as large body size to overcome sources of threat (Cardillo *et al.* 2005, Purvis *et al.* 2005b, Cardillo *et al.* 2006). Thus, biological traits may to be more important than external factors for smaller species whereas larger species are influenced by a combination of environmental factors and intrinsic traits. Because the greatest threat to Mexican mammals is habitat loss, small bodied species of restricted distribution seem to be facing higher risks than larger-bodied, more widely distributed ones. In addition to this, small-mammals are often poisoned by humans because they are seen as pest that destroy crops and grazing land (Ceballos *et al.* 2002a).

7.4.3 Rarity, Endemicity and Extinction Risk

Endemicity, rarity and extinction risk show clear relationships with body size, range size and latitudinal distribution. These results are similar to findings for several taxonomic groups including mammals, fish and plants (Taylor and Gotelli 1994, Jones *et al.* 2003b, Pilgrim *et al.* 2004, Cardillo *et al.* 2005).One must be careful, however, because the criteria to classify a species as rare or widespread already include notions of endemicity and range size.

Concluding remarks

Because of the growing number of complete, detailed phylogenies, large bioinformatics databases (such as PanTHERIA, a database of mammals' life

history traits assembled by Jones and collaborators at www.biodiversitydata.group.cam.ac.uk/pantheria/data_outputs.html), and increasingly sophisticated methods of analysis, the comparative method is likely to be used with more frequency in conservation planning in the near future. This will help to identify sites and taxa that are likely to be vulnerable to a variety of human pressures. Identifying possible future environmental scenarios may then help to make predictions that allow more precise regional planning. For instance, incorporating "latent extinction risk" patterns into conservation planning could help guard against future biodiversity loss by anticipating and preventing species decline before it begins (Cardillo *et al.* 2006).

CHAPTER 8. GENERAL DISCUSSION

The present geological period has more species than any previous one, yet the current rate of extinction is greater now than at any time in the past (Primark 2002). In the past, major changes to the world's biota appear to have been driven by processes such as climate change, tectonic movements (leading to continental interchange), and even events of extra-terrestrial origin (as in the case of the K-T event). The current biodiversity crisis results primarily from processes almost exclusively derived from human activities that alter or destroy natural habitats. These processes (anthropogenic drivers) include rapid climate change, land use change, exploitation, pollution, pathogens, and the introduction of alien species (Perlman and Adelson 1997, Primark 2002, Gaston and Spicer 2004, Ricklefs 2004, Mace *et al.* 2005). Because of these anthropogenic drivers, whole ecosystems and communities are being degraded and destroyed while species are being driven to extinction. On the other hand, the species that persist are losing genetic variation as the number of individuals in their populations shrinks, unique populations and subspecies are destroyed, and the remaining populations become increasingly isolated from one another (Magurran 1988, Perlman and Adelson 1997, Primark 2002, Ricklefs 2004). In consequence, the conservation of biodiversity, including the conservation of essential ecological and evolutionary processes, is one of the most important issues in current biological research (Ferson and Burgman 2000, Mace *et al.* 2000, Pullin 2002, Balmford *et al.* 2005).

Biodiversity value has been identified as the option value for future use or the ability to evolve under changing circumstances (Hopkins *et al.* 2007). From this viewpoint, rather than investigating the genetic diversity of every species in a community, a simpler and most direct measure of species diversity could be devised by taking into account the taxonomic or phylogenetic diversity of the community (Williams *et al.* 1996a, Reyers *et al.* 2000, Faith *et al.* 2003). Estimates of phylogenetic diversity can be used in different ways to inform us of the potential impact of the current extinction crisis and to help inform policy makers of the best ways to ameliorate human impacts. Conservation policy makers must set priorities in the face of limited resources to minimize the impacts of the current human-caused extinction crisis.

Many conservation priority-setting exercises are area or species-based, focusing on distinctive areas or species to preserve as much biological diversity as possible (e.g., biodiversity hotspots; Myers *et al.*, 2000). Phylogenetic diversity is an attribute that is starting to be recognized as being important for conservation-policy decisions (Purvis *et al.* 2005b). For example, it is important to know if areas with larger numbers of species are also those with the highest phylogenetic diversity. Evidence suggests this is the case (Polasky *et al.* 2001, Sechrest *et al.* 2002), but more complete information for different taxonomic groups is needed to address this question comprehensively. Phylogenetic information can be used to indicate the processes that have created the pattern of current biodiversity. For example, the phylogeny could be used to differentiate between rapidly diversifying clades and ancient clades with little recent diversification.Combined with geographic information, the phylogenetic approach might then enable us to locate

and differentiate "cradles" and "museums" of diversity (Chown and Gaston 2000, Mace *et al.* 2003).

A most effective way of preserving biodiversity is by maintaining populations of native species in their natural ecosystems through the establishment of natural reserves (Margules and Pressey 2000, Cabeza and Moilanen 2001, Posadas *et al.* 2001). Ecologists typically want to know if one area is more diverse than another. This requires the development of appropriate concepts and methodology, as well as collection of the relevant data, to set long-term conservation priorities (systematic conservation planning;(Margules and Pressey 2000). It is unlikely that present reserves are sufficient to represent and to maintain the total variety of biodiversity (Margules and Pressey 2000), among other things because most current reserves were not chosen to meet specific biodiversity objectives (Pressey *et al.* 1996, Possingham *et al.* 2000). Nevertheless, the national systems of protected areas need to be carefully (re)designed if large gaps in the protection of biodiversity are to be avoided (Kerr, 1997). The steps to achieve this are: 1) compile information on the biodiversity of the region of interest; 2) select the criteria for measuring conservation value; 3) review existing conservation areas; 4) select additional areas which fill the gaps in the reserve network (i.e. where elements of biodiversity are not adequately protected); 5) implement conservation actions; and finally, 6) maintain the required values of conservation areas.

The purpose on this dissertation was then to quantify the biodiversity of mammals in Mexico and its distribution, and to identify areas of conservation value.

8.1 DATA GATHERING: BIODIVERSITY DATABASES

The first step in conservation is to gather relevant data; in this case, biodiversity databases from the National Commission on Biodiversity (CONABIO) were the sources of information on the distribution of species. Databases such as CONABIO's are becoming increasingly important in the study of the distribution of biodiversity (Webb *et al.* 2002, Magurran 2004). Their usefulness as tools for conservation, however, depends on the reliability of their information. Therefore, careful consideration to taxonomic and geographic accuracy is paramount (Allard *et al.* 1996, Golubov and Soberon 2003, Isaac *et al.* 2004, Hortal *et al.* 2007). The heterogeneous origin of these databases makes quality control even more important (Canhos *et al.* 2004, Soberon and Peterson 2004). A good understanding of errors and error propagation can lead to effective quality control and improvement. Nowadays, web-based tools for validating georeferences, taxonomic identifications, and collection dates (or at least for flagging records with high probabilities of error), such as The SpeciesLink (http://splink.cria.org.br/) and ORNIS (http://olla.berkeley.edu/ornisnet/) projects, are developing a number of data cleaning tools which are currently being tested and evaluated (Canhos *et al.* 2004, Soberon and Peterson 2004, Stein and Wieczoreck 2004)

The first attempt of this dissertation was to measure phylogenetic diversity for two groups of organisms with wide taxonomic and ecological diversity. Unfortunately, data validation (correct name and distribution) was unevenly achieved because of the dissimilar quantity of reliable information for the two biological groups chosen (mammals and seed plants). In spite of these differences, some specimen data errors were common for the three groups: wrong

spelling of taxa, synonymy, misidentification and errors in geo-referencing. Whereas there were some groups which were well known taxonomically, such as gymnosperms and mammals, for some angiosperm families the information was incomplete and not easily accessible. Databases were corrected and made as reliable as possible. Nonetheless, the amount of work required on the data for seed plants made it prohibitive to carry out equivalent analyses to those performed on the mammal dataset in the time available for this investigation. An important aspect highlighted by this study is the representativeness of the collections as significant areas of Mexico are still poorly represented. Thus, the geographic and ecological coverage of the study taxa was uneven. Systematic inventories and analyses of geographic, ecological, taxonomic and genetic diversity are needed to avoid this problem (Crisp *et al.* 2001, Navarro-Siguenza *et al.* 2002, Hortal *et al.* 2007).

Despite their imperfections, databases are the most useful tool to attempt to determine the distribution of species and its possible causes. They have proved effective to record information on the complex interactions that determine biodiversity, the effects of disease, pollution, agriculture, etc. (Knyazhnitskiy *et al.* 2000), as well as documenting species decline (Shaffer *et al.* 1998). Undoubtedly, information from museum specimens is invaluable in all aspects of the study and conservation of biological diversity (Parker *et al.* 1998, Golubov and Soberon 2003).

8.2 SETTING BIODIVERSITY CONSERVATION PRIORITIES: THE ROLE OF PHYLOGENY

In order to set priorities for conservation, it is necessary to define operational measures of biodiversity. The most popular measure of biodiversity used in conservation is *Species Richness* (Magurran 1988, Perlman and Adelson 1997). Recent work in conservation suggests that taking into account measures of the degree of relatedness of species in a sample (community, locality, region) may be a convenient surrogate of the more difficult to quantify component of genetic diversity (Vane-Wright *et al.* 1991, Vazquez and Gittleman 1998, Posadas *et al.* 2001, Sechrest *et al.* 2002, Mace *et al.* 2003, Purvis *et al.* 2005b). Phylogeny has become an important tool for conservation and for understanding of both the processes that have generated the current diversity and the processes that threaten it (Bininda-Emonds *et al.* 2000, Rodrigues and Gaston 2002a, Purvis *et al.* 2005b). Thus, Mace *et al.* (2003) strongly support the use of the measure of phylogenetic diversity (*PD*;(Faith 1992) as a "natural measure of biodiversity" and a convenient means to value it. In their view, areas that contain higher phylogenetic diversity (longer path length of the phylogenetic tree) merit conservation over less differentiated ones.

Two indices of phylogenetic diversity that take these ideas into account have been proposed: Phylogenetic Diversity: Phylogenetic Diversity (*PD*; Faith 1992) and Taxonomic Distinctiveness (*TD*; Clarke & Warwick 1998). These measures are based on phylogenetic information to estimate the length of the branch structure of the phylogenetic or taxonomic tree of a taxon of interest in a particular area, mammals in this dissertation. Mammals are a particularly relevant

group in the identification of priority areas for conservation because their ecological requirements make them good indicators of the wealth of ecological processes collectively known as functional diversity. Additionally, mammals are a taxonomically well understood taxon with immense popular appeal.

Both total and average measures of *PD* and *TD* were calculated, as well as the variation of TD. These indices required detailed taxonomic and/or phylogenetic information of the selected taxon. Two classifications were employed: a straightforward Linnaean taxonomy and a hypothetical phylogenetic supertree of Mexican mammals. To calculate those indices, species records were aggregated into approximately square cells in a geo-referenced latitude × longitude grid. In order to evaluate the effect that sampling intensity (completeness of data) had on the perceived (calculated) diversity, two scales were used: 30' × 30' (S30') and 10'×10' (S10').

Measures of biodiversity based on relatedness of species employing presence/absence data were successfully calculated. The resolution of the classification had a relatively small effect on the relationship between biodiversity and *S*. That means that, despite its simplicity, species richness explains a large proportion of the variation in biodiversity. Whereas values of *TD* for both scales employing either classification tend to overlap, the *PD(t)* curve diverges from the *PD(p)* one at both scales. Nonetheless, employing a taxonomic classification *TD(t)* and *PD(t)* produces more dispersion and higher values than *PD(p)* at both scales. Thus, the use of a phylogenetic classification is preferable over the use of a taxonomic classification. Both *TD* and *PD* increased faster at S30' than at S10'. *TD* showed linear relationships with *S* while *PD* approximated power relationships

with *S*, regardless of the classification employed. Both *TD* and *PD* showed wider dispersion when using a taxonomic classification than when employing a phylogenetic classification, at both scales. All relationships were strongly correlated (r^2>0.85; p<0.01).

Because total biodiversity indices (*PD* and *TD*) are correlated with Species Richness, they cannot possibly be independent of sampling effort. Unless completeness of records can be guaranteed (and this is unlikely ever to be the case) intermediate scales that balance ecological detail (spatial heterogeneity) with sampling effort (number of records) are preferable over large or small ones (Arita *et al.* 1997, Crisp *et al.* 2001, Bickford *et al.* 2004). A grid cell of 30' (S30'~2,835.77 km^2) worked reasonably well in this case. Moreover, a grid cell of 30' × 30' has been found to reduce the effect of bias in sampling effort, common in herbarium and museum data (Margules *et al.* 1994, Crisp *et al.* 2001, Chapman 2005), while still representing the variability of the phenomenon studied (Arita *et al.* 1997, Bickford *et al.* 2004). A larger one would lose ecological detail, while a smaller one would suffer from small sample size per cell.

This study also found that *AveTD* is not an indicator of diversity in the general sense of the word. It is a measure of heterogeneity of taxonomic or phylogenetic relatedness. On *AveTD* the use of phylogeny rather than taxonomy expressed more information on the relationship among samples. *AvePD* values decreased markedly as the number of species increased, indicating phylogenies tend to be more symmetrical as *S* increases. It would therefore be ambiguous to compare *AvePD* across studies with different levels of sampling effort. On the other hand, the results of the simulated 95% probability funnel plots of *AveTD*

showed that these were close to their observed means. The mean values of *AveTD* index for both scales and both classifications were indeed independent of sample size and the number of species, but were not independent of the type of classification (taxonomic *vs.* phylogenetic) employed. Such independence implies that, unlike *AvePD*, *AveTD* can be compared across studies with differing and uncontrolled degrees of sampling effort (Warwick *et al.* 2002). It also confirms that *AveTD* is not a surrogate of species richness.

The variability of *TD* (*VarTD*) is a consequence of the complexity of the phylogenetic or taxonomic tree. However, because museum records are always incomplete, it is difficult to separate the effect of phylogenetic complexity from the effect of the error produced by the incompleteness of the records. Alternative measures of variability may help shed light on the relative contribution of these two effects.

This dependency on sample size is true for both total and average measures (*PD*, *TD*, *AvePD* and *AveTD*). Supporters of the idea that Clarke and Warwick's *AveTD* index is preferable over (total) *PD* (von Euler and Svensson 2001, Bhat and Magurran 2006) are therefore mistaken when they say that *AveTD* is insensitive to sampling effort and should be preferred. On the other hand, supporters of *PD* are mistaken in their dismissal of *AveTD* based on the argument that it ignores the contribution that Species Richness makes to diversity. Both indices contain similar information: one can work "downwards" from (total) *PD* to *AvePD* or "upwards" from *AveTD* to (total) *TD*. Provided we compare like with like (*PD* with *TD*, *AveTD* with *AvePD*), these indices quantify, albeit with different

algorithms, essentially the same thing: either the total or average distance between species in the tree of life.

In summary, total Biodiversity Indices for Mexican mammals were highly correlated with Species Richness as they tend to follow species richness rather closely (Warwick and Clarke 2001). However, *PD* provided more information on the relatedness of the species making up an assemblage. The relationship between *PD* and *S* departed from linearity and the reason for this seems obvious: as sample size and *S* increase, the probability of adding higher taxonomic levels (say, a new order or family) decreases, while the probability of adding a new species of a higher taxa already in the sample increases. Thus, adding new species decreases their relative contribution to *PD* as species number gets larger. This is also why, by being built with different algorithms (either buttom-up or top-down), *PD* and *TD*, yield different results. Thus, although qualitatively similar, care must be taken in the use and interpretation of these two indices: they are not interchangeable. Finally, although closely correlated with *S*, *TD* and *PD* do add information and are therefore preferable over the simpler species-richness count.

This dissertation also looked at the effect that the shape of the phylogenetic tree produced on the values of *PD*. Local phylogenies varied from perfectly balanced (diversity skewness=0) to perfectly imbalanced (diversity skewness=1). Tree shape became more balanced as S (and *PD*) increased. The low Diversity Skweness found for richer local assemblages (those with high *S* and/or *PD*) may be due to the pervasiveness of rodent (the dominant Euarchontoglires order) and bat species (the dominant Laurasiatheria order), which tend to balance each other (see Fig 4.3). That is, areas with high *S*/*PD* will tend to be rich in rodents and bats

and, given that these two groups balance the tree, I_c will tend to be low. This pattern is the opposite of what other studies of global phylogenies have documented, where skewness increases with diversity at different phylogenetic scales (Mooers and Heard 1997, von Euler 2001, Purvis and Agapow 2002). Phylogenetic tree imbalance is thus assumed to be originated by differences in evolutionary rates within trees. However, tree incompleteness and low quality of data are also possible sources of imbalance (Mooers 1995, Stam 2002).

8.3 THE DISTRIBUTION OF BIODIVERSITY

Overall, the diversity of mammals measured as *S*, *PD*, and *TD* and endemic richness (*ESR)*, increased from the north to the south. Areas of high *TD* (mostly) corresponded to areas with high *S*, whereas areas with higher values of *PD* did not necessarily match with those areas with larger number of species. This means that, although with some coincidences, the distribution of *PD* and *TD* showed different patterns. Although conceptually similar, their different methods of calculation yield different answers. Thus, care must be taken in the use and interpretation of these two indices.

Once biodiversity indices were computed and analyzed, Faith's *PD*, calculated with a phylogenetic classification and using a scale of 30'×30', was chosen to identify areas of high diversity. Grid cells of high diversity (53 cells) hold 350 species from the sample. These grid cells were identified as high-priority areas. Cells with high *PD* values (distantly related species) were found across the TVB as well as in the Tropical region, predominantly in the States of Hidalgo,

Puebla, Veracruz, Oaxaca and Chiapas. The area of highest *PD* (and *S*) was found in the State of Oaxaca, on the boundaries between The Sierra Madre del Sur and The Gulf of Mexico Plateau. The main explanation for this distribution of *PD* is related to the geographical pattern that each mammal order displays in the country. Biogeographic features have influenced the geographical distribution on native mammals of Mexico. For instance, Orders Lagomorpha, Soricomorpha and Erinaceamorpha are more diverse in both the Central Plateau and TVB. Members of order Rodentia (the one with the larger number of species) are abundant on the Central Plateau, spreading from the north to the highlands of Chiapas. Orders Cingulata, Pilosa, Primates, Chiroptera and Perissodactyla, are mostly restricted to the tropical zones of the Yucatan Peninsula and the tropical coastal zones. Members of order Chiroptera are also diverse on the central part of the country and the TVB (Arita and Ceballos 1997, Fa and Morales 1998).

In addition, analysis of the correlation between diversity measures (*PD*, *TD* and *DS)* and some attributes from the environment (temperature, precipitation and altitude) were carried out. The results showed that while in some cases there is no apparent relation, for instance temperature, in others, e.g., precipitation, the "envelop" of the points in the scatterplot suggests limits to the values that these relations can have (See Table 6.4 and Appendix E). Both *PD* and *TD (*but also *S* and *ESR), show a* tendency to be higher in low and middle elevations.

Finally, Diversity Skewness (I_c) did not show any relation with environmental variables except precipitation, and local phylogenies tend to be more balanced at precipitations between 2300mm and 3300mm. Moreover, although there is not a clear relation between *DS* and Altitude, when the map of I_c

is superimposed onto the elevation map, balanced phylogenies tend to concentrate over The Sierra Madre del Sur and, further North, over The Sierra Madre Oriental.

Once areas of high phylogenetic diversity were identified, the correlation between traditional biodiversity surrogates (species richness, endemic species and threatened species) and phylogenetic diversity was explored. Levels of endemism were positively correlated with species richness as well as with *PD*. When considering latitude, the number of endemic species increases towards lower latitudes. Most rare species were distributed in the North of the Baja California Peninsula and in the South region of the country (mostly in the States of Oaxaca and Chiapas). 27.99% of the species were endemic (predominantly rodents), 18.8% narrow endemics and 21.37% threatened. There were 23 endemic species inhabiting the TVB, nine of them belonging to six endemic genera. The total number of species with narrow range size (rare) was110 (26.32%); these were mainly small mammals. As with endemics, most rare species are distributed in the North of the Baja California Peninsula and in the South region of the country (mostly in the States of Oaxaca and Chiapas). Although, at a global scale, rarity and threat do not tend to coincide (Grenyer *et al.* 2006), in this study 64.54% rare species are listed under some risk category. This may be due to the similarity of the criteria used to define both attributes. Threatened species were concentrated in the tropical regions of the country; most of them were endemic species too.

8.4 HIGH PRIORITY AREAS

The minimum number of grid cells needed to include all 416 species was 51. Endemic and rare species were fully represented in the complementary system. Complementary cells are spread across the country; 33.33% of them overlap with the distribution of high diversity areas and 17 complementary cells match the distribution of some NPAs.

The number of areas identified as high priority areas (HPA) was 85, as measured firstly in terms of high *PD* and complementarity and, secondly, on the number of endemic, rare and threatened species. The distribution of areas rich in endemic, rare and threatened species overlaps with those of high diversity or complementarity or both, predominantly in the tropical states. However, some rare species hotspots are included in the complementarity cells that are particularly relevant in the Baja California Peninsula. The map of HPA is shown in Figure 6.12.The position of 28 HPA apparently coincides with the distribution of 40 NPA in the reserve network. Those 40 NPAs are concentrated in the Centre and Transvolcanic Belt (TVB) CONANP region, and most of them are National Parks. The results showed that there were several NPAs in the reserve system that did not match the distribution of any area rich in *PD, S,* or some other biodiversity measure, nor do they overlap the distribution of any complementary area (except in northern Baja California). Those reserves are located in the northern states. On the other hand, more protected areas are needed in the states of Michoacán, Mexico, Puebla, Oaxaca, Veracruz and Tabasco, where the long-term persistence of high diversity is not yet assured.

Other studies have analysed the distribution of mammal diversity in Mexico. For instance, Escalante *et al.* (2003) conducted a Parsimony analysis of endemicity (PEA) for the terrestrial mammals of Mexico to identify areas of endemism. PEA is a biogeographical method that uses a parsimony algorithm to obtain an area cladogram, based on taxa inhabiting the area (Morrone and Escalante 2002). They recognized seven areas of importance in endemism: three of them in Baja California (BC1,BC2 and BC3); North High Plateau (NA), Chiapas (Ch), Isthmus (Is) and Yucatan Peninsula (YP). Some HPAs fall within these areas of high endemism.

The evaluation of the effectiveness of the Mexican network of reserves to represent high levels of mammal *PD* indicates that the SINANP does not yet cover a sufficiently representative proportion of areas worth conserving. Therefore, additional reserves are needed in the HPAs highlighted in chapter 6. Finally, it is important to be aware that, by themselves, reserves are not enough to ensure the long-term persistence of species., It is also necessary to understand the ecological and biological factors that maintain their populations. For this reason, studies using occurrence data should be complemented with population viability analysis, predictive habitat modelling, and more detailed inventories that provide information on the long-term abundance and health of populations.

It is important to highlight that the identification of HPAs employing collection records is no guarantee that the high diversity identified in some areas represents the current situation. These areas may have already suffered severe habitat transformation. An analysis that took into account the temporal component of diversity would be ideal, but no collection would have the level of temporal detail

that would be required. Prospecting the HPAs identified by this study to determine their current conservation status is simpler and more economical.

8.5 RELATIONSHIP BETWEEN LIFE HISTORY TRAITS, ENVIRONMENTAL AND BIOGEOGRAPHIC ATTRIBUTES AND BIODIVERSITY SURROGATES (ENDEMICITY, RARITY AND THREATEN)

The final part of the dissertation focused on the investigation of the species' life history characteristics as predictive measures of distribution and threat. There is evidence in the literature that life-history may predispose some species to rarity and extinction risk (Martins 2000, Pilgrim *et al.* 2004).

Body size is one of the most fundamental ecological parameters, correlating with many other life-history attributes (Fa and Purvis 1997, Pyron 1999, Murray and Dickman 2000, Orme *et al.* 2002, Lovegrove and Haines 2004, Isaac *et al.* 2005) and this was found to be the case here too. Large size species have bigger neonates, later weaning, later maturity, small litters and low litters per year than small sized species. Similarly, large species have lower reproductive rates and longer life expectancy than small sized species. This pattern agrees with the general tendency in mammals of an inverse relationship between reproductive rate (age at maturity, litter size, frequency of reproduction) and body size (Read and Harvey 1989, Millar and Hickling 1991). Although these correlations were all significant, considerable variation was evident; resulting in strong correlations among body weight traits and weak correlations with survival- and litter-related traits. Finally, although body size tended to decrease towards lower latitudes, body

size did not appear to be correlated with either latitude or any of the environmental attributes considered in this study.

Range size was significantly positively correlated with latitude and altitude. In other words, species that present larger geographic range sizes tend to have the midpoint of their distribution towards higher latitudes. The same relationship has been documented in other studies and it has been suggested that decreasing latitudinal range size towards the equator (Rapoport's Rule) increases species richness in the tropics (Stevens 1989). Similarly, latitudinal variation among species in life-history traits is often suggested to contribute to high tropical species richness (Cardillo 2002). In the present study, mammals' life-history traits showed more variation towards the lower latitudes. This coincides with the distribution of Phylogenetic Diversity, where values of high diversity tend to be concentrated towards lower latitudes.

Positive interspecific relationships between body size and geographical range size have been documented in areas holding the complete ranges of most, if not all, study species; whereas at smaller-scale studies tend to reveal both positive and negative relationships with equal frequency (Gaston and Blackburn 1996b). Since the present study was carried out at a national scale, and is intended to cover "complete" species ranges of continental mammals, the results of our study indicate that Mexican mammals do not fit this generalisation for body size-range size relationships.

The ecological-evolutionary characteristics associated with endemic/ rare species were small body size and small geographic range, whereas the most likely

candidates for extinction were those species with large body size and small range sizes. The results of the test for correlations between body size and both endemicity and rarity revealed that larger-bodied species tend to be non-endemic and widespread. On the contrary, most small body size species were endemic and rare. Association between body size and range size revealed that larger species have larger range sizes than small species: endemic and rare species are small bodied and show small range size. Relationships of body size, range size and risk category show that large size and smaller geographic ranges characterise those species prone to extinction. These results are similar to findings in other taxonomic groups including mammals, fish and plants (Taylor and Gotelli 1994, Jones *et al.* 2003b, Pilgrim *et al.* 2004, Cardillo *et al.* 2005).

8.6 FURTHER STUDIES

It would be of interest to explore the patterns found in this study in other taxonomic groups. In particular, given the role of plants as providers of the energy for the whole ecosystem, investigating the relationship between the distribution of their phylogenetic diversity and that of mammals would provide evidence as to the drivers of diversity at different levels of the food web. Similarly, ecological niche modelling for a variety of plant and animal groups would provide valuable information on the possible impacts of global climate change on biodiversity. The integration of these tools with Population Viability Analysis (PVA) of key species would enable us to explore more detailed, targeted management strategies to safeguard our otherwise irreplaceable biodiversity.

REFERENCES

Ackerly, D. D. 2000. Taxon sampling, correlated evolution, and independent contrasts. Evolution **54**:1480-1492.

Adkins, R. M., A. H. Walton, and R. L. Honeycutt. 2003. Higher-level systematics of rodents and divergence time estimates based on two congruent nuclear genes. Molecular Phylogenetics and Evolution **26**:409-420.

Agapow, P. M., O. R. P. Bininda-Emonds, K. A. Crandall, J. L. Gittleman, G. M. Mace, J. C. Marshall, and A. Purvis. 2004. The impact of species concept on biodiversity studies. Quarterly Review of Biology **79**:161-179.

Agapow, P. M., and N. J. B. Isaac. 2002. MacroCAIC: revealing correlates of species richness by comparative analysis. Diversity and Distributions **8**:41-43.

Agapow, P. M., and A. Purvis. 2002. Power of eight tree shape statistics to detect nonrandom diversification: A comparison by simulation of two models of cladogenesis. Systematic Biology **51**:866-872.

Alexander, L. F., and B. R. Riddle. 2005. Phylogenetics of the new world rodent family heteromyidae. Journal of Mammalogy **86**:366-379.

Allard, M. W., B. E. McNiff, and M. M. Miyamoto. 1996. Support for interordinal eutherian relationships with an emphasis on primates and their Archontan relatives. Molecular Phylogenetics and Evolution **5**:78-88.

Arita, H. T. 1993. Rarity in Neotropical bats - Correlations with phylogeny, diet, and body-mass. Ecological Applications **3**:506-517.

Arita, H. T., and G. Ceballos. 1997. The mammals of Mexico: distribution and conservation status. Revista Mexicana de Mastozoología **2**:33-71.

Arita, H. T., and F. Figueroa. 1999. Geographic patterns of body-mass diversity in Mexican Mammals. Oikos **85**:310-319.

Arita, H. T., F. Figueroa, A. Frisch, P. Rodriguez, and K. SantosDelPrado. 1997. Geographical range size and the conservation of Mexican mammals. Conservation Biology **11**:92-100.

Arita, H. T., and P. Rodriguez. 2004. Patrones geográficos de diversidad de los mamíferos terrestres de América del Norte. Base de datos SNIB-Conabio proyecto Q068. Instituto de Ecología, UNAM-CONABIO.

Arnason, U., J. A. Adegoke, K. Bodin, E. W. Born, Y. B. Esa, A. Gullberg, M. Nilsson, R. V. Short, X. F. Xu, and A. Janke. 2002. Mammalian mitogenomic relationships and the root of the eutherian tree. Proceedings of the National Academy of Sciences of the United States of America **99**:8151-8156.

Balmford, A., P. Crane, A. Dobson, R. E. Green, and G. M. Mace. 2005. The 2010 challenge: Data availability, information needs and extraterrestrial insights. Philosophical Transactions of the Royal Society B-Biological Sciences **360**:221-228.

Balmford, A., A. H. M. Jayasuriya, and M. J. B. Green. 1996. Using higher-taxon richness as a surrogate for species richness .2. Local applications. Proceedings of the Royal Society of London Series B-Biological Sciences **263**:1571-1575.

Balmford, A., A. J. E. Lyon, and R. M. Lang. 2000. Testing the higher-taxon approach to conservation planning in a megadiverse group: the macrofungi. Biological Conservation **93**:209-217.

Barker, G. M. 2002. Phylogenetic diversity: a quantitative framework for measurement of priority and achievement in biodiversity conservation. Biological Journal of the Linnean Society **76**:165-194.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. Journal of Applied Ecology **43**:413–423.

Beintema, J. J., H. J. Breukelman, J. F. Dubois, and H. W. Warmels. 2003. Phylogeny of ruminants secretory ribonuclease gene sequences of pronghorn (*Antilocapra americana*). Molecular Phylogenetics and Evolution **26**:18-25.

Bell, D. M., M. J. Hamilton, C. W. Edwards, L. E. Wiggins, R. M. Martinez, R. E. Strauss, R. D. Bradley, and R. J. Baker. 2001. Patterns of karyotypic megaevolution in *Reithrodontomys:* evidence from a cytochrome-b phylogenetic hypothesis. Journal of Mammalogy **82**:81-91.

Bennett, P. M., and I. P. F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society B: Biological Sciences **264**:401-408.

Bennett, P. M., and I. P. F. Owens. 2002. Life histories, mating systems and extinction. Oxford University Press, Oxford.

Bhat, A., and A. E. Magurran. 2006. Taxonomic distinctness in a linear system: a test using a tropical freshwater fish assemblage. Ecography **29**:104-110.

Bickford, S. A., S. W. Laffan, R. P. J. Kok, and L. A. Orthia. 2004. Spatial analysis of taxonomic and genetic patterns and their potential for understanding evolutionary histories. Journal of Biogeography **31**:1715-1733.

Bielby, J., G. M. Mace, O. R. P. Bininda-Emonds, M. Cardillo, J. L. Gittleman, K. E. Jones, C. D. L. Orme, and A. Purvis. 2007. The fast-slow continuum in mammalian life history: An empirical reevaluation. The American Naturalist **169**:748-757.

Bininda-Emonds, O. R. P. 2004. The evolution of supertrees. Trends in Ecology and Evolution **19**:315-322.

Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise of present-day mammals. Nature **446**:507-512.

Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biological Reviews of the Cambridge Philosophical Society **74**:143-175.

Bininda-Emonds, O. R. P., D. P. Vazquez, and L. L. Manne. 2000. The calculus of biodiversity: integrating phylogeny and conservation. Trends in Ecology and Evolution **15**:92-94.

Blackburn, T. M., and K. J. Gaston. 1998. Some methodological issues in macroecology. The American Naturalist **151**:68-83.

Blum, M. G. B., and O. Francois. 2006. Which random processes describe the Tree of Life? A large-scale study of phylogenetic tree imbalance. Mathematical Biosciences **195**:1-16.

Bonn, A., A. S. L. Rodrigues, and K. J. Gaston. 2002. Threatened and endemic species: are they good indicators of patterns of biodiversity on a national scale? Ecology Letters **5**:733-741.

Bottu, G., and M. Van Ranst. 2003. Sequence databases: Theory. Pages 24-36 *in* M. Salemi and A.-M. Vandamme, editors. The Phylogenetic Handbook. A practical approach to DNA and protein Phylogeny. Cambridge University Press, Cambridge.

Bradley, R. D., C. W. Edwards, D. S. Carroll, and C. W. Kilpatrick. 2004. Phylogenetic Relationships of Neotomine-Peromyscine Rodents: based on DNA sequences from the mitochondrial cytochrome-b gene. Journal of Mammalogy **85**:389-395.

Brashares, J. S. 2003. Ecological, Behavioral, and Life-History Correlates of Mammal Extinctions in West Africa. Conservation Biology **17**:733-743.

Brooks, D. R., R. L. Mayden, and D. A. MacLennan. 1992. Phylogeny and Biodiversity: conserving our evolutionary legacy. Trends in Ecology and Systematics. **7**:55-59.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, Ecology and Behavior. A research program in comparative biology. The University of Chicago Press, Chicago.

Brooks, T. M., R. A. Mittermeier, G. D. A. d. Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. Rodrigues. 2006. Global biodiversity conservation priorities. Science **313**:58-61.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat Loss and Extinction in the Hotspots of Biodiversity. Conservation Biology **16**:909-923.

Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages - effects of energetic constraints and species dynamics on the diversification of the north-american avifauna. The American Naturalist **130**:1-17.

Brummitt, N., and E. N. Lughadha. 2003. Biodiversity: Where's hot and where's not. Conservation Biology **17**:1442-1448.

Cabeza, M. 2003. Habitat loss and connectivity of reserve networks in probability approaches to reserve design. Ecology Letters **6**:665-672.

Cabeza, M., and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. Trends in Ecology and Evolution **16**:242-248.

Caley, J., and D. Schulter. 1997. The relationship between local and regional diversity. Ecology **78**:70-80.

Canhos, V. P., S. C. Souza, R. Giovanni, and D. A. L. Canhos. 2004. Global Biodiversity Informatics: Setting the scene for a "New World" of ecological Modelling. Biodiversity Informatics **1**:1-13.

Cantu, C., G. Wright, J. M. Scott, and E. Strand. 2004. Assessment of current and proposed nature reserves of Mexico based on their capacity to protect geophysical features and biodiversity. Biological Conservation **115**:411-417.

Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. Proceedings of the Royal Society of London Series B-Biological Sciences **266**:1221-1225.

Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? Journal of Animal Ecology **71**:79-87.

Cardillo, M., G. M. Mace, J. L. Gittleman, and A. Purvis. 2006. Latent extinction risk and the future battlegrounds of mammal conservation. PNAS **103**:4157-4161.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science **309**:1239-1241.

Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M. Mace. 2004. Human population density and extinction risk in the world's carnivores. Plos Biology **2**:909-914.

Carstens, B. C., B. L. Lundrigan and P Myers. 2002. A phylogeny of the neotropical nectar-feeding bats (Chiroptera: Phyllostomidae) based on morphological and molecular data. Journal of Mammalian Evolution **9**:23-53.

CBD. 1996. Convention on Biological Diversity: Practical approaches for capacity building for Taxonomy. Second Meeting. Subsidiary body on scientific, technical and technological advice.

Ceballos, G. 2007. Conservation priorities for mammals in megadiverse Mexico: The efficiency of reserve networks. Ecological Applications **17**:569-578.

Ceballos, G., J. Arroyo-Cabrales, and R. A. Medellin. 2002a. Mamiferos de Mexico.*in* G. Ceballos and J. A. Simonetti, editors. Diversidad y Conservacion de los Mamiferos Neotropicales. CONABIO-UNAM, Mexico, D. F.

Ceballos, G., J. Arroyo-Cabrales, and R. A. Medellín. 2002b. The mammals of México: composition, distribution, and conservation. . Occasional Papers. Museum of Texas Tech University **218**:1-27.

Ceballos, G., P. Rodriguez, and R. A. Medellin. 1998. Assessing conservation priorities in megadiverse Mexico: Mammalian diversity, endemicity, and endangerment. Ecological Applications **8**:8-17.

Cervantes, F. A., C. Lorenzo, and T. L. Yates. 2002. Genic variation in populations of Mexican lagomorphs. Journal of Mammalogy **83**:1077-1086.

Chapman, A. D. 2005. Uses of primary species-occurrence data. version 1.0, Global Biodiversity Information Facility, Copenhagen.

Chown, S. L., and K. J. Gaston. 2000. Areas, cradles and museums: the latitudinal gradient in species richness Trends in Ecology and Evolution **15**:311-315.

Clarke, K., and R. Warwick. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology **35**:523-531.

Clarke, K. R., and R. N. Gorley. 2001. PRIMER v5: User manual/tutorial. PRIMER-E, Plymouth, UK.

Clarke, K. R., and R. M. Warwick. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology-Progress Series **216**:265-278.

Colwell, R. K. 1996. BIOTA. The biodiversity database manager. Sinauer Associates, Inc, Sunderland, Massachusetts.

Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R. K., C. X. Mao, and B. H. J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology **85**:2717-2727.

CONABIO. 2005. Comision Nacional para el Conocimiento y Uso de la biodiversidad en Mexico.

Conroy, C. J., and J. A. Cook. 2000. Molecular Systematics of Holartic Rodent (*Microtus*:Muridae) Journal of Mammalogy **81**:344-359.

Cook, J. A., A. M. Runck, and C. J. Conroy. 2004. Historical biogeography at the crossroads of the northern continents: molecular phylogenetics of red-backed voles (Rodentia: Arvicolinae). Molecular Phylogenetics and Evolution **30**:767-777.

Coppolillo, P., H. Gomez, F. Maisels, and R. Wallace. 2004. Selection criteria for suites of landscape species as a basis for site-based conservation. Biological Conservation. **115**:419-430.

Cowling, R. M., R. Pressey, M. Rouget, and A. T. Lombard. 2003. A conservation plan for a global biodiversity hotspot - the Cape Floristic Region, South Africa. Biological Conservation **112**:147-167.

Crisp, M. D., S. Laffan, H. P. Linder, and A. Monro. 2001. Endemism in the Australian Flora. Journal of Biogeography **28, pp.** :183-198.

Crozier, R. H. 1997. Preserving the information content of species: Genetic diversity, phylogeny, and conservation worth. Annual Review of Ecology and Systematics **28**:243-268.

Crozier, R. H., P. M. Agapow, and L. J. Dunnet. 2006. Conceptual issues in phylogeny and conservation: a reply to Faith and Baker. Evolutionary Bioinformatics Online **2**:197-199.

Crozier, R. H., L. J. Dunnett, and P. M. Agapow. 2005. Phylogenetic biodiversity assessment based on systematic nomenclature. Evolutionary Bioinformatics Online **1**:1-36.

Cruz-Neto, A. P., T. Garland, and A. Shinya-Abe. 2001. Diet, phylogeny, and basal metabolic rate in phyllostomid bats. Zoology **104**:49-58.

Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, A. R. Kiester, B. Downs, R. Hamilton, M. Huso, and K. Sahr. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biological Conservation **80**:83-97.

D'Elia, G. 2003. Phylogenetics of sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics-the International Journal of the Willi Hennig Society **19**:307-323.

Darwin, C. 1859. On the origin of the species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

Daugherty, C. H., A. Cree, J. M. Hay, and M. B. Thompson. 1990. Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). Nature **347**:177-179.

Davies, R. G., C. D. L. Orme, A. J. Webster, K. E. Jones, T. M. Blackburn, and K. J. Gaston. 2007. Environmental predictors of global parrot (Aves: Psittaciformes) species richness and phylogenetic diversity. Global Ecology and Biogeography **16**:220-233.

DeBry, R. W. 2003. Identifying conflicting signal in a multigene analysis reveals a highly resolved tree: The phylogeny of Rodentia (Mammalia). Systematic Biology **52**:604-617.

DeBry, R. W., and R. M. Sagel. 2001. Phylogeny of Rodentia (mammalia) inferred from the nuclear- encoded gene IRBP. Molecular Phylogenetics and Evolution **19**:290-301.

Delsuc, F., F. M. Catzeflis, M. J. Stanhope, and E. J. P. Douzery. 2001. The evolution of armadillos, anteaters and sloths depicted by nuclear and mitochondrial phylogenies: implications for the status of the enigmatic fossil Eurotamandua. Proceedings of the Royal Society of London Series B-Biological Sciences **268**:1605-1615.

Delsuc, F., M. Scally, O. Madsen, M. J. Stanhope, W. W. de Jong, F. M. Catzeflis, M. S. Springer, and E. J. P. Douzery. 2002. Molecular phylogeny of living xenarthrans and the impact of character and taxon sampling on the placental tree rooting. Molecular Biology and Evolution **19**:1656-1671.

Demastes, J. W., T. A. Spradling, M. S. Hafner, D. J. Hafner, and D. L. Reed. 2002. Systematics and phylogeography of pocket gophers in the genera Cratogeomys and Pappogeomys. Molecular Phylogenetics and Evolution **22**:144-154.

Demboski, J. R., and J. A. Cook. 2003. Phylogenetic diversification within the *Sorex cinereus* (Soricidae). Journal of Mammalogy **84**:144-158.

Diniz-Filho, J. A. 2004. Macroecology and the hierarchical expansion of evolutionary theory. Global Ecology and Biogeography **13**:1-5.

Diniz-Filho, J. A., P. Carvalho, L. M. Bini, and N. M. Tôrres. 2005. Macroecology, geographic range size-body size relationship and minimum viable population analysis for new world carnivora. Acta Oecologica-International Journal of Ecology **27**:25-30.

Douady, C., N. Carels, O. Clay, F. Catzeflis, and G. Bernardi. 2000. Diversity and Phylogenetic Implications of CsCl Profiles from Rodent DNAs. Molecular Phylogenetics and Evolution **17**:219-230.

Doughty, P. 1996. Statistical analysis of natural experiments in evolutionary biology: Comments on recent criticisms of the use of comparative methods to study adaptation. The American Naturalist **148**:943-956.

Dragoo, J., R., and R. L. Honeycutt. 1997. Systematics of mustelid-like carnivores. Journal of Mammalogy **78**:426-443. .

Earle, C. J. 1997. Gymnosperms Database. http://www.conifers.org.

Edwards, C. W., and R. D. Bradley. 2001. Molecular phylogenetics of the *Neotoma floridana* species group. Journal of Mammalogy **82**:791-798.

ERIN. 1999. Environmental Resources Information Network. http://www.environment.gov.au/erin/. Australian Goverment. Department of the Environment and Water Resources.

Ernest, S. K. M. 2003. Life history characteristics of placental non-volant mammals. Ecology **84**:3402.

Escalante, T., D. Espinosa, and J. J. Morrone. 2003. Using parsimony analysis of endemicity to analyze the distribution of Mexican land mammals. Southwestern Naturalist **48**:563-578.

ESRI. 2004. ArcGIS 9.1.

Fa, J. E., and S. M. Funk. 2007. Global endemicity centres for terrestrial vertebrates: an ecoregions approach. Endangered Species Research **3**:31-42.

Fa, J. E., and L. M. Morales. 1998. Patrones de Diversidad de Mamiferos de Mexico. Pages 315-351 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. E. Fa, editors. Diversidad Biologica de Mexico. Instituto de Biologia. UNAM, Mexico, D. F.

Fa, J. E., and A. Purvis. 1997. Body size, diet and population density in afrotropical forest mammals: A comparison with neotropical species. Journal of Animal Ecology **66**:98-112.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation **61**:1-10.

Faith, D. P. 1994. Genetic diversity and taxonomic priorities for conservation. Biological Conservation **68**:69-74.

Faith, D. P. 1996. Conservation priorities and phylogenetic pattern. Conservation Biology **10**:1286-1289.

Faith, D. P. 2003. Biodiversity conservation and the tree-of-life. Science. **300**:Published E-Letter responses,1-3.

Faith, D. P., and A. M. Baker. 2006. Phylogenetic diversity (PD) and biodiversity conservation: some bioinformatics challenges. Evolutionary Bioinformatics Online **2**.

Faith, D. P., G. Carter, G. Cassis, S. Ferrier, and L. Wilkie. 2003. Complementarity, biodiversity viability analysis, and policy- based algorithms for conservation. Environmental Science & Policy **6**:311-328.

Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist **125**:1-15.

Ferguson, S. H., and S. Lariviere. 2002. Can comparing life histories help conserve carnivores? Animal Conservation **5**:1-12.

Ferrusquia-Villafranca, I. 1998. Geologia de Mexico: una sinopsis. Pages 3-108 *in* T. P. Rammamoorthy, R. Bye, A. Lot, and J. E. Fa, editors. Diversidad Biologica de Mexico. Instituto de Biologia. UNAM, Mexico, D.F.

Ferson, S., and M. A. Burgman. 2000. Quantitative Methods for Conservation Biology. Springer-Verlag, New York.

Fisher, D. O., and I. P. F. Owens. 2004. The comparative method in conservation biology. Trends in Ecology & Evolution **19**:391-398.

Fjeldsa, J. 2000. The relevance of systematics in choosing priority areas for global conservation. Environmental Conservation **27**:67-75.

Flynn, O. J., J. A. Finarelli, S. Zehr, J. Hsu, and M. A. Nedbal. 2005. Molecular Phylogeny of the Carnivora (Mammalia): Assessing the Impact of Increased Sampling on Resolving Enigmatic Relationships. Systematic Biology **54**:317-337.

Flynn, O. J., and M. A. Nedbal. 1998. Phylogeny of the Carnivora (Mammalia): Congruence vs incompatibility among multiple data sets. Molecular Phylogenetics and Evolution **9:**:414-426.

Franco, M., and J. Silvertown. 1996. Life history variation in plants: An exploration of the fast-slow continuum hypothesis. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **351**:1341-1348.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: A test and review of evidence. The American Naturalist **160** 712–726.

Freitag, S., and A. S. Van Jaarsveld. 1998. Sensitivity of selection procedures for priority conservation areas to survey extent, survey intensity and taxonomic knowledge. Proceedings of the Royal Society of London Series B-Biological Sciences **265**:1475-1482.

Freitag, S., A. S. vanJaarsveld, and H. C. Biggs. 1997. Ranking priority biodiversity areas: An iterative conservation value-based approach. Biological Conservation **82**:263-272.

Garland, T. J., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology **41**:18-32.

Gaston, K. J. 1996a. Biodiversity:a biology of the numbers and differences. Blackwell Science, Oxford.

Gaston, K. J. 1996b. Species-range-size distributions: Patterns, mechanisms and implications. Trends in Ecology and Evolution **11**:197-201.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature **405**:220-227.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford.

Gaston, K. J., and T. M. Blackburn. 1996a. Global scale macroecology: Interactions between population size, geographic range size and body size in the Anseriformes. Journal of Animal Ecology **65**:701-714.

Gaston, K. J., and T. M. Blackburn. 1996b. Range size body size relationships: Evidence of scale dependence. Oikos **75**:479-485.

Gaston, K. J., and J. I. Spicer. 1998. Biodiversity: An Introduction. Blackwell Science, Oxford.

Gaston, K. J., and J. I. Spicer. 2004. Biodiversity. An introduction. 2nd edition. Blackwell Publishing, Oxford.

Gaston, K. J., and P. C. Williams. 1996. Spatial patterns in taxonomic diversity. Pages 202-229 *in* K. J. Gaston, editor. Biodiversity:a biology of the numbers and difference. Blackwell Scince.

Geisler, J. H. 2001. New morphological evidence for the phylogeny of Artiodactyla, Cetacea, and Mesonychidae. American Novitates **3344**:1-53.

Gittleman, J. L., and A. Purvis. 1998. Body size and species-richness in carnivores and primates. Proceedings of the Royal Society of London Series B-Biological Sciences **265**:113-119.

Golubov, J., and J. Soberon. 2003. Bioinformatics methods in the planning of collecting efforts in Mexico. The international Newsletterof the partners of the Millenium Seed Bank Project **4**:1-2.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution **19**:497-503.

Graur, D., L. Duret, and M. Gouy. 1996. Phylogenetic position of the order Lagomorpha (rabbits, hares and allies). Nature **379**:333-335.

Graur, D., M. Gouy, and L. Duret. 1997. Evolutionary affinities of the order Perissodactyla and the phylogenetic status of the superordinal taxa Ungulata and Altungulata. Molecular Phylogenetics and Evolution **7**:195-200.

Grenyer, R., C. D. L. Orme, S. F. Jackson, G. H. Thomas, R. G. Davies, T. J. Davies, K. E. Jones, V. A. Olson, R. S. Ridgely, P. C. Rasmussen, T. S. Ding, P. M. Bennett, T. M. Blackburn, K. J. Gaston, J. L. Gittleman, and I. P. F. Owens. 2006. Global distribution and conservation of rare and threatened vertebrates. Nature **444**:93-96.

Grenyer, R., and A. Purvis. 2003a. A composite species-level phylogeny of the 'Insectivora' (Mammalia : Order Lipotyphla Haeckel, 1866). Journal of Zoology **260**:245-257.

Grenyer, R., and A. Purvis. 2003b. A composite species-level phylogeny of the 'Insectivora' (Mammalia:Order Lipotyphla Haeckel, 1866). Journal of Zoology **260**:245-257.

Hafner, M. S., T. A. Spradling, J. E. Light, D. J. Hafner, and J. R. Demboski. 2004. Systematic revision of pocket gophers of the *Cratogeomys gymnurus* species group. Journal of Mammalogy **85**:1170-1183.

Hafner, M. S., P. D. Sudman, F. X. Villablanca, T. A. Spradling, J. W. Demastes, and S. A. Nadler. 1994. Disparate Rates of Molecular Evolution in Cospeciating Hosts and Parasites. Science **265**:1087-1090.

Halanych, K. M., J. R. Demboski, B. J. van Vuuren, D. R. Klein, and J. A. Cook. 1999. Cytochrome b phylogeny of North American hares and jackrabbits (*Lepus*, Lagomorpha) and the effects of saturation in outgroup taxa. Molecular Phylogenetics and Evolution **11**:213-221.

Halanych, K. M., and T. J. Robinson. 1997. Phylogenetic relationships of cottontails (*Sylvilagus*, Lagomorpha): Congruence of 12S rDNA and cytogenetic data. Molecular Phylogenetics and Evolution **7**:294-302.

Harper, J. L., and D. L. Hawksworth. 1995. Preface. Pages 5-12 *in* D. L. Hawksworth, editor. Biodiversity: measurement and estimation. Chapman and Hall., London.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, New York.

Hassanin, A., and E. J. P. Douzery. 2003. Molecular and morphological phylogenies of ruminants, and the alternative position of the Moschidae. Systematic Biology **52** 206-228.

Heard, S. B. 1992. Patterns in tree balance among cladistic, phenetic and randomly generated phylogenetic trees. Evolution **46**:1818-1826.

Heard, S. B., and G. H. Cox. 2007. The shapes of phylogenetic trees of clades, faunas, and local assemblages: exploring spatial pattern in differential diversification. The American Naturalist **169**:E-Article.

Heard, S. B., and A. O. Mooers. 2000. Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. Proceedings of the Royal Society of London Series B-Biological Sciences **267**:613-620.

Helgen, K. M. 2003. Major mammalian clades: a review under consideration of molecular and palaeontological evidence. Mammalian Biology **68**:1-15.

Helmus, M. R., T. J. Bland, C. K. Williams, and A. R. Ives. 2007. Phylogenetic measures of biodiversity. The American Naturalist **169**

E-Article.

Hendricks, J., K. Hill, R. Osborne and D. Stevenson. 1998. The Cycad Page. http://plantnet.rbgsyd.nsw.gov.au/PlantNet/cycad/.

Hernadez-Fernandez, M., and E. Urba. 2005. A complete estimate of the phylogenetic relationships in Rumiantia: a dated species-level supertree on the extant rumiants. Biological Reviews of the Cambridge Philosophical Society **80**:269-302.

Herron, M. D., T. A. Castoe, and C. L. Parkinson. 2004. Sciurid phylogeny and the paraphyly of Holarctic groundsquirrels (*Spermophilus*). Molecular Phylogenetics and Evolution **31**:1015-1030.

Heywood, V. H., I. Baste, B. Dias, R. Gamez, T. Janetos, W. V. Reid, and G. Ruark, editors. 1995. Global Biodiversity Assessment: Summary for Policy-Makers. UNEP and Cambridge University Press, Melbourne, Australia.

Hijmans, R., L. Guarino, C. Bussink, P. Mathur, M. Cruz, I. Barrantes, and E. Rojas. 2004. DIVA-GIS. A geographic information system for the analysis of biodiversity data.

Hijmans, R., L. Guarino, C. Bussink, P. Mathur, M. Cruz, I. Barrantes, and E. Rojas. 2005. DIVA-GIS. A geographic information system for the analysis of biodiversity data. Manual. International Potato Center, Lima, Peru.

Hijmans, R. J., and D. M. Spooner. 2001. Geographic distribution of wild potato species. Am. J. Bot. **88**:2101-2112.

Hill, K., R. Osborne, and D. Stevenson. 2004. The Cycad Pages. http://plantnet.rbgsyd.gov.au/PlantNet/cycad. Royal Botanical Garden, Sidney.

Hopkins, J. J., H. M. Allison, C. A. Walmsley, M. Gaywood, and G. Thurgate. 2007. Conserving biodiversity in a changing climate: guidance on building capacity to adapt. DEFRA and the UK Biodiversity Partnership.

Hortal, J., J. Lobo, and A. Jimenez-Valverde. 2007. Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. Conservation Biology **21**:853-863.

Huchon, D., F. M. Catzeflis, and E. J. P. Douzery. 2000. Variance of molecular datings, evolution of rodents and the phylogenetic affinities between Ctenodactylidae and Hystricognathi. Proceedings of the Royal Society of London Series B-Biological Sciences **267**:393-402.

Huchon, D., and E. J. P. Douzery. 2001. From the old world to the new world: A molecular chronicle of the phylogeny and biogeography of Hystricognath rodents. Molecular Phylogenetics and Evolution **20**:238-251.

Huchon, D., O. Madsen, M. Sibbald, K. Ament, M. J. Stanhope, F. Catzeflis, W. W. de Jong, and E. J. P. Douzery. 2002. Rodent phylogeny and a timescale for the evolution of glires: Evidence from an extensive taxon sampling using three nuclear genes. Molecular Biology and Evolution **19**:1053-1065.

Hudelot, C., V. Gowri-Shankar, H. Jow, M. Rattray, and P. G. Higgs. 2003. RNA-based phylogenetic methods: application to mammalian mitochondrial RNA sequences. Molecular Phylogenetics and Evolution **28**:241-252.

Humphries, C. J., P. H. Williams, and R. I. Vane-Wright. 1995. Measuring biodiversity value for conservation. Annual Review of Ecology and Systematics **26**:93-111.

InfoNature. 2004. Species Index: Class Mammalia. http://www.natureserve.org/infonatura/.

Isaac, N. J. B., K. E. Jones, J. L. Gittleman, and A. Purvis. 2005. Correlates of species richness in mammals: Body size, life history, and ecology. The American Naturalist **165**:600-607.

Isaac, N. J. B., J. Mallet, and G. M. Mace. 2004. Taxonomic inflation: its influence on macroecology and conservation. Trends in Ecology and Evolution **19**:464-469.

IUCN. 2001. Red List Categories and Criteria : Version 3.1. IUCN Species Survival Commission. Gland, Switzerland and Cambridge.

Jones, K. E., O. R. P. Bininda-Emonds, and J. L. Gittleman. 2005a. Bats, Clocks, and Rocks: Diverisfication Patterns in Chiroptera. Evolution **59**:2243-2255.

Jones, K. E., and A. Purvis. 1997. An optimum body size for mammals? Comparative evidence from bats. Functional Ecology **11**:751-756.

Jones, K. E., A. Purvis, and J. L. Gittleman. 2003a. Biological correlates of extinction risk in bats. American Naturalist **161**:601-614.

Jones, K. E., A. Purvis, and J. L. Gittleman. 2003b. Biological correlates of extinction risk in bats. The American Naturalist **161**:601-614.

Jones, K. E., A. Purvis, A. MacLarnon, O. R. P. Bininda-Emonds, and N. B. Simmons. 2002. A phylogenetic supertree of the bats (Mammalia : Chiroptera). Biological Reviews **77**:223-259.

Jones, K. E., W. Sechrest, and J. Gittleman. 2005b. Age and area revisited: identifying global patterns and implications for conservation. Pages 141-165 *in* A. Purvis, J. Gittleman, and T. Brooks, editors. Phylogeny and Conservation. Cambridge University Press.

Judd, W. S., C. S. Campell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2002. Plant Systematics. A phylogenetic approach. Sinauer Associates, Inc., Sunderland, Massachusetts.

Justus, J., and S. Sarkar. 2002. The principle of complementarity in the design of reserves networks to conserve biodiversity: a preliminary history. Journal of Biosciences **27**:421-435.

Keith, M., C. T. Chimimba, B. Reyers, and A. S. van Jaarsveld. 2005. Taxonomic and phylogenetic distinctiveness in regional conservation assessments: a case study based on extant South African Chiroptera and Carnivora. Animal Conservation **8**:279-288.

Kent, M. 2005. Biogeography and macroecology. Progress in Physical Geography **29**:256-264.

Kerr, J. 1997. Species richness, endemism and the choice of areas for conservation. Conservation Biology **11**:1094-1100.

Khrishtalka, L., and P. S. Humphrey. 2000. Can natural history museums capture the future. Bioscience **50**:611-617.

Knyazhnitskiy, O. V., R. R. Monk, N. C. Parker, and R. J. Baker. 2000. Assignment of global information system coordinates to classical museum localities for relational database analyses. Occasional Papers. Museum of Texas Tech University:1-15.

Koepfli, K. P., and R. K. Wayne. 2003. Type ISTS markers are more informative than cytochrome b in phylogenetic reconstruction of the Mustelidae (Mammalia : Carnivora). Systematic Biology **52**:571-593.

Korth, W. W. 2001. Comments on the systematics and classification of the beavers (Rodentia: Castoridae). Journal of Mammalian Evolution **8**:279-296.

Lehmann, A., J. M. Overton, and M. P. Austin. 2002. Regression models for spatial prediction, their role for biodiversity and conservation. Biodiversity and Conservation **11**:2085-2092.

Leigh, E. G. 1981. The average lifetime of a population in a varyieng environment. Journal of Theoretical Biology **90**:213-239.

Liu, F. G. R., M. M. Miyamoto, N. P. Freire, P. Q. Ong, M. R. Tennant, T. S. Young, and K. F. Gugel. 2001. Molecular and morphological supertrees for eutherien (placental) mammals. Science **291**:1786-1789.

Lovegrove, B. G., and L. Haines. 2004. The evolution of placental mammal body sizes: evolutionary history, form, and function. Oecologia **138**:13-27.

Mace, G. M. 2004. The role of taxonomy in species conservation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**:711-719.

Mace, G. M., A. Balmford, L. Boitani, G. Cowlishaw, A. P. Dobson, D. P. Faith, K. J. Gaston, C. J. Humphries, R. I. Vane-Wright, P. H. Williams, J. H. Lawton, C. R. Margules, R. M. May, A. O. Nicholls, H. P. Possingham, C. Rahbek, and A. S. van Jaarsveld. 2000. It's time to work together and stop duplicating conservation efforts. Nature **405**:393-393.

Mace, G. M., J. L. Gittleman, and A. Purvis. 2003. Preserving the tree of life. Science **300**:1707-1709.

Mace, G. M., H. Masundire, J. Baillie, T. Ricketts, T. Brooks, M. Hoffmann, S. N. Stuart, A. Balmford, A. Purvis, B. Reyers, J. Wang, C. Revenga, E. Kennedy, S. Naeem, R. Alkemade, T. Allnutt, M. Bakarr, W. Bond, J. Chanson, N. Cox, G. Fonseca, C. Hilton-Taylor, C. Loucks, A. S. Rodrigues, W. Sechrest, A. Stattersfield, B. Janse van Rensburg, and C. Whiteman. 2005. Biodiversity *in* R. Hassan, R. Scholes, and N. Ash, editors. Ecosystems and Human Well-Being: Current State and Trends: Findings of the Condition and Trends Working Group Island Press.

Maddison, D. R., and W. P. Maddison. 2003. MacClade 4. Analysis of phylogeny and character evolution. Sinauer Associates, Suderland, Massachussets.

Maddock, A., and G. A. Benn. 2000. Identification of Conservation-Worthy Areas in Northern Zululand, South Africa. Conservation Biology **14**:155-166.

Madisson, D. R., and W. P. Madisson. 2003. MacClade 4. Analyis of Phylogeny and Character Evolution. Sinauer Associates, Suderland, Massachussets.

Madsen, O., M. Scally, C. J. Douady, D. J. Kao, R. W. DeBry, R. Adkins, H. M. Amrine, M. J. Stanhope, W. W. de Jong, and M. S. Springer. 2001. Parallel adaptive radiations in two major clades of placental mammals. Nature **409**:610-614.

Magurran, A. 1988. Ecological diversity and its measures. Princeton University Press, Princenton, NJ.

Magurran, A. 2004. Measuring Biological Diversity. Blackwell Science, Oxford.

Margules, C. R., M. P. Austin, D. Mollison, and F. Smith. 1994. Biological models for monitoring species decline - construction and use of data-bases. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **344**:69-75.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature **405**:243-253.

Margules, C. R., R. L. Pressey, and P. H. Williams. 2002. Representing biodiversity: data and procedures for identifying priority areas for conservation. Journal of Biosciences **27**:309-326.

Martins, E. P. 2000. Adaptation and the comparative method. Trends in Ecology and Evolution **15**:296-299.

Matthee, C. A., B. J. van Vuuren, D. Bell, and T. J. Robinson. 2004. A molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. Systematic Biology **53**:433-447.

Maurer, B. A. 1994. Geographical population analysis: tools for the analysis of biodiversity. first edition. Blackwell Scientific Publications, Utah.

May, R. M. 1990. Taxonomy as destiny. Nature **347**:129-130.

McKenna, M. C., and S. K. Bell. 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York.

Michaux, J., A. Reyes, and F. Catzeflis. 2001. Evolutionary history of the most speciose mammals: Molecular phylogeny of muroid rodents. Molecular Biology and Evolution **18**:2017-2031.

Millar, J. S., and G. J. Hickling. 1991. Body size and the evolution of mammalian life histories. Functional Ecology **5**:588-593.

Millar, J. S., and R. M. Zammuto. 1983. Life histories of mammals: an analysis of life tables. Ecology **64**:631-635.

Mirov, N. T. 1967. The genus *Pinus*. Ronald Press, New York.

Mittermeier, R. A., P. Robles, and M. Goettsch. 1997. Megadiversidad. Los paises biologicamente mas ricos del mundo. Agrupacion Sierra Madre, S. C. and CEMEX, Mexico, D. F.

Montgelard, C., F. M. Catzeflis, and E. Douzery. 1997. Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome b and 12S rRNA mitochondrial sequences. Molecular Biology and Evolution **14**:550-559.

Montgelard, C., S. Ducrocq, and E. Douzery. 1998. What is a Suiforme (Artiodactyla)? Contribution of cranioskeletal and mitochondrial DNA data. Molecular Biology and Evolution **9**:528-532.

Mooers, A. O. 1995. Tree balance and tree completeness. Evolution **49**:379-384.

Mooers, A. O., and S. B. Heard. 1997. Inferring evolutionary process from phylogenetic tree shape. The Quarterly Review of Biology **72**:31-54.

Morrone, J. J. 2004. Homologia biogeografica. Las coordenadas espaciales de la vida. Instituto de Biologia. Universidad Nacional Autonoma de Mexico, Mexico, D. F.

Morrone, J. J., and T. Escalante. 2002. Parsimony analysis of endemicity (PAE) of Mexican terrestrial mammals at different area units: when size matters. Journal of Biogeography **29**:1095-1104.

Murphy, W. J., E. Eizirik, W. E. Johnson, Y. P. Zhang, O. A. Ryderk, and S. J. O'Brien. 2001. Molecular phylogenetics and the origins of placental mammals. Nature **409**:614-618.

Murray, B. R., and C. R. Dickman. 2000. Relationships between body size and geographical range size among Australian mammals: has human impact distorted macroecological patterns? Ecography **23**:92-100.

Myers, P., R. Espinosa, C. S. Parr, T. Jones, G. S. Hammond, and T. A. Dewey. 2006. The Animal Diversity Web (online). Museum of Zoology. University of Michigan.

Myers, R., R. Mittermeier, C. Mittermeier, G. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853-858.

Navarro-Siguenza, A. G., T. Peterson, and A. Gordillo-Martínez. 2002. A mexican case study on a centralised data base from world natural history museums. CODATA Journal **1**:45-53.

NBN. 2004. How real are your records? Exploring data quality. Summary Report.*in* 4th Annual Conference for National Societies and Recording Schemes. National Biodiversity Network, Biological Records Centre and Natural History Museum, The Natural History Museum, London.

Nee, S., and R. M. May. 1997. Extinction and the loss of evolutionary history. Science **278**:692-694.

Neyra, L., and L. Durand. 1998. Recursos Naturales: Biodiversidad. La diversidad Biologica de Mexico: Estudio de Pais. CONABIO, Mexico, D. F.

Norman, J. E., and M. V. Ashley. 2000. Phylogenetics of Perissodactyla and tests of the molecular clock. Journal of Molecular Evolution **50**:11-21.

Novacek, M. J. 2001. Mammalian phylogeny: Genes and supertrees. Current Biology **11**:R573-R575.

Oli, M. K. 2004. The fast-slow continuum and mammalian life-history patterns: an empirical evaluation. Basic and Applied Ecology **5**:449-463.

Olifiers, N., M. V. Vieira, and C. E. V. Grelle. 2004. Geographic range and body size in Neotropical marsupials. Global Ecol Biogeography **13**:439-444.

Orme, C. D. L., N. J. B. Isaac, and A. Purvis. 2002. Are most species small? Not within species-level phylogenies. Proceedings of the Royal Society of London Series B-Biological Sciences **269**:1279-1287.

Ortega-Baes, P., God, H. nez-Alvarez, and ctor. 2006. Global Diversity and Conservation Priorities in the Cactaceae. Biodiversity and Conservation **15**:817-827.

Page, R. M. 1996. TREEVIEW: An application to display phylogenetic trees on personal computers. Computer Applications in the Biosciences **12**:357-358.

Pagel, M. 1992. A method for the analysis of comparative data. Journal of Theoretical Biology **156**:431-442.

Parker, N. C., R. D. Bradley, J. M. Burns, G. F. Edson, D. R. Haragan, C. Jones, R. R. Monk, C. J. Phillips, D. J. Schmidly, and R. J. Baker. 1998. Bioinformatics: a multidisciplinary approach for the life sciences. Occasional Papers. Museum of Texas Tech University:1-8.

Pereira, H. M., and G. C. Daily. 2006. Modeling biodiversity dynamics in countryside landscapes. Ecology **87**:1877-1885.

Perez-Lozada, M., and K. A. Crandall. 2003. Can taxonomic richness be used as a surrogate for phylogenetic distinctness indices for ranking areas for conservation. Animal Biodiversity and Conservation **26**:77-84.

Perlman, D. L., and G. Adelson. 1997. Biodiversity. Blackwell Science, Malden, Massachussetts.

Peterson, A. T., A. G. Navarro-Siguenza, and H. Benitez. 1998. The need for continued scientific collections: a geographic analysis of mexican specimens. Ibis **140**:288-294.

Peterson, T. A., S. Egbert, V. Sanchez-Cordero, and K. Price. 2000. Geographic analysis of conservation priority: endemic birds and mammals in Veracruz, Mexico. Biological Conservation **93**:85-94.

Pielou, E. C. 1975. Ecological diversity. Wiley, New York.

Pilgrim, E. S., M. J. Crawley, and K. Dolphin. 2004. Patterns of rarity in the native British flora. Biological Conservation **120**:161-170.

Pitra, C., R. Furbass, and H.-M. Seyfert. 1997. Molecular phylogeny of the tribe Bovini (Mammalia: Artiodactyla): alternative placement of the *Anoa*. Journal of Evolutionary Biology **10**:589-600.

Polasky, S., B. Csuti, C. A. Vossler, and S. M. Meyers. 2001. A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities for North American birds. Biological Conservation **97**:99-105.

Posadas, P., D. R. M. Esquivel, and J. V. Crisci. 2001. Using phylogenetic diversity measures to set priorities in conservation: An example from southern South America. Conservation Biology **15**:1325-1334.

Possingham, H. P., I. R. Ball, and S. J. Andelman. 2000. Mathematical Methods for Identifying Representative Reserve Networks. Pages 291-306 *in* S. Ferson and M. A. Burgman, editors. Quantitative Methods for Conservation Biology. Springer-Verlag, New York.

Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature **365**:355-364.

Pressey, R. L., H. P. Possingham, and C. R. Margules. 1996. Optimality in reserve selection algorithms: When does it matter and how much? Biological Conservation **76**:259-267.

Price, A. R. G., M. J. Keeling, and C. J. O'Callaghan. 1999. Ocean-scale patterns of biodiversity of Atlantic asteroids determined from taxonomic distinctness and other measures. Biological Journal of the Linnean Society **66**:187-203.

Price, S. A., O. R. P. Bininda-Emonds, and J. Gittleman. 2005. A complete phylogeny of the whales, dolphins and even-toed hoofed mammals (Cetartiodactyla). Biological Review **80**:445-473.

Primark, R. B. 2002. Essentials of Conservation Biology. Sinauer Associates, Sunderland.

Pullin, A. S. 2002. Conservation Biology. First edition. Cambridge University Press, Cambridge.

Purvis, A., and P. M. Agapow. 2002. Phylogeny imbalance: Taxonomic level matters. Systematic Biology **51**:844-854.

Purvis, A., M. Cardillo, R. Grenyer, and B. Collen. 2005a. Correlates of extinction risk: phylogeny, biology, threat and scale. Pages 295-316 *in* A. Purvis, J. Gittleman, and T. Brooks, editors. Phylogeny and Conservation. Cambridge University Press, Cambridge.

Purvis, A., and T. Garland. 1993. Polytomies in comparative analyses of continuous characters. Systematic Biology **42**:569-575.

Purvis, A., J. L. Gittleman, and T. M. Brooks. 2005b. Phylogeny and Conservation. Cambridge University Press, Cambridge.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London Series B-Biological Sciences **267**:1947-1952.

Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. Nature **405**:212-219.

Purvis, A., and A. Rambaut. 1995. Comparative-analysis by independent contrasts (CAIC) - an Apple-Macintosh application for analyzing comparative data. Computer Applications in the Biosciences **11**:247-251.

Pyron, M. 1999. Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. Journal of Biogeography **26**:549.

Rabinowitz, D. 1981. Seven forms of rarity. Pages 205-207 *in* H. Synge, editor. The biological aspects of rare plants conservation. John Wiley and Sons, New York.

Ramamoorthy, T. P., R. Bye, A. Lot, and J. E. Fa. 1998. Diversidad Biologica de Mexico. Instituto de Biologia. UNAM.

Rambaut, A. 1999. TreeThief (computer programme): a tool for manual phylogenetic tree entry from scanned images. Department of Zoology, University of Oxford, Oxford.

Rambaut, A. 2006. FigTree v1.0. A graphical viewer of phylogenetic trees. Institute of Evolutionary Biology. University of Edinburgh.

Ramirez-Pulido, J., J. Arroyo-Cabrales, and A. Castro-Campillo. 2005. Estado Actual y Relacion Nomenclatural de los Mamiferos Terrestres de Mexico. Acta Zoologica Mexicana (n. s.) **21**:21-82.

Ramírez-Pulido, J., A. Castro-Campillo, J. Arroyo-Cabrales, and F. A. Cervantes. 1996. Lista taxonómica de los mamíferos terrestres de México: A taxonomic list of the terrestrial mammals of Mexico. Occasional Papers. Museum of Texas Tech University **158**:1-62.

Randi, E., N. Mucci, M. Pierpaoli, and E. Douzery. 1998. New phylogenetic perspectives on the Cervidae (Artiodactyla) are provided by the mitochondrial cytochrome b gene. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **265**:793-801.

Read, A. F., and P. H. Harvey. 1989. Life history differences among the eutherian radiations. Journal of Zoology **219**:329-353.

Rebelo, A. G. 1994. Iterative selection procedures: centres of endemism and optimal placement of reserves. Strelitzia **1**:231-257.

Rebelo, A. G., and W. R. Sigfried. 1992. Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of diversity. Conservation Biology **6**:243-252.

Redford, K. H., P. Coppolillo, E. W. Sanderson, G. A. B. Da Fonseca, E. Dinerstein, C. Groves, G. Mace, S. Maginnis, R. A. Mittermeier, R. Noss, D. Olson, J. G. Robinson, A. Vedder, and M. Wright. 2003. Mapping the conservation landscape. Conservation Biology **17**:116-131.

Reeder, S. A., D. S. Carroll, C. W. Edwards, C. W. Kilpatrick, and R. D. Bradley. 2006. Neotomine-peromyscine rodent systematics based on combined analyses of nuclear and mitochondrial DNA sequences. Molecular Phylogenetics and Evolution **40**:251-258.

Reid, F. A. 1997. A field guide to the mammals of Central America and Southeast Mexico. Oxford University Press, New York.

Reyers, B., and A. S. van Jaarsveld. 2000. Assessment techniques for biodiversity surrogates. South African Journal of Science **96**:406-408.

Reyers, B., A. S. van Jaarsveld, and M. Kruger. 2000. Complementarity as a biodiversity indicator strategy. Proceedings of the Royal Society of London Series B-Biological Sciences **267**:505-513.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters **7**:1-15.

Robinson, M., F. Catzeflis, J. Briolay, and D. Mouchiroud. 1997. Molecular phylogeny of rodents, with special emphasis on murids: Evidence from nuclear gene LCAT. Molecular Phylogenetics and Evolution **8**:423-434.

Robinson, T. J., and C. A. Matthee. 2005. Phylogeny and evolutionary origins of the Leporidae: a review of cytogenetics, molecular analyses and a supermatrix analysis. Mammal Review **35**:231-247.

Rodrigues, A. S., T. M. Brooks, and K. J. Gaston. 2005. Integrating phylogenetic diversity in the selection of priority areas for conservation: does it make a difference? Pages 101-119 *in* A. Purvis, J. L. Gittleman, and T. M. Brooks, editors. Phylogeny and Conservation. Cambridge University Press.

Rodrigues, A. S. L., S. J. Andelman, M. I. Bakarr, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. C. Fishpool, G. A. B. da Fonseca, K. J. Gaston, M. Hoffmann, J. S. Long, P. A. Marquet, J. D. Pilgrim, R. L. Pressey, J. Schipper, W. Sechrest, S. N. Stuart, L. G. Underhill, R. W. Waller, M. E. J. Watts, and X. Yan. 2004. Effectiveness of the global protected area network in representing species diversity. Nature **428**:640-643.

Rodrigues, A. S. L., and K. J. Gaston. 2002a. Maximising phylogenetic diversity in the selection of networks of conservation areas. Biological Conservation **105**:103-111.

Rodrigues, A. S. L., and K. J. Gaston. 2002b. Optimisation in reserve selection procedures - why not? Biological Conservation **107**:123-129.

Rose, J. R., M. J. Dewey, and W. D. Dawson. 2004. PeroBase. The *Peromyscus* Database at the University of South Carolina. http://wotan.cse.sc.edu/perobase/. Biological Sciences. *Peromyscus* Stock Center.

Rosenzweig, M. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Roy, K., D. Jablonski, and J. W. Valentine. 1996. Higher taxa in biodiversity studies: Patterns from eastern Pacific marine molluscs. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **351**:1605-1613.

Rzedowski, J. 1998. Diversidad y origenes de la flora fanerogamica de Mexico.*in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. E. Fa, editors. Diversidad Biologica de Mexico. Instituto de Biologia. UNAM, Mexico, D. F.

Sanchez-Cordero, V., P. Illoldi-Rangel, M. Linaje, S. Sarkar, and A. T. Peterson. 2005. Deforestation and extant distributions of Mexican endemic mammals. Biological Conservation **126**:465-473.

Sanderson, M. J., A. Purvis, and C. Henze. 1998. Phylogenetic supertrees: assembling the trees of life. Trends in Ecology and Evolution **13**:105-109.

Savitsky, B. G., and T. E. Lacher Jr., editors. 1998. GIS Methodologies for Developing Conservation Strategies. Columbia University Press, New York.

Schneider, I., H. Schneider, M. P. Schneider, and A. Silva. 2004. The prion protein and New World primate phylogeny. Genetics and Molecular Biology **27**:505-510.

Sechrest, W., T. M. Brooks, G. A. B. da Fonseca, W. R. Konstant, R. A. Mittermeier, A. Purvis, A. B. Rylands, and J. L. Gittleman. 2002. Hotspots and the conservation of evolutionary history. Proceedings of the National Academy of Sciences of the United States of America **99**:2067-2071.

SEMARNAT. 2002. Norma Oficial Mexicana. NOM-059-ECOL-2001: Proteccion ambiental. Especies nativas de Mexicode flora y fauna silvestres, categorias de riesgo y especificaciones para su inclusion, exlusion o cambio. Lista de especies en riesgo. Pages 1-56. Diario Oficial, 6 de Marzo de 2002.

Shaffer, H. B., R. N. Fisher, and C. Davidson. 1998. The role of natural history collections in documenting species declines. Trends in Ecology and Evolution **13**:27-30.

Simmons, N. B., and T. Conway. 2001. Phylogenetic relationships of mormoopid bats (Chiroptera: Mormoopidae) based on morphological data. Bulletin of the American Museum of Natural History **258**:1-97.

Slattery, J. P., and S. J. O'Brien. 1998. Patterns of Y and X chromosome DNA sequence divergence during the Felidae radiation. Genetics **148**:1245-1255.

Soberon, J., R. Jimenez, J. Golubov, and P. Koleff. 2007. Assessing completeness of biodiversity databases at different spatial scales. Ecography **30**:152-160.

Soberon, J., and A. T. Peterson. 2004. Biodiversity Informatics: managing and applying primary biodiversity data. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**:689-698.

Sogin, M. L., and G. Hinkle. 1997. Common measures for studies of biodiversity: molecular phylogeny in the Eukaryotic microbial world. Pages 109-122 *in* M. Reaka-Kundla, D. E. Wilson, and E. O. Wilson, editors. Biodiversity II. The National Academies Press

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. The principles and practice of statistics in Biological Research. 3rd edition. W. H. Freeman and Company, New York.

Springer, M. S., M. J. Stanhope, O. Madsen, and W. W. de Jong. 2004a. Molecules consolidate the placental mammal tree. Trends in Ecology and Evolution **19**:430-438.

Springer, M. S., M. J. Stanhope, O. Madsen, and W. W. de Jong. 2004b. Molecules consolidate the placental mammal tree. Trends in Ecology & Evolution **19**:430-438.

Stam, E. 2002. Does imbalance in phylogenies reflect only bias? Evolution **56**:1292-1295.

StatSoft-Inc. 2003. STATISTICA (data analysis software system) v 6. www.statsoft.com.

Stein, B. R., and J. Wieczoreck. 2004. Mammals of the world: MaNIS as an example of data integration in a distributed network environment. Biodiversity Informatics **1**:14-22.

Steppan, S. J., R. M. Adkins, and J. Anderson. 2004. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Systematic Biology **53**:533-553.

Stevens, G. C. 1989. The latitudinal gradient in geographic range - how so many species coexist in the tropics. The American Naturalist **133**:240-256.

Stockwell, D., and A. T. Peterson. 2003. Comparison of resolution of methods used in mapping biodiversity patterns from point-occurrence data. Ecological Indicators **3**:213-221.

Stoner, C. J., O. R. P. Bininda-Emonds, and T. Caro. 2003. The adaptive significance of colouration in lagomorphs. Biology Journal of the Linnean Society **79**:309-328.

Stuart-Fox, D., and I. P. F. Owens. 2003. Species richness in agamid lizards: chance, body size, sexual selection or ecology? Journal of Evolutionary Biology **16**:659-669.

Styles, B. T. 1998. El genero *Pinus*: su panorama en Mexico. Pages 385-408 *in* T. P. Rammamoorthy, B. R., L. A., and J. E. Fa, editors. Instituto de Biologia. Universidad Nacional Autonoma de Mexico, Mexico, D.F.

Symonds, M. R. E. 1999. Life histories of the Insectivora: the role of phylogeny, metabolism and sex differences. Journal of Zoology **249**:315-337.

Taylor, C., and N. Gotelli. 1994. The macroecology of Cyprinella: Correlates of phylogeny, body size, and geographical range. The American Naturalist **144**:549-569.

Teeling, E. C., M. S. Springer, O. Madsen, P. Bates, S. J. O'Brien, and W. J. Murphy. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science **307**:580-584.

Tellez-Valdes, O., and P. DiVila-Aranda. 2003. Protected areas and climate change: a case study of the Cacti in the Tehuacan-Cuicatlan Biosphere Reserve, Mexico. Conservation Biology **17**:846-853.

Vamosi, J. C., and S. M. Vamosi. 2007. Body size, rarity and phylogenetic community structure: insights from diving beetle assemblages of Alberta. Diversity and Distributions **13**.

Vane-Wright, R. I., C. J. Humphries, and P. H. Williams. 1991. What to protect?. Systematics and the agony to choice. Biological Conservation **55**:235-254.

Vazquez, D. P., and J. L. Gittleman. 1998. Biodiversity conservation: Does phylogeny matter? Current Biology **8**:R379-R381.

Vazquez, L.-B., and K. J. Gaston. 2004. Rarity, commonnes and patterns of species richness: the mammals of Mexico. Global Ecology and Biogeography **13**:535-542.

Villa R., B., and F. A. Cervantes. 2003. Los mamiferos de Mexico. Grupo Editorial Iberoamerica, S. A. de C. V e Instituto de Biologia, UNAM, Mexico City.

Villalobos, F., A. A. Valerio, and A. P. Retana. 2004. A phylogeny of howler monkeys (Cebidae: *Alouatta*) based on mitochondrial, chromosomal and morphological data. Revista De Biologia Tropical **52**:665-675.

Villaseñor, J. L., G. Ibarra-Manriquez, J. A. Meave, and E. Ortiz. 2005. Higher taxa as surrogates of Plant Biodiversity in a Megadiverse country. Conservation Biology **19**:232-238.

Virgos, E., S. Cabezas-Diaz, and J. A. Blanco-Aguiar. 2006. Evolution of life history traits in Leporidae: a test of nest predation and seasonality hypotheses. Biological Journal of the Linnean Society **88**:603-610.

Virolainen, K. M., T. Virola, J. Suhonen, M. Kuitunen, A. Lammi, and P. Siikamaki. 1999. Selecting networks of nature reserves: methods do affect the long-term outcome. Proceedings of the Royal Society of London Series B-Biological Sciences **266**:1141-1146.

Viveiros, C. E. 2002. Is higher-taxon analysis an useful surrogate of species richness in studies of Neotropical mammal diversity? Biological Conservation **108**:101-106.

von Euler, F. 2001. Selective extinction and rapid loss of evolutionary history in the bird fauna. Proceedings of the Royal Society of London Series B-Biological Sciences **268**:127-130.

von Euler, F., and S. Svensson. 2001. Taxonomic distinctness and species richness as measures of functional structure in bird assemblages. Oecologia **129**:304-311.

von Willert, D. J. 1994. Welwitschia mirabilis Hook. fil.- das Überlebenswunder der Namibwüste [the survival miracle of the Namib desert]. . Naturwissenschaften **81**:430-442.

Voss, R. S., and S. A. Jansa. 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: Separate and combined analyses of didelphine relationships with denser taxon sampling. Bulletin of the American Museum of Natural History:1-82.

Vovides, A. 1998. Identification of the case Mexico, States of Veracruz and Chiapas. Conservation of cycads through propagation in peasant-run sustainable management nurseries. The world bank/WBI's CBNRM Initiate.

Waddell, P. J., H. Kishino, and R. Ota. 2001. A Phylogenetic Foundation for Comparative Mammalian Genomics. Genome Informatics **12**:141-154.

Waddell, P. J., and S. Shelley. 2003. Evaluating placental inter-ordinal phylogenies with novel sequences including RAG1, gamma-fibrinogen, ND6, and mt-tRNA, plus MCMC-driven nucleotide, amino acid, and codon models. Molecular Phylogenetics and Evolution **28**:197-224.

Walker, P. A., and D. P. Faith. 1994. DIVERSITY-PD: Procedures for conservation evaluation based on phylogenetic diversity. Biodiversity Letters **2**:132-139.

Warwick, R. M., C. M. Ashman, A. R. Brown, K. R. Clarke, B. Dowell, B. Hart, R. E. Lewis, N. Shillabeer, P. J. Somerfield, and J. F. Tapp. 2002. Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Mar. Ecol. Progr. Ser **234**:1–13.

Warwick, R. M., and K. R. Clarke. 2001. Practical measures of marine biodiversity based on relatedness of species. Pages 207-231 Oceanography and Marine Biology, Vol 39. Taylor & Francis Ltd, London.

Watson, F. D., and J. E. Eckenwalder. 1993. Cupressaceae.*in* F. o. N. A. E. Committee, editor. Flora of North America North of Mexico. Oxford University Press.

Wayne, R. K., E. Geffen, D. J. Girman, K. P. Koepfli, L. M. Lau, and M. CR. 1997. Molecular systematics of the Canidae. Systematic Biology **46**:622-653.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogeny and community ecology. Annual Review of Ecology and Systematics **33**:475-505.

Weksler, M. 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae : Sigmodontinae) based on the nuclear IRBP exon. Molecular Phylogenetics and Evolution **29**:331-349.

Wilkinson, G. S., and J. M. South. 2002. Life history, ecology and longevity in bats. Aging Cell **1**:124-131.

Williams, P. C., K. J. Gaston, and C. J. Humphries. 1994. Do conservationists and molecular biologists value differences between organisms in the same way? Biodiversity Letters **2**:67-78.

Williams, P. H. 1999. WORLDMAP 4 Windows: Software and help document 4.2 (see www.nhm.ac.uk/curation-research/projects/worldmap). The Natural History Museum, London.

Williams, P. H., K. J. Gaston, and C. J. Humphries. 1997. Mapping biodiversity value worldwide: Combining higher-taxon richness from different groups. Proceedings of the Royal Society of London Series B-Biological Sciences **264**:141-148.

Williams, P. H., D. Gibbons, C. Margules, A. Rebelo, C. Humphries, and R. Pressey. 1996a. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. Conservation Biology **10**:155-174.

Williams, P. H., D. Lees, M. B. Araujo, C. Humphries, R. I. Vane-Wright, and I. J. Kitching. 2002a. Biodiversity and Worldmap

http://www.nhm.ac.uk/science/projects/worldmap/index.htm. The Natural History Museum.

Williams, P. H., C. R. Margules, and D. W. Hilbert. 2002b. Data requirements and data sources for biodiversity priority area selection. Journal of Biosciences **27**:327-338.

Williams, P. H., G. T. Prance, C. J. Humphries, and K. S. Edwards. 1996b. Promise and problems in applying quantitative complementary areas for representing the diversity of some neotropical plants (families Dichapetalaceae, Lecythidaceae, Caryocaraceae, Chrysobalanaceae and Proteaceae). Biological Journal of the Linnean Society **58**:125-157.

Wilson, D. E., and D. M. Reeder. 1993. Mammal species of the world: a taxonomic and geographic reference. Smithsonian Institution Press.

Wilson, E. O. 1988. Biodiversity. National Academy Press, Smithsonian Institution, Washington.

Xuan Mao, C., R. K. Colwell, and J. Chang. 2005. Estimating the species accumulation curve using mixtures. Biometrics **61**:433-441.

Zaldivar, M. E., O. Rocha, K. E. Glander, G. Aguilar, A. S. Huertas, R. Sanchez, and G. Wong. 2004. Distribution, ecology, life history, genetic variation, and risk of extinction of nonhuman primates from Costa Rica. Revista De Biologia Tropical **52**:679-693.

Zarza, H., G. Ceballos, and M. A. Steele. 2003. *Marmosa canescens*. Mammalian Species. American Society of Mammalogists **745**:1-4.

APPENDICES

APPENDIX A. NOMENCLATURE SOURCES EMPLOYED FOR SEED PLANTS

Group	Nomenclature
Gymnosperms	
- Earle, C. J. 1997. Gymnosperms database. http://www.conifers.org. - Reveal, J. L. 1998. Norton-Brown Herbarium, University of Maryland - Judd, W. S., Campell, C. S., Kellogg, E. A., Stevens, P. F. and Donoghue, M. J. 2002. Plant systematics. A phylogenetic approach. Sinauer Associates, Inc., Sunderland, Massachusetts. 575 pp.	
Zamiaceae	- Hendricks, J., K. Hill, R. Osborne and D. Stevenson. The Cycad Pages (http://plantnet.rbgsyd.gov.au/PlantNet/cycad)
Cupressaceae	- Gadek, P.A., D.L. Alpers, M.M. Heslewood and C.J. Quinn. 2000. Relationships within Cupressaceae sensu lato: a combined morphological and molecular approach. American Journal of Botany 87(7):1044-1057.
Gnetaceae	- Stevenson, Dennis W. 1993. Ephedraceae. Flora of North America Editorial Committee (eds.): Flora of North America North of Mexico, Vol. 2. Oxford University Press.
Pinaceae	- Frankis, M. P. 1989. Generic inter-relationships in Pinaceae. Notes Royal Botanical Garden. Edinburgh 45: 527-548. - Frankis, M. P. 1989 Classification of the genus Pinus. In http://www.pinetum.org/Lovett/classification.htm - Styles, B. T. 1998. El genero Pinus: Su panorama en Mexico. In: Rammamoorthy, T.P., R. Bye, A. Lot and J.E Fa. (Eds). Instituto de Biologia. Universidad Nacional Autonoma de Mexico. Mexico, D.F. pp 385-40 -Richardson, D.M. (ed.). 1998. Ecology and Biogeography of *Pinus*. Cambridge University Press.
Podocarpaceae	- Farjon, A. 1998. World Checklist and Bibliography of Conifers. The Royal Botanic Gardens, Kew. UK.
Taxaceae	- Hils, M. H. 1993. Taxaceae. Flora of North America Editorial Committee (eds.): Flora of North America North of Mexico, Vol. 2. Oxford University Press.

Group	Nomenclature
Angiosperms	
- L. Watson and M. J. Dallwitz (1992 onwards). The Families of Flowering Plants: Descriptions, Illustrations, Identification, Information Retrieval. Version: 13th January 2005. http://delta-intkey.com'. - Angiosperms Phylogenetic Group: http://www.mobot.org/MOBOT/research/APweb/welcome.html - Judd, W. S., Campell, C. S., Kellogg, E. A., Stevens, P. F. and Donoghue, M. J. 2002. *Plant systematics. A phylogenetic approach.* Sinauer Associates, Inc., Sunderland, Massachusetts. 575 pp.	
Agavaceae and Nolinaceae	- Davidse, G., M. Sousa S. & A. O. Chater (eds). 1994. Alismataceae a Cyperaceae. Flora Mesoamericana 6: i--xvi, 1--543 http://www.mobot.org/MOBOT/fm/
Arecaceae	- Henderson, A., Galeano, G. and Bernal, R. 1995. Field guide to the palms of the Americas. Princeton University Press. 352 pp + plates.
Commelinaceae	- Hunt, D. R. 1998. Commelinaceae de Mexico. In: Rammamoorthy, T.P., R. Bye, A. Lot and J.E Fa. (Eds). Instituto de Biologia. Universidad Nacional Autonoma de Mexico. Mexico, D.F. pp 409-425.
Orchidaceae	- Romero-González, G., G. C. Fernández-Concha, R. L. Dressler, L. K. Magrath & G. W. Argus . Family Orchidaceae. Flora of North America. http://www.mobot.org/MOBOT/fm/
Poaceae	- Grass Genera of the World (Watson & Dallwitz, 2005?) - Catalogue of new world grasses (Poaceae) R. J. Soreng, G. Davidse, P. M. Peterson, F. O. Zuloaga, E. J. Judziewicz, T. S. Filgueiras & O. Morrone
Acanthaceae	- Daniel, T. 1998. Acanthaceae de Mexico: diversidad y distribucion. In: Rammamoorthy, T.P., R. Bye, A. Lot and J.E Fa. (Eds). Instituto de Biologia. Universidad Nacional Autonoma de Mexico. Mexico, D.F. pp pp 527- 544.
Asteraceae	- Judd, W. S., Campell, C. S., Kellogg, E. A., Stevens, P. F. and Donoghue, M. J. 2002. Plant systematics. A phylogenetic approach. Sinauer Associates, Inc., Sunderland, Massachusetts. 575 pp. - Turner, B. and G. L. Nesom. 1998. Biogeografia, diversidad y situacion de peligro o amenaza de Asteraceae de Mexico. In:

	Rammamoorthy, T.P., R. Bye, A. Lot and J.E Fa. (Eds). Instituto de Biologia. Universidad Nacional Autonoma de Mexico. Mexico, D.F. pp 545-561.
Cactaceae	- Anderson, E. F. 2001. The cactus family. Timber Press. 776 pp.
Fabaceae	- Sousa, M and C. Delgado. 1998. Leguminosas mexicanas: fitogeografia, endemismo y origenes. In: Rammamoorthy, T.P., R. Bye, A. Lot and J.E Fa. (Eds). Instituto de Biologia. Universidad Nacional Autonoma de Mexico. Mexico, D.F. pp 449-500. - Doyle, J. and Luckow, M. A. 2003. The rest of the iceberg: Legume diversity and evolution in a phylogenetic context. Plant Phys. 131: 900-910.
Fagaceae	- Nixon, K. C. 1997. Family Fagaceae, Flora of North America. - Nixon, K. C. 1998. El genero Quercus in Mexico. In: Rammamoorthy, T.P., R. Bye, A. Lot and J.E Fa. (Eds). Instituto de Biologia. Universidad Nacional Autonoma de Mexico. Mexico, D.F. pp 435-447

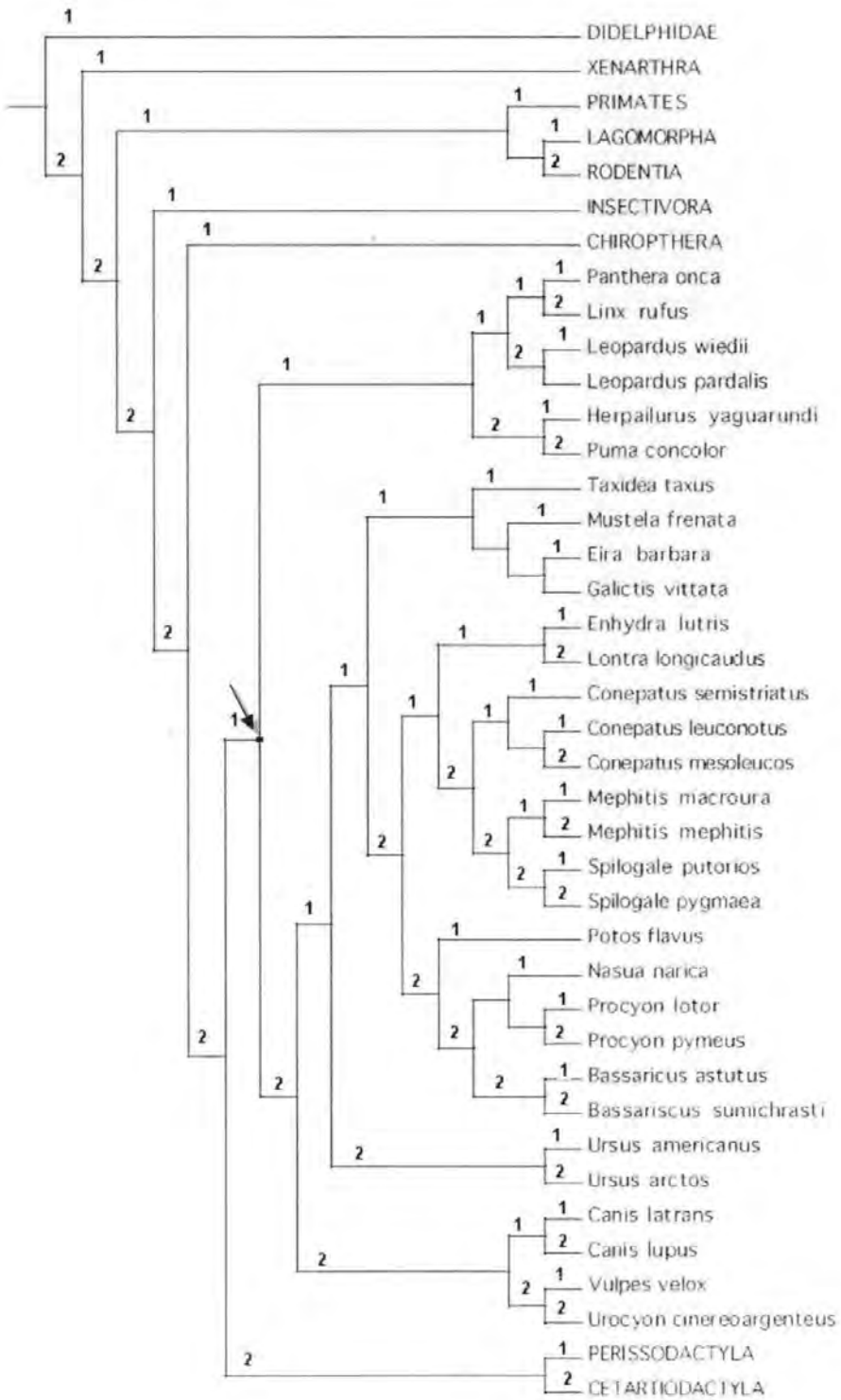
APPENDIX B: SOURCES OF PHYLOGENETIC INFORMATION

Taxonomic group	Source
Eutherian Mammals	McKenna and Bell (1997), Liu *et al.* (2001), Madsen *et al.* (2001), Murphy *et al.* (2001), Novacek (2001), Waddell *et al.* (2001), Arnason *et al.* (2002), Delsuc *et al.* (2002), Helgen (2003), Hudelot *et al.* (2003) and Springer *et al.* (2004b).
Didelphidae	Voss and Jansa (2003).
Xenarthra	Delsuc *et al.* (2001, 2002).
Primates	Purvis 1995, Schneider *et al.* (2004) and Villalobos *et al.* (2004)
Leporidae	Graur *et al.* (1996), Halanych and Robinson (1997), Halanych *et al.* (1999), Cervantes *et al.* (2002), Matthee *et al.* (2004), Robinson and Matthee (2005), and Virgos *et al.* (2006).
Rodentia	Hafner *et al.* (1994), Robinson *et al.* (1997), Conroy and Cook (2000) , Douady *et al.* (2000), Huchon *et al.* (2000), DeBry and Sagel (2001), Huchon and Douzery (2001), Korth (2001), Michaux *et al.* (2001), Bell *et al.* (2001), Demastes *et al.* (2002), Edwards and Bradley (2001), Huchon *et al.* (2002), Adkins *et al.* (2003), D'Elia (2003), Weksler (2003), Bradley *et al.* (2004), Cook *et al.* (2004), Hafner *et al.* (2004), Herron *et al.* (2004), Rose *et al.* (2004), Steppan *et al.* (2004), Alexander and Riddle (2005) and Steppan *et al.* (2005), and Reeder *et al.* (2006).
Insectivora	Demboski and Cook (2003), Grenyer and Purvis (2003a)

Taxonomic group	Source
Carnivora	Dragoo and Honeycutt (1997), Wayne *et al.* (1997), Slattery and O'Brien (1998), Bininda-Emonds *et al.* (1999), Koepfli and Wayne (2003) and Flynn *et al.* (2005)
Chiroptera	Simmons and Conway (2001), Carstens *et al.* (2002), Jones *et al.* (2002), Hernadez-Fernandez and Urba (2005), Jones *et al.* (2005a) and Teeling *et al.* (2005).
Perissodactyla	Graur *et al.* (1997) Norman and Ashley (2000)
Artiodactyla	Pitra *et al.* (1997), Montgelard *et al.* (1997, 1998), Randi *et al.* (1998), Murphy *et al.* (2001), Beintema *et al.* (2003), Hassanin and Douzery (2003) and Hernadez-Fernandez and Urba (2005), Geisler (Geisler 2001)

APPENDIX C: PHYLOGENETIC ENCODING

Encoding method for the Order Carnivora, as an example. All member species are shown, together with all the other orders (in capitals). The arrow indicates where Order Carnivora splits from the ungulates, *sensu latissimo.*



APPENDIX D: ENVIRONMENTAL DATA

Table D.1 Average Precipitation values

Number	Rank (mm)	Average (mm)
1	0 - 125	62.5
2	125 - 400	262.5
3	400 - 600	500
4	600 - 800	700
5	800 - 1200	1000
6	1200 - 1500	1350
7	1500 - 2000	1750
8	2000 - 2500	2250
9	2500 - 4000	3250
10	>4000	3250

Table D.2 Average Temperature values

Number	Mean Annual Temperature (°C)	Average	Thermal Zone
1	>26		Very Hot
2	22-26	24	Hot
3	18-22	20	Warm
4	12-18	15	Temperate
5	5-12	8	Cool
6	<5		Cold and very cold

Table D.3 Average Altitude values

Number	Rank (mm)	Average (mm)
1	1-200	100
2	201-400	300
3	401-600	500
4	601-800	700
5	801-1000	900
6	1001-1200	1100
7	1201-1400	1300
8	1401-1600	1500
9	1601-1800	1700
10	1801-2000	1900
11	2001-2200	2100
12	2201-2400	2300
13	2401-2600	2500
14	≥2601 (up to 5401 m)	>2600

Figure D.1 ELEVATION

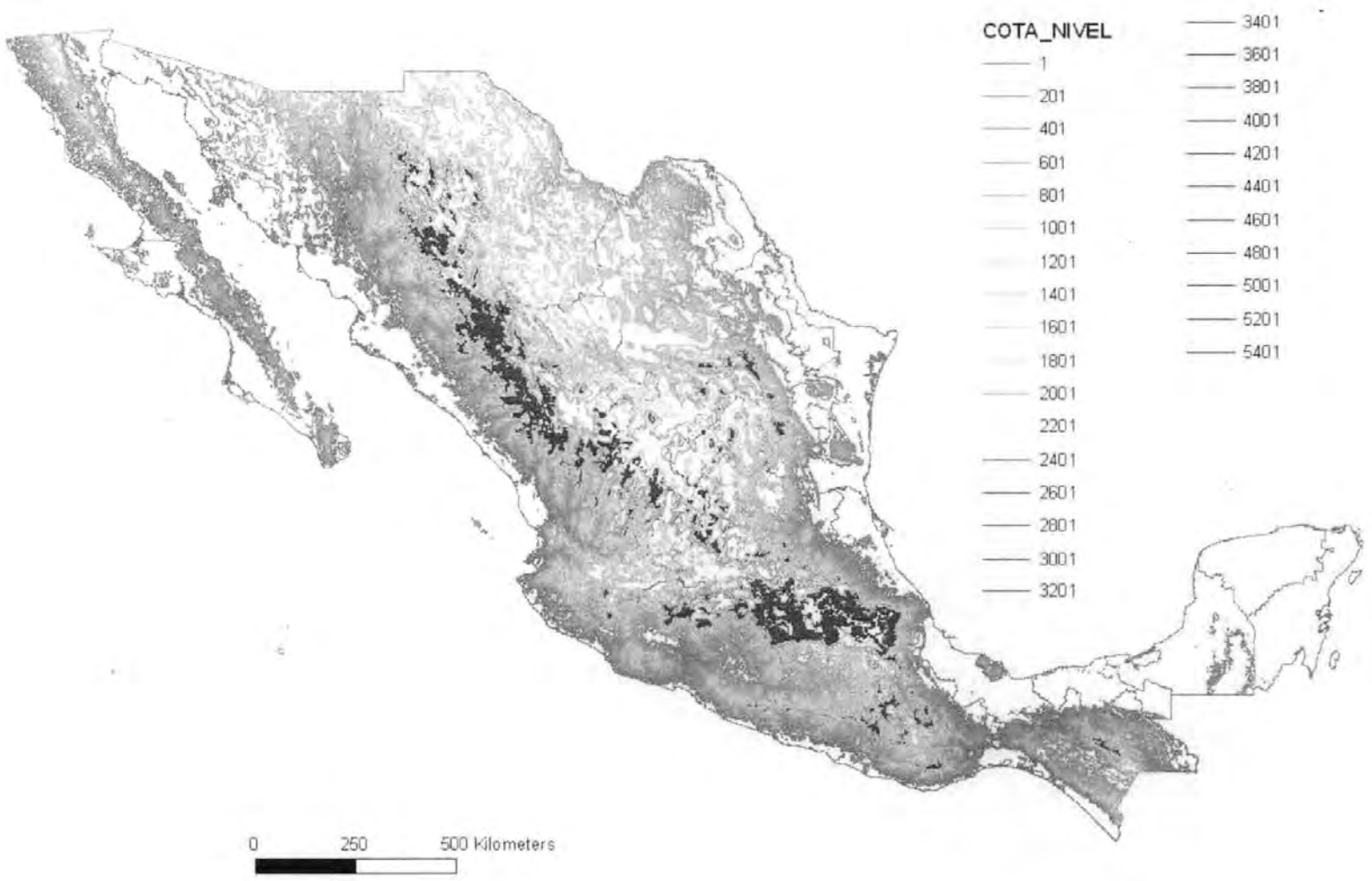


Figure D.2 ELEVATION (RASTERS)

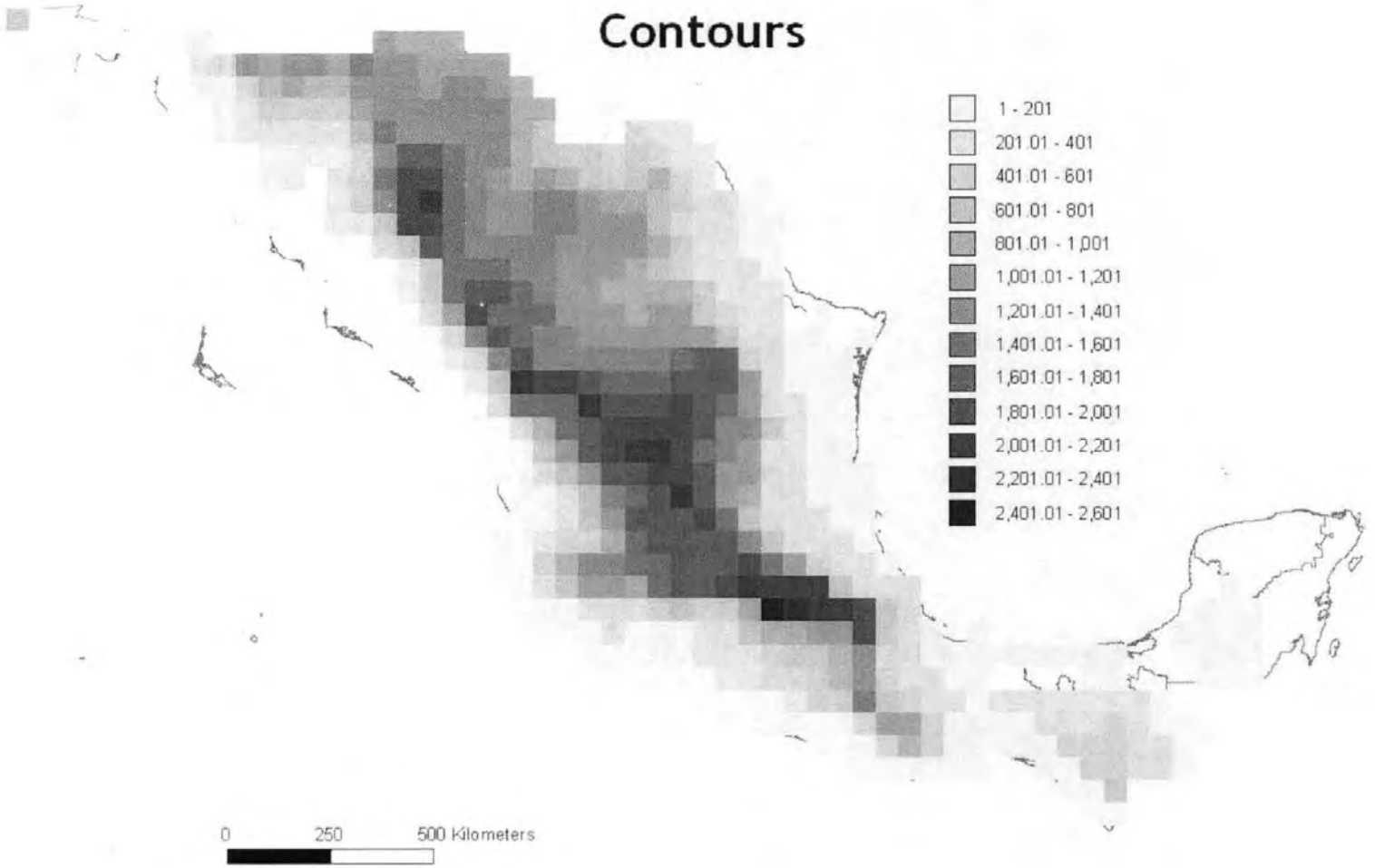


Figure D.3 PRECIPITATION

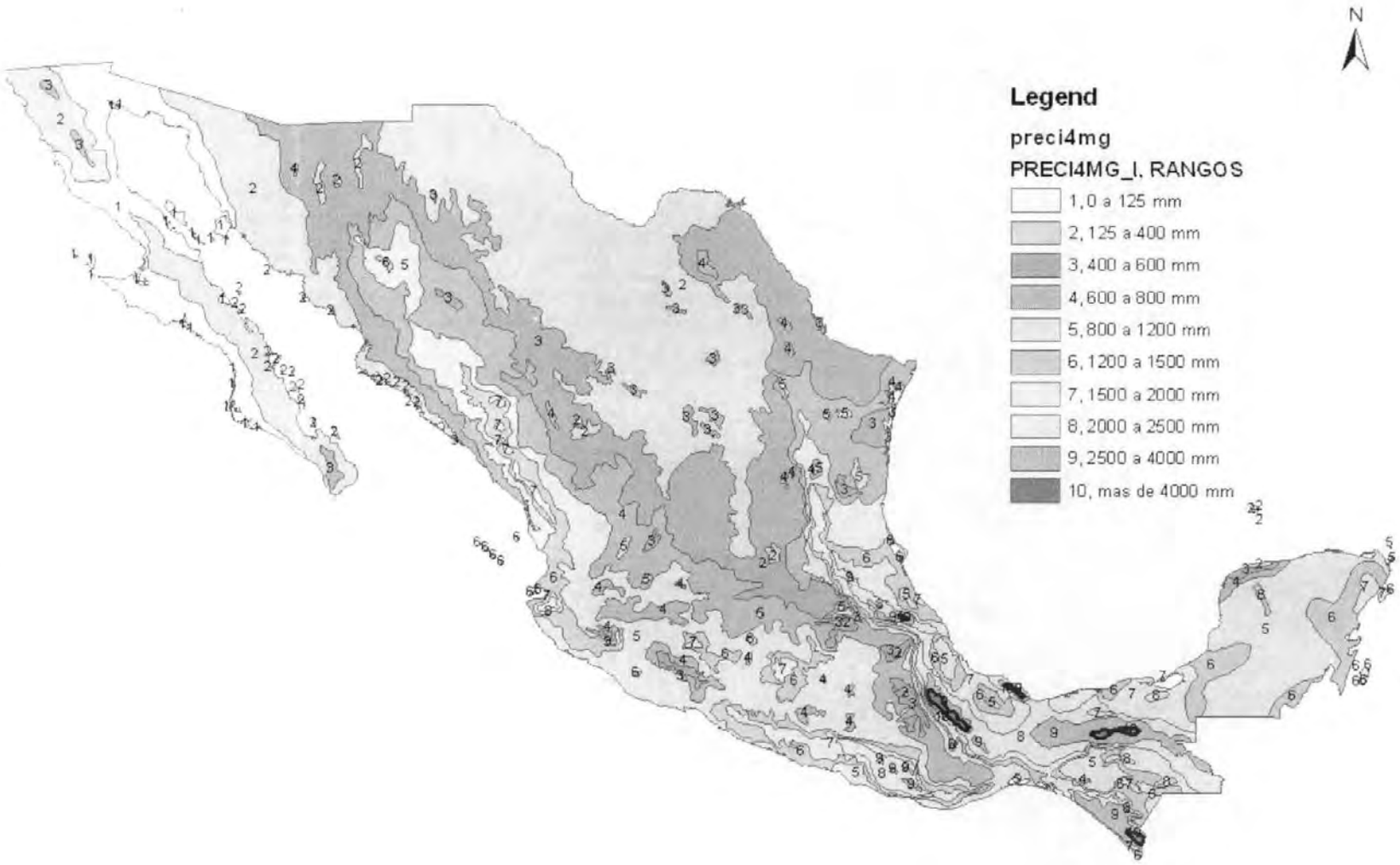
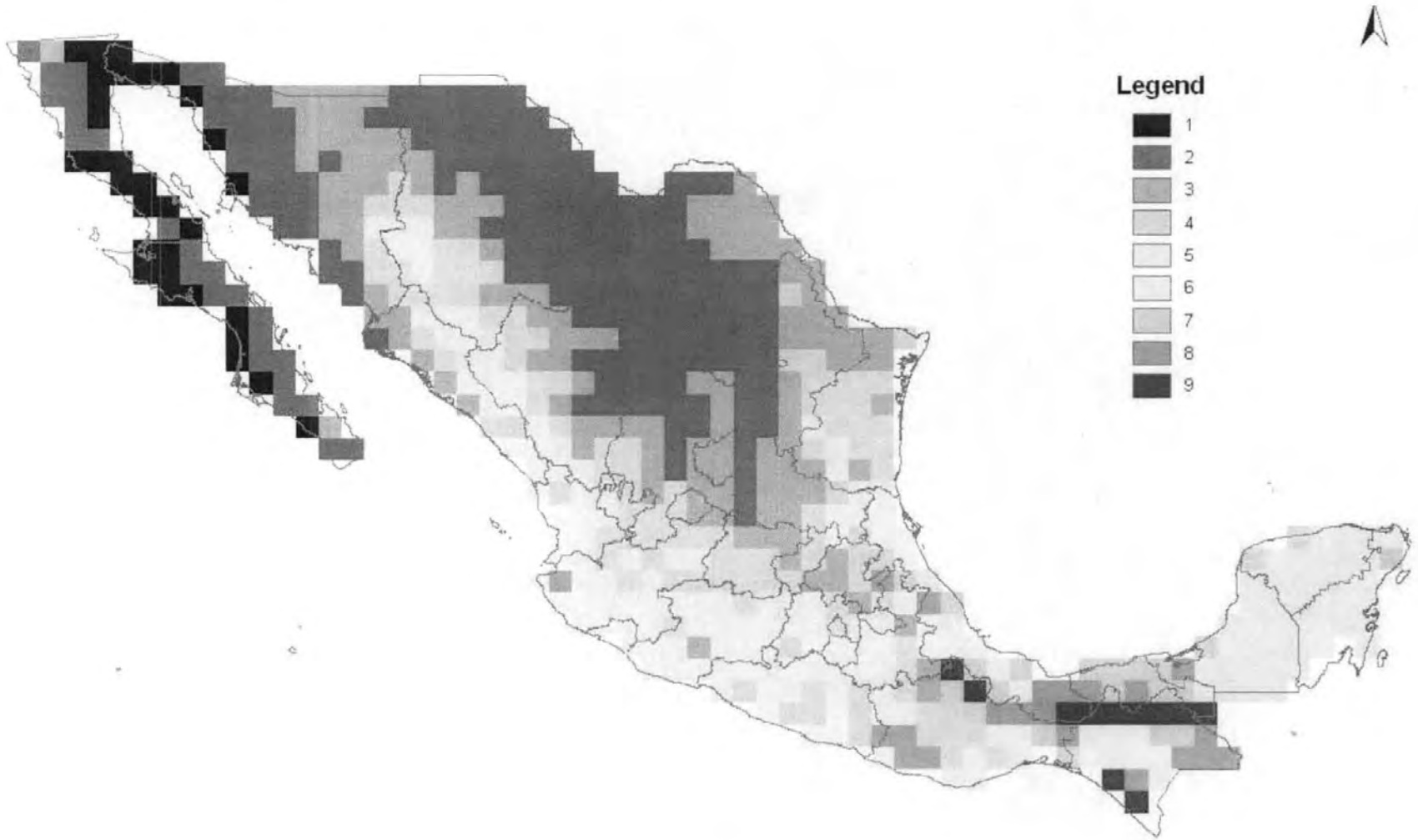


Figure D.4 PRECIPITATION (RASTERS)



APPENDIX E: DIVERSITY, GEOGRAPHIC GRADIENTS AND ENVIRONMENTAL VARIABLES

Figures E.1 Scatter plots of species richness (*S*) versus geographic gradients, endemism and environmental variables.

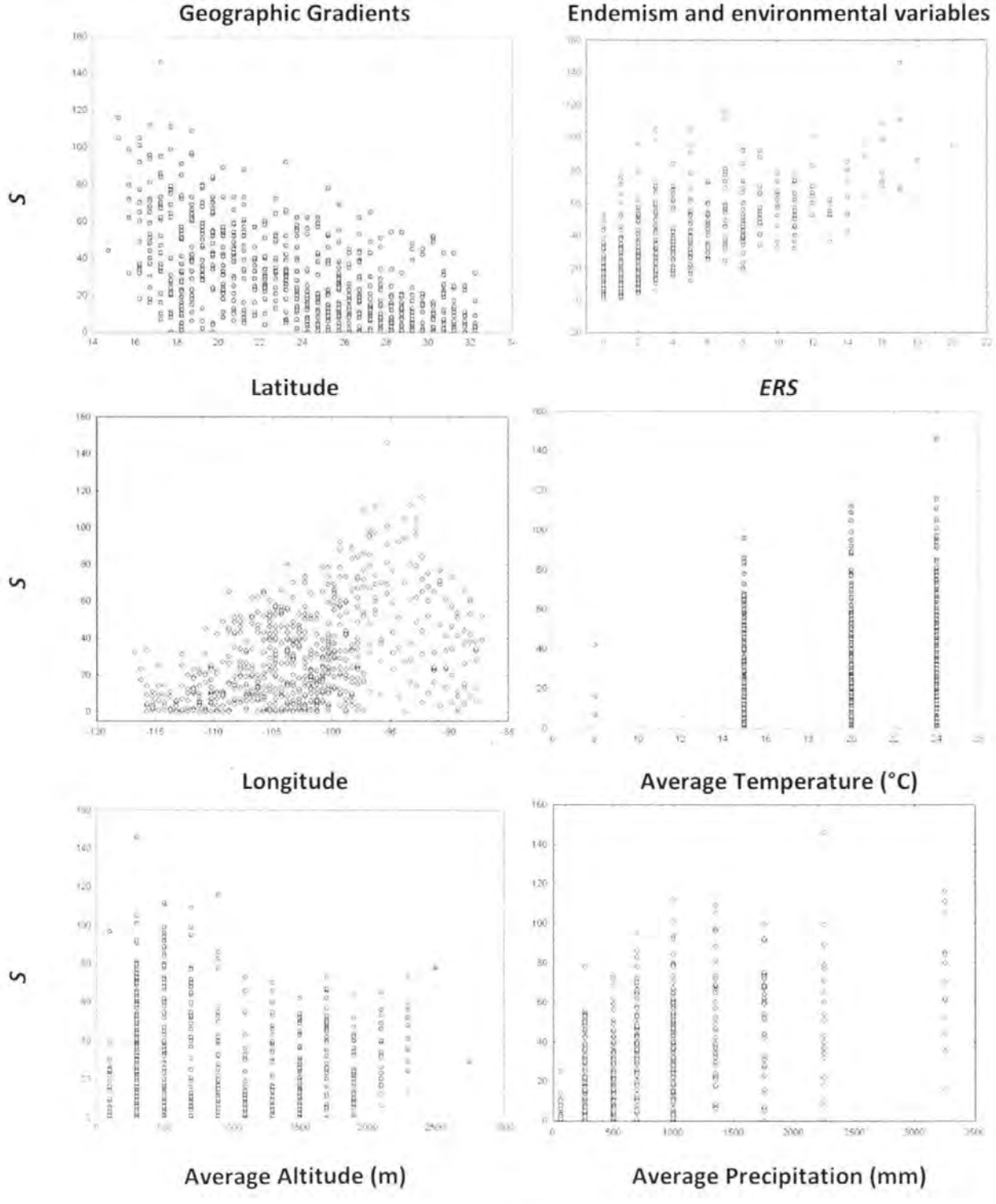


Figure E.2 Scatter plots of Phylogenetic Diversity versus geographic gradients, endemism and environmental variables.

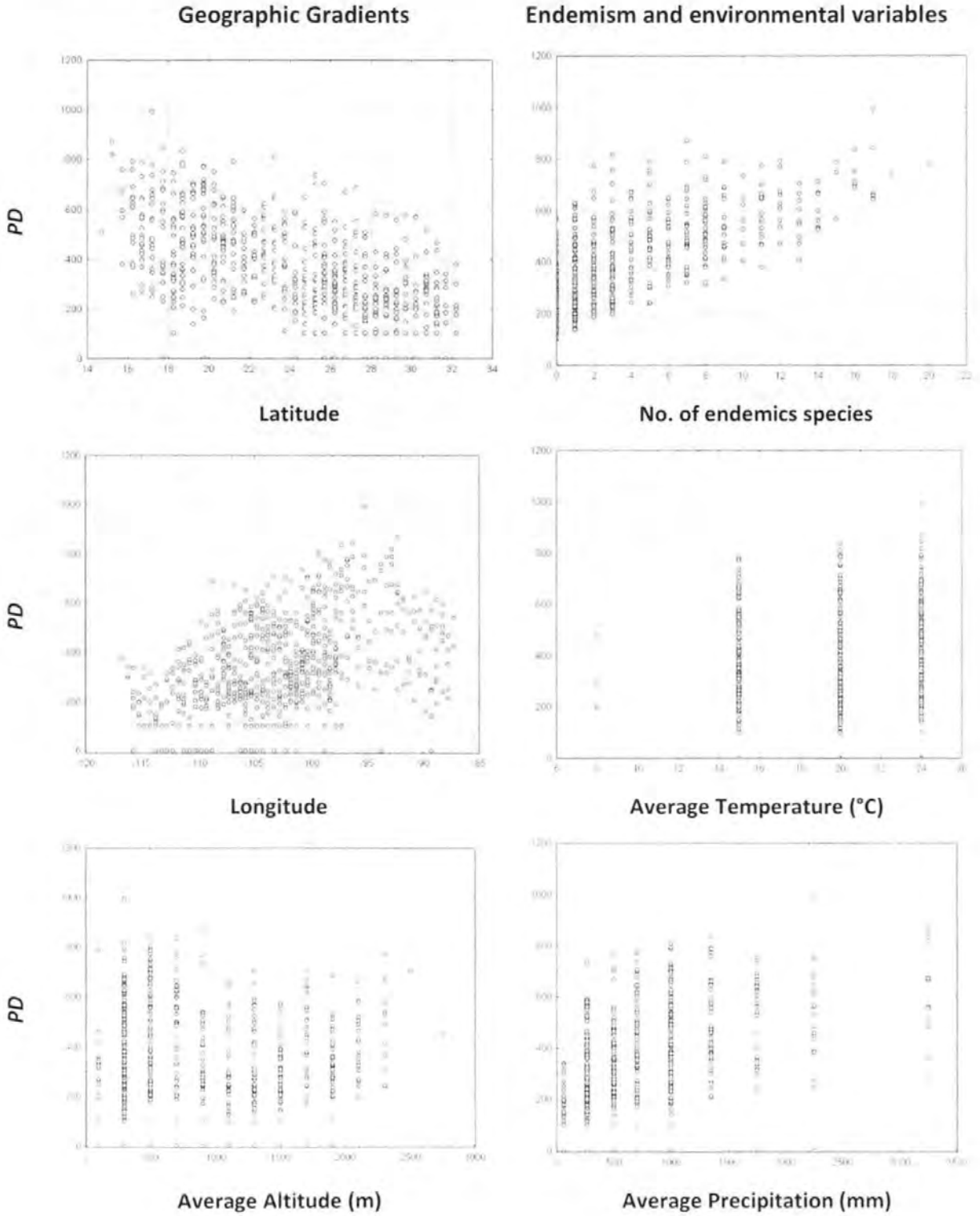


Figure E.3 Scatter plots of Taxonomic Distinctness *versus* geographic gradients, endemism and environmental variables.

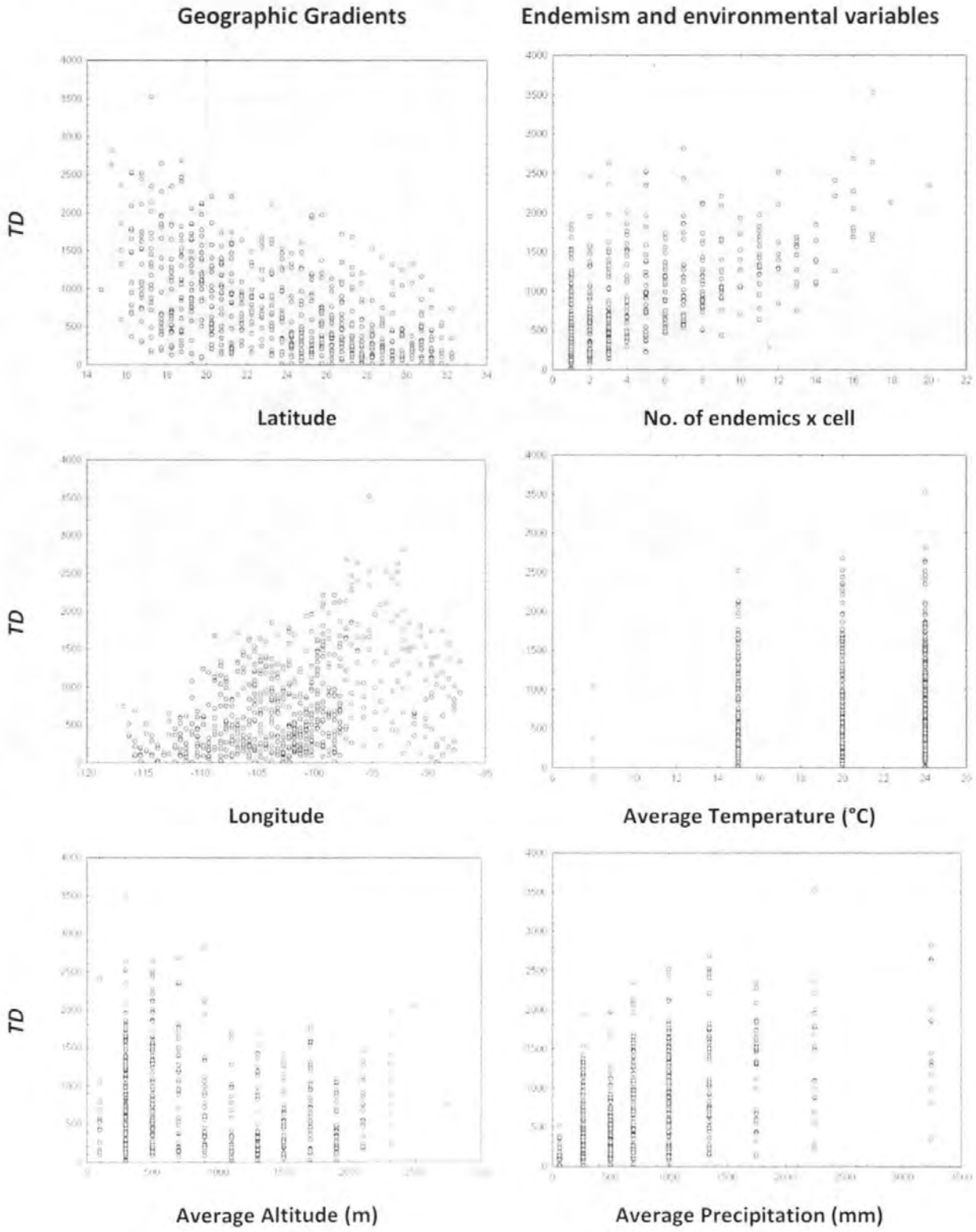


Figure E.4 Scatter plots of Diversity Skewness (Tree imbalance index, I_c) *versus* geographic gradients, endemism and environmental variables.

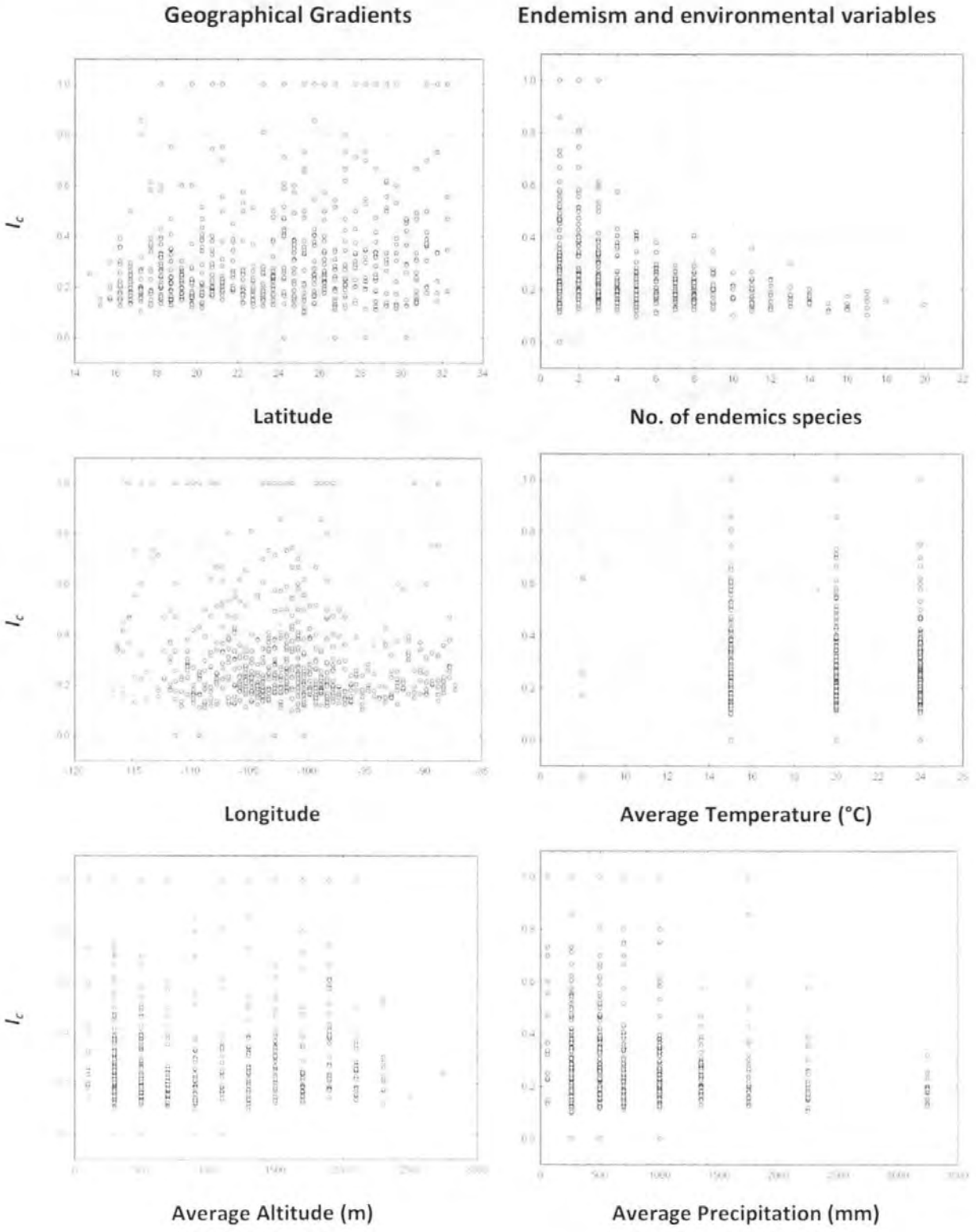
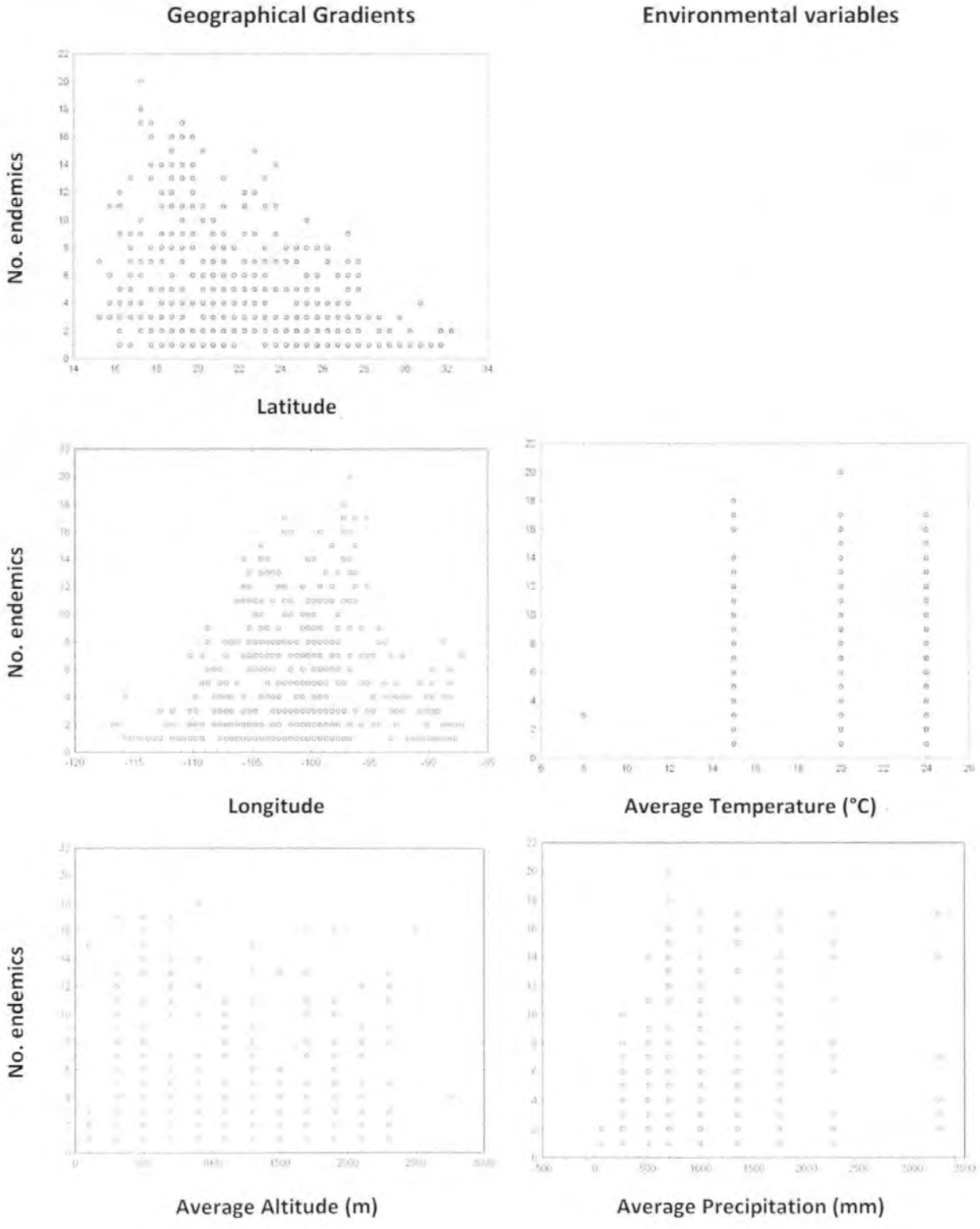


Figure E.5 Scatter plots of richness of endemic species *versus* geographic gradients, phylogenetic diversity and environmental variables.



Appendix F: High Priority Areas

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA1	32.25	-116.75	32	yes	2	9	14	378.261	-43.78633	0.18	N/A		Baja California Norte
HPA2	32.25	-114.75	9	yes	0	1	3	213.043	-34.97921	0.56	N/A		Sonora
HPA3	31.75	-115.75	4	yes	1	1	2	182.609	7.602702	0.33	Constitucion of 1857	Xeric Scrubland	Baja California Norte
HPA4	31.75	-114.25	9	yes	1	1	4	313.043	65.02079	0.22	El Pinacate y Gran Desierto de Altar	Xeric Scrubland	Sonora
HPA5	31.75	-113.75	11	yes	0	1	4	213.043	-57.33118	0.15	El Pinacate y Gran Desierto de Altar	Xeric Scrubland	Sonora
HPA6	31.25	-115.25	11	yes	1	3	5	234.783	-35.59205	0.36	N/A		Baja California Norte
HPA7	30.75	-115.75	33	yes	4	10	15	334.783	-98.85618	0.16	N/A		Baja California Norte
HPA8	30.25	-108.25	51	yes	2	2	7	569.565	46.66081	0.15	N/A		Chihuahua
HPA9	30.25	-107.75	49	yes	0	1	7	408.696	-105.2905	0.13	N/A		Chihuahua
HPA10	29.75	-104.75	19	yes	0	1	8	260.87	-81.13443	0.3	N/A		Chihuahua
HPA11	29.25	-110.75	45	yes	1	3	9	439.13	-56.3751	0.17	N/A		Sonora
HPA12	28.25	-105.25	54	yes	1	1	6	582.609	46.69304	0.11	N/A		Chihuahua
HPA13	27.25	-108.75	65	yes	9	0	8	686.957	106.5666	0.13	Sierra de Alamos and Rio CuchuJaqui	Oak Forest (transformed for agriculture and grazing)	Sonora
HPA14	26.75	-106.75	62	no	4	0	8	669.565	100.8491	0.13	N/A		Chihuahua
HPA15	26.75	-100.25	38	yes	0	1	3	469.565	8.805956	0.18	N/A		Nuevo Leon
HPA16	26.25	-107.75	5	yes	2	0	1	186.957	-5.673613	1	N/A		Sinaloa-Durango

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA17	25.75	-103.75	55	yes	6	2	4	591.304	51.14352	0.17	N/A		Durango
HPA18	25.75	-100.25	69	no	3	1	8	704.348	108.8609	0.16	N/A		Nuevo Leon
HPA19	25.25	-111.75	23	yes	3	2	9	339.13	-32.15687	0.18	N/A		Baja California Sur
HPA20	25.25	-100.75	78	yes	10	6	12	734.783	107.0599	0.1	Cumbres de Monterrey (boundery)	Pine Forest	Coahuila-Nuevo Leon
HPA21	25.25	-100.25	78	no	5	2	9	700	72.27734	0.12	N/A		Coahuila-Nuevo Leon
HPA22	23.25	-109.75	42	yes	3	1	11	521.739	40.71781	0.16	Sierra la Laguna	Thorn Forest	Baja California Sur
HPA23	23.25	-104.25	66	yes	13	2	9	639.13	54.9177	0.15	La Michilia	Thorn Forest	Durango
HPA24	23.25	-99.25	92	yes	8	2	12	808.696	134.795	0.12	N/A		Tamaulipas
HPA25	22.75	-104.25	53	yes	15	3	6	569.565	37.93978	0.12	N/A		Durango
HPA26	22.25	-99.25	60	yes	6	2	5	560.87	0.115843	0.16	N/A		San Luis Potosi
HPA27	22.25	-97.75	30	yes	2	1	3	413.043	-3.18258	0.26	N/A		Tamaulipas-Veracruz
HPA28	21.25	-101.75	52	yes	11	1	4	530.435	3.14596	0.18	N/A		Jalisco-Guanajuato
HPA29	21.25	-99.75	69	yes	8	2	9	643.478	47.99133	0.18	Sierra Gorda		Queretaro
HPA30	21.25	-99.25	88	no	9	0	13	791.304	130.1625	0.15	Sierra Gorda		Queretaro
HPA31	20.75	-89.75	73	yes	6	2	15	647.826	37.73321	0.17	Dzibilchantun (boundaries)	Subdeciduous Tropical Forest (transformed for agriculture and grazing)	Yucatan
HPA32	20.25	-102.25	57	no	11	1	7	700	151.4789	0.17	no	Thorn Forest	Jalisco and Michoacan

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA33	20.25	-98.25	89	no	15	2	13	747.826	83.46402	0.12	Cuenca Hidrologica del Rio Necaxa/Barranca de Meztitlan	Cloud Forest	Hidalgo-Puebla
HPA34	20.25	-97.75	73	no	7	0	11	678.261	68.16799	0.13	N/A		
HPA35	19.75	-103.25	70	yes	13	2	8	704.348	105.1651	0.16	N/A	transformed for agriculture and grazing (Deciduous Tropical Forest)	Jalisco
HPA36	19.75	-102.25	73	no	16	2	9	700	89.90712	0.13	N/A	transformed for agriculture and grazing (Pine Forest)	Michoacan
HPA37	19.75	-101.75	64	no	16	2	9	686.957	110.4231	0.17	N/A	transformed for agriculture and grazing	Guanajuato y Michoacan
HPA38	19.75	-100.75	65	no	12	0	7	660.87	80.47963	0.16	N/A	transformed for agriculture and grazing (Coniferous Forest)	Michoacan
HPA39	19.75	-99.25	52	no	12	0	4	673.913	146.6242	0.22	N/A	Thorn Forest	Mexico
HPA40	19.75	-98.75	73	no	11	0	11	773.913	163.8202	0.12	N/A	Thorn Forest	Hidalgo-Mexico

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA41	19.75	-98.25	83	no	12	1	13	769.565	124.8459	0.13	N/A	Coniferous andForest (transformed for agriculture and grazing)	Hidalgo-Puebla-Tlaxcala
HPA42	19.75	-97.75	84	no	8	1	18	717.391	69.34324	0.16	N/A		
HPA43	19.75	-97.25	54	yes	14	4	9	530.435	-5.480873	0.17	Cofre de Perote	Pine Forest (transformed for agriculture and grazing)	Veracruz
HPA44	19.25	-103.75	80	yes	14	2	12	669.565	34.97142	0.15	Las Huertas	Deciduous Tropical Forest	Colima
HPA45	19.25	-102.25	70	yes	17	3	8	643.478	44.29554	0.17	Pico de Tacintaro		Michoacan
HPA46	19.25	-99.25	78	no	16	1	11	704.348	76.62517	0.15	Desierto de los Leones, Lomas de Padierna, Cumbres del Ajusco, Ins. M. Hidalgo y Costilla)	Coniferous and Oak Forest	Mexico y DF
HPA47	19.25	-98.75	59	yes	13	1	10	665.217	108.5017	0.18	Iztaccihuatl-Popocatepetl	Coniferous Forest (transformed for agriculture and grazing)	Mexico
HPA48	19.25	-97.25	68	yes	17	5	15	665.217	73.45691	0.19	Pico de Orizaba (boundaries)	Coniferous Forest	Veracruz-Puebla
HPA49	19.25	-96.75	79	no	7	2	16	695.652	64.48155	0.17	N/A		Veracruz
HPA50	18.75	-102.75	40	yes	12	3	4	469.565	-1.469506	0.24	N/A		Michoacan

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA51	18.75	-99.75	66	no	9	2	7	660.87	76.65683	0.18	N/A		Mexico-Guerrero
HPA52	18.75	-98.25	66	yes	11	1	7	656.522	72.309	0.16	N/A		Puebla
HPA53	18.75	-97.25	109	no	16	3	23	834.783	109.9119	0.13	Cañon del Rio Blanco	Oak Forest (transformed for agriculture and grazing)	Veracruz
HPA54	18.75	-96.75	96	no	2	0	19	773.913	87.56602	0.15	N/A		Veracruz
HPA55	18.75	-96.25	97	yes	15	3	18	786.957	97.54431	0.15	N/A	Deciduous Tropical Forest	Veracruz
HPA56	18.25	-97.25	72	no	14	2	12	713.043	106.5584	0.17	Tehuacan-Cuicatlan	Deciduous Tropical Forest and Thorn Forest	Puebla
HPA57	18.25	-96.75	85	no	14	4	16	665.217	13.86312	0.15	N/A	Evergreen Tropical Forest (transformed for agriculture and grazing)	Veracruz-Puebla-Oaxaca
HPA58	18.25	-96.25	74	no	11	3	9	665.217	51.54474	0.2	N/A	Evergreen Tropical Forest (transformed for agriculture and grazing)	Veracruz-Oaxaca
HPA59	18.25	-95.25	91	no	5	1	18	743.478	72.73715	0.15	N/A		
HPA60	18.25	-93.75	27	yes	0	1	9	317.391	-80.39841	0.2	N/A		

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA61	17.75	-99.25	78	yes	16	2	15	713.043	85.32082	0.17	General J. N. Alvarez (Boundary)	transformed for agriculture and grazing (Oak Forest)	Guerrero
HPA62	17.75	-97.75	62	yes	13	6	13	547.826	-20.89005	0.18			Oaxaca
HPA63	17.75	-96.75	99	no	16	3	16	752.174	56.68492	0.12	Tehuacan-Cuicatlan	Oak Forest (transformed for agriculture and grazing)	Oaxaca
HPA64	17.75	-96.25	111	no	17	6	22	843.478	112.9181	0.13	N/A	Evergreen Tropical Forest (transformed for agriculture and grazing)	Oaxaca
HPA65	17.75	-94.75	77	no	7	0	14	686.957	62.70711	0.19	N/A		Veracruz
HPA66	17.75	-92.75	79	no	2	5	24	673.913	42.74242	0.15	N/A		Tabasco
HPA67	17.25	-97.25	86	no	18	3	15	734.783	80.14423	0.16	N/A	Oak Forest and Aquatic and Subaquatic Vegetation	Oaxaca
HPA68	17.25	-96.75	95	no	20	3	19	778.261	94.99728	0.14	N/A	agriculture and grazing (Coniferous and	Oaxaca

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA69	17.25	-95.25	146	yes	17	7	34	991.304	169.3667	0.1	N/A	Transformed for agriculture and grazing (Evergreen Tropical Forest)	Oaxaca (Sierra Mixe)
HPA70	17.25	-92.25	84	yes	4	6	23	673.913	25.86498	0.18	Cascada de Agua Azul		Chiapas
HPA71	16.75	-93.75	94	no	8	3	18	730.435	50.27319	0.15	N/A		Chiapas
HPA72	16.75	-93.25	112	no	7	3	24	786.957	53.57346	0.13	Cañon del Sumidero	Subdeciduous Tropical Forest (transformed for agriculture and grazing)	Chiapas
HPA73	16.75	-92.75	96	yes	5	9	16	786.957	100.6095	0.16	N/A		Chiapas
HPA74	16.75	-91.75	68	yes	4	5	11	573.913	-17.84744	0.22	N/A		Chiapas
HPA75	16.75	-90.75	71	yes	1	5	20	565.217	-37.63115	0.19	Lacan_tun/Chan-Kin/Yaxchilan		Chiapas
HPA76	16.25	-96.25	60	yes	12	1	12	626.087	65.33323	0.18	N/A		Oaxaca
HPA77	16.25	-95.25	101	yes	12	2	22	791.304	89.80816	0.13	N/A	Subdeciduous Tropical Forest	Oaxaca
HPA78	16.25	-94.25	92	no	9	4	14	691.304	17.40367	0.16	N/A	Subdeciduous Tropical Forest	Oaxaca-Chiapas
HPA79	16.25	-93.75	105	no	5	4	18	756.522	43.21139	0.14	La Sepultura	Evergreen Tropical Forest (Cloud Forest)	Chiapas
HPA80	16.25	-91.75	60	yes	1	2	7	608.696	47.94193	0.21	Lagunas de Montebello	Evergreen Tropical Forest	Chiapas

HPA_ID	Latitude centroid	Longitude centroid	*S*	Compl	*ESR*	Rare	Risk	*PD*	*PD resid*	*Ic*	PNA	Main vegetation type	States
HPA81	16.25	-90.75	77	yes	1	6	27	626.087	1.837549	0.17	Montes Azules	Evergreen Tropical Forest (Cloud Forest)	Chiapas
HPA82	15.75	-93.25	80	yes	4	8	18	669.565	34.97142	0.15	El Triunfo/ La Encrucijada	Evergreen Tropical Forest (Cloud Forest)	Chiapas
HPA83	15.75	-92.75	99	no	3	7	19	756.522	61.03275	0.16	El Triunfo/ La Encrucijada	Evergreen Tropical Forest (Cloud Forest)	Chiapas
HPA84	15.25	-92.75	105	yes	3	9	22	817.391	104.081	0.15	El Triunfo/ La Encrucijada	Evergreen Tropical Forest (Cloud Forest)	Chiapas
HPA85	15.25	-92.25	116	yes	7	11	25	869.565	125.032	0.12	Volcan Tacana	Evergreen Tropical Forest (Cloud Forest)	Chiapas

APPENDIX G: SOURCES OF LIFE HISTORY TRAIT DATA

Taxonomic group	Source
Didelphidae	Ernest (2003), Myers (2006), Pereira and Daily (2006), Reid, (1997) and Zarza *et al* (2003).
Xenarthra	Ernest (2003), Myers (2006), Pereira and Daily (2006), Reid, (1997), Villa and Cervantes (2003)
Primates	Ernest (2003); Myers (2006), Zaldivar et al (2004), Purvis 1995, Villalobos *et al.* Reid, (1997)
Leporidae	Ernest (2003), Graur *et al.* (1996), Reid, (1997); AnAge: http://genomics.senescence.info/species/index.html; Villa and Cervantes (2003)
Rodentia	Ernest (2003); Myers (2006), Pereira and Daily (2006), PeroBase http://wotan.cse.sc.edu/perobase/testperobase.htm, Reid (1997) and Villa and Cervantes (2003)
Insectivora	Pereira and Daily (2006), Symonds (1999) Reid, (1997)
Carnivora	Ernest (2003), Ferguson and Lariviere (2002), Pereira and Daily (2006) Reid, (1997), Millar and Zammuto (1983), Villa and Cervantes (2003)
Chiroptera	Ernest (2003), Cruz-Neto *et al.*, (2001), Jones et al (2003b), Wilkinson and South (2002), AnAge: http://genomics.senescence.info/species/index.html, Villa and Cervantes (2003).
Perissodactyla	Ernest (2003), Pereira and Daily (2006) and Reid (1997).
Artiodactyla	Ernest (2003); Myers (2006), Pereira and Daily (2006), Reid, (1997). and Villa and Cervantes (2003)