DETECTION, CHARACTERIZATION AND CONSERVATION OF EVOLUTIONARILY ISOLATED SPECIES

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

In the
Department of Biological Sciences

SIMON FRASER UNIVERSITY

Spring 2010

APPROVAL

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ABSTRACT

Most published phylogenetic trees are imbalanced, meaning that while many species have many close relatives a minority have few. Importantly, these few isolated species have few closely-related species with which they can share the burden of their slice of the world's biodiversity, i.e. they are non-redundant. Of the ten or so published measures of evolutionary isolation, several overlap in the information they contain and therefore need not be used concurrently in analyses. Interestingly, isolated species that score highly using many such measures are generally overdispersed in a phylogeny, and therefore might collectively represent the shared branches contained within that phylogeny. This property is important if we consider isolated species as targets for increased conservation attention under an 'agony of choice' framework. One way to target them is using the novel 'expected loss' method, which multiplies our 'value' measure (evolutionary isolation) with an 'urgency' rating (threat of extinction) to prioritise those species that are both isolated and threatened. I show that evolutionary isolation and expected loss in primates is correlated with how far from the mean a species scores for many different biological, ecological and geographical traits, suggesting perhaps some link between evolutionary isolation and ecological distinctiveness. Lastly, evolutionarily isolated species are, in general, found in the most species rich areas of the world with geographic isolation playing a limited role in explaining their distribution. Overall,

evolutionarily isolated species are both phylogenetically infrequent and morphologically unusual suggesting they may well warrant greater future conservation attention.

Keywords: Phylogeny; conservation; evolutionary distinctiveness; evolutionary isolation; EDGE; range size.

DEDICATION

To the family and friends whose support this work is built on.

ACKNOWLEDGEMENTS

Thanks to Aki Mimoto, Klaas Hartman, Carolyn Hudson, Karen Magnusson-Ford, Walter Jetz for guidance and technical help. Thanks to Arne Mooers for his immense support, astute guidance and, overall, his faith that I would get there in the end.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1: COMPARING MEASURES OF EVOLUTIONARY ISOLATION

1.1 Introduction

Approximately one fifth of assessed species are considered vulnerable to extinction (IUCN, 2009). Worryingly, for most taxonomic groups the proportion of species considered threatened is increasing over time. A common estimate for the minimum amount of money needed to be spent to protect all threatened species is approximately $20 billion per year (James et al. 2001). The combined amount being spent on conservation initiatives by the majority of the richest countries and largest conservation organisations, however, is approximately $10 billion globally per year, leaving a significant shortfall (Waldron et al. in prep).

Conservation science, therefore, has to make important decisions about which threatened species to conserve first. If we make decisions about the conservation attention awarded to species solely using their threat status, we assume all species are equal, except in their degree of threat. From an evolutionary perspective, however, species have contrasting evolutionary histories and this information can be used to preferentially select those threatened species that can play a disproportionate role in conserving evolutionary history (Vane-Wright 1991, Crozier, 1994).

The most common situation is that, within the ‘Tree of Life’, a species has several close relatives (Mooers and Heard, 1997; Blum et al., 2006). For

example, the house mouse (*Mus musculus*) shares its genus *Mus* with 35 other species, and given that the *Mus* genus itself is relatively young (~8 million years, Steppan et al. 2004), most *Mus* species have split off from their nearest 'sister' species in only the last one or two million years (indeed, under a random speciation model, approximately 1.4 million years [A.O. Mooers, pers. comm.]).

Occasionally, there are species that have just a few close relatives, such as the platypus (*Ornithorhynchus anatinus*). It is the sole member of its own family (Ornithorhynchidae), splitting from its nearest 'sister' species over 30 million years ago and, therefore, has a long unique evolutionary history. If 'evolutionarily isolated' species, such as the platypus, go extinct, we would lose a much larger amount of unique evolutionary history from the tree of life than we would by losing, for instance, a mouse species from the *Mus* genus.

Furthermore, the platypus is from a species-poor area of the tree. If we lost it and its 5 sister species in the *Echindna* genus, we would lose a further 100 million years of evolutionary history. If, instead, we lost 6 *Mus* species we would expect to lose on the order of 10 million years of evolution (6 multiplied by 1.4 million years). This is because the internal branch that represents the stem of the Mus genus is represented by 36 species, so that if 6 species go extinct, the common branch is still well represented. The Platypus/Echidna stem branch has no such redundancy: when all 6 species go extinct, their common branch does also.

There are, therefore, two elements to evolutionary isolation, as outlined in the phylogenetic tree in Figure 1: The amount of unique evolutionary history

attributed to a species (Figure 1, for *T.alba* this is represented by the red branch) and the redundancy of evolutionary history it shares with other species (Figure 1, for *T.alba* shared history is represented by the blue branches). In Figure 1, *T.alba* has a short unique evolutionary history (Figure 1, branch labelled ‘a’) but, importantly, little redundancy for the long internal branch representing shared the evolutionary history with *T. delicatula* (Figure 1, branch ‘b’). In contrast, in the same figure the species *B. bubo* has a long unique evolutionary history but high redundancy for all its internal branches that lead to the root of the tree.

The ‘evolutionary isolation’ of a species, simply defined as the number of close relatives a species has, was first used in a conservation context by the US Federal government in relation to its ‘Endangered Species Act’ (ESA 1973. Under policy associated with the act, conservation priority is given to species that are monotypic within their genus over non-monotypic species (Fay & Thomas, 1983). Using a measure of evolutionary isolation based on taxonomic information will have inherently poor discrimination power because all the species in the family or genus will be awarded the same degree of isolation. Treating families and genera as equal units is also often unfounded, as taxonomies are biased by subjective decisions that do not reflect either a group’s estimated actual time of appearance, relative diversity or even its morphological differentiation from other taxa (Larson, 1998).

Another suggestion is that we could use ‘phylogenetic diversity’ to make decisions about the conservation priorities of species (Faith, 1992). ‘Phylogentic diversity’ is a measure of the total information content in tree, or subtree,

calculated by summing all the branch lengths connecting the tips to each other and to the root (Faith 1992). It is an effective way to rank which subsets of species best represent the total information contained within a tree of candidate species, which is a logical target for conservation biology.

Unfortunately, ‘phylogenetic diversity’ is uninformative for any single species on an ultrametric time-based evolutionary tree, as the values for all tips are the same. Thus, given the strong bias for conservation policy to be set at the species level (Possingham et al. 2002) incorporating ‘phylogenetic diversity’ into conservation decision making remains problematic. Even if conservation policy could be adapted to rank sets of species, on any given phylogeny there is rarely just a single subset of species that captures the maximum amount of phylogenetic diversity (Redding et al. 2008), further complicating this process. There have, therefore, been several attempts to create evolutionary isolation measures on a tip-by-tip basis to better dovetail information taken from the evolutionary relationships amongst species with current conservation policy.

1.1.1 Measures of evolutionary isolation

Below I detail all published measures of evolutionary isolation known to me:

1) May’s (1990) modification of Vane-Wright et al.’s (1991) measure (referred to as VW), is the inverse of the summed number of splits, or nodes, between each species’ tip and the root of the tree.

2) The Nixon and Wheeler (1992) unweighted index (NWU) is effectively an extension of the VW node-counting measure, where the node is only counted

if the candidate species is in the most species-poor daughter clade at any given split.

3) The Nixon and Wheeler (1992) weighted index (NWW) is again closely related to VW; at each node, the inverse of the number of species in each daughter clade to which the candidate species is a member, is summed.

4) The Pendant Edge value (PE, Altschul and Lipman 1990), is a different type of measure to the first three presented above. It disregards the internal structure within a tree, and is the distance from any tip on a tree to where it subtends the tree of life. This gives it the advantage of being an absolute measure that only changes if the phylogenetic relationships of sister species are revised or re-dated.

5) Equal-splits (ES; Redding & Mooers 2006), represents a different family of evolutionary isolation scores that combine information from the shape (as in 1-3) and branch lengths (as in 4) of an evolutionary tree. It distributes the phylogenetic diversity contained within the tree uniquely among the species at the tips. This is achieved by dividing the phylogenetic distance represented by each branch equally among its daughter branches. The sum of the equal-splits value from every internal branch between a species tip and the root is a representation of the amount of unique evolutionary history a species embodies. This process gives species from species-poor clades a higher weighting, as less of the path length between the tip and the root is shared by other species. Sharing all branch lengths among all the tips in the tree ensures that the sum of

the equal-splits measure equals the total phylogenetic diversity, or length, of the tree (Pauplin 2000; Semple & Steel 2004).

6) Fair Proportion (FP; Isaac et al., 2007; Redding 2003) is a conceptually similar metric to ES (5), but instead distributes internal branches fairly, not to descendant clades as in ES, but to all descendant species.

7) The average patristic distance (PAT; Webb et al. 2002) differs from the previous six measures, as it is based on the distances between a focal species and all other species. To calculate this value, one sums the branch lengths following the minimum path between the single candidate tip and all possible other species on a tree. The average patristic distance score is the total summed pairwise distance, for a single tip, divided by the number of species in a tree minus one. If the tree is represented by a patristic pairwise distance matrix, PAT for a tip is simply the average of its row values. Consider a species isolated on a long terminal branch, its distance to any other single species on the same tree must always take a path that uses this long branch. For another tip in the same tree with many close relatives, however, the distances to most other tips on the tree will be comparatively shorter.

8) Quadratic Entropy (QE; Rao 1982) is an essentially pairwise measure that was initially proposed as a measure of the biodiversity for a species assemblage. As a biodiversity measure, QE considers both relative abundance of a species and its relatedness to other species in a sample, and returns the expected patristic distance between two randomly chosen individuals. Pavoine et al. (2005) observed that a solution that assigns idealized individual species

proportions to yield the maximal diversity value satisfies the criteria of a distinctiveness measure: if species-pairs are sampled in proportion to their distinctiveness, pair-wise patristic distance is maximized.

9) The Shapley value is a concept used in game theory that distributes "a 'fair' distribution of the total worth of the entire set" amongst the players of a game (Haake et al. 2007). This value represents the expected contribution of diversity any player adds to the group and, therefore, can be used to rank players. When applied to evolutionary trees, however, we can interpret this value as the expected phylogenetic diversity a species is likely to contribute to future subsets of the tree (Haake et al. 2007).

1.1.2 Practical Applications

The first conservation programme to use a species-specific measure of evolutionary isolation was the EDGE project, started in 2007. This programme uses a two-component ranking score to determine the conservation priorities for a set of species (Isaac et al. 2007). A species' EDGE score is calculated by summing the logarithm of the species' evolutionary isolation score (in this case 'Fair Proportion', called "Species-specific PD" in Redding, 2003) and a measure of the species' global threat status. Importantly, there has been no sensitivity analysis to date that tests the stability of such a ranking if one of the other published measures of evolutionary isolation were used instead of Fair Proportion.

While some subsets of these measures have been compared to one another (Pavoine et al. 2005, Redding et al. 2008) there has been no systematic

comparison of all the known published evolutionary isolation measures when setting conservation priorities. Importantly, no one has yet determined whether the simple patristic measures, such as distance to nearest neighbour (effectively the PE score) and average pair-wise distance are viable alternatives to the more (conceptually) complex approaches. Here, I suggest a framework to choose among evolutionary isolation measures for selecting species for conservation priority:

Candidate measures must correctly identify those species with fewer close relatives. Given this, preferred measures should discriminate more finely among species in different phylogenetic positions. Lastly, for measures of evolutionary isolation to be of practical use, there must be a clear explanation of what they actually measure.

To examine how these statements apply to each of the published measures, I collated a set (n=30) of ultrametric empirically-derived evolutionary trees, a set (n=272) of non-ultrametric empirically-derived trees, and also investigated a very large set (n=10000) of simulated trees. To address the first aspect of the comparison framework, I looked at the pair-wise rank correlation among the scores to see whether they measure the same information, considering that at least some of the measures have been shown to approximate the number of close relatives a species has (QE, Pavoine 2005; PE Altschul & Lipman 1990). Second, I determined how the variance and range of scores differ among the measures. Third, I assessed the ability of each of the measures to resolve differences between tips. Fourth, I recalculated the EDGE scores for mammals,

using the measures outlined above, and then examined differences in the respective lists of top 100 EDGE species. I end with recommendations about which measures should be used in the future when setting conservation rankings.

1.2 Methods

I calculated the scores of the 9 different measures of evolutionary isolation (for all measures using code based on the R package ape, except for: FP N. Isaac pers. comm., ES K. Magnusson-Ford pers. comm. and QE, NWW, NWU the R package ade4), on a dataset of 5000 128-tip ultrametric trees simulated using the Yule (1924) process, a set of 5000 128-tip trees simulated using the Hey process (1992) and, finally, on an empirical dataset of 30 ultrametric and 242 non-ultrametric phylogenies (McPeek & Brown, 2007). The simulated trees were built using Bio::Phylo package (Vos, 2006) and were selected to give as wide a range of tree shapes as possible under the Yule model. The empirically derived trees have a large range of tip number (4 to 192 tips) and a diverse taxonomic cross-section (including flagellate protists, dicotyledons, birds and mammals; McPeek & Brown, 2007).

To evaluate the first two aspects of the comparison framework outlined above, for each tree in each of the above four tree sets I measured the bivariate spearman rank correlations across all 9 scores and the number of unique scores given by each measure, once they had been rounded to 3 significant figures. In addition, to examine how the measures gave different relative scores to species tips in the tree I compared the maximum and minimum score to the mean score in each tree.

Finally, I created nine EDGE ranking lists (Isaac et al. 2007) for all mammal species, one for each of the 9 measures. This time, however, I also included the number of species per genus as a further taxonomic measure of evolutionary isolation, to make 10 EDGE lists in total. Each set of evolutionary isolation scores was first standardised by their mean such that they had a mean value of 1. Given that the scores are on different scales, in order to balance the input of different scores against the threat status component, each evolutionary isolation measure was multiplied by the correct factor that resulted in the sum of scores for all tips equalling the length of the tree (the common scale for the Fair Proportion used by Isaac et al., 2007, see below).

To compare with the results of Isaac et al. (2007) I used an ordinal variable to represented 'Global Endangerment', with a value of zero to represent the IUCN category 'Least Concern' (IUCN, 2009) through to a value of 4 for the most threatened 'Critical Endangered' category (IUCN, 2009). Finally, to calculate the EDGE score we used the equation from the original publication (Isaac et al. 2007).

$$EDGE_i = \ln(ED_i + 1) + (\ln(GE_i) \times \ln(2)) \quad (1)$$

where EDGE score for species *i* is the sum of the logarithm of the evolutionary isolation score (ED_i) and, the product of the natural logarithm of 2 and the natural logarithm of the global endangerment category (GE_i).

(I note here that the authors in the original EDGE publication used the logarithm of two multiplied by threat status value to weight the relative input of threat against that of the evolutionary score. This is only one of many possible

weighting schemes and there is an urgent need to make transparent, objective decisions about combining these values; for an alternative that does not directly use a weighting, see Redding & Mooers, 2006).

For a set of EDGE-type scores I first plotted each of the different evolutionary isolation scores against its corresponding EDGE-type value, to determine how the different distributions of evolutionary isolation values contribute to the final composite EDGE score. I then chose the top 100 highest scoring EDGE species, as dictated in the EDGE methodology (Isaac et al 2007), from each of the ten EDGE lists and compared them to see which species the lists had in common.

1.3 Results

The triumvirate of ES, FP and PE were the most closely correlated measures on the set of 30 ultrametric trees (Spearmans $\rho \sim 0.95$; table1), while VW and NWU were also strongly related (Spearmans $\rho = 0.91$). It is worth noting that QE had the highest average correlation with all of the other measures (Spearmans $\rho = 0.85$, with none below 0.7; table 1) and, at least, on this set of trees seems to offer the best 'average' measure of evolutionary isolation. The least correlated set was NWW and PE (Spearmans $\rho \sim 0.36$; table1.1), and NWW has the lowest average correlation coefficient with the others (Spearmans $\rho = 0.65$).

Similarly, on the non-ultrametric trees, FP and ES were the most similar (Spearmans $\rho = 0.96$) along with VW and NWU (Spearmans $\rho = 0.92$). The correlation coefficients were, overall, noticeably lower for this set of trees

(average Spearmans ρ of 0.65 for non-ultrametric and 0.77 for ultrametric trees) while the standard deviations were higher (average Spearmans ρ of 0.074 for non-ultrametric and 0.044 for ultrametric trees). For this second set of trees, the two Nixon and Wheeler (1982) measures had low correlations especially with ES, FP and PE (Spearmans ρ = 0.44; table 1.1). QE cannot be measured on non-ultrametric trees.

The Yule and Hey simulated tree sets appear to have different properties when compared to each other. The Yule tree set has again ES, FP and PE closely correlated, as are the node-based measures NWW, NWU and VW. In this set PE is only weakly correlated to both PAT and NWW (Spearmans ρ = 0.13 & 0.17 respectively; table 1.3), with PAT being only weakly correlated to all the other measures, including QE (Spearmans ρ = 0.57; table 1.3).

The Hey based trees, conversely, gave surprisingly different results. For instance, ES and QE are more strongly related (Spearmans ρ = 0.9), and ES much less correlated to PE (Spearmans ρ = 0.66) than on other tree sets (table 1.3).

On the empirical ultrametric trees, the MDS ordination (Figure 1.2a) suggests that as expected ES/FP and PE group together, as do VW, NWW and NWU. Both QE and PAT have fairly equal correlation with all the other measures (table 1.1) placing them away from both groups.

In comparison, on the ordination from the dataset of non-ultrametric trees (Figure 1.2b), the relative separation between the topological measures (NWW, NWU, VW) and branch-based measures (ES, FP, PE) is amplified. As expected

the interrelationships between VW, NWW, and NWU remain virtually constant (table 1.1). Average pair-wise distance (PAT) remains reasonably well correlated to the topological measures (Spearmans ρ ~ 0.53) while being strongly correlated to the branch-length measures (average Spearmans ρ of ES, FP, PE = 0.76; table 1.1).

The simulated trees show similar groupings of measures, with the exception that PAT appears to be more different to the other measures than on the trees inferred from empirical data (figure 1.3 a & b). The only other noticeable difference, consistent with the results above, is that ES, FP and PE are more distantly related on Hey trees, with ES being more allied with QE (fig. 1.3b).

A comparison on the mammal tree gives only one sample of a taxonomy-based measure but, for mammals at least, the taxonomic evolution isolation measure (species per genus) had a low correlation with most other measures (Spearman ρ = 0.36, n=4900, p<0.001).

At the extremes, NWW on average considers the most isolated species as being ~5 times larger than mean score, while the least isolated is ~0.5 times the size of the mean score (tables 1.2 & 1.4). PAT, conversely considers the most isolated species as being ~1.5 times larger than mean score on average, while the least isolated is ~1 times the size of the mean score (tables 1.2 & 1.4).

The node-based measures give many tips similar scores (tables 1.2 & 1.4). In contrast, QE, FP and ES provide the greatest differentiation (tables 1.2 & 1.4), often giving the maximum number of unique ranks possible on the tree (results not shown).

The NWW EDGE measure, when comparing the top 10% of species, has a strong correlation to the NWW component alone (spearman's $\rho = 0.66$, $n=490$, $p<0.001$). Alternatively the PAT measure had a weaker correlation with the PAT EDGE measure, due to the reported small range in PAT scores, (spearman's $\rho = 0.31$, $n=490$, $p<0.001$) such that threat plays a large part in deciding a species PAT EDGE score, even for the top 10% of species.

As expected, the top 100 list that was most different to the original FP-based list (Isaac et al. 2007) was the one derived from the evolutionary isolation score NWW, with only 32 species shared in the respective list of top 100 highest ranked species. The highest correlation was with the PE-based EDGE list, with 84 species shared in the top 100. The average number of species shared with the FP based EDGE list was 62, meaning that across the lists there was generally much agreement. All of the top 15 ranked species using FP based EDGE were in the top 100 species using the other measures of evolutionary isolation, with the exception of NWW (which included only four of these species).

Overall, out of 4900 mammal species in total, there were 302 different species found in the 9 top 100 lists, not counting the taxonomy based (GENUS) EDGE list. Most species (126 out of 302) were found in just a single list, but two-thirds of the 302 different species were in the top 250 using the original FP based ranking.

1.4 Discussion

1.4.1 Measuring Evolutionary Isolation

As there is strong correlation among nearly all the measures of evolutionary isolation on most empirically-inferred and simulated trees, they all appear to choose evolutionary isolated species well; satisfying the first component of the comparison framework I set out above. Possible exceptions were PAT and NWW, which appear to measure slightly different information when compared to the other measures. For all trees considered in this study, however, the highest scoring tip was the same for all measures (results not shown).

There are ready explanations for most of the subtle differences seen between the correlations on sets of trees. For instance, the different patterns seen between the two sets of simulated trees could be because Hey trees have more speciation events near the present than trees built using the Yule model (Hey, 1992), and therefore there is likely to be lower variation in the lengths of the species tips (i.e. most are short).

Also, in the MDS plots of non-ultrametric trees, the strong separation of the topology-based measures from the branch-length based measures is due to the branch-length based scores being based on slightly different information in this set of trees. FP and ES, for instance, are both calculated by awarding each tip a proportion of the total path length from root-to-tip; the total amount awarded depending on the number of close relatives a species has. On ultrametric trees all root-to-tip lengths are equal. This is not the case with non-ultrametric trees,

where tips have different root-to-tip path lengths, providing an extra source of variation for scores calculated using the branch-length based measures. In contrast, this extra variation does not affect scores calculated using topology-based ones causing the two sets of evolulationary isolation measures to be less correlated.

Although it is a limited comparison, the taxonomy-based measure of evolutionary isolation used here had the lowest average correlation to all the others. Species-per-genus does measure some of the same information as the other evolutionary isolation measures, but with only 3% unique tip scores within the mammal tree (compared to ES, FP and QE with 35% unique scores) its resolution is very low, potentially accounting for the weak correlations. We note, however, that taxonomy-based measures are often the only alternative for poorly-known species groups and more work is needed to assess whether they provided a reasonably proxy for measures based on phylogenetic information.

The ‘Shapley Index’ is not recorded in most of the results listed below, as its correlation with the FP value is almost always 1. The exception can be seen in table 1.3 where, for simulated Hey trees, which has an average correlation of 0.99. This finding is robust to examining different subsets of the data and it appears that on some shapes of tree there are very slight differences between the values. Given the very strong correlation still present, this finding is of academic as opposed to conservation interest.

One of the key findings of this study is the consistent groupings of the different measures of evolutionary isolation on each of the tree sets. These

groupings appear to align well with the underlying mechanism by which the scores are constructed, i.e. branch-length based, topology-based or pair-wise. To represent the different mechanisms by which the measures quantify how many close relatives a species has, therefore, one does not need to apply all the possible measures of evolutionary isolation to a candidate tree. Instead, calculating scores using one measure from the three sets (NWW, NWU and VW; ES, FP/Shapley, PE; and QE), most of the variation across the 9 measures of evolutionary isolation will be captured.

1.4.2 Score Differentiation

From conservation ranking perspective the occurrence of many equal scores of evolutionary isolation presents problems detecting real differences between the evolutionary positions of species on a tree. Measures that include more information from the tree, i.e. both branch lengths and topology consider more species to have distinct values of evolutionary isolation in nearly all cases, compared to those measures that use just topological information.

If maximising the number of unique tip scores is the aim then QE, ES & FP are clearly superior in this respect. However, the differences could be due to slight differences in the node heights of otherwise similar clades. We need, therefore, to investigate whether these subtle differences are worthy of their higher conservation rank and the subsequent preferential application of conservation resources. For instance, upon consideration it may be that the topological measures provide a more reasonable assessment of the number of different scores in a tree. An alternative approach is to use the branch-length

based measures, but use a predetermined cut-off e.g. a % difference in scores, to prevent subtle differences in branch lengths strongly influencing important conservation decisions.

1.4.3 Metric Conceptualization

The evolutionary and conservation meaning of the topological node-based measures ('May', 'Nixon & Wheeler Weighted', 'Nixon & Wheeler Unweighted') is not clear. There has been a suggestion that these node-based measures approximate how basally rooted a species is (Redding et al. 2008) or, alternatively, the amount of historic speciation there has been in the clade of which the candidate species tip is a member. While 'Pendant Edge', 'Fair Proportion' and 'Equal Splits' give strong or complete weighting to the most recent split, the node-based measures, for the majority, are calculated with equal weighting on a path from root to tip. These measures could be considered to weight 'basal' taxa higher, but only in comparison to those measures (FP, ES, PE) that weight information nearer the tip strongly. Furthermore, this distinction is blurred when a species pendant edge tends towards the height of a tree, as it is then restricted to meeting the rest of the tree near the root, and all measures will give this tip a high isolation score. Thus, the topology based measures can only been seen to give more relative weight to the basal rooting for species with a low or medium-low pendant edge score.

The pair-wise based measures ('Quadratic Entropy' and 'Average Pairwise Difference'), likewise, suffer from a lack of clear understanding of what the resulting evolutionary isolation units mean in terms of the evolution and

conservation of a species. The ‘Quadratic Entropy’ evolutionary isolation score “Maximize(s) the expected (phylogenetic) dissimilarity between two species randomly drawn from the set” (Pavoine, 2005). The ‘Average Pairwise Difference’ score is straight-forwardly the average amount of evolutionary history between a species and all the other species in the tree. While it is clear that if a species is more distant to other species on average, or more dissimilar, then it will have fewer close relatives but the units that result from these algorithms are artificial and difficult to interpret.

Conversely, within an evolutionary biology context the understanding of the units resulting from the ‘Pendant Edge’ measure is straight-forward: When applied to a dated ultrametric phylogeny it is the amount of time since the speciation of the common ancestor of a species, into the candidate species and its sister clade. This is useful information from a conservation perspective as it potentially highlights genetic information that is unique to the species.

‘Pendant edge’ has also been used to approximate the “age” of a species and, subsequently, analysed alongside a variety of traits, such as geographic range size (Webb & Gaston, 2000), response to habitat degradation (Meijaard et al. 2007), and species diversity (Ricklefs et al. 2006). Further research that takes into account fossil records and molecular phylogenies (using e.g. marine molluscs) is needed to assess how well ‘Pendant Edge’ scores, calculated on a tree of currently extant species, approximates true species age.

One downside of ‘Pendant Edge’ as a metric of evolutionary isolation can be demonstrated in figure 1.1. The tips ‘*T.alba*’ and ‘*T. delicatula*’ have short

species tips or pendant edges, but a long internal branch that connects the two species to the rest of the tree. Therefore, the ‘Pendant Edge’ approach gives them a low rank (8^{th}) meaning that they are the least isolated tips in the whole tree. This is not a contrived example; the Kiwis (family Apterygidae) are an avian group containing five species that have recently split from one another (Baker et al. 1995). Similar to the example in figure 1.1, the Kiwi family meets the rest of the tree almost near the root of the whole tree of Aves, between 50 and 80 million years ago (Baker et al. 1995). It is clearly an evolutionary isolated group but using the ‘Pendant Edge’ measure the five species would be considered not isolated. The closely-related measures ‘Equal Splits’ and ‘Fair Proportion’ measures cannot be ‘fooled’ in this way, as they give the evolutionary isolated group of ‘*T.alba*’ and ‘*T. delicatula*’ both relatively high rankings by dividing the long internal branch that connects them to rest of the tree amongst the two species (figure 1.1).

The strong positive correlation between ‘Fair Proportion’ (and less so ‘Equal Splits’) and the ‘Shapley Index’ is surprising. ‘Fair Proportion’ was initially created as an algorithm to simply divide an evolutionary tree up amongst its tips such that the most isolated species are allocated a greater proportion of the tree (Redding, 2003). Neither it, nor Equal Splits, has a simple conceptual explanation and this is a strong criticism of their general use. The ‘Shapley Index’, conversely, is derived from game theory and can be simply conceptualized as the expected phylogenetic diversity a species is expected to contribute to future subsets of the tree (Haake et al. 2008). Indeed, the Shapley index is a measure

of future pendant edge under a fully random extinction process. Hartmann (2008) proved formally that the ‘Shapley Index’ converges on the FP as trees become large. Therefore, although they derive from different roots, both isolation measures (‘Fair Proportion’ and to a lesser extent ‘Equal Splits’) can be seen as computational cheap ways to measure the more conceptually straight-forward ‘Shapley Index’.

1.4.4 EDGE rank lists

The differences seen between the EDGE-like lists were not just a factor the correlation between the measures of evolutionary isolated used and their ability to resolve differences but also the distribution of scores amongst the tips. For instance, due to distribution of very high and low scores, the most isolated species calculated using the NWW measures will be given much more weight in an EDGE list compared to their threat status, than when compared to an EDGE list using the PAT measure.

These different distributions are reflected when we compare the scores for EDGE against the corresponding ED element (figures 1.3 & 1.4). At the low end of EDGE score for QE, for instance, the score is entirely decided by the threat status of the species, whereas for the higher EDGE scoring species the value is correlated to the QE value much more strongly than it is for the threat score (figure 1.3). For ES, in contrast, there is variation in EDGE scores for nearly all values of ES, meaning that threat status plays a part in deciding EDGE score across the range of values (figure 1.4).

As discussed above, using the different evolutionary isolation measures also affects what the priority “EDGE species” that are selected for conservation attention actually represent. For instance, using the ‘Fair Proportion’ measure in the EDGE ranking is preferentially conserving threatened species that add the largest expected amount of evolutionary history to future trees. I note that it is not clear if this is the aim of the EDGE programme: there needs to be a critical examination of results of any EDGE list, and an informed choice of which ‘evolutionary isolation’ measure to use. Alternatively, conservation organizations might consider using a combined ‘average’ score to provide a more comprehensive picture of which species are considered “evolutionarily distinct.” It is less clear, however, what such a group of species would represent from an evolutionary biology perspective and, therefore, what the specific aims would be of a conservation approach based on such a measure.

1.4.5 Suggestions for Future Work

What the imperfect overall correlations between the measures demonstrate is hard to determine unless there is some common ground upon which to make a comparison. One option is to consider our two suggested components of evolutionary isolation: The unique evolutionary history apportioned to a species and the redundancy (or vulnerability) of the internal branches which connect the species tip to the root. Clearly, ‘Pendent Edge’ represents the extreme of the first component. We have not yet created a measure of the second component. If we could do this, then we could compare how the measures give different weight to the two.

1.5 Conclusion

Evolutionary or phylogenetic isolation, as I define it here, is a statistical measure that can be applied to rooted trees of extant species or populations and also to gene trees (capturing gene duplications and divergence as well as the lineages in which they are found), or phylogenies of extinct species. Above and elsewhere in this thesis, I focus on species-level molecular phylogenies, where such measures are already commonly used. Most of the concepts and terms I use will have analogous interpretations in most other fields for which analyses based on rooted trees are integral.

Given the strong correlations amongst the different measures of evolutionary isolation, we must use other factors to select which score to use. For example, we can use the scores' ability to differentiate tips, their simplicity, and their biological interpretation to help make decisions about which to use. Indeed, the lack of clear interpretation for many of the measures remains perhaps the strongest criticism of their use (Faith 2008).

Given this, I recommend using 'Fair Proportion' as the measure of evolutionary isolation within a conservation prioritization context. It is already used (Isaac et al., 2007), it has high resolution on most tree shapes, it has low computational overhead and it ranks highest, those species that have the highest potential contribution to future evolutionary trees. Usefully, groups that are selected as having the highest FP score also capture the total information in the tree considerably better than random choice (Redding et al 2008). It is also readily extendable (see, e.g. Steel et al., 2007).

1.6 This thesis

In the balance of this thesis, I use subsets of the evolutionary isolation scores I have introduced above to begin to examine the difference between those species that score high and those that score low. I look, firstly, to see what properties high scoring (evolutionarily isolated) species have when chosen as a group, and secondly, how we can prioritise them for conservation attention. Thirdly, I examine whether their evolutionary isolation leads to unusual ecological, morphological and geographic characteristics Lastly, I ask how evolutionarily isolated species are geographically distributed.

Note, the chapters of this thesis were written and finalized in the following chronological order: Chapter 3, 2, 4, 1, 5. I have attempted to standardize terminology throughout and have moved sections around for clarity (particularly from chapter 2 to chapter 1). However, some redundancies remain: in particular, chapter 3 re-introduces one of the evolutionary isolation measures (ES) also considered in chapters 1 and 2.

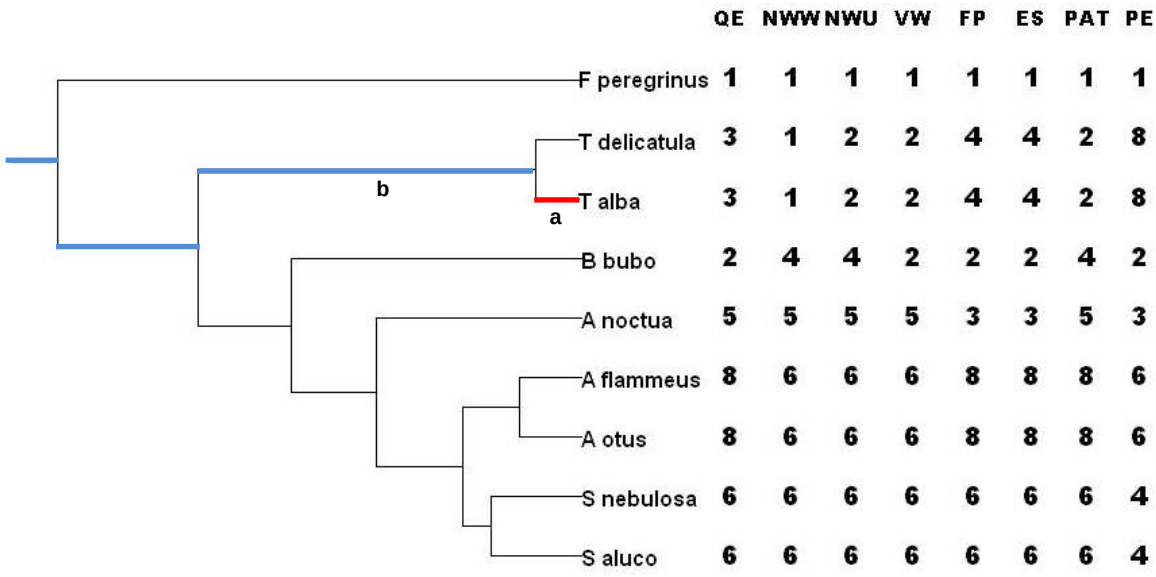

Figure 1.1 **Cartoon of a 9-tip phylogenetic tree, with a table of ranks based on real scores from 8 measures of evolutionary isolation. Numbers indicate the corresponding species rank, with the highest score being rank 1 (most isolated) to lowest score being rank 6 or 8 (least isolated). QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, NWU: Nixon & Wheeler weighted, VW: Vane-Wright, FP: fair proportion; ES: equal splits; PAT: Average pairwise difference, PE: pendant edge. See text for details of the measures. For tip 'T alba', red branch (a) is unique evolutionary information and blue branches are shared evolutionary information.**

Table 1.1 **Average rank correlations (to 2 s.f.) with standard deviation (in brackets; to 3 s.f.) taken from correlations of pairs of 8 evolutionary isolation measures across a collection of 30 ultrametric (bottom left of diagonal) and 242 non-ultrametric (top right of the diagonal) phylogenetic trees estimated from empirical data (McPeek & Brown, 2006). QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, NWU: Nixon & Wheeler weighted, VW: Vane-Wright, FP: fair proportion; ES: equal splits; PAT: Average pairwise difference, PE: pendant edge. See text for details of the measures**

QE	--	--	--	--	--	--	--
0.7 (0.079)	**NWW**	0.88 (0.016)	0.79 (0.026)	0.4 (0.141)	0.43 (0.118)	0.57 (0.11)	0.44 (0.135)
0.83 (0.015)	0.86 (0.038)	**NWU**	0.92 (0.008)	0.43 (0.132)	0.48 (0.107)	0.55 (0.12)	0.51 (0.109)
0.91 (0.007)	0.77 (0.073)	0.91 (0.005)	**VW**	0.46 (0.121)	0.53 (0.099)	0.52 (0.122)	0.58 (0.078)
0.91 (0.012)	0.49 (0.124)	0.65 (0.058)	0.75 (0.038)	**FP**	0.96 (0.003)	0.86 (0.021)	0.83 (0.042)
0.89 (0.01)	0.51 (0.084)	0.66 (0.041)	0.77 (0.029)	0.97 (0)	**ES**	0.79 (0.029)	0.86 (0.022)
0.9 (0.005)	0.75 (0.094)	0.79 (0.019)	0.82 (0.017)	0.77 (0.043)	0.72 (0.036)	**PAT**	0.65 (0.084)
0.82 (0.026)	0.36 (0.14)	0.54 (0.101)	0.65 (0.073)	0.96 (0.001)	0.95 (0.002)	0.61 (0.064)	**PE**

Table 1.2 **Series of statistics (with standard deviation in brackets) taken from applying 8 evolutionary isolation measures on a set of 30 ultrametric trees (ULT) and 242 non-ultrametric trees (NULT). QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, NWU: Nixon & Wheeler weighted, VW: Vane-Wright, FP: fair proportion; ES: equal splits; PAT: Average pairwise difference, PE: pendant edge. See text for details of the measures**

Type	Analysis	QE	NWW	NWU	VW	ES	PAT	PE	FP
Ultra-metric	Unique tip values (%)	--	57.5 (12)	48.3 (13.8)	37 (13.8)	94.1 (9.2)	88.9 (12.8)	68.3 (7.8)	93.3 (9.5)
Ultra-metric	Maximum score /mean	--	3.31 (2.58)	2.01 (0.78)	2.51 (1.07)	2.07 (0.89)	1.39 (0.31)	2.03 (0.91)	2.47 (1.18)
Ultra-metric	Minimum score /mean	--	0.51 (0.19)	0.49 (0.13)	0.58 (0.11)	0.51 (0.17)	0.81 (0.07)	0.31 (0.25)	0.45 (0.18)
Non-Ultra.	Unique tip values (%)	64.8 (6.9)	53.5 (11.7)	42.7 (10.3)	31.3 (10.7)	64.5 (6.2)	57 (13.2)	63.9 (6.6)	63.8 (7.7)
Non-Ultra.	Maximum score /mean	3.06 (1.81)	4.52 (4.21)	2.56 (0.93)	2.33 (1.01)	1.91 (0.82)	1.24 (0.23)	2.75 (1.51)	1.86 (0.77)
Non-Ultra.	Minimum score /mean	0.37 (0.22)	0.46 (0.16)	0.53 (0.14)	0.61 (0.11)	0.5 (0.21)	0.88 (0.07)	0.26 (0.19)	0.61 (0.16)

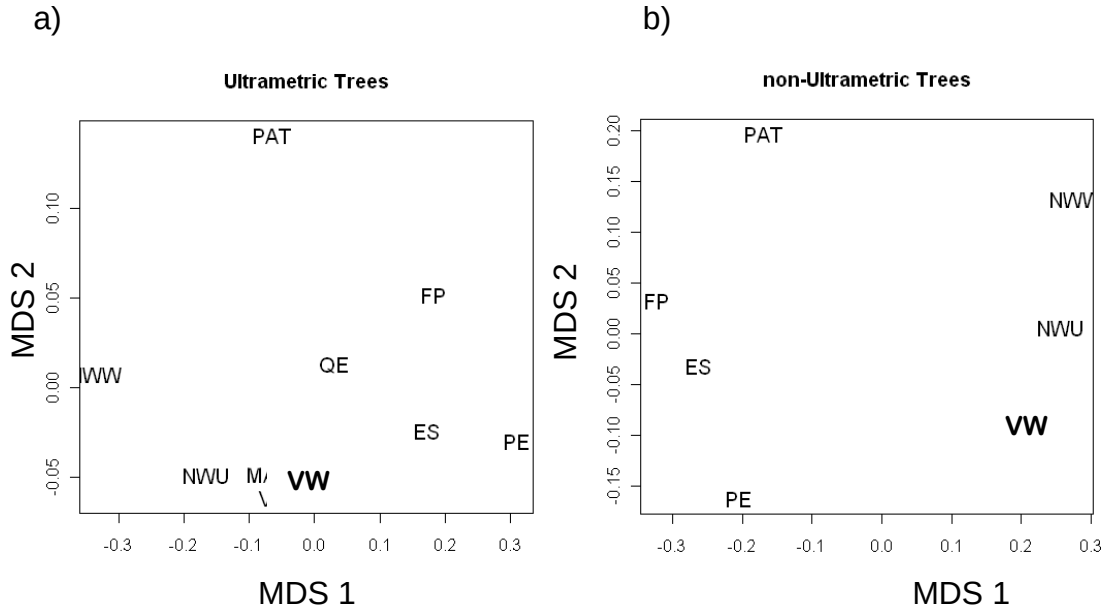

Figure 1.2 **The relative differences, using multi-dimensional scaling, in pairwise correlation coefficients between 8 measures evolutionary isolation applied to a) 30 ultrametric trees and b) 242 non-ultrametric trees. QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, NWU: Nixon & Wheeler weighted, VW: Vane-Wright, FP: fair proportion; ES: equal splits; PAT: Average pairwise difference, PE: pendant edge. See text for details of the measures**

Table 1.3 **Average rank correlations (to 2 s.f.) with standard deviation (in brackets, to 2 s.f.) taken from correlations of pairs of 9 evolutionary isolation measures across a collection of 5000 128-tip ultrametric phylogenetic trees simulated using the Hey process (Hey, 1982; bottom left of diagonal) and of 5000 128-tip ultrametric phylogenetic trees simulated using the Yule process (Yule, 1924; top right of the diagonal). QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, NWU: Nixon & Wheeler weighted, VW: Vane-Wright, FP: fair proportion; ES: equal splits; PAT: Average pairwise difference, PE: pendant edge, SHAP: Shapley index. See text for details of the measures**

QE	0.62 (0.137)	0.78 (0.07)	0.88 (0.017)	0.79 (0.029)	0.65 (0.049)	0.6 (0.104)	0.8 (0.03)	0.8 (0.036)
0.68 (0.115)	**NWW**	0.76 (0.016)	0.74 (0.019)	0.29 (0.107)	0.75 (0.18)	0.13 (0.115)	0.32 (0.163)	0.31 (0.162)
0.82 (0.058)	0.76 (0.016)	**NWU**	0.89 (0.014)	0.57 (0.062)	0.59 (0.088)	0.33 (0.122)	0.53 (0.1)	0.52 (0.1)
0.9 (0.009)	0.74 (0.019)	0.89 (0.015)	**VW**	0.7 (0.047)	0.65 (0.104)	0.45 (0.104)	0.66 (0.067)	0.65 (0.07)
0.93 (0.007)	0.53 (0.128)	0.79 (0.06)	0.9 (0.014)	**ES**	0.34 (0.08)	0.87 (0.009)	0.95 (0.001)	0.95 (0.001)
0.51 (0.161)	0.78 (0.176)	0.52 (0.124)	0.53 (0.177)	0.36 (0.146)	**PAT**	0.17 (0.08)	0.42 (0.11)	0.4 (0.115)
0.57 (0.236)	0.15 (0.173)	0.33 (0.184)	0.46 (0.144)	0.66 (0.122)	0.08 (0.108)	**PE**	0.87 (0.013)	0.88 (0.012)
0.87 (0.029)	0.68 (0.236)	0.67 (0.101)	0.78 (0.05)	0.8 (0.05)	0.67 (0.223)	0.55 (0.26)	**SHAP**	1 (0)
0.88 (0.025)	0.63 (0.257)	0.66 (0.119)	0.78 (0.052)	0.83 (0.03)	0.58 (0.253)	0.6 (0.224)	0.99 (0.001)	**FP**

Table 1.4 Series of statistics (with standard deviation in brackets) taken from applying 8 evolutionary isolation measures on a set of 5000 128-tip ultrametric phylogenetic trees simulated using the Hey process (Hey, 1982) and 5000 128-tip ultrametric phylogenetic trees simulated using the Yule process (Yule, 1924). The standard deviation for each statistic is given in brackets. QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, NWU: Nixon & Wheeler weighted, VW: Vane-Wright, FP: fair proportion; ES: equal splits; PAT: Average pairwise difference, PE: pendant edge. See text for details of the measures

Type	Analysis	QE	NWW	NWU	VW	ES	PAT	PE	FP
Hey	Unique tip values (%)	82.21 (2.964)	64.188 (5.815)	19.992 (2.628)	11.772 (1.855)	84.794 (2.494)	80.715 (2.959)	82.614 (2.808)	84.271 (2.55)
Hey	Maximum score /mean	12.068 (7.238)	6.829 (8.189)	5.323 (0.785)	2.768 (1.026)	8.598 (3.816)	1.705 (0.744)	16.704 (10.97)	4.809 (3.395)
Hey	Minimum score /mean	0.053 (0.031)	0.458 (0.129)	0.413 (0.044)	0.577 (0.052)	0.087 (0.034)	0.818 (0.075)	0.008 (0.008)	0.496 (0.082)
Yule	Unique tip values (%)	82.8 (2.774)	64.344 (5.777)	19.988 (2.649)	11.783 (1.833)	85.359 (2.404)	85.293 (2.427)	85.351 (2.404)	85.352 (2.407)
Yule	Maximum score /mean	8.041 (3.827)	6.73 (8.026)	5.334 (0.775)	2.762 (1.031)	3.19 (0.556)	1.186 (0.116)	5.362 (1.231)	2.821 (0.564)
Yule	Minimum score /mean	0.089 (0.041)	0.458 (0.13)	0.412 (0.044)	0.576 (0.051)	0.22 (0.059)	0.915 (0.03)	0.016 (0.015)	0.436 (0.055)

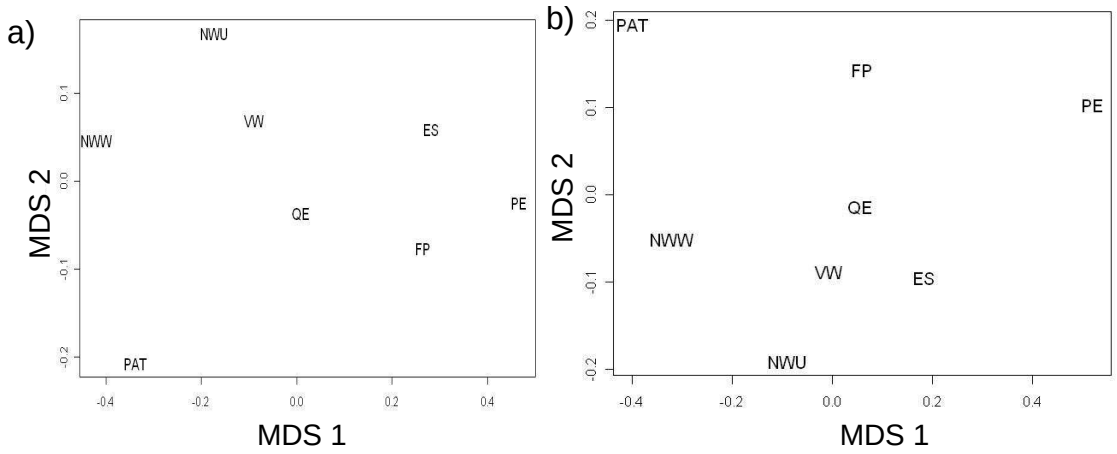

Figure 1.3 The relative differences, using multi-dimensional scaling, in pairwise correlation coefficients between 8 measures evolutionary isolation applied to a) 5000 128-tip ultrametric phylogenetic trees simulated using the Yule process (Yule, 1924) and b) 5000 128-tip ultrametric phylogenetic trees simulated using the Hey process (Hey, 1982). QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, NWU: Nixon & Wheeler weighted, VW: Vane-Wright, FP: fair proportion; ES: equal splits; PAT: Average pairwise difference, PE: pendant edge. See text for details of the measures

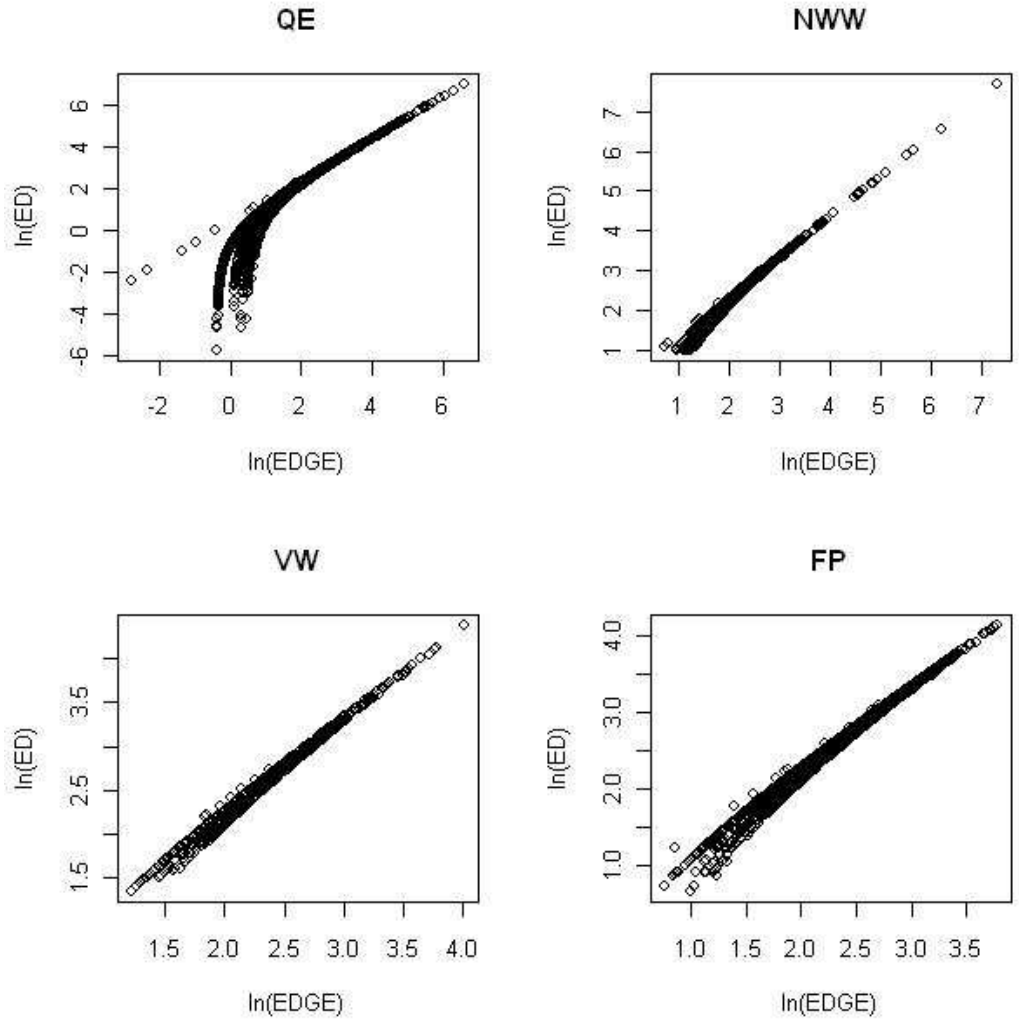

Figure 1.4 **EDGE scores for 4900 species of mammal created from two component variables: a score representing a species evolutionary isolation (ED) and a score of the specie global endangerment (GE), plotted against one of the components of that score evolutionary isolation (ED). Each panel represents an EDGE score created using the same value for global endangerment but using different methods of calculating evolutionary isolation. QE: quadratic entropy; NWW: Nixon & Wheeler unweighted, VW: Vane-Wright, FP: fair proportion. See text for details of the measures**

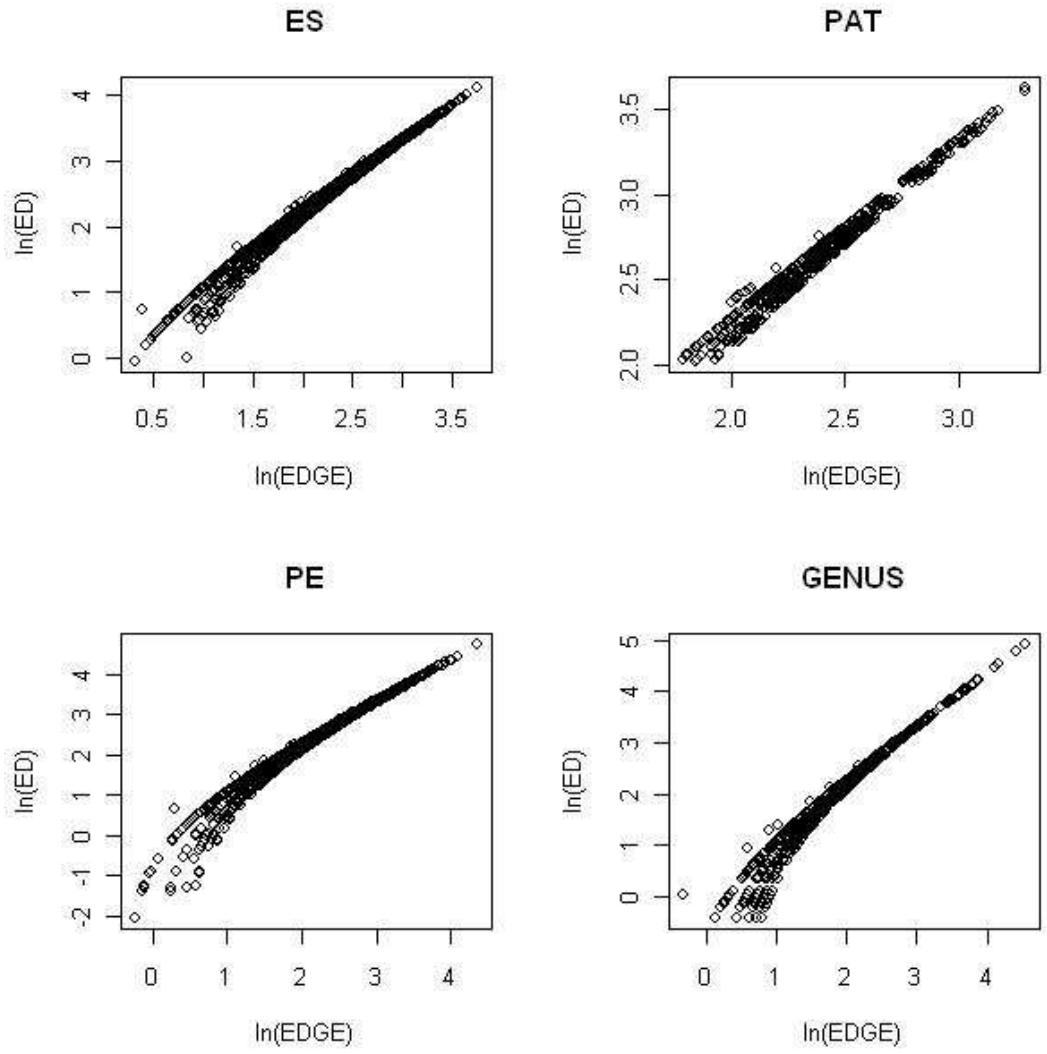

Figure 1.5 **EDGE scores for 4900 species of mammal created from two component variables: a score representing a species evolutionary isolation (ED) and a score of the specie global endangerment (GE), plotted against one of the components of that score evolutionary isolation (ED). Each panel represents an EDGE score created using the same value for global endangerment but using different methods of calculating evolutionary isolation. ES: equal splits; PAT: Average pairwise difference, PE: pendant edge, GENUS: number of species in the species' genus. See text for details of the measures**

2: EVOLUTIONARILY ISOLATED SPECIES OFTEN CAPTURE MORE PHYLOGENETIC DIVERSITY THAN EXPECTED[1]

2.1 Introduction

With increasing extinction there is a pressing need to effectively prioritize species for conservation. Many nonexclusive currencies are used, e.g. threat status, ecological importance, social or intrinsic value, and financial cost (for discussion, see Crozier 1992; Weitzman 1998; Andelman 2004; Avise 2005). Here I focus on the evolutionary isolation of species in the context of their conservation. In particular, I examine the trade off between prioritizing the most evolutionary distinctive species in a tree and prioritizing sets of species that best represent the whole tree.

Conservation biologists have approached the goal of representing a phylogenetic tree from two angles. Both approaches use information about the relatedness among tips (usually species), but one (phylogenetic diversity) is a group measure, while the other (evolutionary isolation) is a species-specific property.

To illustrate the connections between the two approaches, consider the order Sphenodontia. This order contains the two species of tuatara and is sister

[1] A version of this chapter has been published as (Redding, D. W., K. Hartmann, A. Mimoto, D. Bokal, M. DeVos, and A. O. Mooers. 2008. Evolutionarily distinctive species often capture more phylogenetic diversity than expected. Journal of Theoretical Biology 251:606-615.) I gathered all the data and did all the analyses, and wrote the first draft of the published paper.

to Squamata (Snakes, Lizards, Amphisbaenians), which contains ~6200 species. From a macroevolutionary perspective, if one species from each order were equally threatened, priority should go to a tuatara before any lizard, snake or amphisbaen species, because both tuatara species are highly distinctive and so contain a disproportionately large proportion of the phylogenetic diversity contained within the two orders. However, if only two species of the ~6202 species were to be preserved (an unlikely scenario), the tree would be best represented with a set that included only one of the two tuataras, and one Squamate. More generally, any *subset* that did not contain *one* of the tuataras would be suboptimal.

The idea of comparing the relative phylogenetic diversity represented by *sets* of species in order to prioritize sets that contribute more unique evolution was pioneered by Vane-Wright et al. (1991) and by Faith (1992). The phylogenetic diversity (PD) of a set of species is generally measured as the sum of the branch lengths of the tree containing those species and the root (see Figure 1 and Faith & Baker, 2006) and sets of species with maximal PD can be found using simple algorithms (Steel 2005, Pardi and Goldman 2005, Minh et. al. 2006). The PD approach has also been extended to include species survival probabilities and conservation costs and budgets (Weitzman 1998, Hartmann and Steel, 2006, Pardi and Goldman 2007).

In parallel, systematists have proposed metrics for how much unique evolution a particular species contributes to some larger set (again, see Vane-Wright et al. 1991; see also May 1990, Nixon & Wheeler 1992, Pavoine et al.

2005, Redding 2003, Redding & Mooers 2006, Isaac et al., 2007). Early attempts to attribute a score of evolutionary isolation to individual species (May 1990, Nixon and Wheeler 1992, Vane-Wright et al., 1991) used only tree topology, and relied on the fact that basal and evolutionary isolated species have fewer nodes between the tip and the root. Recent workers (Isaac et al., 2007, Pavoine et al. 2005, Redding and Mooers 2006, Steel et al., 2007, Weitzman 1998) have suggested isolation measures (outlined below) that use both topology and internal branch lengths to measure species isolation. All such measures have one thing in common: they give species that have many and closer relatives less value than they give species with fewer and more distant relatives.

Evolutionary isolation measures and PD approaches differ in substantial ways. PD is uninformative for any one species on an ultrametric tree - all single species are the same distance from the root and so receive the same value. Many current conservation approaches (e.g. endangered species lists) rely on having species ranked in order of priority. Current PD approaches offer no such order. To overcome this, species within any optimal set chosen could be ordered by arranging them according to their evolutionary isolation, or, alternatively, species could be chosen according to natural species-specific indices that ensure optimal sets (DB, MdV, KH, unpublished results). However, there will be as many possible rankings of species produced by these approaches as there are PD maximizing solutions for the set of candidate species, and thus may be difficult to implement at the management level.

More importantly, the amount of PD saved is only optimal if *all* the species that are selected are subsequently protected. If any species in the selection are lost, new optimal sets are possible. Finally, it may be difficult to find optimal sets of species if there are large numbers of species to prioritize and other complex factors such as cost of conserving individual species are considered (Weitzman, 1998).

The recently developed species-specific measures of evolutionary distinctiveness may, in comparison, represent a flexible and transparent conservation tool to promote “evolutionary value” in the current legislative climate. However and importantly, they have not been designed to capture total phylogenetic diversity. If sets of evolutionary distinctive species did capture substantial PD, then the species-specific measures would be doubly useful, highlighting the most individually distinctive species whilst helping to preserve more of the tree of life. This is the focus of the present study. I first outline the distinctiveness measures I tested, and then consider aspects of the underlying tree that might affect the relationship between distinctiveness measures and PD.

The measures that I used were introduced in Chapter 1 (section 1.2.1). I considered five of them here: Pendant Edge (PE), Vane-Wright’s node-counting measure (VW), Pavoine’s quadratic entropy measure (QE), which all measure different information from the tree and combined explain a good proportion of the total variation in published evolutionary isolation measures (Figure 1.2). In addition, the two apportionment measures Equal Splits (ES) and Fair Proportion (FP) are included as they have the simple interpretation of being the likelihood of

contributing to future subsets of the tree. Finally, for comparison, I included the expected value of PD if species were chosen randomly (AVG, following Nee and May, 1997).

2.1.1 Tree Shape

Tree shape is likely to be an important factor in determining how effectively distinctiveness measures capture PD. I outline three measures of tree shape and how I think they will affect the PD 'capture rate'.

The balance of the tree towards the root (I_c; Colless 1982; Heard, 1996) will dictate whether, when randomly selecting species some internal branches are more likely to be chosen than others. Repeatedly selecting closely related species will decrease the total amount of PD represented, since the same internal branches are chosen again and again. Random selection on trees with imbalance at the root will have this effect.

The tree shape measure I_2 (Mooers and Heard 1997) measures the imbalance over the entire tree (Matsen, 2006). In balanced trees or areas of the tree, tips will have similar distinctiveness scores (e.g. there will be the same number of nodes between the tips and the root). Distinctiveness measures will then rank these species similarly, and will choose closely-related species, decreasing the total PD captured. On small trees, I_2 is strongly correlated with the number of terminal pairs, or cherries, there are in a tree (For 16-tip Yule trees, this relationship is very strong: Pearson's P = 0.988, n = 5005, $p<0.001$). Cherries will have the same distinctiveness measure. On larger trees, there are

more complex sub-tree shapes that can act like cherries. Consider a large tree with high imbalance at the root but balanced elsewhere. The species on the species-poor side of the tree are likely to have fewer edges separating them from the root relative to the species on the other side of the tree. A simple distinctiveness measure such as VW (see equation 1 below) is likely to choose species exclusively from the species-poor side of the tree without crossing the root, decreasing the PD captured.

The final aspect of tree branching structure that is likely to affect capture rate is average node depth. This can be measured using the 'gamma statistic', a value which quantifies whether the splits in an evolutionary tree are, in general, near the tips or near the root (Pybus and Harvey, 2000).This, therefore, approximates how much of the tree there is to "share" among the tips. Consider a star phylogeny (gamma <<0), where species contribute equally to PD value (~PD/n): each species contributes the same amount to total PD; at the other extreme, where most of the nodes are at the present (gamma>>0), the first species chosen captures ~PD/2, and most additional species contribute little. In these extreme cases the capture rates are fixed and irrelevant of the order in which species are chosen and all the measures therefore must perform similarly.

Trees with gamma values between these two extremes are expected to have much more complicated PD capture curves but must be bounded by these two examples. In this middle range of gamma there are many different possible tree topologies, with, therefore, much greater variation in the proportion of the

tree a tip can represent, and as a result, tip choice must be an important factor for capturing PD.

To test how efficiently distinctiveness metrics capture PD, and to explore how tree shape might affect this efficiency, I undertook simple simulations, and then formalized some of the results using a graph-theoretical approach, and finally applied the metrics to a sample of trees derived from empirical data.

2.2 Methods

Our primary dataset consisted of 5000 simulated Yule trees (Yule 1924) with 16 tips, created using Bio::Phylo package (Vos, 2006). In order to test the sensitivity of the findings to the process model used, I also simulated “Hey trees” (Hey, 1992): these are the tree shapes expected under the Moran coalescent (Moran, 1951) and have Yule topologies, but different waiting times, with more splits occurring near the present. Using Yule trees in this situation is conservative, as the principal way they differ to “real trees” is their limited imbalance (Heard and Mooers, 1997). Thus, if as predicted, the greater imbalance leads to better performance by distinctiveness measures over random choice, samples of real trees should show a stronger relationship.

In this study I only use ultrametric trees. This allows us to set a constant “currency”, time. I note that many of the arguments I present apply to trees with different currencies, such as trait richness, but that QE is only applicable to ultrametric trees. Though there is a loss of generality by using just ultrametric trees, at present I can think of no measure besides time that can be as widely applied across the Tree of Life.

For each simulated 16-tipped tree, I used the five metrics to rank the 16 tips (ES, FP, QE, VW, and PE). I then recorded the cumulative PD captured (as a proportion of that represented by the entire tree) when selecting 2,4,6,8 and 10 species. When ranks of species tied, I took the mean (expected) value of PD (i.e., that if the choice among tied species were random).

I first attempted to predict the amount of PD captured (by the five distinctiveness measures and the AVG algorithm) using a series of exploratory logistic regression models, with the y variable being percentage of the tree captured, and our three measures of tree shape as the x variables: I_c, I_2, and Gamma . In total, five separate models were constructed with the PD captured by 2,4,6,8 and 10 species as the respective dependent variables. For statistical independence, I recorded the proportion of PD captured by only one of 6 measures (the 5 distinctiveness metrics, and the average (expected) proportion) for each of the 5000 trees, yielding n=833 in our models. I concentrate on the differences between random choice and the choice using the distinctiveness metrics.

I selected models in a step-wise manner using the conservative Bayesian Information Criteria (BIC) score as the selection criterion (in the R environment; *step* function Venables & Ripley, 2002). Because highly unbalanced tree topologies are highly constrained, model residuals were non-normally distributed. I therefore used bootstrapping (*lmboot* in R, Peng 2005) to estimate the error residuals about the coefficients.

Finally, I applied the five distinctiveness metrics to a selection of 50 “real trees”, representing a large range of tip number (4 to 89 tips) and diverse taxonomic cross-section (including flagellate protests, dicotyledons, birds and mammals; McPeek & Brown, 2007) and asked how much PD was represented by the most original set of species at two different group sizes: 25% and 50% of total species number, using the same methods as for the simulated dataset. I then compared these values to the expected PD when randomly choosing groups of the same size from these trees.

2.3 Results

For our small simulated trees, all five distinctiveness metrics perform well at capturing PD for the majority of tree shapes, and generally capture significantly more of the tree than would a random sample (Table 2.1). The extra amount of the tree that would be captured by selecting species using an distinctiveness measure as opposed to randomly selecting them, e.g. the difference between random selection and ES, ranges from 4 to 9%.

When two species are chosen from the trees, the measures capture between 28% (VW) and 30% (ES) of the total PD, with all five measures doing better than random in this regard; corresponding numbers for 8 species are 72-77%; (Table 2.1). The Equal-Splits measure captured significantly more PD than the other distinctiveness measures (Tukeys HSD, all pairwise comparisons $p<0.001$).

Across all group sizes and measures the BIC criterion approach retains only gamma and I_2 as explanatory variables for the amount of PD captured. For example the model selected for ES at group size 6 was

$$Log\ (odds) = 0.22 + 0.12 \times gamma + 3.17 \times I2$$

The amount of PD that was captured by random choice, however, was chiefly dictated by models that contained only gamma and I_c - again the example at group size 6:

$$Log\ (odds) = 0.30 + 0.08 \times gamma - 0.45 \times Ic$$

The only discrepancies to this pattern are at the largest of the group sizes (i.e. 8 and 10 of 16 tips), where the models for each of the ES, FP and PE also contain I_c (Table 2.2), and at the smallest group size (2 tips chosen), where the model for AVG also contains I_2.

The relative value of the coefficient estimate for gamma were similar for all distinctiveness measures and for random choice, and across all groups sizes, showing that this factor of tree shape has little effect on their relative performance. I_c and I_2 alternatively had greater variation in coefficients, which suggests they play a key role in determining the relative performance of the different tip-choosing methods on different shaped trees.

Hey trees gave qualitatively similar results with respect to the relative performance of the measures averaged across 5000 trees. ES again captured the most PD but for Hey trees VW and QE captured the next highest amounts, with no significant difference between them, and PE captured the least (see Table 2.1). FP performed noticeably worse on Hey trees than on Yule trees,

capturing only just more than random at the small group sizes. Because they have very high Gamma values the absolute amount of the tree captured by the metrics was higher for Hey trees than for Yule trees, especially for groups of 2 species, which captured nearly twice as much PD. When selecting large subsets of species, however, the percentages captured were much more similar (Table 2.1).

The models produced from the Hey data were qualitatively similar in terms of the parameters chosen by the algorithm, differing only slightly in the coefficient values. Given these similarities, I concentrate on the most significant characteristics that are shared by both datasets in our discussion.

When choosing 25% of the species from each of the 50 “real trees,” all distinctiveness measures selected groups that had higher PD than the upper 95% c.i. of randomly chosen groups on at least 82% of the trees. ES and QE select equal to, or higher than random, for 92% of the trees, while VW achieved a similar result on the fewest number, 43 out of the 50 trees (86%).

When choosing groups that contained 50% of the species on each tree, ES and PE increased the number of trees on which they capture significantly more than random, with ES increasing from 88% to 90%, and PE from 84% to 90% (Table 2.3).

Those trees on which none of the measures captured more than random were both more (ANOVA, df = 51 $p<0.01$) and had higher gamma (at 50%; ANOVA, df = 48, $p=0.05$), in line with the results of the simulation study.

2.4 Discussion

I highlight four main findings: First, for the small trees considered here, all five distinctiveness metrics perform well at capturing PD for the majority of tree shapes, and generally capture significantly more of the tree than would randomly selecting species (Table 1). The absolute improvement, however, was modest. For example, on the tree of Aves (an a phylotaxonomy constructed, for comparison purposes, using Monroe & Sibely, 1993), selecting 50% of the species in the tree using ES captures a further 8 billion years of (concurrent) evolution, which is approximately 9.5% of the total tree, when compared to randomly selecting the same number of species (unpublished results). The absolute amount of the tree captured by any of the metrics is a strong function of gamma, as expected. Second, ES consistently captured PD better than all the other measures, and the simplest measure, the pendant edge (PE) also performed well. Third, the effects of tree shape on the effectiveness of capturing PD are unsurprising and suggest that distinctiveness may prove a useful metric for conservation. Fourth, while I do not know the extent of “real” tree space, and indeed how widely our 50 sampled trees represent this space, the concordance of the patterns from our simulations and the “real” trees suggests that the results are likely to be replicated throughout most of the plausible range of ”real” tree space.

In contrast to random selection, the metrics are unaffected by the overall balance of tree (I_c). They are affected, however, by the average balance throughout the tree (measured as I_2) and therefore for a small proportion of tree

shapes they capture PD only as well as random choice. I do not further discuss VW due to its consistently poor performance and the general problem it has with multiple ties among candidate species.

Random Choice – Random choice does capture a fairly large proportion of total PD (Nee and May, 1997). I note, however, that random choice may not be a realistic model for how species will survive into the future; though the patterns are currently weak, it may be that extinction will be clumped on the phylogenetic tree. In particular, as seen by the negative coefficient estimate (Table 2) random choice performs poorly with increasing tree imbalance. To the extent that published trees are more imbalanced than Yule (Mooers and Heard, 1997; Blum et al., 2006), random choice is compromised.

ES and FP- The Equal Splits measure is highly related to the Pendant Edge measure and for Yule trees is expected to represent a larger proportion of a set of clades than the Pendant edge Measure alone (Redding et al. 2008). However, the biases that affect the PE measure are expected to also affect ES, due to their correlation. Findings applicable to ES are also likely to be similarly applicable to Fair Proportion (FP), due to the fact that they are methodologically similar. It is not known why ES performs better, especially on high gamma trees, and further study is needed to investigate this property.

Quadratic Entropy – QE is an explicitly pair-wise measure, quite different from the others surveyed here. It is also the most computationally complex of the distinctiveness measures and captures PD at the same rate as PE in the Yule tree dataset, but slightly better in the Hey tree dataset.

A useful property of QE is that it sets absolute relative relationships between tips (DB, unpublished observations) irrespective of the size of the tree considered: If one species is twice as evolutionarily isolated as another on a small tree, then if these tips are considered as part of a much larger clade, the relative distinctiveness will remain 2:1. I propose that more work be done investigating the properties of QE, perhaps expanding it from a pairwise to a multispecies framework (c.f. Haake et al., 2008; Hartmann and Steel, 2006).

2.4.1 Conclusion: implications for conservation

The criterion most often used to prioritize species for conservation is threat status (Possingham et al. 2002). While threatened species tend to come from species-poor groups (Purvis et al. 2000) threat status may not be much more effective at capturing PD than choosing species at random (Redding and Mooers 2006). Likewise, evolutionary distinctiveness and threat are only very weakly correlated for birds and mammals (see section 3.3 for birds; also AOM and DWR, unpublished). If one conservation goal is the preservation of the tree of life, we must attend to explicit tree-based measures.

Quadratic Entropy and the Vane-Wright node counting measure are both good at picking out the most relictual species (e.g. they would correctly identify both the tuataras as of highest rank within the squamates) but with the handicap that they do not capture species from across the tree, and therefore do not capture PD.

PE performed surprisingly well for most of the simulation study and in the 50 sample trees, and using PE as a measure of distinctiveness certainly has many advantages: it is easy to understand, easy to measure, and, perhaps most importantly, it is an absolute measure, meaning any set of species can be compared. Obviously, more work with real trees is required to evaluate how well PE does on average: the relative length of pendant edges to interior nodes, and the extent to which pendant edge length predicts structure deeper in the tree are open questions (see, e.g. Burlando 1990). In addition, PE is likely to be very sensitive to alternative species designations (c.f. Isaac et al. 2007).

Of the five distinctiveness measures tested here, Equal Splits (ES) is consistently better than the other measures at capturing PD, at least in the tree space I tested, and is relatively simple to calculate. Fair Proportion (FP) performed similarly to ES but in most cases captured slightly less PD. The cases where I observed VW, PE or QE to perform better than ES were relatively rare, occurring only in tree shapes where all ranking measures perform badly, i.e. near star-like trees with very low gamma, and where random choice is as good as any other method.

To conclude, I propose that several distinctiveness measures be applied to a wider range of real trees and taxonomies to further explore their properties. I also suggest that the relationship between distinctiveness and other measures of conservation value, particularly conservation status, be explored in more detail and I examine this in more detail in the next chapter. Finally, we must continue the hard work of finding a framework that allows measures of distinctiveness to

be compared with other measures of species value, particularly ecological importance, charisma, and costs of recovery and probability of success.

Table 2.1 Proportion of entire tree (PD captured) when 2, 4, 8 and 10 species are selected on a 16-species tree (n=5000 trees). For each column, groups that are significantly different at the 0.05 level are designated by different letters.

	Species selected on Yule Trees					Species selected on Hey Trees				
	2	**4**	**6**	**8**	**10**	**2**	**4**	**6**	**8**	**10**
ES	0.296[b]	0.505[b]	0.658[b]	0.772[b]	0.859[b]	0.477[b]	0.696[b]	0.811[b]	0.882[b]	0.931[b]
FP	0.283[d]	0.480[c]	0.630[c]	0.748[c]	0.842[c]	0.411[e]	0.610[e]	0.750[e]	0.846[d]	0.912[c]
PE	0.289[c]	0.486[c]	0.633[c]	0.747[c]	0.837[c]	0.444[c]	0.649[d]	0.767[d]	0.846[d]	0.904[d]
QE	0.281[d]	0.482[c]	0.631[c]	0.747[c]	0.840[c]	0.438[d]	0.663[c]	0.785[c]	0.864[c]	0.921[c]
VW	0.280[d]	0.467[d]	0.613[d]	0.727[d]	0.823[d]	0.448[c]	0.663[c]	0.783[c]	0.861[c]	0.916[c]
AVG	0.270[e]	0.440[e]	0.570[e]	0.679[e]	0.773[e]	0.413[e]	0.591[f]	0.704[f]	0.788[e]	0.855[e]

Table 2.2 Parameter estimates of best approximating models for capturing PD by each distinctiveness measure and random choice (AVG), for 8 of 16 tips chosen. Variables are those included in the top BIC model for each species and significant at P < 0.01.

	ES	β	SE
ES	*u*	0.5407	0.0534
	γ	0.1419	0.0111
	l_2	4.3079	0.5633
	lc	-0.196	0.0175
FP	*u*	0.4566	0.0587
	γ	0.1089	0.0121
	l_2	0.236	0.5616
	lc	-0.9051	0.0248
PE	*u*	0.4344	0.0545
	γ	0.1067	0.0108
	l_2	4.7053	0.5634
QE	*u*	0.4832	0.0537
	γ	0.1284	0.011
	l_2	3.4899	0.5766
VW	*u*	0.4345	0.0541
	γ	0.1409	0.0108
	l_2	2.7524	0.5662
AVG	*u*	0.6023	0.0222
	γ	0.0924	0.0044
	lc	-0.4515	0.0603

β, coefficient; SE, standard error; *u*, intercept; γ, gamma

Table 2.3 Percentage of the 50 trees derived from empirical data, on which the measures achieved more than the upper 95% confidence limit of the expected amount of the tree captured (upper), within the confidences limits of the expected amount (Same), and lower the than the lower confidence limit (Lower). Table (a) when 25% species are chose, table (b) when 50% are chosen.

a)

Measure	Lower	Same	Higher
ES	8	4	88
QE	8	8	84
FP	10	6	84
PE	10	6	84
VW	12	4	84

b)

Measure	Lower	Same	Higher
ES	8	2	90
QE	14	2	84
FP	14	2	84
PE	8	2	90
VW	16	2	82

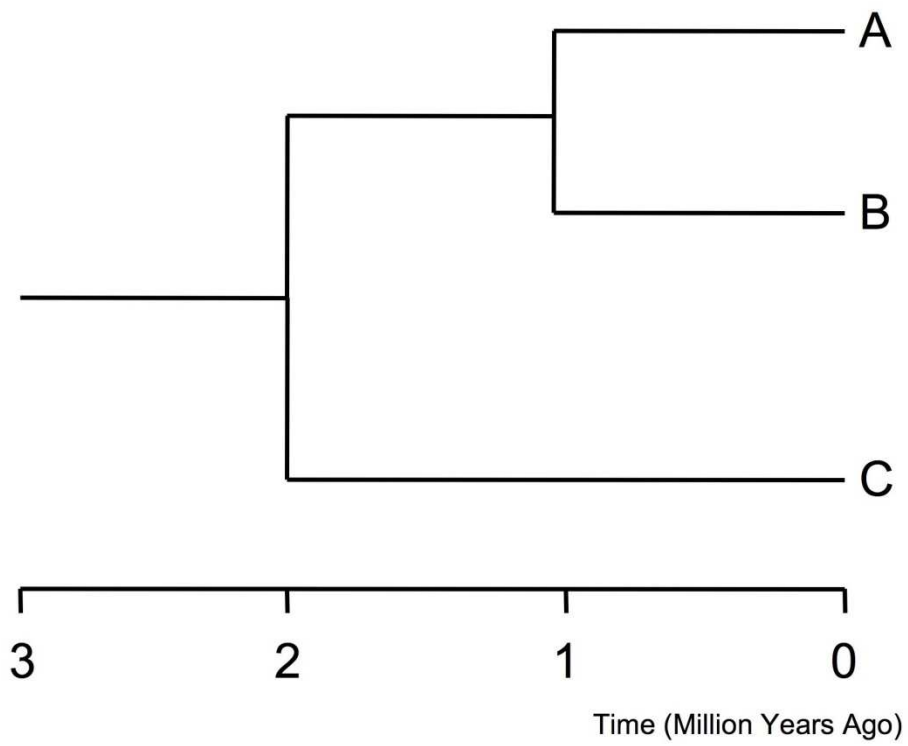

Figure 2.1 This figure shows a tree connecting a hypothetical group of species. The phylogenetic diversity (PD) of all the species is found by summing up the branch lengths in the tree, here 6 million years. The PD of a subset of species is found by summing up the branch lengths of the tree connecting those species and the root, for group AB it is 4 million years. In this paper we investigate how well species prioritizations based on simple indices capture the PD of the tree.

3: INCORPORATING EVOLUTIONARY ISOLATION INTO CONSERVATION PRIORITISATION[2]

3.1 Introduction

The most widely recognized system to determine the threat status of a species is the IUCN (World Conservation Union) Red List (Gardenfors et al. 2001). The IUCN Red List provides scientific decision-making guidelines with which to assign species into categories of threat based on threshold values of population parameters, such as range of occurrence and population decline (Mace & Lande 1991). The categories, indicating decreasing risk of extinction, are critically endangered (CR), endangered (EN), vulnerable (VU), lower risk/conservation dependent (LR/cd), lower risk/near threatened (LR/nt), and least concern (LC). Although it was not intended as a prioritization metric, the lack of a globally accepted alternative means that the IUCN Red List status or other threat status measures are often seen as being synonymous with conservation priority (Avise, 2005; Possingham et al. 2002). Categorizations used in this way assume that all species are of equal worth except for their threat status.

Species differ substantially in the amount of unique genetic information they embody (May 1990; Vane-Wright et al. 1991; Faith 1992; Crozier 1992). Several metrics have been developed to capture genetic variation (reviewed in

[2] This work was published as part of "Redding, D.W., Mooers, A.O., 2006. Incorporating Evolutionary Measures into Conservation Prioritization. Cons. Biol. 20, 1970-1978."

Diniz 2004). If species were ranked for conservation purposes based on these metrics, resources would be preferentially allocated to those species that embody disproportionately large amounts of unique genetic information above those with many close relatives.

May (1990) discusses the genetic value of species in relation to the conservation of tuataras (*Sphenodon* spp.). He cites a study by Daugherty et al. (1990) that suggests that there are two species of tuatara within the suborder Rhynchocephalia, the sister group to Squamata (the snakes, lizards and amphisbaenians, a group containing over 6000 species): these two tuatara species are thought to represent 0.3 to 7% of the unique genetic information found in both suborders (Vane-Wright et al. 1991). Until 1990 all tuatara were considered a single species (*Sphenodon punctatus)* that was “neither rare nor endangered” (Williams & Given, 1981). Prior to its recognition as a full species, the Cook Island Tuatara *Sphenedon gutheri* became extinct in one of only two sites where it occurred (Daugherty et al. 1990). The IUCN now ranks *S. guntheri* as vulnerable. There are, however, 100 species in Squamata and Rhynchocephalia with the same threat rank and 65 that are deemed more threatened.

However, if a prioritization system that explicitly incorporated genetic distinctness had been applied earlier to this species, it is likely the taxonomic uncertainty would have been resolved, perhaps preventing the loss of key populations. We propose and evaluate a potential prioritization system.

Meffe and Carroll (1997) suggest that evolutionary and ecological value should be the key components of any system that assigns conservation priority. Evolutionary importance, however, is difficult to quantify because of problems such as the difficulties in determining what constitutes “Evolutionary Significant Units” (e.g. Erwin 1991) and the relationship between phenotypic and genetic variation (e.g., see Diniz 2004). In our heuristic analysis, we applied the precautionary principle and sought to maximize genetic distinctness.

Promoting species for conservation priority based solely on high levels of genetic information would fail in the opposite way from that which led to *S. gutheri’s* demise by potentially ignoring those species in greatest peril (Possingham et al. 2002). However, by calculating the expected loss of genetic information for a group of species, which is the product of the probabilities of extinction and a value of genetic diversity, the two approaches can be combined (Witting, et al. 1994). We applied this thinking to the bird species on the IUCN Red List.

Little is known about how threat status and measures of genetic diversity are related. Previous work suggests that species with high levels of unique genetic information are more likely to be threatened (e.g. Purvis & Hector, 2000). This suggests that prioritization based solely on threat status may also capture genetic uniqueness, but the overlap between ranking species for their genetic value and by threat has yet to be quantified.

Therefore, we carried out a comparative assessment to determine whether threat status and expected loss of genetic information produce similar rankings of

taxa. We asked whether species in higher threat categories embody more genetic uniqueness, and how the rankings of bird species are different if they are ranked by a prioritisation metric that combines statues and genetic value, as suggested by Witting et al. (1994), as opposed to one based on their threat status alone.

3.2 Methods

Following von Euler (2001), we used Monroe & Sibley's (1993) 13-level taxonomy of 9702 bird species to estimate the shape and branch lengths of the evolutionary tree for the global avifauna. Node ages were estimated using a calibration factor of ΔTH_{50} 1.0 = 4.7 MY (Sibley & Ahlquist 1990), which is consistent with a hypothesised Eoaves-Neoaves split at ~130 MY (Cooper & Fortney 1998; for alternative dates see e.g. Feduccia 1995). The tree was produced from a manual analysis of the taxonomy. As this is a heuristic analysis the Sibley and Monroe based tree was considered appropriate due to its relative simplicity and wide taxonomic coverage.

Each species in the tree was allocated a threat status category from the IUCN red list (downloaded from the www.redlist.org). We used only the major threat categories, with the three lower risk/conservation dependent and all lower risk/near threatened species condensed into the lower risk category, which left us with five categories in total: CR, EN, VU, LR, and LC. We designated any species classified as CR, EN or VU as threatened and any LR or LC species as unthreatened. We used Avibase (LePage 2003) as a reference to resolve categorization disputes due to name changes. Species from the 9702 in the

Sibley and Monroe taxonomy that were extinct, extinct in the wild, data deficient or taxonomically uncertain (156 species) were excluded from the analysis, and the final data set contained 9546 species, of which 1090 were categorized as threatened.

3.2.1 Assigning Extinction Probabilities to Threat Categories

The threshold probability of extinction (criteria E) can be used, under the IUCN Red List Guidelines, to assign species to the three threatened species categories (Mace & Lande 2001). Species that have a predicted probability of extinction p_e > 0.5 in 10 years are designated CR; those with p_e >0.2 in 20 years are designated EN, and those with p_e >0.1 in 100 years are designated VU. Ideally, extinction probabilities are estimated for each species based on a standardized approach, such as population viability analysis (PVA). In anticipation of future precision and to allow quantitative comparisons among species in the absence of such data, we used the criteria E value to assign p_e values to each bird species.

To do this, we first extrapolated the extinction probabilities to a common timescale (here, 100 years). Because such extrapolations are problematic (Kindvall & Gärdenfors 2003), we also calculated values of p_e for categories CR and EN based on published p_e data derived from full PVAs (O'Grady et al. 2004). We compared these values to our extrapolations. There was an average of 12 bird-species values for the CR and EN categories, always at the 100-year time frame. For the EN category the p_e value was qualitatively very similar to the extrapolated p_e calculated by assuming extinction risk remains constant over 100

years (mean 0.315 vs. extrapolated 0.328), and for CR the mean probability of extinction value suggested that a lower score was more appropriate (mean 0.786 vs. extrapolated 0.999). The category VU has a designated criteria E value of 0.1 over a 100-year period, so there was no need to extrapolate.

For LC species there is no associated p_e value in the IUCN guidelines. Therefore, we hypothesized that approximately 0.01% or 7 out of the ~7000 LC species will go extinct within 100 years. This seems a reasonable estimate because over the next century the extinction rate could be 10 times higher than the current rate (Pimm et al. 1995) and because over the previous 100-year period approximately two previously abundant species became extinct (*Ectopistes migratorius*, *Conuropsis carolinensis*).

Finally, we fit a power curve ($y=0.007x^{4.1234}$, $R^2 = 0.999$) to these four probability measures to interpolate a p_e for the LR category, which assigned LR species a p_e of 0.02. Our measures are heuristic only; the approach we apply below can be used for any set of species with associated p_e values. It also possible to perform a sensitivity analysis to measure the effect of assigning different probability values to the categories. This would be an important step if a system, such as the one we suggest, were put into practise.

3.2.2 Assigning Species Evolutionary Isolation Values

Based on the average age of each taxonomic level (Sibley & Ahlquist 1990), the global evolutionary tree of avifauna contains approximately 79.9×10^9 years of evolution history (EH; Nee & May, 1997). We apportioned this history

among all the species, based on their position in the tree, with an equal-splits approach (see Chapter 1.2.1):

$$\mathrm{ES} = \sum_{j=1}^{r} \frac{B_j}{\prod_{k=1}^{j} (d(k-1)-1)} \qquad (3.1)$$

where j is the internal node on direct path from i to the root (r), B_j is the edge length from internal node j to j -1, and $d(k)$ is the degree (3 for bifurcation, one edge entering plus two leaving) of node k.

The equal-splits approach divides the evolutionary time represented by a branch equally among its daughter branches. The sum of the equal-splits value from every taxonomic level is the estimated amount of evolutionary time each species embodies (Fig. 3.1). This measure reflects how evolutionarily isolated a species is and therefore approximates how genetically distinct it is from the other species in the tree.

Our measure differs from calculating PD (Faith 1992) and GD (Crozier 1992) for a single species. A single species value for PD for a species is calculated either as the distance from the species to the root, which is the same for all species, or its age, or pendant edge value (Altschul & Lipman 1990) i.e. the length of the branch from the tip to where it joins the tree. Our measure distributes the whole tree among its entire constituent species. Under a simple model of tree production (Hey 1992), equal-splits values are positively correlated with pendant edge (PE) scores (Spearman's correlation coefficient, $\rho = 0.71$, $p<0.05$; 100 16-taxa trees) [see chapter 1]. This correlation is not perfect, and

shows that these two measures incorporate different information. Clearly, where the species joins the tree is a key factor in determining its equal-splits score, but the value also depends on the length of all branches between it and the root, and the number of species that share those branches with the focal species at each node.

Indeed, this is its strength. More of the total evolutionary history of the clade is apportioned to those taxa that have long pendant edges, are members of species-poor clades, and that diverged from the tree nearer its root. The equal splits measure captures more information about how isolated that species is on the tree, weighing more isolated species more highly. In this way, it takes into account the evolutionary redundancy present in the surrounding tree, giving greater value to species whose genetic history is not shared with many other species. The measure also apportions the entire tree uniquely among its tips, such that the sum of the equal-splits measure across the tips equals the total phylogenetic diversity of the tree (Pauplin 2000; Semple & Steel 2004). For the global avifauna the distribution of equal-splits scores is highly skewed and could not be normalized using any common transformation. Therefore it was used in this analysis in an untransformed state.

To test how evolutionary isolation and threat are related, we used Monte Carlo simulation, a nonparametric approach that uses resampling with replacement (in the Poptools program; Hood 2003). We created a distribution, based upon 10000 random samples from all 9546 bird species, of the summed equal-splits values from 1090 species to estimate the population mean μ and

variance σ^2. This group size corresponds to the total number of species from the categories CR, EN, and VU. The null hypothesis is that any difference between the sum of the equal-splits values observed in the 1090 IUCN threatened bird species and the estimated population mean is due to chance. Therefore, the number of samples taken that exceeded the observed total seen in threatened species, can be divided by the number of replications (in this case 10000) to give a “true” probability of the likelihood of the observed value occurring by chance.

We also modelled the distribution of species within the threatened (VU and worse) and non-threatened (LR & LC) categories by applying a logistic regression with equal-splits as the covariate (see Purvis & Hector, 2000). This was done to test whether a logistic model containing equal-splits adequately described whether a species was designated as threatened or not, and therefore to assess the strength of the relationship between threat status and evolutionary isolation.

We then created five more distributions (again *n*=10000) for total equal-splits in groups of species the same size as each of the five IUCN categories (158, 291, 641, 716, 7740). Using the same assumptions, we calculated how many samples exceeded the observed amount of summed equal-splits values, seen in each threat category, with the null hypothesis that any variation was due to chance.

To see how equal-splits compared with a measure previously used to assess the relationship between evolutionary isolation and threat (family species richness; Purvis & Hector, 2000), we compared our results from the above tests

to those based on family species richness. We first tested for a correlation between equal-splits and family species richness and then repeated the resampling tests above with family species richness instead of equal-splits values.

We created a null distribution, with 10000 samples, of the average size of families to which 1090 randomly drawn species belong, reapplying the Monte Carlo method we used the for equal-splits measure. From this distribution we can determine how often values the same as or greater than the average family species richness for all 1090 threatened species occurred, and therefore the probability of this value occurring by chance. We then modelled the distribution of species within the threatened and non-threatened categories with a logistic regression, this time with family species richness as the covariate (see Purvis & Hector, 2000).

Finally, we created five additional distributions (n=10000) for average family species richness in groups the same size as each of our categories (158, 291, 641, 716, 7740) and used the same assumptions tested to see if family species richness in each of the individual categories was significantly different from the estimated mean.

3.2.3 Incorporating Evolutionary Values into Conservation Prioritization

The species-specific expected loss of evolutionary history (EL) was calculated using an equation modified from one used to determine expected loss

of evolutionary history for groups of species (Witting & Loeschcke 1994; Weitzman, 1998):

$$\mathrm{EL} = ES_i \bullet Pe_i \qquad (3.2)$$

where ES_i is the evolutionary history embodied by species *i* and Pe_i is the probability that the species *i* will become extinct within the time frame of interest.

All species were then ranked by expected-loss and again separately by IUCN threat category. We compared the two rank orders to determine the percent overlap in species at five different points in the rank sequences. These points were the first 158, 449, 1090, and 1806 species, corresponding to the group sizes of CR, CR and EN, all threatened species, and threatened and LR species. Finally, we used two cumulative distributions of evolutionary-history values (expected-loss and threat) to determine the difference in history captured at the same five points in the ranking sequence.

3.3 Results

The avian tree is highly imbalanced (von Euler 2001) and as a result species-specific phylogenetic diversity is highly skewed, with the 73% of species having values lower than the mean (Fig. 3.2). The mean is 8.319 million years (MY) (SD = 4.79 MY). *Strutho camelus* (Southern Ostrich) had the highest value, 92.31 MY, due to its basal and monotypic status.

Threatened species collectively embodied more evolutionary history than expected by chance (Monte Carlo, n=10000, p<0.001). This relationship did not

seem to be influenced specifically by any of the threat categories (i.e., CR, EN, VU; Monte Carlo for the three subsamples n=10000, all p>0.05).

Equal-splits significantly but poorly predicted whether a species was threatened or not (logistic regression, pseudo r^2 = 0.01, p<0.05). Although there was more evolutionary history embodied by threatened species than expected in a group that size, the difference only represented a 3.8% increase over the population mean or 348 MY (0.4% of the phylogenetic diversity of the entire tree) more evolutionary history in threatened species than expected.

As a point of comparison, if the most threatened species had the highest ES scores, giving a perfect positive correlation between level of threat and evolutionary history embodied, then there would be 20939 MY more evolutionary history in the 1090 threatened species (a 229% increase over the mean) than the evolutionary history in 1090 species chosen at random.

Family species richness was a different but related measure to equal-splits (Spearman's correlation coefficient, ρ = 0.196, p<0.001). The weak positive correlation suggests the two measures do capture different information. Threatened species came from smaller families (Monte Carlo, n=10000, p<0.001) and again this was not influenced by any particular threat category (Monte Carlo, n=10000, all p>0.05). Family species richness also significantly but poorly predicted whether a species was threatened or not, giving qualitatively similar results to equal-splits (logistic regression, pseudo r^2 = 0.01, p<0.05).

Because ranking by expected loss incorporated IUCN threat status, the two systems identified broadly similar sets of species. Of the 1090 threatened

species, 1086 were captured in the first 1090 species ranked by equal-splits (the missing taxa were the vulnerable species *Nectarinia thomensis, Turdus celaenops, Turdus feae, Turdus menachensis*).

Ranking by expected loss did, however, order species differently. The addition of ES is expected to create a large difference if the correlation is weak and ES has reasonable variance. Indeed, there were only 68 species common to both the first 158 species ranked by threat (the CR species) and the first 158 ranked by expected loss. Ranking by expected loss chose 40% more total evolutionary history in the first 158 species, but only 2% more in the first 1090 species (Fig. 3.3).

3.4 Discussion

We considered how to incorporate a value of worth into conservation prioritization in order to help to direct conservation action toward important species. An example of a potentially important species is the Plains Wanderer (*Pedionomus torquatus*). This species and 270 others are considered the 159th most important for conservation action according to the IUCN Red List. As the sole member of the family Pedionomidae, however, its equal-splits score is 53.6 MY of evolutionary history (compared with the average 8.139 MY). If this species' evolutionary history "value" is incorporated in the prioritization approach with the expected-loss calculation, the species moves up 140 places to the 19th species most in need of conservation action.

Ranking species by the expected loss of genetic distinctness incorporated 40% more evolutionary history in the first 150 species when compared with ranking by the expected loss of species (i.e. the IUCN Red List). The two ranking approaches shared 99.6% of the first 1090 species, meaning that ranking by expected loss changed only the order of the threatened species. Importantly, conservation efforts will still be concentrated on largely the same cohort of species if they are applied based on our rankings.

Although threat and evolutionary isolation are related, there was a large increase in the amount of genetic information captured in the first 150 species when prioritising all species with a metric that included evolutionary isolation and threat, as opposed to the one that contained only threat. This occurred because only an estimated 1% of the variation in the distribution of species within threat categories was explained by equal-splits values or species per family. This means threat is a poor surrogate for conserving phylogenetic information and needs to be considered as a separate component when prioritising species.

Measures of evolutionary isolation

The U.S. Fish and Wildlife Service is one of few prioritization bodies that already assess species evolutionary isolation when allocating resources. They use a system which, after a species has been awarded a score based on its threat status, gives a secondary score of 1 point to members of monotypic genera, 0 points to full species and minus 1 point to subspecies. The final result is an overall Species Listing Score that determines where each taxon will enter the Endangered Species List relative to the others already listed.

This measure is designed to be simple to apply (Andelman et al. 2004) and is essentially a categorical estimate of a taxon's pendant edge value. Thus, this score is influenced by the shape of the tree toward the tips and does not take into account how close to the base of the tree the taxa are rooted. This distinction can be seen in the Kiwi family (Apterygidae), which, with around five species, is not monotypic. Under the U.S. system, they would not receive any increased priority, despite the fact that they are genetically (and phenotypically) distinct from the majority of other bird species (May 1991).

Family species richness, as considered in this study, is another simple measure of evolutionary isolation. It offers more differentiation than the U.S. system, but again the overall shape of the family subtree, or its position relative to the root, has no impact on an individual species' score. If all 9546 bird species were ranked by their family species richness in ascending order, the five Kiwi species and 10 other taxa would rank as the 108th most evolutionarily isolated.

The equal-splits measure we propose captures different evolutionary "information" when compared to family species richness, and although correlated, it has the potential to take into account the shape of the entire tree. With the equal splits measure each Kiwi species receives an evolutionary history value of 28.34 MY; equal to the 61st highest equal-splits value out of all species. The equal-splits score also has the advantage that it can be widely applied across taxonomic groups because it is measurable for both phylogenies and taxonomies. It is, however, measured from a particular root (here the root of the

bird clade) and therefore is relative to the other species being considered, rather than being an absolute value.

Results of several studies show how measures of evolutionary isolation respond to tree shape. These measures when independently applied to the same clade give different levels of interspecies variation and contrasting weights to “basal” species and “pendant” species (Pavoine et al. 2005). Rao (1982) states that the key properties of evolutionary isolation measures are their straightforward calculation and applicability to less studied groups. Studies are needed to investigate the properties of such measures and how these correspond to the needs of the conservation community.

Combining Evolutionary Isolation and Threat

In many countries (e.g. Species at Risk Act – Canada, Wildlife and Countryside Act – UK) there is strong link between threatened species lists and conservation legislation (Possingham 2002). Therefore, either the individual listing procedures used in such legislation need to be altered in scope to incorporate other values deemed important by the scientific community, as the US system adjusts a species listing priority number by its degree of taxonomic isolation, or a widely-adopted approach of prioritising species needs to be developed and put into practise.

A prioritisation system, analogous to the US approach, but instead building upon the framework of the widely-used IUCN threat listing protocols, could use a threshold of expected-loss as one of many criteria to assign species into categories of conservation importance. This would ensure that species with more

than an acceptable level of expected-loss are entered into priority categories above the level that would be assigned by population parameters alone.

A key implementation problem of using an approach that uses broad categories, as shared with the U.S. system, is that there are only a few levels of conservation concern and therefore large numbers of species with equal priority. Another potential drawback is that this prioritization system would only increase the number of species considered worthy of protective measures and not downgrade those species with many close relatives.

The quantitative approach we used to create a prioritization metric (expected-loss) is separate from but integrates threat status. It has the functional benefit that it reflects the true distribution of the input variables (i.e., very isolated species receive much greater priority than moderately isolated species). It also produces a ranked order of species, rather than several groups with equal priority, and the combined quantitative values create understandable units (millions of years of evolutionary history that are expect to be lost in 100 years) rather than just a combined rank score, such as the listing priority number.

By reflecting the distribution of the input variables accurately expected-loss is highly sensitive to the shape of variable's distribution, unlike the listing system used by the U.S. Fish and Wildlife Service. Our results showed that most species with high equal-splits values are in the LC and LR categories (85.3% of the upper 10^{th} percentile), but only a few of these have moved above the rank of any threatened species. This is because the LC, LR, and VU categories were, coincidently, given p_e values with approximately the same difference in

magnitude as between the highest and lowest equal-splits scores for all species. Therefore, ranking by expected loss as we have implemented it can only affect the intercategory order for most species within LC and LR. Whether this is a desirable characteristic is uncertain, and more work is needed in assigning p_e values to individual species.

Unlike this analysis, previous example systems to combine threat and evolutionary isolation measures (Weitzman 1998, Avise 2005) were based on very small groups of species (15 and 4 respectively) for which large amounts of detailed information was available. Avise (2005) suggests a mechanism which sums, for each species, the weighted ranks of five different criteria (rarity, distribution, ecology, charisma, phylogeny), and both studies advise that prioritisation measures need to take into account the economic feasibility of conserving chosen species. These studies offer a possible path to develop our prioritisation measure; however, it is important such measures are simple enough to be applicable in data-poor species groups to ensure the widest taxonomic relevance.

3.4.1 Conclusion

Our study represents an initial step toward developing and incorporating a value of evolutionary importance into a species prioritization approach. We showed how threat status can be used, not as the only measure of conservation importance, but as a way to focus conservation attention on the important species we identified. We note here that Isaac et al. (2007) presented a measure which is simply the logarithm of ‘expected loss’, but using the Fair Proportion

rather than the Equal Splits measure (see chapter 1). This is the basis of a major conservation initiative by the London Zoological Society called the EDGE of Existence programme (www.edgeofexistence.org), to which we are contributing (see also Chapter 4).

However it is incorporated, and whichever measure is used, it is imperative that this accessible and valuable information be included in conservation prioritization efforts. It seems inadvisable to risk the loss of large amounts of evolutionary history by waiting until valuable species have become highly threatened before conservation action occurs. Conservation science is working hard to understand the odds we are betting with; it also needs to consider the value of chips being held.

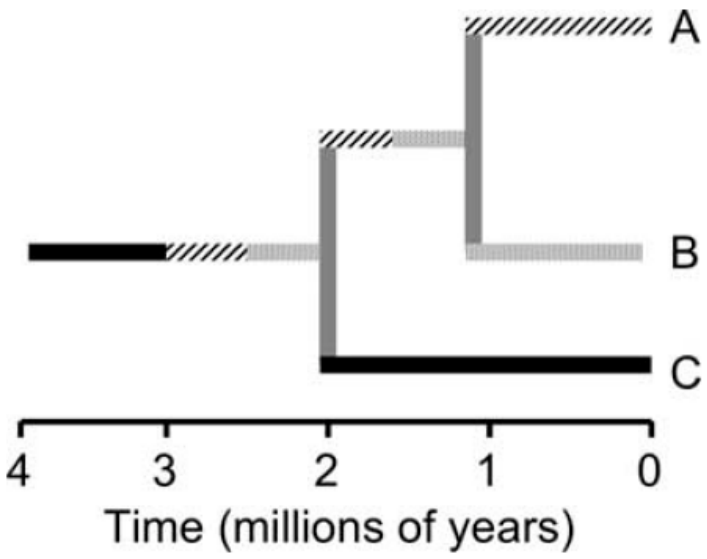

Figure 3.1 The equal-splits approach is used to apportion the total EH (Nee & May, 1997) of this tree (7 million years) among the three constituent species in the tree (A, B and C). The branch that represents the common ancestor to all three species from 4 MY to 2 MY ago is divided equally among clade (AB) and clade C, and therefore each group is awarded 1 MY. The branch for the common ancestor of (AB) is divided equally between A and B, awarding each 0.5 MY. Summing these with their individual branch lengths, the equal-splits value for species A is 2 MY, for species B, 2 MY and for species C, 3 MY. The sum of these values equals the total EH of the clade.

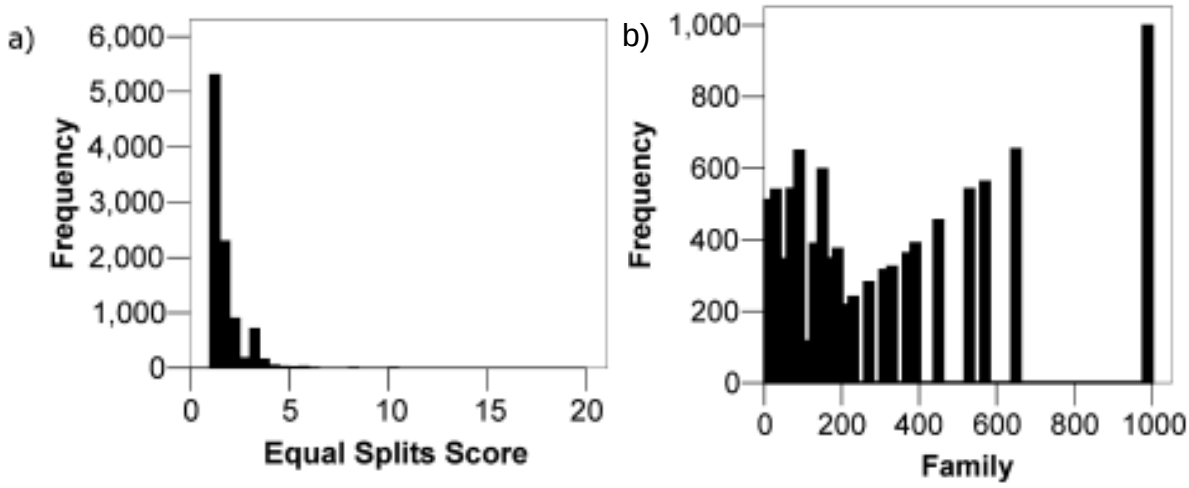

Figure 3.2 Frequency distributions of (a) the equal-splits scores and (b) family species richness for 9546 bird species. The y-axis for both graphs is log10 transformed.

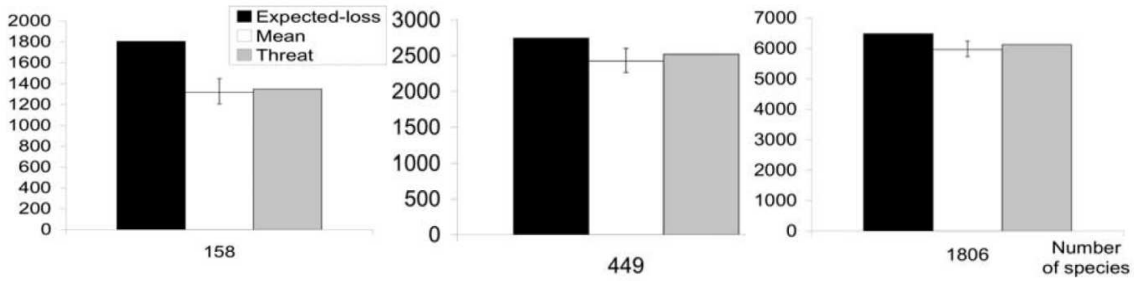

Figure 3.3 Total evolutionary history represented using different ranking metrics. The black bar in each chart, e.g. left handmost panel, represents the summed equal-splits scores, a measure of embodied evolutionary history, of the top (here, 158) species when all 9546 birds species are ranked by their expected-loss of evolutionary history. The grey bar represents the summed equal-splits scores of the top (158) species when all 9546 birds species are ranked by their how threatened they are, with the most threatened first. The white bar represents the average summed equal-splits scores of the same number of species (here, 158) chosen at random from the total pool, from 10000 resamples with replacement. Error bars represent 95% confidence limits. The numbers chosen are equal to the all the critically endangered bird species (left panel), all the critically endangered plus endangered species (middle panel), and all the critically endangered, endangered, vulnerable, and lower risk/near threatened species (right panel).

4: EVOLUTIONARY ISOLATION, THREAT STATUS AND ECOLOGICAL ODDITY IN PRIMATES[3]

4.1 Introduction

If this is the era of conservation triage (Marris 2007; Bottril et al. 2008; Joseph et al. 2009), then threatened species must be differentiated from each other so that the most important species can be attended to first. Attending to species on the basis of threat status is inefficient and risks "unnecessary extinctions" (Joseph et al. 2009). Therefore, a prioritization system is needed that can objectively assign values to species. The London Zoological Society's EDGE program (evolutionarily distinct and globally endangered) (Isaac et al. 2007; see also Redding & Mooers 2006) offers such a system. The program ranks species on the basis of their global threat status, taken directly from the International Union for Conservation of Nature (IUCN) Red List rankings (Mace & Lande 1991), and their evolutionary isolation to prioritize "those species that are both endangered and evolutionarily distinctive" (www.edgeofexistence.org).

The EDGE approach is comparable to the project prioritization protocol (Joseph at al. 2009), which uses a greedy algorithm to objectively select the optimal group of species that minimizes potential future extinctions within a fixed budget and maximizes taxonomic uniqueness if every selected species is

[3] This paper is to appear in Conservation Biology: "Redding, D.W., DeWolf, C. & A.O.Mooers. In press. Evolutionary isolation, threat status and ecological oddity in primates. Conservation Biology". I supervised Mr. DeWolff closely in data collection and also gathered much of the ecological data myself, and I did all the analyses and wrote the paper.

conserved. The EDGE listing procedure differs from the project prioritization protocol by being a two-stage procedure. First, a single, ranked EDGE list is published and those species that are receiving the least amount of attention from current conservation initiatives are selected as “focal species” (Isaac et al. 2007). Second, funds gathered primarily from private sources are allocated preferentially to these focal species, with the number of species allocated resources depending on the amount of funds gathered. The current EDGE process includes objective and subjective aspects; thus, it can be flexible to changes in the threat status of focal species.

The measure of evolutionary isolation in the EDGE score, evolutionary distinctiveness (ED), is one of a family of such measures (e.g., Vane-Wright et al. 1990; Crozier 1992; reviews in Pavoine et al. 2005; Redding et al. 2008). By assessing one clade at a time (e.g., order Primata), we used EDGE measures to preferentially rank those species within that clade that have fewer or more distant relatives. High-ranked species are candidates for higher conservation priority because they have potentially more unique genetic information (Redding & Mooers 2006), but they also have fewer close relatives and therefore less redundancy in the genetic information they contain.

Some suggest that species with high EDGE scores stand out as being unusual with respect to the other species in their clade (for a list of examples see appendix A). For example, the platypus (*Ornithorhynchus anatinus*) has a high EDGE score and is very unusual. The platypus is an egg-laying, teatless, cold-blooded (32 deg.) animal with poisonous spurs and a remarkable genome

(Warren et al. 2008). It is part of a small clade (it and four species of Echidna) that is the sister group to all (roughly 5400) other species of mammal. Although it seems justifiable to consider the platypus as an irreplaceable component of biodiversity, it is unknown whether it is representative of high species with high EDGE species.

If species with high EDGE scores are generally odd, where we define *odd* as absolute distance from the average phenotype (or in the case of categorical data, species that populate categories with few members), then a selection of species with the highest EDGE scores should represent a disproportionally broad set of biological characteristics from the overall group. Given that they are all threatened, their imminent extinction would therefore result in a large loss of character diversity.

Character diversity itself is a valid measure of biodiversity (Faith 1992; Hector & Purvis 2000). However, if evolutionarily distinct species have odd morphologies and such odd morphologies are associated with rare ecological roles, then groups of species with high EDGE scores may have increased functional importance (for related work with communities see Cadotte et al. 2008; Cadotte et al. 2009). Conversely, if evolutionarily distinct species express predominantly relictual characters, then Erwin's (1991) contention that species isolated on the tree of life are relictual is true and such species may therefore offer little to future evolutionary potential.

We first tested, solely within Primates, for an overall correlation between EDGE score and biological oddness, as well as the correlations between EDGE's

two components (distinctiveness and endangerment) and oddness. We then determined whether the traits represented when choosing threatened and evolutionarily isolated species were likely to resemble those traits attributed to ancestral primates (i.e., whether the most threatened evolutionarily isolated species were generally relics).

4.2 Methods

From a variety of sources, we collected as much physical, ecological, and reproductive data as possible on the world's 233 primate species (Wilson & Reeder 1993) (see Supporting Information for variables and references). We used this older taxonomy because it was used to create the EDGE list, although more recent taxonomies include many more species (e.g., Groves 2001 [350 species]; Rylands & Mittermeier 2009 [424 species]). For each data point (e.g., adult male body mass for *Gorilla gorilla)*, if there was more than one source the mean of the values was used. From approximately 85 data variables, those variables with <50% coverage of species or over 70% correlation with any other variable were removed leaving 20 variables that we treated as independent in the final data set. For correlations, the variable with the highest average correlation coefficients over all other variables was the one removed. Finally, we discarded species that had no EDGE score (Isaac et al. 2007) (i.e., they were "data deficient" according to the IUCN Red List (IUCN 2009), which left 217 species in our final data set.

For the 15 continuous variables, we transformed scales to remove the effect of outliers (e.g., by log transformation) and then calculated the absolute

distance of each species' score to the median score for that variable (Fig 1a). For each of the five categorical variables, the value assigned to a species was the frequency of that category in the entire data set. So, for example, if we had a categorical data variable "coat color" that contained 100 species and 75 species had brown coats and 25 had black coats, the brown primates would all be given a value of 75 for that category, representing the frequency of brown coats across the data set, and, similarly, the black-coated species would be given a value of 25.

We then tested for a correlation (using cor.test; "base" package in R language) for each of the 20 variables between our statistical approximations of oddness and each species' EDGE score (Fig. 1b). A negative correlation coefficient for categorical data variables indicated a positive relationship between oddness and EDGE score. Because our correlations do not correct for phylogenetic relationships amongst the tips, the *p*-values we report should not be seen as tests of the general hypothesis across other clades. As well, because we repeated the same test over 20 variables, the *p*-value for a single test does not provide a valid probability of committing a type 1 (false-positive) error. Therefore, we used the false discovery rate to adjust the *p*-values so they would take this into account (p.adjust; "stats" package in the R language; Benjamini& Hochberg 1995). This procedure accounted for the number of false-positive hypotheses that would be accepted with raw *p*-values, given a predefined significance (alpha) value (in this case 0.05). This procedure ranked all the observed *p*-values from each test and, working from the largest value down, accepted the null hypothesis

only for those tests where $p \geq k \times \alpha/n$, where k is the rank of the p-value, α is the chosen level of significance, and n is the number of p-values considered (Garcia 2004).

To estimate the relationship between oddness and EDGE score over all 20 variables, we calculated the mean correlation coefficient and a combined p-value with the Stouffer method (Whitlock 2005), which weighed the input values from each of the 20 independent tests on the basis of their sample size to give greater weight to correlations with more data points (Hunter & Schmidt 2004). Last, we repeated all the analyses with the infraorder Lemuriformes removed to ensure the relationship was not entirely driven by this geographically peripheral, endemic clade (Spathelf & Waite 2007)

To assess whether traits represented by species with high EDGE scores were more likely to be ancestral, we attributed values for 7 of the 20 variables to two hypothesized ancestral species (*Dryomomys szalayi* and *Ignacius clarkforkensis*) on the basis of recent fossil finds (Bloch et al. 2007). These species are members of the Plesiadapiformes, which are thought to be “stem primates” and thus to express characteristics that we expected to be exhibited by the ancestor to modern-day primates (Bloch et al. 2007). The seven traits were the variables that could be reasonably inferred from the fossil record: diet (from teeth shape), mass, length to mass ratio, tail to body length ratio, diurnality, terrestiality (mostly arboreal or mostly terrestrial), and habitat (Forest or savannah-scrub). We scored a species as ancestral if it was placed in the same (e.g., diet) category as the ancestral species or, for continuous variables, if it was

in the closest 15% of species when all species, including the ancestral ones, were placed in rank order by that variable. To test the sensitivity of this 15% value we repeated the procedure three more times coding the closest 5%, 10%, and then 20% of species in rank order as ancestral for the continuous variables. We then tested for a correlation (using cor.test; "base" package in the R language) between each species' ancestral score (ranging from 0, no ancestral traits, to 7, all traits ancestral) and its EDGE score.

4.3 Results

Overall, primate species' EDGE scores were positively related to trait oddness in 18 of the 20 variables and were significantly positively related to oddness for half of them (10 out of 20; Table 1). When all 20 tests were combined, the global result was a highly significant positive correlation (mean correlation = 0.14, $p=1.74\times10^{-14}$). The mean correlation of only the variables with significant, adjusted *p*-values was more strongly positive (mean *correlation* = 0.36). Lemuriformes did not drive this relationship because the patterns seen were very similar when they were removed (Table 1; combined $p=4.3\times10^{-13}$).

Geographical traits were most significant (100%) and were followed in decreasing order by behavioral and ecological traits (50%), morphological traits (40%), and reproductive traits (25%) (Table 1).

Primate species with high EDGE scores did not appear to be more likely to express ancestral characters than low-scoring species because there was no relationship between the ancestral character score and EDGE score (Pearson product correlation coefficient $\rho=-0.003$, $n=217$ $p=0.96$). Using other cut-offs

(5%, 10%, 15%, and 20%) to categorize species for the continuous variables as ancestral or not produced very similar results (*p* value range: 0.92-0.98).

When analyzing ED (evolutionary distinctiveness) and GE (threat) separately for 13 of 20 variables, oddness was significantly correlated to ED (mean correlation = 0.13, combined $p=3.13\times10^{-27}$), whereas oddness was significantly correlated to GE for only 3 of the 20 variables (Table 2). There was a noticeably lower mean correlation coefficient for GE as well (mean correlation = 0.07), although the combined *p*-value was still strongly significant ($p<0.001$).

4.4 Discussion

For a large proportion of the traits we examined, we found a positive relationship between a primate species' EDGE score and how far it is from the average morphological and ecological phenotype. Therefore, our approach to conservation evaluation prioritized a sample of the most evolutionarily isolated and threatened primates for conservation attention and captured a larger-than-expected proportion of the total ecological and phenotypic variation in the clade.

If we accept that "ancestral" species might be less likely to contribute to future evolutionary radiations (Erwin 1991), then the EDGE ranking approach would have proven undesirable if, by choosing primate species with high EDGE scores, it had preferentially selected relictual species.. If species with high EDGE scores harbor remnant ancestral characteristics, they may still be unusual compared with the rest of the clade. We found no strong tendency for species with high EDGE scores to have "ancestral" characteristics, which suggests they

possess both rare and derived characters. There is no evidence yet, therefore, that these species are less likely to contribute to the future ecological landscape.

It is logical to ask how the two components of EDGE interact to produce the positive relationships we report here. As ED and GE are uncorrelated in primates (ED to GE correlation; r = 0.001, *n*=219, *p*=0.89), one might expect that for each of the traits we used in our analysis either ED or GE would drive the correlation with overall EDGE score. This proposition appears to hold generally (Table 2). Considering only the 10 traits that were significantly and positively correlated to EDGE, the ED score drove the relationship between trait oddness and EDGE score for seven traits: female mass, group size, latitudinal midpoint, gestation duration, activity period, population density, and solitariness. This relationship between trait oddness and ED is consistent with results from a few studies that show species in smaller taxonomic groups, compared with more species-rich groups at same taxonomic level, are found on the edge of multidimensional ecological and morphological space (Ricklefs 2006; Latiolais et al. 2006; Magnuson-Ford et al. 2009).

Threat status by itself was correlated to just 2 of the same 10 traits: geographic range and body shape (defined here as the residuals of a body mass - body length regression). Geographic range size is relatively straightforward to interpret. Small range species are listed as threatened on the basis of their range size (Mace & Lande 1991), whereas species with large ranges are more likely to be affected by human encroachment (Blackburn & Gaston 2002; Cardillo et al. 2005). As for the latter correlation, we can think of no obvious mechanism that

explains why primates with odd weight-to-size ratio (i.e. long with low mass or short with high mass) were at a higher risk of extinction. Particular body shapes could be associated with habitats (e.g., tall primary forests) that are more affected by human activities, but this remains to be tested.

"Distance to center of continent" was significantly related to both threat status and evolutionary isolation: species that were more threatened or that had fewer close relatives tended to be geographically peripheral. Although vertebrate threat status is unevenly distributed globally (Grenyer et al. 2006), our results are the first to suggest that in some clades it may also be distributed toward a more-encompassing clade's range edge. Potentially, the positive correlation between threat and distance to the center of the clade's range is explained by preferential human development on coastlines. This relationship also may be affected by the observations that geographic range size gets smaller toward continental edges (e.g., Gaston 2003) and that smaller range species are more likely to be listed as threatened (Mace &Lande 1991). Primates with high EDGE scores were also more likely to be found on the geographical edge of the continent on which they occur. Ricklefs (2005) suggests that such peripheral, evolutionarily isolated patterns may hold for passerine birds as well. This variable could act as a mechanism to drive some of the relationships we saw between EDGE score and the traits we tested in primates. If primate groups with higher average scores of evolutionary distinctiveness are geographically peripheral compared with their encompassing continental clades (e.g., macaques in Africa and tarsiers in Southeast Asia), they may also have developed unusual traits to survive and

reproduce in habitats and seasonal regimes that are rare for the group as a whole.

The patterns we discovered need to be tested in other groups (see, e.g. Magnuson-Ford et al. 2009). Primates are somewhat restricted geographically and in their use of habitat (i.e., they are dominated by dwellers of tropical forests). These factors make it difficult to generalize all our findings to other mammal groups. For instance, we do not know if clades with pole-to-pole latitudinal distributions will have the same relationship between ED score and distance to the centre of the continent. We can think of no obvious reason, however, why the evolution of traits in primate species should be different overall from those of any other mammal group.

All geographic variables were significantly related to EDGE score, whereas only one of the reproductive traits was. This result was unexpected because reproductive traits often map well onto species phylogenies, whereas geographical traits do not (e.g., Gaston 2003). However, whether or not a trait is strongly heritable is irrelevant to whether isolated species have unusual characteristics. Even with a very strongly inherited trait, the most unusual values could be common to all the members of a small clade within a “bushy” (and therefore low-ED-scoring) part of the candidate tree.

The consensus for the variables studied here is that primate species with few close relatives are morphologically, ecologically and behaviorally different to those with many. This finding, if found in subsequent analyses of other groups, may provide support for the suggestion that phylogenetic branch lengths can

approximate gross phenotypic differences between species (Faith 1992 2004). The frequency by which such a relationship is detected in other taxa will depend on how well the topology of phylogenetic trees reflect the 'true' evolutionary relationships amongst species and, more generally, whether branch lengths measured as the expected number of base substitutions separating species within many different (often mitochondrial) genes correlate similarly to the phenotypic differences between species. A strong and consistent relationship would be useful from a conservation perspective, potentially allowing us to select a subset that maximizes the gross phenotypic diversity amongst a set of species.

Sets of primates that have high ED scores not only represent more biological diversity (the present study), but also represent a greater than expected proportion of the tree from which they are sampled (Redding et al. 2008). That is, as a collective, such species embody both higher than expected phylogenetic (Faith 1992) and ecological diversity. These two findings are interesting in light of a proposed "ideal" framework for conservation-evaluation ranking that includes a measure of phylogenetic (taxon by taxon), evolutionary (future evolutionary potential), and ecological (present-day ecosystem function) importance (Bowen 1999; Bowen & Roman 2005).

Bowen suggests that these three perspectives may often be in conflict. If, however, species with high evolutionary distinctiveness scores (Bowen and Roman's first axis) represent a greater than random set of future evolutionary routes (Redding et al. 2008), then conserving them would be a logical bet-hedging strategy for retaining evolutionary potential, the second axis of

conservation worth outlined by Bowen (1999; Bowen & Roman 2005). This means that Bowen and Roman's first and second axes need not conflict. Our results here suggest that, within primates, there is potential for some agreement between the first (phylogenetic) and third axes (ecosystem functioning). Interestingly, results of studies of artificially constructed communities suggest that "phylogenetic relatedness is an indicator of the ecological uniqueness of species" (Cadotte et al. 2008; Cadotte et al. 2009) such that evolutionarily isolated species are likely to be more ecologically distinct. Artificially constructed communities of less-related species in turn have higher ecosystem function (Cadotte et al. 2008; Cadotte et al. 2009; Maherali & Klironomos 2007).

Instead of communities of interacting species, ED methods have, so far, been predominately applied to clades. If, in future work, ED measures can be applied across communities and a link between evolutionary distinctiveness and ecological role is demonstrated, then using ED to rank at-risk species could retain a larger than expected selection of ecosystem functional diversity. So far, the EDGE framework seems to offer at least as much as advertised for conservation biology, and if our findings are replicated throughout the tree of life, perhaps more.

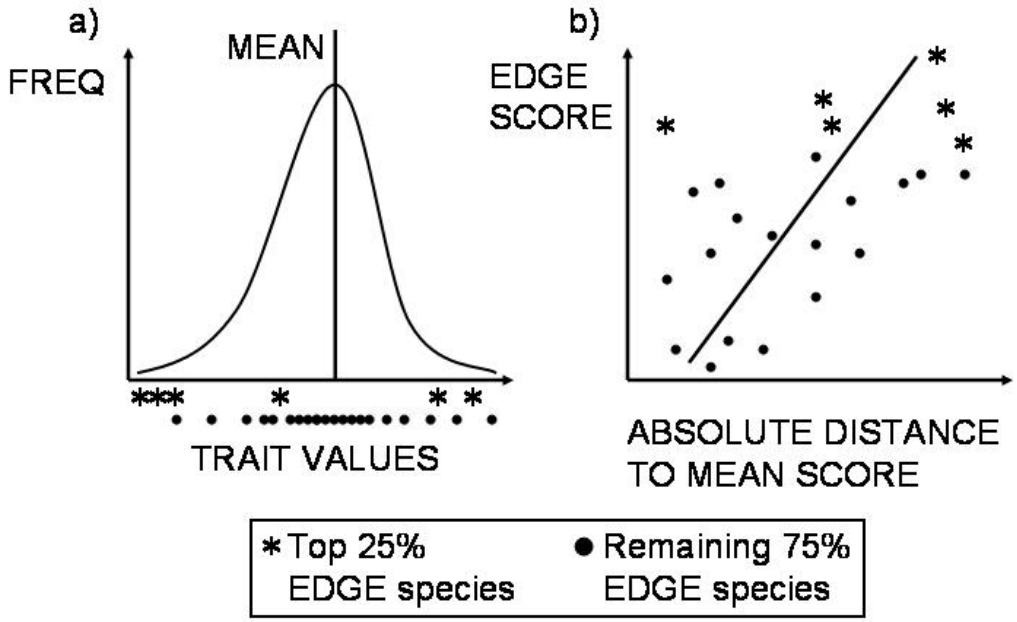

Figure 4.1 Cartoon showing how the position of high EDGE scoring species further from a trait's median score shown on the frequency distribution (a), translates into a positive correlation, plot (b), between EDGE score and 'trait oddness'. The data points are illustrative and not part of the dataset.

Table 4.1 Pearson correlations (ρ) of the EDGE scores for primate species and distance of species specific traits from the average for the order. Variables described in Appendix B.

		EDGE			
Group[c]	Variable	df	ρ	p[a]	p[b]
M	Female Mass	216	0.158	0.039	0.051
M	Tail Length – Body Residuals	217	-0.007	0.918	0.762
M	Body Length – Mass Residuals	217	0.163	0.035	0.051
M	Maximum Age	146	0.068	0.552	0.327
M	Sexual Weight Dimorphism	200	0.054	0.560	0.167
G	Geographic Range Size	217	0.248	0.001	0.003
G	Latitudinal Midpoint	211	0.257	0.001	0.003
G	Distance to Continental Centroid	217	0.347	0.000	0.003
BE	Population Density	143	0.293	0.001	0.025
BE	Home Range Size	160	0.153	0.093	0.045
BE	Group Size	146	0.187	0.035	0.067
BE	Solitariness	163	-0.230	0.011	0.000
BE	Activity Period	217	-0.188	0.015	0.051
BE	Terrestrially	182	-0.102	0.282	0.051
BE	Habitat	200	0.087	0.318	0.572
BE	Diet Class	217	-0.041	0.645	0.760
R	Gestation Duration	212	0.291	0.000	0.000
R	Litter size	217	0.083	0.318	0.268
R	Mating System	137	0.028	0.830	0.754
R	No of Males in Group	174	0.014	0.895	0.754

a - Corrected for multiple testing using the false discovery rate (Benjamini& Hochberg 1995)

b - Corrected value but when Lemuriformes are excluded

c - Column key: G – Geographical traits, BE - Behavioral/Ecological traits, M - Morphological traits, R- Reproductive traits

Table 4.2 Pearson correlations (ρ) of (ED) scores and membership IUCN Redlist threat category (GE; scored 1:5 most threatened first) for primate species, and distance from the average for the order. Variables described in Appendix B.

			ED		GE	
Group[b]	Variable	df	ρ	p[a]	ρ	p[a]
M	Female Mass	216	0.27	0.000	-0.01	0.957
M	Tail Length – Body Residuals	217	-0.05	0.554	0.05	0.642
M	Body Length – Mass Residuals	217	0.03	0.821	0.21	0.012
M	Maximum Age	146	0.12	0.195	-0.01	0.957
M	Sexual Weight Dimorphism	200	-0.16	0.049	0.12	0.136
G	Geographic Range Size	217	0.02	0.821	0.28	0.000
G	Latitudinal Midpoint	211	0.15	0.049	0.16	0.070
G	Distance to Continental Centroid	217	0.17	0.040	0.32	0.000
BE	Population Density	143	0.19	0.049	0.20	0.070
BE	Home Range Size	160	0.17	0.049	0.05	0.642
BE	Group Size	146	0.27	0.002	0.05	0.642
BE	Solitariness	163	-0.62	0.000	0.10	0.330
BE	Activity Period	217	-0.72	0.000	0.15	0.074
BE	Terrestriality	182	0.15	0.068	-0.14	0.126
BE	Habitat	200	0.00	0.960	0.13	0.126
BE	Diet Class	217	-0.06	0.533	0.00	0.986
R	Gestation Duration	212	0.34	0.000	0.14	0.107
R	Litter size	217	0.01	0.918	0.12	0.136
R	Mating System	137	0.20	0.049	-0.05	0.642
R	No of Males in Group	174	0.17	0.049	-0.05	0.642

a - Corrected for multiple testing using the false discovery rate (Benjamini& Hochberg.1995)

b - Column key: G – Geographical traits, BE - Behavioral/Ecological traits, M - Morphological traits, R- Reproductive traits

Table 4.3 Spearman rank correlations coefficients between the continuous variables used in this study.

	MASS	GEOG RANGE	POP DENS	HOME RANGE	DAY JOURN	GROUP SIZE	SEX DIMW	LAT MID	TAIL/ LENGTH	LEN/ MASS	GEST LEN	LITTER SIZE	MAX AGE
GEOG RANGE	0.02												
POP DENS	-0.15	-0.07											
HOME RANGE	0.44	0.08	-0.19										
DAY JOURN	0.06	0.29	-0.16	0.47									
GROUP SIZE	0.2	0.06	-0.12	0.5	0.26								
SEX DIMW	0.46	0.15	-0.19	0.48	0.25	0.41							
LAT MID	0.2	0.04	-0.33	0.26	0.07	0.36	0.29						
TAIL/ LENGTH	0.1	-0.03	0.03	0.01	-0.12	-0.03	-0.02	-0.01					
LEN/ MASS	0.03	-0.02	-0.1	0.13	0.05	0.11	0.05	0.05	0.33				
GEST LEN	0.5	-0.01	-0.36	0.28	0.07	0.3	0.26	0.47	0.04	0.07			
LITTER SIZE	-0.19	-0.04	0.24	-0.16	-0.01	-0.22	-0.31	-0.28	0.05	-0.01	-0.45		
MAXAGE	0.54	0.05	-0.24	0.33	0.16	0.31	0.22	0.24	0.04	0.1	0.64	-0.44	
DISTANCE	-0.09	-0.35	0.24	-0.22	-0.24	-0.15	-0.04	-0.11	0.03	0.05	-0.14	0.06	-0.1

5: GEOGRAPHIC AND EVOLUTIONARY ISOLATION IN MAMMALS

5.1 Introduction

Most species in the tree of life belong to species-rich clades, but species-rich clades are greatly outnumbered by those that contain just a few species: this is the classic taxonomic hollow curve first noted by Willis (1922). Species with few close relatives have been proposed as important targets for conservation (see, e.g. Vane-Wright et al. 1991, Redding & Mooers, 2006, Isaac et al, 2007; this thesis). We know little about the spatial distribution of species-poor clades at a global scale (but see Fjeldsa et al. 2001, Davies et al. 2009). Such knowledge would be useful to set effective geographical conservation targets (e.g. a "hotspots" approach) for species with few close relatives, and may also provide a useful insight into the macro-evolutionary processes that underlie global patterns of biodiversity.

As there is lower species richness and lower population density in more poleward areas, when compared to those in the tropics (Gaston, 2003), we might naively expect clades of species found near the poles to be species-poor as well. Distributional data do not support this prediction though. If we consider the class Aves, for example, 4 out of 8 bird orders with fewer than 20 species are exclusively found in the tropics, while 7 of these are found in tropical and temperate habitats (unpublished results).

Theories developed to explain the latitudinal biodiversity gradient provide a source of possible explanations of why species-poor clades may often be located in the tropics. For instance, one hypothesis is that the tropics have lower extinction rates than other areas of the world (tropics as museums; Stenseth, 1984; Weir and Schluter, 2007). This lower extinction rate would mean that species-poor clades are simply more likely to survive over time there than in other areas of the world. Potential mechanisms driving lower extinction rates in the tropics include the lack of extreme climatic variation in the tropics, reducing mass extinction events (e.g. Wallace, 1855), or more “ideal” biological conditions (heat and humidity) in the tropics (Svenning et al. 2007) that increase persistence.

It has also been suggested that species in species-poor clades are older, and from a phenotypic standpoint “relics” (Simpson 1944, Irwin 1981). Species age is not always correlated with the number of close relatives a species has: For instance, two species in different clades with the same age of appearance could have very different evolutionary isolation scores due to disproportionate extinction rates, for instance, in one of the two clades. However, if species from species-poor clades are found to be, in general, older then this finding might suggest that they are located mainly in the tropics, as unlike the tropical rainforests, many polar and temperate habitats have changed in size, shape and location during the course of recent mammal evolution (Stenseth, 1984).

If, however, species from species-poor clade are also ‘relics’ and the term relic implies obsolescence, then we might expect a different pattern of spatial

distribution for such species. As relics, it seem reasonable to propose that species with few close relatives only survive in ‘refuge’ habitats with lower inter-specific (and inter-lineage) competition, rather than in species rich-habitats. One well-known example of a member of a species-poor lineage that could fit this pattern is the Platypus (*Ornithorhynchus anatinus*), which is geographically isolated from ‘modern’ placental mammals. If it is true that species with few close relatives are ‘relics’, whose obsolete characteristics means that they generally cannot survive in areas with ‘modern’ species, we can hypothesise that they may be found, in general, at the edges of continents, on remote islands or in habitats that are marginal for mammals in general (i.e. habitats that have low mammal species richness irrespective of the latitude, such as deserts)

To determine the spatial distribution of species from species-poor clades and to assess which of the above arguments explains the patterns seen most effectively, I assigned a measure of evolutionary isolation (see chapter 1) to each species of mammal, and then (i) I mapped areas of the world that contain the 10% most evolutionary isolated species, and compared this spatial distribution to that of overall species richness using habitat polygons as sampling units. (ii) I determined those areas of the world that have a higher average evolutionary isolation score and more highly evolutionarily isolated species than expected. (iii) I then asked, using habitat polygons, whether geographic isolation (see below) is correlated with the number of highly evolutionarily isolated species found in a habitat, both in terms of raw frequency and then using average evolutionary isolation score and expected numbers of highly evolutionarily isolated species.

Finally, I compare the spatial patterns of recent speciation to that of highly evolutionarily isolated species, to test whether there are similar patterns seen in both groups of species.

5.2 Methods

5.2.1 Calculating Geographic Measures

Ranges (extents of occurrence) for all mammal species (n=5488) were downloaded from the IUCN Red list website (IUCN, 2009). The mammal evolutionary tree used was a recently published supertree (Fritz et al. 2009). I removed all marine mammals, and then, using available literature (Wilson & Reeder 2005), I attempted to match the species for which there were range maps available (n=5488) to the species tips on the tree (n=4200). Mismatches were of three types: taxonomic splits leading to species found only in the range database, taxonomic splits leading to species on the tree with no range data, and new species. For each of the species found only in the range database, I identified the most closely related species found in the phylogenetic tree using a taxonomy (Wilson & Reeder 2005) and took the union of the ranges of these two species and attributed the range to the single tip in the phylogenetic tree.

I pruned species that were found on the tree but not in the range database from the tree, substituting names from the range database onto the tree if necessary. Those species that were new full species in either the tree or range dataset and could not be matched were removed from the relevant database. This left me with 4767 species in the dataset.

I calculated the ‘Fair Proportion’ (FP; Redding, 2003; Isaac et al. 2007) metric on the mammal supertree, as it is a measure that differentiates well amongst tips and has a fairly straightforward interpretation (Chapter 1). To examine the effects of the polytomies present within the mammal supertree, I artificially resolved all polytomies 10,000 times, assuming a Yule pattern for topologies and uniform random edge lengths generated with a broken stick model. These lengths approximate the Yule model as well, since every edge on a Yule tree has very nearly the same expected length (Steel and Mooers, in review). From this distribution, I created a mean score for FP for each mammal species, to test whether the lack of resolution in the tree made a difference to the results.

Using a 0.25 degree by 0.25 degree grid, I mapped the following quantities:

1. The number of ranges that overlap each grid cell, to calculate the species richness of each cell.

2. The number of the 10% (467 spp) most evolutionary isolated species in each grid cell. Initially I used the isolation measure FP but repeated the analysis using VW (Vane-Wright et al. 1990, Redding, 2008) and QE for comparison (Pavoine, 2005). If the findings are robust to the method of measuring evolutionary isolation then this provides some credibility to the analysis, suggesting that we are examining the distribution of species with few close relatives, irrespective of the particular assumptions made by the method used to determine this value (see Chapter 1 for a discussion).

3. The number of highly evolutionarily isolated species more or less than expected, weighting the probability of any species being found in any cell by the total number of cells a species is found in (see Jetz et al. 1995), in order to control for the species richness of the grid cell.

4. The average logged evolutionary isolation score of all the species that overlapped each grid cell, also in order to control for the species richness of the grid cell.

5. The species richness of those mammal species with the bottom 10% shortest terminal branches (or species tips). These are the most recently-speciated species.

6. The overlap of 'hotspots' of the species richness of highly evolutionarily isolated species with the "hotspots" of the species richness of recently speciated species. To achieve this, I took the top 10% highest scoring grid cells for both group of species and mapped where they overlapped and where they did not.

Following this, I divided the world up into areas that represent 22 distinct habitats (ecofloristic provinces, Leemans, 1990) resulting in 13,469 separate polygons. For each habitat polygon over 10,000 m^2 with at least one mammal species present (n=1085), I averaged the values of the grid cells found in it for all the variables above, so that I had a value for the mean species richness of a habitat polygon, the mean number of top 10% most evolutionarily isolated species and so on. I then undertook a series of regressions using habitat polygon as the sampling unit, with the arc distance between each habitat polygon centroid used to correct for spatial autocorrelation (calculations from GeoDa, Anselin

2009). As explanatory variables in the models I used: Latitude of habitat polygon centroid, the area of habitat polygon, total average species richness per grid cell contained with the habitat polygon, habitat type of the polygon (as a grouping variable). As separate dependent variables I then used the number of top 10% most evolutionarily isolated species, the number of the 10% most recently diverged species and in order to control for the species richness in a polygon the expected number of top 10% evolutionarily isolated species and the mean evolutionary isolation score. All four dependent variables noted above were calculated by taking the mean value across grid cells found in each habitat polygon.

I then divided the dataset into islands and continental habitat polygons, and created models using the same dependent variables as above, but using the distance from the centroid of habitat polygon or island to the nearest continental coastline (Asia, Africa, North or South America combined) as an additional explanatory variable.

All continuous variables were log transformed to correct for the effects of outliers, and all models recorded here used a Spatial Error structure as recommended by internal diagnostics (GeoDa, Anselin 2009).

5.3 Results

5.3.1 Spatial distribution of species with few close relatives and comparison to overall species richness

The isolation scores from the tree before and after resolving polytomies are very closely related (correlation between resolved-FP and polytomy-FP was

0.83; figure 1.5). The same patterns of significance were found for all tests, with only slightly different coefficient estimates - therefore, only the FP scores averaged across the resolved tree set will be reported further.

The majority of top 10% of evolutionarily isolated species are found in continental areas (72% on continents; 72 & 70% for top 15 and 5% respectively), as expected, as the continents represent about 85% of the mammal inhabited land area. There are no more highly evolutionarily isolated species on islands than expected (Chi-square test (χ-squared = 0.0368, df = 1, p = 0.85). Most of the top 10% evolutionarily isolated species are also found in the tropical forests of South and Central America (22% of all top 10% species), Central Africa (19%) and South-East Asia (2%) and Indonesia (8%). Overall, tropical forests contain 68% of the top 10% most evolutionarily isolated species (despite comprising only 29% of the total mammal inhabited grid squares). This figure reflects the disproportionate total species richness of the tropics with 67% of all mammal species being located in tropical habitats.

Indeed, the spatial distribution of highly evolutionarily isolated species and total species richness were qualitatively similar (Fig. 1.1). This observation is supported by the spatial regression predicting the number of top 10% most evolutionarily isolated species from the overall species richness, which has a β of 0.76 (c.i. 0.73-0.78) and an r^2 of 0.82 ($p<0.001$, n=1085 polygons). A similar relationship was seen in maps of the top 5% (β of 0.69 and an r^2 of 0.79, $p<0.001$, n=1085) and 15% (β of 0.80 and an r^2 of 0.91, $p<0.001$, n=1085) most evolutionarily isolated species (Fig 1.4). Additional explanatory variables, such as

latitude, habitat and area of polygon increased the variance explained by just a few percent (e.g. full model $r^2 = 0.93$, n=1085). In all models reported herein the spatial element was strongly significant ($p<0.001$).

5.3.2 Comparison of the spatial distribution of species with few close relatives when controlling for species richness

When controlling for species richness (i.e. using mean ED and expected number of the most evolutionarily isolated species per habitat polygon, as dependent variables, Fig. 1.2) polygons with the highest mean evolutionary isolation score were at lower latitudes ($\beta = -1.26$, $r^2 = 0.11$, n=1085, $p<0.001$, spatial error model in GeoDa), as were the higher than expected numbers of top 10% most evolutionarily isolated species ($\beta = -0.46$, $r^2 = 0.82$, n=1085, $p<0.001$, spatial error model in GeoDa). Interestingly, the most species rich areas still contain a higher mean evolutionary isolation and more top 10% evolutionarily isolated species than expected ($\beta = 1.25$, $r^2 = 0.10$, n=1085, $p<0.001$, spatial error model in GeoDa and $\beta = 0.32$, $r^2 = 0.80$, n=1085, $p<0.001$ respectively, spatial error models in GeoDa). Both these dependent variables (mean isolation and expected number of top 10% ED species) gave very similar results despite an imperfect correlation (Pearsons $\rho = -0.4$, n=1085, $p<0.001$).

Nearly all the tropical shrub-land areas within Africa, such as the ‘Horn of Africa’ and the Kalahari plains, appear to have high mean evolutionary isolation and higher than expected numbers of the most evolutionarily isolated species (Fig 1.2). Also the Indian sub-continent, which has had a very different recent geological history to the rest of south-east Asia, is clearly delineated with a high

average evolutionary isolation. Papua New Guinea, which shares many Marsupial species with Australia, has a much higher mean evolutionary isolation score than Borneo and the other neighbouring Indonesian islands. The very high values within Australia correspond well to the combined ranges of the monotremes (Order Monotrema), which are the mammal species with, by far, the highest evolutionary isolation scores.

5.3.3 Spatial distribution of species that have recently speciated

Again, total species richness is a significant but weaker predictor of the number of recently speciated species ($\beta = 0.4$, $r^2 = 0.61$, $n=1085$, $p<0.001$, spatial error model in GeoDa), when compared to models predicting numbers of highly evolutionarily isolated species. Overall, there is not a strong concordance of areas with high numbers of highly evolutionary isolated species and number of recently speciated species (48% of high value grid cells overlap, figure Fig. 1.4). This is, perhaps, suprising as both variables are positively correlated to species richness so there is an expection of strong overlap in all of the most species rich areas. India is, again, notably different to the continent it adjoins, with much lower numbers of recently speciated species. Also, Papua New Guinea has many recently speciated species, whereas islands to the east of it have few. Most centres of high, recent speciation outside South America appear associated with tropical or sub-tropical mountain systems e.g. Altai range, the Sierra Madre, the western Himalayas and the Arc Mountains of Eastern Africa (Fig 1.4). Unlike evolutionarily isolated species, the regressions suggest that all forest habitats

have lower numbers of recently speciated species than expected given its species richness (β = -0.23 to -0.46, $p<0.03$, n=1085).

5.3.4 Spatial distribution of species with few close relatives using different measures of evolutionary isolation

Very similar overall results were seen with models using the different measures of evolutionary isolation. For example, for the simple model predicting number of the top 10% most evolutionarily isolated species using the species richness of a polygon were all strongly significant, with β estimates of 0.8, 0.71 and 0.68 for the measures 'Quadratic Entropy', 'Fair Proportion' and 'Vane-Wright' respectively. Both the 'Quadratic Entropy' method and the 'Vane-Wright' methods identify areas within Australasia and South America as having higher numbers of the most evolutionarily isolated species than 'Fair Proportion' but, in general, there is good agreement with high value areas mainly located in South America and Central Africa (Fig. 1.3).

5.4 Discussion

I show that species-rich areas of the world not only have the highest absolute number of highly evolutionarily isolated mammal species, as expected, but often the highest proportion of such species. Interestingly, there is a weaker relationship between species richness and numbers of species that have recently speciated, and a limited overlap of 'hotspots' of recent speciation and 'hotspots' of species with few close relatives. This may suggest that the "tropics as museums" hypothesis has some validity, where areas of high species richness

are often ones that hold on to species-poor lineages, rather than ones with high current speciation rates.

Many tropical and sub-tropical mountainous areas appear, for the world's mammals at least, an important area for speciation. Interestingly, these areas do not appear to have the highest numbers of highly evolutionarily isolated species. Montane habitats have high habitat heterogeneity which promotes speciation (Fjeldsa et al. 2001). Perhaps, due to small population sizes there, they also have relatively high extinction rates, which limits not only the total species richness but also prevents species-poor lineages persisting.

The role of geographical isolation in the spatial distribution of species-poor lineages is not clear. The single result that somewhat supports a role of isolationis that while the most evolutionarily isolated species tend to be found in the species-rich tropical rainforests, the marginal scrub and dry forests surrounding the rainforests have more highly evolutionarily isolated species than expected.

Conversely, there seems little evidence to suggest that the more remote an island, the more evolutionarily isolated species are present. Indeed, there are also no more highly evolutionarily isolated species on islands overall, than expected. Also, the polar and sub-polar regions, which, if isolation was the primary driver of the spatial distribution of the most evolutionarily isolated species we would expect to have the highest proportion of such species, but they instead appear to have, consistently, the expected number of the most evolutionarily isolated species. At least at the spatial scale considered by this study, we must,

overall, reject isolation as a mechanism than strongly explains present day patterns of evolutionary isolation.

The situation presented above, where some highly evolutionarily-isolated species are found in species-rich areas, while others are in more species-poor habitats and on islands (e.g. the platypus), could be caused by two discrete types of evolutionary isolated species: Those that are the remnants of historically species-rich ‘dying’ clades versus those groups that have experienced historically low speciation rates. Our geographic expectation for these groups might be different. It could be that, for instance, remnant species survive because they are located on islands or other refuges, while species from groups with low speciation rates exist in long-term unchanging niches for which they are ideally adapted, and which promote low speciation. Thus, we would have no reason to expect that the species richness of the latter group would not map well onto that of overall species richness, whereas the former group would have a very different relationship to total species richness. According to our results, the latter type of evolutionarily isolated species would appear to be the most frequent. Ideally, we would test these ideas on groups for which the fossil record is relatively complete, e.g. corals (Order Sceletaria), so that we can identify the mechanism that has resulted in the species-poor nature of particular lineages, before testing whether this evolutionary history is related to their present day distribution.

From a geographical conservation perspective actions that protect the highest species richness areas for mammals would also protect those areas that have the highest incidence of evolutionary isolated species. With the higher than

expected numbers of highly evolutionarily isolated species in medium species-richness habitats, it is possible that, while effective, ‘hotspots’ of species richness may not provide an optimum geographical solution to protect those species with the fewest close relatives (but see Rodrigues & Gaston 2002).

From a single-species conservation perspective, this study provides evidence that species with few close relatives are not, in general, geographically isolated (c.f. chapter 4). Instead, they appear to co-exist directly with many other species in species-rich habitats. Thus, there is no evidence to suggest that they are not ecologically or functionally as important as any other set of species, therefore, they appear to offer valid targets for conservation, as they house a large amount of unique evolutionary history.

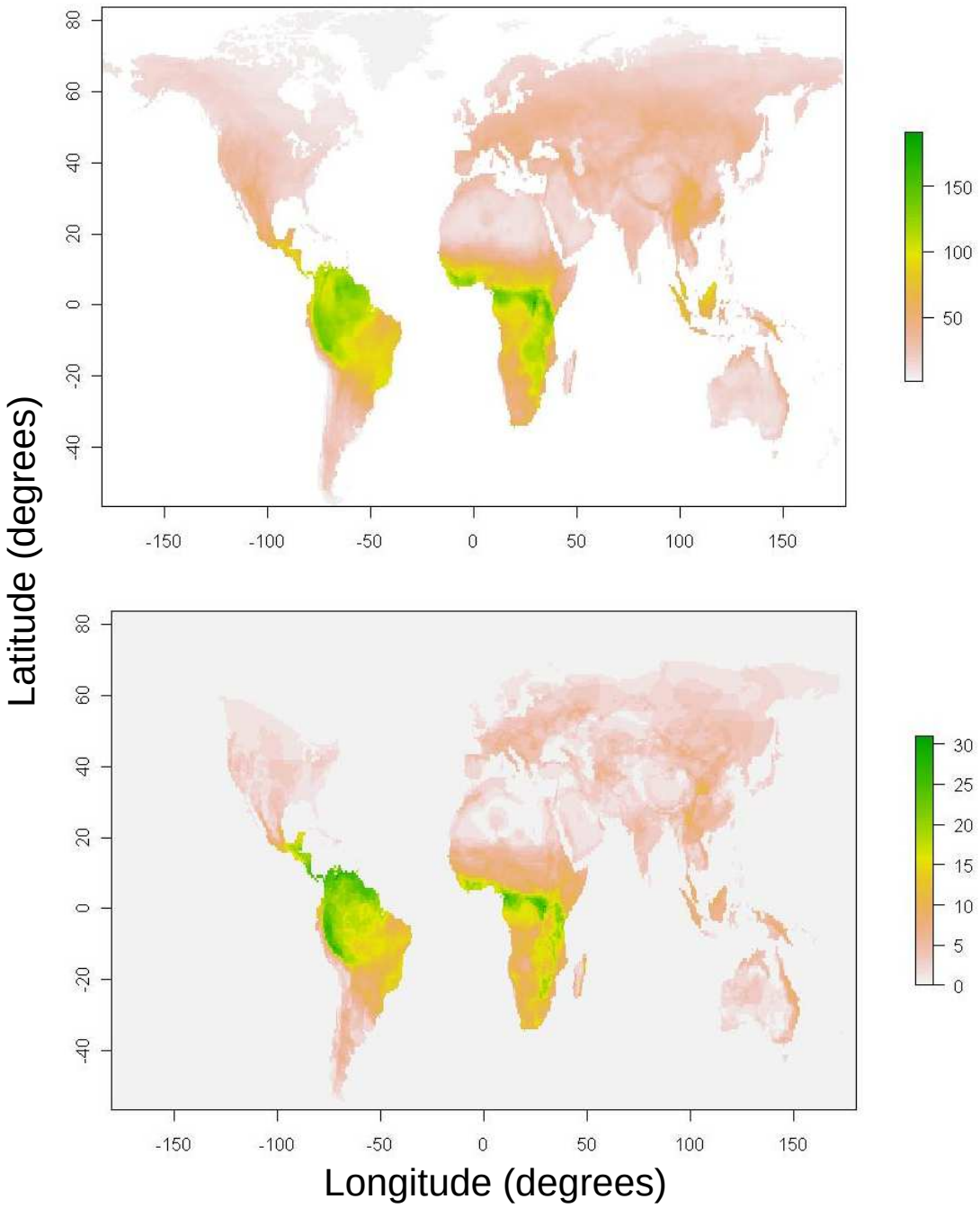

Figure 5.1 **The total number (top panel) of world's mammal species (n = 4767) and number of species that have the top 10% highest evolutionary isolation scores (bottom panel), found in each quarter by quarter degree grid square. Evolutionary isolation scores calculated using the 'Fair Proportion' measure (Redding, 2003) which approximates how many close relatives a species has in the evolutionary tree of the world's mammals. The higher the evolutionary isolation score the fewer close relatives a species has.**

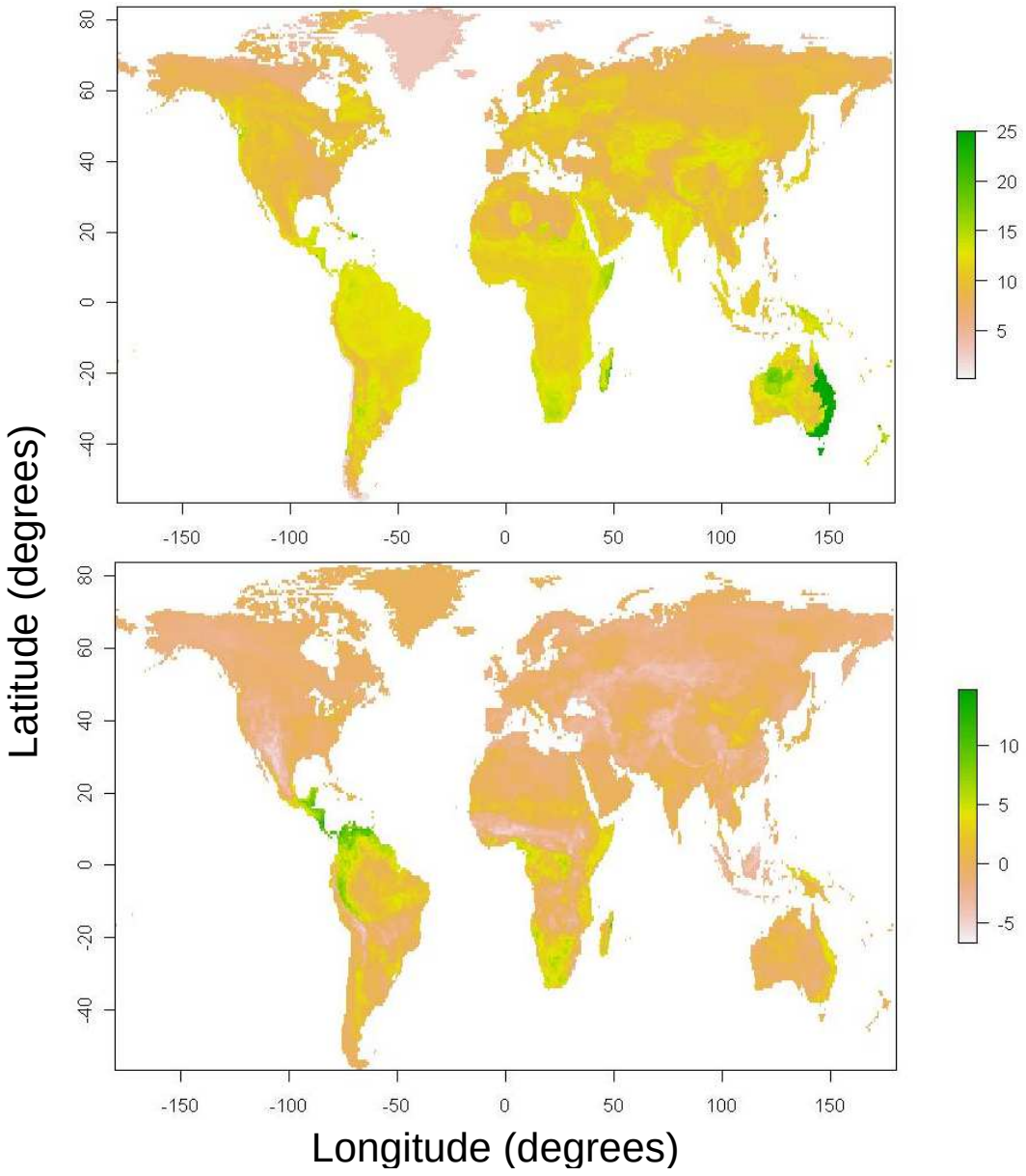

Figure 5.2 **Mean evolutionary isolation score (top panel) of mammal species found in each quarter by quarter degree grid square. Bottom panel uses the same grid but values represent the difference from the expected number of top 10% most evolutionarily isolated species found in each grid cell. Higher values mean there are more evolutionarily isolated species than expected, given the species richness of the grid cell. Evolutionary isolation score calculated using the 'Fair Proportion' measure (Redding, 2003) which approximates how many close relatives a species has in the evolutionary tree of the world's mammals. The higher the evolutionary isolation score the fewer close relatives a species has.**

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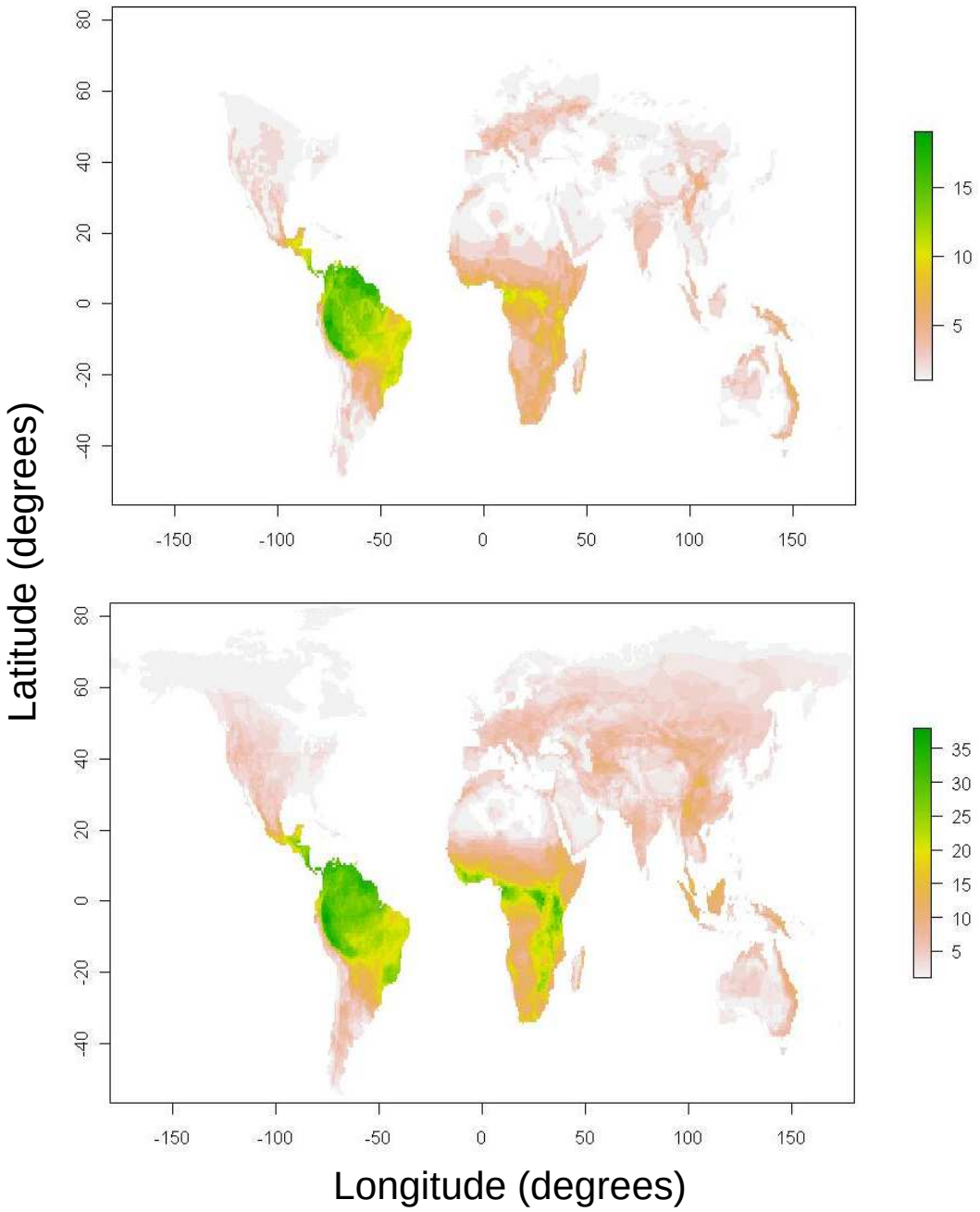

Figure 5.3 **The number of top 5% (top panel) and top 15% (bottom panel) most evolutionarily isolated species found in each quarter by quarter degree grid cell. Higher values mean there are more evolutionarily isolated species in the grid cell. Evolutionary isolation score calculated using the 'Fair Proportion' measure (Redding, 2003) which approximates how many close relatives a species has in the evolutionary tree of the world's mammals. The higher the evolutionary isolation score the fewer close relatives a species has.**

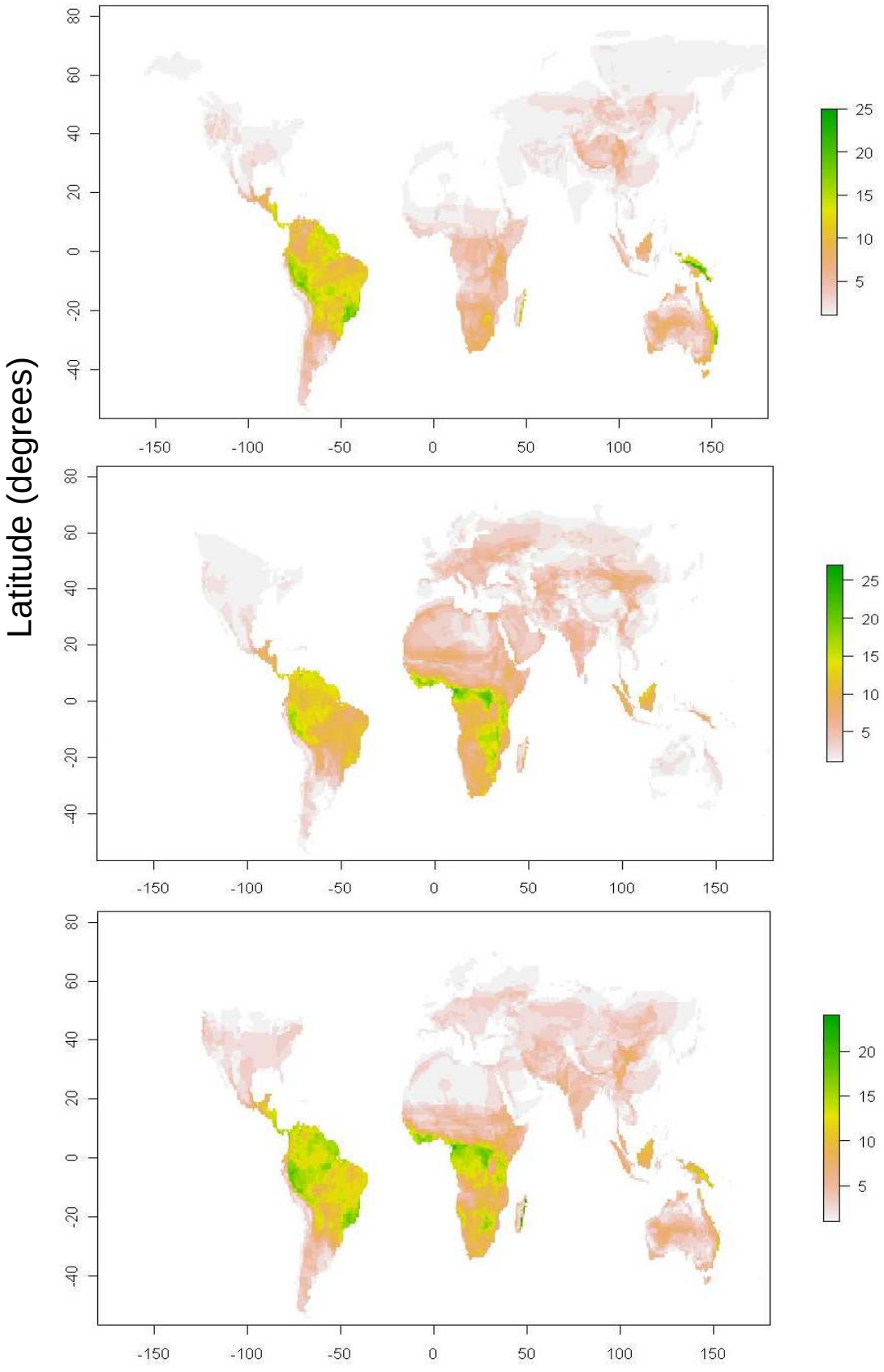
Latitude (degrees)
80
60
40
20
0
-20
-40
-150
-100
-50
0
50
100
150
25
20
15
10
5
Longitude (degrees)

Figure 5.4 Figures overleaf: The number of top 10% most evolutionarily isolated species found in each quarter by quarter degree grid cell. Higher values mean there are more evolutionarily isolated species in the grid cell. Evolutionary isolation score calculated using the Vane-Wright measure (top panel; Vane-wright, 1991), 'Fair Proportion' measure (middle panel; Redding, 2003) and Quadratic Entropy (bottom panel; Pavione, 2005) which all approximate how many close relatives a species has in the evolutionary tree of the world's mammals. The higher the evolutionary isolation score the fewer close relatives a species has.

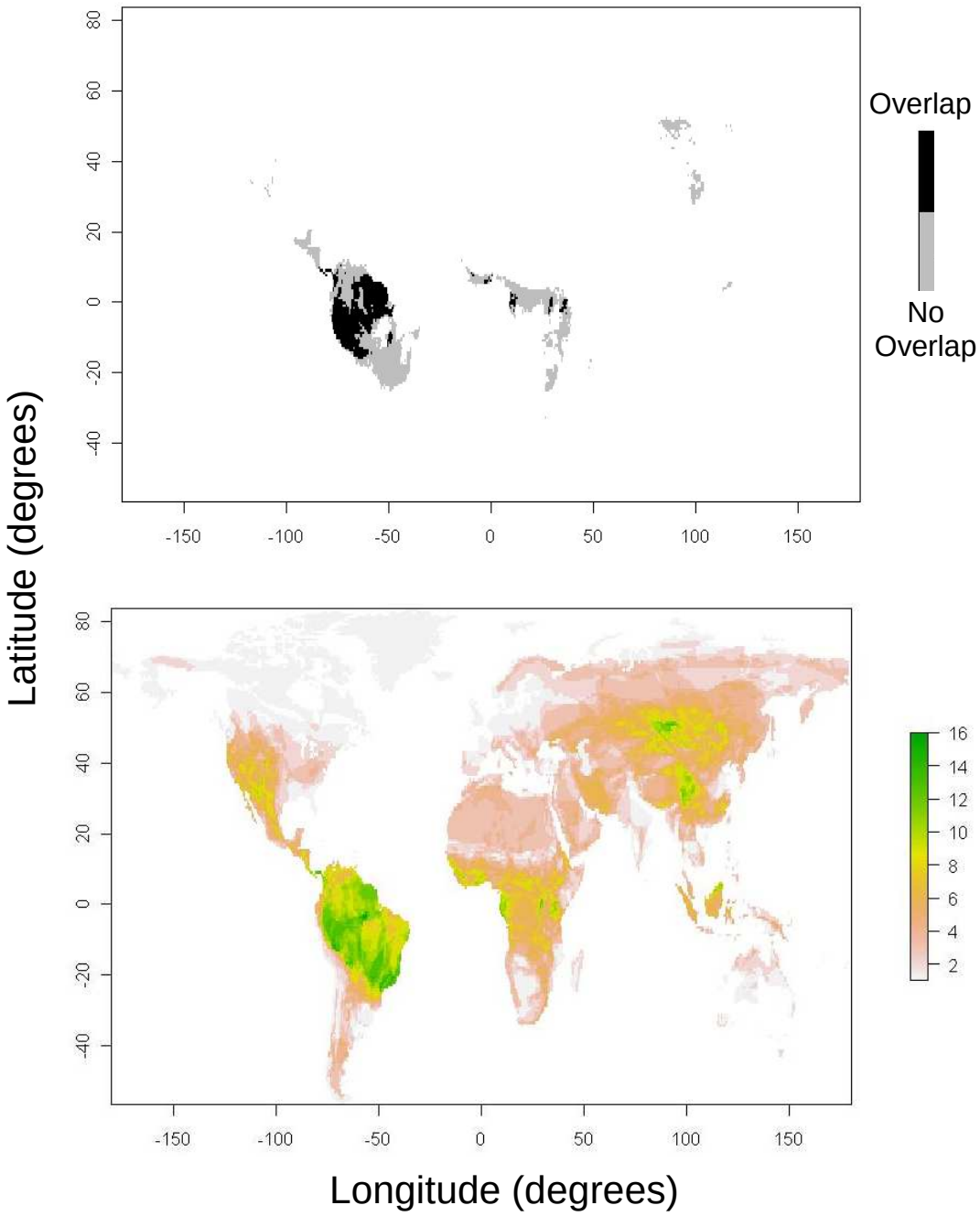

Figure 5.5 The overlap of highest 10% most species rich grid cells of recently speciated species with those species with the few close relatives (top panel) and the number of 10% most recently speciated mammal species (bottom panel) found in each quarter by quarter degree grid cell. Higher values mean there are more recently speciated species in the grid cell. Species age was calculated by measuring the species tip, or terminal branch, of each species in the tree of the world's mammals.

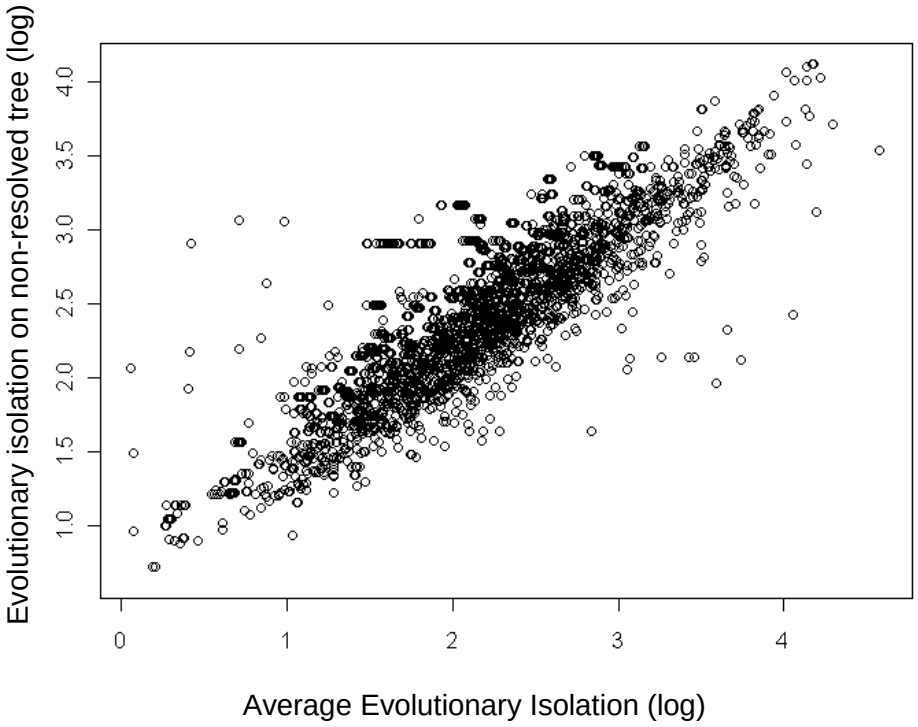

Figure 5.6 Correlation between log evolutionary isolation score 'Fair Proportion' (FP; Redding 2003) calculated for all species of mammal (n=4768), and log average FP taken from a distribution of 10,000 randomly resolved full bifurcating versions of the mammal tree. Spearman rank correlation is 0.89.

APPENDICES

Appendix A

List of hyperlinks to major news organisations covering the EDGE project:

http://www.edgeofexistence.org/species/default.php
http://www.independent.co.uk/environment/nature/worlds-weird-amphibians-face-extinction-771339.html
http://environment.uk.msn.com/wildlife/gallery.aspx?cp-documentid=7455038
http://www.timesonline.co.uk/tol/news/environment/article3221833.ece
http://www.newscientist.com/article/dn10962-conservation-bid-targets-worlds-100-weirdest-creatures.html
http://news.bbc.co.uk/1/hi/sci/tech/6263331.stm
http://www.guardian.co.uk/environment/2008/jan/21/conservation
http://www.telegraph.co.uk/earth/earthnews/3322467/Weirdest-and-most-endangered-creatures.html
http://www.spiegel.de/international/0,1518,459951,00.html
http://www.msnbc.msn.com/id/22784864/ns/technology_and_science-science/
http://www.nzherald.co.nz/strange-but-true/news/article.cfm?c_id=500835&objectid=10488166
http://www.foxnews.com/story/0,2933,324627,00.html

Appendix B

Raw data used in chapter 4 - 20 biological, ecological and geographical data variables for 216 primate species

Label	Description	Mean Value Used	Data Group	Transf-ormation used	Data Type	Sources
Female Mass	Body mass in grams of adult female	Y	M	log	Cont	4-7, 9-19, 23,25,27
Tail Length – Body Length Residuals	The residuals of linear model of tail length (cm) and body length (cm)	Y	M	sqrt	Cont	6,11,13,20, 21,24,27
Body Length –Mass Residuals	The residuals of linear model of body length (cm) and adult female mass (g)	Y	M	sqrt	Cont	4-6,9-12,14-19,20,22,23, 24,27
Maximum Age	Maximum age reported in years	Y	M	log	Cont	3-5,8-10,18,19
Sexual Dimorphism	Adult male average weight divided by adult female average weight	Y	M	log	Cont	4-6,9,10,14-19,22,23,25,27
Geographic Range Size	Geographical extent (km^2) of species' occurrence	N	G	log	Cont	28-44
Latitudinal Midpoint	Latitude of species' geographic range mid-point	N	G	sqrt	Cont	28-44
Distance to Continental Centroid	Distance of geographic range mid-point to mid-point of the combined area of all species found in that continent	N	G	none	Dist	28-44
Population Density	Average number of individuals per km^2	N	E-B	log	Cont	4,5,9,10,14-19,23,25
Home Range Size	Size in m^2 of group or individual's land use	N	E-B	log	Cont	14-17,23
Group Size	Number of individuals in social group	N	E-B	log	Cont	4-6, 9,10,13-19, 21-23, 25, 26
Solitariness	Whether the species is solitary (Yes or No)	N	E-B	none	Cat	14-17, 23,27
Activity Period	Marked as Diurnal or Nocturnal	N	E-B	none	Cat	2,6,13-17,21, 23,26
Terrestrially	Marked as either Arboreal (arb) or Terrestrial (terres)	N	E-B	none	Cat	14-17, 23, 26, 27
Habitat	Species marked as dwelling in Forest or Savanna/Scrub forest	N	E-B	none	Cat	6,13,26
Diet Class	Diet according to 7 categories	N	E-B	none	Cat	2, 6, 13-17, 21,23,26, 27

Gestation Duration	Duration in months of gestation periods	Y	R	none	Cont	1, 3, 6, 11-13, 22, 25, 26, 27
Litter size	Size of litter	Y	R	none	Cont	3,6,11,13,25
Mating System	Marked as monogamy (M), polygyny (PG), polyandry (PA), polygyandry (PGA)	N	R	none	Cat	6-8,13,21,22
No of Males in Group	Number of male individuals in social group (SM – single male, MM – Multi-male, SMM – Single and Multi-male Groups	N	R	none	Cat	4,5,9,10,18,19

Key: Data Group: E-B = Eco-Behavioral; R = Reproductve; M = Mophological; G = Geographic; **Data Type**: Cat = Categorical; Cont=Continuous; Dist=Distance

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	Female Mass	Tail Length	Body Length	Maximum Age	Sexual Dimorphism	Geographic Range Size	Latitudinal Midpoint
Allenopithecus nigroviridis	4750	77.19411	3.240048	1.439333	1.380475	5.804242	0.423124
Allocebus trichotis	78.9	-391.487	-112.41	NA	1.046536	3.000975	4.073514
Alouatta belzebul	6180	-8.01021	-105.199	NA	1.154772	6.414663	2.608528
Alouatta caraya	5590	-19.4368	-47.784	1.510545	1.221468	6.244777	4.510807
Alouatta coibensis	6400	170.4178	23.48378	NA	1.249	3.431364	2.762605
Alouatta fusca	5190	1.487341	89.41618	NA	1.231673	5.823667	4.596877
Alouatta palliata	6580	322.5749	42.97435	1.342423	1.152947	5.739817	2.637219
Alouatta pigra	7200	29.17238	-12.5326	1.30103	1.335927	4.803297	4.336537
Alouatta sara	6610	565.4676	197.5464	NA	1.249	6.199215	3.836833
Alouatta seniculus	6420	258.1189	132.4078	1.39794	1.133491	6.693506	0.824876
Aotus azarai	1246	-98.6302	-104.255	1.477121	0.983984	6.006802	4.129945
Aotus brumbacki	603	358.8683	85.22991	NA	1	5.350508	NA
Aotus hershkovitzi	800	181.9342	130.5154	NA	1	NA	1.869041
Aotus infulatus	1240	27.88752	27.71149	NA	0.989906	6.301613	NA
Aotus lemurinus	881	353.4282	68.80686	1.528917	1.008612	5.545941	2.493362
Aotus miconax	800	350.5933	91.40888	NA	1	4.981358	2.442096
Aotus nancymaae	795	8.744094	-11.6179	NA	1.00453	5.281021	2.14419
Aotus nigriceps	1060	7.765156	-3.81288	NA	0.959463	6.310299	2.780073
Aotus trivirgatus	912	-22.6631	12.10182	1.398808	1.033776	5.896038	2.037198
Aotus vociferans	873	-42.0605	0.256415	1.344392	1.003518	6.036693	1.033577
Arctocebus aureus	235	366.1506	6.694773	NA	NA	5.919434	0.642915
Arctocebus calabarensis	258	278.8835	77.40577	1.113943	1.008087	5.202848	2.350069
Ateles belzebuth	6720	-18.7474	80.88175	1.454845	1.028353	6.053192	1.784108
Ateles chamek	7130	241.715	77.46564	1.523746	0.994878	6.058408	2.647856
Ateles fusciceps	9070	427.5749	-9.52565	1.564074	0.992307	5.171605	2.538053
Ateles geoffroyi	7610	-61.3063	-100.825	1.673021	1.033048	5.858951	3.519394
Ateles marginatus	6240	50.52176	41.57362	1.643453	1	5.107303	2.166932
Ateles paniscus	8710	-311.867	-229.377	1.596597	1.042474	5.981238	1.437924
Avahi laniger	1020	-21.2016	86.5637	NA	0.932224	4.952581	4.413317
Brachyteles arachnoides	10600	374.6518	254.0506	1.477121	1.087893	4.959948	4.650358
Cacajao calvus	3420	-306.368	352.1808	1.446382	1.094608	5.105529	2.394939
Cacajao melanocephalus	3140	260.5967	46.24699	NA	1.07994	5.701226	0.734324
Callicebus brunneus	852	-48.363	-119.886	NA	1.021325	5.714371	3.174432
Callicebus	992	261.1065	62.18188	NA	1	5.949834	NA

caligatus							
Callicebus cinerascens	992	-75.8263	-62.6782	NA	NA	4.903185	2.897837
Callicebus cupreus	1120	246.6776	97.62895	1.421604	0.954439	5.993264	1.773526
Callicebus donacophilus	899	215.5662	91.89528	1.39794	1.044034	5.680572	3.984334
Callicebus dubius	992	-356.264	-26.1499	NA	NA	4.903185	NA
Callicebus hoffmannsi	1070	-67.5486	-137.906	NA	1.028555	5.281021	1.99472
Callicebus modestus	992	-126.363	-133.402	NA	NA	3.899964	3.868616
Callicebus moloch	965	-61.0201	-117.633	1.281033	1.030047	6.164158	2.775157
Callicebus oenanthe	992	-136.399	-58.109	NA	NA	3.899964	2.360892
Callicebus olallae	992	-196.457	-160.154	NA	NA	3.899964	3.868616
Callicebus personatus	1390	-426.459	-138.137	NA	0.959333	5.980755	4.063413
Callicebus torquatus	1220	20.58294	11.0858	NA	1.021966	6.199209	0.518044
Callimico goeldii	558	-23.7644	20.88246	1.302114	0.991555	5.65743	2.309541
Callithrix argentata	369	419.6518	156.0506	1.217484	0.966927	5.915436	3.238883
Callithrix aurita	388	-226.565	-156.792	NA	1	5.107303	4.812223
Callithrix flaviceps	375	-1.25591	-19.1179	NA	0.991546	4.903185	4.600157
Callithrix geoffroyi	342	-360.296	33.56313	1.245513	1	5.202848	4.357868
Callithrix humeralifera	375	262.5545	45.63696	1.138303	0.972892	5.183186	2.316277
Callithrix jacchus	291	343.7374	46.20589	1.149219	0.99538	5.997636	2.566494
Callithrix kuhlii	375	505.8755	109.2943	1.199618	1.09975	4.677352	3.952933
Callithrix penicillata	340	309.0637	78.60422	1.187521	1.029746	6.158296	3.5609
Cebuella pygmaea	125	448.7307	63.52968	1.269513	0.951635	6.194364	2.442547
Cebus albifrons	2520	382.5104	86.12406	1.625312	1.148366	6.53019	0.910386
Cebus apella	2760	103.5004	57.60974	1.653213	1.198395	7.042208	3.367534
Cebus capucinus	3010	206.6334	278.1161	1.702861	1.206663	5.554708	2.95746
Cebus olivaceus	2800	-29.7467	68.84937	1.672098	1.147791	6.226214	2.188538
Cercocebus agilis	7120	191.4532	119.4176	1.503109	1.234726	5.980235	0.737377
Cercocebus galeritus	7080	112.9012	70.37268	1.278754	1.352585	5.493734	1.451528
Cercocebus torquatus	7290	-55.2191	-42.2488	1.562293	1.324212	5.870794	2.111225
Cercopithecus ascanius	3540	-221.717	-233.081	1.428944	1.131891	6.472314	1.647035
Cercopithecus campbelli	3640	14.84874	-58.0604	1.477121	1.291051	5.758362	2.920638
Cercopithecus cephus	3440	-196.628	-253.788	1.462398	1.208814	5.928003	0.653373
Cercopithecus diana	4370	-103.873	-223.32	1.543447	1.149925	5.511202	2.579176
Cercopithecus dryas	2780	-8.48559	-14.8202	NA	1	3.899964	1.263144

Cercopithecus erythrogaster	3440	206.946	50.3532	1.380211	1.306863	4.998729	2.462327
Cercopithecus erythrotis	3250	-414.872	87.48689	NA	1.08067	5.046502	2.23138
Cercopithecus hamlyni	4620	-415.545	92.85284	1.456366	1.278256	5.459082	1.326628
Cercopithecus lhoesti	5320	-426.265	-159.182	1.382017	1.321826	5.628633	1.066451
Cercopithecus mitis	5040	-265.778	22.34404	1.460898	1.329662	6.507775	3.23981
Cercopithecus mona	3980	-18.9674	-48.8368	1.414973	1.361606	5.797302	2.614741
Cercopithecus neglectus	5320	326.5348	63.76718	1.421604	1.324422	6.445605	1.057412
Cercopithecus nictitans	5260	208.1189	96.40782	1.491362	1.252144	6.352914	1.300129
Cercopithecus petaurista	3240	-176.73	-235.475	1.462398	1.208601	5.745028	2.989456
Cercopithecus pogonias	3580	5.664883	6.244149	1.371068	1.21485	6.10618	1.240693
Cercopithecus preussi	5140	265.3349	148.199	1.414973	1	4.777239	2.187805
Cercopithecus sclateri	3070	203.7033	76.20731	NA	1.193732	4.299515	2.325463
Cercopithecus solatus	5260	236.821	64.45834	NA	1.34005	3.999852	0.898024
Cercopithecus wolfi	3260	206.1269	132.0193	NA	1.188084	6.14766	1.343105
Cheirogaleus major	448	-415.015	91.12512	1.045323	1.108528	5.037816	4.331364
Cheirogaleus medius	197	-413.853	81.85667	1.206826	1.023872	5.168104	4.363437
Chiropotes albinasus	2800	155.8822	53.97053	1.243038	1.124715	5.821546	2.900919
Chiropotes satanas	2970	156.2289	51.20625	1.292256	1.041245	6.166072	1.528465
Chlorocebus aethiops	4030	76.47763	87.06072	1.437751	1.197525	7.151683	2.769295
Colobus angolensis	8990	296.2085	36.36885	1.547775	1.127796	6.408109	2.040666
Colobus guereza	10000	-44.0343	-118.02	1.456745	1.20457	6.515635	2.27086
Colobus polykomos	8610	-391.915	26.40924	1.507856	1.101293	5.7233	3.011125
Colobus satanas	9150	-173.553	-145.373	NA	1.18401	5.532912	1.405436
Daubentonia madagascariensis	2750	-80.1696	-9.91409	1.357935	1.022915	5.046502	4.335135
Erythrocebus patas	8010	297.3098	42.58821	1.396896	1.384122	6.813277	2.823951
Eulemur coronatus	1700	197.9012	72.87268	1.431364	1.051671	3.821791	3.614227
Eulemur fulvus	2390	-126.297	-118.922	1.515741	0.982975	5.372223	4.326139
Eulemur macaco	2480	230.0493	90.47542	1.500236	1.009502	3.969452	3.734817
Eulemur mongoz	1770	380.4572	37.22333	1.488057	0.978019	4.32123	4.014853
Eulemur rubriventer	2040	280.0493	110.4754	1.301003	1.010406	4.781582	4.296425
Euoticus elegantulus	296	-196.571	-196.743	NA	1.048636	5.919434	0.519569
Euoticus pallidus	278	-185.026	-208.101	NA	0.995245	4.677352	2.212332
Galago alleni	250	-81.2559	100.8821	1.079181	1.015324	5.615428	1.806093
Galago gallarum	214	128.0915	-18.9146	NA	NA	6.00826	0.574682

Galago matschiei	194	56.64346	-32.3696	NA	0.994054	5.459082	3.670111
Galago moholi	216	-170.41	-85.9954	1.218798	1.049541	6.718536	1.396774
Galago senegalensis	269	-175.408	-86.0116	1.225309	1.086666	6.970426	0.630986
Galagoides demidoff	67.1	-249.33	-240.68	1.120574	0.981047	6.674815	1.051438
Galagoides zanzibaricus	148	-137.702	-119.686	NA	1.049348	5.706121	3.441375
Gorilla gorilla	114000	370.7973	4.782838	1.713991	1.466217	5.821225	0.938277
Hapalemur aureus	1570	-80.345	-8.51569	NA	1.037674	3.000975	4.654131
Hapalemur griseus	956	-57.6053	-23.2241	1.246745	1.049063	5.059531	4.378873
Hapalemur simus	2040	-79.8046	-12.8247	1.245513	1.285986	3.000975	4.665091
Homo sapiens	58700	165.6374	60.92178	2.0463	1.075259	NA	NA
Hylobates agilis	5860	-342.848	74.05059	1.690196	1.011462	5.480796	0.408805
Hylobates concolor	6430	64.86846	-11.1907	1.613313	1.006818	5.155076	4.681239
Hylobates gabriellae	8500	229.6415	93.72751	NA	1	5.202848	3.832859
Hylobates hoolock	6700	-19.9432	-14.719	1.618048	1.00797	5.480796	4.841619
Hylobates klossii	5850	144.3696	116.1652	1.568202	0.977961	3.80442	1.460453
Hylobates lar	5630	-361.368	32.18081	1.645913	1.047823	5.560667	3.699652
Hylobates leucogenys	7320	158.6184	107.0196	1.644439	0.998669	4.677352	4.573021
Hylobates moloch	5870	19.77124	12.55746	1.60206	1.01128	4.647468	2.646954
Hylobates muelleri	5930	-334.006	102.513	1.716003	1.02739	5.836918	1.065568
Hylobates pileatus	5600	-412.038	67.38487	1.585461	1.005507	5.406966	3.594827
Hylobates syndactylus	10900	-5.10009	-41.8126	1.591065	1.044287	5.202848	0.378152
Indri indri	8650	-80.1859	-9.78401	NA	0.936659	4.573121	4.151561
Lagothrix flavicauda	8270	-356.44	-90.7838	NA	1.191873	4.503634	2.80937
Lagothrix lagotricha	6270	-296.831	-234.672	1.461799	1.065106	6.511655	1.888589
Lemur catta	2640	20.0017	10.72003	1.507856	1.027833	5.098617	4.801227
Leontopithecus caissara	605	-19.9432	-14.719	NA	1	3.504756	5.068193
Leontopithecus chrysomelas	574	229.6618	93.5649	1.32838	1.062827	4.503634	3.874927
Leontopithecus chrysopygus	656	20.05676	10.281	1.252853	1.001263	4.503634	4.689393
Leontopithecus rosalia	593	132.4559	46.28808	1.359551	1.020002	4.203971	4.701169
Lepilemur dorsalis	509	198.5164	87.83265	NA	NA	3.756647	3.713937
Lepilemur edwardsi	822	-68.257	-80.2311	NA	NA	4.729467	4.161078
Lepilemur leucopus	600	-160.928	-106.865	NA	1.009636	4.54272	4.949992
Lepilemur microdon	957	-145.29	-86.9547	NA	NA	4.781582	4.637261
Lepilemur mustelinus	671	-190.743	-113.345	NA	0.9469	4.620893	3.982675

Lepilemur ruficaudatus	763	-155.015	-109.15	NA	NA	4.76421	4.646053
Lepilemur septentrionalis	764	79.29475	96.49178	NA	NA	3.383154	3.586942
Lophocebus albigena	7360	82.53748	10.63767	1.556303	1.187465	6.456913	0.314356
Loris tardigradus	249	-80.3348	-8.59699	1.194514	1.024572	5.902062	3.684047
Macaca arctoides	9400	-35.9092	28.11783	1.471292	1.191602	6.453616	4.142935
Macaca assamensis	8560	-21.273	-105.117	1.49693	1.259967	6.186106	4.797277
Macaca cyclopis	5760	77.90792	107.5489	NA	1.121917	4.329271	4.890305
Macaca fascicularis	4590	363.044	86.73445	1.580241	1.218942	6.415836	2.034233
Macaca fuscata	10100	191.0861	122.3445	1.553276	1.155429	5.264781	5.990437
Macaca maura	7290	30.67305	35.43503	1.518514	1.286793	4.292357	2.231864
Macaca mulatta	6450	-158.812	86.53146	1.537819	1.1959	6.781949	5.007924
Macaca nemestrina	7870	-307.25	-308.077	1.504403	1.282005	6.400992	3.338995
Macaca nigra	7380	-196.53	-227.068	1.414973	1.31045	4.305428	1.007419
Macaca ochreata	2750	227.7177	109.3361	1.462398	1.427677	4.3782	2.169239
Macaca radiata	5000	-320.711	299.2419	1.477121	1.352861	5.762499	3.820424
Macaca silenus	6000	-141.711	-105.621	1.591065	1.193073	4.717745	3.632945
Macaca sinica	4660	-19.9432	-14.719	1.472025	1.322165	4.864791	2.806082
Macaca sylvanus	11500	128.6421	1.695128	1.407391	1.161895	4.942347	5.849603
Macaca thibetana	10600	-2.80589	63.24005	1.371068	1.305856	6.184353	5.327694
Macaca tonkeana	10100	-46.3579	146.6951	1.453318	1.286628	4.961216	1.053144
Mandrillus leucophaeus	14200	38.66252	44.03252	1.528917	1.286205	5.147076	2.284514
Mandrillus sphinx	16800	-415.036	88.78773	1.619771	1.611859	5.564733	0.872455
Microcebus coquereli	328	-258.991	55.80063	1.212853	0.97274	4.58615	4.283494
Microcebus murinus	66.6	-68.2957	-84.9221	1.225568	0.975847	5.224563	4.354308
Microcebus rufus	48.5	-68.1285	-96.7555	NA	1.004252	5.076902	4.396279
Miopithecus talapoin	1250	-225.916	118.4416	1.442245	1.126238	5.875646	2.772783
Nasalis concolor	7937.5	-136.328	-140.662	NA	1.296405	5.92812	NA
Nasalis larvatus	12300	-134.114	-143.689	1.285557	1.311027	3.000975	1.193087
Nycticebus coucang	971	-413.302	77.46635	1.320146	1.032196	6.579561	3.033004
Nycticebus pygmaeus	344	-250.562	95.35355	1.268344	1.108478	5.650171	4.116184
Otolemur crassicaudatus	1250	98.23089	40.10911	1.275311	1.043497	6.609962	3.835882
Otolemur garnettii	814	-104.73	53.84866	1.246745	1.049762	5.806517	2.148401
Pan paniscus	35200	-19.6822	-16.8003	1.676694	1.161435	5.519964	1.289837
Pan troglodytes	45100	19.86709	11.79322	1.802774	1.121373	6.228003	1.483881

Papio hamadryas	16900	-322.704	60.23579	1.562887	1.350706	6.921965	2.544065
Perodicticus potto	1080	-409.631	208.1975	1.390317	1.000638	6.527446	1.330699
Phaner furcifer	410	-19.9432	-14.719	1.39794	0.957978	4.729467	4.210316
Pithecia aequatorialis	2380	-355.178	224.0435	NA	NA	5.046502	1.570401
Pithecia albicans	2800	346.2052	101.5307	NA	1.035098	4.981358	2.046134
Pithecia irrorata	2320	249.492	75.18953	NA	1.042473	6.10618	2.855973
Pithecia monachus	2110	231.1506	-158.305	1.39794	1.086057	6.274788	2.508289
Pithecia pithecia	1670	-334.987	263.065	1.395763	1.105396	6.080097	1.709097
Pongo pygmaeus	52100	331.7388	2.141136	1.764662	1.465068	5.437167	1.155007
Presbytis comata	8430	223.7612	135.8814	NA	0.998907	4.936473	3.114079
Presbytis femoralis	6620	440.0835	135.474	NA	1.002761	5.678079	2.602277
Presbytis frontata	7000	-67.0024	-64.2474	NA	0.993647	5.406966	2.169711
Presbytis hosei	6160	-80.7366	-5.39368	NA	1.051325	5.406966	0.484538
Presbytis melalophos	6300	-424.986	-29.3775	1.30103	1.009515	5.248314	1.917672
Presbytis potenziani	6470	-404.736	274.1725	NA	0.988312	3.80442	1.827301
Presbytis rubicunda	6460	462.8571	38.35978	NA	1.013584	5.862976	1.460453
Presbytis thomasi	6410	19.58294	-38.9142	NA	0.993095	4.981358	1.193087
Procolobus badius	6690	-102.269	-124.15	NA	1.033505	6.194186	2.111779
Procolobus pennantii	9160	26.50069	-41.2314	NA	1.084307	6.184349	1.318843
Procolobus preussi	8910	-21.2016	86.5637	NA	NA	4.503108	2.273916
Procolobus rufomitratus	8070	326.0539	-9.83067	NA	NA	3.50311	1.607098
Procolobus verus	3980	-20.7325	-58.4262	NA	1.061095	5.480218	2.646879
Propithecus diadema	6600	275.7598	-30.0538	1.30103	0.985042	4.798954	4.227969
Propithecus tattersalli	3540	-80.1064	-10.4182	1.30103	0.977249	3.000975	3.61755
Propithecus verreauxi	3650	-101.175	-124.898	1.386231	1.00347	5.298393	4.480934
Pygathrix avunculus	9550	-74.8861	4.825708	NA	1.288161	3.98248	3.882443
Pygathrix bieti	9120	443.8835	109.9058	NA	1.208714	4.408089	4.697857
Pygathrix brelichi	11000	443.3125	114.4587	NA	1.364734	3.98248	5.356414
Pygathrix nemaeus	12300	20.21584	9.012686	1.258278	1.14305	5.650171	5.227811
Pygathrix roxellana	13500	-354.325	255.7585	1.469822	1.265079	4.503634	5.685842
Saguinus bicolor	465	-99.9609	-116.605	1.278754	0.997587	4.654465	1.32007
Saguinus fuscicollis	394	-55.3287	-133.146	1.396199	0.982667	6.302924	2.299404
Saguinus geoffroyi	493	439.696	66.06348	1.311754	0.9825	4.790837	2.623485
Saguinus imperator	410	-159.663	-137.495	1.308564	0.998974	5.317108	3.038435
Saguinus inustus	803	265.2262	9.335765	NA	0.904868	5.545941	0.80456
Saguinus	510	-21.1812	86.40109	1.3117	0.962058	5.405249	2.531461

labiatus				54			
Saguinus leucopus	457	-388.417	-85.1336	1.181844	1.003014	4.548226	2.510234
Saguinus midas	541	-37.1302	-111.255	1.233631	0.950267	6.192038	0.417771
Saguinus mystax	559	-7.82462	-56.6783	1.30103	0.97584	5.752197	2.497935
Saguinus nigricollis	450	82.49402	39.09239	1.231724	0.983763	5.223492	1.403004
Saguinus oedipus	464	443.7612	110.8814	1.297761	1.014256	4.757709	3.037589
Saguinus tripartitus	385	-50.9263	-96.8815	0.778151	NA	4.803297	1.414444
Saimiri boliviensis	805	-48.518	-115.65	1.481443	1.163334	6.010636	3.324171
Saimiri oerstedii	714	290.2533	35.09937	NA	1.137893	3.868516	2.962149
Saimiri sciureus	750	-221.734	-235.442	1.40824	1.088731	6.628161	0.804535
Saimiri ustus	890	-194.24	-235.394	NA	1.073608	5.823889	2.997514
Saimiri vanzolinii	784	-146.418	-227.963	NA	1.209095	3.98248	1.510831
Semnopithecus entellus	12600	-7.44547	-23.113	1.431364	1.160525	6.513839	4.503022
Tarsius bancanus	114	-170.598	-94.4994	1.150756	1.04599	5.949834	0.75026
Tarsius dianae	111	-19.9432	-14.719	NA	NA	3.20075	NA
Tarsius pumilus	122.5	17.72103	24.17423	NA	1	4.203971	1.585842
Tarsius spectrum	166	379.6822	43.4023	1.079181	1.046257	5.354373	1.021481
Tarsius syrichta	116	-256.805	-224.872	1.168792	1.070008	5.046502	1.855028
Theropithecus gelada	16000	-414.995	90.96252	1.441302	1.278568	5.214977	3.310374
Trachypithecus auratus	9720	376.6946	162.6282	1.49276	1	5.202848	2.073295
Trachypithecus cristatus	7130	-80.3348	-8.59699	1.451786	1.072139	6.135137	2.365599
Trachypithecus francoisi	8170	-124.509	122.2219	1.419956	1.017765	5.167284	4.664875
Trachypithecus geei	8360	-291.665	-210.995	NA	1.06338	3.80442	5.176221
Trachypithecus johnii	10600	-415.484	94.86503	1.531479	1.048652	3.98248	3.279724
Trachypithecus obscurus	7120	185.9263	138.4834	1.5302	1.124604	5.36489	2.612158
Trachypithecus phayrei	7700	-80.3348	-8.59699	1.451786	1.112228	6.11177	4.526497
Trachypithecus pileatus	11200	-194.469	-732.28	1.401401	1.103079	5.650171	4.983133
Trachypithecus vetulus	7860	192.473	41.28737	1.416641	1.151686	4.903185	2.835336
Varecia variegata	3870	366.5315	-26.0709	1.389166	1.022716	4.859755	4.3675
	Distance to Continental Centroid	Population Density	Home Range Size	Group Size	Solitariness	Activity Period	Terrestriality
Allenopithecus nigroviridis	86221.21	NA	NA	1.60206	no	Diurnal	terres
Allocebus trichotis	2935800	NA	NA	NA	yes	Nocturnal	arb
Alouatta belzebul	936187	1.210429	NA	1.023252	no	Diurnal	arb
Alouatta caraya	1422481	1.974934	0.770852	0.929419	no	Diurnal	arb

Alouatta coibensis	2709096	NA	NA	1.100371	no	Diurnal	arb
Alouatta fusca	2282677	2.027287	0.754016	0.946125	no	Diurnal	arb
Alouatta palliata	3159899	1.624307	1.47273	1.154323	no	Diurnal	arb
Alouatta pigra	4227805	1.013892	1.774593	0.682747	no	Diurnal	arb
Alouatta sara	989647.9	NA	NA	NA	NA	Diurnal	arb
Alouatta seniculus	991673.9	1.789707	1.07616	0.867271	no	Diurnal	arb
Aotus azarai	1307853	1.484427	NA	0.582631	no	Nocturnal	arb
Aotus brumbacki	1620133	NA	NA	NA	NA	Nocturnal	arb
Aotus hershkovitzi	1620133	NA	NA	NA	NA	Nocturnal	arb
Aotus infulatus	844269.4	NA	NA	0.60206	no	Nocturnal	arb
Aotus lemurinus	2213970	1.652245	NA	0.544068	no	Nocturnal	arb
Aotus miconax	1730544	NA	NA	NA	NA	Nocturnal	arb
Aotus nancymaae	1294925	1.524698	0.963788	0.60206	no	Nocturnal	arb
Aotus nigriceps	551433.1	1.590922	NA	0.531479	no	Nocturnal	arb
Aotus trivirgatus	1044663	1.455491	0.815171	0.544068	no	Nocturnal	arb
Aotus vociferans	1313082	1.306036	NA	0.518514	no	Nocturnal	arb
Arctocebus aureus	759905	NA	NA	NA	NA	Nocturnal	NA
Arctocebus calabarensis	1447403	NA	NA	NA	yes	Nocturnal	arb
Ateles belzebuth	1313738	1.198038	2.556564	1.352183	no	Diurnal	arb
Ateles chamek	722197.8	0.667896	2.274152	NA	NA	Diurnal	arb
Ateles fusciceps	2237577	NA	NA	1.356981	no	Diurnal	arb
Ateles geoffroyi	3920838	1.243361	2.142952	1.547159	no	Diurnal	arb
Ateles marginatus	726966.1	NA	NA	NA	NA	Diurnal	NA
Ateles paniscus	1098542	1.375214	2.321065	1.510545	no	Diurnal	arb
Avahi laniger	2935800	1.770337	0.289399	0.455457	no	Nocturnal	arb
Brachyteles arachnoides	2447380	0.930674	2.292526	1.295933	no	Diurnal	arb
Cacajao calvus	1241316	1.250907	2.726999	1.477121	no	Diurnal	arb
Cacajao melanocephalus	1077223	NA	3	1.477121	no	Diurnal	arb
Callicebus brunneus	536729.8	NA	0.838849	0.574031	no	Diurnal	arb
Callicebus caligatus	254443	NA	NA	NA	NA	Diurnal	NA
Callicebus cinerascens	215464.7	NA	NA	NA	NA	Diurnal	NA
Callicebus cupreus	954711.8	0.644544	NA	0.491362	no	Diurnal	NA
Callicebus donacophilus	1117889	1.495544	NA	0.568202	no	Diurnal	arb
Callicebus dubius	804478.8	NA	NA	NA	NA	Diurnal	NA
Callicebus	468915.5	NA	NA	NA	NA	Diurnal	NA

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Callicebus modestus	934459.7	NA	NA	NA	NA	Diurnal	NA
Callicebus moloch	689338.3	1.425254	0.624916	0.50965	no	Diurnal	arb
Callicebus oenanthe	1785573	NA	NA	NA	NA	Diurnal	NA
Callicebus olallae	1122167	NA	NA	NA	NA	Diurnal	NA
Callicebus personatus	2431759	1.160781	0.811647	0.579784	no	Diurnal	arb
Callicebus torquatus	813102.7	1.144575	1.138338	0.575957	no	Diurnal	arb
Callimico goeldii	1234049	0.319245	1.648736	0.869232	no	Diurnal	arb
Callithrix argentata	904209.2	NA	1.217484	0.977724	no	Diurnal	arb
Callithrix aurita	2327277	NA	1.137506	0.778151	no	Diurnal	NA
Callithrix flaviceps	2489631	1.175679	1.550228	0.991226	no	Diurnal	NA
Callithrix geoffroyi	2385340	NA	NA	NA	NA	Diurnal	arb
Callithrix humeralifera	124422.5	1.478566	1.292962	1.055951	no	Diurnal	arb
Callithrix jacchus	2070847	2.929419	0.832558	0.927712	no	Diurnal	arb
Callithrix kuhlii	2373435	1.770852	1	0.788875	no	Diurnal	NA
Callithrix penicillata	1688948	NA	0.463055	0.863323	no	Diurnal	arb
Cebuella pygmaea	1124348	1.357464	-0.274	0.78295	no	Diurnal	arb
Cebus albifrons	936877.3	1.236264	2.078979	1.196821	no	Diurnal	arb
Cebus apella	498945.1	1.410357	2.34815	1.073107	no	Diurnal	arb
Cebus capucinus	3041344	1.163894	1.841093	1.31492	no	Diurnal	arb
Cebus olivaceus	1292754	1.39794	2.409933	1.197281	no	Diurnal	arb
Cercocebus agilis	259414.2	NA	NA	1.220108	no	Diurnal	arb
Cercocebus galeritus	1620133	1.922553	1.943823	1.276845	no	Diurnal	terres
Cercocebus torquatus	2355135	1.966611	2.395326	1.4133	no	Diurnal	terres
Cercopithecus ascanius	236447	1.993774	1.459953	1.430559	no	Diurnal	arb
Cercopithecus campbelli	3112492	1.176091	1.185637	1.099796	no	Diurnal	arb
Cercopithecus cephus	759059.3	1.345839	1.535289	0.973128	no	Diurnal	arb
Cercopithecus diana	3016563	1.542618	2.164353	1.355068	no	Diurnal	arb
Cercopithecus dryas	230721.4	NA	NA	NA	NA	Diurnal	NA
Cercopithecus erythrogaster	1906845	NA	NA	1.190332	no	Diurnal	arb
Cercopithecus erythrotis	1381529	NA	NA	1.290035	no	Diurnal	arb
Cercopithecus hamlyni	722810.2	NA	NA	NA	NA	Diurnal	arb
Cercopithecus lhoesti	773384.1	0.759668	2.929419	1.240549	no	Diurnal	terres
Cercopithecus mitis	1270874	1.920921	1.737826	1.247052	no	Diurnal	arb

Cercopithecus mona	1754500	NA	0.477121	NA	NA	Diurnal	arb
Cercopithecus neglectus	171266.7	1.776889	0.869232	0.791223	no	Diurnal	terres
Cercopithecus nictitans	1089867	1.423306	2.169919	1.133539	no	Diurnal	arb
Cercopithecus petaurista	3105643	NA	1.612784	1.079181	no	Diurnal	arb
Cercopithecus pogonias	696148	1.118344	2.158965	1.117271	no	Diurnal	arb
Cercopithecus preussi	1410704	NA	NA	0.69897	no	Diurnal	terres
Cercopithecus sclateri	1593805	NA	NA	1.352183	no	Diurnal	NA
Cercopithecus solatus	904468.1	NA	NA	1.070038	no	Diurnal	terres
Cercopithecus wolfi	298954	1.645422	NA	1.079181	no	Diurnal	arb
Cheirogaleus major	2935800	1.823583	0.60206	NA	yes	Nocturnal	arb
Cheirogaleus medius	2935800	2.348844	0.573064	0.327359	no	Nocturnal	arb
Chiropotes albinasus	340062.2	0.875061	2.477121	1.342423	no	Diurnal	arb
Chiropotes satanas	1437444	1.242965	2.380362	1.064458	no	Diurnal	arb
Chlorocebus aethiops	183722.1	1.738212	1.825944	1.426511	no	Diurnal	terres
Colobus angolensis	581931.6	1.83123	2.60206	1.045323	no	Diurnal	arb
Colobus guereza	939678.6	2.137497	1.296299	0.937852	no	Diurnal	arb
Colobus polykomos	3459924	1.371068	1.518126	1.084129	no	Diurnal	arb
Colobus satanas	964635.5	1.300165	1.853981	1.167317	no	Diurnal	arb
Daubentonia madagascariensis	2935800	NA	1.682354	NA	yes	Nocturnal	arb
Erythrocebus patas	1684412	-0.1549	3.579381	1.441564	no	Diurnal	terres
Eulemur coronatus	2935800	2.10618	0.919078	0.924279	no	Diurnal	arb
Eulemur fulvus	2935800	2.660787	1.442903	0.953438	no	Diurnal	arb
Eulemur macaco	2935800	2.11059	0.732394	0.946943	no	Diurnal	arb
Eulemur mongoz	2935800	NA	0.80529	0.546131	no	Diurnal	arb
Eulemur rubriventer	2935800	1.477121	1.336768	0.50515	no	Diurnal	arb
Euoticus elegantulus	757480.7	1.243038	NA	NA	yes	Nocturnal	arb
Euoticus pallidus	1317913	NA	NA	NA	yes	Nocturnal	NA
Galago alleni	1015735	1.243038	1.270006	0.30103	no	Nocturnal	arb
Galago gallarum	2207496	NA	NA	NA	NA	Nocturnal	NA
Galago matschiei	942111	NA	NA	NA	yes	Nocturnal	NA
Galago moholi	1596729	2.230865	0.86697	NA	yes	Nocturnal	arb
Galago senegalensis	1058577	1.491362	0.975432	NA	yes	Nocturnal	arb
Galagoides demidoff	496939	1.812913	0.072785	NA	yes	Nocturnal	arb
Galagoides zanzibaricus	2089457	2.227887	0.351699	NA	yes	Nocturnal	arb

Gorilla gorilla	611305.5	-0.13116	3.253687	0.971682	no	Diurnal	terres
Hapalemur aureus	2935800	NA	1.766703	0.477121	no	Diurnal	arb
Hapalemur griseus	2935800	1.824996	0.788128	0.486667	no	Diurnal	arb
Hapalemur simus	2935800	NA	2	0.90309	no	Diurnal	arb
Homo sapiens	NA	NA	NA	NA	NA	Diurnal	terres
Hylobates agilis	2453123	1.276462	1.451018	0.643453	no	Diurnal	arb
Hylobates concolor	896036.3	NA	1.942008	0.607455	no	Diurnal	arb
Hylobates gabriellae	938064.9	NA	1.544068	NA	NA	Diurnal	NA
Hylobates hoolock	3324793	0.845098	1.573742	0.544068	no	Diurnal	arb
Hylobates klossii	2889224	NA	1.264453	0.550228	no	Diurnal	arb
Hylobates lar	1125881	0.879127	1.564333	0.5864	no	Diurnal	arb
Hylobates leucogenys	2232847	0.462398	NA	0.740363	no	Diurnal	arb
Hylobates moloch	1620133	0.782047	1.232149	0.518514	no	Diurnal	arb
Hylobates muelleri	1620133	1.053078	1.556303	0.531479	no	Diurnal	arb
Hylobates pileatus	1620133	1.374748	1.539016	0.574031	no	Diurnal	arb
Hylobates syndactylus	1620133	0.484579	1.481423	0.572097	no	Diurnal	arb
Indri indri	2935800	0.948366	1.275229	0.50515	no	Diurnal	arb
Lagothrix flavicauda	1752852	NA	NA	0.959041	no	Diurnal	arb
Lagothrix lagotricha	1294917	0.941234	2.706505	1.254669	no	Diurnal	arb
Lemur catta	2935800	2.203416	1.132795	1.202761	no	Diurnal	terres
Leontopithecus caissara	2467480	NA	NA	0.812913	no	Diurnal	NA
Leontopithecus chrysomelas	2345173	NA	1.649943	0.770852	no	Diurnal	arb
Leontopithecus chrysopygus	2147309	NA	2.005093	0.556303	no	Diurnal	arb
Leontopithecus rosalia	2593144	NA	1.531142	0.822822	no	Diurnal	arb
Lepilemur dorsalis	2935800	NA	NA	NA	yes	Nocturnal	NA
Lepilemur edwardsi	2935800	1.755875	0.018713	NA	yes	Nocturnal	NA
Lepilemur leucopus	2935800	2.66701	-0.6338	NA	yes	Nocturnal	arb
Lepilemur microdon	2935800	NA	NA	NA	yes	Nocturnal	NA
Lepilemur mustelinus	2935800	2.125839	-0.29747	NA	yes	Nocturnal	arb
Lepilemur ruficaudatus	2935800	2.404771	NA	NA	yes	Nocturnal	NA
Lepilemur septentrionalis	2935800	2.226493	0	NA	yes	Nocturnal	NA
Lophocebus albigena	192126.9	1.212748	2.261531	1.281033	no	Diurnal	arb
Loris tardigradus	1947115	NA	0	NA	yes	Nocturnal	arb
Macaca arctoides	1129622	NA	NA	NA	NA	Diurnal	terres

Macaca assamensis	468954.5	NA	NA	1.322219	no	Diurnal	arb
Macaca cyclopis	2765933	NA	1.810569	1.258877	no	Diurnal	terres
Macaca fascicularis	2156246	1.672801	1.924343	1.445215	no	Diurnal	arb
Macaca fuscata	4695737	1.498311	2.294208	1.688815	no	Diurnal	terres
Macaca maura	3807866	1.676694	1.39794	1.376577	no	Diurnal	terres
Macaca mulatta	593420.5	1.804823	2.820672	1.640647	no	Diurnal	terres
Macaca nemestrina	1306084	1.370351	2.491065	1.41761	no	Diurnal	terres
Macaca nigra	3700128	1.63098	2.390346	1.502086	no	Diurnal	terres
Macaca ochreata	3938333	1.176091	NA	NA	NA	Diurnal	arb
Macaca radiata	1993340	1.544068	2.239682	1.434569	no	Diurnal	terres
Macaca silenus	2105084	NA	1.913997	1.380211	no	Diurnal	arb
Macaca sinica	2002824	1.74194	1.70898	1.338954	no	Diurnal	arb
Macaca sylvanus	4639199	1.277463	2.696542	1.343409	no	Diurnal	terres
Macaca thibetana	1898213	NA	2.477121	1.407957	no	Diurnal	terres
Macaca tonkeana	3564843	1	NA	NA	NA	Diurnal	terres
Mandrillus leucophaeus	1390733	NA	3.653213	1.230449	no	Diurnal	terres
Mandrillus sphinx	961509.1	NA	3.553176	1.666206	no	Diurnal	terres
Microcebus coquereli	2935800	2.086241	0.490484	NA	yes	Nocturnal	arb
Microcebus murinus	2935800	2.628403	0.273741	NA	yes	Nocturnal	arb
Microcebus rufus	2935800	2.013566	NA	NA	yes	Nocturnal	arb
Miopithecus talapoin	789444.6	1.799022	2.0863	2.031004	no	Diurnal	arb
Nasalis concolor	2486554	1.048645	2.175361	0.875061	no	Diurnal	NA
Nasalis larvatus	2916502	1.332705	2.253294	0.877947	no	Diurnal	arb
Nycticebus coucang	1312525	1.30103	NA	NA	yes	Nocturnal	arb
Nycticebus pygmaeus	1153003	NA	NA	NA	yes	Nocturnal	arb
Otolemur crassicaudatus	1476111	1.972155	0.906243	NA	yes	Nocturnal	arb
Otolemur garnettii	1835861	1.562293	1.163753	NA	yes	Nocturnal	arb
Pan paniscus	100998.4	0.230803	3.436928	1.867025	no	Diurnal	terres
Pan troglodytes	698519.6	0.329022	3.48181	1.719515	no	Diurnal	terres
Papio hamadryas	295154.4	0.540437	3.304896	1.211299	no	Diurnal	terres
Perodicticus potto	635446.3	1.049218	1.137598	NA	yes	Nocturnal	arb
Phaner furcifer	2935800	2.488553	0.596597	0.30103	no	Nocturnal	arb
Pithecia aequatorialis	1675281	NA	NA	NA	NA	Diurnal	NA
Pithecia albicans	507424.8	0.973128	2.363988	0.662758	no	Diurnal	arb

Pithecia irrorata	456956.9	1.118285	NA	0.643453	no	Diurnal	NA
Pithecia monachus	1329274	0.929583	1.620656	0.60206	no	Diurnal	arb
Pithecia pithecia	1076585	0.76502	0.845098	0.430156	no	Diurnal	arb
Pongo pygmaeus	2754463	0.454084	2.789266	NA	yes	Diurnal	arb
Presbytis comata	2898755	1.433144	1.478676	0.954243	no	Diurnal	arb
Presbytis femoralis	1620133	NA	1.113943	0.69897	no	Diurnal	NA
Presbytis frontata	3048190	NA	NA	1.09691	no	Diurnal	arb
Presbytis hosei	2875169	NA	1.544068	0.845098	no	Diurnal	arb
Presbytis melalophos	1033163	1.785181	1.353937	1.092838	no	Diurnal	arb
Presbytis potenziani	2486554	NA	1.307317	0.568202	no	Diurnal	arb
Presbytis rubicunda	2949211	NA	1.871289	0.773299	no	Diurnal	arb
Presbytis thomasi	1712493	1.370497	1.42757	1	no	Diurnal	arb
Procolobus badius	550779.3	2.239929	1.774482	1.52277	no	Diurnal	arb
Procolobus pennantii	2920164	NA	NA	1.526339	no	Diurnal	NA
Procolobus preussi	1620133	NA	NA	1.60206	no	Diurnal	NA
Procolobus rufomitratus	1620133	2.27054	0.954243	1.443263	no	Diurnal	NA
Procolobus verus	1620133	1.322219	1.440778	0.835691	no	Diurnal	arb
Propithecus diadema	2935800	0.837562	1.560191	0.70757	no	Diurnal	arb
Propithecus tattersalli	2935800	NA	1.050185	0.694605	no	Diurnal	arb
Propithecus verreauxi	2935800	2.141655	0.726316	0.73706	no	Diurnal	arb
Pygathrix avunculus	1108485	0.697807	3.440049	1.365207	no	Diurnal	arb
Pygathrix bieti	1008381	0.453958	3.510362	1.424882	no	Diurnal	NA
Pygathrix brelichi	1653887	1.098831	3.252748	1.884144	no	Diurnal	arb
Pygathrix nemaeus	1848186	NA	NA	1.186674	no	Diurnal	arb
Pygathrix roxellana	1644842	0.683197	3.518382	2.099819	no	Diurnal	terres
Saguinus bicolor	465092.5	NA	1.079181	0.826075	no	Diurnal	arb
Saguinus fuscicollis	1073271	1.286483	1.490966	0.716003	no	Diurnal	arb
Saguinus geoffroyi	2482264	1.329666	1.418759	0.838849	no	Diurnal	arb
Saguinus imperator	1197379	1.041309	1.62376	0.72632	no	Diurnal	arb
Saguinus inustus	479397.8	NA	NA	NA	NA	Diurnal	arb
Saguinus labiatus	2204017	1.131701	1.469794	0.781755	no	Diurnal	arb
Saguinus leucopus	737424.1	1.181844	NA	0.78533	no	Diurnal	arb
Saguinus midas	1085033	1.320885	0.954243	0.79588	no	Diurnal	arb
Saguinus mystax	918733.6	1.481833	1.506756	0.739375	no	Diurnal	arb

Saguinus nigricollis	1455356	1.297884	1.63092	0.799341	no	Diurnal	arb
Saguinus oedipus	2409988	1.553883	1.155772	0.834897	no	Diurnal	arb
Saguinus tripartitus	1709881	NA	0.929419	NA	NA	Diurnal	arb
Saimiri boliviensis	933562.1	1.439614	NA	1.778151	no	Diurnal	arb
Saimiri oerstedii	3004527	1.919078	1.623668	1.627195	no	Diurnal	arb
Saimiri sciureus	3005225	1.791394	2.292625	1.521705	no	Diurnal	arb
Saimiri ustus	804035.5	NA	NA	NA	NA	Diurnal	NA
Saimiri vanzolinii	332781.6	NA	0.439333	1.60206	no	Diurnal	NA
Semnopithecus entellus	686792.6	1.586257	2.065813	1.361728	no	Diurnal	terres
Tarsius bancanus	1643537	1.794136	0.591728	NA	yes	Nocturnal	arb
Tarsius dianae	2776018	NA	-0.18709	NA	yes	Nocturnal	NA
Tarsius pumilus	3596355	NA	0.176091	NA	yes	Nocturnal	arb
Tarsius spectrum	3701384	2.411506	0.354026	0.42529	no	Nocturnal	arb
Tarsius syrichta	3296104	NA	0.176091	NA	yes	Nocturnal	arb
Theropithecus gelada	2369170	1.79212	2.299943	1	no	Diurnal	terres
Trachypithecus auratus	2741430	1.623249	0.765296	1	no	Diurnal	arb
Trachypithecus cristatus	2179676	2.161368	1.280275	1.403121	no	Diurnal	arb
Trachypithecus francoisi	1130045	0.69897	NA	1.20412	no	Diurnal	terres
Trachypithecus geei	985384.7	0.414973	2.574031	1.073107	no	Diurnal	arb
Trachypithecus johnii	2125405	NA	1.968196	1.136192	no	Diurnal	arb
Trachypithecus obscurus	1550140	1.67415	1.431188	1.22617	no	Diurnal	arb
Trachypithecus phayrei	473092.6	NA	1.720159	1.177536	no	Diurnal	arb
Trachypithecus pileatus	602452.5	1.839896	1.537382	0.94035	no	Diurnal	arb
Trachypithecus vetulus	2020419	NA	0.690629	0.939519	no	Diurnal	arb
Varecia variegata	2935800	2.026873	2.043901	0.74364	no	Diurnal	arb
	Habitat	Diet Class	Gestation Duration	Litter size	Mating System	No of Males in Group	
Allenopithecus nigroviridis	forest	frugivore	NA	1	NA	MM	
Allocebus trichotis	forest	insectivore	7.745967	1	Mon	SM	
Alouatta belzebul	forest	folivore, frugivore	13.67479	1	NA	MM	
Alouatta caraya	forest	folivore, frugivore	13.67479	1	NA	MM	
Alouatta coibensis	forest	folivore, frugivore	13.67479	1	PG	MM	
Alouatta fusca	forest	folivore, frugivore	13.67479	1	NA	MM	
Alouatta palliata	forest	folivore, frugivore	13.64063	1	PG	MM	
Alouatta pigra	forest	folivore, frugivore	13.58921	1	NA	MM	

Alouatta sara	forest	folivore	13.41641	1	PG	NA	
Alouatta seniculus	forest-savanna	folivore, frugivore	13.80821	1.066667	PG	MM	
Aotus azarai	forest	frugivore	11.37981	1	Mon	SM	
Aotus brumbacki	forest	frugivore	11.24722	1	Mon	SM	
Aotus hershkovitzi	forest	frugivore	11.24722	1	Mon	SM	
Aotus infulatus	forest	frugivore	11.24722	1	Mon	SM	
Aotus lemurinus	forest	frugivore	11.56143	1	Mon	SM	
Aotus miconax	forest	frugivore	11.24722	1	Mon	SM	
Aotus nancymaae	forest	frugivore	11.53256	1	Mon	SM	
Aotus nigriceps	forest	frugivore	11.24722	1	Mon	SM	
Aotus trivirgatus	forest	frugivore	11.6857	1.016847	Mon	SM	
Aotus vociferans	forest	frugivore	11.24722	1	Mon	SM	
Arctocebus aureus	NA	insectivore	11.61895	1	NA	NA	
Arctocebus calabarensis	forest	insectivore	11.55783	1	PG	SM	
Ateles belzebuth	forest	frugivore	13.42262	1	PGA	MM	
Ateles chamek	NA	frugivore	15.0333	1	NA	MM	
Ateles fusciceps	forest	frugivore	15.07758	1	NA	MM	
Ateles geoffroyi	forest	frugivore	15.16575	1	NA	MM	
Ateles marginatus	NA	frugivore	15	1	NA	NA	
Ateles paniscus	forest	frugivore	15.13688	1	NA	MM	
Avahi laniger	forest	folivore	12.68858	1	Mon	SM	
Brachyteles arachnoides	forest	folivore	15.0333	1.007814	PGA	MM	
Cacajao calvus	forest	frugivore	13.49074	1	Mon	MM	
Cacajao melanocephalus	forest	frugivore	13.52775	1	NA	NA	
Callicebus brunneus	forest	frugivore	12.4499	1	Mon	MM	
Callicebus caligatus	forest	frugivore	12.4499	1	NA	NA	
Callicebus cinerascens	forest	frugivore	12.4499	1	NA	NA	
Callicebus cupreus	forest	frugivore	11.42074	1	Mon	NA	
Callicebus donacophilus	NA	frugivore	12.4499	1	NA	MM	
Callicebus dubius	forest	frugivore	12.4499	1	NA	NA	
Callicebus hoffmannsi	forest	frugivore	12.4499	1	NA	NA	
Callicebus modestus	forest	frugivore	12.4499	1	NA	NA	
Callicebus moloch	forest	frugivore	12.75735	1	Mon	SM	
Callicebus oenanthe	forest	frugivore	12.4499	1	NA	NA	
Callicebus olallae	forest	frugivore	12.4499	1	NA	NA	
Callicebus personatus	forest	frugivore	12.95183	1	Mon	MM	
Callicebus torquatus	forest	frugivore	12.4499	1	Mon	SM	

Callimico goeldii	forest	frugivore	12.34234	1.010793	PG	SM	
Callithrix argentata	forest	insectivore	12.02082	1.957778	NA	SM	
Callithrix aurita	forest	frugivore	12.40967	2	NA	NA	
Callithrix flaviceps	NA	gummnivore	12.04159	2	Mon	NA	
Callithrix geoffroyi	forest	gummnivore	12.26784	2	Mon	NA	
Callithrix humeralifera	forest	omnivore	12.13466	2	PA	NA	
Callithrix jacchus	forest	frugivore	12.05543	2.09996	Mon	SM	
Callithrix kuhlii	forest	frugivore	11.58123	2	Mon	NA	
Callithrix penicillata	forest-savanna	gummnivore	12.24745	2	Mon	NA	
Cebuella pygmaea	forest	gummnivore	11.4528	1.943333	Mon	MM	
Cebus albifrons	forest	frugivore	12.51	1	NA	MM	
Cebus apella	forest	frugivore	12.48666	1.189517	NA	MM	
Cebus capucinus	forest	omnivore	12.72792	1	NA	MM	
Cebus olivaceus	forest	omnivore	12.68858	1	PG	MM	
Cercocebus agilis	forest	frugivore	13.60147	1	NA	MM	
Cercocebus galeritus	forest	frugivore	13.18459	1	NA	SMM	
Cercocebus torquatus	forest	frugivore	12.96791	1	NA	SMM	
Cercopithecus ascanius	forest	frugivore	12.62933	1	PG	NA	
Cercopithecus campbelli	forest	frugivore	13.45239	1	NA	SM	
Cercopithecus cephus	forest	frugivore	13.08689	1	PG	SM	
Cercopithecus diana	forest	folivore, frugivore	12.34909	1	PG	SM	
Cercopithecus dryas	forest	frugivore	12.34909	1	NA	NA	
Cercopithecus erythrogaster	forest	frugivore	12.34909	1	NA	SM	
Cercopithecus erythrotis	forest	omnivore	12.34909	1	NA	SM	
Cercopithecus hamlyni	forest	frugivore	12.95183	1	NA	SM	
Cercopithecus lhoesti	forest	frugivore	12.34909	1	NA	SM	
Cercopithecus mitis	forest	frugivore	11.80184	1	PG	SM	
Cercopithecus mona	forest	frugivore	12.95183	1	PG	SM	
Cercopithecus neglectus	forest	frugivore	13.37286	1.001328	PG	SM	
Cercopithecus nictitans	forest	frugivore	13.0767	1	PG	SM	
Cercopithecus petaurista	forest	frugivore	12.94218	1	PG	SM	
Cercopithecus pogonias	forest	frugivore	12.92285	1	PG	SM	
Cercopithecus preussi	forest	frugivore	12.34909	1	PG	SM	
Cercopithecus sclateri	forest	frugivore	12.34909	1	PG	MM	
Cercopithecus solatus	forest	frugivore	12.34909	1	PG	SM	

Cercopithecus wolfi	forest	frugivore	12.34909	1	PG	SM	
Cheirogaleus major	forest	frugivore	8.266398	2.066667	Mon	MM	
Cheirogaleus medius	forest	frugivore	7.833688	2.25	Mon	NA	
Chiropotes albinasus	forest	frugivore	12.64252	1	NA	MM	
Chiropotes satanas	forest	frugivore	12.49166	1	NA	MM	
Chlorocebus aethiops	forest-savanna	omnivore	12.73905	1	PG	MM	
Colobus angolensis	forest	folivore	12.74755	1	PG	SM	
Colobus guereza	forest	folivore	13.18459	1	PG	SM	
Colobus polykomos	forest	folivore	13.30445	1	PG	SM	
Colobus satanas	forest	gramnivore	13.96424	1	PGA	SM	
Daubentonia madagascariensis	forest	insectivore	12.89703	1	PG	SM	
Erythrocebus patas	forest-savanna	omnivore	12.94797	1.003327	PG	SM	
Eulemur coronatus	forest	frugivore	11.18928	1.346154	PG	MM	
Eulemur fulvus	forest	folivore, frugivore	10.87811	1.061931	NA	MM	
Eulemur macaco	forest	folivore	11.16915	1.04305	PG	MM	
Eulemur mongoz	forest	folivore, frugivore	11.41928	1.062037	Mon	SM	
Eulemur rubriventer	forest	folivore, frugivore	11.35782	1	Mon	SM	
Euoticus elegantulus	forest	gummnivore	11.33578	1	PG	NA	
Euoticus pallidus	NA	gummnivore	10.95445	1	NA	NA	
Galago alleni	forest	frugivore	11.53256	1.2	PG	NA	
Galago gallarum	NA	frugivore	NA	2	NA	NA	
Galago matschiei	NA	frugivore	NA	1	NA	NA	
Galago moholi	forest-savanna	insectivore	11.09054	2	Mon	SM	
Galago senegalensis	forest-savanna	gummnivore	11.21903	1.45129	PG	SM	
Galagoides demidoff	forest	insectivore	10.55936	1.303281	PG	SM	
Galagoides zanzibaricus	forest	insectivore	10.95445	1.295	PG	SM	
Gorilla gorilla	forest	folivore	16.15498	1.018028	PG	SM	
Hapalemur aureus	forest	folivore	11.74734	1	Mon	SM	
Hapalemur griseus	forest	folivore	11.83216	1.114286	Mon	SM	
Hapalemur simus	forest	folivore	12.06234	1	NA	NA	
Homo sapiens	forest-savanna	omnivore	16.56804	1	Mon	SM	
Hylobates agilis	forest	frugivore	14.61164	1	Mon	SM	
Hylobates concolor	forest	frugivore	14.63728	1	Mon	SM	
Hylobates gabriellae	forest	frugivore	14.61164	1	Mon	SM	
Hylobates hoolock	forest	frugivore	14.61164	1	Mon	SM	

Hylobates klossii	forest	frugivore	14.63301	1	Mon	SM	
Hylobates lar	forest	frugivore	14.62399	1	Mon	SM	
Hylobates leucogenys	NA	frugivore	14.61164	1	NA	NA	
Hylobates moloch	forest	frugivore	15.28071	1	Mon	SM	
Hylobates muelleri	forest	frugivore	14.43087	1	Mon	SM	
Hylobates pileatus	forest	frugivore	14.54304	1	Mon	SM	
Hylobates syndactylus	forest	frugivore	15.19265	1	Mon	SM	
Indri indri	forest	folivore	12.0727	1	Mon	SM	
Lagothrix flavicauda	forest	frugivore	14.93318	1	NA	MM	
Lagothrix lagotricha	forest	frugivore	14.9283	1	NA	MM	
Lemur catta	forest	folivore	11.58954	1.088015	PG	MM	
Leontopithecus caissara	NA	frugivore	11.31371	2	Mon	NA	
Leontopithecus chrysomelas	forest	frugivore	11.33578	2	NA	NA	
Leontopithecus chrysopygus	forest	frugivore	11.33578	2	Mon	SM	
Leontopithecus rosalia	forest	frugivore	11.36002	1.96626	Mon	SM	
Lepilemur dorsalis	NA	folivore	11.51086	1	NA	NA	
Lepilemur edwardsi	NA	folivore	11.51086	1	NA	NA	
Lepilemur leucopus	forest	folivore	11.72071	1	PG	SM	
Lepilemur microdon	NA	folivore	11.51086	1	NA	NA	
Lepilemur mustelinus	forest	folivore	11.61895	1	PG	SM	
Lepilemur ruficaudatus	NA	folivore	11.61895	1	NA	SM	
Lepilemur septentrionalis	forest	folivore	11.61895	1	PG	NA	
Lophocebus albigena	forest	omnivore	13.34447	1	PGA	MM	
Loris tardigradus	forest	insectivore	12.89199	1.18	Mon	SM	
Macaca arctoides	forest	frugivore	13.31415	1	NA	MM	
Macaca assamensis	forest	frugivore	12.34909	1	NA	MM	
Macaca cyclopis	forest-savanna	frugivore	12.75735	1	PG	MM	
Macaca fascicularis	forest-savanna	frugivore	12.79323	1	PG	SMM	
Macaca fuscata	forest	frugivore	13.17161	1.166667	NA	MM	
Macaca maura	forest	frugivore	13.06182	1	NA	MM	
Macaca mulatta	forest-savanna	omnivore	12.86468	1.001299	NA	MM	
Macaca nemestrina	forest	frugivore	13.0958	1	NA	MM	
Macaca nigra	forest	frugivore	13.20606	1	NA	MM	
Macaca ochreata	forest	frugivore	12.34909	1	NA	MM	
Macaca radiata	forest	frugivore	12.77756	1	NA	MM	
Macaca silenus	forest	frugivore	13.16929	1	PG	MM	

Macaca sinica	forest	frugivore	12.74755	1	NA	MM	
Macaca sylvanus	forest	omnivore	12.8342	1.167665	NA	MM	
Macaca thibetana	forest	frugivore	13.0384	1	NA	MM	
Macaca tonkeana	forest	frugivore	13.15295	1	NA	MM	
Mandrillus leucophaeus	forest	frugivore	13.38189	1	NA	SM	
Mandrillus sphinx	forest	frugivore	13.24638	1.055556	PG	SM	
Microcebus coquereli	forest	frugivore	9.461227	1.766667	NA	NA	
Microcebus murinus	forest	insectivore	7.803845	1.975	PG	NA	
Microcebus rufus	forest	frugivore	7.794229	2.5	PG	SM	
Miopithecus talapoin	forest	frugivore	12.84079	1	NA	MM	
Nasalis concolor	forest	folivore	12.8841	1	Mon	SM	
Nasalis larvatus	forest	folivore, frugivore	12.8841	1.083333	PG	SM	
Nycticebus coucang	forest	omnivore	13.78993	1.019247	Mon	SM	
Nycticebus pygmaeus	forest	omnivore	13.71131	1.75	PG	SM	
Otolemur crassicaudatus	forest	gummnivore	11.44552	1.58058	Mon	SM	
Otolemur garnettii	forest	frugivore	11.48695	1	PG	SM	
Pan paniscus	forest	frugivore	15.24248	1	PGA	MM	
Pan troglodytes	forest-savanna	frugivore	15.12173	1.015639	PGA	MM	
Papio hamadryas	forest-savanna	gramnivore	13.26716	1	PG	SM	
Perodicticus potto	forest	frugivore	13.18459	1.0225	PG	NA	
Phaner furcifer	forest	gummnivore	NA	1	Mon	SM	
Pithecia aequatorialis	forest	frugivore	13.01922	1	Mon	MM	
Pithecia albicans	forest	frugivore	13.01922	1	Mon	MM	
Pithecia irrorata	forest	frugivore	13.01922	1	Mon	MM	
Pithecia monachus	forest	frugivore	13.0384	1	Mon	MM	
Pithecia pithecia	forest-savanna	frugivore	12.72792	1	Mon	MM	
Pongo pygmaeus	forest	frugivore	15.96872	1.0178	PG	MM	
Presbytis comata	forest	folivore	13.52775	1	PG	SM	
Presbytis femoralis	forest	frugivore	12.96148	1	PG	SM	
Presbytis frontata	forest	folivore	13.52775	1	NA	NA	
Presbytis hosei	forest	folivore	13.52775	1	PG	NA	
Presbytis melalophos	forest	folivore	13.80217	1	PG	SMM	
Presbytis potenziani	forest	folivore	13.52775	1	Mon	SM	
Presbytis rubicunda	forest	folivore	13.52775	1	PG	SM	
Presbytis thomasi	forest	folivore, frugivore	12.95183	1	PG	SM	
Procolobus badius	forest	folivore	13.2382	1	PA	MM	

Procolobus pennantii	NA	folivore	12.34909	1	NA	MM	
Procolobus preussi	NA	folivore	NA	1	NA	MM	
Procolobus rufomitratus	forest	folivore	12.34909	1	PG	MM	
Procolobus verus	forest	folivore	12.9976	1	PG	MM	
Propithecus diadema	forest	folivore	12.99573	1	Mon	SM	
Propithecus tattersalli	forest	folivore, frugivore	12.7181	1	NA	MM	
Propithecus verreauxi	forest	folivore	12.33703	1	PG	MM	
Pygathrix avunculus	forest	folivore	14.14214	1	NA	SMM	
Pygathrix bieti	forest	folivore	14.08013	1	NA	SM	
Pygathrix brelichi	forest	folivore	14.14214	1	NA	SM	
Pygathrix nemaeus	forest	folivore	13.26231	1	PG	SMM	
Pygathrix roxellana	forest	folivore	14.12887	1	PG	SM	
Saguinus bicolor	forest	omnivore	12.4499	1.815	Mon	SM	
Saguinus fuscicollis	forest	omnivore	12.15182	1.874	PA	MM	
Saguinus geoffroyi	forest	omnivore	11.92686	1.966667	PA	SM	
Saguinus imperator	forest	omnivore	12.06752	2	Mon	SM	
Saguinus inustus	forest	omnivore	12.4499	2	NA	NA	
Saguinus labiatus	forest	omnivore	12.06924	1.903333	Mon	SM	
Saguinus leucopus	forest	omnivore	12.4499	2	NA	SM	
Saguinus midas	forest	omnivore	11.57944	2	PA	MM	
Saguinus mystax	forest	omnivore	12.07615	1.968333	Mon	SM	
Saguinus nigricollis	forest	omnivore	11.83216	1.87092	NA	NA	
Saguinus oedipus	forest	omnivore	12.74428	1.937661	PA	MM	
Saguinus tripartitus	forest	omnivore	11.83216	2	NA	NA	
Saimiri boliviensis	forest	frugivore, insectivore	12.51998	1	PGA	NA	
Saimiri oerstedii	forest	frugivore, insectivore	14.61164	1	NA	MM	
Saimiri sciureus	forest	frugivore, insectivore	12.67264	1.000633	PGA	MM	
Saimiri ustus	NA	frugivore, insectivore	13.0384	1	NA	NA	
Saimiri vanzolinii	forest	frugivore, insectivore	12.4499	1	PGA	NA	
Semnopithecus entellus	forest	folivore	13.98913	1	NA	SMM	
Tarsius bancanus	forest	insectivore	12.81275	1	Mon	SM	
Tarsius dianae	NA	insectivore	13.52775	1	NA	NA	
Tarsius pumilus	forest	insectivore	13.34166	1	Mon	NA	
Tarsius spectrum	forest	insectivore	12.70171	1	Mon	NA	
Tarsius syrichta	forest	insectivore	13.4102	1	Mon	NA	
Theropithecus gelada	forest-savanna	gramnivore	13.23558	1	PG	SM	

Trachypithecus auratus	forest	folivore	14.24781	1	NA	SM	
Trachypithecus cristatus	forest	folivore	13.52775	1	PG	SM	
Trachypithecus francoisi	forest	folivore	14.61164	1	NA	SM	
Trachypithecus geei	forest	folivore	13.52775	1	NA	SM	
Trachypithecus johnii	forest	folivore	14.61164	1	NA	SMM	
Trachypithecus obscurus	forest	folivore	12.1621	1	PG	SMM	
Trachypithecus phayrei	forest	folivore	13.31666	1	NA	SMM	
Trachypithecus pileatus	forest	folivore	14.14214	1	NA	SM	
Trachypithecus vetulus	forest	folivore	14.47699	1	NA	SM	
Varecia variegata	forest	frugivore	10.00833	1.733333	Mon	SM	

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