Risks to Global Primate Diversity from Climate Change and Other Pressures

GAFFNEY, LIAM,ROBERT

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Risks to Global Primate Diversity from Climate Change and Other Pressures

Liam R. Gaffney

Abstract:

Primate species are widely threatened from the impact of deforestation and other human activities, with many species already facing high risk of extinction. Climate change poses an additional threat to the world's biota. However, the extent to which future climate change poses a risk to primates in conjunction with the other threats remains largely unclear. This study will utilise bioclimate models in order to assess the potential changes in primate species richness under future climate change scenarios. These results will then be combined with country-level data on forest loss and projected increases in human populations, to establish the potential synergy between these drivers of environmental change and quantify the regions facing the greatest risks to primate species diversity. The response of primate species richness to future climate change was shown to vary between regions and to depend upon the climate model and emissions scenario used. Madagascar generally displayed the largest increase in suitable climate, whereas on the whole, African primates may potentially be impacted the most from adverse climate change. The greatest risk to primate species from the correlating threats of adverse climate change, forest loss and human population pressure, was found in countries of north-west Africa and Asia, in particular the south-east. The results demonstrate the complexity of the link between climate and biodiversity and highlight the importance of the choice of model used to assess climate change impacts on biodiversity. In addition, it is clear that there is a need for urgent conservation measures to be adopted in high risk regions in order to combat threats from climate change to already fragile primate populations.

Acknowledgments

Primate species distributions (ArcMap shapefiles), in addition to their current endangered status and population trend, were obtained from the International Union for the Conservation of Nature (IUCN). Taxonomic data on primate species was obtained from www.bucknell.edu/MSW3/ (Wislon and Reeder 2005).

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List of Abbreviations:

Δ^+	–	Taxonomic Distinctness
GCMs	–	Global climate models
SSTs	–	Sea surface temperatures
IUCN	–	International Union for Conservation of Nature
PCM	–	Parallel Climate Model
HadCM3	–	Hadley Centre Coupled Model, version 3
IPCC AR4 SRES	–	Intergovernmental Panel on Climate Change, Fourth Assessment Report, Special Report on Emission Scenarios

Chapter 1

General Introduction

Climate determines the baseline conditions for life on earth. The distribution of species and ecosystems, at large spatial scales, is primarily determined by climatic conditions. Past changes in climate have led to shifts in species and habitats across continents (e.g. Hewitt 2000) as well as species extinctions (e.g. Mayhew *et al.* 2008; Nogués-Bravo *et al.* 2010). Recent anthropogenic climate change has already led to range shifts in a number of species (e.g. Hickling *et al.* 2006; Parmesan 2006) and the key task for conservationists is to assess and quantify the threat to species and ecosystems from future climate change.

This study will assess the potential risks from climate change and other pressures on the mammalian order *Primates*, comprising of over 400 species and primarily found throughout the tropics in four key biogeographic regions; Asia, Africa, Madagascar and the Neotropics (Fleagle, *et al.* 1999). Primates comprise of the following groups: the Tarsiers, Lemurs and Lorises, new- and old-world monkeys, the Colobines and the Hominoids (Moynihan 1976; Morales *et al.* 1999).

Primates have critical ecological roles as pollinators and seed dispersers (Jernvall and Wright 1998) and therefore have an important place in tropical forest ecosystems across the world. Results from the most recent IUCN assessment of the world’s mammals indicate that primates are among the most endangered vertebrate groups, with up to 50% facing the threat of extinction (Mittermeier *et al.* 2009). Within the main primate-inhabited biogeographic regions species diversity has been found to correlate, at individual sites, with mean annual rainfall, excluding Asia for which the pattern is more complex (Reed and Fleagle 1995), with moist tropical forests forming the primary habitat for 90% of species (Reed and Fleagle 1995; Chapman and Peres 2001; Isabirye-Basuta and Lwanga 2008). Therefore the impacts of climate change on tropical forest ecosystems and patterns of rainfall will be highly important for primate species.

In this chapter, I will briefly introduce the key concepts relevant to this thesis: (i) the nature of future climate change (ii) the general patterns in which species may (and have) respond to changes in climate, (iii) the link between climate and extinction risk, (iv) the current methods used to model changes in biodiversity in response to climate change and (v) the current threats faced by primate species.

Climate Change

Future projections derived from global climate models for a wide range of scenarios indicate an increase in the Earth's mean surface temperature of 1.4 to 5.8°C by the end of the twenty-first century (IPCC 2007). The projected rate of warming is very likely to be unparalleled during at least the last 10,000 years, with land masses warming more than oceans and high latitudes warming more than the tropics (IPCC 2007). In addition to rising temperatures, precipitation levels are projected to increase in high latitude and equatorial areas and decrease in the subtropics (IPCC 2007).

The potential effects warming may have on the frequency and magnitude of large scale climatic events such as the El Niño/Southern Oscillation (ENSO) could have major implications for biodiversity (McCarty 2001) especially since ENSO has displayed an increased intensity since the 1970's compared with the previous 100 years (IPCC 2007). However the impacts associated with ENSO can vary between regions and the upper extremes do not always occur (Latif and Keenlyside 2008). Additionally, sea level is expected to rise in response to melting of the ice caps and increased sea surface temperatures (IPCC 2007) posing a risk to low lying coastal regions.

Ecosystem productivity and species diversity are globally determined by geographic variations in temperature, rainfall and seasonality, therefore ecosystems will respond to projected changes in these variables which will subsequently have an impact on biodiversity (Thomas *et al.* 2008). For instance, the combination of temperature and precipitation is significant in the distribution of global vegetation, which is sensitive to changes in temperature on the scale of years to decades (McCarty 2001).

A wide range of literature has documented changes in natural systems that are already taking place under recent climate change (e.g. Gitay *et al.* 2002; Walther *et al.* 2002; Parmesan and Yohe 2003). However, it is important to consider that factors influencing ecosystems and populations interact in complex ways (Forchammer and Post 2000), for instance temperature is related to moisture availability, which is of high importance to vegetation and general habitat requirements of species (Root *et al.* 2003). Additionally the current, historically unprecedented levels of carbon dioxide will affect plant species and ecosystems, leading to the potential for the development of novel species assemblages and interactions that will further impact biodiversity (Sala *et al.* 2000; Cox *et al.* 2004; Thomas *et al.* 2004). Primates are very habitat specific (tropical forest) and therefore the nature and extent of climate and ecosystem changes will be particularly important.

Climate and Species Diversity

Several changes may take place in species' traits due to warming climates including changes in phenology, species range changes, changes in morphology (body size, behaviour) and shifts in genetic frequencies (Root *et al.* 2003). The anomalous climate of the past half century has been shown to have already affected the physiology, distribution and phenology of some species (Thuiller *et al.* 2005). McCarty (2001) demonstrates how increased global temperatures and observed changes in the timing of seasonal events over recent years have affected ecosystems and a wide range of species. The earlier onset of spring and thus the growing season, brought on by increased temperatures associated with climate change, has been observed and this change in seasonality is occurring in a wide variety of locations and affecting many species (Sparks and Menzel 2002). For instance, frugivorous primates may be affected by changes in seasonal fruit production. Changes in phenology such as this are regarded to be the most responsive aspects of nature to global warming (Sparks and Menzel 2002) and will have fundamental impacts for most species.

The climatic changes in recent years have seen numerous shifts in the distributions and abundance of species (e.g. Hickling *et al.* 2006), with increasing impacts expected for the future, with general patterns including shifts in geographic distributions of species towards the poles and higher elevations (Thomas *et al.* 2004; Thuiller *et al.* 2005; Levinsky *et al.* 2007). The importance of climate on species distributions and richness can be seen by the greater number of species present in areas that have displayed relatively stable climatic conditions for long periods, compared to regions of fluctuating climate in which species numbers tend to be lower and vary over time (Janson 2002; Ohlemüller *et al.* 2006). Although, results from a study by Menéndez *et al.* (2006) indicate that the species richness and composition of communities may take centuries to adjust to current climates.

Janson (2002) explains how species have survived previous climatic shifts by tracking their preferred habitat, or inhabiting climatically stable areas, however the rapid human transformation of the Earth's ecosystems will make such movements in response to current and future climate change much more difficult. Species are likely to respond individually to climate change (Menéndez *et al.* 2006), for instance, species often displayed differential movements during rapid climate changes in the past and if similar trends take place this may disrupt interactions of many species in current ecosystems (Walther *et al.* 2002; Root *et al.* 2003). Many primates, however, will have restricted dispersal abilities on account of tropical forest forming the primary habitat for the majority of species, therefore the impacts of climate change on this biome could have major connotations for primate species.

Climate and Extinction Risk

Of the various threats to global biodiversity, global warming provides the most concern given its potential to even affect areas far from human habitation (Malcolm *et al.* 2006). Moreover, the threat from climate change will be elevated due to widespread human activities weakening the resilience of the natural landscape (Gardner *et al.* 2009). According to the Gitay *et al.* (2002) the current rate of biodiversity loss is greater than the natural background rate of extinction, with widespread losses being an expected ecological consequence of global warming and the magnitude of climate-driven extinctions in particular, having the potential to be very large (Schwartz *et al.* 2006).

Species facing the greatest risk of extinction from climate change are those restricted to shrinking climates, especially small range endemic species and species already under significant strain for which even a small reduction in survival or reproductive success could lead to extinction (Ohlemüller *et al.* 2008; Thomas *et al.* 2008). The projected extinction risks vary between parts of the world and between taxonomic groups, a concern is that the risks might be higher than anticipated if future locations of suitable climate do not coincide with other essential resources such as soil type or food sources (Thomas *et al.* 2004), or in case of most primate species, areas of tropical forest. Furthermore, local species that are lost may be replaced by exotic invasive species (McCarty 2001), which can have a detrimental effect on what would be already fragile ecosystems. Species extinctions can lead to cascading effects throughout communities, particularly in complex ecosystems such as tropical forests, where many species are strongly interlinked (Koh *et al.* 2004).

For species such as primates, already facing high levels of threat from local pressures and environmental change, such as those imposed by human activities, ongoing climate change may present an additional source of stress, increasing the risk of extinction (McCarty 2001). The most severe impacts arising from climate change are likely to arise from a combination of interacting threats, rather than climate change acting in isolation (Sala *et al.* 2000; Thomas *et al.* 2004; Brook *et al.* 2008). For example, the substantial rise in human population throughout the twentieth century from 1.6 to around 6 billion has amplified the pressure on the environment, with human impacts on the environment believed to have increased at least as fast as the population (McCarty 2001). Therefore the pressures on many ecosystems and species are already significant even without anticipated climate change. Although ecosystems and populations are dynamic, varying over time, even in the absence of human disturbance and global warming, species have become extinct or changed their specific ranges (McCarty 2001).

Bioclimate Models

The complexity of the Earth's climate needs to be considered when assessing future impacts on biodiversity (Forchhammer and Post 2000). Large regional differences exist with substantial disparity between regional and global mean changes, which combined with projected increases in climatic variability (IPCC 2007), serve to complicate future predictions. Therefore the type, scale and resolution of models used to assess climate change impacts are particularly important.

A range of bioclimatic models are used to estimate relationships between the distributions of species and climate (Guisan and Zimmermann 2000; Guisan and Thuiller 2005). Bioclimate models in their simplest form comprise of only climate variables, excluding biotic or other environmental factors such as land cover that may also influence species distributions (Pearson and Dawson 2003). Bioclimate models can be developed based on the relationship between observed species distributions and environmental variables, in which climate variables are correlated with observed distributions and as such represent a species' realised niche, since observed species distributions are constrained by non climatic factors (Pearson and Dawson 2003). The development of these models has been driven by the need for better data that can be used for biodiversity management in response to the increased rate of global change (Araújo and Rahbek 2006). Cane (2005) explains the increased importance of models in assessing potential impacts of climate change because past records do not provide a true analogue for the climate that human activity is creating. The scale used by models is particularly important given how observed relationships in ecology tend to vary with local conditions (Jetz *et al.* 2005). However, current bioclimatic envelope models for forecasting the effects of global warming on biodiversity have limitations and the validity of them has to be questioned (Botkin *et al.* 2007). Although, these models can be viewed as a useful first approximation of the potential impact of climate change on the distribution of species (Levinsky *et al.* 2007) and ecosystems as a whole.

A problem arises when evaluating model performance under climate change; to overcome this models are calibrated with current species relationships and then tested against reconstructed species distributions from the fossil record, however this is limited to a few species and regions for which sufficient fossil records are available (Araújo and Rahbek 2006). Historically calibrated models, that generate results that can be evaluated through time, before projecting into the future, are more likely to provide accurate projections of future change (Algar *et al.* 2009). Predictions of future species distributions from bioclimatic models gain uncertainty due to the difficulty accounting for local climate change, inaccurate estimates of species climatic tolerances and unforeseen evolutionary adaptations in populations in response to changes (Araújo and Rahbek 2006).

Accurate predictions of future changes in species diversity in response to global climate change are critical if useful conservation strategies are to be developed (Algar *et al.* 2009). If reliable models predicting the occurrences and richness of rare and threatened species can be produced, they can allow the development of adaptive measures such as land use planning and allow prioritisation for conservation (Parviainen *et al.* 2009).Therefore, given the documented pressures on primate species from deforestation and other human activities, such as hunting and agriculture (Cowlishaw and Dunbar 2000; Chapman and Peres 2001), the future impacts of climate change on primate species richness will need to be investigated in order to determine the potential for climate change to exacerbate, or alleviate these threats.

Current Threats to Primate Species

The major threats that primates currently face are primarily related to habitat modification such as wild fires and deforestation as a result of agriculture and logging operations (Cowlishaw and Dunbar 2000; Chapman and Peres 2001). The impact of wild forest fires is already a significant threat but can be devastating especially when combined with the results of selective logging, which leaves behind large quantities of dead wood acting as additional fuel for fires (Chapman and Peres 2001). With the increased frequency and severity of El Niño dry seasons anticipated under climate change scenarios, wildfires may become one of the most significant destructive forces in tropical forests (Chapman and Peres 2001; Gitay *et al.* 2002). In addition to habitat modification, commercial hunting is another significant threat, for example primates are being hunted in great numbers and in an unsustainable fashion in many areas of Africa and parts of South America (Chapman and Peres 2001; Chapman *et al.* 2006; Corlett 2007).

The already high levels of threat experienced by many primates may be exacerbated by projected climate change. For instance the effect of changing levels of precipitation and temperature will have a significant impact on tropical forests (Wiederholt and Post 2010), a habitat common to most primate species. Possibly one the most important consequences of climate change for tropical forests would be the impact of warming on ENSO, which is the greatest source of interannual climatic variation in the tropics, affecting regional differences in precipitation and temperature (Wright and Calderon 2006; IPCC 2007; Wiederholt and Post 2010).

The interaction between climate change and other pressures, such as those arising from human activities in the form of changing land use can have serious consequences for primates (Chapman *et al.* 2006). The combination of increasingly large areas of agricultural land surrounding primate habitats, often supporting high human densities, and the loss of habitat with climate change will put primate populations under increasing strain (Chapman *et al.* 2006). Furthermore, the loss of particular plant species’ and changes in phenology as a result of climate change can alter ecosystems, affecting primate populations

(Chapman *et al.* 2006). Findings in Eeley and Lawes (1999) suggest that even relatively small environmental change may threaten a relatively large number of primate species.

Very little is known about how climate change is affecting primate populations and how they will be impacted in the future (Wiederholt and Post 2010). Primates are particularly sensitive to habitat loss and with tropical forests already being reduced by deforestation and forest fires in addition to the impacts of commercial and subsistence hunting on populations, the largely unknown impact of global climate change on forest ecosystems will have a considerable outcome on the survival of many species (Chapman and Peres 2001; Chapman *et al.* 2006).

Aims and structure of this thesis

The aim of this study is to assess the risks to global primate diversity from climate change, habitat loss and human population pressures, quantifying which regions on earth are at greatest risk of primate species extinctions. To this end there are three objectives to this study:

1. To assess global primate biodiversity patterns and identify hotspots of high diversity and threatened species (chapter 2).
2. To model current drivers of primate species richness and use future climate data to project potential changes in primate species richness (chapter 3).
3. To investigate the combined additive risk to primate diversity from human population, forest cover and climate (chapter 4).

Chapter 5 will provide an overall discussion of our primate-specific results in the wider context of current literature surrounding potential climate change impacts on biodiversity.

Chapter 2

Patterns of Global Primate Diversity

1.1 Introduction

Primates are widely distributed across the globe, primarily throughout the tropics and in four key biogeographic regions; Asia, Africa, Madagascar and the Neotropics (Fleagle *et al.* 1999). Moist equatorial and tropical forests form the primary habitat for most species (Mittermeier 1988), with many having critical ecological roles as pollinators and seed dispersers (Jernvall and Wright 1998). Primates, therefore, have an important role in tropical forest ecosystems across the world.

There are currently 412 primate species on Earth, excluding *Homo sapiens* (IUCN 2009). The species richness and abundance of non-human primates varies greatly across each biogeographic region, in addition to the levels of taxonomic diversity, although similar trends in the location of species-rich areas can be observed with latitude (Stevens 1989; Peres and Janson 1999) and area of tropical forest (Mittermeier 1988; Reed and Fleagle 1995). The particular patterns of primate species richness and taxonomic diversity are not simply explained by the overall area of tropical forest, although there is a high correlation between the two on a continental scale (Reed and Fleagle 1995), moreover aspects such as rainfall, habitat heterogeneity and physical barriers such as rivers play important roles in shaping primate species richness and distributions at local scales (e.g. Ayes and Clutton-Brock 1992; Reed and Bidner 2004). In addition, the role of historical environmental change through glacial and interglacial cycles since the Pleistocene has set a platform from which current distributions have arisen (Chapman *et al.* 1999; Eeley and Foley 1999; Eeley and Lawes 1999).

The Pleistocene and Quaternary periods have played a significant role in shaping current species distributions and taxonomic diversity. The result of cooling during glacial periods and then subsequent warming in interglacials has led to a sequence of forest contraction and expansion, in which primate species will have been isolated and fragmented for significant periods encouraging speciation, and then dispersal during interglacial periods allowing various species to reintegrate (Eeley and Lawes 1999). This pattern of environmental change would have led to a variety of evolutionary forces operating on primate species (Chapman *et al.* 1999), giving rise to modern day patterns of taxonomic diversity and species richness.

In recent times primate species have come under increasing threat from human activities and changing environmental conditions, and at present nearly half of all the world's primates are threatened with extinction (Mittermeier *et al.* 2009). In order to understand better the current threats faced by primates, a comprehensive review of their global distribution is necessary, taking into account global hotspots of species richness and the diversity of taxa within key biogeographic zones.

1.2 Aims

This chapter will utilise spatial datasets and the latest Red List data (IUCN 2009) on primate species distributions and their respective levels of threat to address the following aims:

1. To calculate and map global patterns of primate species richness, identifying any latitudinal trends.
2. To calculate and map global patterns of primate taxonomic distinctness.
3. To identify global hotspots of threatened and vulnerable species.

2. Methods

Species data

Current distributions for 406 primate species were obtained from IUCN (2008) and combined with a 0.5° resolution grid of the earth's landmass using ArcGIS. The grid cells which overlapped by at least 10% with the species' shape file were recorded as "present" for that species. The presence/absence data were used to produce a species richness table showing the number of species present in each 0.5° grid cell, which was then displayed in ArcMap. The Red List (IUCN 2009) has distinguished 415 primate species, however in this study we can only account for 406 species due to the following five species having a distribution too small to be accounted for within a particular grid cell; *Lepilemur tymerlachsonorum*, *Macaca pagensis*, *Mircrocebus mamirata*, *Procolobus kirkii*, *Tarsius sangirensis*. In addition, two species included on the Red List of primate species: *Palaeopropithecus ingens* and *Xenothrix mcgregori* are already classed as extinct. The other species, *Miza zaza*, is acknowledged despite no species shape file being available, due to limited knowledge of its distribution at the time of writing. The final species included on the Red List but not here are *Homo sapiens*, which are not relevant to this study which focuses on non-human primates, therefore only 406 species have been accounted for.

We analysed latitudinal trends in species richness by plotting species richness against latitude at two resolutions: globally and for the four main biogeographic zones (Asia, Africa, Madagascar, and the Neotropics) separately.

Taxonomic Distinctness

We calculated the taxonomic distinctness of the species present in each grid cell in order to attain a more adequate measure of biodiversity, rather than simply using species richness, providing data on the 'relatedness' of species (Clarke and Warwick 1998). First, a primate taxonomy was obtained from the Bucknell website (Wilson and Reeder 2005; http://www.bucknell.edu/MSW3/) and was used to produce a taxonomic table based on the Linnean classification, with the following levels: *order, suborder, infraorder, superfamily, family, genus, species*. Sub species was not included due to insufficient data. The taxonomic table, in conjunction with the presence/absence data, was used to deduce the taxonomic distinctness of each grid cell with at least two species present, similar to the methods used in several previous studies (e.g. Clarke and Warwick 1998; Warwick and Clarke 1998; Clarke and Warwick 1999; Mouillot *et al.* 2005), using the following equation:

$$\Delta^{+} = [\sum\sum_{i<j} \omega_{ij}]/[m(m-1)/2]$$

Clarke and Warwick (1999)

Where m is the total number of species in a particular study and ω_{ij} is the weight (path length) given to the taxonomic relationship between species i and j (Clarke and Warwick 1999). Taxonomic distinctness (Δ^{+}) can range from 0, low values of diversity through to 1, indicating the highest diversity/taxonomically distinct assemblage.

Taxonomic distinctness (Δ^{+}) is the average number of steps up the hierarchy that must be taken to reach a taxonomic rank common to two species, computed across all possible pairs of species in an assemblage (Clarke and Warwick 1999; von Euler and Svensson 2001; Mouillot *et al.* 2005), i.e. within each grid cell, therefore presenting an estimate of the average evolutionary distance between different species within an assemblage. Δ^+ provides an adequate measure of taxonomic diversity when only presence/absence data are available, with the impact of an individual species depending upon the overall species composition of the assemblage (von Euler and Svensson 2001). Using Δ^+ is beneficial because it utilises simple species lists such as presence/absence data, it attempts to capture phylogenetic diversity rather than simply the number of species and is more closely linked to functional diversity (Clarke and Warwick 1999). Additionally, Δ^+ has been shown to decline monotonically in response to environmental degradation whilst being relatively insensitive to major habitat variations, removing the limitations associated with species richness measures of biodiversity, which are more strongly affected by habitat type and complexity (Warwick and Clarke 1998), therefore Δ^+ allows comparisons to be made across various habitats.

Threatened Species Data

Data collected from the IUCN Red List website provided information on the conservation status of each species: Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern (IUCN 2009). The upper limits in terms of the level of threat a particular species is facing; Critically Endangered, Endangered and Vulnerable were combined for each species and a total was calculated for each grid cell to provide an overall sum of threatened primate species. From this the percentage of threatened species in each grid cell was calculated and displayed in a global map. Similarly, the population status of each species was obtained i.e. decreasing, stable, increasing, unknown, from the Red List (IUCN 2009), and the percentage of primate species with decreasing populations was calculated for each grid cell.

3. Results

3.1 Species richness

Primate species occur in four biogeographic regions; Asia, Africa, Madagascar and the Neotropics (Fig. 2.1). Areas with the highest concentration of species richness are the Amazon River Basin in South America and the Congo River Basin in Africa. Outside of these two regions, Madagascar has the highest number of primate species, which is concentrated around the coasts with the narrow central spine of the country being mostly devoid of primates. For much of Asia the number of species per-grid cell is lower than in Africa and Madagascar even though the total number of primate species in this region is higher than in the latter two. Grid cells with only one species present predominantly occur on the edges of more primate-rich areas and at greater latitudes (Fig. 2.1). This is particularly noticeable in areas of North Africa and those bordering the Sahara desert, northern parts of India and China, and upper and lower reaches of the Neotropics.

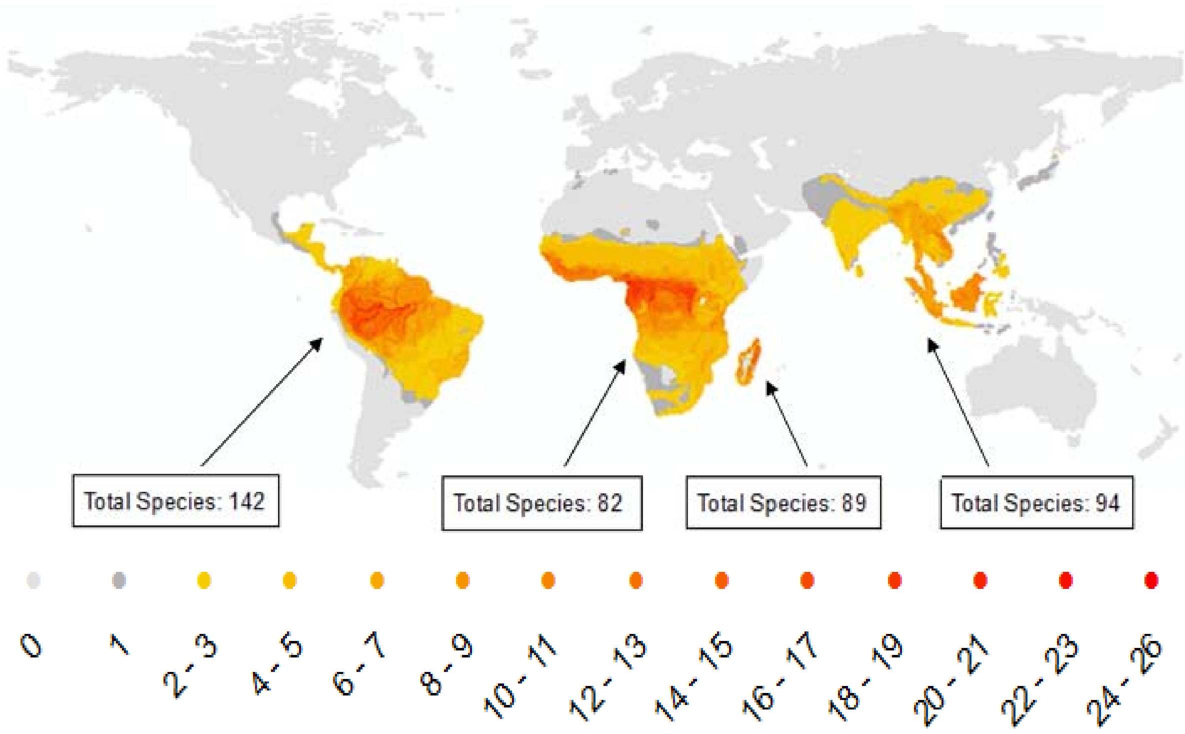


Figure 2.1: Total species richness - the numbers in each box represent the number of primate species present in each biogeographic zone; The Neotropics, Africa, Madagascar and Asia.

Given the distribution of species richness against latitude (Fig. 2.2) it is evident that primate species richness declines with increasing distances from the equator, with the areas of high species richness concentrated between 20° North and South. Africa and the Neotropics follow a similar pattern with the greatest species richness occurring between 15° North/South, although in the Neotropics this is weighted towards -15° South. The pattern for Madagascar is restricted due to the comparatively small area of the island and it being constrained to southern latitudes. Similarly the distribution for Asia is weighted towards northern latitudes due to most of the land mass being situated north of the equator.

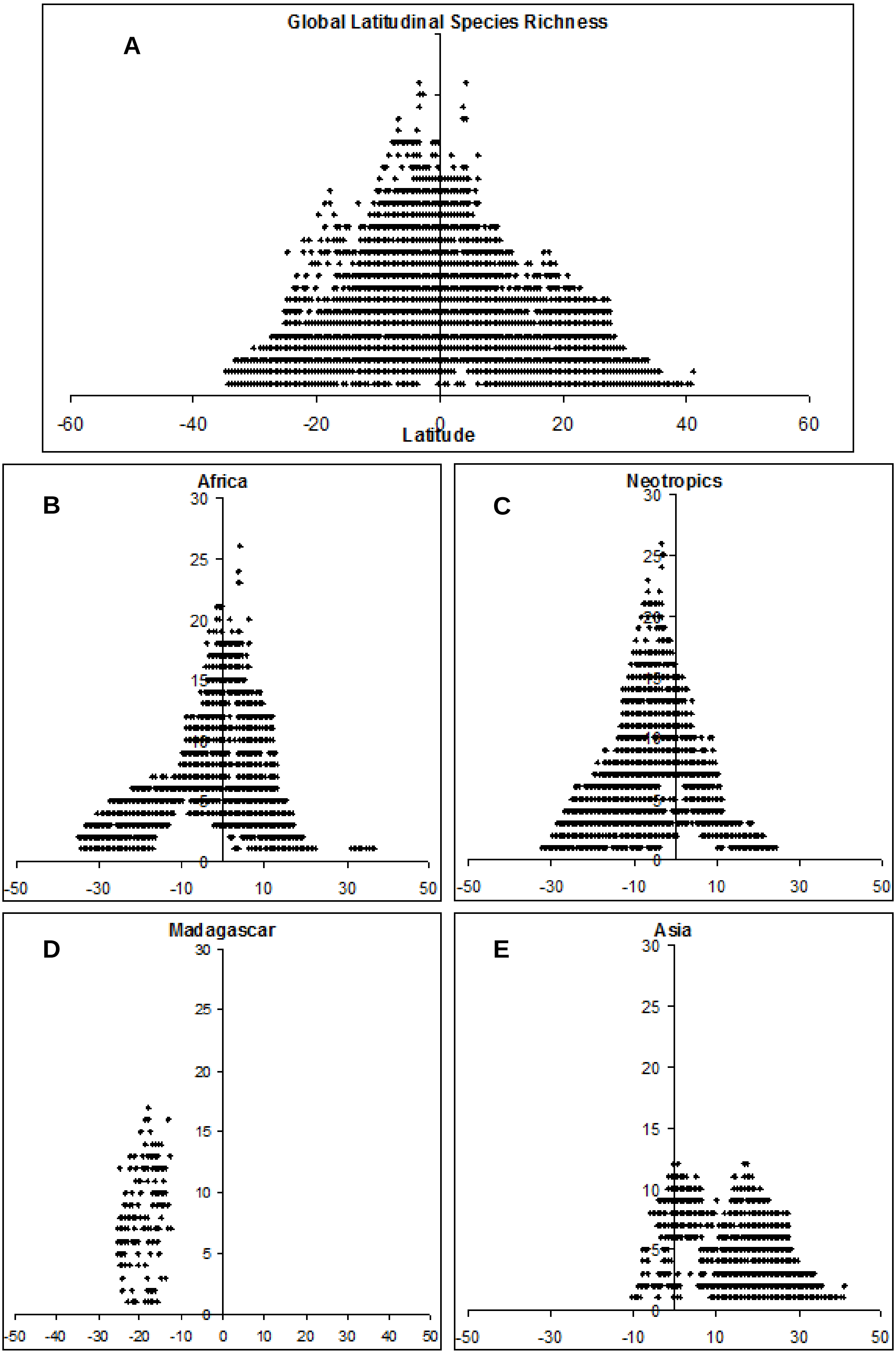


Figure 2.2: Latitudinal primate species richness gradients - shown globally (**A**) and for the four biogeographic regions separately (**B**-**E**). It is clear that the majority or primate species are located between 20° North and South of the equator.

3.2 Taxonomic distinctness

The global taxonomic distinctness (Δ^+) of primate species (Fig. 2.3) provides a value of the unrelatedness of species within a grid cell and it is apparent that Africa possesses the highest levels of taxonomically distinct species, excluding southern Africa, with large areas containing Δ^+ values close to 1, which relates to the most irregular observed taxonomic tree (Mouillot *et al.* 2005). Outside of Africa, areas of south-east Asia and southern India possess relative high levels of Δ^+, particularly along the Sunda Shelf region. In contrast, the lowest levels of Δ^+ occur throughout the northern parts of Asia and Central America, with the bulk of South America and Madagascar displaying similarly high levels of Δ^+.

In comparison with the species richness map (Fig. 2.1) large differences between species richness and Δ^+ become apparent; particularly for Africa, which has almost universally high levels of Δ^+ despite moderate levels of species richness for most of the continent outside of the west-central band around the Congo Basin. Similarly the high levels of Δ^+ for parts of Asia such as the southern extent of India are not matched by particularly high levels of species richness.

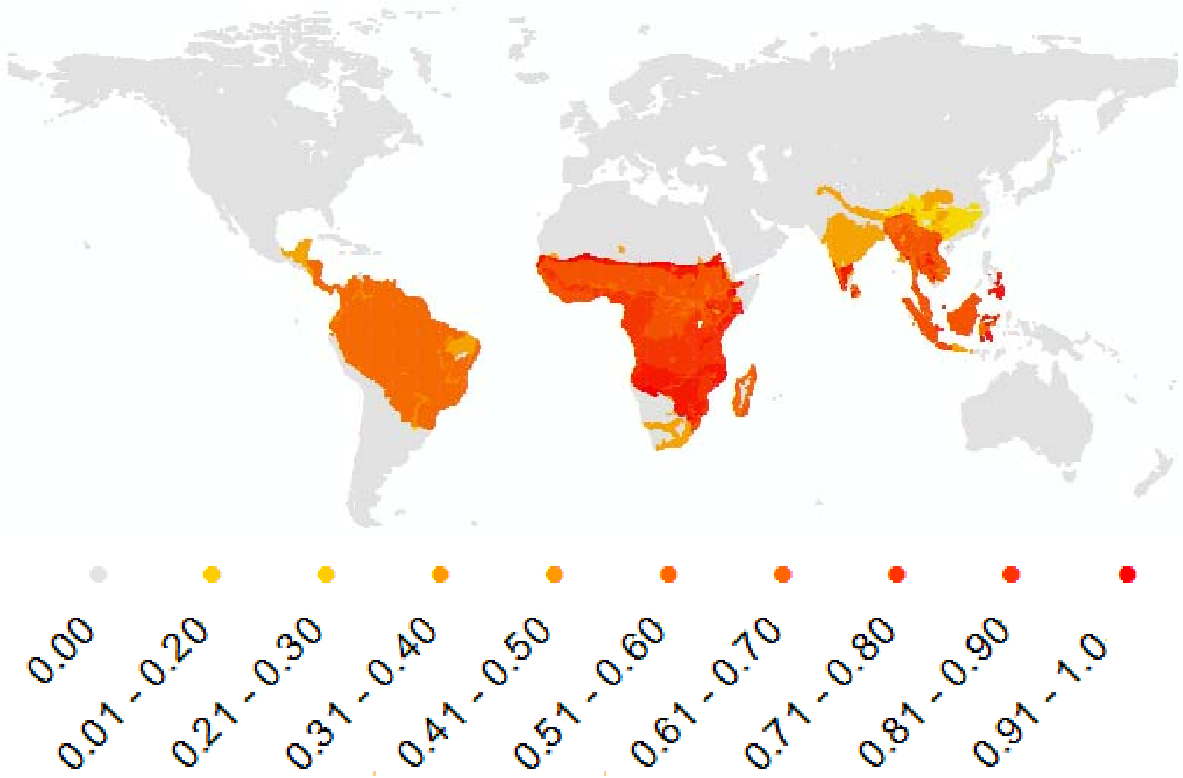


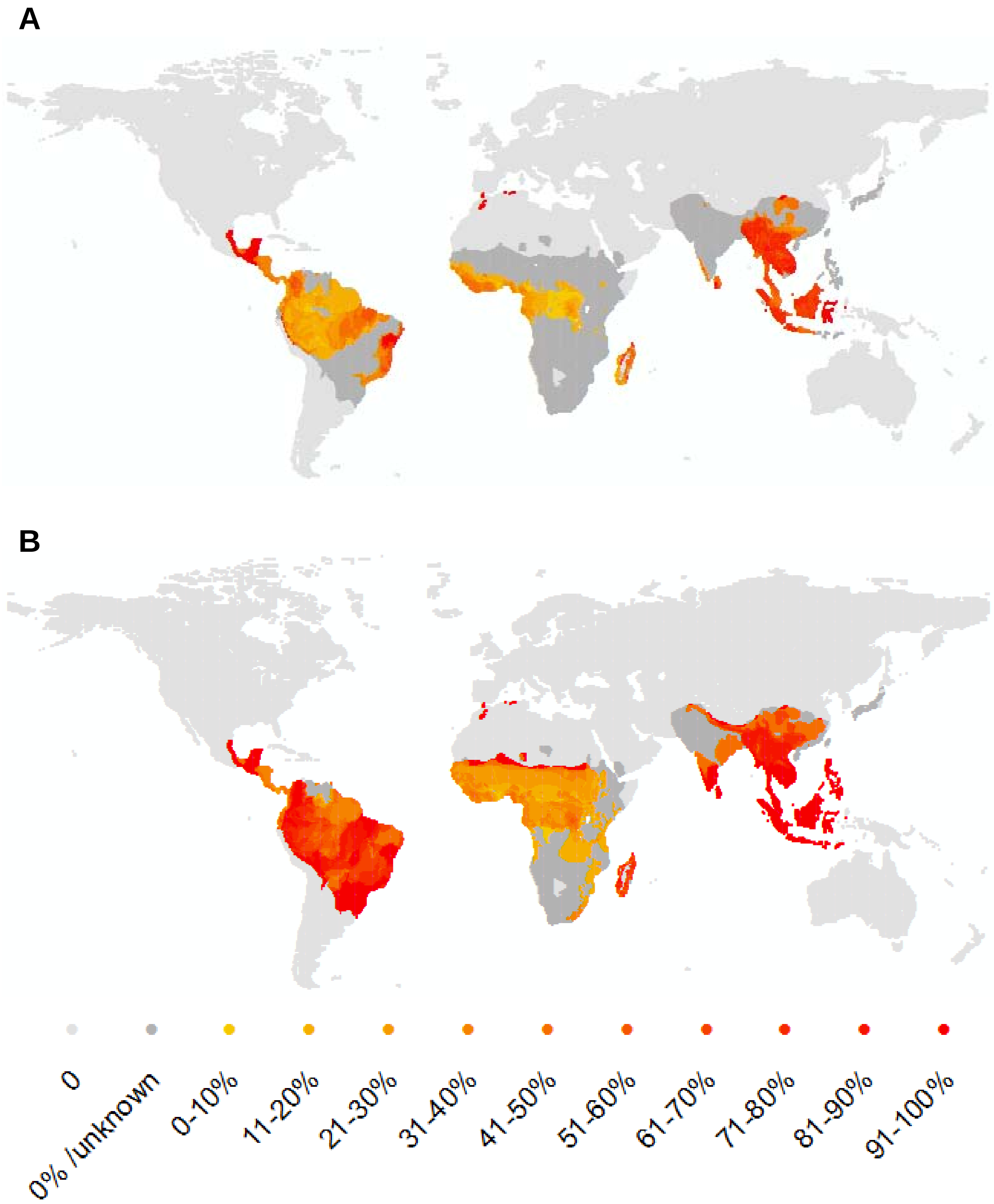
Figure 2.3: Global primate taxonomic distinctness (Δ+) - the higher values indicate a more taxonomically distinct species assemblage. Africa is shown to have the most unrelated, taxonomically distinct species assemblage, followed by the Sunda Shelf region of south-east Asia, and southern India.

3.3 Threatened species

The regions with the highest percentage of threatened primate species are south-east Asia, upper Central America and along the eastern coast of Brazil (Fig. 2.4A). Africa on the whole, except for small areas in the Mediterranean region of North Africa and the central-western band covering the Congo River Basin, has comparatively few threatened species present. In stark contrast, there is a much larger geographic area of primate species exhibiting a declining population trend (Fig. 2.4B), incorporating regions that have no threatened species currently present.

Much of South America, Madagascar and the majority of Asia, excluding a section of India and Pakistan, have very high percentages (around 70%) of primate species with decreasing populations. Africa is the region with the lowest levels of decreasing primate populations similar to the trend displayed in the percentage of threatened species map (Fig. 2.4A). However, there is a larger geographic area of decreasing populations in Africa in comparison to the area of threatened species, with particular concern for the locations just below/bordering the Sahara desert, and the northern Mediterranean region. Madagascar is home to a large number of primate species, especially given its size in comparison to other the biogeographic regions, however it is almost entirely comprised of high percentages of threatened and decreasing primate populations. The percentage of decreasing populations per grid cell in particular, are considerably high in Madagascar (60-70% plus), and it could be expected that this will eventually lead to elevated numbers of threatened species.

Thus, when considering the percentage of threatened species, in addition to the percentage of primate species with decreasing populations, the main hotspots of threatened species are Madagascar, south-east Asia, west-central Africa, roughly covering the area of the Congo River Basin, Central America, large parts of Amazonia and the coastal areas of Brazil.



<u>Figure 2.4</u>: Distribution of threatened primate species – showing the percentage of threatened species per grid cell (**A**) and the percentage of decreasing primate populations per grid cell (**B**). The dark grey areas represent areas in which primate species are present but have either 0% threatened species/decreasing populations or insufficient data on the conservation status/population trend were available. It is clear that there is a much greater amount of decreasing primate populations, leading to the possibility that the numbers of threatened species will increase.

4. Discussion

4.1. Species Distributions and Richness

Areas with the highest levels of primate species richness are the Amazon River Basin in South America and the Congo River Basin in Africa (Fig. 2.1) as has been previously observed (Eeley and Foley 1999; Fleagle *et al.* 1999; Peres and Janson 1999). One of the areas with the highest values of primate species richness is western Amazonia, which is regarded to have one of the most diverse mammalian communities in the Americas (Costa *et al.* 2000). The high values of primate diversity for Madagascar are well documented, in particular by Ganzhorn *et al.* (1999) who claimed that the island holds the third highest primate diversity of any country on Earth, supported in part by our results, which indicate Madagascar to have the third highest number of primate species out of the four biogeographic zones (Fig. 2.1). Although, in the case of Madagascar it has been proposed that little mammalian competition on the island has made such high levels of primate species richness possible (Ganzhorn *et al.* 1999).

The clear pattern in which high species richness follows the tracks of the Amazon River (Fig. 2.1) may be a result of very high tree density with a wide variety of vegetation due to the river providing fertile soils, and consequently resource rich areas capable of supporting multiple species, although observer bias will need to be considered as people use the rivers as a transport mechanism throughout the forests, thus increasing the likelihood of sightings along tracks of the Amazon. Costa *et al.* (2000) suggest this pattern along the Amazon has arisen in response to historic climatic and vegetation fluctuations in response to major glacial cycles.

The general increase in species richness from east to west across the Amazon (Fig. 2.1) has also been observed by Peres and Janson (1999) who show how the interfluvial regions of the western Amazon are substantially richer than those of east Amazonia. Peurtas and Bodmer (1993) link these superior levels of species richness present in the western Amazon to the greater floral diversity within the area which has greatly influenced species diversity. In addition, the important role rivers have played in constraining the dispersal of Amazonian primates is highlighted by Ayres and Clutton-Brock (1992), who discuss how species that evolve in areas closely bounded by major rivers are likely to have smaller geographic ranges than those evolving at a greater distance from permanent rivers. Furthermore, the considerable density of rivers found in the

Amazon rainforests probably contributes to the high diversity of mammals associated with them (Ayres and Clutton-Brock 1992), supporting our results which show how the reaches of the Amazon have some of the highest concentrations of primate rich grid cells (Fig. 2.1). This impact from rivers on species richness is also apparent in Africa with the high levels of species richness throughout the Congo River Basin, although again this could be a result of observer bias with rivers providing the easiest routes to travel through the dense tropical forests, increasing the likelihood of sightings along the rivers path.

In addition to riverine barriers, elevational barriers are known to exist and may present a major obstacle to primate distributions. Gradients of species richness tend to be steeper near higher elevations, a pattern that is prominent in South America where there is a rapid decline in species richness over a relatively short distance adjacent to the Andes Mountains (Fig. 2.1) (Eeley and Lawes 1999). Hence the patterns of primate distribution and diversity in South America are partly a consequence of the combined influence exerted by riverine and elevational barriers. Alternatively, higher altitude locations may have provided areas of forest refugia during periods of increased aridity in tropical lowlands (Eeley and Lawes 1999) providing a refuge for species which would have become isolated and subsequently followed different evolutionary paths. This could explain areas of lower species richness or where just one species is present, due to these populations being isolated at higher altitudes.

The clearest evidence of any kind of natural barrier to species dispersal is the Sahara desert in northern Africa, which appears to restrict the northward distribution of primate species, with an abrupt end in primate-inhabited grid cells along the edge of the region. This is the largest part of Africa that is devoid of primates. In contrast, the highest primate numbers in Africa have been found to occur at sites composed of a complex mixture of different habitats (Fleagle *et al.* 1999) such as the areas throughout the Congo River Basin (Fig. 2.1). This supports Lehman (2004), who found a positive relationship between primate species richness and habitat heterogeneity, a relationship driven by the increased number of ecological niches in diverse habitats.

Much of Asia has moderate level of species richness despite having a greater number of species present across the continent than Africa and Madagascar, a finding that is supported in other assessments of primate diversity (Reed and Fleagle 1995; Fleagle *et al.* 1999; Reed and Bidner 2004). There are several possibly reasons for this; site to site variation in primate communities and various habitat parameters across south-east Asia have been observed by Gupta and Chivers (1999), who attributed it to the existence of human-induced microhabitats, suggesting that these microhabitats may account for variations in primate community structure at broader scales. The impacts of human activity throughout the continent may have reduced primate numbers, particularly considering the high population densities of countries such as Bangladesh, India and China. Alternatively, Reed and Bidner (2004) suggest it potentially could be due to Asia possessing more primate species in the 5-10kg category, and that this may be related to resource acquisition in such a way that species numbers within a community are restricted.

The region with the highest species richness in Asia is situated along the Sunda Shelf, a region characterised by intermittent volcanic activity over the last 100million years producing large mountainous areas, which were separated by rising sea levels during the Holocene forming many small islands (Heaney 1984). The distribution of primates across the islands of the Sunda Shelf is believed to be best explained by extinctions of species from smaller islands after they became isolated from the main land due to the rising sea level (Harcourt 1999; Harcourt and Schwartz 2001). Additionally, large variations in rainfall across south-east Asia associated with the monsoon have produced a varied vegetation structure and a uniquely rich fauna along the Sunda Shelf (Gupta and Chivers 1999) which could account for greater numbers of primate taxa due to the large variety of habitats and available food resources being able to accommodate more diverse species assemblages.

4.2 Causes of Species Distributions and Richness

Tropical Forest

Reed and Fleagle (1995) analysed primate communities in South America, Africa, Madagascar and Asia, with their results displaying a high positive correlation between the number of primate species present and the area of tropical forest, in addition to a correlation, at individual sites, between species diversity and mean annual rainfall in each biogeographic region except Asia. There are few primate species adapted to either temperate or non-forest habitats (Reed and Fleagle 1995), something that is also evident from the latitudinal distribution of primate species (Fig. 2.2). This could imply that primate diversity at a continental level is determined primarily by the area of tropical forest (Reed and Fleagle 1995). Thus it could be concluded that the large areas of tropical forest on Madagascar may have played a key role in supporting the high species richness on the island.

Mittermeier (1988) demonstrates how the equatorial regions of South America have extensive forest cover and boast some of the highest levels of primate diversity and endemism in the world; our results also show this area with high concentrations of species-rich grid cells (Fig. 2.1). Similarly the habitats in south Asia that hold some of the higher levels of primate species richness, span two main forest formations; the deciduous monsoon rainforests of mainland Asia and the evergreen forests on the Sunda Shelf Islands (Gupta and Chivers 1999), which include species-rich areas such as Sumatra, Java, Borneo and Malaysia.

In a typical forest environment, a high value of tree density can be associated with greater amounts of food and resources that primate communities require, thus it could be expected that more diverse primate communities will feature in areas of high tree density (Gupta and Chivers 1999), a theory supported by the species-rich areas synonymous with the tropical regions of South America, Africa and Asia in addition to providing a possible explanation for the large numbers of primate species on the tropical island Madagascar. Therefore assuming that it is simply the area of forest cover that dictates primate species richness is an oversimplification, and although it may be the case on a broad scale, the complexity of habitats that comprise these primate rich regions will have a significant impact on levels of primate species richness (Eeley and Lawes 1999).

In addition to forest cover, several authors have shown the importance of rainfall in relation to primate species richness (Reed and Fleagle 1995; Chapman *et al.* 1999; Peres and Janson 1999). For example, Asia is subject to monsoon rainfall providing high levels over a short period each year, which could be expected to encourage very different patterns of plant productivity than that found on other continents (Reed and Fleagle 1995). Following this, the vegetation structure and composition throughout south-east Asia can be accounted for by the variation in rainfall across the region, for example; low tree species diversity and density in the drier regions of western India, to the high tree species diversity and density in the high rainfall areas of south-east Asia (Gupta and Chivers 1999) promoting a gradient in the habitats across the region and potentially explaining the higher levels of primate species richness observed over south-east Asia (Fig.

2.1). However, even within a single forested region that receives similar levels of rainfall, primate communities that occupy different areas can vary (Chapman *et al.* 1999) and in some cases this may be a consequence of physical and biotic barriers.

Other Factors

Physical and biotic barriers can restrict the dispersal of individuals, limiting the distribution of taxa and preventing gene flow by splitting species ranges (Eeley and Lawes 1999). Barriers to species dispersal can include large rivers (Ayres and Clutton-Brock 1992), mountain ranges (Eeley and Lawes 1999), or more subtle features such as forest types that do not provide appropriate food items at certain times of the year (Chapman *et al.* 1999).

Habitat diversity may operate in conjunction with riverine barriers, for example interfluvial regions are characterised by habitat variability (Lehman 2004) and such regions are generally the areas with the greatest numbers of primate species, for example, the Amazon. Riparian forests typically border the banks of large rivers and are often backed by a variety of moist woodland habitats (Ayres and Clutton-Brock 1992) in which primate diversity and abundance can vary considerably, for instance between non flooded moist forest and flooded forest (Lehman 2004). The effect of rivers inhibiting species dispersal and the habitat heterogeneity created by interfluvial regions could be expected to promote speciation leading to the high levels of species richness observed in South America around the Amazon and across tropical west-central Africa throughout the Congo River Basin (Fig. 2.1). The action of rivers dissecting large areas of forest or the topography of a region can potentially have an impact on species distribution and richness. For example, the patterns of species richness throughout South America could be attributed to this, due to the combined effect of the Amazon River and mountains such as the Andes (Ayes and Clutton-Brock 1992; Eeley and Lawes 1999).

However, there is debate about the contribution of rivers such as the Congo and Amazon to patterns of diversity, with other factors such as forest fragmentation often thought to initiate population differentiation with rivers acting later to limit dispersal and therefore reinforce and maintain differentiation (Chapman *et al.* 1999). Although in areas where there is a high density of rivers, such as the Congo and Amazon River basins, it may have a more fundamental effect by influencing the pattern of forest refugia (Eeley and Lawes 1999). In such regions forest contraction is likely to have encouraged the separation of a number of local populations promoting diversity and endemism (Ayres and Clutton-Brock 1992). The importance of rivers acting as a hindrance to dispersal abilities of primates is such that they may slow the spread of a population, allowing two different, but related taxa to spread out from centres of differentiation on opposite river banks (Chapman *et al.* 1999).

4.3 Variations in Latitudinal Species Richness

The distribution of primate species is found to be concentrated around tropical and equatorial latitudes (Fig. 2.2). Generally there are fewer numbers of species at higher latitudes due to the greater climatic variability and seasonal extremes demanding species to be better adapted, often with greater range sizes, compared to the smaller range sizes of the more specialized species located at lower latitudes, with a lower environmental tolerance (Stevens 1989; Stevens 1992; Eeley and Foley 1999; Eeley and Lawes 1999; Gaston 2000; Harcourt 2000; Harcourt *et al.* 2002; Willig *et al.* 2003). In particular for primates, the location of tropical forest will lead to greater species numbers at tropical latitudes. However, it is more than simply the location of tropical forest that determines the range of many primate species, rather it is a result of constraints on species dispersal at greater latitudes outside the tropics (Harcourt and Schreier 2009).

Several patterns have been proposed to explain latitudinal gradients in species richness; variation in habitat seasonality, extreme temperature fluctuations, net primary productivity, floristic diversity and parasite diversity (Stevens 1989; Peres and Janson 1999; Willig *et al.* 2003). For instance, Harcourt and Schreier (2009) demonstrate how high speciation rates in the tropics compared with the ecological and thus evolutionary constraints on diversity at higher latitudes have led to greater diversity within the tropics.

The Neotropics and Africa show the most distinct relationship between species richness and latitude. Cowlishaw and Hacker (1997) observed similar trends of latitudinal gradients in primate species richness for Africa as those displayed in our results (Fig. 2.2), highlighting how African primates are predominantly tropical, although there are species that do exist outside the tropics. Similarly, Eeley and Lawes (1999) demonstrate how anthropoid primate species richness across Africa and the Neotropics was focused in equatorial regions and declined with increasing latitudes. Peres and Janson (1999) explain how latitude is one of the most important predictors of Neotropical primate diversity due to the gradual increase in species richness towards the equator in a number of phylogenetically independent taxa.

In Africa the pattern of primate richness has been shown to reflect vegetation types, with decreasing species richness from wetter to more arid areas (Grubb 1982), thus potentially explaining why extreme north- and southerly latitudes have reduced numbers of primates. Hence a species' latitudinal extent is heavily determined by their ability to adapt to greater climatic variations that are experienced at higher latitudes (Willig *et al.* 2003). Furthermore, species occupying more extreme latitudes can be expected to have an increased geographic range and are often generalist species that can tolerate a broader set of climatic conditions, allowing them to spread across a wider range of habitats (Cowlishaw and Hacker 1997), whereas species exclusively located at equatorial latitudes can be expected to be specialised with smaller ranges and therefore a narrower environmental tolerance (Stevens 1992; Harcourt 2000). Within Africa for example, species richness declines with increasing latitude north and south of the equator (Fig. 2.2), at the same time Eeley and Foley (1999) found that the average species range size, habitat and dietary breadth all increase. The broader climatic variability experienced at more extreme latitudes could explain the areas on the outer reaches of the major biogeographic zones in which only one species is present, such as Mediterranean- and southern-Africa and northern regions of Asia (Fig. 2.1).

The Neotropics follow a similar pattern to Africa in that species richness has a strong latitudinal gradient (Eeley and Lawes 1999) and the regions of greatest diversity are strongly linked to the distribution of the forest biome (Mittermeier 1988). Peres and Janson (1999) explain how the reduction in species richness at high latitudes in Neotropical primates is a product of greater seasonality, lower floristic diversity and the substantial decrease in areas of tropical forest with increased distance from the equator. An alternative theory to the patterns of latitudinal species richness for Africa and the Neotropics has been proposed by Eeley and Lawes (1999), who speculate the degree to which patterns observed between species richness and latitude could be due to the shape of each continent, with both being widest at the equator.

4.4 Global Primate Taxonomic Distinctness

Africa has the highest levels of taxonomic distinctness (Δ^+), which equates to the most unrelated assemblage of taxa (Fig. 2.3). Hacker *et al.* (1998) found that hotspots of taxon richness were clustered in west Central Africa, which would coincide with the hotspots of species richness we found in Africa (Fig. 2.1). The species composition of African primates is believed to have resulted from long-term historical processes of dispersal, extinction and evolution (Chapman *et al.* 1999) therefore more diverse primate communities will have evolved over time. Climatic changes since the Pleistocene, associated with glacial and interglacial periods, have constructed a sequence of forest contraction (glacial) and expansion (interglacial) within which forest vegetation would have been rarely stable for long periods, the consequence of this pattern of environmental change would have led to a variety of evolutionary forces operating on primates living in African forests (Chapman *et al.* 1999), therefore encouraging the development of evolutionary distinct species assemblages (Fig. 2.3).

Forest contraction leads to separation of primate populations, encouraging speciation and when the forest expands there is potential for these new populations to interact, encouraging further adaptations and hybridization (Chapman *et al.* 1999). However it is not just forest expansion and contraction, the effect of barriers such as rivers and mountains can further separate populations, as previously discussed (Ayes and Clutton-Brock 1992; Eeley and Lawes 1999; Lehman 2004), consequently isolating populations and promoting the development of taxonomically distinct species assemblages in different habitats, therefore providing a possible explanation for high levels of Δ^+ in Africa and South America.

The location of regions with high levels of Δ^+ could be expected to coincide, to a certain extent, with areas that contain the highest levels of species richness, and this could explain why Madagascar has a relatively high Δ^+ value, due to the high density of primate species on the island given its total area when compared to regions such as the whole of Africa. Although Madagascar's unique evolutionary history will have played a major role in the development of the taxonomically distinct species assemblages present on the island (Reed and Bidner 2004). In comparison, large parts of Asia are classed as having high levels of Δ^+ despite intermediate levels of species richness. Although areas of high Δ^+ across Asia primarily feature in the south-east of the continent (Fig. 2.3) and the pattern of species richness follows a similar trend, with the islands of the Sunda Shelf supporting some of the highest values (Fig. 2.1). The reasons for this could be due to the isolation of small primate populations across the many small islands that make up the Sunda shelf, which have been subject to unique evolutionary conditions promoting diversification. Furthermore, Holocene sea level rise that produced the islands of the Sunda shelf (Heaney 1984) will have separated primate populations and may have promoted speciation. Primates present only on larger Sunda Shelf islands are thought to have gone extinct on the smaller islands, with those species that remain on smaller islands being the ones least susceptible to extinction (Harcourt and Schwartz 2001). Thus the primate communities across the Sunda Shelf vary with island size (Harcourt 1999) and species that became isolated following the creation of the islands will have subsequently followed different evolutionary paths, developing more unrelated and therefore taxonomically distinct species assemblages. Additionally, historical environmental change comparable to that described for Africa and South America (Fleagle *et al.* 1999; Chapman *et al.* 1999; Eeley and Lawes 1999) could have altered the monsoon cycles acting over south-east Asia and subsequently impacted the structure of forests and vegetation across the region, creating varied habitats, promoting the development of new, distinct primate species assemblages.

The lowest levels of Δ^+ are found in north/north-east Asia, upper central America and southern Africa (Fig. 2.3). The low levels of Δ^+ are in higher latitude regions which experience greater climatic variability, limiting the number of primate species occurring in these environments (Stevens 1989; Harcourt and Schreier 2009). Additionally, there is a possibility that areas in which Δ^+ is lower may be due to previous extinctions and reduced population sizes, consequently reducing the dissimilarity in taxa as susceptible species die out from communities.

Reed and Bidner (2004) explain that greater competitive interaction is expected among closely related species, therefore potentially explaining the low levels of species richness recorded for north and north-eastern parts of Asia (Fig. 2.1), being a result of this region holding the some of the most closely related species assemblages across all continents, i.e. the lowest levels of Δ^+ (Fig. 2.3). Although considering the area in question covers part of China, it is possible that the high human population and its associated pressures on habitats may have significantly reduced the taxa in this region.

4.5 Primates Under Threat

The most alarming observation from our results is the much larger area of decreasing primate populations when compared to the areas of threatened species (Fig. 2.4). Schipper *et al.* (2008) observe this trend for all mammals and explain that 52% of mammal species for which population trends are known are declining, including 22% of those classified as least concern. This indicates that the levels of threatened species could be expected to rise. Furthermore, the areas composed of high percentage of threatened species and decreasing primate populations coincide with the regions of the globe that harbour some of the highest levels of Δ^+ and species richness, such as south-east Asia, leading to concern over potential losses from hotspots of primate diversity. However, this link could be attributed to areas of high primate diversity primarily being tropical forest, which are impacted greatly by human practices (Hacker *et al.* 1998) reducing the size of populations and ultimately increasing the risk of extinction.

Primates have the challenge of coping with the dynamics of their habitats, which are continually changing, demanding them to adapt in order to survive or face potential extinction (Isabirye-Basuta and Lwanga 2008). Habitats are under threat worldwide from a variety of pressures, ranging from human activities such as farming and deforestation to the relatively uncertain effects associated with climate change (Cowlishaw and Dunbar 2000), however the influence of different threats will vary geographically (Schipper *et al.* 2008).

Many of the habitats in south-east Asia are heavily impacted by human activities, with hardly any primate habitat unaffected (Gupta and Chivers 1999), most likely accounting for the high percentage of threatened species across the region, in addition to the even larger coverage of decreasing populations. Schipper *et al.* (2008) support this observation and estimate that potentially up to 79% of primate species in this region are threatened with extinction, a similar level to that displayed in our results (Fig. 2.4A). Furthermore the coastal areas of Brazil are of particular concern due to the potential pressure on habitats associated with the high human population density in this region, which also provides a possible explanation for the high levels of threatened species present along the Atlantic coast (Fig. 2.4A).

Much of Africa is classed as having 0% threatened species, or Data Deficient (Fig. 2.4A), however, when considering the high levels of species richness and known human pressures upon common primate habitats throughout

Africa (Chapman *et al.* 1999), it was expected that there would be a larger percentage of threatened species across the continent. The largest area of threatened primates in Africa is centred over the same area in which the highest species numbers occur – roughly over west- and west-central Africa (Fig. 2.1 and Fig. 2.4A) leading to concern over the prospect of maintaining the high primate diversity of this region.

It is important to appreciate that species not marked as threatened are not necessarily safe; many species have experienced range shifts and large population declines in the past that have not been accounted for in the current Red List status (Schipper *et al.* 2008). Furthermore, some species may already be committed to extinction as a result of habitat destruction, with extinction often occurring some time after habitat loss occurs (Tilman *et al.* 1994; Chapman *et al.* 2006). This time lag between habitat destruction and extinction of a species is termed 'extinction debt' (Tilman *et al.* 1994). There are also primate species for which there is insufficient or unavailable data, therefore the percentage of threatened species and decreasing populations may be higher or lower in some areas.

Madagascar has been shown to hold some of the highest levels of primate diversity on Earth (Fig. 2.1 and 2.3). However, given high percentages of decreasing primate populations on the island, combined with already high percentages of threatened species (Fig. 2.4), it makes it one of the regions of most concern. Ganzorn *et al.* (2001) highlight the ongoing loss of primary vegetation across the island, something which may explain why Madagascar harbours high percentages of threatened primate species. Many species have previously become extinct on Madagascar due to previous environmental change in which the island became drier, in addition to the onset of human habitation which accentuated the process and has been estimated to have eliminated at least one third of all lemur species on the island (Ganzhorn *et al.* 1999). Continued pressure on habitats, coupled with the potential effects of climate change, is a concern and may considerably reduce the number of primate species present in Madagascar, especially given current levels of threatened species (Fig. 2.4A).

A limitation with showing the percentage of threatened/decreasing species per grid cell is that there is a slightly biased rating towards grid cells containing fewer species, for example; some grid cells only contain one species, which may be threatened/have a decreasing population status, resulting in that grid cell being classed as 100% threatened even though there is only one species present. Conversely a grid cell may contain 14 threatened species, but with three species not threatened and therefore it will be given a lower percentage.

5. Conclusions

The Neotropics hold the greatest numbers of primate species, followed by Asia, Madagascar and Africa. The particular areas which have the greatest concentration of primate rich grid cells feature the throughout the Amazon River Basin, particularly towards western-Amazonia, across west- and west-central Africa throughout the Congo River Basin, Madagascar and the Sunda Shelf region in south-east Asia. Primate species are linked to areas of extensive tropical forest with the latitudinal distribution of primate species richness highlighting how the majority of species are present between 20° North/South of the equator, a pattern shown most clearly for Africa and the Neotropics.

Africa comprises the most unrelated/evolutionary distinct primate species assemblages, illustrated by high levels of taxonomic distinctness (Δ^+) over much of the continent. High levels of Δ^+ are likely to have been brought about by a combination of historical environmental and evolutionary change, with the actions of physical and biotic barriers fragmenting populations leading to further differentiation (Ayres and Clutton-Brock 1993; Chapman *et al.* 1999).

The threat to primate species as a consequence of human activities and environmental change is a major concern. The number of threatened primate species could be set to increase given the much larger numbers of decreasing primate populations. Of particular concern are Madagascar, south-east Asia, Central America and coastal areas of Brazil which all have high percentages of threatened species, in addition to declining primate populations. Moreover, areas with a high percentage of threatened and decreasing primate populations tend to coincide with regions of the globe that harbour some of the highest levels of Δ^+ and species richness, such as Madagascar and south-east Asia in particular. This raises possibility of reductions in the overall primate diversity of these regions as a consequence of species extinctions.

Chapter 3

Climate and Primate Diversity: Current Relationships and Projected Future Changes

1.1 Introduction

At large spatial scales, climate is the primary determinant of species distributions and diversity (Pearson and Dawson 2003), with energy availability being an important factor, particularly with regards to the occurrence of greater species richness in warmer climates (Schipper *et al.* 2008). Gaston (2000) explains how energy availability can enable a greater biomass to be supported in a region, allowing more individuals to coexist. These relationships with climate and environmental energy are linked with gradients of latitude and elevation, with current and historical states of these factors shaping the variation in distribution and diversity of species (Gaston 2000). Changes in climate will therefore inevitably impact upon species ranges, subsequently altering species numbers at a given location, with many studies documenting the influence climate change has already had on a variety of taxa (e.g. Hughes 2000; McCarty 2001; Gitay *et al.* 2002; Walther *et al.* 2002; Hickling *et al.* 2006).

The IPCC (2007) anticipates a general rise in the Earth's mean surface temperature over the twenty first century; this is expected as a result of rising levels of anthropogenic greenhouse gas concentrations. Alterations in global precipitation patterns are more varied however, with increases expected for equatorial areas and higher latitudes and a reduction in the subtropics (IPCC 2007). Tropical Africa and eastern Asia are projected to receive amplified winter and summer precipitation levels respectively, with large year to year variations expected (IPCC 2007), which will be of particular importance to primate species located in these regions.

The impact of global warming on large scale patterns of climatic variability such as the El Niño/Southern Oscillation (ENSO), which impacts climate worldwide because of the associated changes in heating of the tropical atmosphere, potentially altering global atmospheric circulation (Cane 2005), has the potential to affect primate-rich regions across the globe. Furthermore it is likely that global warming will lead to an increase in the variability of Asian summer monsoon precipitation (IPCC 2007), which will affect Asian primates, many of which already face high risks of extinction and would struggle to cope with any further negative impacts on their habitats. In addition to global climate change, altered regional and local climate aspects can affect population abundance, species' distribution and behaviour, and may also impact upon community structure (Easterling *et al.* 2000).

Climate regimes influence species distributions and numbers, often through species-specific physiological thresholds of temperature and precipitation (Walther *et al.* 2002). In terms of primates, climate change may have a direct effect by creating unfavourable conditions, and subsequently impacting upon the bodily functions and physiology of individuals or it may have indirect effects by reducing food availability and influencing biological aspects such as competition, predation and disease (Hoffman and Parsons 1997). The extent to which a species may be impacted upon by projected climate change will depend on the size of its current range, its dispersal ability and its level of environmental tolerance, however, in the case of primates, dispersal ability will be restricted to areas of tropical forest for many species.

Wiederholt and Post (2010) explain the need to quantify the role of climate change in the dynamics of primates due to the already large numbers (up to one third) of primate species threatened with extinction. This is particularly disconcerting considering that under projected climate change the extinction risk of vulnerable species is likely to increase (Dunbar 1998; Cowlishaw and Dunbar 2000; *Gitay et al. 2002*; Thomas *et al. 2004;* Malcolm *et al.* 2006). As previously discussed (Chapter 2), primates are mainly located in tropical forests throughout tropical and equatorial regions; therefore the impact of any climatic changes on these areas will have important knock-on effects. For example, forest development is significantly linked with levels of rainfall (Reed and Fleagle 1995; Cowlishaw and Dunbar 2000; Reed and Bidner 2004), moreover floristic diversity, and the availability of food resources will be governed by climate, as plants can only successfully reproduce and grow within specific ranges of temperature and precipitation (Hughes 2000; McCarty 2001).

Lucht *et al.* (2006) use Dynamic Global Vegetation Models to map the responses of terrestrial vegetation to climate change, concluding that climate change will cause widespread shifts in the distribution of major vegetation functional types on all continents by 2100. However, using similar methods Schapoff *et al.* (2006) explain the difficulty in anticipating the response of sub-tropical and tropical ecosystems to climate change due to large variations in simulated precipitation patterns from different global climate models. Nevertheless it is clear that climate change has the potential to impact primate species through a combination of factors acting across ecosystems.

1.2 Aims

In this chapter we investigate the relationship between current climatic conditions and primate species diversity at the global scale and how future climate change might affect global patterns of primate diversity. There are three main aims to this chapter:

1. Establish the current climatic determinants on primate diversity, thus providing an understanding of the key climatic drivers in primate-inhabited regions.
2. To develop a model to predict possible changes in primate species richness in response to projected future climate change.
3. Use the model predictions to identify areas in which climatic conditions are set to improve/deteriorate and the possible effects on primate species.

2. Methods

Climate and Species Data

Climatic conditions that may have led to the observed patterns of primate diversity were established using baseline climate data covering the last pre-warming "normal" period 1931-1960. For this, the CRU TS 2.1 dataset was used providing mean values of baseline temperature and precipitation for June/July/August and December/January/February for each 0.5° grid cell (www.cru.uea.ac.uk/data/hrg); thus providing data for summer and winter, respective of which hemisphere. The total species richness of each grid cell, obtained in chapter 2, was used to build a model of species richness as a function of climate.

Future climate data, for the period 2031-2060 (referred to hereafter as the “2050s”), were derived from the TYN S.C. 2.0 dataset, (www.cru.uea.ac.uk/data/hrg) providing June/July/August and December/January/February temperature and precipitation values from two different global climate models (GCMs): *PCM* and *HadCM3* under two different IPCC AR4 SRES greenhouse gas emission scenarios: A2 and B1. The A2 scenario depicts a heterogeneous world harbouring a continuously increasing population with technological change more fragmented and slower than other scenarios (IPCC 2007). In contrast, the B1 scenario describes a convergent world with the same global population, in which the focus is on social and environmental sustainability with the introduction of clean and resource efficient technologies (IPCC 2007). Using a range of GCMs and scenarios allows for a better assessment of future changes, given the many uncertainties associated with future climate predictions.

The Global and Continental Model

The climate data and the values of species richness were organised into five datasets: one with a global coverage, incorporating all grid cells, representing the *global* model and one for each of the four main primate-inhabited biogeographic zones: Asia, Madagascar, Africa and the Neotropics, which constitute the *continental* model. The *continental* model uses a restricted dataset for each biogeographic zone, which may allow the model to account better for the specific climatic conditions that may be of greater or lesser importance in different regions, without adding a large number of negative values, i.e. absence records in areas clearly climatically unsuitable for primates. The *global* model incorporates all the grid cells and will be used to provide an indication of where climate conditions, suitable for primates, persist outside of primate-inhabited zones, in addition to providing a useful comparison with the *continental* model output. The geographic extent of the four biogeographic zones used in the *continental* model can be seen below in Table 3.1.

Table 3.1: Latitude/Longitude extent of each biogeographic region incorporated in the *continental* model.

Region	Number of Grid Cells	Latitudinal extent	Longitudinal extent
Neotropics	6701	24.25; -55.25	-99.25; -34.75
Africa	10869	36.75; -34.75	-17.25; 46.75
Madagascar	211	-12.25; -25.25	43.25; 50.25
Asia	6507	41.25; -10.25	63.75; 141.75

The Species Richness Model

Two stepwise multiple OLS regression models were built, using SPSS 17, with species richness used as the dependent variable, and the linear, second and third order climate variables as independent variables. The benefit of using a stepwise regression is that it provides the most parsimonious model, i.e. retaining the least number of variables while explaining maximum amounts of variation in the dependent variable. These regression models were applied to the global dataset, i.e. all grid cells (*global* model*)* and then to each biogeographic region, (*continental* model*)*, thus providing two models of baseline species richness. In order to assess the accuracy of the models before using them for future predictions, they were compared to the observed values of species richness illustrating areas which may have been over or under-predicted. Graphs of observed against modelled species richness were plotted in order to illustrate model performance. In addition, graphs of modelled and observed species richness over latitude were produced to identify areas in which the model was most accurate and where it had over or under predicted species richness.

The linear, second and third order baseline climate variables were also individually used in a regression analysis for each of the five datasets; the global coverage of grid cells and each biogeographic region, to provide the R^2 values of the climate variables in each model (including the linear, second and third order terms). This will highlight the most important aspects of the climate acting in each of the biogeographic regions, and on a global scale in determining primate species richness. Additionally, the root mean square error (RMSE) was calculated providing an indication of model performance compared to observed data.

The regression equations from the *global* and *continental* models were applied to the future climate variables to predict future primate species richness. The aim is to develop an accurate model that can be used to provide an approximation of species richness under future climate. Therefore, the projected change in species richness was calculated using the difference between the model output for future and baseline species richness, rather than with the observed values of species richness. This method was used because the model outputs for future and baseline species richness are relative to each other, on account of the way the model calculates species richness in terms of the climate variables, and therefore will provide better predictions of future changes.

The model projections for future changes in species richness were compared to the elevation for each grid cell to identify any links between altitude and changes in future climate. This could highlight regions of higher altitude which may act as a buffer against adverse climate change, or conversely show high altitude regions which will be more severely impacted by climate change than lower lying land masses.

3. Results

3.1 Explanatory power of individual climate variables

For each model the individual climate variables (linear, second and third order terms) were used as the single independent variable with total species richness as the dependent variable, providing the R^2 values, all of which were significant, for each climate variable. The one climate variable with a relatively high R^2 for each model is December, January, February (*djf*) temperature, which appears to be an important factor for current primate species richness (Table 3.2A). However, the one exception to this is Madagascar, in which June, July, August (*jja*) precipitation appears to be the one important variable, with all the others possessing very low R^2 values. In a similar trend to Madagascar, the Asia model demonstrates just *djf* temperature as the main climatic determinant with an R^2 of 0.36 compared to 0.1 and 0.02 for the linear *jja* and *djf* precipitation variables respectively. Temperature also appears to be an important factor for Neotropical primates, as indicated by all the *jja* and *dfj* temperature variables having high R^2 values compared with much lower values for the precipitation variables. In contrast, the Africa model displays relatively high R^2 values of 0.23 for *jja* and *djf* precipitation, although the highest R^2 values are those relating to each *djf* temperature variable. On a global scale the two most important climate variables in relation to primate species are shown to be djf temperature and precipitation.

Following the stepwise regression analysis the *β* coefficient values (Table 3.2B) were used to build each model, with the subsequent regression equations enabling the prediction of species richness for the baseline climate conditions and for the projected future climate from each GCM and scenario. The Neotropics and Africa in particular, are best represented by the model parameters, demonstrated by the higher adjusted R^2 values. Although both of these contain the largest number of grid cells and therefore data points, which will increase the R^2. Madagascar is the poorest-performing model indicated by the lowest R^2 value. The

Asia and Global model both have a relatively high adjusted R^2 value, each explaining 54% of the variation in species richness, although the *global* model comprises the largest dataset consisting of all the grid cells.

Table 3.2: Total species richness regression analysis. A: The R square value for each individual climate variable. B: The β coefficients produced from the stepwise regression, with total species richness as the dependent variable. The variables left in the model after stepwise regression analysis represent the minimal adequate model. NOTE: All the values were classed as significant; this could be a result of the large number of points in the models.

A

Individual R Square Values

Climate Variable	Global	Asia	Madagascar	Africa	Neotropics
jja_Temperature	0.15	0.15	0.08	0.05	0.43
jja_Temperature^2	0.15	0.13	0.08	0.09	0.45
jja_Temperature^3	0.13	0.11	0.08	0.13	0.44
djf_Temperature	0.26	0.36	0.02	0.45	0.27
djf_Temperature^2	0.00	0.11	0.02	0.48	0.29
djf_Temperature^3	0.16	0.26	0.02	0.48	0.30
jja_Precipitation	0.05	0.10	0.13	0.23	0.00
jja_Precipitation^2	0.06	0.05	0.17	0.13	0.01
jja_Precipitation^3	0.04	0.00	0.18	0.07	0.01
djf_Precipitation	0.20	0.02	0.03	0.23	0.10
djf_Precipitation^2	0.17	0.00	0.03	0.16	0.08
djf_Precipitation^3	0.12	0.00	0.03	0.12	0.05

B

B Coefficients

Variable	Global	Asia	Madagascar	Africa	Neotropics
constant	-2.54	2.24	-20.40	-11.23	-18.00
jja_Temperature	-0.38	-	-	0.29	-0.68
jja_Temperature^2	0.04	0.00	-	0.03	0.03
jja_Temperature^3	0.00	-	-	0.00	-
djf_Temperature	-0.01	0.26	-	-	2.34
djf_Temperature^2	0.00	0.00	-	-	-0.10
djf_Temperature^3	0.00	-	0.00	-	0.00
jja_Precipitation	0.41	0.36	-	1.29	-
jja_Precipitation^2	0.02	-0.04	-	-0.09	0.09
jja_Precipitation^3	0.00	0.00	2.37	-	-0.01
djf_Precipitation	0.19	0.55	-	3.39	0.83
djf_Precipitation^2	0.07	-0.14	-	-0.55	-
djf_Precipitation^3	-0.01	0.01	-	0.03	0.00
Adj R2	0.54	0.54	0.26	0.75	0.62
RMSE	2.52	5.52	6.55	3.12	5.07

3.2 Predicting Current Species Richness

On the whole, the *continental* model has identified the patterns of high species richness within the biogeographic zones with more success than the *global* model, in particular for areas over central/western Africa around the Congo Basin, in addition to areas of south-east Asia (Fig. 3.1). Furthermore, the areas possessing the highest levels of species richness are concentrated around the tropics similar to the observed data. However, the *continental* model has failed to identify a relatively large area of primate species that are present in the observed data over southern Africa and some parts of eastern Africa. The *global* and *continental* model outputs are similar in that the same areas within each of the main biogoegraphic regions contain the highest values of species richness, and areas such as the Sahara Desert are devoid of primate species as in the observed data. In addition, both models class Madagascar as having high levels of species richness, the *continental* model in particular. However, the clearest difference between the *global* and *continental* model output is the difference in species numbers predicted by each model, with the *global* having a maximum of eight species in a particular grid cell, compared to 20 for the *continental* model.

The *global* model also illustrates areas currently uninhabited by primates that may have suitable climatic conditions for primate species (under the baseline climate conditions); specifically these areas are along the east and upper north-west of North America, and much of Australasia in particularly northern Australia. Additionally, the far east of Russia, up into the arctic is classed as having species present, although they are low numbers.

The maps illustrating the difference between observed and predicted species richness (Fig. 3.1) show how the *global* model over-estimates species richness in areas such as Australia, where in reality there are no species present, but this is because the model calculates that the baseline climate was suitable for primate populations in that region. Both models identify areas in which primate species are present with differing accuracy; the *global* model tends to underestimate species richness whereas the *continental* model over estimates it, this is further supported in Table 3.3. Although the *continental* and *global* models both under-predict African primates, on average by -2.15 and -2.62 species per grid cell respectively. Furthermore, the areas around the Congo River Basin are considerably lower in primate species than the observed data (Fig. 3.1), in particular for the *global* model.

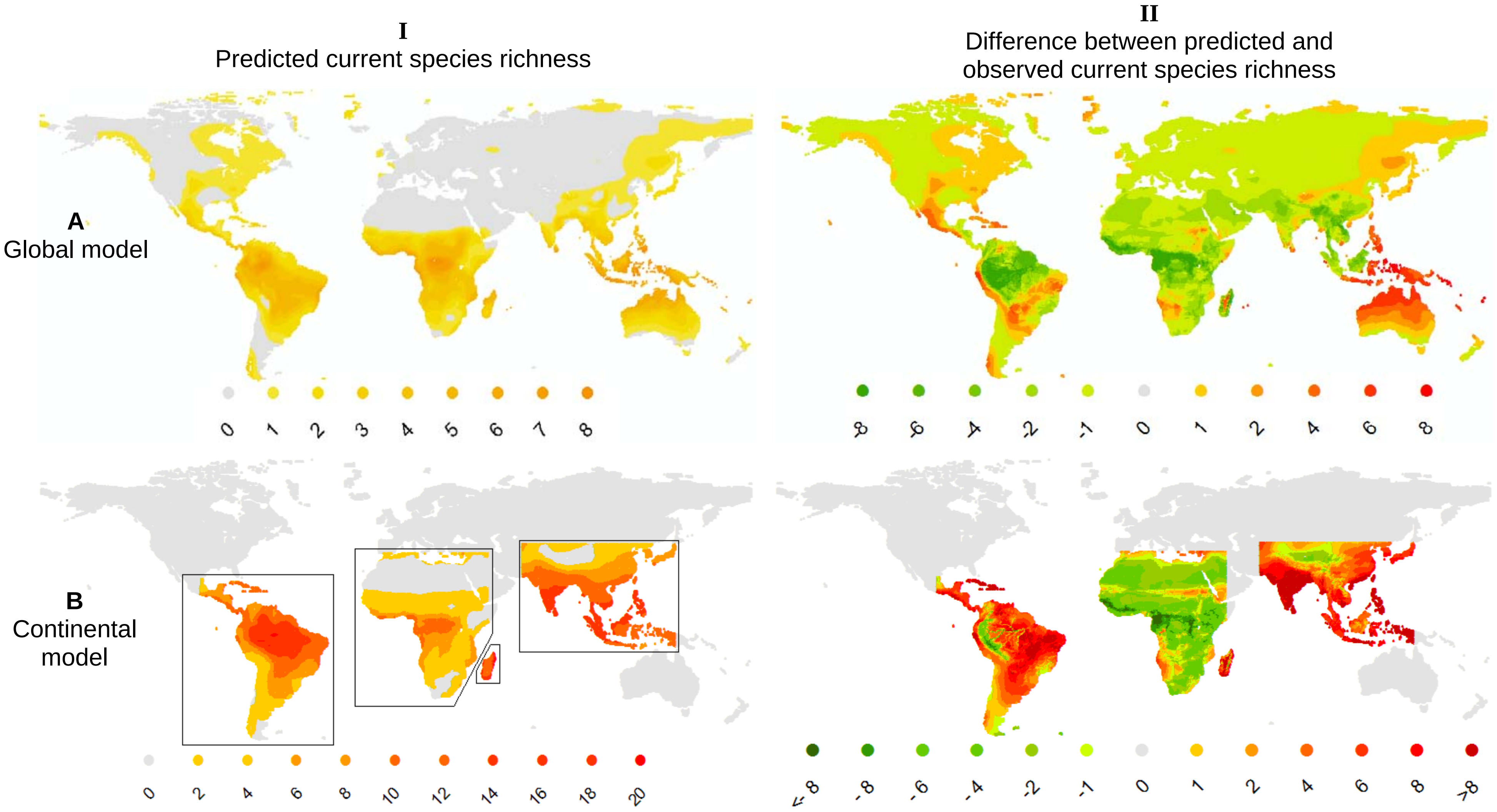


Figure 3.1: Predicted (baseline-climate) primate species richness. I: Predicted primate species richness under baseline climatic conditions for the *global* (A) and *continental* (B) model; II: Difference between predicted and observed primate species richness for the two models. The most apparent difference between the *global* and *continental* model outputs is the scale, with the *global* model predicting much lower species numbers than the *continental* model.

Within the Neotropics the *continental* model over-estimates species richness in Central America and it is noticeable how it lacks detail in species-rich areas concentrated along the Amazon River Basin unlike in the observed data, whereas in comparison the *global* model largely undervalues the species richness in the Amazon Basin. On average, for the Neotropics, the *global* model under-estimates species richness by -1.99 per grid cell compared to the *continental* model that over-estimates by 3.88 species per grid cell (Table 3.3). Both models class the central area of Madagascar as having species present; indicating that baseline climatic conditions in this area are suitable for primate species and their absence in the observed data is due to other factors. Asia brings contrasting results from each model, with the *continental* model over-predicting species richness on average by 4.09 species per grid cell (Table 3.3), although it is primarily India and far-east Asia that are over-estimated (Fig. 3.1). In contrast the *global* model under-values the whole region, with the exception of south-east Asia. For both models the patterns across continents such as Africa and South America are not as well pronounced as in the observed data and tend to be blurred, particularly the *global* model output.

Table 3.3: **Average difference between modelled and observed species richness** - in addition to the absolute difference between each model prediction. Important to consider that this table just shows the average difference - the actual patterns of species richness predicted by each model may be different.

	Continental Model	Global Model	*Absolute Difference Between Models*
Asia	4.09	-1.4	*5.49*
Madagascar	5.24	-3.18	*8.42*
Africa	-2.15	-2.62	*0.47*
Neotropics	3.88	-1.99	*5.87*

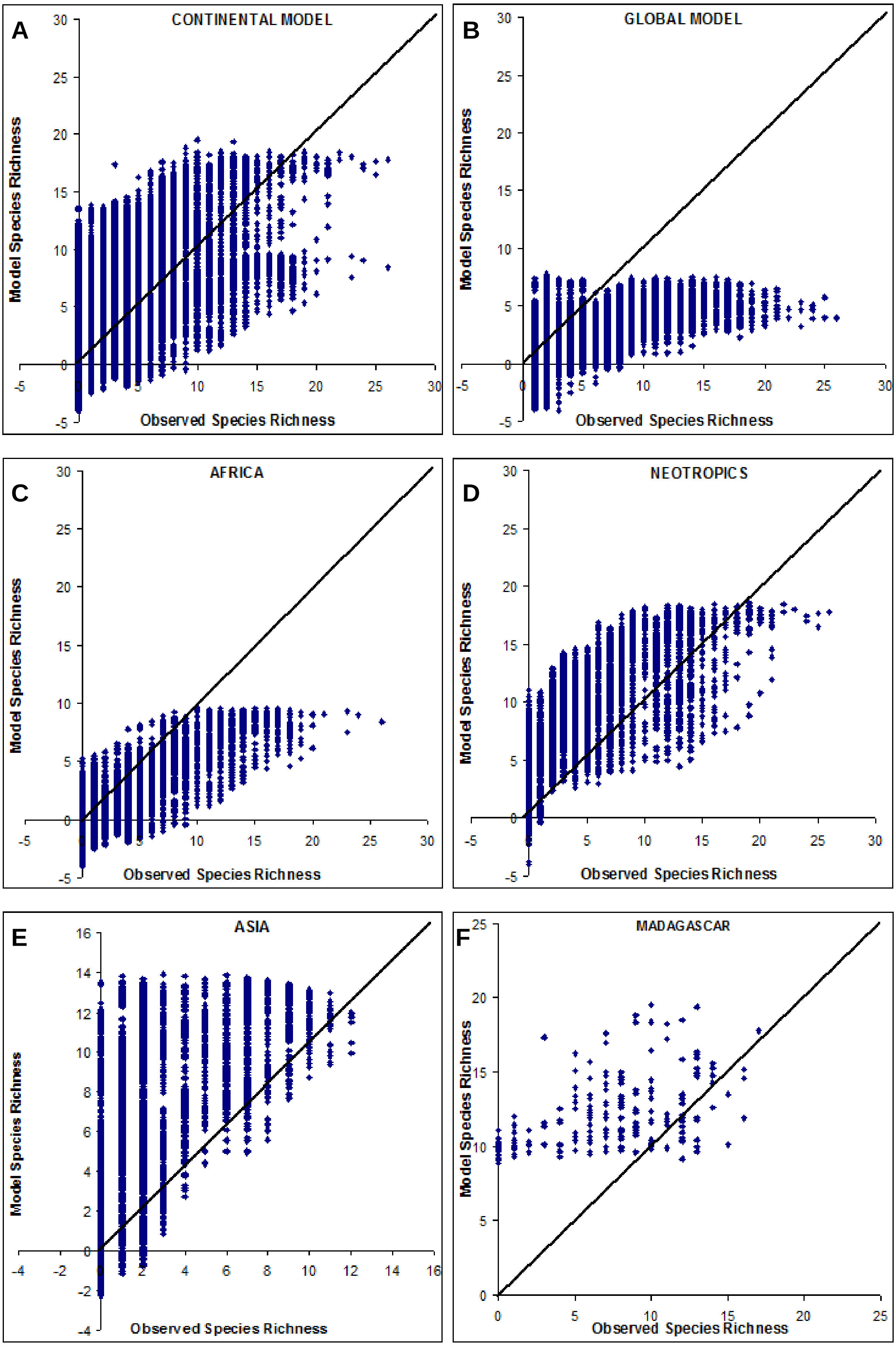
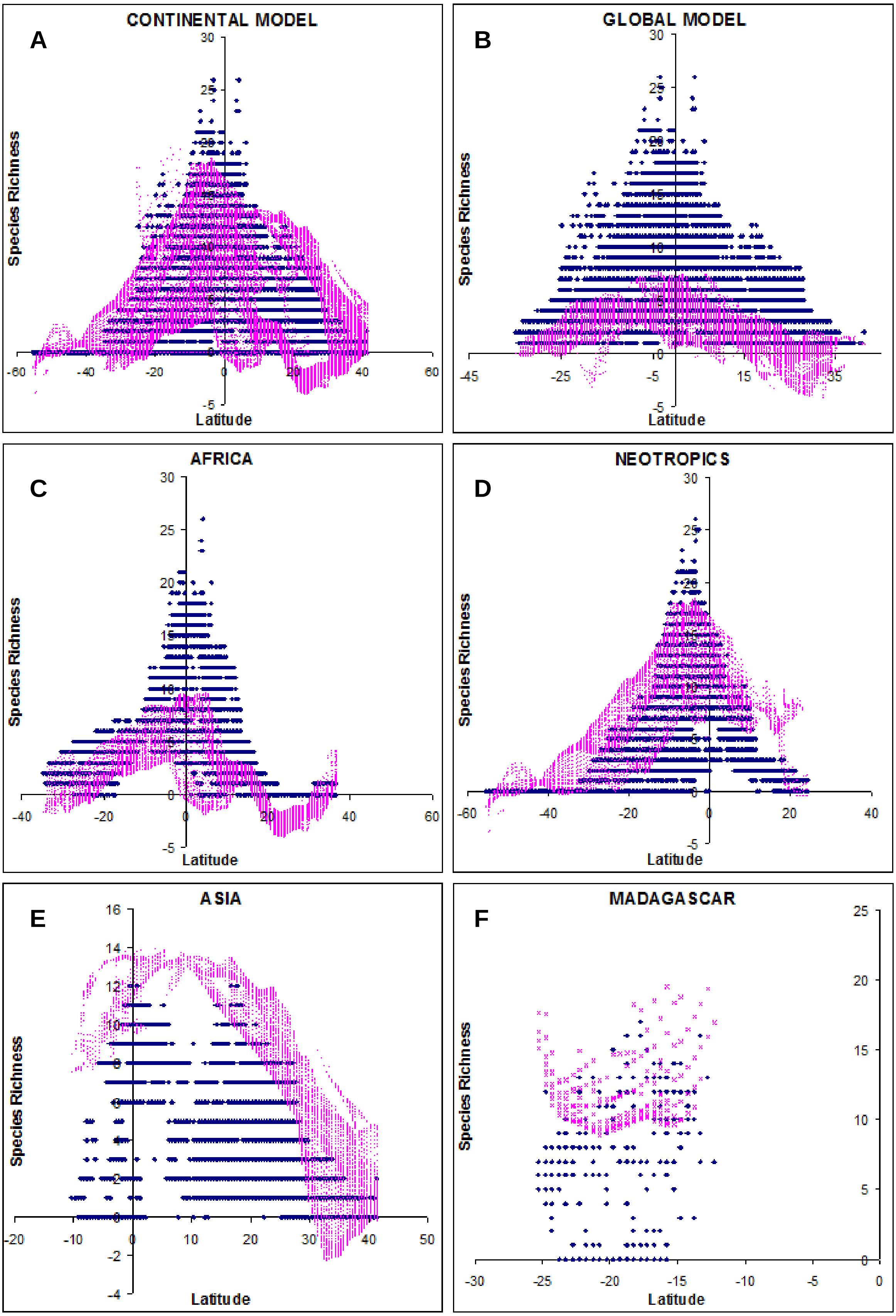


Figure 3.2: Observed vs. predicted primate species richness - for the continental model (A), the global model (B) and for each biogeographic region (C-F), with a 1:1 (*x*=*y*) line.



<u>Figure 3.3:</u> Observed (blue) and predicted species richness (pink) against latitude - for the continental model (A), the global model (B) and for each biogeographic region (C-F). The *continental* model predicts the baseline species richness with greater accuracy than the *global* model, with the latitudinal patterns of species richness reproduced better, except for Asia.

The predictions of baseline species richness vary considerably between each biogeographic zone (Fig. 3.2 and 3.3), with the best representation of current patterns of species richness being produced by the Neotropics, Africa and Madagascar models. Asia displays an unusual pattern compared to the observed pattern of species richness, with a heavy concentration of species present between 25 and 40° north of the equator (Fig. 3.3). The *continental* model outputs for the Neotropics and Africa also successfully duplicate the latitudinal pattern across the continents, although the Africa model produces lower levels of species richness. Conversely, the Madagascar model over-estimates species richness. The *global* model considerably under-estimates species richness with every biogeographic region under-predicted, by -3.18 species per grid cell in the case of Madagascar (Table 3.3). This under-estimation is also evident in the baseline maps (Fig. 3.1), however the model still roughly picks up on the latitudinal patterns of species richness.

Generally the separate models for each biogeographic zone (*continental* model) tend to over-estimate species richness, by as much as 5.24 and 4.09 species per grid cell on average for Madagascar and Asia respectively (Table 3.3). Although in contrast, the Africa model does under-predict species richness. However, given the more accurate representation of latitudinal patterns and numbers of species (Fig. 3.3), and the fact that the *global* model under values species numbers for each region (Table 3.3), the outputs from separate biogeographic zone models have been combined into the *continental* model, which will be used with future climate projections to assess potential changes in primate species richness.

3.3 Future Projections of Species Richness

When assessing the model predictions of future primate species richness it is important to consider that areas anticipated to increase or decrease in primate species are doing so on account of an improvement or deterioration in suitable climate, respectively. Hence the models calculate potential change in species under projected future climate change given the current climate-primate species relationships, even though the actual numbers of primates in a particular grid cell may or may not change. There is a clear difference in scale of changes for each model; the *continental* model predicts increases of up to 20 species per grid cell and decreases of 12, compared to the *global* model which ranges from 7 to -30.

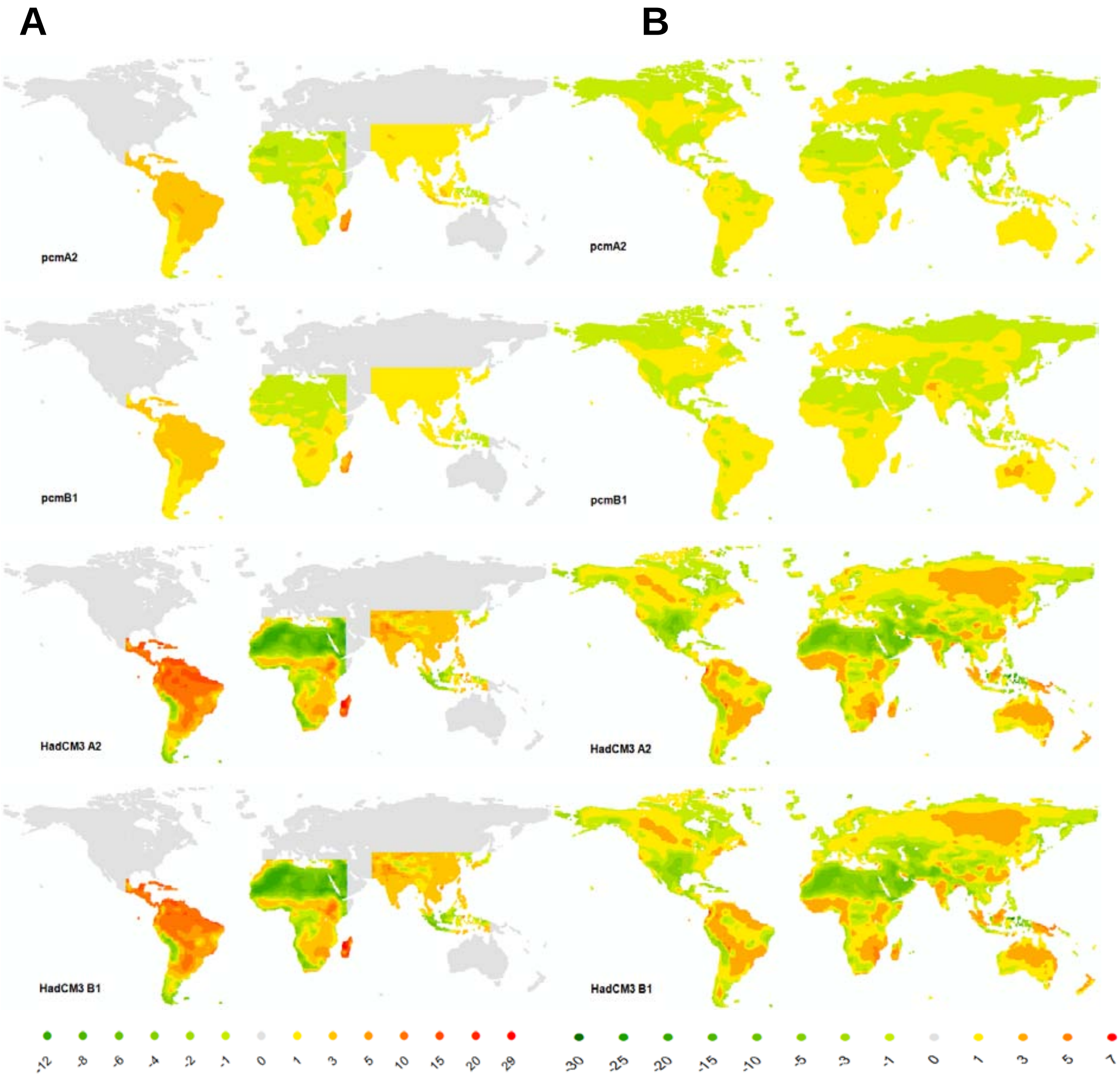


Figure 3.4: Projected changes in future primate species richness – for (A) *Continental* Model and (B) *Global* Model**.** Calculated as the difference between current-modelled and future-modelled species richness. Increase in species numbers indicates potential improvements in climate given current climate-primate species relationships, whereas decreases in species numbers indicate a potential decline in suitable climatic conditions. The *HadCM3* model predicts greater changes in species numbers than the *PCM*, although both models display similar trends, with the largest decrease in species over the Sahara Desert.

Continental Model

The *continental* and *global* model predictions of future primate species richness vary considerably between each GCM (Fig. 3.4). For instance, for both the *continental* and *global* model *PCM A2* and *B1* outputs, there are only moderate levels of change in primate species richness compared to the range of changes projected by the *HadCM3 A2* and *B1* outputs. Some general trends can be detected across each GCM and scenario, such as Madagascar being predicted to increase in species richness, and regions bordering the Sahara Desert in Africa expected to decrease in primate species, again both of these changes occur on a greater scale under the *HadCM3* model. With regards to Madagascar, it is the only model in which each GCM and scenario projects that 100% of the grid cells will become more climatically suitable for primate species (Table 3.4).

The *PCM* outputs follow similar spatial patterns to the *HadCM3* model outputs; with both anticipating an increase in species richness across much of the Neotropics, with the *HadCM3 A2* model predicting an increase in species richness for South America, in particular. This indicates more favourable climatic conditions for primate species arising in this region. Furthermore, each GCM and scenario predicts that over 90% of grid cells throughout the Neotropics will have an improved future climate given current climate-species relationships, with *HadCM3* B1 being the exception in which it is 88.69% (Table 3.4).

Under both GCMs there is a moderate rise in species richness predicted for much of mainland Asia. However the islands of south-east Asia along the Sunda Shelf are predicted to decrease in species richness by the *HadCM3 A2* and *B1* model, with the *PCMB1* model also predicting declines in this region, albeit by a much smaller amount and over a reduced area. Between the *PCM* and *HadCM3* models there is clear difference in the percentage of grid cells increasing in species richness for the Asia, with the *HadCM3 B1* predicting the lowest rise of 86.81% of grid cells compared to 97.22% predicted under *PCM A2*.

Africa displays the most variation across the continent in terms of the pattern of changes in species richness. The conditions in the Sahara desert region and much of northern Africa are predicted to become even more climatically unsuitable for primate species, as indicated by the high negative values, with the *HadCM3* model predicting a considerable decrease in species richness in these areas. Moreover, out of all the components of the *continental* model, Africa has the lowest percentage of grid cells set to improve in climatic suitability for each GCM and scenario (Table 3.4). The greatest percentage occurs under the *PCMB1,* with 41.59% of grid cells experiencing a rise in species numbers, compared to just of 39% for each *HadCM3* output and only 35.86% under the *PCM A2*. However, despite these decreases, large parts of Africa are also predicted to have elevated levels of species richness, particularly along the east of the continent, with the *HadCM3* GCM output projecting high levels in east-central Africa.

Table 3.4: Percentage of grid cells predicted to increase in species richness (improved future climate) - This shows the proportion of grid cells that are predicted to either increase or decrease in species richness under future climate for the Continental Model and the equivalent biogeographic regions within the Global Model.

	% Grid cells projected to increase in species richness (improved climate)			
	PCMA2	PCMB1	hadCM3A2	hadCM3B1
Global Model				
Asia	58.43	45.66	51.65	50.65
Madagascar	99.05	100.00	81.99	75.83
Africa	55.34	56.14	47.46	43.83
Neotropics	74.84	79.14	75.47	76.23
Continental Model				
Asia	97.22	96.11	88.47	86.81
Madagascar	100.00	100.00	100.00	100.00
Africa	35.86	41.59	39.22	39.19
Neotropics	98.93	99.19	90.29	88.69

Global Model

In a similar trend to the output from the *continental* model, the *HadCM3* projections display a greater range of results than the *PCM* output, ranging from -30 through to +7 species per grid cell, compared to -3 to +3 species respectively. The scenarios used with each GCM do offer slightly different outcomes; however the same patterns are clearly evident, just in some cases slightly more pronounced under one scenario than another. The *global* model also provides an indication of climatically suitable regions for primates in areas which they are not present, as can be observed for each GCM and scenario for much of Australia. In addition, parts of central/eastern Europe, large parts of Russia and some central areas of North America, particularly under the *HadCM3* output, are suggested as having future climate that may be suitable for primate species. Furthermore, a greater area than that already occupied by primates in South America is predicted to become climatically suitable. Clearly there are many aspects other than climate that would determine as to whether primate species could survive in these regions but these future projections highlight the potential suitability of such areas.

The area most unsuitable for primate species under the *global* model is centred over North Africa and the Sahara desert, spreading into Arabia and the Gulf, a feature common to each GCM and scenario. This suggests that the already harsh climate in this region is expected to intensify, becoming more unsuitable for primate species. The greatest impact of this will be on the primate species located in areas bordering the Sahara Desert. Further to this, the models have shown how similar unsuitable areas are present down towards central Africa just below the Sahara region, extending into the Congo River basin as well as in the Mediterranean region of North Africa, which is also predicted to decrease in primate species by the *global* model. On the whole, Africa, as it was for the *continental* model, is the continent which displays the lowest area of improving future climate, with only 43.83% of the continent predicted to increase in species richness under *HadCM3 B1* (Table 3.4). However, the GCM and scenario outputs for the *global* model do have a higher percentage of grid cells increasing in primate species than the equivalent in the *continental* model.

The Neotropics show clear variation in the numbers of species present between the *PCM* and *HadCM3* outputs (Fig. 3.4B), with the main difference in the patterns and numbers of species occurring over South America. Each *HadCM3* scenario has predicted very similar patterns and amounts of change (Table 3.4). In contrast, the *PCM* outputs have lower levels of species richness over much of the continent, with a slight difference between each scenario in the number grid cells expected to become more climatically suitable for primate species (Table 3.4).

The common prediction across all the outputs for Asia is that the south of India will decrease in species richness, in addition to parts of China. However, the Sunda Shelf region will experience a split response, with the northern extent increasing in species compared to scattered areas of lower species richness along the central and southern extent of the islands. Similarly to Africa, Asia has a low percentage of grid cells increasing in primate species. There is little difference between the *HadCM3* outputs, however, there is a difference of over 10% between the *PCMA2* and *B1* outputs. Moreover, when compared to the *continental* model, each GCM and scenario predicts a much smaller percentage of the Asian landmass to increase in species richness; for example, *PCMB1* has less than half the amount of grid cells increasing in species richness than it does under the *continental* model.

Madagascar displays a pattern of rising levels of species richness for all the model outputs, although the northern extent of the island is shown to have reduced species richness by the *HadCM3 A2* and *B1* outputs (Fig. 3.4B). However, the percentage of grid cells on the island increasing in species varies from 99/100% for the *PCM* outputs, to only 81.99% and 75.83% under *HadCM3 A2* and *B1* respectively (Table 3.4). This provides a contrast to the *continental* model, in which every GCM and scenario output predicts 100% of grid cells to increase in primate species.

3.4 Future Changes in Species Richness at Higher Elevations

The change in primate species richness at higher elevations produces varying results under each GCM and for the *continental* and *global* model (Fig. 3.5). Each scenario, however, generates similar results except for the *global* model *PCM* output, in which the A2 scenario displays a reduction in species at lower elevations, followed by a gradual increase at higher ones, in contrast to a reduced number of species at all elevations under the B1 scenario. The *HadCM3 continental* model output displays the greatest reduction in climatic suitability at higher elevations, indicated by the reduction in species numbers over 4400m. However the *global* model *HadCM3* and *continental* model *PCM* projections predict improved climatic conditions across all elevations, as indicated by the increases in species numbers, although at the highest elevations the size of the increases is slightly reduced.

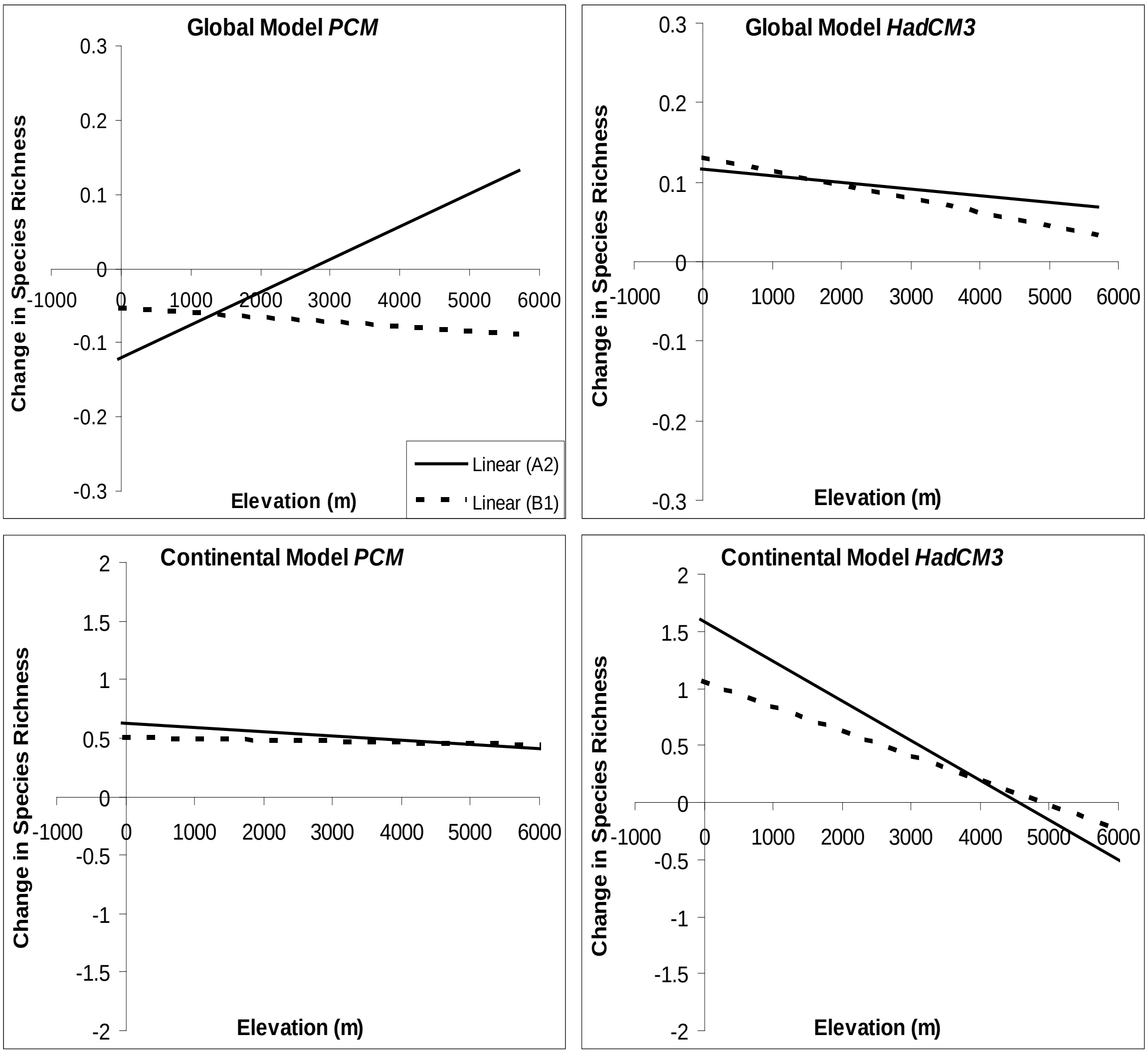


Figure 3.5: Projected changes in species richness with elevation - displaying the change in the number of species per grid cell between baseline and future (2050s) climate conditions (i.e. change in suitable climate) against elevation. The linear lines of best fit represent the A2 scenario (solid line) and the B2 scenario (dashed line) for each GCM. The *global* model *PCM* outputs produce the most varied results when compared to the other models. This is particularly apparent for the *PCMA2* scenario (*global* model), which is the only output to predict an increase in species richness at the highest elevations.

4. Discussion

4.1 The *Global* and *Continental* Models

The difference between the *global* and *continental* models is the restricted space used i.e. reduced number of grid cells and therefore climate data, for the four main biogeographic zones that were subsequently combined in the *continental* model. Thuiller *et al.* (2004) explain how restricting the input data can have several implications with possible consequences for model performance due to the fact that absences are often true absences, providing potentially relevant information on species ecology. This may account for the higher estimation of species numbers from the *continental* models, with up to 20 species present in a grid cell and generally much higher species numbers than in reality as can be seen from the observed/predicted difference maps (Fig. 3.1), possibly because the restricted environmental space used in the *continental* models incorporates mainly favourable conditions for primate species from grid cells comprising the key primate-inhabited biogeographic zones. In comparison, the *global* model includes a greater range of environmental conditions, including more climatically unsuitable grid cells from regions such as northern Canada, for example, possibly leading to the much lower values of primate species richness predicted, with no more than 8 species present in one particular grid cell, in addition to much of the biogeographic zones being under-valued compared to observed species data (Fig. 3.1).

The *global* model does not reproduce levels of species richness across biogeographic regions as accurately as the *contitnental* model (Fig. 3.1). This could be due to its inability to account for the varying importance of different climatic variables, such as the relationship between primate species and rainfall, between each of these regions (Reed and Fleagle 1995; Kay *et al.* 1997; Reed and Bidner 2004), due to the greater amount of environmental data used in the *global* model, which may obscure such regionally important climatic characteristics. In addition, the *global* model under-values species richness for baseline climate in each of the main biogeographic zones (Table 3.3), compared to the *continental* model, which over-values species richness for each region. This could again be due to the restricted dataset of the *continental* model including mainly favourable environmental variables and therefore elevating the subsequent predictions of species richness by the model. However, a restricted dataset, such as that used in the *continental* model, may not incorporate the complete range of environmental conditions in which a species may occur (Thuiller *et al.* 2004).

4.2 Baseline Representations and Observed vs. Predicted Species Richness

Despite a restricted environmental dataset, the *continental* models appear to reproduce the baseline patterns of species richness accurately across each region, in addition to accounting for the latitudinal variations in species richness (Fig. 3.3). The greatest differences between observed and predicted species richness, from both the *global* and *continental* model, occurred for Madagascar (Table 3.3), this could be due to the large differences in the number of grid cells and environmental data present in the small Madagascar model compared to the much larger, unrestricted dataset in the *global* model.

An interesting aspect of the Madagascar outputs is that both models account for the presence of primate species along the central spine of the island under baseline climatic conditions, despite the observed data showing no species present in this location, due to this central plateau of Madagascar consisting primarily of grassland and savannas on account of human disturbances (Reed and Bidner 2004). This further highlights the well documented negative impact of anthropogenic activities on the island (Ganzhorn *et al.* 1999; Reed and Bidner 2004; Dunham *et al.* 2008), in that climatic conditions are currently suitable, and are even projected to become more favourable for primate species (Fig. 3.4), yet due to human influences there are areas in which primates are absent. Human modifications to the habitat and environment, which are not accounted for in the model, such as a loss of forest due to deforestation, reduce the numbers of primate species present despite suitable climatic conditions. Although this provides hope that suitable climatic conditions will prevail and benefit primates across the island. The anthropogenic activities on Madagascar could also account for the lower R^2 value of the model (Table 3.2B), although the lower number of grid cells and therefore data points in the model will also be a contributing factor.

The Asian model could be affected in a similar way to Madagascar, with the negative impacts of human activities being documented along areas of the Sunda Shelf and for much of the continent (Gupta and Chivers 1999; Reed and Bidner 2004). Much of Asia is over-estimated in numbers of species present by the *continental* model, possibly an indication of the impact of human activities extensively reducing species numbers in reality, something not affecting the baseline model predictions due to the climate being suitable for primates.

Both the *continental* and *global* model under predict the numbers of species present in Africa, however, on average, both models have similar outputs (Table

3.3). The Africa component of the *continental* model is the one with the most grid cells and therefore environmental data included. This means it will incorporate a wider range of climate data, similar to the *global* model, some of which will be negatively correlated with primate occurrence, for instance the grid cells that constitute the Sahara Desert region, which will have an unsuitable climate for primates.

A visible difference between the baseline model outputs and the observed values of species richness for Africa and the Neotropics, is the reduced accuracy around the Congo River and the western extent of the Amazon River respectively, this is also apparent in the future predictions. This may be a consequence of the models not being able to account for the work of rivers in creating diverse habitats and resources, which can promote high species diversity within interfluvial regions (Ayres and Clutton-Brock 1992; Lehman 2004).

The R^2 values for each model (Table 3.2) can be considered to be relatively high given that only climate variables were used, which are not the only factors determining primate species occurrence. This is particularly evident for Africa and the Neotropics, although the greater number of grid cells and therefore environmental data used in these models may have contributed towards the higher R^2 value.

4.3 Regional Impacts of Climate Change on Primate Species Richness

Climate change is not uniform across all areas of the globe; some regions will experience large changes whereas others remain relatively stable (IPCC 2007). However, the interlinked nature of the climate system will result in feedbacks associated with changing climate being conveyed across all parts of the world (IPCC 2007). Chivers (1991) explains how flexibility in feeding strategies allows primates to cope with short- and long-term environmental changes, however the primary concern is the current pace of change being experienced across ecosystems, in particular climate, which can impose new types of threat. For instance the effect of climatic stress might decrease primate species richness, highlighted by the decrease in primate species present at more extreme latitudes and with distance from the equator (Chapter 2); a pattern that might exist due to many species struggling to cope with greater environmental variability (Cowlishaw and Dunbar 2000). This can be supported by Neotropical primates, in which the small-bodied taxa are less likely to be found at higher latitudes due to them being unable to sustain the high energy costs of thermoregulation or to survive long periods of food scarcity (Cowlishaw and Dunbar 2000).

In comparing the *global* to the *continental* model outputs for the main primate-inhabited biogeographic zones, similar patterns become apparent between both sets of results. For instance, the broad patterns of increasing and decreasing species richness over much of Africa and Madagascar are similar. The main difference is the scale of changes, with the *global* model predicting lower levels of increases within these regions, in particular the *PCM* outputs. Asia provides the greatest variation between models; mainland Asia under the *global* model displays a more varied change in species richness, with a mix of increasing and decreasing areas, compared to the *continental* model output for this region which is largely comprised of areas of greater species richness, this is further supported in the percentage of increasing grid cells across the region (Table 3.4). The Neotropics are widely predicted to increase in species richness under the *continental* model output. However the *global* model, especially the *HadCM3 A2* output, displays scattered areas of decreasing species richness in South America, particularly over central areas of the Amazon, with a lower area of the continent expected to increase in species richness (Table 3.4). Although there is still a relatively high percentage of the Neotropics predicted have an improved future climate under the *global* model, with the possibility of increases in primate species richness. Below I will discuss the potential impacts of climate change on each primate species within each biogeographic region individually:

4.3.1 The Neotropics

Generally much of the Neotropics are predicted to increase in species richness by the model outputs, indicating beneficial changes in climatic conditions. However, the Gitay *et al*. (2002) anticipated an increased rate of biodiversity loss in this region due to climate change, with analysis by Cox *et al.* (2004) suggesting that the primary cause of Amazonian climate change is an El Niño like sea surface temperature warming under increased levels of carbon dioxide. Wiederholt and Post (2010) found that climate change related variation in ENSO events posed a serious threat to South American Ateline primates, by impacting resource availability with a sequence of high and then low fruit production during El Niño and La Niña years respectively. This would be a result of an intensification of ENSO, which has been linked to precipitation anomalies in many regions of the world (Thomson *et al.* 2003), and is something that has been evident in recent years and anticipated due to global warming (Wright and Calderon 2006; Latif and Keenlyside 2008). However our results suggest otherwise with both the *continental* and *global* model indicating that the majority of the Neotropics are set to improve in suitable climate for primate species richness (Table 3.4).

Ripe fruit is the major source of energy for many Neotropical primates, although its availability varies seasonally (Kay *et al.* 1997). The seasonality of fruit production increases with length of the dry season, and thus may play a role in limiting species richness (Kay *et al.* 1997), especially if climate change alters the length of the dry season. A high correlation between mean annual rainfall and primate species richness has been found at sites in the Neotropics, in addition to sites in Africa and Madagascar (Reed and Fleagle 1995; Peres and Janson 1999), even though the strength of this relationship is quite variable (Fleagle *et al.* 1999). The explanation for this correlation is assumed to be because of the link between rainfall, primary productivity and the diversity of tree species, with plant productivity suggested to be an important determinant on primate species richness (Reed and Fleagle 1995; Chapman *et al.* 1999). For instance, Kay *et al.* (1997) discuss how Neotropical primate species richness can be linked to plant productivity, which declines with rainfall beyond levels of ~2,500mm, possibly due to soil nutrient levels being depleted on account of leaching, and subsequently depressing plant growth and thus the quantity and quality of important resources for primates. Despite the majority of the Neotropics being predicted to increase in species richness for both the *continental* and *global* models (Table 3.4), there are also areas predicted to decline; mainly the west of South America. These areas of decreasing species richness indicate negative changes in climate.

Rivers can also affect Neotropical primate habitats through flooding, leaving many forests seasonally inundated, with such forests generally comprised of lower species numbers (Reed and Bidner 2004). Therefore increased levels of rainfall could increase the amount of forest flooding or flood new areas of forest, reducing primate numbers, particularly primates not adapted to coping with flooded forests; such as those that feed on insects in the lower canopy, which will not be present when the forest is flooded (Reed and Bidner 2004).

In the case of flooding, an aspect of climate change not taken into account in this study is the impact of rising sea levels. Gitay *et al.* (2002) explains how Mangrove ecosystems will be degraded or lost due to sea level rise, in addition, coastal mangrove forests in Asia, such as those in the Sundarbans, are also said to be vulnerable to climate change induced sea level rise, with a 1m rise in sea level being enough to make the Sundarbans disappear. This would cause a subsequent loss of primate habitat threatening species survival and placing greater strain on already fragile populations.

4.3.2 Africa

Africa has the driest climate of each of the main biogeographic zones investigated here, yet despite this it hosts the second largest expanse of tropical forest in the world (Chapman *et al.* 1999; Reed and Bidner 2004). In addition Africa also has vast amounts of permanent swamp- and seasonally flooded forests (Reed and Bidner 2004). Primate species richness is constrained by the length of the dry season for much of Africa, as demonstrated by Chapman *et al.* (1999), with habitats that receive more rainfall generally having a greater level of plant productivity, which is likely to support a larger number of primates.

The impact of high latitude warming is evident in the model outputs for Africa, in which future predictions of species richness are much reduced over northern Africa (Fig. 3.4). This will come as a consequence of shifting rainfall patterns and seasonality with a rise in temperatures, potentially followed by an increase in size of the Sahara Desert (Gitay *et al.* 2002), thus explaining the low percentages of grid cells in the African model anticipated to improve in suitable climate (increase in primate species) (Table 3.4). Desertification is predicted to intensify in accordance with reduced rainfall and/or increases in the evaporative demand, subsequently reducing soil moisture, particularly for north, west and southern Africa (Gitay *et al.* 2002) with our results also showing these areas to be declining in suitable climate, with lower species numbers predicted by each model (Fig. 3.4). Following a potential reduction in rainfall and increased desertification there will inevitably be negative effects on vegetation and consequently food resources in these areas. Moreover, shifts in temperature generated by global warming are expected to have implications for the distribution of vegetation zones (e.g. Dunbar 1998; Lucht *et al.* 2006) which will impact a wide range of taxa.

The future predictions of species richness (Fig. 3.4) display areas of greatest reduction over south, north-west and northern Africa. Considering the high diversity currently present in west- and west-central Africa this could be of great significance. Additionally the few species that inhabit areas of southern

Africa and areas bordering the Sahara Desert, in some cases just one species (Chapter 2) may become extinct as consequence of such climate change, removing primates from these areas completely. Furthermore, the region of decreasing suitable climate (species richness) present in southern Africa (Fig. 3.4) corresponds with an area where droughts occur in the December-March rain season after the onset of an El Niño event (Thomson *et al.* 2003), thus it is possible the model has taken account of this and the potential strengthening of ENSO and consequently predicted reduced numbers of species in this region.

4.3.3 Madagascar

Madagascar has been subject to a unique evolutionary history, once being a part of Africa, the island has since experienced a period of extended isolation (Storey *et al.* 1995; Yoder *et al.* 2003; Reed and Bidner 2004). This in addition to the arrival of humans on the island, which greatly affected all forms of taxa, will have played a part in creating distinct species assemblages (Ganzhorn *et al.* 1999; Reed and Bidner 2004). The primate habitats of Madagascar range from dry desert in the south; to the eastern tropical rainforest and the western tropical deciduous forest (Reed and Bidner 2004). The island of Madagascar is a global extinction hotspot due to its high endemism and high rate of habitat degradation (Dunham *et al.* 2008), however the results from the models used in this study indicate a general increase in primate species richness, or at least a beneficial improvement in the climatic conditions for primates (Fig. 3.4). Reed and Bidner (2004) detail the current climatic influences acting on lemur habitats in Madagascar; they include extreme fluctuations in rainfall, with cyclical patterns of drought and cyclones, in addition to periodic extreme drops in temperature.

Thomson *et al.* (2003) found that ENSO events have caused severe droughts in Madagascar and the south of Africa, thus the potential for enhanced ENSO events in response to global warming is of particular importance, especially considering the already high levels of anthropogenic threats to primates on the island (Dunham *et al.* 2008). This may act by impacting primate species directly through changes in precipitation and temperature and indirectly by affecting vegetation structure and consequently food resources (Dunham *et al.* 2008). Many habitats may be affected by heavy droughts, in particular the west and south-west areas of the island (Reed and Bidner 2004). Model results from a Dunham *et al.* (2008) study found that a higher frequency of El Niño events directly affected primate species, in this case *P. edwardsi*, with fecundity rates dropping by 65.5% reducing the average population size and increasing the risk of decline. However despite these negative impacts associated with climate change and ENSO, the model output in this chapter clearly displays an increase in primate species richness, across all scenarios (Fig. 3.4), particularly in the *continental* model in which across each GCM and scenario 100% of the grid cells are predicted to become more climatically suitable for primate species (Table 3.4).

The reasons for the larger increases generally occurring on the western side of the Madagascar (Fig. 3.4) may be a result of a reduced length of the dry seasons experienced in the western deciduous Malagasy forests, which are currently particularly long compared to the eastern rainforests, which also receive a greater amount of annual rainfall (Reed and Bidner 2004). This may explain why the increases are not as large on the east of the island. One potentially negative aspect, difficult to assess with the models used here, is the impact of global warming on the cyclones, originating in the Indian Ocean, which periodically hit the island, destroying large areas of forest and subsequently reducing food supply (Reed and Bidner 2004).

4.3.4 Asia

Asian primates currently inhabit a band extending from the south-east, around the Philippines, along the Sunda Shelf Islands and the Malaysian Peninsula up to India and parts of China and Japan (Chapter 2; Gupta and Chivers 1999; Reed and Bidner 2004). The continent offers a vast array of habitats, with five different types of forest being recognised on the Malay Peninsula alone (Reed and Bidner 2004). The highest levels of species richness are currently concentrated around south-east Asia, along the Sunda Shelf Islands. Despite much of mainland Asia predicted to increase in species richness in our study, although in most parts by low levels and primarily by the *continental* model (Table 3.4), there are important areas which display a reduction in species richness; the lower reaches of the Sunda Shelf Islands, and north-western Japan; both with more prominent reductions under the *HadCM3* GCM. These two areas are of concern due to the high levels of diversity present across the Sunda Shelf meaning a greater risk to a wider variety of primate taxa; whereas in contrast, Japan has few species currently present meaning any future deterioration in climatic conditions could permanently remove primates from the country.

The climate supporting the forests of Asia comprises two monsoon seasons; in December-January and a milder one in late spring (Reed and Bidner 2004). Many Asian forests experience particularly high levels of rainfall, which are elevated by the monsoon to annual levels of ~5,000mm, with low levels of 2,000mm in other regions (Reed and Bidner 2004). It has been proposed that the monsoon and associated high levels of rainfall constrain species richness throughout Asia (Reed and Bidner 2004), due to high rainfall potentially limiting primary productivity and hence the overall species richness (Kay *et al.* 1997; Reed and Bidner 2004). Additionally, greater cloud cover, which is inevitable with higher levels of rainfall, will reduce solar radiation, limiting plant photosynthesis and therefore productivity (Kay *et al.* 1997). Furthermore, Peres and Janson (1999) discuss how, within the Neotropics, beyond a certain level of rainfall primate species richness has not been found to noticeably increase, with the possibility that species richness may decline in areas with extreme levels of rain because of a reduction in plant productivity associated with lower soil nutrients (Kay *et al.* 1997; Peres and Janson 1999). This may also be relevant to Asian primates, with a considerable number of primate communities in Asia that already experience in excess of 2500mm of annual rainfall (Gupta and Chivers, 1999), thus the predicted decline in species richness over south-east Asia (Fig. 3.4) may be a result of altered patterns, or even increased amounts of rainfall possibly associated with changes in the activity of the Asian Monsoon.

The IPCC (2007) report speculates as to whether increased global temperatures may increase the variability of the Asia summer monsoon precipitation. However, other studies such as Yu *et al.* (2004) found that the East Asian Monsoon weakens in response to tropospheric cooling in east Asia during July and August, causing the upper-level westerly jet stream over east Asia to move southward, resulting in decreased rainfall and a heightened risk of drought in northern China.

The distribution and extent tropical rainforest in south-east Asia has been historically sensitive to climatic change according to Heaney (1991), who examined changes in vegetation and climate since the Miocene (25 million years BP), Pleistocene (2 million years BP) and the last glacial maximum (18,000 years BP) up to modern day times. This demonstrates the important link between changes in climate and primate habitat. Moreover, considering the many habitats already under high levels of anthropogenic pressure for much of Asia (Gupta and

Chivers 1999; Reed and Bidner 2004), beneficial changes in climate may help to ameliorate current pressures over areas of mainland Asia, whereas adverse changes, such as predicted by some model outputs for the Sunda Shelf, may exacerbate them (Fig. 3.4).

4.4 Altitudinal Changes in Species Richness

Generally, species that are confined to high altitude vegetation zones with small ranges may be more at risk from climate change than more mobile low altitude species (Dunbar 1998; Ohlemüller *et al.* 2008). Our results indicate that higher altitudes may witness improvements in climatic suitability, with the exception of *global* model *PCM* B1and both *continental* model *HadCM3* outputs, whereas lower elevations generally witness the greatest improvements in climatic suitability, with the exception of the *global* model *PCM* outputs (Fig. 3.5).

Climate change has been shown to have a detrimental impact on species at higher elevations, for instance Gitay *et al.* (2002) predicts that adverse effects on cloud (mist) forests will take place over Latin America, something which is supported by Pounds *et al.* (1999) who investigated the changes in species distribution as a consequence of warming in highland forests at Monte-Verde, Costa Rica. In this is example, atmospheric warming has accelerated the rise in sea surface temperatures (SSTs) leading to enhanced evaporation, generating large amounts of water vapour, with latent heat being released as this moisture condenses (Pounds *et al.* 1999; Hughes 2000). Thus the decline in temperature with elevation is significantly reduced, increasing the warming trend at higher altitudes, and subsequently raising the average altitude at the base of the orographic cloud bank, as predicted by the lifting-cloud base hypothesis (Pounds *et al.* 1999; Still *et al.* 1999).

Montane species are particularly prone to extinction as vegetation can be driven up the altitudinal slope by warming (Peters 1991). However, topographic regions of high diversity can also act as a buffer in the face of climate change, providing areas of stable climate (Midgley *et al.* 2003). This appears to occur under *global* model *PCM* A2 output (Fig. 3.5) in which lower elevations have reduced species richness compared to increases at higher elevations, indicative of an improvement in climatic conditions given current primate species–climate relationships.

Dunbar (1998) carried out a study assessing the impact of global warming on the distribution and survival of the Gelada baboon situated on the high montane grasslands of the Ethiopian plateau, with their current population density constrained by agriculture practices at lower latitudes. The Gelada baboon species' lower altitudinal limit is predicted to rise by around 500m for every 2°C rise in global temperature (Dunbar 1998). The importance of temperature is its impact on the nutritional content of the grasses, on which the Gelada baboons depend (Dunbar 1998). Moreover, the indirect effects of climate change on agricultural practice in the Ethiopian highlands, with warming allowing more intensive cultivation of profitable crops at higher altitudes, is likely to further constrain available habitat and exacerbate associated impacts of temperature increases on these primates (Dunbar 1998). This provides an example of the detrimental effects of rising temperatures on montane species.

4.5 New Climatically Suitable Areas

The benefit of the *continental* model is that the representations of baseline species richness are the most accurate, possibly because it better acknowledges the varying importance of the different climate variables across each biogeographic zone (Table 3.2). Thus it can be expected that the future projections of species richness will also be more accurate. However, the *continental* model is limited in that it only accounts for the areas within the biogeographic zones for which primate species are already present (Fig. 3.1), therefore other regions which may become more suitable for primate species under future climate change, will not be detected.

The advantage of the *global* model in this study is that it provides an indication of areas which are climatically suitable for primates outside of the main biogeographic zones (and outside of areas where primates are currently found). This is important as future climate change will alter the spatial distributions of habitats and climatically suitable areas (Williams and Jackson 2007). The development of novel climates that will promote new species formations could increase the risk of extinction for species with small ranges and poor tolerance to climatic variability (Williams *et al.* 2007). Furthermore, dispersal limitations will elevate the risk of a species experiencing a loss of suitable climate or the occurrence of a novel climate (Williams *et al.* 2007); this is particularly important for primates due to most species being constrained to areas of tropical forest.

High latitude areas such as parts of North America and a large section of north Asia are predicted to become more climatically suitable (Fig. 3.4B) possibly on account of a global rise in temperature accompanied by enhanced levels of precipitation at high latitudes (IPCC 2007). The other region shown to harbour suitable climatic conditions for primate species is northern Australia (Fig.3.1 and 3.4B), which already hosts areas of tropical rainforest. However, Gitay *et al.* (2002) anticipate large parts of Australasia to become drier and adds that much of the area has relatively nutrient-poor soils. Thus, it is unlikely that required levels of resources can be sustained in this region for primate species. Furthermore, Williams *et al.* (2003) demonstrate how tropical ecosystems of Australia are severely threatened by climate change themselves.

Although new climatically suitable areas may occur across the globe, there are many difficulties facing primate species before they could successfully colonise. Firstly, as tropical forest is the common habitat for the majority of primate species, with only 5 primate species with a geographic distribution entirely outside of the tropics; *Macaca fuscata, M. sylvanus, Rhinopithecus bieti, R. brelichi, R. roxellana* (Cowlishaw and Dunbar 2000), it would generally fit that any region of suitable climate would also need this form of habitat. Reaching new climatically suitable areas can be complicated due to habitat fragmentation, in addition, the region would need to meet the specific food requirements of a particular species and there would also be potentially adverse effects of competition with new unfamiliar species and the prospect of new types of predators and diseases (Thomas *et al.* 2004).

4.6 Model Limitations

Pearson and Dawson (2003) demonstrate how the complexity of the natural system fundamentally limits model performance, making predictive errors inevitable. The models used in this chapter are primarily limited in that they only account for two climate variables; temperature and precipitation, although seasonal values in these are taken into account. The results provide an indication of how primate species richness may alter given predicted changes in these variables from each GCM and scenario, in addition to providing an indication of future climatically suitable areas. However, the impact of changing climatic conditions on vegetation, in particular tropical rainforests, is not accounted for and neither are factors such as changes in evapotranspiration and carbon dioxide levels, all of which will impact upon primate species and their habitats. In addition, the models in this study fail to account for dispersal and migration of primate species, therefore the ability of species to reach areas that will be more climatically suitable in the future is unclear. However, as previously discussed, primates are generally confined to areas of tropical forest, therefore restricting dispersal abilities.

5. Conclusions

The *continental* model, incorporating a more relevant regional rather than global environmental space, accounts for the regional patterns and latitudinal trends in species richness more accurately than the *global* model, possibly due to a better representation of the varying importance of the climate variables between the main biogeographic regions. However, the *continental* model generally over-estimated baseline species richness, except for Africa, whereas the global model under-estimated it.

The projected changes in future primate species richness varied between each model used; *continental* or *global,* and with each GCM and emissions scenario. However, some general patterns became apparent, such as Madagascar being predicted to have an improved future climate for primate species and Africa having the lowest percentage improvement in grid cells with suitable future climate, although this is affected by the size of the Sahara Desert. Similarly the impact of climate change on higher elevations is also shown to have a varied impact on future primate species richness, with lower elevations generally having greater increases in species richness (improved climate), except under the *global* model *PCM* outputs. Thus it is unclear as to whether high altitude zones may provide areas of refuge under changing climates.

There are several locations that are predicted to have a suitable future climate for primate species which are not currently inhabited, in particular northern Australia. However, there are many factors that would make colonisation of new areas extremely complicated and unlikely, such as competition within new environments and the potential threats from new predators and diseases (Hoffman and Parsons 1997; Cowlishaw and Dunbar 2000). Moreover, one key restraint for primate species is the requirement of areas of tropical forest, which limits the regions in which they could locate.

The model results only provide an indication of future temperature and rainfall patterns, both of which are important to primate species, however, many other aspects will determine the effect of climate change on species richness, ranging from the impacts of warming on large scale climatic events such as ENSO, to the potential impact of new invasive species colonising primate habitats with changing temperatures.

Chapter 4

Multiple Threats to Primate Diversity: Climate, Forest Loss and Humans

1.1 Introduction

Global biodiversity is changing at an unprecedented rate as a complex response to several human-induced changes in the global environment (Sala *et al.* 2000). Kerr and Burkey (2002) illustrate how extinction rates have risen and can be attributed to the influences of habitat loss on regions of the world with moist tropical forest. When anthropogenic impacts are combined with the effects of climate change the pressure on natural systems can be amplified, for instance habitat loss, as a consequence of human activity, reduces the ability of a species to adapt and keep pace with changes in climate (Travis 2003). Furthermore, Hoffman and Parsons (1997) explain how the effects of global changes will be exacerbated by human activities, such as those involving the destruction of local habitats, which can subsequently affect local climate. Such human modification of ecosystems is threatening biodiversity, of particular concern are the tropical forests that are experiencing rapid anthropogenic transformation with high rates of deforestation in the Americas, Africa and Asia (Chapman and Peres 2001; Schipper *et al.* 2008).

One of the greatest threats primate species currently face is habitat destruction in the form of deforestation (Bearder 1991; Chapman and Lambert 2000; Chapman and Peres 2001; Ganzhorn *et al.* 2001). Cowlishaw and Dunbar (2000) discuss how agriculture is often the primary mechanism leading to deforestation, with human population growth being the driving force behind this. Large economic development programs such as resettlement and infrastructure development, in addition to large scale projects such as mining and hydroelectric power developments, that further promote deforestation are also ultimately driven by increases in human population (Cowlishaw and Dunbar 2000; Chapman and Peres 2001).

The threat imposed on primate species from increases in human population is related to the greater demand on resources that are required to support growing human populations. Human population growth promotes greater encroachment into habitats which are subsequently degraded and destroyed by anthropogenic activities, such as deforestation, therefore limiting the areas of suitable habitat while further fragmenting populations (Hoffman and Parsons 1997). A rise in human population can therefore be seen as one of the key driving forces behind the threats currently faced by primate species. Although the way in which population growth and resources are managed will vary between countries, with developing countries generally having greater rates of human population growth and thus more likely to over exploit natural resources such as forests.

The results in Chapter 3 of this study demonstrate, given the current climate-primate species relationships, how, depending on the region, future climate change may provide better or worse climatic conditions for primate species. When coupled with the effects of increased human population and subsequent habitat disturbances such as deforestation, negative aspects of climate change can be exacerbated. For instance, Phillips *et al.* (1998) demonstrate how tropical forests contain up to 40% of the total carbon stored as terrestrial biomass and help to buffer the rate of increases in atmospheric carbon dioxide (CO_2), reducing the impacts of global climate change. Therefore the exploitation of the tropical forest biome from logging and large scale deforestation has the potential to accelerate global warming.

The correlation of the threats faced by primates will ultimately exacerbate the impacts and subsequent risk to species (Chapman *et al.* 2006; Mora *et al.* 2007; Brook *et al.* 2008; Darling and Côté 2008). Therefore in this chapter we attempt to combine the three main threats to primate species (human population growth; forest loss; future climate change) in order to highlight the countries facing the greatest risk of species loss.

1.2 Aims

This chapter aims to:

1. Identify the primate-inhabited countries facing the highest levels of threat from forest loss, population growth and climate change.
2. Address the ability of countries to mitigate the threats their primate species are facing.

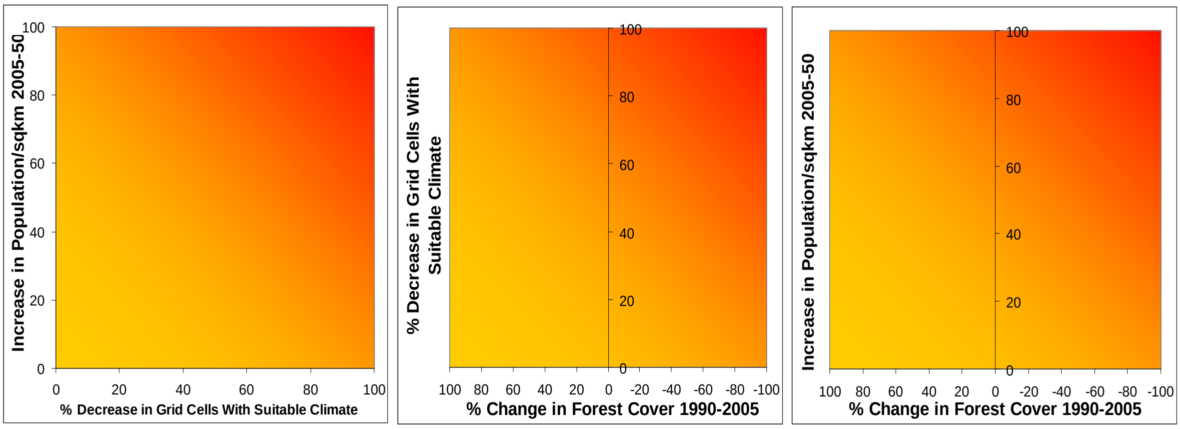
2. Methods

All primate-inhabited countries were ranked according to three measures indicating their importance for primate biodiversity: total species richness, taxonomic distinctness and percentage of threatened primate species. To calculate species richness, the total number of primate species in each grid cell of a particular country was combined to provide the country-total species richness. Similarly, using the Red List data (IUCN 2009), the number of Critically Endangered, Endangered and Vulnerable species per country was deduced and displayed as a percentage of total species present, providing the percentage of threatened species per country. In the case of taxonomic distinctness (Δ^+), which rather than a simple count like species richness, is a measure of the average evolutionary distance between different species in an assemblage (see Chapter 2; Clarke and Warwick 1998), the average Δ^+ value across all the grid cells that constitute a particular country was calculated providing a country average value of Δ^+. From this data 88 primate-inhabited countries were identified. These countries were then ordered separately by species richness, taxonomic distinctness and percentage of threatened species, to provide a top and bottom 25 list for each category (Appendix 1).

Data regarding the human population density (per km^2), in addition to the forest area (1000 ha per country), were obtained from the Food and Agriculture Organisation (FAO). Using this data, the change in population density from 2005 to 2050 was calculated for each country, in addition to the percentage change in forest cover from 1990 to 2005. Although the change in forest cover does not include future projections, the change over this period will provide an indication of countries which have experienced forest loss and may continue to do so. Furthermore, using our model projections from Chapter 3, the percentage of grid cells predicted to decrease in climatic suitability for primate species was calculated for each country. These datasets were used to analyse the threats faced by the primate-inhabited countries (Fig. 4.1), with the different threats faced by the top and bottom 25 value countries being assessed.

The 88 primate-inhabited countries were ranked according to the three threats; population increase, forest loss and decrease in suitable climate, with 1 indicating lowest and 88 indicating the highest threat. All countries were then ordered by the combined sum of these rank values (greater rank sum equates to higher threat), which allowed the identification of countries facing the greatest combined threats to primate species. From the sum of the rank values the countries were split into 8 categories of 11 countries, ranging from the highest risk countries, category 8, to the lowest risk, category 1. These categories were mapped using ArcGIS to provide a global hazard map of primate countries facing greatest combination of threats to species diversity.

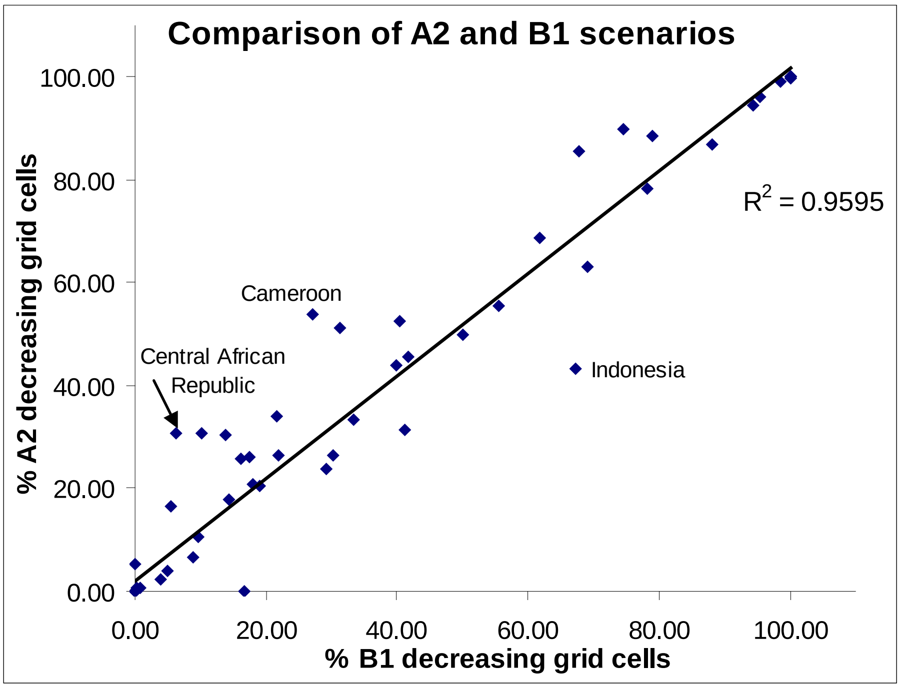
In order to appreciate the ability of countries to mitigate the threats faced to primate species, the 2004 average government score (Kauffman *et al.* 2005) in addition to the Gross Domestic Product (GDP) (World Bank 2005) of each country was used to highlight those countries which may struggle or be best suited to address the threats faced to their primate populations. The average government score accounts for each government's score for; voice and accountability; political stability; government effectiveness; regulatory quality; rule of law; and control of corruption (Kauffman *et al.* 2005). The government score was plotted against the rank sum of the combined threats to identify to potential for high risk countries to be able to mitigate the threats faced to primate species. The GDP of each country, providing an indication of wealth, was combined with the average government score to provide an indication of the economic and political stability of primate-inhabited countries, which can be used to infer the ability of a nation to mitigate threats from population pressure, forest loss and climate change.



<u>Figure 4.1:</u> Conceptual graphs - illustrating how the high threat countries were identified. Countries which fall in the dark red area are those facing the highest levels of combined threat from population increase, forest loss and climate change. The percent decrease in grid cells with suitable climate refers to the model outputs from Chapter 3; a grid cell may predicted to decline in future primate species richness (suitable climate) based on the current climate-primate species relationships.

3. Results

For the purpose of this chapter, the outputs from the two global climate models used in Chapter 3, *HadCM3* and *PCM* were averaged, providing the percentage of grid cells decreasing in suitable climate per country for the A2 and B1 scenarios. There is a close similarity between the two scenarios (Fig. 4.2), supported by the high R^2 value of 0.9595. The main outliers have been identified as Cameroon, Central African Republic and Indonesia. Furthermore, as can be seen in IPCC (2007) report, the scenarios are very similar up until 2050, with little variation between them. Due to this similarity, only the A2 scenario was used throughout the analysis.



<u>Figure 4.2</u>: **Comparison of changes in climate under A2 and B1 scenarios** - the average of the two global climate models *HadCM3* and *PCM,* used in the future predictions of species richness (Chapter 3), was taken and just two scenarios were used. % decreasing grid cells refers to number of grid cells predicted to decrease in climatic suitability (i.e. species richness) given current climate-primate species relationships (Chapter 3). Only the A2 scenario is used throughout the analysis in this chapter, due to the similarity between the A2 and B1 scenarios.

3.1 High- and Low-Value Primate Countries

The benefit of identifying high-value primate countries based on species richness, average taxonomic distinctness and percentage threatened is that it allows the countries with the highest importance in terms of primate species to be identified and analysed in relation to the threats they face.

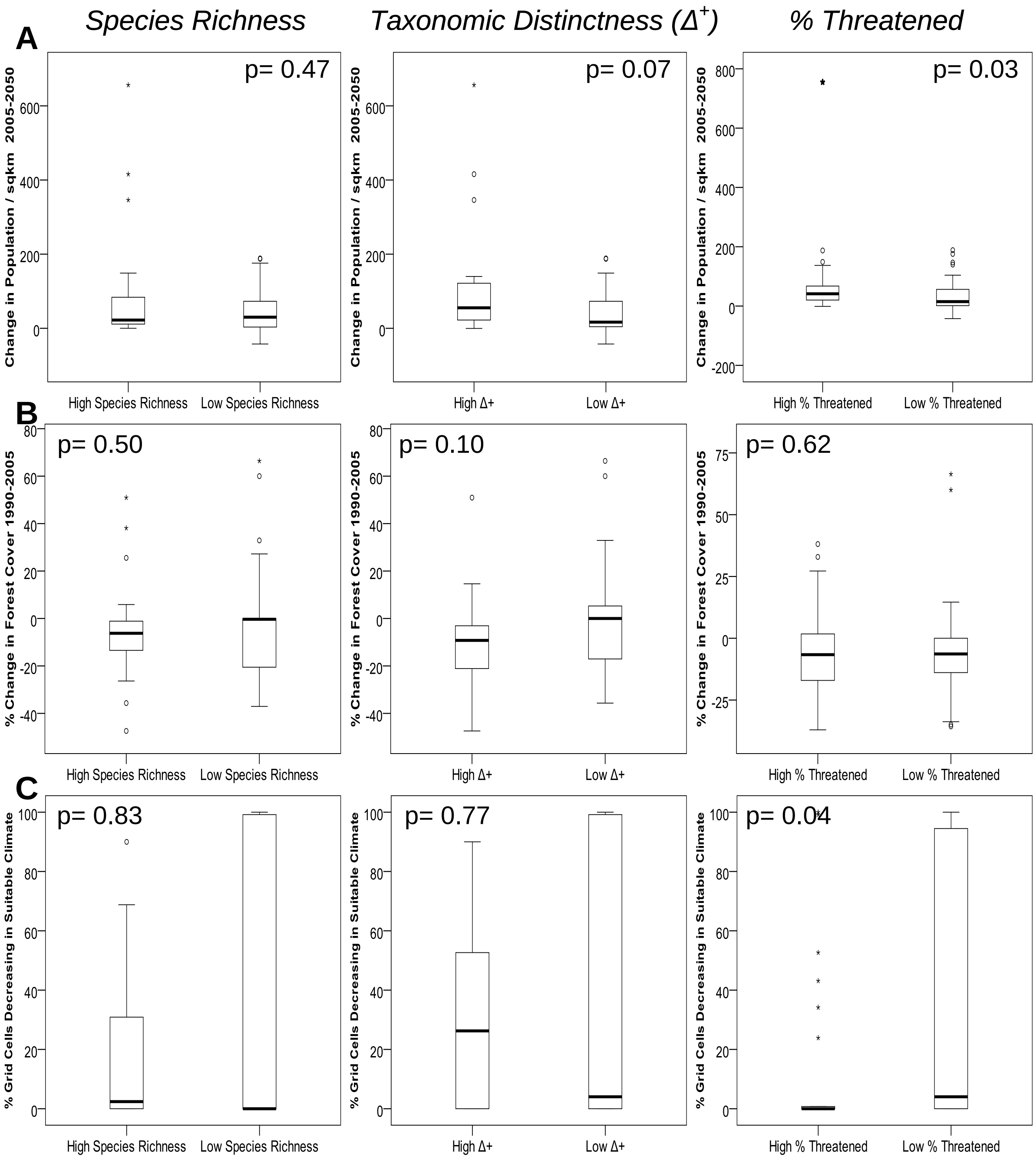
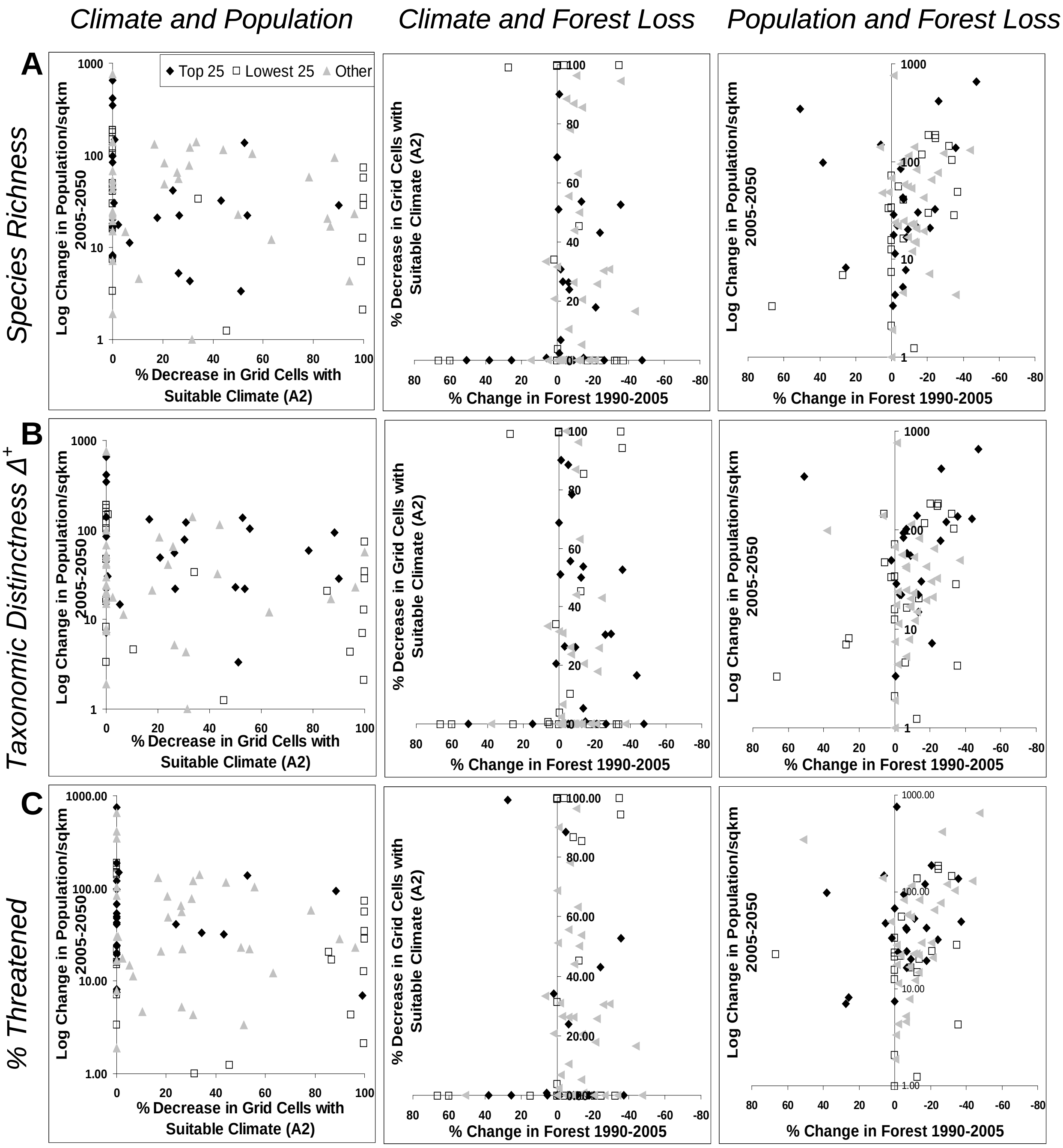


Figure 4.3: Difference in threats faced by high- and low-value primate countries – the threat from increases in human population (A), forest loss (B) and future climate (C), to the high-value (left) and low-value primate countries (right). Future climate is shown as the percentage of grid cells, per country, predicted to decrease in future primate species richness based on current climate-primate species relationships (Chapter 3).

A contrasting assessment of the threats faced by the higher and the lower value countries indicates that generally there is little variation between the threats faced by the top and bottom 25 primate value countries (Fig. 4.3). The greatest differences occur under the threat of future climate change. In which, generally the countries facing the greatest percentage decrease in grid cells with suitable climate are countries of lower primate importance. The difference between the countries with high and low proportions of threatened primate species is shown to be significant ($p < 0.05$) for the percentage of grid cells decreasing in suitable climate (p=0.04) and for the change in population per km^2 (p=0.03). This shows that the countries with high percentages of threatened primate species are at greater risk from increases in human population yet at much less risk from adverse climate change, compared to the countries with lower values of threatened primate species for which it is the opposite.

There is a large proportion of primate-inhabited countries that have witnessed a decrease in forest cover from 1990-2005 (Fig. 4.4), in which most of the points are in the negative values. Although this change in forest cover is only from 1990-2005, rather than 2005-2050 like population change, it still provides an indication of countries which have experienced decreases in forest cover, which potentially may continue to decline, placing local primate species at greater risk. Furthermore, the majority of countries are predicted to witness increases in human population per km^2 which will likely compound the threat faced from forest loss by placing further pressure on the remaining habitat.

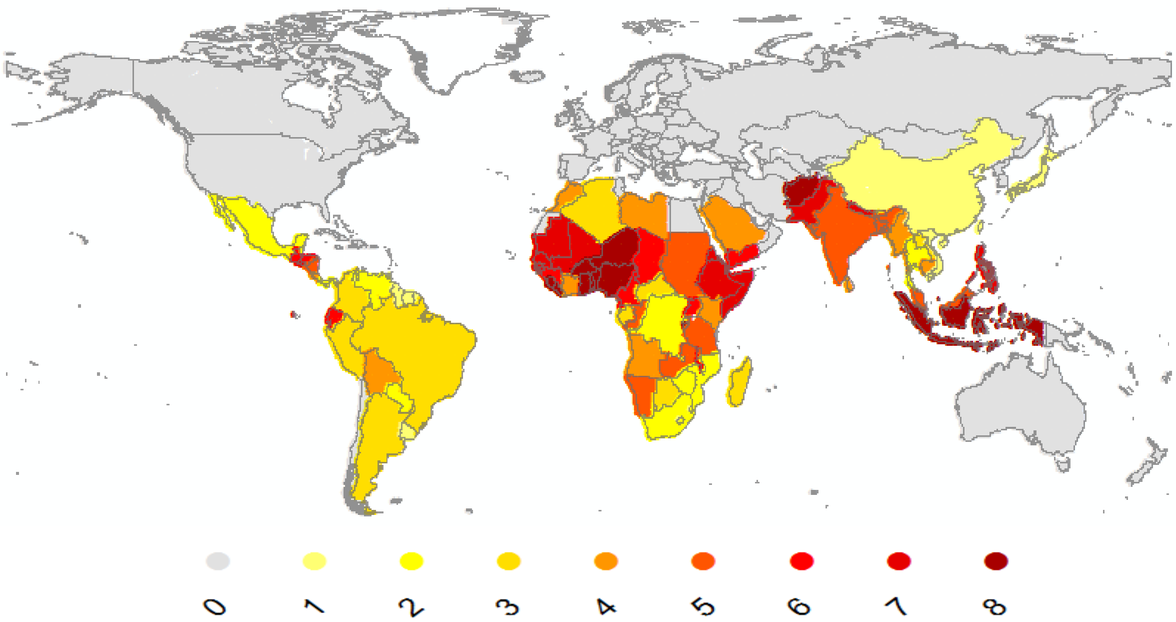
The top 25 countries with a high percentage of threatened species face a greater risk from decreasing forest cover and population increase, than from future climate change (Fig. 4.4C). In both graphs displaying population change and forest loss against percentage of grid cells decreasing in suitable climate, only six of the top 25 countries with the greatest percentage of threatened species were shown to be under threat from future climate change. Although in contrast, a larger number of the bottom 25 countries, all of which currently have zero percent threatened species, face a greater threat from future climate, which could potentially lead to these countries witnessing a rise in the number of Critically Endangered, Endangered and Vulnerable species.



<u>Figure 4.4:</u> Comparison of combined threats per country - showing the high-value primate countries (black), low-value primate countries (hollow square) and the other countries (grey) in terms of Species Richness (A), Average Taxonomic Distinctness Δ+ (B) and Percent Threatened (C) in relation to the combination of threats faced by each country. NOTE: The percentage change in forest cover is in 1000 ha per country and percent decreasing grid cells per country refers to the percentage of grid cells decreasing in suitable climate, given current species-climate relationships. The change in population is not calculated as a percentage.

3.2 High Risk Countries

The primate-inhabited countries facing the highest levels of threat from human population growth, forest loss and climate change have been grouped into eight categories consisting of 11 countries (Fig. 4.5), ranging from 1, lowest risk, to 8, highest risk (see Appendix 2 for full list of countries in each group). The most notable aspect of the global hazard map is how the countries facing the highest additive risk predominantly feature across Africa from north-west to east, and Asia, particularly south-east Asia. However, it is important to acknowledge that category 1 countries may still face a particularly high risk from one of the threats, but not across all three. On a continental scale, the Neotropics appear to face the lowest combined levels of threat, whereas Africa and Asia, with the exception of China and Japan, face the greatest levels.



<u>Figure 4.5:</u> **Additive risk from forest loss, population pressure and climate change for primate-inhabited countries.** Every country was given a rank value according to each of the three threats; human population increase, forest loss and decreasing suitable climate (a higher value was assigned to a greater threat). The sum of these rank values was calculated to identify the countries facing the highest combined levels of threat. The countries were then grouped into eight categories of 11 countries based on their overall rank sum. 1 to 8 represents lowest to highest risk. The highest risk countries are located across the Sahara Desert region of Africa, in addition to the north-west and south-east of Asia, along the Sunda Shelf in particular. Much of the Neotropics appear to have moderate levels of risk, apart from Central America, with the exception of Mexico.

Countries in category 1 face the least risk and benefit from an average increase in forest cover in addition to no adverse impact from climate change (Fig. 4.6A). However, there is still an average overall population increase anticipated for these countries. China, which is in category 1, is already known to have a large population with the associated pressures on land and habitat well documented, therefore the analysis here may be misleading. The highest risk group, category 8, displays the highest levels of forest loss and population growth, and some of the highest levels of adverse climate change. From category 1 to 8 there is a rise in the level of forest loss, and a general increase in climate change impacts, although the category 7 countries actually have a higher average percentage than 8. In contrast, the average change in population does not increase with increased risk category, i.e. 1 to 8, with category 2 and 5 having particularly large population growth, possibly due to presence of Mexico in category 2 and Bangladesh in category 5, increasing the overall average.

Consideration needs to be made over the average values for primate diversity and threatened species levels across the 11 countries in each category (Fig. 4.6B), because it allows identification of a high risk group of countries that may have particularly high values of primate diversity. The percentage of threatened species per country is of particular importance due to the fact that countries with already high numbers of endangered primate species may face high levels of additive threat, and will therefore be at a greater risk of having species becoming extinct. Across the risk groups, the highest levels of threatened species are present in category 4 and 3 countries, making their primate species especially vulnerable to additive threats, with the lowest levels in category 7.

Taxonomic distinctness (Δ^+) is similar across all the risk groups (Fig. 4.6B), although of concern is category 8, the highest risk group of countries, which host some of the highest levels of Δ^+. Similarly to the Δ^+ values, species richness remains similar on average, across each of the categories, with the exception of category 3, which has almost double the amount of the other groups. Hence the threats in these countries can affect a large proportion of primate species.

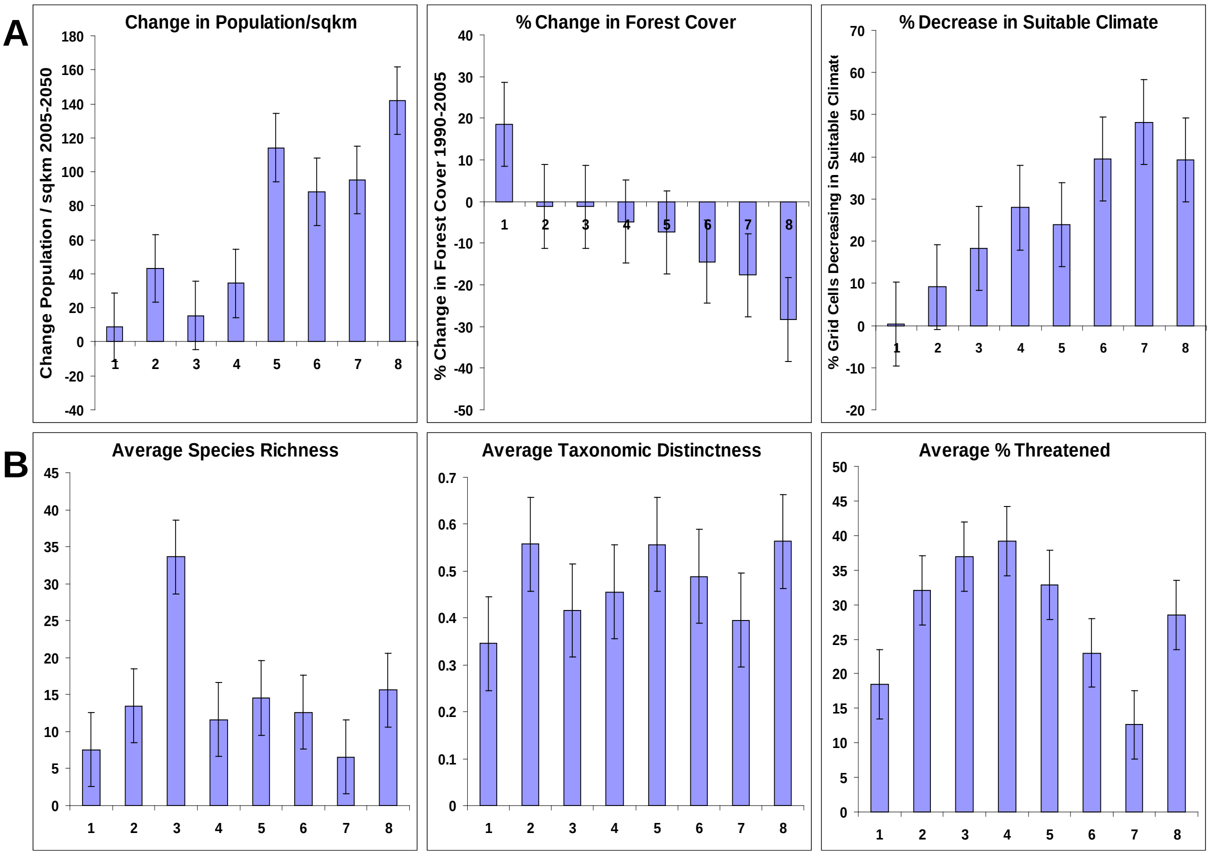


Figure 4.6: Risk category averages – A: Charts showing the average values of each threat from the 11 countries in each category. B: The average value for species richness, taxonomic distinctness ($(_{\Delta+})$) and percent threatened for each country in a category. The risk categories range from lowest risk, 1, up to the highest risk category 8.

3.3 Mitigation Potential

To assess the potential for countries to mitigate the threats imposed by projected climate change, population growth and forest loss, the 2004 average government score (Kaufmann *et al.* 2005) was used. A low government score could be indicative of a government/country that may disregard conservation and protection of forests and habitats, or consider them to be of low importance/priority. There is a general trend for lower government scores within higher risk categories, which leads to concern for the higher risk primate species, since low government scores could be indicative of a potential exacerbation of threats faced by countries due to poor management (Fig. 4.7). Of primary concern is that the group of highest risk countries are also the ones with the lowest average government score. This leads to concern over the potential management of issues such as growing populations and adverse climate change, which risk category 8 countries face on a greater scale. Furthermore, the risk category 8 countries face the highest levels of forest loss as previously discussed (Fig. 4.6A), which could potentially be coupled in part with a low government score. Thus it is no surprise that the group of countries with the highest levels of forest loss also have the lowest combined average government score.

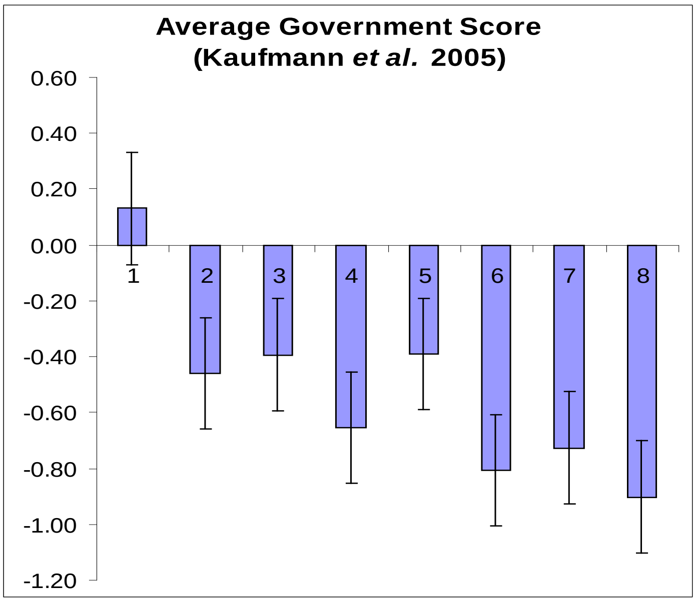


Figure 4.7: Average government score for each risk category - the average government scores for all the countries in each risk category was combined to provide an overall average value per category. The risk categories range from lowest risk, 1, up to the highest risk category 8.

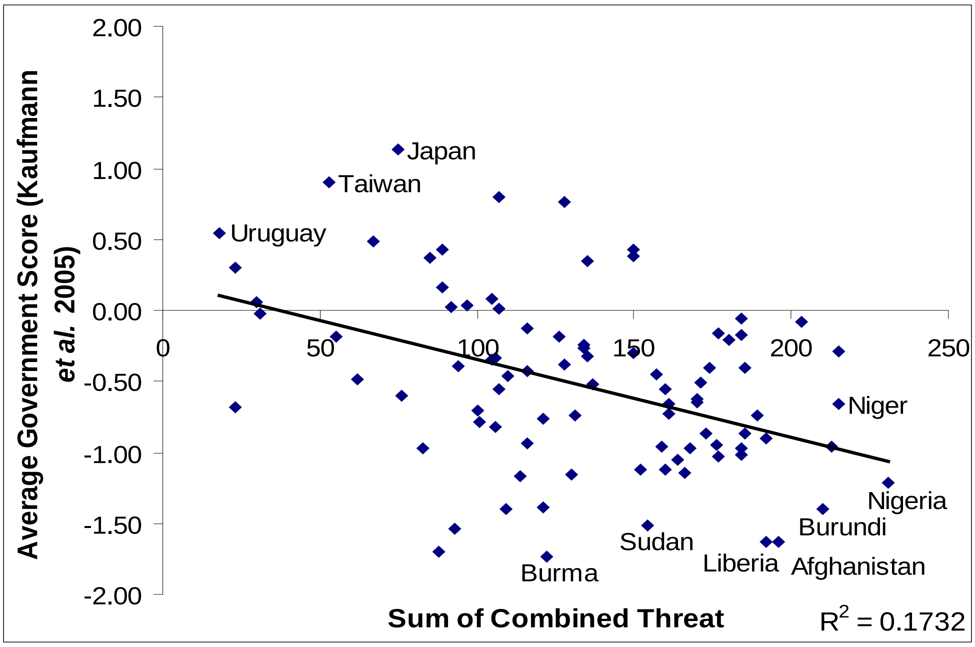
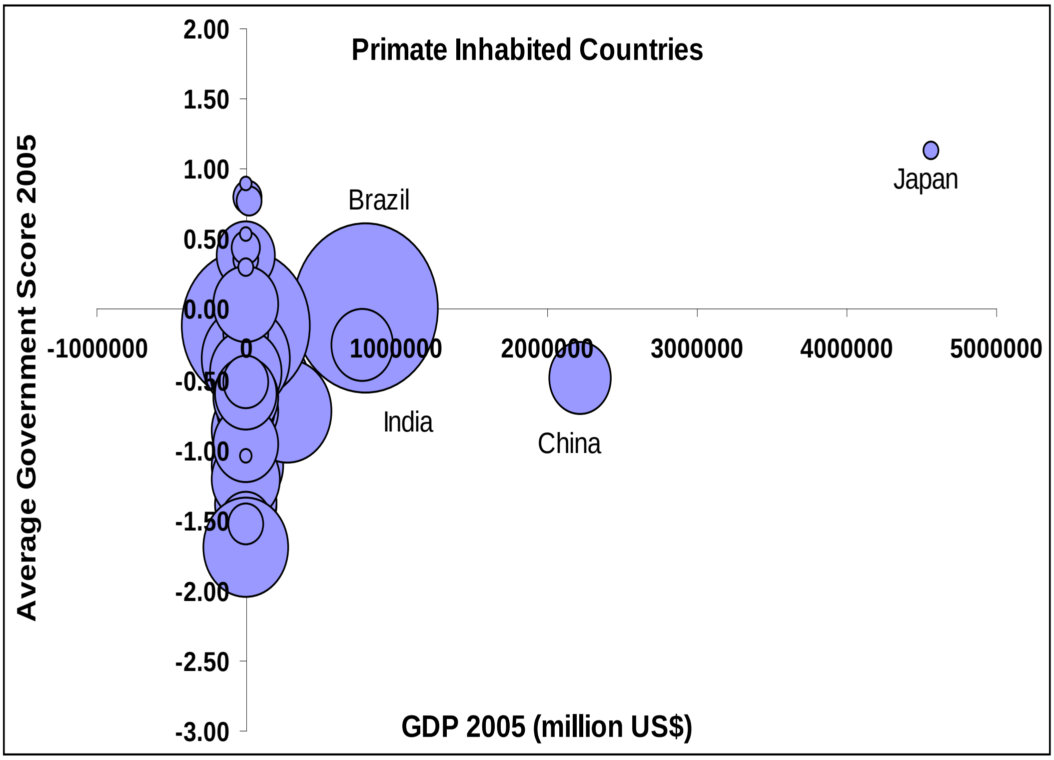


Figure 4.8: Average government score (2004) plotted against combined threat - the sum of combined threat relates to the sum of the rank position of each country for population increase, forest loss and decreasing area of suitable climate, with a higher value assigned to countries with greater levels of threat.

The countries that have the highest combined levels of threat tend to have the lowest government scores (Fig. 4.8), with a general increase across the 8 risk categories (Fig. 4.7). Of concern would be the large number of countries that have a negative (low) score. The impact of this is that countries facing multiple threats can be assumed to be less able to mitigate the effects of such threats, on account of their low average governance scores. Additionally, the results could provide an indication of how a low government score leads to a higher level of threat (Fig. 4.8). Although this is mainly relevant with forest loss, as in many cases it is the governments who decide whether to permit deforestation activities such as logging and how much forest area they are prepared to protect.



<u>Figure 4.9</u>: Comparison of GDP (2005), average government score (2005) and total species present per country - the size of the bubble represents the number of primate species present per country. Apart from Japan and China, primate-inhabited countries are characterised by a low GDP. Furthermore, given the size of the bubbles, the majority of primate species are indeed located within the poorer countries.

The majority of primate-inhabited countries have a low Gross Domestic Product (GDP), with the exception of Japan and China, which have the largest GDP, followed by Brazil and India (Fig. 4.9). Furthermore, the countries with the lowest GDP also tend to have a lower average government score. Hence it is clear that primates are predominantly located in poorer, developing countries.

4. Discussion

Each of the main threats analysed here has implications when acting in isolation, although their combined effects are what place populations under the greatest risk. The potential for primate species to adapt and tolerate the threats they face depends on their ability to locate adequate food and suitable habitat in order to breed successfully and maintain their populations (Chivers 1991).

4.1 Human Population Pressure

Despite the intelligence and adaptability for which primates are renowned, many species are struggling to cope with the environmental changes imposed by rising human population densities (Bearder 1991). The threat faced by primate species from population growth will be in the form of increased pressures on land and resources, promoting greater encroachment onto, and destruction of habitats. In our analysis we have found a significantly higher threat from future population pressure in countries of high percentages of threatened primate species compared to those with low percentages (Fig. 4.3), which may subsequently lead to extinctions as a result of population related pressures. However there was no significant difference between the threat faced by high and low species-rich countries or between high and low taxonomic distinctness (Δ^+) countries (Fig. 4.3).

Bomhard *et al.* (2005) discuss how habitat destruction and degradation, mostly because of agriculture and urbanisation are the main past and present threats to biodiversity. For instance countries such as Bangladesh, which face the greatest increases in population, will require increased space to house the growing numbers of people, while simultaneously placing more pressure on agriculture within the country. The associated change in land use as a response to growing populations is anticipated to have the greatest impact on terrestrial ecosystems, with model projections by Sala *et al.* (2000) predicting the greatest levels of land use change to occur in tropical forests, which will most likely impact primate species diversity. Considering that the majority of primate-inhabited countries are predicted to increase in human population (Fig. 4.4), it could to lead to greater instances of forest loss and climate change related threats due to the interaction between these different pressures (Brook *et al.* 2008).

Cowlishaw and Dunbar (2000) explain how shifting cultivation, practised by small scale farmers, involving clearing and planting crops in small patches of forest over periods of three years, causes minimal damage as the land is allowed to recover. However, at increased population densities, inappropriate agricultural methods have been adopted leading to this form of agriculture causing considerable losses of tropical forest (Cowlishaw and Dunbar 2000). The results presented in this chapter support this link between high population countries and forest loss, with higher population countries often displaying a greater percentage of forest loss (Fig. 4.4). Considering that population pressure will lead to increased demand on agriculture as the need for food increases, it can be expected that more intense farming methods will be adopted, putting a greater strain on the environment, and subsequently leading to greater levels of forest loss (Saunders *et al.* 1991; Ewers and Laurance 2006). Conversely, a reduction in agriculture can promote an increase in the size of forest, as demonstrated by Matlack (1997).

In addition to agriculture, high population increases will place a greater demand on resources, for example Laurance (1998) documents an increase in mining and the numbers of major mineral oil and natural gas developments observed in the Amazon. The development of these large scale projects promotes extensive road building, opening up previously inaccessible forest, subsequently promoting settlement and agriculture, in addition to small towns to house the workforce (Cowlishaw and Dunbar 2000), all of which will place strain on the local environment and consequently primate species. Cowlishaw and Dunbar (2000) discuss how fires can be used to clear forest, which can spread easily with devastating consequences, for example in Madagascar the use of fire has become a cultural habit, removing large areas of tropical forest that is subsequently replaced by grassland (Chapman and Peres 2001). Therefore, with regards to the countries in risk category 8 of the high risk countries map (Fig. 4.5 and 4.6), that face the highest levels of population growth, it can be expected that the already high levels of forest loss will become a more serious problem due to the links between forest loss and population. Moreover, countries that face high levels of population growth and relatively little forest loss could potentially be expected to witness a rise in future forest loss.

A more direct effect of human population increases on primate populations could be a result of increased hunting and trade. Peres (2001) demonstrates how subsistence hunting has had negative effects on species diversity within Amazonian forests. Growth of human populations in some countries, particularly those of South America and Africa could lead to a rise in subsistence and commercial hunting of primate species (Chapman and Peres 2001). For instance, Laurance (1998) show how hunting has increased throughout the Amazon due to improved access following infrastructure developments in the forest and similarly Corlett (2007) describes how high human population densities are leading to increased levels of hunting throughout almost all remaining tropical forest in Asia. Furthermore, Nekaris *et al.* (2010) demonstrate the detrimental impact of trade, driven by economic factors and cultural traditions together with increased forest access, on primate species in Asia. The result is that precarious populations are put under greater strain, with serious impacts on primate populations already observed in many regions of Africa (Chapman *et al.* 2006).

Considering the majority of primate-inhabited countries have a low GDP (Fig. 4.9) these countries may have an increased dependence on their own natural resources to generate capital from exports, which may result in elevated levels of primate hunting. Further negative impacts can arise due to increased human contact and presence within habitats which is likely to facilitate the incidence of diseases and the threat of parasites to primate populations (Chapman *et al.* 2006). However despite this, the greatest threat from human population growth is the impact on primate habitat, particularly the area and quality of tropical forest.

4.2 Forest Loss

Forest loss can be considered one of the most serious threats to primate species, given how the majority of primate-inhabited countries display a reduction in forest cover from 1990-2005 (Fig. 4.4). Moreover, when combined with the number of countries with expanding populations (Fig. 4.4), which can exacerbate forest loss, this threat will be heightened. Additionally, there was no significant difference between the threat from forest loss on high- and low-value primate countries (Fig. 4.3), providing a further indication that it is a threat common to most primate-inhabited countries.

Tropical deforestation has occurred predominantly in response to expansion of agriculture and large scale economic development programs (Chapman and Peres 2001). In addition to forest clearing, selective logging is having an impact on forests, particularly in Asia where alternative sources of timber are sought with the tropical forests already considerably reduced in size (Cowlishaw and Dunbar 2000). This along with the known high population pressure in Asia explains why a large number of primate-inhabited Asian countries are classed as facing the highest risk levels, particularly those in south-east Asia

(Fig. 4.5). In addition to the threat posed by logging operations in south-east Asia, the conversion of the remaining tropical forest habitat for oil palm cultivation is a major problem. Gaveau *et al.* (2009) explain how the expansion of high-revenue oil palm plantations, due to increased prices and demand from the food, cosmetic and biofuel industries, along with development of road networks, required to move palm oil from the remote forests to market destinations, is the most important threat to lowland forests in south-east Asia. This places primates such as the orangutan under increased risk of extinction, as has been documented for Indonesia and Malaysia (e.g. Gaveau *et al.* 2009; Swarna Nantha and Tisdell 2009). Furthermore, logging operations from Malaysia and Indonesia are expanding into the Amazon, with a new trend in which selective removal of valuable tree species, rather than whole areas of forest occurs (Laurance 1998). This can be as equally damaging as any other form of logging due to the potential to affect specific food resources required by certain species.

The effect of selective logging can lead to reductions in primate populations before the effects of deforestation have been delivered (Chapman and Peres 2001). One of the main impacts on primate populations from selective logging will be reduced food availability (Chapman *et al.* 2000). However, Ganzhorn (1995) found that small scale logging on a Madagascan forest increased the availability of sunlight and resources for the remaining trees, leading to a greater abundance of fruit and better quality leaves with a subsequent rise in lemur populations. Although, the various other aspects associated with logging can offset any benefits and even prevent increased productivity. For instance, many logging operations often remove the important food trees (Chapman *et al.* 2006), in addition to the development of road networks and infrastructure during operations; which can cause tree mortality; changes in local microclimates and open up the forest to further human settlement and agriculture (Laurance 1998). Johns (1991), for example, demonstrate how tree diversity in the Amazon is important for maintaining numerous species within a community, but is being impacted by selective logging.

Although selective logging may not result in large areas of forest being cleared, detrimental effects may arise as a consequence of changes in the forest structure, such as making the forest more flammable and prone to devastating forest fires (Cowlishaw and Dunbar 2000), something which can be exacerbated by an intensification of El Niño, predicted under climate change scenarios (IPCC 2007), promoting longer periods of drought (Dunham *et al.* 2008).

Infrastructure developments associated with logging operations, such as road networks and sites to house workers, will further fragment the forest, resulting in the size of primate populations confined to a particular fragment being greatly reduced, consequently increasing the risk of extinction (Cowlishaw and Dunbar 2000). This is supported by Harcourt and Doherty (2005) who demonstrate that for most regions, with the exception of Africa, the number of primate species declines linearly with fragment area. In addition to the direct threat of small fragment size, edge effects and changing microclimates will inflict further stresses on strained primate populations (Saunders *et al.* 1991; Cowlishaw and Dunbar 2000; Harcourt *et al*. 2001). Fragmented habitats are also more susceptible to invasive species such as weeds and pests, promoting further deterioration of the habitat (Hoffman and Parsons 1997). Furthermore these habitats become much more accessible for humans, prompting an increase in threats to primate species in relation to human population pressures as previously discussed, for example Peres (2001) explains how forest fragmentation can promote hunting due to greater accessibility.

In addition to being closely linked to population pressures, changes in forest are also related to changes in climate, with deforestation having the capacity to exacerbate climate change, just as climate change can promote forest loss (Laurance 1998; Cox *et al*. 2004). Laurance *et al.* (2000) document synergisms between forest fragmentation and natural climatic variability due to fragmented forest being more susceptible to desiccation making them more vulnerable to droughts and fire. Therefore it can be expected that the countries which are currently impacted by just one threat and those in lower risk categories (Fig. 4.5 and 4.6), may soon face greater levels of other threats due these correlating factors (Mora *et al.* 2007; Darling and Côté 2008). An example of the link between human impacts on forest loss and subsequently climate, is the effect on forest microclimates which have been found to be sensitive to adjacent deforestation (Phillips and Gentry 1994), with instances of higher tree mortality in the Amazon being attributed to increased desiccation and wind turbulence near forest edges (Laurance 1998).

4.3 Climate Change

The threat from climate change is inherently linked to the threats from human population and forest loss, mainly due to the influence of changing land cover, such as deforestation and urbanisation, which can influence climate through a range of feed back mechanisms (Cox *et al.* 2004). For instance, tropical forest clearing decreases evapotranspiration rates, which in turn can reduce precipitation, potentially leading to a further decline in forest cover (Laurance 1998; Gitay *et al.* 2002). Consequent changes in the hydrological cycle have also been observed (Laurance 1998) which can affect entire ecosystems. Based on these feedbacks, the countries with a low percentage of grid cells decreasing in suitable climate, but have high levels of population growth and forest loss in particular (Fig. 4.4), could potentially experience a deterioration in suitable climate. Furthermore, countries with a low percentage of threatened species were found to be at significantly greater risk from climate change than countries with a high percentage (Fig. 4.3), leading to the possibility that these countries could witness an increase in threatened species on account of the impacts of adverse climate change. Alternatively, the countries with a high percentage of threatened species are under less threat from climate change, meaning any added strain, from detrimental changes in climate, on these fragile primate populations may be avoided.

Clearing of tropical forests contributes further towards the already increasing levels of greenhouse gas emissions, due to the role of forests in storing carbon, consequently accelerating the rate of climate change (Gitay *et al.* 2002). Similarly Cox *et al.* (2004) demonstrate the potential of the biosphere to effect climate due to the responses of vegetation to elevated carbon dioxide levels, with tropical forests having the potential to buffer the rate of climate change. Thus further highlighting the important interactions between these key threats, in that deforestation not only contributes towards climate change, but reduces the capacity for ecosystems to moderate and restrict the magnitude and rate of change.

A decline in suitable climate, potentially in the form of increased temperatures, could promote drought conditions, which along with logging activities can substantially increase the risk of disastrous forest fires. For example, Chapman and Peres (2001) discuss how catastrophic wildfires in tropical forests will be aggravated by the synergistic effects of climate change, through stronger

El-Niño mediated dry seasons and anthropogenic forest disturbance that breaks up the forest, promoting rapid drying, in addition to activities such as logging which can provide large amounts of fuel wood (Laurance 1998; Gould *et al.* 1999; Dunham *et al.* 2008). Sala *et al.* (2000) demonstrate the synergistic interactions between drivers of global change with the example of how human disturbance and changes in climate can lead to the invasion of exotic species. Chapman *et al.* 2006 explains how primate species would be able to respond to such pressures associated with climate change by migrating to a new area of tropical forest, however, human habitation and agriculture have curtailed this ability.

4.4 Combined Threat

The effects of just one threat can lead to adverse consequences for primate diversity, with a combination of threats having a greater potential to simultaneously impact upon primate species (Mora *et al.* 2007; Brook *et al.* 2008; Darling and Côté 2008). It is clear how population pressure, forest loss and climate change are interlinked through a variety of feedbacks. Due to this, the global map of high risk countries was produced taking account of the combination of these threats (Fig. 4.5).

One of the regions facing the greatest combined levels of threat is south-east Asia (Fig. 4.5), where almost every primate habitat has been impacted by human activities (Gupta and Chivers 1999). These human induced land use and land cover changes have been linked to changes in the East Asian monsoon (Fu 2003), providing another example of the correlation between threats. Furthermore, Brook *et al*. (2003) present results suggesting that the current rate of habitat destruction in south-east Asia will result in the loss of 12-42% of regional populations over the next century, half of which will be global extinctions, indicating the severity of the threats faced by the region. The other region identified as being at particularly high risk is the area across north-west to east Africa (Fig. 4.5). Previous studies, such as Chapman *et al.* (2006) highlight how African forests and their primate communities are seriously threatened, and when combined with the impacts of future climate change, in which northern Africa was projected to have large areas decreasing in climatic suitability (Chapter 3), it explains the band of countries across this region that display high levels of additive risk (Fig. 4.5).

Countries such as Brazil in South America have been assigned a lower threat category based on the sum of their combined threats. However, it is widely documented how Amazon deforestation is taking place (Laurance 1998; Cowlishaw and Dunbar 2000; Ewers and Laurance 2006). The annual percentage rate of deforestation in the Neotropics is around half that of Asia but destroys an area twice as large (Cowlishaw and Dunbar 2000), thus the sheer size of the area of tropical forest throughout the Amazon means what would be significantly large proportions of forest loss in other countries, is relatively small within the countries of the Amazon.

Madagascar is in category 3 (Fig. 4.5), one of the lower risk groups, despite being documented to have witnessed significant reductions in forest cover (Ganzhorn *et al.* 2001; Dunham *et al.* 2008), this could potentially be a due to the limitation of assessing percentage change in forest cover, as with some of the countries in the Amazon, or due to most forest removal occurring outside the time frame used in this study (1990-2005). Additionally, the fact that Madagascar did not possess any grid cells decreasing in suitable climate may have reduced the overall additive risk.

It is important to appreciate that the charts in Fig. 4.6 display the average values across countries in each category, therefore individual countries with high values can alter the pattern significantly. For example, category 3 is classed as having a much larger average number of species present than the other categories (Fig. 4.6B); the reason for this is the presence of Brazil and Madagascar in this category, the two countries that hold the greatest number of primate species. The aim of these charts is to provide an indication of the primate- and risk-values for each category. Furthermore, the countries classed as facing lower threat levels and may be in category 2, 3 or 4, could still have high population growth, forest loss or negative climate change impacts, but because the categories were assigned based on the combination of the three threats, some countries that face a particularly high threat from one hazard, such as adverse climate change, for example, may not face any forest loss or population related threats.

4.5 Mitigation potential

The majority of the primate-inhabited nations can be classed as developing countries, indicated by the low GDP commonly displayed for most countries (Fig. 4.9). These countries can be very poor and characterised by political instability, often with high rates of population growth, making issues such as forest protection a low priority (Ewers 2006; Isabirye-Basuta and Lwanga 2008), leading to elevated pressures on the environment and consequently primate species. The average government score (Kaufmann *et al.* 2005) provides an indication of a country which may be politically unstable and could be expected to make protection of primate species and their habitat relatively low on their agenda. With this in mind, it is of great concern that the countries facing the greatest overall threat from forest loss, population increase and climate (Fig. 4.7 and 4.8) have the lowest government scores. This could explain the high levels of forest loss (1990 to 2005) already experienced in these countries, due to issues such as conservation and forest protection being a low priority (Isabirye-Basuta and Lwanga 2008), in addition to raising the possibility of further losses in the future.

The African continent hosts some of the highest rates of human population growth coupled with some of the lowest per capita incomes in the world, leaving people heavily reliant on natural resources, explaining factors such as the high rates of forest loss (Chapman *et al.* 2006) and therefore supporting the high risk levels assigned to much of the continent, particularly northern Africa (Fig. 4.5). Furthermore, throughout the continent there is great political and economic instability, which could serve to undermine any conservation efforts (Chapman *et al.* 2006).

The majority of primate species occur in countries with a low GDP and a low government score (Fig. 4.9), with the exception of Japan, China, Brazil and India. Ewers (2006) provides results showing how economic wealth has a direct effect on deforestation rate, with natural resources such as forests shown to be essential to the economic development of many countries and the main source of export earnings, with more wealthy countries having a lower reliance on environmental capital such as forest resources. This can be similar for countries in which hunting for primates is a common practice as it provides much needed capital from exports (Cowlishaw and Dunbar 2000).

According to Tol *et al.* (2004) poorer people will be more vulnerable to the impacts of climate change due to their limited capacity for adaptation. Given that primate-inhabited countries can be predominantly considered to be ‘poor’ the ability to mitigate threats such as climate change will be reduced, and when combined with the low government scores displayed by most of these countries (Fig. 4.8 and 4.9) it will likely consign primate species to greater risks of extinction. Additionally, Ewers (2006) explains how the quality of the government and the money available will determine the ability of a nation to make the switch from deforestation to afforestation. In this study these two variables can be represented by the average government score and GDP respectively, with it apparent that the majority of primate species are located in countries with low values for each (Fig. 4.9).

4.6 Limitations

Care has to be taken when interpreting percentage or absolute change in forest cover and population over their respective timescales. For example, Ewers (2006) explains that when a nation has low forest cover, a small change in the absolute amount of forest cover will be represented as a large percentage change, therefore nations with low forest cover being more likely to display greater rates of change. This could explain the lower percentage forest loss in the Amazon compared to areas of Asia and Africa. However, in the case of primates for which tropical forest is the primary habitat, a country with low forest cover will already have a small area for primates; therefore any further decrease is very important as there will be very little remaining habitat. The actual increases in population per km^2 from 2005-2050 were calculated rather than the percentage for this reason. However, Cincotta *et al*. (2000) discuss how population growth can be a misleading indicator of risk due to growth rates masking the spatial distributions of increasing human populations.

5. Conclusions

In the presence of continuing deforestation, agricultural expansion and climate change, primate populations are going to find their forest habitats increasingly fragmented, which poses a severe threat to their survival (Chapman *et al.* 2006). Human activity in the form of population growth can be seen as the ultimate driver behind threats to primate diversity, as it can promote deforestation, contributing towards climate change, which in turn can lead to reductions in forest cover. For instance within forests, the different forms of anthropogenic disturbance often coincide, with their effects operating synergistically (Peres 2001), with projected climate change having the capacity to magnify the impacts of these disturbances on primate habitats, consequently having serious implications to the extinction risk faced by primate species.

The results in this chapter provided no significant differences in the levels of threat faced by primate-inhabited countries with high and low diversity. However, the countries that currently have low percentages of threatened species face increased risk from adverse future climate change, possibly leading to a rise in threatened species. Moreover, countries with high percentages of threatened species are at significantly greater risk from increases in human population. The greatest risk countries are those facing the combined action of various threats to primate diversity, which can intensify the overall impacts through associated feed back mechanisms. The ability for countries to mitigate these threats and protect primate species can be largely determined by their wealth and political stability (Chapman *et al.* 2006). However, it appears that the countries facing the highest additive risk from a combination of threats are also the ones with some of the lowest average government scores, placing an added concern over the future of primate diversity in these countries.

Chapter 5

General Discussion

Primate species are widely threatened with nearly half of all species being classed as endangered (Mittermeier *et al.* 2009). Different species face different levels of threat from the various facets of ongoing environmental change. In this study, we have investigated the impact of future climate change and other threats on primate species, including to what extent these different threats act in synergy or in isolation, in addition to identifying regions in which the total threat is likely to be highest.

The greatest threat currently faced by primate species is from deforestation as a result of various human activities, driven by the unprecedented growth and expansion of the human population over the last century (Chapman and Peres 2001). Our model results illustrate the varied impact of future climate change on primate species across different geographic regions; with some areas set to witness improvements in climate, such as Madagascar, whereas others face deterioration in suitable conditions, such as northern Africa. The way in which climate change impacts upon primate habitats, many of which are characterised by high levels of human disturbance, could determine the fate of many species.

In this chapter, I will summarise and discuss the primate-specific results of this study in the wider context of three issues: i) the relevance of past climatic conditions for current global biodiversity patterns and extinction risk, ii) changing climate dynamics and their effects on the biota, and iii) the interacting impacts of climate change and habitat loss.

Global Primate Biodiversity, past Climatic Signals, and Extinction Risk

Past Climate Change and Primate Diversity

Modern day patterns of primate species richness have arisen as a result of ecological and historical factors associated with regional geomorphology and climate (Eeley and Foley 1999; Peres and Janson, 1999; Cowlishaw and Dunbar 2000). There is considerable evidence that major environmental change during the late Quaternary has shaped present day patterns of primate distribution and diversity, in addition to those of many other species (Eeley and Lawes 1999;

Hewitt 2000). An example in which historical environmental change has helped shaped present day primate species assemblages and richness can be seen from the Sunda Shelf islands of south-east Asia. These islands were formed as a consequence of climatic warming leading to a rise in sea level during the Holocene period (Heaney 1984). The subsequent isolation of primate species on the various islands helped create distinct species assemblages due to extinction of primate species from smaller islands (Harcourt 1999; Harcourt and Schwartz 2001).

Growth and decline of tropical forests in response to climatic change during the Pleistocene acted as a driving force behind historical evolution of primate species (Eeley and Lawes 1999; Cowlishaw and Dunbar 2000). As forests contracted with a changed climate and species composition, primate populations would have been fragmented and during times of isolation, evolutionary processes, adaptation to changing local conditions and competition would have often caused populations to differentiate (Chapman *et al.* 1999). Equally when forests expanded, species dispersal would have led to further adaptive change, and differing dispersal abilities and ecological tolerances influenced various species' ability to establish new niche habitats (Chapman *et al.* 1999).

Historical events and adaptive responses have played a major role in producing the patterns of modern day primate diversity (Chapman *et al.* 1999; Eeley and Foley 1999; Eeley and Lawes 1999), and potentially explain the global patterns of taxonomic distinctness for primates (Fig. 2.3). The way in which historical environmental change has shaped primate species distributions and abundance highlights the importance of climate and the potential for future climate change to impact species.

Climate Change and Extinction Risk

Mass extinction events have occurred across a wide range of taxa throughout the geological and fossil records and can often be associated with changes in climate (Hoffman and Parsons 1997; Mayhew *et al.* 2008; Nogués-Bravo *et al.* 2010). Many studies accept that we are currently experiencing a mass extinction event driven by human activities (Cowlishaw and Dunbar 2000; Gitay *et al.* 2002). Benton and Twitchett (2003) study the end-Permian event, 600 million years ago, which saw the loss of around 95% of all species on Earth. There are several theories behind what triggered this mass extinction, with evidence of asteroid impact and/or mass volcanism contributing towards a spiral of positive feedbacks which subsequently led to a dramatic rise in global temperatures, termed the ‘Runaway Greenhouse Effect’ (Benton and Twitchett 2003). The Runaway Greenhouse Effect results from a breakdown in global environmental mechanisms and consideration needs to be made of the risk for modern day global warming to reach a point that causes natural systems break down resulting in cascading effects similar to those proposed for the ‘runaway greenhouse effect’.

Environmental stochasticity such as seasonal fluctuations in temperature and rainfall, changes in large scale circulation systems such as the El Niño/Southern Oscillation (ENSO) and incidence of extreme events such as hurricanes, drives most natural fluctuations in population size through the associated effects on food availability, predation and disease (Cowlishaw and Dunbar 2000). Thus the projected impact of climate change on these activities may significantly affect extinction risk, with changes in the frequency and intensity of extreme events already being predicted under climate change scenarios (Easterling *et al.* 2000; IPCC 2007). However, fluctuations in the numbers of individuals over time and space are typical for all animal populations (Heino, *et al.* 1997) with many species adapting to changing conditions in order to maintain their populations.

Gitay *et al.* 2002 explain how future extinctions as a result of climate change will vary between regions, with no globally uniform trend; climate change will vary depending on the location. Our results corroborate this, with the varied impact of future climate change on primate species richness being demonstrated by large improvements in climate predicted for regions such as Madagascar and the Neotropics in particular, compared to Africa, in which the majority of the continent is set to decrease in climatic suitability, given current climate-primate species relationships (Fig. 3.4 and Table 3.4). Furthermore, extinctions will also vary between different countries, with some potentially better placed, economically and politically, to mitigate threats faced to primate species (Fig. 4.8 and 4.9) which may ultimately determine the ability of species to survive current pressures.

Despite the general consensus by many authors that anthropogenic climate change has the potential to increase extinction rates (e.g. Gitay *et al.* 2002; Thomas *et al.* 2004), there is contrasting evidence between the fossil record and molecular data and recent ecological research (Bininda-Emonds *et al.* 2007; Botkin *et al.* 2007). This along with specific problems with current forecasting methods led Botkin *et al.* (2007) to conclude that recent projections of extinction rates are overestimates; based on the relatively few extinctions that have occurred during the recent ice ages, as displayed in the fossil record, compared to modern forecasts. This miss-match between future predictions and historical data is described as the ‘Quaternary Conundrum’ (Botkin *et al.* 2007). Possible explanations for this are that projected climate change is considerably different to that experienced during the Quaternary and even though species have responded to climate changes throughout their evolutionary history, it is the rapid rate of change coupled with increased pressures from human activities that could lead to a much greater number of extinctions (Root *et al.* 2003). Conversely, current forecasting methods do not account for the genetic and ecological mechanisms that may allow the persistence of many species even under rapid climate change (Botkin *et al.* 2007), potentially reducing the susceptibility of species to many threats. For example, Wright and Muller-Landau (2006) explain how large reductions in forest cover during Pleistocene glacial events may have allowed tropical forest species to develop a natural resilience to deforestation. This may be the case, however, the pace and scale of changes experienced by ecosystems, from a combination of anthropogenic activity and global warming, is unparalleled when compared with the slow changes experienced through previous Ice Ages (Travis 2003; Brook *et al.* 2006). Moreover, the impact of climate change combined with the threats from deforestation and human population pressure, places ecosystems, and therefore primate species, under greater strain. Hence the countries facing the highest additive risk from these threats (Fig. 4.5) will be most likely to witness extinctions of primate fauna.

Changing Climate Dynamics

Given global distributions of primate species, two of the most important aspects of the climate system that will have a major bearing on primates are ENSO and the Asian Monsoon.

ENSO

ENSO arises from large-scale ocean-atmosphere interactions, with the combination of sea surface temperatures (SSTs), Walker circulation and the thermocline depth being responsible for the development of the two ENSO extremes – El Niño and La Niña (Latif and Keenlyside 2008). Cane (2005) explain how paleoclimate records highlight the sensitivity of ENSO towards changing climatic conditions, thus it can be expected for this phenomena to behave differently in the future. The way in which climate change affects the feedbacks in the development of ENSO will underpin any changes in characteristics (Latif and Keenlyside 2008).

Equatorial Pacific SSTs have increased over the latter half of the twentieth century concordant with global warming, however ENSO activity displayed nothing above what could be attributed to internal background variability, with no sustained long-term trend observed (Latif and Keenlyside 2008). However despite this, a potential shift towards more frequent and severe El Niño conditions has been observed (e.g. Gitay *et al.* 2002; Wright and Calderon 2006). Although the model predictions for the impact of climate change on ENSO face large uncertainties, particularly due to complex nature in which ENSO develops (Latif and Keenlyside 2008).

A model developed by Cox *et al.* (2004) incorporating vegetation and the carbon cycle demonstrates a switch towards an El Niño state, which could potentially reduce rainfall in northern Brazil and over Amazonia – both of which comprise high primate species richness and taxonomic distinctness (Fig. 2.1 and 2.3). The result would lead to the Amazon rainforest drying out and becoming more susceptible to forest fires, which could further reduce the forest size (*Cox et al.* 2004), placing the high primate diversity within this region at risk. Moreover vegetation feedbacks will further reduce rainfall and increase atmospheric carbon dioxide levels, acting as a positive feedback and subsequently accelerating global warming (*Cox et al.* 2004). Thus the importance of ENSO can be demonstrated by the way that plants in tropical forests, the primary habitat for the majority of primate species, will respond to changes in temperature and moisture due to plant metabolism (Wright and Calderon 2006), for example Peres and Janson (1999) explain how annual rainfall throughout the Neotropics is positively correlated with floristic diversity and large scale primate species richness. Moreover, Wright and Calderon (2006) discuss the potential for El Niño events to decrease plant productivity due to reduced rainfall causing water stress or higher temperatures increasing respiration costs, however the effects could be weakened through greater irradiance alleviating periods of light limitation, potentially allowing productivity to increase.

Isabirye-Basuta and Lwanga (2008) suggest that climate change can have severe effects on food resource base for primates and this has been displayed through the potential for ENSO events to affect the timing, quantity and quality of fruit production in tropical forests (e.g. Wiederholt and Post 2010). For example, Gould *et al.* (1999) studied the impact of a 2-year drought, in which food resources were severely depleted, on *Lemur catta* in south-western Madagascar, during this period of environmental stress, increases in infant and juvenile mortality rates were recorded, with a general decrease in the entire population. Furthermore, during drought conditions large areas of forest can become defoliated exacerbating the risk of forest fires (Gould *et al.* 1999). This may increase the risk of extinctions due to the high percentages of threatened primate species already present in Madagascar (Fig. 2.4). Similarly, extended droughts associated with El Niño events have caused elevated tree mortality and increased the risk of forest fires in certain tropical forests of Asia and South America (Chapman and Peres 2001; Wright and Calderon 2006). When this threat is considered alongside the high levels of threatened species over South America and much of Asia, in addition to the high percentage of species displaying a declining population trend (Fig. 2.4), it raises concern over the long term viability of primate populations in these regions. Asian primates in particular, will be of concern due to several countries in the region currently at high risk from a combination of threats (Fig. 4.5 and 4.6).

Asian Monsoon

Like ENSO, the Asian Monsoon develops from interplay between the ocean, atmosphere and land surface, with many factors affecting its strength, ranging from the SSTs in the Indian and Pacific Ocean to the snow cover and soil moisture over Asia, in addition to the strength and direction of the prevailing winds and variations in solar output (Wahl and Morrill 2010). However, a lack of information on these factors and the short observational record make it difficult to forecast and predict how the Asian monsoon might be affected by global climate change (Wahl and Morrill 2010) adding uncertainty to model predictions. Kumar *et al.* (1999) describe how the inverse relationship between the Indian summer monsoon and ENSO, in that a weak monsoon develops following a warm ENSO event, has diminished in recent decades. The possible reason for this lies behind Eurasion warming enhancing the land-ocean thermal gradient that is conductive towards a strong monsoon, thus sustaining monsoon rainfall at normal levels despite strong ENSO events (Kumar *et al.* 1999). Other future projections have indicated a potential decrease in rainfall for the East Asian monsoon (Yu *et al.* 2004). Fu (2003) concludes that human induced changes in land cover, which alter the exchanges of water and energy between the land and atmosphere, have weakened the East Asian monsoon resulting in decreased precipitation. Therefore, these human induced changes could potentially offset any increases in monsoon activity predicted due to global warming.

Any change in Asian Monsoon frequency or intensity may have significant consequences for primates across the continent, primarily due to the widespread impacts of human activities across the region (Gupta and Chivers 1999; Sodhi *et al.* 2004). Additionally, Asia holds some of the countries facing the highest levels of combined threat to primate species (Fig. 4.5), and therefore may also be particularly vulnerable to any adverse changes in climate related to the Asian Monsoon. However, the impact of future climate change on primate species richness varies across Asia (Fig. 3.4), with, for example, an improvement in climatic conditions predicted for much of mainland Asia under the *continental* model outputs, whereas a deterioration in suitable climate for parts of south-east Asia.

The Interacting Impacts of Climate Change and Habitat Loss

Despite beneficial improvements in climate projected for certain regions (Fig. 3.4 and Table 3.4), the warmer conditions anticipated under global climate model (GCM) outputs (IPCC 2007) will have effects on many aspects of ecosystems that are not included in our models.

Changes in Phenology

As a consequence of pressures arsing from climate change, plant species must alter their phenology to avoid increased risks of extinction, with advanced timing of events such as fruiting and flowering anticipated (Hughes 2000; Berteaux *et al.* 2004), which could potentially affect the feeding patterns of frugivorous primates, for example. Thus the way in which primates adapt to changes in phenology, in order to mitigate these effects, will determine how much they are impacted. Furthermore, Menzel (2002) explains how shifts in phenological phases due to climate change can have impacts on the climate system itself, especially regional climate, by feedback mechanisms of evaporation, carbon dioxide levels and surface albedo effects.

Dispersal and Adaptation

In order to survive in the presence of environmental change species must either adapt to novel environmental conditions, or, more commonly, migrate to track their preferred ecological niche (Pearson and Dawson 2003; Martinez-Mayer *et al.* 2004; Malcolm *et al.* 2006). This will be problematic for primate species due to their restricted dispersal ability, on account of tropical forest being the primary habitat for most species (Mittermeier 1988), added to the fact that populations of trees expand at a much slower rate, in many cases dispersal being inadequate to keep up with climate change (Hoffman and Parsons 1997).

Cowlishaw and Dunbar (2000) provide an overview of how changes in climate led to the extinction of the *Theropithecus* baboon, which was once prominent across Africa until rising temperatures promoted shifts of the temperate grasslands, which the species depended on, upward in altitude consequently leading to their demise as this habitat became highly fragmented due to the limited distribution of high altitude sites. The only surviving member of this genus was the Gelada on the Ethiopian Plateau, which is currently facing a significant threat from climate change and changing agricultural practices (Dunbar 1998; Cowlishaw and Dunbar 2000). This provides an indication of the difficulty species face when tracking their habitat through time and space, and even if this is accomplished, the pace and magnitude of changes may be too much for many populations to persist.

The rapid pace of climate change may reduce the ability of plant species to track their preferred climates, with the only response being one of adaptation to the new environmental conditions (Jump and Penuelas 2005). Increasingly fragmented ecosystems, however, combined with rapid climate change, may negate the adaptation ability of plants, leading to altered genetic compositions yielding unpredictable species assemblages and an increased susceptibility to pest and disease outbreaks, which can further reduce populations (Jump and Penuelas 2005). Clearly this will play a huge role in determining primate survival in such habitats as essential food sources may no longer be available. In addition, the adaptability of primate populations to the cascading effects of various environmental changes may also be reduced due to the rapid pace of change. However, an example of a mammal species successfully adapting to a new climate regime is provided by Réale *et al.* (2002) who report how the timing and breeding of red squirrel populations in the Yukon, Canada have advanced as a consequence of microevolutionary changes in phenology and genetics in response to rapid climate change altering their ecosystem. Therefore, some primate species may be able to adapt similarly.

The combination habitat destruction and climate change can be enough to overpower species ability to adapt and cope with changes, ultimately leading to their extinction. For example, McLaughlin *et al.* (2002) report how two populations of checkerspot butterfly became extinct in response to increased precipitation variability. These populations will have most likely survived similar or even greater climatic fluctuations throughout their history due to their once extensive habitat allowing for persistence under climatic variability (McLaughlin *et al.* 2002). However the destruction of this habitat increased their vulnerability to climate change and subsequently led to their extinction (McLaughlin *et al.* 2002). Similarly, Warren *et al.* (2001) demonstrate how British butterflies will have reduced numbers of species due to the combined effects of habitat modification and climate change, with mobile and widespread habitat generalists dominating communities. Therefore, the countries facing the greatest risk from additive threats to primates, such as those in north-west Africa, Central America and south-east Asia (Fig. 4.5), are of primary concern due to the synergy between drivers of extinction (Sala *et al.* 2000; Brook *et al.* 2008; Darling and Côté 2008).

Disease and Invasive Species

Climate change may encourage movement of non-native species into new areas, potentially adding a new source of competition for local inhabitants (Thomas *et al.* 2004). In some cases climate change can lead to invasive species and epidemic diseases spreading into new areas, particularly with rising temperatures, which has seen expanding mosquito-borne diseases in the high lands of Asia, east Africa and Latin America (Walther *et al.* 2002).

Other studies have demonstrated the impact climate change can have on invasive species and disease outbreaks. For example, amphibians, which primarily occur in the tropics like primates, face a significant risk from infectious disease with climate change anticipated to exacerbate this threat, with the small geographic ranges of many species making them susceptible to extinction (Wake and Vredenburg 2008). Pounds *et al*. (2006) show how recent amphibian extinctions in the mountains of Costa Rica are associated with warming temperatures promoting infectious disease. Similarly, Kiesecker *et al.* (2001) report how amphibian populations in western USA are coming under increasing threat from pathogen outbreaks due to changes in precipitation as a result of climate change, altering the UV-B exposure of species.

Impacts on the Tropical Forest Biome

Potentially one of the most detrimental affects of climate change on primate species will be related to the potential impacts on forest ecosystems, with the species composition of forests likely to change with climate (Gitay *et al.* 2002; Jump and Penuelas 2005; Brook *et al*. 2006). Ecosystems dominated by long lived plant species, such as tropical rainforest, are often slow to show any indication of change but they will also be slow to recover from any changes imposed by climate related stress (Gitay *et al.* 2002; Brook *et al*. 2006).

Wright and Muller-Landau (2006) suggest that the mass extinction of tropical forest species may be avoided and that many tropical forest species will be able to survive through the current rates of deforestation and human population pressures. This conclusion is based on anticipated increases in rural to urban migration and therefore a subsequent rise in urban populations, reducing the human population pressure in forested areas (Wright and Muller-Landau 2006); allowing for natural forest regeneration to take place, which will eventually exceed the rate of deforestation and result in a stabilisation or increase in forest cover (Wright and Muller-Landau 2006). If this does occur, then it could be expected, for example, that the primate species of Madagascar may be able to recover from current pressures due to a rejuvenated tropical forest habitat and flourish in potentially improved climatic conditions as predicted by our models (Fig. 3.4 and Table 3.4). However, Brook *et al.* (2006) disagree with the results presented by Wright and Muller-Landau (2006) due to the link between rural and urban population densities and deforestation being much more complex. For instance, urban populations can damage ecosystems many kilometres away due to the demands of such high population densities in urban centres, for example the need for water, energy (e.g. fuel wood, hydroelectric power plants, both of which are sourced outside urban areas) and areas for waste disposal (Cincotta *et al.* 2000). Moreover the strong likelihood that the essential habitat for most species will have already been eliminated or degraded to the point of no return, removes the potential for successful regeneration of forest (Brook *et al.* 2006). For example, fragmented habitats often experience changes in microclimates and edge effects, altering the plant and animal species present (Saunders *et al.*1991; Collinge 1996;

Turner 1996). In addition, the large number of indigenous species present in tropical forests, most of which have a low environmental tolerance, places them at greater risk of being lost due to forest fragmentation (Turner 1996).

Time lags observed between habitat loss and species extinctions may give secondary forests the chance to mature (Wright and Muller-Landau 2006), however, the small population sizes of species in highly fragmented and secondary forests are often already committed to extinction due to extinction debt (Tilman *et al.* 1994; Brook *et al.* 2006). For instance, Cowlishaw (1999) performed tests based on the species-area relationships that indicate the likely existence of extinction debts amongst African forest primates as a result of historical deforestation, with the debt in most countries comprising around 30% of the forest primate fauna. These findings illustrate how forest regeneration or even conservation measures such as protected forest areas during time lags of extinction debt may not be enough to prevent extinctions induced through habitat loss (Cowlishaw 1999).

Conclusions

The magnitude and pace in which modern environmental change is occurring is unlike anything previously experienced by species, with the various impacts of climate change and human modification of the environment having an impact at global, regional and local scales. Several drivers of environmental change may act in synergy resulting in the potential of additive threats at a location or across a region.

The highest levels of threatened primate species are located in south-east Asia, Central America and the coastal areas of Brazil. Concern arises over the much larger amount of primate species with decreasing populations, which could be expected to lead to a greater number of threatened species, and thus a greater chance of species loss. Furthermore, the areas with a high percentage of threatened and decreasing primate populations tend to coincide with regions of the globe that harbour some of the highest levels of taxonomic distinctness (Δ^+) and species richness, such as Madagascar and south-east Asia in particular. The threat from climate change was found to be significantly greater in countries with a low percentage of threatened primate species compared to countries with high percentages of threatened species, however, it is the opposite for human population pressure, with countries holding the highest levels of threatened primates facing a significantly greater threat.

Bioclimate models using a more relevant regional, rather than global, environmental space reproduced the distribution and patterns of global primate species richness for each biogegraphic zone more accurately. Running these models with future climate data produced results demonstrating how the impact of future climate change on primate species varies within and between regions. Given current climate-primate richness relationships, areas such as northern Africa are predicted to decrease in climatic suitability, in addition to parts of south-east Asia, under some model outputs, whereas Madagascar is predicted to increase in climatic suitability for primate species richness. This study highlights differences in projections of climatic suitability, depending on which climate model and greenhouse gas emission scenario is used for model fitting. However, many other factors need to be considered when assessing the impact of climate change, such as the complex interactions between changing land use and climate, and the response of large scale climatic systems such as ENSO and the Asian Monsoon.

Primate species facing the greatest risk of extinction can be found in countries facing the highest levels of combined action of the various threats to primate diversity; climate change, forest loss and human population pressure, which can intensify the overall threat to species due to synergy and associated feed back mechanisms between threats. Conservation measures will need to be implemented in high risk regions in order to prevent species losses, however, the ability for countries to mitigate these threats and protect primate species could largely be determined by their economic wealth and political stability, with the majority of primate species shown to be located in economically poor countries, with low government scores, indicating that conservation may be a low priority. Furthermore, the countries facing the highest risk from a combination of threats are generally the ones with some of the lowest average government scores, with low GDPs, such as Nigeria, for example, placing added concern over the future of primate diversity in these countries.

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Appendix 1

Appendix 1: Top 25 high-value primate countries (A) and top 25 low-value primate countries (B)

A	Top 25 - HIGH VALUE PRIMATE COUNTRIES		
	Total Species	**% Threatened**	**Average Δ^+**
Country	Brazil	Belize	Zimbabwe
	Madagascar	Algeria	Mozambique
	Colombia	Morocco	Swaziland
	Peru	Vietnam	Angola
	Indonesia	Cambodia	Malawi
	Zaire (Dem Rep Congo)	Laos	Zambia
	Cameroon	Indonesia	Burundi
	Congo	China	Tanzania
	Bolivia	Thailand	Congo
	Tanzania	Malaysia	Gabon
	Nigeria	Brunei	Rwanda
	Ecuador	Myanmar (Burma)	Equatorial Guinea
	Thailand	Bangladesh	Senegal
	Uganda	Guatemala	Kenya
	Venezuela	Mexico	Guinea
	China	Sri Lanka	Cameroon
	India	India	Burkina Faso
	Vietnam	Costa Rica	Ivory Coast
	Central African Republic	Honduras	Togo
	Gabon	El Salvador	Nigeria
	Angola	Panama	Uganda
	Kenya	Bhutan	Zaire
	Malaysia	Madagascar	Benin
	Rwanda	Nigeria	Guinea-Bissau
	Burundi	Burkina Faso	Ghana

B	Bottom 25 - LOW VALUE PRIMATE COUNTRIES		
	Total Species	**% Threatened**	**Average Δ^+**
Country	Algeria	Libya	Algeria
	Libya	Saudi Arabia	Libya
	Morocco	Taiwan	Morocco
	Saudi Arabia	Uruguay	Saudi Arabia
	Taiwan	Yemen	Spain
	Uruguay	Japan	Taiwan
	Yemen	Argentina	Uruguay
	Afghanistan	Afghanistan	Yemen
	Belize	Pakistan	Japan
	Djibouti	Mauritania	Argentina
	El Salvador	Lesotho	Afghanistan
	Japan	Djibouti	Pakistan
	Lesotho	Niger	Mexico
	Pakistan	Namibia	China
	Philippines	Philippines	Mauritania
	Trinidad and Tobago	Somalia	Lesotho
	Guatemala	Nepal	Djibouti
	Mexico	South Africa	El Salvador
	Nicaragua	Chad	Niger
	Costa Rica	Botswana	Guatemala
	Eritrea	Paraguay	Namibia
	Honduras	Trinidad and Tobago	Bhutan
	Namibia	Eritrea	Philippines
	Nepal	Malawi	Somalia
	Niger	Swaziland	India

Appendix 2

Appendix 2: Rank table of combined threats for each country - Every country was given a rank value according to each of the three threats; human population increase, forest loss and decreasing suitable climate (a higher value was assigned to a greater threat). The sum of these rank values was calculated to identify the countries facing the highest combined levels of threat. The countries were then grouped into 8 categories of 11 countries based on their overall rank sum. 1 to 8 represents lowest to highest risk.

Country	Rank Totals			Sum	Risk Category
	Population	Forest Loss	ClimateA2		
Afghanistan	72	82	42	196	8
Benin	75	80	60	215	8
Burkina Faso	69	38	78	185	8
Burundi	87	88	35	210	8
Ghana	66	78	59	203	8
Indonesia	49	75	65	189	8
Liberia	63	74	55	192	8
Niger	46	83	86	215	8
Nigeria	77	84	70	231	8
Sierra Leone	73	53	66	192	8
Togo	76	87	50	213	8
El Salvador	83	70	31	184	7
Eritrea	61	36	87	184	7
Ethiopia	67	65	52	184	7
Guinea-Bissau	71	42	72	185	7
Mali	42	54	81	177	7
Mauritania	15	85	80	180	7
Nepal	82	76	18	176	7
Pakistan	84	77	16	177	7
Philippines	80	81	13	174	7
Senegal	62	47	75	184	7
Somalia	36	64	76	176	7
Cameroon	40	62	71	173	6
Chad	32	51	77	160	6
Djibouti	51	22	88	161	6
Ecuador	37	73	51	161	6
Equatorial Guinea	41	57	68	166	6
Guatemala	74	67	29	170	6
Guinea	60	52	56	168	6
Honduras	58	86	27	171	6
Malawi	78	60	22	160	6
Uganda	86	79	5	170	6
Yemen	65	14	85	164	6
Bangladesh	88	30	41	159	5
Brunei	59	55	36	150	5
Congo	45	28	79	152	5
Gambia, The	79	8	63	150	5
India	81	9	44	134	5
Malaysia	53	43	54	150	5
Namibia	10	58	67	135	5

Nicaragua	47	71	17	135	5
Sudan	25	56	73	154	5
Tanzania, United Republic of	48	66	43	157	5
Zambia	27	63	47	137	5
Angola	38	34	58	130	4
Bolivia	18	41	57	116	4
Cambodia	64	23	34	121	4
Costa Rica	52	44	32	128	4
Ivory Coast	57	11	53	121	4
Kenya	68	37	26	131	4
Libya	12	20	84	116	4
Morocco	50	12	64	126	4
Myanmar (Burma)	34	69	19	122	4
Saudi Arabia	26	19	83	128	4
Sri Lanka	55	68	11	134	4
Algeria	19	5	82	106	3
Argentina	17	40	49	106	3
Bhutan	56	10	39	105	3
Botswana	8	61	38	107	3
Brazil	22	48	37	107	3
Central African Republic	16	32	61	109	3
Colombia	33	29	45	107	3
Gabon	14	27	69	110	3
Laos	44	45	25	114	3
Madagascar	54	39	23	116	3
Peru	24	33	48	105	3
Belize	21	24	40	85	2
Mexico	30	46	21	97	2
Mozambique	39	35	20	94	2
Panama	43	31	15	89	2
Paraguay	28	59	14	101	2
Rwanda	85	3	12	100	2
South Africa	9	18	62	89	2
Thailand	35	50	7	92	2
Venezuela	31	49	3	83	2
Zaire (Dem Rep Congo)	1	13	74	88	2
Zimbabwe	20	72	1	93	2
China	23	6	33	62	1
French Guiana	11	26	30	67	1
Guyana	6	21	28	55	1
Japan	4	25	46	75	1
Lesotho	5	2	24	31	1
Suriname	3	17	10	30	1
Swaziland	7	7	9	23	1
Taiwan	29	16	8	53	1
Trinidad and Tobago	2	15	6	23	1
Uruguay	13	1	4	18	1
Vietnam	70	4	2	76	1

Appendix 3

Appendix 3: Taxonomic Table Order: *Primates*

SUBORDER	INFRAORDER	SUPERFAMILY	FAMILY	GENUS	SPECIES
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Allenopithecus*	*Allenopithecus nigroviridis*
Strepsirrhini	Lemuriformes	Cheirogaleoidae	Cheirogaleidae	*Allocebus*	*Allocebus trichotis*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta arctoidea*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta belzebul*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta caraya*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta discolor*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta guariba*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta juara*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta macconnelli*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta nigerrima*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta palliata*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta pigra*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta puruensis*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta sara*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta seniculus*
Haplorrhini	Simiiformes		Atelidae	*Alouatta*	*Alouatta ululata*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus azarae*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus brumbacki*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus griseimembra*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus jorgehernandezi*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus lemurinus*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus miconax*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus nancymaae*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus nigriceps*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus trivirgatus*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus vociferans*
Haplorrhini	Simiiformes		Aotidae	*Aotus*	*Aotus zonalis*
Strepsirrhini	Lorisiformes		Lorisidae	*Arctocebus*	*Arctocebus aureus*
Strepsirrhini	Lorisiformes		Lorisidae	*Arctocebus*	*Arctocebus calabarensis*
Haplorrhini	Simiiformes		Atelidae	*Ateles*	*Ateles belzebuth*
Haplorrhini	Simiiformes		Atelidae	*Ateles*	*Ateles chamek*
Haplorrhini	Simiiformes		Atelidae	*Ateles*	*Ateles fusciceps*
Haplorrhini	Simiiformes		Atelidae	*Ateles*	*Ateles geoffroyi*
Haplorrhini	Simiiformes		Atelidae	*Ateles*	*Ateles hybridus*
Haplorrhini	Simiiformes		Atelidae	*Ateles*	*Ateles marginatus*
Haplorrhini	Simiiformes		Atelidae	*Ateles*	*Ateles paniscus*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi betsileo*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi cleesei*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi laniger*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi meridionalis*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi occidentalis*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi peyrierasi*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi ramanantsoavanai*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Avahi*	*Avahi unicolor*
Haplorrhini	Simiiformes		Atelidae	*Brachyteles*	*Brachyteles arachnoides*
Haplorrhini	Simiiformes		Atelidae	*Brachyteles*	*Brachyteles hypoxanthus*
Haplorrhini	Simiiformes		Pitheciidae	*Cacajao*	*Cacajao ayresi*
Haplorrhini	Simiiformes		Pitheciidae	*Cacajao*	*Cacajao calvus*

Haplorrhini	Simiiformes		Pitheciidae	*Cacajao*	*Cacajao melanocephalus*
Haplorrhini	Simiiformes		Pitheciidae	*Cacajao*	*Cacajoa hosomi*
Haplorrhini	Simiiformes		Cebidae	*Callibella*	*Callibella humilis*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus aureipalatii*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus baptista*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus barbarabrownae*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus bernhardi*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus brunneus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus caligatus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus cinerascens*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus coimbrai*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus cupreus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus discolor*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus donacophilus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus dubius*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus hoffmannsi*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus lucifer*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus lugens*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus medemi*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus melanochir*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus modestus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus moloch*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus nigrifrons*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus oenanthe*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus olallae*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus ornatus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus pallescens*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus personatus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus purinus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus regulus*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus stephennashi*
Haplorrhini	Simiiformes		Pitheciidae	*Callicebus*	*Callicebus torquatus*
Haplorrhini	Simiiformes		Cebidae	*Callimico*	*Callimico goeldii*
Haplorrhini	Simiiformes		Cebidae	*Callithrix*	*Callithrix aurita*
Haplorrhini	Simiiformes		Cebidae	*Callithrix*	*Callithrix flaviceps*
Haplorrhini	Simiiformes		Cebidae	*Callithrix*	*Callithrix geoffroyi*
Haplorrhini	Simiiformes		Cebidae	*Callithrix*	*Callithrix jacchus*
Haplorrhini	Simiiformes		Cebidae	*Callithrix*	*Callithrix kuhlii*
Haplorrhini	Simiiformes		Cebidae	*Callithrix*	*Callithrix penicillata*
Haplorrhini	Simiiformes		Cebidae	*Cebuella*	*Cebuella pygmaea*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus albifrons*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus apella*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus capucinus*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus cay*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus flavius*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus kaapori*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus libidinosus*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus macrocephalus*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus nigritus*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus olivaceus*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus robustus*
Haplorrhini	Simiiformes		Cebidae	*Cebus*	*Cebus xanthosternos*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercocebus*	*Cercocebus agilis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercocebus*	*Cercocebus atys*

Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercocebus*	*Cercocebus chrysogaster*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercocebus*	*Cercocebus galeritus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercocebus*	*Cercocebus sanjei*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercocebus*	*Cercocebus torquatus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus ascanius*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus campbelli*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus cephus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus diana*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus dryas*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus erythrogaster*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus erythrotis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus hamlyni*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus lhoesti*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus mitis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus mona*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus nictitans*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus neglectus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus petaurista*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus pogonias*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus preussi*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus sclateri*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Cercopithecus*	*Cercopithecus solatus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Cheirogaleus*	*Cheirogaleus adipicaudatus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Cheirogaleus*	*Cheirogaleus crossleyi*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Cheirogaleus*	*Cheirogaleus major*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Cheirogaleus*	*Cheirogaleus medius*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Cheirogaleus*	*Cheirogaleus minusculus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Cheirogaleus*	*Cheirogaleus ravus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Cheirogaleus*	*Cheirogaleus sibreei*
Haplorrhini	Simiiformes		Pitheciidae	*Chiropotes*	*Chiropotes albinasus*
Haplorrhini	Simiiformes		Pitheciidae	*Chiropotes*	*Chiropotes chiropotes*
Haplorrhini	Simiiformes		Pitheciidae	*Chiropotes*	*Chiropotes satanas*
Haplorrhini	Simiiformes		Pitheciidae	*Chiropotes*	*Chiropotes utahickae*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Chlorocebus*	*Chlorocebus aethiops*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Chlorocebus*	*Chlorocebus cynosuros*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Chlorocebus*	*Chlorocebus djamdjamensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Chlorocebus*	*Chlorocebus pygerythrus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Chlorocebus*	*Chlorocebus sabaeus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Chlorocebus*	*Chlorocebus tantalus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Colobus*	*Colobus angolensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Colobus*	*Colobus guereza*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Colobus*	*Colobus polykomos*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Colobus*	*Colobus satanas*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Colobus*	*Colobus vellerosus*
Strepsirrhini	Chiromyiformes		Daubentoniidae	*Daubentonia*	*Daubentonia madagascariensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Erythrocebus*	*Erythrocebus patas*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur albifrons*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur cinereiceps*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur collaris*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur coronatus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur fulvus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur macaco*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur mongoz*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur rubriventer*

Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur rufifrons*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur rufus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Eulemur*	*Eulemur sanfordi*
Strepsirrhini	Lorisiformes		Galagidae	*Euoticus*	*Euoticus elegantulus*
Strepsirrhini	Lorisiformes		Galagidae	*Euoticus*	*Euoticus pallidus*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides cocos*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides demidovii*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides granti*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides nyasae*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides orinus*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides rondoensis*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides thomasi*
Strepsirrhini	Lorisiformes		Galagidae	*Galagoides*	*Galagoides zanzibaricus*
Strepsirrhini	Lorisiformes		Galagidae	*Galago*	*Galago gallarum*
Strepsirrhini	Lorisiformes		Galagidae	*Galago*	*Galago matschiei*
Strepsirrhini	Lorisiformes		Galagidae	*Galago*	*Galago moholi*
Strepsirrhini	Lorisiformes		Galagidae	*Galago*	*Galago senegalensis*
Haplorrhini	Simiiformes	Hominoidea	Hominidae	*Gorilla*	*Gorilla beringei*
Haplorrhini	Simiiformes	Hominoidea	Hominidae	*Gorilla*	*Gorilla gorilla*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Hapalemur*	*Hapalemur alaotrensis*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Hapalemur*	*Hapalemur aureus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Hapalemur*	*Hapalemur griseus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Hapalemur*	*Hapalemur meridionalis*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Hapalemur*	*Hapalemur occidentalis*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hoolock*	*Hoolock hoolock*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hoolock*	*Hoolock leuconedys*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hylobates*	*Hylobates agilis*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hylobates*	*Hylobates albibarbis*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hylobates*	*Hylobates klossii*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hylobates*	*Hylobates lar*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hylobates*	*Hylobates moloch*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hylobates*	*Hylobates muelleri*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Hylobates*	*Hylobates pileatus*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Indri*	*Indri indri*
Haplorrhini	Simiiformes		Atelidae	*Lagothrix*	*Lagothrix cana*
Haplorrhini	Simiiformes		Atelidae	*Lagothrix*	*Lagothrix lagotricha*
Haplorrhini	Simiiformes		Atelidae	*Lagothrix*	*Lagothrix lugens*
Haplorrhini	Simiiformes		Atelidae	*Lagothrix*	*Lagothrix poeppigii*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Lemur*	*Lemur catta*
Haplorrhini	Simiiformes		Cebidae	*Leontopithecus*	*Leontopithecus caissara*
Haplorrhini	Simiiformes		Cebidae	*Leontopithecus*	*Leontopithecus chrysomelas*
Haplorrhini	Simiiformes		Cebidae	*Leontopithecus*	*Leontopithecus chrysopygus*
Haplorrhini	Simiiformes		Cebidae	*Leontopithecus*	*Leontopithecus rosalia*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur aeeclis*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur ahmansonorum*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur ankaranensis*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur betsileo*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur dorsalis*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur edwardsi*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur fleuretae*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur grewcockorum*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur hubbardorum*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur jamesorum*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur leucopus*

Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur mustelinus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur microdon*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur milanoii*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur mittermeieri*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur otto*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur petteri*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur randrianasoloi*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur ruficaudatus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur sahamalazensis*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur seali*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur septentrionalis*
Strepsirrhini	Lemuriformes	Lemuroidea	Lepilemuridae	*Lepilemur*	*Lepilemur wrightae*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Lophocebus*	*Lophocebus albigena*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Lophocebus*	*Lophocebus aterrimus*
Strepsirrhini	Lorisiformes		Lorisidae	*Loris*	*Loris lydekkerianus*
Strepsirrhini	Lorisiformes		Lorisidae	*Loris*	*Loris tardigradus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca arctoides*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca assamensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca cyclopis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca fascicularis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca fuscata*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca hecki*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca leonina*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca maura*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca mulatta*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca munzala*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca nemestrina*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca nigra*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca nigrescens*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca ochreata*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca radiata*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca siberu*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca silenus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca sinica*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca sylvanus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca thibetana*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Macaca*	*Macaca tonkeana*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Mandrillus*	*Mandrillus leucophaeus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Mandrillus*	*Mandrillus sphinx*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico acariensis*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico argentatus*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico chrysoleucus*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico emiliae*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico humeralifer*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico intermedius*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico leucippe*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico manicorensis*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico marcai*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico mauesi*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico melanurus*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico nigriceps*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico saterei*
Haplorrhini	Simiiformes		Cebidae	*Mico*	*Mico sp. nov.*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus berthae*

Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus bongolavensis*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus danfossorum*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus griseorufus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus jollyae*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus lehilahytsara*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus mittermeieri*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus murinus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus myoxinus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus ravelobensis*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus rufus*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus sambiranensis*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus simmonsi*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Microcebus*	*Microcebus tavaratra*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Miopithecus*	*Miopithecus ogouensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Miopithecus*	*Miopithecus talapoin*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Mirza*	*Mirza coquereli*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Nasalis*	*Nasalis larvatus*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Nomascus*	*Nomascus concolor*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Nomascus*	*Nomascus gabriellae*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Nomascus*	*Nomascus hainanus*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Nomascus*	*Nomascus leucogenys*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Nomascus*	*Nomascus nasutus*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Nomascus*	*Nomascus siki*
Strepsirrhini	Lorisiformes		Lorisidae	*Nycticebus*	*Nycticebus bengalensis*
Strepsirrhini	Lorisiformes		Lorisidae	*Nycticebus*	*Nycticebus javanicus*
Strepsirrhini	Lorisiformes		Lorisidae	*Nycticebus*	*Nycticebus coucang*
Strepsirrhini	Lorisiformes		Lorisidae	*Nycticebus*	*Nycticebus menagensis*
Strepsirrhini	Lorisiformes		Lorisidae	*Nycticebus*	*Nycticebus pygmaeus*
Haplorrhini	Simiiformes		Atelidae	*Oreonax*	*Oreonax flavicauda*
Strepsirrhini	Lorisiformes		Galagidae	*Otolemur*	*Otolemur crassicaudatus*
Strepsirrhini	Lorisiformes		Galagidae	*Otolemur*	*Otolemur garnettii*
Haplorrhini	Simiiformes	Hominoidea	Hominidae	*Pan*	*Pan paniscus*
Haplorrhini	Simiiformes	Hominoidea	Hominidae	*Pan*	*Pan troglodytes*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Papio*	*Papio anubis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Papio*	*Papio cynocephalus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Papio*	*Papio hamadryas*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Papio*	*Papio papio*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Papio*	*Papio ursinus*
Strepsirrhini	Lorisiformes		Lorisidae	*Perodicticus*	*Perodicticus potto*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Phaner*	*Phaner electromontis*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Phaner*	*Phaner furcifer*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Phaner*	*Phaner pallescens*
Strepsirrhini	Lemuriformes	Cheirogaleoidea	Cheirogaleidae	*Phaner*	*Phaner parienti*
Haplorrhini	Simiiformes		Pitheciidae	*Pithecia*	*Pithecia aequatorialis*
Haplorrhini	Simiiformes		Pitheciidae	*Pithecia*	*Pithecia albicans*
Haplorrhini	Simiiformes		Pitheciidae	*Pithecia*	*Pithecia irrorata*
Haplorrhini	Simiiformes		Pitheciidae	*Pithecia*	*Pithecia monachus*
Haplorrhini	Simiiformes		Pitheciidae	*Pithecia*	*Pithecia pithecia*
Haplorrhini	Simiiformes		Hominidae	*Pongo*	*Pongo abelii*
Haplorrhini	Simiiformes		Hominidae	*Pongo*	*Pongo pygmaeus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis melalophos*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis chrysomelas*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis comata*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis femoralis*

Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis frontata*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis hosei*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis natunae*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis potenziani*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis rubicunda*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis siamensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Presbytis*	*Presbytis thomasi*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Procolobus*	*Procolobus badius*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Procolobus*	*Procolobus gordonorum*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Procolobus*	*Procolobus pennantii*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Procolobus*	*Procolobus preussi*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Procolobus*	*Procolobus rufomitratus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Procolobus*	*Procolobus verus*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Prolemur*	*Prolemur simus*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus candidus*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus coquereli*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus coronatus*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus deckenii*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus diadema*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus edwardsi*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus perrieri*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus tattersalli*
Strepsirrhini	Lemuriformes	Lemuroidea	Indridae	*Propithecus*	*Propithecus verreauxi*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Pygathrix*	*Pygathrix cinerea*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Pygathrix*	*Pygathrix nemaeus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Pygathrix*	*Pygathrix nigripes*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Rhinopithecus*	*Rhinopithecus roxellana*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Rhinopithecus*	*Rhinopithecus avunculus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Rhinopithecus*	*Rhinopithecus bieti*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Rhinopithecus*	*Rhinopithecus brelichi*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Rungwecebus*	*Rungwecebus kipunji*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus bicolor*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus fuscicollis*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus geoffroyi*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus imperator*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus inustus*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus labiatus*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus leucopus*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus martinsi*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus melanoleucus*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus midas*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus mystax*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus niger*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus nigricollis*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus oedipus*
Haplorrhini	Simiiformes		Cebidae	*Saguinus*	*Saguinus tripartitus*
Haplorrhini	Simiiformes		Cebidae	*Saimiri*	*Saimiri boliviensis*
Haplorrhini	Simiiformes		Cebidae	*Saimiri*	*Saimiri oerstedii*
Haplorrhini	Simiiformes		Cebidae	*Saimiri*	*Saimiri sciureus*
Haplorrhini	Simiiformes		Cebidae	*Saimiri*	*Saimiri ustus*
Haplorrhini	Simiiformes		Cebidae	*Saimiri*	*Saimiri vanzolinii*
Strepsirrhini	Lorisiformes		Galagidae	*Sciurocheirus (GALAGO)*	*Sciurocheirus alleni*
Strepsirrhini	Lorisiformes		Galagidae	*Sciurocheirus (GALAGO)*	*Sciurocheirus gabonensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Semnopithecus*	*Semnopithecus ajax*

Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Semnopithecus*	*Semnopithecus dussumieri*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Semnopithecus*	*Semnopithecus entellus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Semnopithecus*	*Semnopithecus hector*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Semnopithecus*	*Semnopithecus hypoleucos*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Semnopithecus*	*Semnopithecus priam*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Semnopithecus*	*Semnopithecus schistaceus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Simias*	*Simias concolor*
Haplorrhini	Simiiformes	Hominoidea	Hylobatidae	*Symphalangus*	*Symphalangus syndactylus*
Haplorrhini	Tarsiiformes		Tarsiidae	*Tarsius*	*Tarsius bancanus*
Haplorrhini	Tarsiiformes		Tarsiidae	*Tarsius*	*Tarsius dentatus*
Haplorrhini	Tarsiiformes		Tarsiidae	*Tarsius*	*Tarsius lariang*
Haplorrhini	Tarsiiformes		Tarsiidae	*Tarsius*	*Tarsius pelengensis*
Haplorrhini	Tarsiiformes		Tarsiidae	*Tarsius*	*Tarsius pumilus*
Haplorrhini	Tarsiiformes		Tarsiidae	*Tarsius*	*Tarsius syrichta*
Haplorrhini	Tarsiiformes		Tarsiidae	*Tarsius*	*Tarsius tarsier*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Theropithecus*	*Theropithecus gelada*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus auratus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus barbei*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus cristatus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus francoisi*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus geei*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus germaini*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus hatinhensis*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus johnii*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus laotum*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus obscurus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus phayrei*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus pileatus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus poliocephalus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus shortridgei*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus vetulus*
Haplorrhini	Simiiformes	Cercopithecoidea	Cercopithecidae	*Trachypithecus*	*Trachypithecus delacouri*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Varecia*	*Varecia rubra*
Strepsirrhini	Lemuriformes	Lemuroidea	Lemuridae	*Varecia*	*Varecia variegata*