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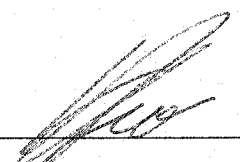

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Biodiversity of Plants: Broad-Scale Patterns and Mechanisms

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Thesis submitted to the Faculty of Graduate and Postdoctoral Studies, University of Ottawa in partial fulfillment of the requirements for the Ph.D. degree in the

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Abstract

One of the most obvious patterns in ecology is the geographic variation in species richness over broad spatial scales. However, despite observations of these patterns of richness for two centuries, mechanisms for the patterns remain controversial. This thesis is a study of the broad-scale biodiversity patterns of plants and the potential mechanisms behind those patterns.

Richness-climate relationships often account for >80% of the spatial variance in richness. However, it has been suggested that richness-climate relationships differ significantly among geographic regions, and that there is no globally consistent relationship. Since there is little point in arguing about mechanisms before the patterns they predict have been documented, I investigated the global patterns of species and family richness of angiosperms in relation to climate. Models relating angiosperm richness to mean annual temperature, annual water deficit and their interaction, or to annual potential evapotranspiration and water deficit, are both globally consistent and very strong, independent of the diverse evolutionary histories and biome assemblies in different parts of the world.

One hypothesized mechanism that predicts strong and consistent richness-climate patterns is the Physiological Tolerances hypothesis. This hypothesis predicts that the number of species found in a given location is a function of the number that can tolerate the climatic conditions in that place. Using global angiosperm family richness distributions and climatic data to estimate the climatic tolerances of plant families, I examined the relationships of potential family richness patterns to both climatic gradients and observed patterns of family richness. Observed family richness was not strongly

related to potential family richness. However, both richness and potential richness were related to climate, but in different ways. Potential family richness necessarily sets an upper limit on observed richness levels, but observed richness did not generally reach that limit. In other words, there are generally many more species that can tolerate the climate in a particular area than actually occur there.

A second hypothetical mechanism predicting strong consistent richness-climate patterns, the Energy-Diversity or Species-Energy hypothesis, suggests that for a species to persist in an area, there must be sufficient energy available in that area to support enough individuals of that species to maintain a viable population. Thus species richness will depend upon the number of individuals, which in turn depends upon energy availability. Using tree counts from 15 forest sites along a latitudinal gradient running from James Bay, Canada to Costa Rica, I tested whether a series of direct correlative links existed from climate to tree density to tree species richness. Despite a positive (but not statistically significant) correlation between AET and richness, the tree density per site was negatively correlated with energy. Even where positive energy-density correlations were observed (e.g. Alwyn Gentry's global observations of tree density and species richness), path models show that the relationship was not strong enough to explain the richness-energy correlation. Among distinct forest populations, any effect of energy on species richness does not operate through tree density.

While neither hypothesis examined here was corroborated, additional observations suggest that broad scale patterns of plant diversity may be related to habitat heterogeneity, which may in turn be constrained by climate.

Résumé

Un des phénomènes écologiques les plus évidents montre que la répartition géographique des espèces varie sur une grande échelle. En revanche, bien que les études en macroécologie des deux derniers siècles aient été consacrées à l'observation de la répartition des espèces, les mécanismes responsables de cette répartition restent controversés. La présente thèse est une étude de la biodiversité des plantes sur une grande échelle, ainsi que des mécanismes pouvant l'influencer.

Dans la majorité des cas, les facteurs climatiques expliquent plus de 80 % de la variabilité spatiale de la diversité des espèces. Cependant, certains ont laissé entendre que l'influence des facteurs climatiques sur la diversité des espèces varie significativement d'une région géographique à une autre, et que les relations climat-diversité ne peuvent pas être généralisées à l'échelle du globe. Puisqu'il serait inutile de discuter des mécanismes régissant la distribution des espèces avant même de connaître cette distribution, j'ai étudié la relation possible entre la répartition à l'échelle du globe des espèces et familles d'angiospermes et le climat. Les modèles reliant la diversité des angiospermes à la température annuelle moyenne, au déficit en eau annuel et à leur interaction, ou encore au potentiel d'évapotranspiration annuel et au déficit en eau, sont l'un et l'autre observables et très marqués partout dans le monde, indépendamment de l'histoire évoutive des espèces ou du biome dans lequel elles se trouvent.

L'hypothèse des tolérances physiologiques est un mécanisme possible prédisant une relation constante et significative entre le climat et la diversité des espèces. Cette hypothèse prédit que le nombre d'espèces se trouvant dans un site donné est fonction du nombre d'espèces pouvant tolérer les conditions climatiques de ce site. En utilisant les

données sur la distribution mondiale de la diversité des familles d'angiospermes et les données sur le climat afin d'évaluer la tolérance de chaque famille de plante au climat, j'ai pu étudier les relations entre la répartition potentielle de la diversité des familles et les gradients climatiques ainsi que la répartition observée de la diversité des familles. Le lien entre la diversité observée des familles et la diversité potentielle des familles était faible. En revanche, les diversités observée et potentielle étaient toutes les deux reliées au climat à leur façon. Bien que la valeur de la diversité potentielle des familles établie nécessairement une limite supérieure quant aux niveaux que peut atteindre la diversité observée, la diversité observée n'atteignait généralement pas cette limite. Bref, dans un site donné, il existe en général beaucoup plus d'espèces pouvant tolérer le climat en théorie, que le nombre d'espèces réellement présentes.

L'hypothèse énergie-diversité, ou l'hypothèse espèce-énergie, est un autre mécanisme proposé prédisant une forte corrélation entre le climat et la distribution des espèces. Elle laisse entendre que, pour qu'une espèce puisse persister dans une région donnée, il doit y avoir suffisamment d'énergie disponible pour assurer la survie d'un assez grand nombre d'individus de cette espèce pour maintenir une population viable. La diversité des espèces dépendra donc du nombre d'individus qui est lui-même dépendant de l'énergie disponible. À l'aide d'un dénombrement d'arbres provenant de quinze sites forestiers suivant un gradient latitudinal allant de la Baie James (Canada) au Costa Rica, j'ai vérifié si des liens corrélatifs directs existaient du climat à la densité des arbres à la diversité des espèces d'arbres. Bien que la corrélation entre l'évapotranspiration annuelle et la diversité soit positive (mais non statistiquement significative), celle entre la densité des arbres par site et l'énergie était négative. De plus, même aux endroits où des

corrélations positives ont été observées entre l'énergie et la densité (par ex., les observations à l'échelle du globe de la densité des arbres et de la diversité des espèces d'Alwyn Gentry), l'analyse des coefficients de direction démontre que cette relation n'était pas assez forte pour expliquer les corrélations entre la diversité et l'énergie. Au sein des populations forestières distinctes, les effets de l'énergie sur la diversité en espèces n'agissent pas par l'entremise de la densité des arbres.

Bien qu'aucune des hypothèses ayant été examinées ici n'aient été corroborées, des observations additionnelles donnent à penser que la répartition sur une grande échelle des espèces de plantes est peut-être reliée à l'hétérogénéité de l'habitat, qui elle à son tour pourrait être limitée par le climat.

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Introduction

Simply put, biodiversity is the assortment of different types of organisms that co-occur in time and space. Biodiversity – or more specifically, the availability and sustainability of high levels of biodiversity – is accorded great value under numerous perspectives. As a source of simple aesthetic beauty, a vast repository of scientific and medical knowledge (Reid et al. 1993), a wellspring of economic opportunity from ecotourism to resource extraction (Balmford et al. 2002), or an integral component of ecosystem health and stability and ipso facto a contributor to fundamental processes that sustain life – human and otherwise – on this planet (Naeem 2002), biodiversity is important to humanity.

Despite this importance, humanity imposes serious negative impacts on biodiversity at multiple scales of time and space. The popular media regale us with stories and reports of the ongoing destruction of natural habitats around the world, impending climate change disasters and other ecological travesties all having potentially dire consequences upon biodiversity. Other sources tell us not to worry, that these problems are overstated and that, while some problems do exist, nature in general – and thereby biodiversity – is sufficiently variable and resilient to cope. The problem is, that after more than 150 years of scientific study, it is still not clear what factors or processes lead to observed patterns of biodiversity. If we are to be able to mitigate the costs associated with the real or potential loss of biodiversity, we must understand the factors or processes responsible for existing levels of biodiversity.

While ecologists and geographers have studied patterns of biodiversity of almost every conceivable taxonomic group, this thesis is a study of the biodiversity patterns of

plants – trees in chapters one and four, angiosperms in chapters two and three. I chose these groups for two important reasons. First, as they make up 99.9% of non-microbial terrestrial biomass on this planet (Paul Keddy *personal communication*), and are the base of almost every terrestrial food web, the study of substantive taxonomic subsets of plants provides a valuable insight into general issues in ecology. Secondly, since plants all occupy the same trophic level within ecosystems, there is generally one less level of complexity relative to other taxonomic groups with regards to defining processes potentially affecting patterns of diversity.

In any study of biodiversity, two important constructs must be clearly defined. First, there are numerous metrics for quantifying biodiversity. The simplest of these, commonly referred to richness, is the total number of taxa (species, genera, etc.) with no reference to the relative abundance of each group. Other measures (e.g. Shannon Weiner diversity index) consider the relative abundance of each taxonomic group, such that the diversity index decreases as taxa become relatively rare. Thus two sites having similar levels of richness may have vastly different diversity levels given different proportions of rare taxa. There are pros and cons to both richness and diversity as measures of biodiversity. Richness will more clearly identify areas that harbour the largest total numbers of taxa. However, if many of the taxa in those high richness areas are so rare as to not make any significant contribution to ecological process of that area, those areas may potentially be diminished in value depending on the ultimate purpose of the initial comparison.

In studies comparing broad reaches of geography however, debate on the appropriateness of richness versus diversity indices as measures of biodiversity generally

becomes irrelevant. As the area over which biodiversity is measured increases, the determination of numbers of individuals per taxa becomes increasingly difficult. For global level studies, such tallies become practically impossible given the quality of current data sets. Thus in this thesis – with exceptions as specified in chapter four – taxonomic richness will be the only measure of biodiversity.

Second, fundamental to the study of biodiversity is the definition of scale. Discussion of this ostensibly simple concept is frequently complicated given both contradictory notions of what constitutes large versus small scale, and multiple attributes of scale. Geographers generally refer to scale in terms of map ratios. The smaller the scale or ratio, the more geography is squeezed onto a map. Thus small scale indicates that broad landscapes are being studied, while larger scales are used for geographically smaller areas. Alternatively, biologists use scale as more direct description of the landscape they are studying. Thus a comparison of continental sized tracts is large scale while a study of neighbouring garden plots would be small scale. In this thesis, I will use terms large (or broad) and small scale in the context of the biologists' lexicon.

The term scale may also be indiscriminately used to refer to any of several components of the size of a study, namely the extent, grain, and number of samples. Extent describes the maximum spatial distance or area among sample points, while grain refers to the actual size of the sample points. All four chapters in this thesis describe studies of large (broad) scale patterns of diversity in reference to the relatively large extent of the sample plots (i.e. continental to global distributions). In this thesis then, scale denotes extent. In all but chapter three, there are discussions of grain as well as extent, but in these cases, I specify matters of quadrat size specifically rather than use

terms of scale. In this thesis, the term scale is not applied to issues of sample size or corresponding statistical power.

At very large scales, as a matter of practicality, it becomes impossible to conduct controlled manipulation experiments comparing potential mechanisms of biodiversity. Moreover, while numerous hypothetical mechanisms have each attributed richness patterns to vastly differing processes, there is no reason to necessarily believe these mechanisms are mutually exclusive. Presumably most, if not all, of the hypothetical mechanisms have some potential to influence patterns of richness.

The approach I have taken in constructing this thesis stems from Popper's (1990) idea of propensities. Most natural systems are intractably complex webs of interacting drivers and processes. It is likely however, that some of the mechanisms have stronger effects than others. Thus some drivers will show strong correlations with richness, at the scale of the patterns that I am studying, while others will not. It may then be possible to extract the most important drivers, i.e. those factors that account for the greatest amount of diversity at large scales. There is little point in arguing about mechanisms before the patterns they predict have been documented. This subject forms the first part of my thesis.

This purely empirical approach identifies propensities of large-scale systems and thus provides some predictive ability. The predictive ability of such correlations, while potentially useful, must of course be regarded as limited as extrapolation and even, to some degree, interpolation of these patterns without clear understanding of their origin. The strength of this approach however is the ability to rank hypothetical mechanisms

according to their potential to predict the propensities of the system. Hypothesized causal factors that cannot statistically account for the strongest propensities of the system at the scale of interest may not be incorrect, but they are not likely to be of great importance to the web of processes driving richness patterns. This is not to say that such mechanism do not warrant study, rather that mechanisms that can produce such patterns should be investigated first. Once these are identified and tested, signals from less important mechanisms may be more easily examined.

Thus the second half of my thesis tests mechanisms that potentially account for the general propensities described in the first half of the thesis. Again, because of the impracticality of conducting controlled manipulations at large scales, the studies are correlative in nature. However, in each case I have deduced predictions of unique correlations from the hypothesized mechanisms and tested them against correlations observed in nature.

This thesis is laid out in four chapters. The first chapter in this thesis is a warning against the inappropriate dismissal of richness-climate correlations. It is a re-examination of the Latham and Ricklefs (1993a) study of global patterns of tree species richness in moist forests. After comparing tree species richness among sites covering several continents, they observed slightly larger differences among continental groups than was (in their view) explainable by climatic differences. They used this observation to reject Energy Diversity Theory in favour of historical explanations of the geographical patterns of tree species richness. Latham and Ricklefs' (1993a) data are, in fact, consistent with the richness-energy hypothesis. While differences among regions do exist beyond those explained by annual evapotranspiration (AET) – the sole climatic measure used in this

study – the richness-climate correlation was nevertheless still very strong. Moreover, since AET was strongly collinear with the regions they distinguished in this particular data set, the data could not provide a strong test to distinguish between the hypotheses pertaining to contemporary climate, versus those suggesting other inter-regional differences.

While the first chapter examines the potential for biologists to overlook existing richness-climate patterns, there is constant debate within the scientific literature as to the qualitative form of the richness climate relationship at large scales – as well as the general consistency of this form among broad regions – when such patterns are observed. Except for some very restricted taxonomic groups (e.g., termites: Eggleton et al. 1994; mangroves: Ricklefs and Latham 1993; corals: Fraser and Currie 1996), there has been no study to date that examines complete global patterns of richness. The second chapter of this thesis provides an investigation of the global patterns of species and family richness of angiosperms in relation to climate. I developed two empirical models, distinct in qualitative form, relating angiosperm richness to climate, then tested the transferability of the models among various global regions. The globally consistent relationships I find may provide a background against which other potential influences on richness may be tested.

Having confirmed the existence of strong and consistent continental and global richness climate patterns, chapters three and four of this thesis test two hypothetical mechanisms potentially contributing to these patterns popular in the scientific literature. The first of these, covered in chapter three, is that observed richness directly reflects the number of species that have evolved the adaptations necessary to survive in a given area,

which varies with climatic conditions. While numerous papers have debated this mechanism, operational predictions of the climatic tolerance hypothesis are not entirely obvious. One strong prediction however is that the number of species found in a given location is the number that can tolerate the climatic conditions in that place. Combining global angiosperm family spatial distributions and climatic data, I estimated the climatic tolerances of angiosperm families among various global regions, then calculated potential richness patterns based under varying levels of allowed spatial dispersal. I then compared observed richness patterns and richness potentials with each other, and to climatic gradients, climatic variability and habitat heterogeneity.

In chapter four, I examined the Species Energy hypothesis proposed by Hutchinson (1959) and elaborated by Brown (1981) and Wright (1983). This bottom-up mechanism links energy balance (as a function of climate) first to numbers of individuals then to numbers of species. While the richness-climate (energy) correlation fits with this hypothesis, the prediction that density of individuals over broad scales is proportional to total energy has not been tested. Chapter four tests this prediction. If the energy-diversity hypothesis is correct, there should be a series of direct correlations from climate to individuals to richness.

Chapter 1: Global Patterns Of Tree Species Richness In Moist Forests: Another Look

Abstract

After examining some perceived inconsistencies in the relationship between species richness and energy, Latham and Ricklefs (1993a) rejected the Energy Diversity Theory in favour of historical explanations of the geographical patterns of tree species richness. I have re-examined Latham and Ricklefs's data, both by itself and pooled with Currie and Paquin's (1987) data. I find that Latham and Ricklefs's (1993a) data are, in fact, consistent with the richness-energy hypothesis. Because of strong collinearity between annual evapotranspiration and region in their particular data sets, the data cannot be used to distinguish between the hypotheses that contemporary climate, versus some other inter-regional difference, is responsible for observed species richness patterns. Finally, there is no particular reason to attribute differences among regions to historical factors rather than to contemporary ones.

Introduction

The hypothesis that the number of species that can co-occur in a particular area may be limited by ambient available energy levels was proposed over four decades ago (Hutchinson 1959). Since then, numerous studies have found strong correlations between continental patterns of species richness and variables related to productivity such as potential annual evapotranspiration (Currie 1991), temperature (Richerson and Lum 1980), solar energy (Turner et al. 1987), and precipitation (Owen 1988).

In a study of the variation of tree species richness across North America, Currie and Paquin (1987) demonstrated that richness at that scale is highly correlated with annual evapotranspiration (AET). Continental-scale variation in AET had previously been shown to be strongly related to primary productivity (Rosenzweig 1968, Lieth 1975). Thus AET can be viewed as a surrogate measure of ambient environmental energy, i.e. the net energy flux through an ecosystem. Furthermore, Currie and Paquin (1987) found that tree species richness in Great Britain and Ireland is close to the level one would predict from the North American relationship between richness and AET, despite the suggestion that British species richness is low because of barriers to post-glacial recolonization (Goudie 1992, Sauer 1988). Currie and Paquin (1987) interpreted these results to mean that diversity patterns in trees appear to reflect contemporary patterns of energy availability, and that there is no need to invoke historical explanations.

Other studies of large-scale species richness patterns are consistent with this conclusion. Adams and Woodward (1989) found that most of the variance in species richness in temperate forests in Europe, eastern North America, eastern Asia and New

Zealand can be explained in terms of present day climatic factors. After controlling for climate, only small differences in richness among these regions remained. Similarly, Wright's (1983) global study of species richness on islands demonstrated that climate variables related to energy could explain 70 to 80% of the variation in species number per island.

Latham and Ricklefs (1993a), however, disagreed with this conclusion. They pointed out that if energy diversity theory has global validity, then forests in different parts of the world should fall on a single richness-energy relationship. To test this prediction, Latham and Ricklefs (1993a) assembled two data sets. The first consists of total tree richness in 28 temperate forests (ranging in size from 1 ha to 7400 km2) in 5 distinct regions of the globe. The second data set described tree richness in 46 small (1 ha) forest plots in several different forest biomes in five separate regions.

From their analysis of these data, Latham and Ricklefs (1993a) concluded that Currie and Paquin's (1987) North American model failed to predict regional species richness in other parts of the world, based on the following observations. First, while Latham and Ricklefs did find significant correlations between species richness and AET, their data suggested that mean species richness is 1.9 times higher in Asia than in eastern North America, independently of AET. Using their small forest plot data set in a series of ANCOVAs, Latham and Ricklefs found that mean richness differed among the five regions of the world represented in their data set. After statistically controlling for region, evapotranspiration could not explain any significant additional variation in species richness. Latham and Ricklefs concluded that their data were inconsistent with Currie and Paquin's (1987) suggestion that evapotranspiration levels determine tree

species richness at the global level. They interpreted the differences in richness among regions of the globe as reflecting the evolutionary history of the different areas. They suggested that richness-AET relationships (Currie and Paquin 1987, Adams and Woodward 1989) are indirect, resulting from the inclusion of multiple biomes that have different numbers of species due to different evolutionary histories.

I feel that re-examination of Latham and Ricklefs's (1993a) data does not necessarily support these conclusions. I do not disagree with Latham and Ricklefs's analyses per se. Rather, I will show below that, because of the peculiarities of their data sets, their data are consistent with several interpretations.

Analysis

First, consider Latham and Ricklefs's (1993a) broad-scale data set (reproduced in Figure 1.1), which included only temperate forest biomes. The relationship between species richness and AET in Latham and Ricklefs's data was essentially the same as that observed in earlier work. Richness was strongly related to AET and quadrat area, even within temperate forests (Table 1.1(1)). One would expect these data to be comparable to Currie and Paquin's (1987) data from North American forests, since their spatial scales are similar. When Currie and Paquin's (1987) data are culled to include only quadrats composed primarily of temperate or warm temperate forest (as defined by the Holdridge Life Zones Aggregated Classification: Leemans 1992), I find that richness again is strongly related to AET (Table 1.1(2)). When plotted together after statistically controlling the effect of quadrat area (Fig. 2), Currie and Paquin's (1987) North American richness data and Latham and Ricklefs's (1993a) global richness data relate to

AET in qualitatively very similar manners. Although small differences between the two data sets can be statistically detected, AET is the strongest covariate of richness in the combined data (Table 1.1(3)). Thus, all the extant broad-scale data - including Latham and Ricklefs's (1993a) - show qualitatively similar relationships between tree richness and AET, even when the data are restricted to a single biome type. Moreover, the relationships are of similar form and strength.

Yet, as Latham and Ricklefs pointed out, there are differences in richness among continents that cannot be attributed to variation in AET. Consider again Latham and Ricklefs's broad-scale data pooled with Currie and Paquin's temperate forest data (i.e. Figure 1.2). Richness does differ, on average, among the three areas of the world represented in the data set (Table 1.2(4)), albeit less strongly than its covariation with AET (Table 1.2(5)). When region and AET are combined in an ANCOVA (Table 1.2(6)), the combined model accounts for 8% more of the variance than the model with AET. This is entirely consistent with Adams and Woodward's (1989) earlier findings: there are strong patterns of richness as a function of AET with additional small differences among continents. These differences could be due to any number of factors. While AET has previously been shown to be strongly related to primary productivity (Rosenzweig 1968, Lieth 1975), AET is still only an approximate measure of ambient environmental energy. The residual variance may be due to other factors that influence productivity (e.g. soil nutrients) and that differ among continents. Alternatively, residual variance could be related to other environmental factors that differ among continents: for example, Currie and Paquin (1987) found that the residual variation in North America, after controlling for AET, was related to elevation. Finally, the residuals could be related

to historical differences among regions. Extant data provide no way to distinguish among these hypotheses.

Consider now Latham and Ricklefs's (1993a) second data set of one-hectare forest plots. As Latham and Ricklefs (1993a) indicated, mean species richness in these forest plots varies among regions. Species richness also varies strongly with AET (Table 1.3(8)). However, when both variables are included in a single model (R^2=0.844), the effect of AET becomes non-significant. Thus, in this data set, richness does not covary with AET within regions, and there are differences in richness among regions that cannot be explained by AET.

Discussion

How should these results be interpreted? First, they do not mean that richness does not covary with AET. In Latham and Ricklefs's (1993a) data, the two independent variables AET and region are strongly collinear. This collinearity is evident in Figure 1.3: there is an obvious sorting of data points by region along the AET axis. Region accounts for 83% of the variability in AET in this data set (Table 1.3(9)). Thus the data are consistent with the interpretation that all the local-scale variation in richness is related to factors other than AET that vary among continents. It is equally consistent with the interpretation proposed above: that richness depends strongly on AET, and that differences among continents account for an additional 11% of the variation in richness. When independent variables are as strongly correlated as they are in this data set (Figure 1.4), it becomes impossible to distinguish their effects on dependent variables (Draper and Smith 1981), and thus it is impossible to distinguish between the two interpretations.

What then is the significance of the fact that none of the within-continent variation in richness could be related to AET in Latham and Ricklefs's local data set? Failure to detect a relationship either means that no relationship exists, or that the design (the data set, in this case) was not powerful enough to detect a relationship. Several characteristics of this data set contribute to its lack of statistical power. First, the number of points within any continent was small: from five to twelve. With five points, for example, only relationships that statistically explain >77% of the variability in the dependent variable are detected as significant. Second, the range of AET within continents was also small: it varies only by a factor of 1.6, on average (versus an order of magnitude in most studies relating richness and AET). When an independent variable is constrained to vary very little, its relationship to other variables becomes weak. Finally, the collinearity between AET and region causes the error estimates associated with their effects to be artificially inflated (Gujarati, 1988). These three factors increase the probability of retaining the null hypothesis and decrease the probability of detecting the effects. Since many other researchers have found relationships between richness and AET within continents (e.g. Richerson and Lum 1980; Currie and Paquin 1987; Adams and Woodward 1989; as well as Latham and Ricklefs 1993a in their first data set), it seems very possible that Latham and Ricklefs's local data set simply lacked the statistical power to detect them.

As an alternative explanation of species richness patterns, Latham and Ricklefs (1993a) proposed that diversity patterns in trees, rather than being related to AET, "reflect very long-term evolutionary and geographical processes coinciding with most of the history of angiosperm evolution". According to this hypothesis, the major variation

in species richness is due to geographical location, not to climate. Since angiosperm evolution began primarily in South East Asia (Latham and Ricklefs 1993b), one might expect more new species to have originated there, thus endowing the region with high species richness. Other regions have been subjected, through their respective histories, to different speciation and extinction rates, generating distinct levels of species richness in each. While regions may potentially be capable of supporting higher levels of richness, the regional disparity is maintained by barriers that prevent or retard the movement of species between regions. Such barriers may be physical, such as oceans or mountains, or physiological, such as a requirement for frost tolerance.

Although this historical hypothesis is interesting and plausible, it is weak (*sensu* Rigler and Peters 1995, Chap. IV) at best. It may even be untestable. Richness models such as that of Currie and Paquin (1987) make explicit, quantitative predictions about richness in particular places. These predictions make the models eminently testable. It is not clear what predictions about the contemporary distribution of species richness, if any, can be derived from historical hypotheses. Without such predictions, these hypotheses cannot be tested (Platt 1964). Indeed, Latham and Ricklefs (1993a) did not try to test it. Further, the inter-regional differences noted by Latham and Ricklefs (1993a) may equally well be due to contemporary environmental factors other than AET that differ among continents. Unless it can be shown that observed patterns of richness are more closely related to some specific pattern predicted by an historical hypothesis than to contemporary factors, there is no scientific reason to prefer the historical hypothesis.

Conclusion

In conclusion, although Latham and Ricklefs (1993a) concluded that the richness-energy hypothesis does not account for variation in species richness, their data are as consistent with that theory as are earlier studies. Latham and Ricklefs's (1993a) particular data sets are equally consistent with the hypothesis that some other factor that varies among continents determines patterns of richness. This ambiguity is due to the strong collinearity between AET and region in Latham and Ricklefs's data that makes it impossible to distinguish between the effects of these two variables on species richness. However, in data sets that do not suffer from this collinearity (e.g. Adams and Woodward's 1989 data, as well as the data presented here in Figure 1.2), richness is strongly related to AET and region explains a relatively small amount of additional variance. This indicates that some other factor that differs among regions other than AET also influences richness. However, the suggestion that richness differences among regions are due to historical factors rather than to contemporary ones is merely speculative at this point.

Tables

Table 1.1 Models relating the log of regional tree species richness to environmental conditions. Latham and Ricklefs's data set consists of total tree richness in 28 temperate forests (ranging in size from 1 ha to 7400 km^2) in five distinct regions of the globe. Currie and Paquin's (1987) data have been culled to include only temperate and warm temperate forest richness data throughout North America. Quadrat area is important in Latham and Ricklefs's data but was not significant in the Currie and Paquin model as their quadrats were all of similar size. Source is a categorical variable indicating whether a point is from the Latham and Ricklefs (1993a) or Currie and Paquin (1987) data set.

Model	Data Source	Independent Variables	Type III SS	d.f.	F	p	n	R^2
1	Latham and Ricklefs	log(area)	0.416	1	10.7	<0.01	26	0.723
		AET, AET^2	1.80	2	23.1	<0.001		
2	Currie and Paquin	AET	0.787	1	84.7	<0.001	53	0.624
3	Both together	log(area)	0.494	1	26.4	<0.001	79	0.710
		AET	1.53	1	81.0	<0.001		
		source	0.343	1	18.3	<0.001		
		source*AET	0.289	1	15.5	<0.001		
		source*AET^2	0.251	1	13.4	<0.001		

Table 1.2 Richness-AET models for temperate forests. Data were pooled from Latham and Ricklefs's (1993a) regional data set and Currie and Paquin's (1987) culled data set. The regions examined were North America, Europe and Asia. n = 79.

Model	Dependent Variable	Independent Variables	Type III SS	d.f.	F	p	R^2
4	log(species)	log(area)	0.686	1	15.2	<0.001	0.282
		region	0.577	2	6.40	0.003	
5	log(species)	log(area)	0.507	1	25.3	<0.001	0.680
		AET, AET^2	2.45	2	92.0	<0.001	
6	log(species)	log(area)	0.420	1	27.7	<0.001	0.765
		AET, AET^2	2.27	2	81.2	<0.001	
		region	0.398	2	13.1	<0.001	

Table 1.3 Latham and Ricklefs's (1993a) local richness data set of mean tree species richness in temperate to tropical forests in five regions - tropical Americas, southeastern Asia, Africa, eastern North America and Japan. Mean AET per region was also examined. n = 46.

Model	Dependent Variable	Independent Variables	Type III SS	d.f.	F	p	R^2
7	log(species)	region	9.08	4	53.3	<0.001	0.839
8	log(species)	AET, AET^2	7.90	2	58.2	<0.001	0.730
9	AET	region	6.20×10^6	4	50.1	<0.001	0.830

Figures

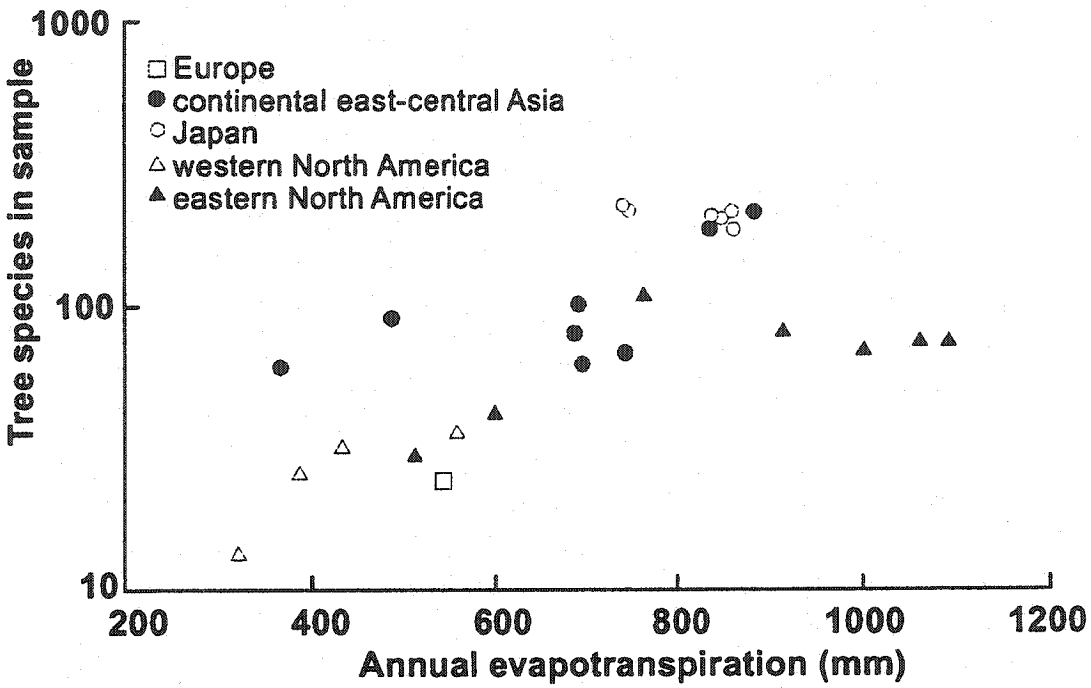


Figure 1.1 Data from Latham and Ricklefs's (1993a) Fig. 1. Tree species richness in 10^0-10^4 km^2 areas in temperate forests from five different regions around the world. Tree richness is strongly related to AET (and quadrat area). Some of the residual variation can also be related to region.

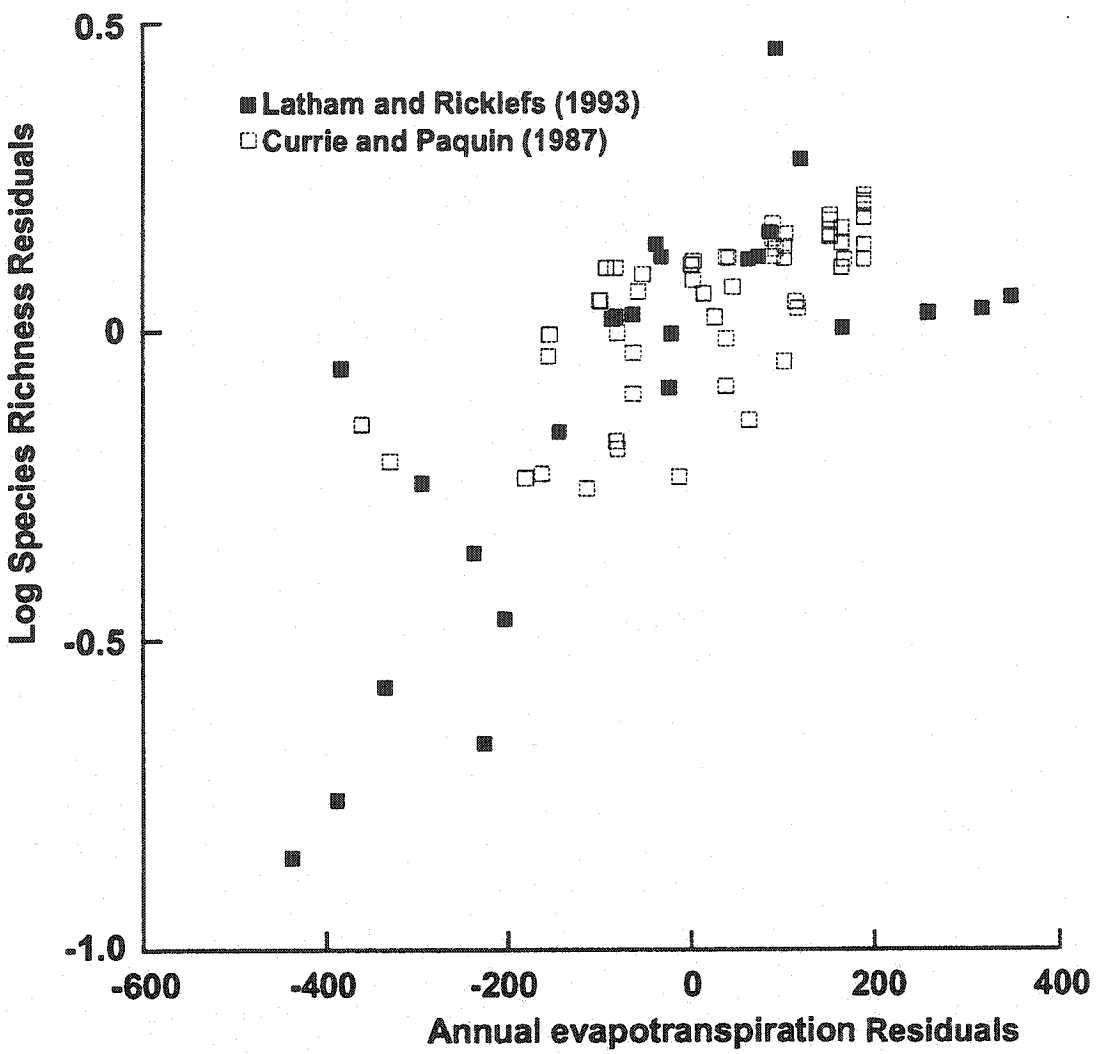


Figure 1.2 A partial plot (controlling for quadrat area) of the square root of tree species richness as a function of annual evapotranspiration. Data are drawn from Currie and Paquin's (1987) data set, culled to include only quadrats composed primarily of temperate or warm temperate forest, and Latham and Ricklefs's (1993a) regional data set. The richness-AET models are qualitatively very similar and richness is strongly related to AET in both, although significant differences between the two can be detected (Table 2).

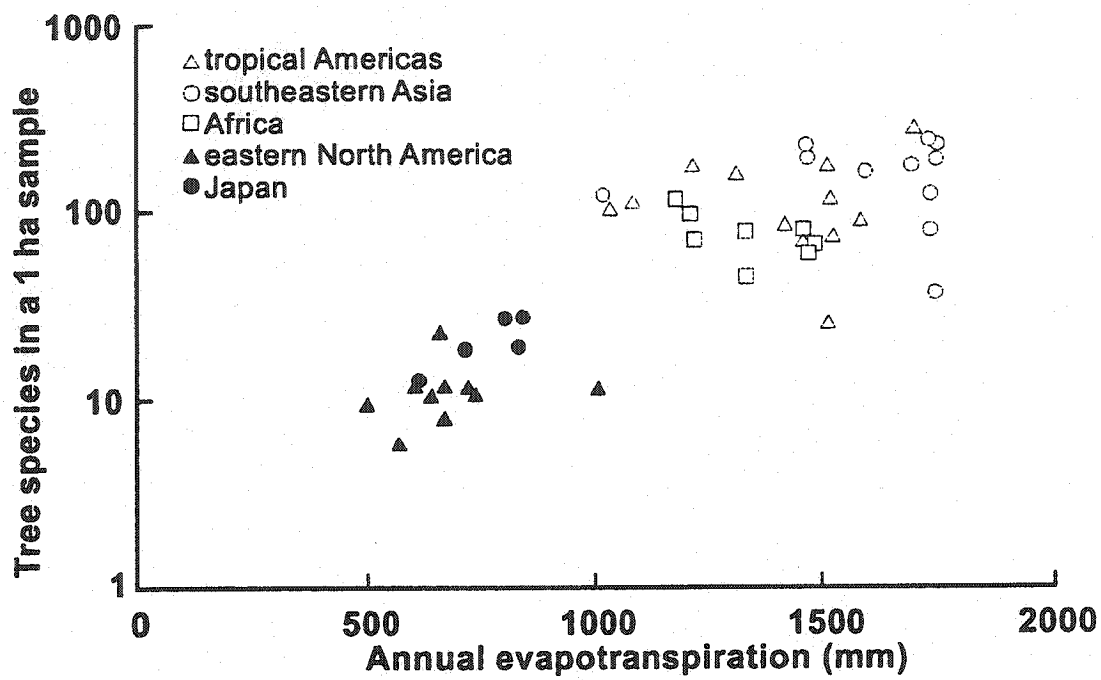


Figure 1.3 Data from Latham and Ricklefs's (1993a) Fig. 2. Tree species richness in 1 ha forest plots from five different regions around the world. Richness covaries strongly with annual evapotranspiration (AET). Mean richness also differs significantly among the five regions of the world represented above. However, AET and region are strongly collinear in this data set: There is an obvious sorting of regions along the AET axis.

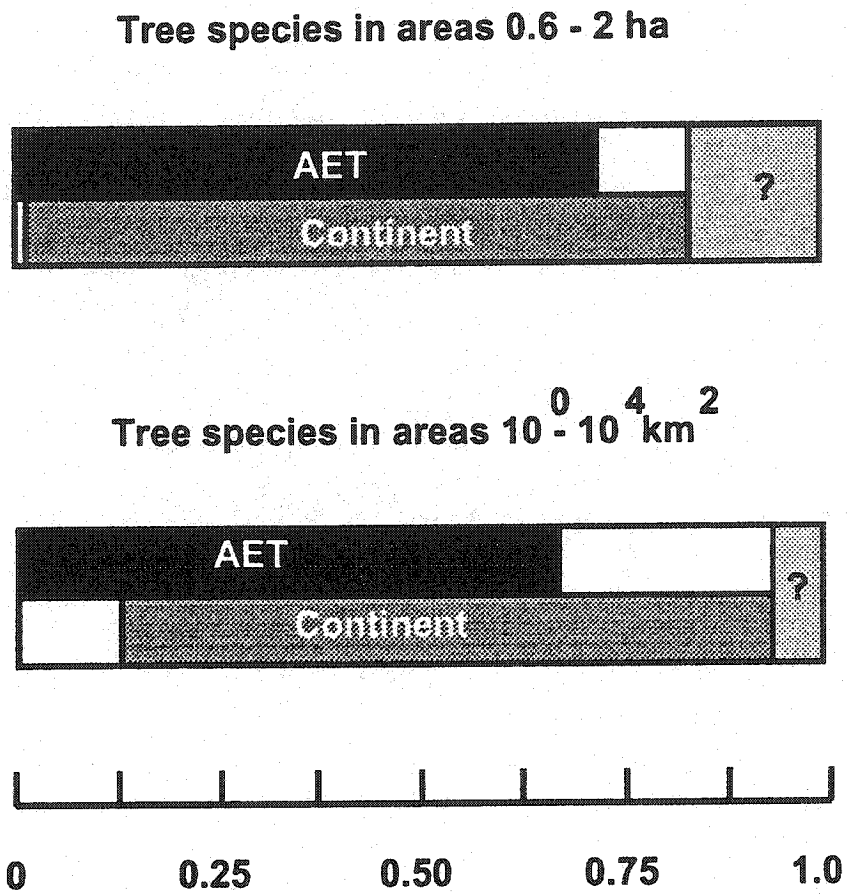


Figure 1.4 The proportion of the variance of species richness explained by AET alone (black bar), by continent alone (gray bar), or by an ANCOVA of both variables. The white bars represent the additional variance explained by including the second variable in the model. The bar marked "?" represents unexplained residual variance. The overlapping portions of the gray and black bars represent the portion of the variance that can equally well be ascribed to either variable, due to their collinearity. Note that most of the explained variance falls in this latter category.

Chapter 2: A Globally Consistent Richness-Climate Relationship For Angiosperms

Abstract

Species richness, the simplest index of biodiversity, varies greatly over broad spatial scales. Richness-climate relationships often account for >80% of the spatial variance in richness. However, it has been suggested that richness-climate relationships differ significantly among geographic regions, and that there is no globally consistent relationship. The present study investigated the global patterns of species and family richness of angiosperms in relation to climate. I found that models relating angiosperm richness to mean annual temperature, annual water deficit and their interaction, or to annual potential evapotranspiration and water deficit, are both globally consistent and very strong, independently of the diverse evolutionary histories and functional assemblages of plants in different parts of the world. Thus, effects of other factors such as evolutionary history, post-glacial dispersal, soil nutrients, topography or other climatic variables must either be quite minor over broad scales (because there is little residual variation left to explain), or they must be strongly collinear with global patterns of climate. The correlations shown here must be predicted by any successful hypothesis of mechanisms controlling richness patterns.

Introduction

One of the most obvious patterns in ecology is the geographic variation in species richness over broad spatial scales. Biologists have noted global scale spatial patterns of richness for at least two centuries (Von Humbolt and Bonpland 1807). While potential mechanisms of richness patterns at many different scales have been proposed and studied, mechanisms for broad-scale patterns remain the subject of long standing controversy (Hutchinson 1959, Schall and Pianka 1978, Rohde 1992).

Several hypotheses postulate that the main factors controlling richness gradients result directly or indirectly from climatic gradients. For example, geographical patterns of species richness may exist because more physiologically distinct species can tolerate areas with benign climates (Hall 1992; Kleidon and Mooney 2000). Alternatively, stable climates may permit specialization and therefore higher richness (Klopfer 1959), or perhaps the total metabolic energy that organisms can derive from the environment is finite, and its partitioning among species limits the total number of species that can coexist (Hutchinson 1959; Brown 1984). These hypotheses all predict a strong, consistent correlation between richness and climatic variables such as heat (i.e. net thermal energy and/or factors contributing to that energy) and water availability, or variables such as primary productivity, whose variability over broad scales depends principally on climate.

A second group of hypotheses suggests that broad-scale gradients of richness are mainly the result of processes independent of climate: e.g., idiosyncratic historical differences among regions in rates of evolution and extinction (Rosen 1988, Latham and

Ricklefs 1993a), residual effects of Quaternary glaciations (Mönkkönen 1994, McGlone 1996), effects of edaphic factors (Huston 1993) or the interaction between gradients of competition intensity and disturbance rates (Huston 1979). These hypotheses give no reason to expect correlations between richness and climate, except insofar as they may also depend upon climate.

If observations of richness-climate patterns were shown to be unimportant, inconsistent or spurious, it would suggest that explanations independent of climate were required. For example, it has been suggested that broad-scale richness-climate gradients may exist only because global studies span multiple biomes (Latham and Ricklefs 1993a, Ricklefs and Schluter 1993). Biomes are defined by both distinct climatic conditions and by unique species assemblages adapted to those conditions. Since biomes segregate along climate gradients, broad-scale richness-climate relationships may simply be an artefact of pooling data from these multiple biomes. It has also often been suggested (e.g. Brown and Lomolino 1998) that areas such as Europe and Great Britain and the southeastern US (O'Brien 1993) are relatively species-poor because of barriers to recolonization of these areas after the Pleistocene glaciations. If this were true, then there would be no reason to expect that climatically similar regions in different parts of the globe should have similar richness.

Does richness relate to climate in a globally consistent manner? Latham and Ricklefs (1993a) examined data on tree richness at 26 sites on several continents. They found that, although richness was correlated with climate, the relationship became non-significant when a dummy variable distinguishing different continents was included in the model. They concluded that climate was a relatively unimportant influence on

richness patterns. Schall and Pianka (1978) observed that richness of birds and mammals is positively correlated with temperature in the US, but negatively correlated in Australia. They argued that there are profound differences in the distribution patterns of vertebrate richness among continents with generally similar climates; presumably then, climate could not have been responsible for richness gradients observed over very broad scales. Kerr and Packer (1997) contend that mammal richness is strongly related to climate only in cold areas such as Canada; in the US, richness-climate relationships become non-significant, and habitat heterogeneity becomes the main determinant of spatial patterns of richness.

Yet other studies have observed consistent richness-climate patterns among different parts of the world. Tree species richness patterns described by Currie and Paquin (1987) in North America are very similar to those in climatically similar areas of the British Isles. Adams and Woodward (1989) found that, although differences exist in richness among continents, richness patterns across four continents can be explained mainly in terms of present day climate. Francis and Currie (1998) demonstrated that the continental variation in richness patterns observed by Latham and Ricklefs (1993a) was also consistent with a general richness-climate relationship. Wright's (1983) study of richness on islands supports a relationship between species richness and climate that is more or less consistent globally.

Except for some very restricted taxonomic groups (e.g., termites: Eggleton et al. 1994; mangroves: Ricklefs and Latham 1993; corals: Fraser and Currie 1996), there has been no study to date that examines complete global patterns of richness. The purpose of the present study is to determine whether richness covaries with climate in a globally

consistent manner. If so, which climatic variables are consistently related to richness? The answers to these questions are central to the entire discussion of the factors that control patterns of broad-scale diversity. A globally consistent relationship between richness and climate (or any other environmental characteristic) would provide the background against which other influences on richness (such as history or human activities) could be tested (Whittaker and Field 2000).

Methods

To test whether richness-climate relationships are in fact globally consistent, I assembled data on global angiosperm family richness patterns. I considered angiosperm families because the global distributions of all angiosperm families are reasonably well characterized (Heywood 1993), whereas the spatial distributions of individual species are unknown in many parts of the world. Patterns of family richness have been shown to be close to those of species richness (Williams and Gaston 1994, Balmford et al. 1996, Williams et al. 1997); however, variation in the number of species per family can modify the spatial distribution of species richness. I therefore repeated this study with the angiosperm species richness patterns compiled and mapped by Barthlott et al. (1996).

All of the data in my study were extracted from published maps using a sampling grid composed of 4394 equal-area quadrats covering all major landmasses except for Antarctica. Each quadrat had a latitudinal span of two degrees and a longitudinal span proportional to the inverse of the cosine of the central latitude – set to equal a two-degree span at 45° N and S (i.e., 34,900 km^2). This resolution corresponds approximately to the areas of the smallest gaps in otherwise continuous ranges depicted in the range maps. It

thus represents the resolution of detection of family presence/absence. To test whether my results depend upon quadrat size, I repeated the study using similarly constructed grids with quadrats spanning 4°, 6°, 8°, and 10°.

Angiosperm family richness was calculated based upon range maps taken from Heywood (1993). Using the Idrisi geographic information system I digitized each family's range map, and I then extracted presence/absence of each family in each quadrat in my sampling grid. The total number of families present in each quadrat was tallied to determine the global spatial distribution of angiosperm family richness.

Climate variables were extracted from digital global climate maps. Most studies that relate characteristics of plant assemblages to environmental characteristics focus on measures of heat and water, either as separate variables (e.g. rainfall and temperature; Schall and Pianka 1978, O'Brien 1993) or as combined variables (e.g. AET; Currie and Paquin 1987, Wright 1983; water deficit: Stephenson 1990). Since there is little consensus on which climatic factors best describe plant distributions (Stephenson 1998), I examined a number of combinations of heat and water variables. I took mean monthly temperature and precipitation data from Legates and Willmott (1992), and monthly potential and actual evapotranspiration levels from Ahn and Tateishi (1994a). Evapotranspiration data were missing for some of the most northerly quadrats (presumably those primarily covered in ice). To allow me to compare richness-climate models based on different climatic factors, I excluded those quadrats from my study, leaving a total of 4224. Following Stephenson (1990), I calculated water deficit as the difference between PET and AET. O'Brien (2000) suggests that rainfall – i.e. the portion of precipitation that falls as liquid water – is more important to plant diversity than total

precipitation. I estimated rainfall as the total monthly precipitation for all months with a mean temperature above 0°C. For each climate variable, I examined annual total (annual mean for temperature), minimum and maximum.

In order to study the consistency of richness-climate relationships among different regions of the world (cf. Latham and Ricklefs 1993a; Adams and Woodward 1989), I used A. R. Wallace's well-known biogeographic provinces (Brown and Lomolino 1998). I identified the province in which each of my quadrats fell. Quadrats that cross interprovincial boundaries, including quadrats in the Sahara, were omitted from analyses that involved provinces. I also omitted quadrats on the islands of New Zealand and Greenland, as it was not clear in which province to include them. Analyses involving biogeographic provinces therefore included 3850 of the 4224 quadrats covering the globe. I also compared richness-climate relationships among Holdridge aggregate life zones (Leemans 1992), which distinguish the world's major biomes. I identified the life zone into which the largest portion of each quadrat fell.

I tested relationships between richness and climate using multiple regressions relating plant richness variables to combinations of heat (temperature), water (precipitation or rainfall) or composite (PET, AET, water deficit) variables. Because all of these variables are collinear to some degree, selection of the best model is non-trivial. To proceed, I examined trivariate surfaces of richness as a function of pairs of heat and water variables. I visually identified possible non-linearities and interactions between variables, and I used multiplicative terms (for interactions) or polynomial terms (for non-linearities) in subsequent regression models to test their significance. I retained regression models with high R^2, and with residuals that were symmetrically distributed

around 0, and whose variance was independent of the expected value of richness.

I only included individual terms in the model that increased R^2 by at least 1% for two reasons. First, when regression models involve very large numbers of observations (as in this case), variables that account for extremely small amounts of variance are often apparently statistically significant. Second, because there is spatial autocorrelation in my data (see below), the true number of degrees of freedom is over-estimated in my models. Indices like Mallows' C_p, a statistic that might allow one to judge how many terms to include in a model, are of little value here. Because of the apparent statistical power, no variable tested contributes sufficiently little to a model to be excluded on the basis of Mallows' Cp, regardless of how many other highly collinear terms were already present. To be conservative, it is prudent not to interpret marginally significant relationships that may be spurious. Further, marginally significant variables in regressions with very high (apparent) power may reflect small amounts of lack-of-fit in the stronger relationships already in the model, if the variables are collinear. Since I was interested in main effects, not weak ones, I excluded the latter from my models.

To test whether richness is related to climate within regions of the world, I observed the relationships between richness and climate within each biome and each province. To test whether richness-climate relationships are consistent among regions, I carried out the following procedure. For each province, I regressed richness as a function of climate, excluding that province. I then used the resulting model to predict richness for each quadrat in the excluded region. I repeated this process for each province. These predicted richness estimates were then compared with observed richness as a test of the consistency of richness climate patterns among biogeographic provinces. I also carried

out this process for each Holdridge biome.

In any data set in which sample quadrats fully cover the study region, spatial autocorrelation is bound to be high. This leads to over-estimation of the true number of degrees of freedom in significance tests. However, all of the relationships reported in this chapter would be significant at $p<0.05$ if <10% of the 3850 to 4224 observations included in the study were statistically independent. Most of the relationships would be significant with <1% of all observations. It is therefore extremely unlikely that spatial autocorrelation is responsible for spuriously significant relationships. I also examine the degree of pseudo-replication resulting from autocorrelation by comparing relationships using different grid sizes.

Results

Angiosperm family richness shows strong spatial patterns (Figure 2.1), as has been known qualitatively at least since the time of Wallace (1878). Average log species density per quadrat, as estimated by Barthlott et al. (1996), was strongly correlated with family richness ($r^2=0.760$, $n=4394$, $p<0.001$). In all analyses reported below, results using the species richness data of Barthlott et al. were qualitatively identical to those using the family richness data. However, Barthlott et al. used climatic information to estimate species richness in some poorly studied parts of the world, which introduces some circularity into richness-climate relationships. Further, even Barthlott et al. regard their species richness estimates as preliminary. I therefore only present results using the family richness data.

How does plant richness relate to climate?

Simple, bivariate relationships between richness and temperature or PET (Figure 2.2a and b) superficially resemble many other similar published relationships (e.g. Kerr and Packer 1997, Currie 1991). Richness covaries strongly with heat in cold areas but the relationship becomes much more variable, apparently plateauing in warm areas. Fitted with polynomial models, this pattern is often described (inaccurately, as I show below) as a peaked relationship between richness and heat (cf. Currie 1991, O'Brien 2000). Bivariate relationships between richness and other climatic variables such as precipitation are noisier (Figure 2.2c).

I identified two models that describe richness as a function of total annual water deficit and either mean annual temperature or total annual PET and that satisfy the statistical criteria described above (Table 2.1) although other similar models involving measures of heat and water, can also account for these patterns nearly as well. Temperature and PET are strongly correlated (Spearman $r = +0.939$, $n=4224$, $p<0.001$), but their relationship is non-linear (PET is an accelerating function of temperature), and richness relates in ostensibly different ways to temperature and PET (Figure 2.3). Water deficit in combination with PET or temperature yielded slightly better richness models – in both adjusted r^2 and general fit – than any other variable describing water availability (such as precipitation or rainfall).

Consider first the relationship between richness, temperature, and water deficit. In areas of the world where water deficit is low, richness increases strongly and linearly with temperature, with stable variance (Figure 2.4a). The relationship shows no evidence of deceleration, even in the hottest parts of the world. In areas where water deficit is near

700 $mm \cdot yr^{-1}$, richness is independent of temperature, and in areas with the highest water deficits, the slope of the relationship with temperature becomes increasingly negative. In no case was a second-degree term statistically significant.

Similarly, the way that richness covaries with water availability depends upon temperature (Figure 2.4b). In the coldest parts of the world (mean annual temperature < +5°C, richness actually increases with water deficit (i.e., there can be too much water). In areas with mean annual temperatures between about +5°C and +15°C, richness is essentially independent of water deficit. In areas that are warmer still, richness decreases with water deficit.

The shape of the overall richness-climate relationship can be inferred from the curves in Figure 2.4, which effectively represent the first partial derivative of the relationship between richness and one variable, holding the other climate variable constant. Thus richness (R) varies linearly (as a first approximation) as a function of temperature (T) at a given water deficit (W):

$$R = a_{1,W} + a_{2,W}T \qquad (1)$$

but the coefficients a_1 and a_2 of the relationship (1) change with water deficit (W), again in an approximately linear fashion:

$$R = (a_3 + a_4W) + (a_5 + a_6W)T \qquad (2)$$

This reduces to:

$$R = a_3 + a_4W + a_5T + a_6WT \qquad (3)$$

where a_i for i=1 to 6 are empirical constants. Analogous reasoning concerning the relationship between R and W also leads to equation 3.

Model (3), fitted by least squares, statistically explains 79.9% of the global variation in family richness (Table 2.1). The negative coefficient on the water deficit – temperature interaction term leads to the appearance of a peaked relationship between richness and temperature. However, richness does not decrease with temperature provided that sufficient water is available: the richest areas of the world are the hottest and the least lacking in water (Figure 2.4).

Richness covaries differently with PET and water deficit. As it does with temperature, richness increases strongly with PET when there is little water deficit (Figure 2.5a). Unlike the case for temperature however, richness continues to increase with PET at higher water deficits - i.e. richness-PET is always approximately monotonic positive, although it is non-linear (Figure 2.5a). The effects of PET and water deficit are additive; only the intercept of the richness-PET relationship depends upon water deficit. The forms of curves appear to vary somewhat at high water deficits. However, the number of quadrats defining the curves at higher water deficits is small, and differences in slope or curvature appear to be minimal.

The richness-water deficit relationship depends upon PET, but to a lesser degree than upon temperature (Figure 2.5b). When PET is low, the richness-water deficit relationship is in fact non-significant, and it is strongly negative at high PET.

Based on logic similar to that used above, richness varies with water deficit (W) and PET (P) as follows:

$$R = a_1 + a_2W + a_3P + a_4P^2 \qquad (4)$$

This model (4) statistically explains 83.7% of the global variation in family

richness (Table 2.1). Richness varies as a monotonically increasing, curvilinear function of PET (with the exception of one artefact), and a linearly decreasing function of water deficit. The richest areas of the world are the wettest and have the highest PET (Figure 2.5).

For both models 3 and 4, additional polynomial terms and polynomial interactions can be added to the models, increasing the adjusted R^2 by 1%-3%. These extra terms may simply reflect statistical artefact or they may represent small deviations from my basic model form. Almost any combination of higher order interactions may appear statistically significant because of the extremely high statistical power of my data set. However, since this power is in part exaggerated by spatial autocorrelation, choosing which of these minor deviations are important is somewhat speculative. My final selection of model form was based on the most parsimonious explanation of apparent shape of the richness topography over the climatic space. I will maintain these simple models.

Effects of spatial scale

Coarse-graining the analysis – that is, increasing the size of quadrats – provides a test of the appropriateness of the size of my quadrats for this study. Coarse-graining has little effect on the overall model forms (Table 2.2). The included terms and the coefficients of those terms remain approximately constant as quadrat area increases, suggesting that the form of the models is not an artefact of my sampling grid design. The intercept of both family richness models increases progressively with quadrat size, indicating that larger quadrats contain more taxa. Thus, 2°quadrats are not simply pseudoreplicates of some larger minimal "real" quadrat. Since, for part of this study, I

wished to compare richness-climate relationships among biomes, and since coarse-graining increases the potential for heterogeneity within quadrats (i.e. the number of biome types included in a quadrat), I retained the 2° quadrats. At least at the scales larger than 2° x 2°, my richness-climate relationships are scale independent.

Testing the general richness model

Some studies have emphasized differences in average richness among geographic regions, rather than climatic correlates of richness (e.g., Schall and Pianka 1978; Latham and Ricklefs 1993a). Richness does differ among geographic regions (e.g. for phytogeographic provinces $F_{5,3844}=729$, $r^2=0.497$, $p<10^{-5}$), but climate does as well (e.g. temperature: $F_{5,3844}=942$, $r^2=0.552$, $p<10^{-5}$). After statistically controlling for climate, differences in mean richness among provinces account for about 3% of the total variability in family richness (e.g. temperature and water deficit: $R^2=0.831$, $p<10^{-5}$ temperature, water deficit and phytogeographic province: $R^2=0.866$, $p<10^{-5}$). Richness also covaries strongly with climate *within* every phytogeographic province and every biome (Table 2.3). Thus, richness-climate relationships are not an artefact of pooling biomes.

Most importantly, richness-climate relationships are, for the most part, globally consistent. Richness in any province or biome can be predicted from the richness-climate relationships derived in the rest of the world (Figure 2.6). After statistically accounting for climate, small systematic differences in richness among regions do remain. These differences account for an additional 3% - 6% of the variance in family richness among regions (Figure 2.6).

Discussion

In this study, I analyze the relationships between angiosperm family richness and climate. I similarly analyzed the species-level data of Barthlott et al. (1996). Despite the limitations in their data (see above), all of the conclusions I present below are equally consistent with the species richness patterns described by Barthlott et al. Although family-level richness is sometimes interpreted as a measure of the diversity of functional groups rather than of species (Huston 1994), I find no evidence that richness relates to climate differently at the different taxonomic levels I examined.

My most important result is that there is a globally consistent relationship between angiosperm family richness and climate. Richness varies with climate within nearly every phytogeographic province and biome in very similar ways (Table 2.3). Moreover, the richness of a given area can be predicted quite well using climate-richness models developed with data from other parts of the world, without the need to postulate other special circumstances for particular regions (Figure 2.6).

Differences in richness among provinces after controlling for climate are small, accounting for only an additional 4% to 6% of the global variance in richness (Figure 2.6). The most extreme outlier is Australia, with 12.5 fewer families per quadrat than climate would predict, while the Oriental province (tropical Asia) has 9.2 families more. Latham and Ricklefs (1993a), based on a comparison of 14 Asian and 11 North American forests, argued that Asian temperate forests have higher diversity than North American forests due to the evolutionary history of Angiosperms. However, I find that Palearctic quadrats in general (which include Asian temperate forests) do not have significantly

more families than Nearctic (North American) quadrats, after accounting for climate (Tukey's test p=0.54, nominal d.f.=2099). Thus, effects of regional differences in, for example, evolutionary history (Latham and Ricklefs 1993a), post-glacial dispersal (Latham and Ricklefs 1993b, Qian and Ricklefs 1999), soil nutrients (Huston 1980), topography (Kerr and Packer 1997) or other climatic variables (O'Brien 2000) must either be quite minor over broad scales (because there is little residual variation left to explain), or they must be strongly collinear with climate.

My second important result is that the form of the relationship between richness and heat depends upon water availability, and the relationship between richness and water depends upon heat. The best models accounting for richness patterns involve water deficit and either temperature or potential evapotranspiration. Essentially the same variables are related to the global distribution of the world's major biomes (Whittaker 1977; Stephenson 1990, 1998). Because of the strong collinearity among alternate measures of heat and water (e.g., precipitation, AET, primary productivity estimated from climate), it makes little sense to belabor the small differences among models using these different variables. It also clearly makes little sense to examine relationships between richness and one climatic variable in the absence of the other.

Richness-climate relationships are not the result of pooling across biomes (cf. Latham and Ricklefs 1993a). If they were, there would be no reason to expect similar patterns within biomes. Yet, I found significant, qualitatively similar, family (and species) richness-climate relationships within all Holdridge life zones (Table 2.3), just as I did in phytogeographic provinces. Richness-climate relationships are generally weaker within life zones than within provinces because life zones are defined largely by climate.

Thus, the ranges of climatic variables within life zones are narrow. The two biomes with non-significant richness-climate relationships had particularly narrow ranges of climatic variables.

My third important result is that, contrary to most recent literature (e.g. O'Brien 1993; Rosenzweig 1995), the broad-scale spatial relationships between richness and heat, and between richness and the climatic drivers of primary productivity, are not peaked. Richness increases monotonically with heat, provided that water is available. Similarly, on the global scale, richness increases as a positive monotonic function of the climate variables that control primary productivity (the simultaneous availability of water and heat, Lieth 1975). Studies in which richness appears to be peaked or negative functions of heat reflect collinearities between water availability (measured by water deficit or by precipitation) and heat (whether measured by temperature or PET) (cf. Figures 4 and 5). Note that, at local spatial scales, richness generally varies as a peaked function of productivity (Rosenzweig and Abramsky 1993; Mittelbach et al. 2001). Thus the relationship between richness and productivity does appear to be scale-dependent, between biogeographic scales and local scales.

Earlier richness-climate models that appear to differ from ours are special cases of the present model, tuned to local subsets of the conditions that exist globally. Studies in predominantly hot, dry places have emphasized the effect of precipitation on richness. For example, Schall and Pianka (1978) reported that vertebrate richness is negatively correlated to temperature in Australia (which is mainly hot and dry), but positively correlated in the US (which has both dry and wet areas) (Figure 2.7). Combining Schall and Pianka's (1978) data for Australian mammals and Currie's (1991) data for North

American mammals, my models 3 and 4 (which were developed for angiosperms) statistically explain more of the variation in species richness patterns (R^2=0.683 and R^2=0.692, respectively) than Schall and Pianka's correlations did, with no statistically significant difference in richness between continents after controlling for climate.

Similarly, Kerr and Packer (1997) pointed out that the strong correlation between mammal richness and PET in cold parts of North America (PET<1000 mm·yr^{-1}) disappears in warm areas with PET>1000 mm·yr^{-1} (Figure 2.8a). However, water deficit is essentially nil in cold parts of North America whereas, further south, it is high in some areas and low in others. Thus, it is not surprising that Kerr and Packer would find that PET alone fails to predict richness in warmer parts of North America. Models 3 and 5, applied to the mammal data used by Kerr and Packer, work about as well as PET alone in cold areas (R^2=0.837 and 0.868 for models 3 and 5, R^2=0.843 for PET). In warm areas, the richness-climate relationships proposed in models 3 and 5 remain strong (R^2=0.677 and 0.662 for models 3 and 5, R^2=0.010 for PET), with no change of form of the sort described by Kerr and Packer (Figure 2.8b and c). Kerr and Packer failed to observe a significant richness-climate correlation in the US because the richness-climate model they used is appropriate only to northern climates.

Finally, O'Brien's (1993) "interim general model" of angiosperm richness in southern Africa (also mainly hot and dry) work equally well as ours for southern Africa (south of 18°S, approximately the Zambezi River). Applied to the global data however, O'Brien's (1998) model (family richness = rainfall + minimum PET + minimum PET^2) performs much less well than the models I present here (r^2=0.629, n=4224, $p<10^{-5}$; cf. Table 2.1)). Over larger scales, O'Brien (2000) argues that rainfall, as opposed to total

precipitation is a more appropriate climatic measure of water, since water falling as snow or ice is not directly useful to biological activity. However, spring melt-water may be an important source of water in some areas. Furthermore, precipitation in excess of demand (i.e. runoff) presumably has little influence on the flora. Thus I propose that richness is more closely related to water deficit than to precipitation or rainfall because water deficit is more indicative of (or at least inversely proportional to) the availability of water to plants, relative to their need.

My fourth important observation is that, although some authors have regarded temperature and PET as interchangeable measures of "environmental energy" (e.g. Currie 1991), richness relates qualitatively differently (albeit about equally strongly) to these two variables (Figure 2.4a and 2.5b). This is partly because temperature and PET are non-linearly related (Figure 2.3). At temperatures above freezing, increasing temperature leads to increased capacity to evaporate water i.e. higher PET. Below 0°C, water is frozen, and PET remains near zero, even while temperature continues to decrease. But moreover, at high water deficits, PET depends upon more than just temperature. Evapotranspiration may be driven by heat, but PET is also affected by such climatic factors as humidity, cloudiness, and wind patterns, and biotic factors such as plant cover (Sellers 1965). As plant cover increases, so too does the surface area from which water is transpired (Sellers 1965). Thus among the hot, dry areas of the world, I observe that areas of high temperature but only moderate PET tend to be found in barren deserts, whereas high temperature, high PET areas occur in more vegetated steppes and savannas (Figure 2.9). If PET incorporates, to some degree, an effect of biomass, this may explain why my model that is based upon PET marginally out-performs the temperature-based

model. It also explains why the forms of richness-temperature relationships and richness-PET relationships are different, even though PET is strongly dependent upon temperature.

What mechanisms produce my observed patterns of richness? I neither believe that mechanisms can be inferred from patterns, nor that a single mechanism need be responsible for these patterns. It is possible that richness-climate patterns represent the aggregate of many processes affecting richness, perhaps including differences in physiological tolerances (Hall 1992; Kleidon and Mooney (2000), frequencies of interspecific interactions (Brown et al. 1996), availability of different microhabitats, differing rates of evolution, etc. That said, one can ask if the patterns I have observed are consistent with mechanisms that have been hypothesized to affect richness.

Energy-richness – Hutchinson (1959) and Brown (1984) hypothesized that richness increases as a function of available energy: every individual requires a certain amount of energy to survive, and populations require a certain number of individuals to persist. Competition for energy could limit species richness, and environments with higher available energy should have more species with populations large enough to persist. This hypothesis is apparently consistent with monotonic positive relationships between richness and the climatic variables that control broad-scale patterns of productivity (e.g. the present results, as well as those of Wright 1983, Turner et al. 1988; Adams and Woodward 1989). However, as Huston (1999) points out, competition operates at local scales, and the relationship between richness and productivity on local scales is often peaked (Mittelbach et al. 2001). It is not obvious what patterns at broad scales would result from local-scale competition. Further, this hypothesis predicts that

the numbers of individuals, as well as richness, should correlate with climate. I find that this is not true (Francis and Currie, unpublished). I provisionally reject the proposed mechanism of the energy-richness hypothesis.

The physical state of water - O'Brien (1998) suggests that the peaked richness-PET relationship she observes in southern Africa reflects availability of liquid water as water changes from ice to water to water vapour along a gradient of increasing PET. However, I find that, for any given level of water deficit (i.e. water availability relative to evaporative demand), richness always covaries positively with PET (Figure 2.5). Thus, the effect of PET cannot simply be on the availability of water. Broad-scale patterns of richness are clearly dependent simultaneously on both heat and water availability.

Physiological tolerance – It has been hypothesized that more physiological configurations can survive in benign (warm and wet) conditions than in marginal (cold and/or dry) conditions (e.g. Hall 1992). Kleidon and Mooney (2000) produced a model of the factors controlling a plant's energy balance. They created hypothetical species having physiological parameters with randomly chosen values. Their model predicts that more hypothetical species have positive energy balances in benign climates than in harsh ones. This hypothesis is at least prima facie consistent with richness-climate correlations, although Kleidon and Mooney did not test their model against real richness patterns. This physiological tolerance hypothesis does not predict a limit to the number of species that can coexist locally. Stohlgren et al. (1999) and Sax (2001) observed that the number of exotic species in particular environments is strongly related to the number of native species. This seems to be consistent with Kleidon and Mooney, since the addition of new species apparently did not eliminate extant ones: i.e., environmental characteristics did

not somehow limit the number of coexisting species. Extant evidence appears to be consistent with the physiological tolerance hypothesis.

Competition and disturbance -- Huston (1979; 1999) suggested that diversity gradients result from the combined effects of competitive exclusion (the rate of which varies as a function of productivity) and disturbance. He hypothesizes that richness is a peaked function of both processes. Mackey and Currie (2000) found that little of the spatial variability in species richness could be related to measures of disturbance, particularly at broad scales and that richness is not generally a peaked function of disturbance. Moreover, I find that richness increases monotonically with the climate factors most closely related to broad-scale patterns of richness. Huston's (1979) hypothesis is either not relevant at broad spatial scales (Huston 1999), or it is simply inconsistent with observed patterns.

Evolutionary history -- Latham and Ricklefs (1993a) argue that richness patterns arise from differences in evolutionary and extinction histories among regions: e.g. the forests of temperate Asia are more speciose than American temperate forests because angiosperms originated in southeast Asia. If non-uniform evolutionary processes (vicariance events, major extinction events, bursts of radiation) were the major source of variation in richness patterns among regions, then richness should be poorly related to climate, and there should be pronounced regional differences in richness, independent of climate. However, I find that there are no major differences in richness among regions after accounting for climate (Figure 2.6).

Alternately, Rohde (1992, Rohde et al. 1993) and Rosenzweig (1995) present

mechanisms describing how speciation occurs at higher rates in tropical regions than in temperate regions. Perhaps evolutionary rates do vary with climate – or at least with geographical variables that covary with climate (e.g., area: Rosenzweig 1995) – over time, which may provide a latitudinal gradient in the number of species adapted to given sets of conditions (i.e. total species pool size). This is an effect that I am currently attempting to measure (Francis and Currie, in prep.). However, unless evolutionary rates and extinction events over very local scales track climate quite closely, then it seems unlikely that tight richness-climate relationships *within* life zones would result. I provisionally reject the hypothesis that differing evolutionary histories are responsible for contemporary gradients of richness.

Conclusion

Among the hypotheses proposed to explain broad-scale patterns of species richness, some predict that richness should be correlated with climate (e.g. "energy-diversity theory"), and others do not. Before evaluating any of these hypotheses, the first question is: is richness consistently related to climate? There is little point in arguing about mechanisms before the patterns they predict have been documented.

I find that there is a globally consistent relationship between richness and climate, despite dramatic differences among regions in evolutionary and geological history, edaphic factors, and other regional characteristics. Broad-scale patterns of richness depend mainly on the simultaneous availability of heat and water; it makes little sense to investigate the influence of these two variables separately. I do not contend that other characteristics play no role in determining regional and global patterns in richness, nor

even that contemporary climate is necessarily the proximate driver of richness patterns (experiments modifying climate would be necessary to demonstrate that). Rather, I maintain that any explanation of broad-scale richness patterns must account for the ubiquitous and strong richness-climate correlation.

Tables

Table 2.1 Global richness climate models. In all cases, n=4224, and F>2000 and $p<10^{-5}$ for the overall model.

Model	Dependent Variable	Independent Variables	Coefficient	SE	Variable p	Model r^2
1	FR	WD	1.17	3.35×10^{-2}	<0.00001	0.799
		Temp	4.14	3.21×10^{-2}	<0.00001	
		WD*Temp	-4.16×10^{-3}	1.13×10^{-4}	<0.00001	
2	FR	WD	-6.41×10^{-2}	8.25×10^{-4}	<0.00001	0.837
		PET	2.20×0^{-1}	2.79×10^{-3}	<0.00001	
		PET*PET	-6.79×0^{-5}	1.41×10^{-6}	<0.00001	

FR=family richness, WD=water deficit ($mm \cdot yr^{-1}$), Temp=average temperature (°C), PET= potential annual evapotranspiration ($mm \cdot yr^{-1}$), SE=standard error of the coefficient

Table 2.2 Global richness climate models of the relationship between family richness and climatic variables, or species richness and climate, constructed using varying quadrat sizes. All models are significant to $p<0.00001$. The coefficients of climatic terms do not change systematically with quadrat size, suggesting that the models do not depend upon spatial scale within this range. The intercepts of the family richness models (i.e. mean richness per quadrat) increase progressively with increasing quadrat size, indicating that smaller quadrats are not simply pseudoreplicates of larger units. This was not the case for the species density.

Latitudinal Span	n	Independent Variable	Coefficient	F	R^2	Independent Variable	Coefficient	F	R^2
2°	4224	Constant	8.01×10^{1}	5607	0.799	Constant	8.79	7235	0.837
		WD	3.41×10^{-2}			WD	-6.41×10^{-2}		
		Temp	4.14			PET	2.20×10^{-1}		
		WD*Temp	-4.16×10^{-3}			PET*PET	-6.79×10^{-5}		
4°	1178	Constant	8.27×10^{1}	1600	0.803	Constant	1.08×10^{1}	2153	0.846
		WD	3.70×10^{-2}			WD	-5.99×10^{-2}		
		Temp	4.18			PET	2.24×10^{-1}		
		WD*Temp	-4.10×10^{-3}			PET*PET	-7.05×10^{-5}		
6°	608	Constant	8.48×10^{1}	802	0.799	Constant	1.30×10^{1}	1160	0.847
		WD	4.07×10^{-2}			WD	-5.61×10^{-2}		
		Temp	4.16			PET	2.27×10^{-1}		
		WD*Temp	-4.08×10^{-3}			PET*PET	-7.26×10^{-5}		

8°	377	Constant	8.65×10^{1}	487	0.797	Constant	1.48×10^{1}	709	0.851
		WD	4.81×10^{-2}			WD	-5.05×10^{-2}		
		Temp	4.15			PET	2.27×10^{-1}		
		WD*Temp	-4.13×10^{-3}			PET*PET	-7.27×10^{-5}		
10°	255	Constant	9.04×10^{1}	348	0.806	Constant	1.44×10^{1}	521	0.862
		WD	4.04×10^{-2}			WD	-4.91×10^{-2}		
		Temp	4.14			PET	2.38×10^{-1}		
		WD*Temp	-3.70×10^{-3}			PET*PET	-7.86×10^{-5}		

WD=water deficit ($mm \cdot yr^{-1}$), Temp=average temperature (°C), PET= potential annual evapotranspiration ($mm \cdot yr^{-1}$)

Table 2.3 Global richness climate models within Wallace's phytogeographic provinces and Holdridge's biomes (Temperature models: richness = water deficit + temperature + temperature*water deficit, PET models: richness = water deficit + PET + PET^2). For all models $p<0.001$ except where noted.

		Temperature Models		PET Models	
Province	**n**	**F**	**r^2**	**F**	**r^2**
Nearctic	691	3.37×10^3	0.936	3.33×10^3	0.936
Neotropical	575	3.80×10^2	0.666	1.03×10^3	0.844
Palearctic	1410	1.72×10^3	0.786	3.66×10^3	0.887
Ethiopian	643	3.36×10^2	0.612	1.67×10^2	0.440
Oriental	256	6.23×10^1	0.426	6.15×10^1	0.423
Australian	275	1.76×10^2	0.661	3.24×10^2	0.782
Biome					
tundra	146	5.45×10^2	0.920	1.08×10^3	0.958
cold parklands	21	7.17×10^1	0.927	3.91×10^2	0.986
forest tundra	232	2.08×10^2	0.732	4.69×10^2	0.861
boreal forest	459	6.23×10^1	0.291	2.14×10^2	0.585
cool desert	70	6.99×10^1	0.761	5.34×10^1	0.708
steppe	221	4.61×10^1	0.389	1.29×10^2	0.641
temperate forest	380	4.84×10^1	0.278	1.84×10^2	0.595
hot desert	336	1.47×10^1	0.117	5.15	0.044
chaparral	219	1.16×10^1	0.140	4.04×10^1	0.360
warm temperate forest	96	2.10×10^1	0.406	3.74×10^1	0.549
tropical semi-arid	295	2.00×10^1	0.171	3.07×10^1	0.240
tropical dry forest	407	7.27×10^1	0.351	1.06×10^2	0.442
tropical seasonal forest	568	3.83×10^1	0.169	4.27×10^1	0.185
tropical rain forest	400	1.48×10^1	0.101	1.68×10^1	0.113

Figures

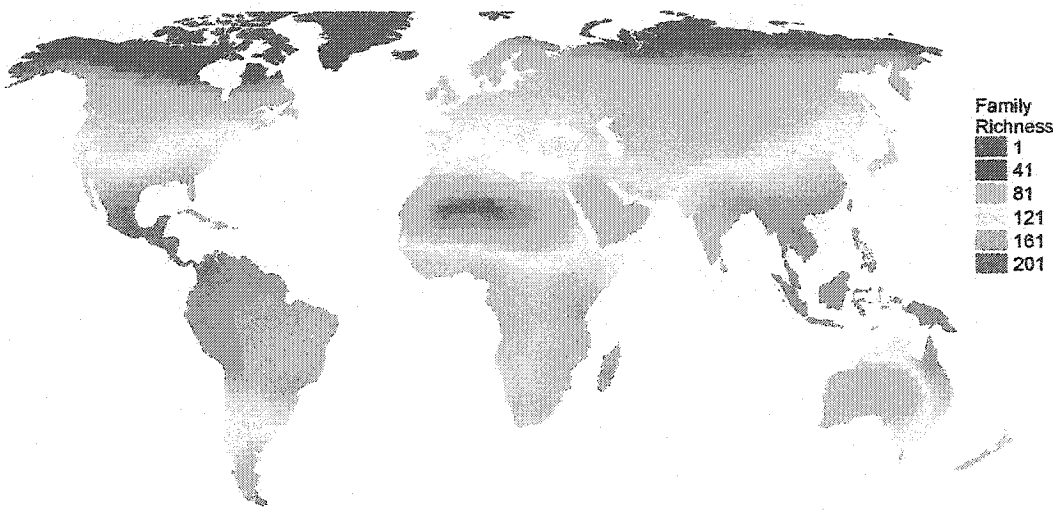


Figure 2.1: A map of the global variation in the number of angiosperm families per 3.5×10^4 km^2 quadrat, based on Heywood's (1993) distribution maps.

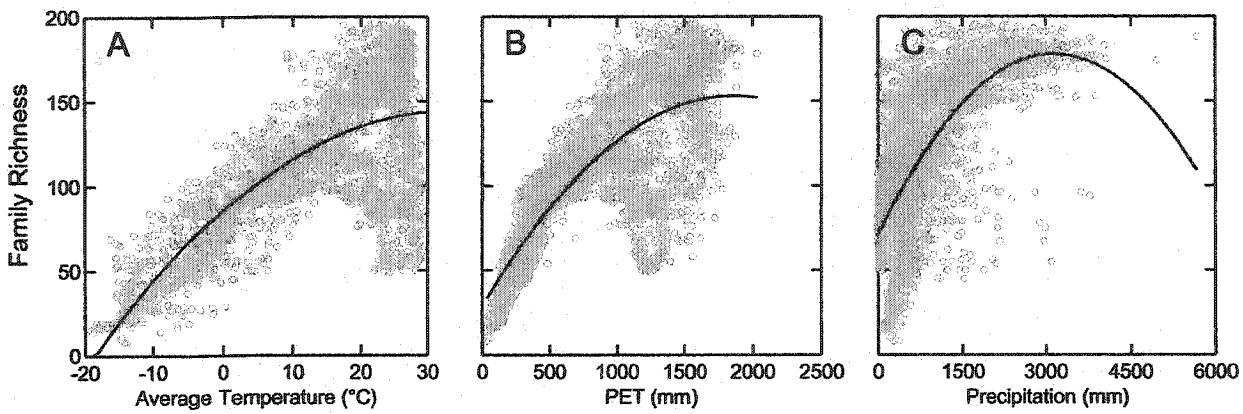


Figure 2.2: The relationships between **A** angiosperm family richness and temperature, **B** family richness and PET, and **C** family richness and precipitation, which are often (poorly) approximated using simple quadratic functions, as shown here.

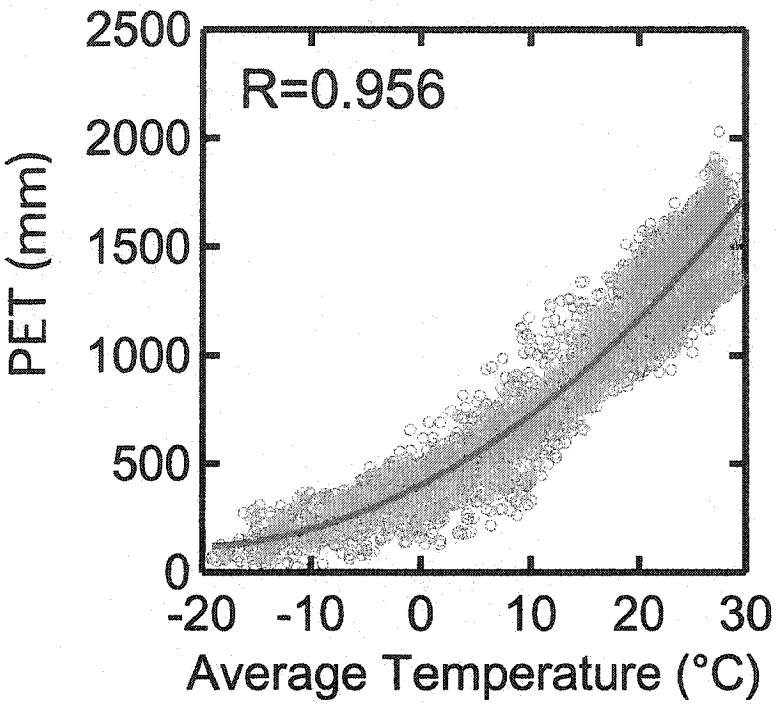


Figure 2.3: The global relationship between annual potential evapotranspiration and mean annual temperature. The relationship between PET and temperature is monotonic positive and approximately quadratic as opposed to linear (r^2=0.92, n=4224, p<0.001).

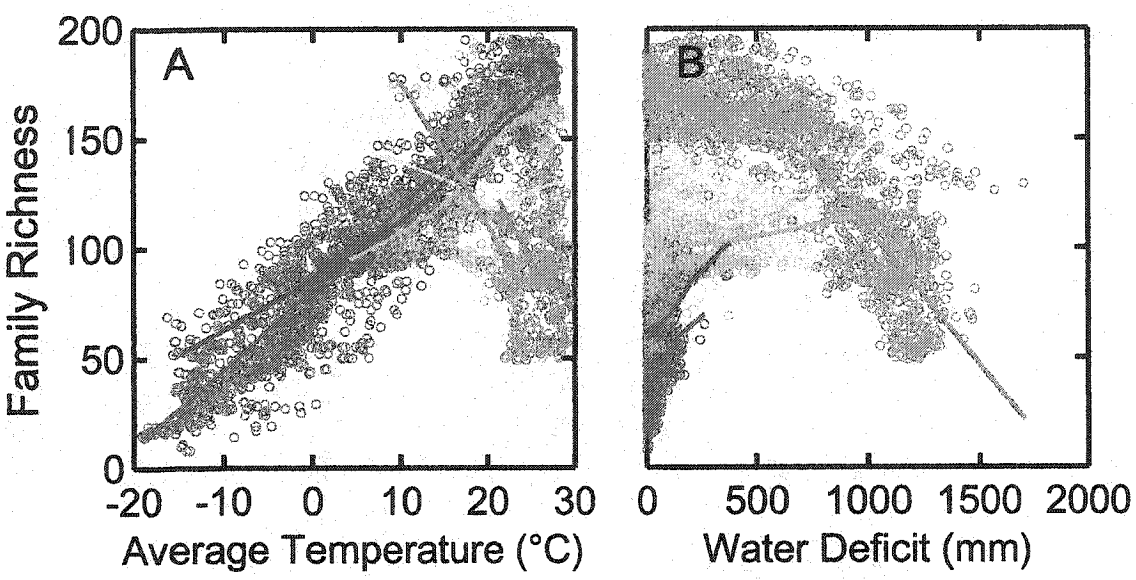


Figure 2.4: **A** The relationship between angiosperm family richness and mean annual temperature, considering quadrats within specified ranges of water deficit (● 0 to 250 mm, ● 250 to 500 mm, ● 500 to 750 mm, ● 750 to 1000 mm, ● 1000 to 1250 mm, ● >1250 mm). **B** The relationship between angiosperm family richness and water deficit, considering quadrats within specified temperature ranges (● -20 to –10°C, ● -10 to 0°C, ● 0 to 10°C, ● 10-20°C, ● >20°C). All smoothed lines are LOWESS curves using a tension of 0.7.

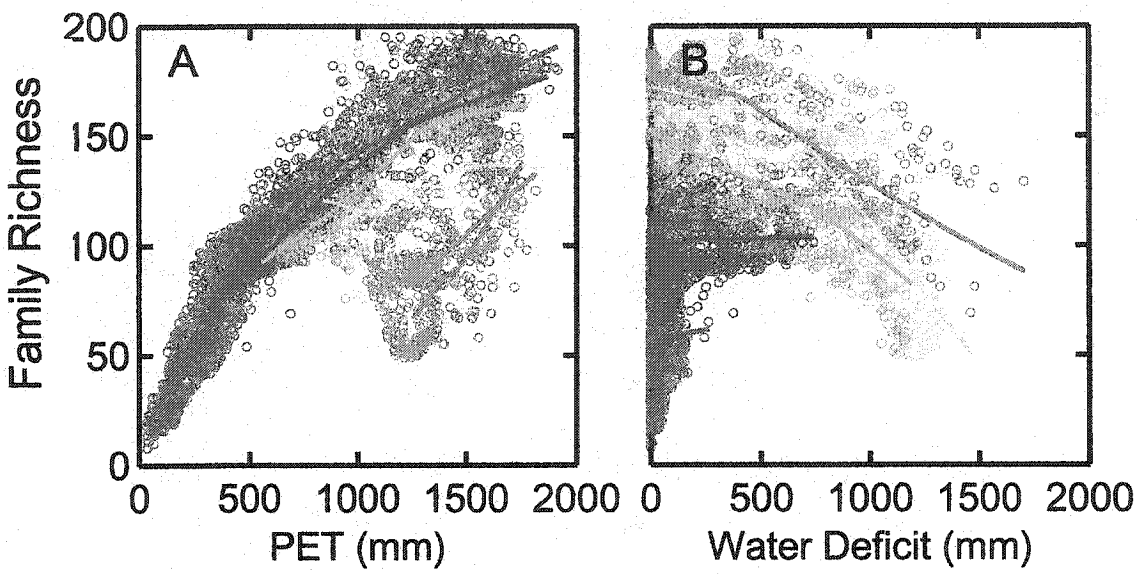
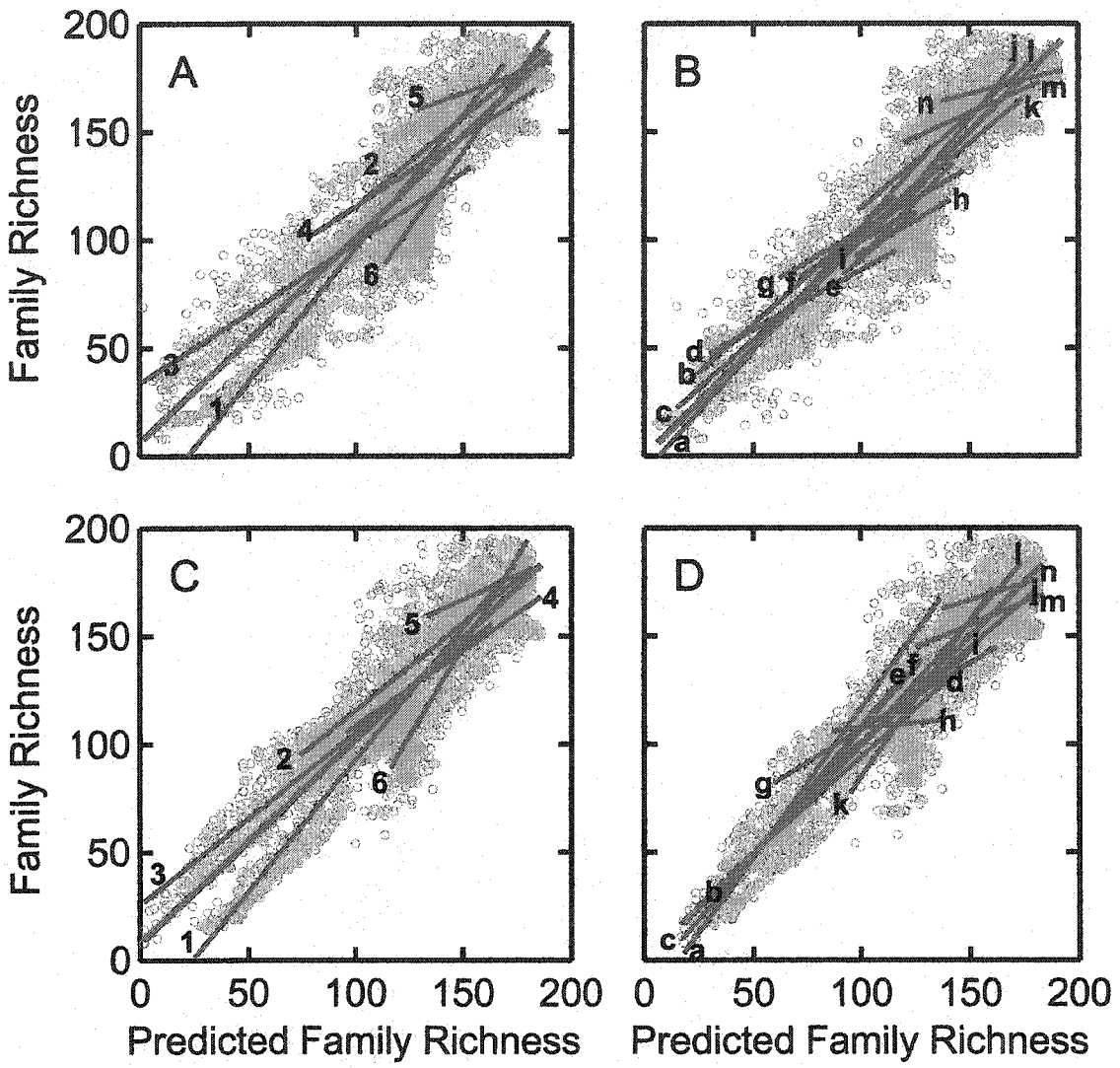


Figure 2.5: **A** The relationship between angiosperm family richness and annual potential evapotranspiration, considering quadrats within specified ranges of water deficit (• 0 to 250 mm, • 250 to 500 mm, • 500 to 750 mm, • 750 to 1000 mm, • 1000 to 1250 mm, • >1250 mm). (b) The relationship between angiosperm family richness and water deficit, considering quadrats within specified PET ranges (• 0 to 400 mm, • 400 to 800 mm, • 800 to 1200 mm, • 1200 to 1600 mm, • >1600 mm). All smoothed lines are LOWESS curves using a tension of 0.7.

Figure 2.6: Observed family richness per quadrat compared to predicted richness using the temperature-water deficit model (A and B) and the PET-water deficit model (C and D) parameterized with extra zonal quadrats. Zones are either biogeographic provinces (1=Nearctic, 2=Neotropical, 3=Palearctic, 4=Ethiopian, 5=Oriental, 6=Australian) or Holdridge aggregate life zones (a=Tundra, b=cold parklands, c=forest tundra, d=boreal forest, e=cool desert, f=steppe, g=temperate forest, h=hot desert, i=chaparral, j=warm temperate forest, k=tropical semi-arid, l=tropical dry forest, m=tropical seasonal forest, n=tropical rain forest). Red lines mark the global relationship. Blue lines mark the relationship between observed and predicted within each zone.


A
B
C
D
Family Richness
Predicted Family Richness
0
50
100
150
200
1
2
3
4
5
6
a
b
c
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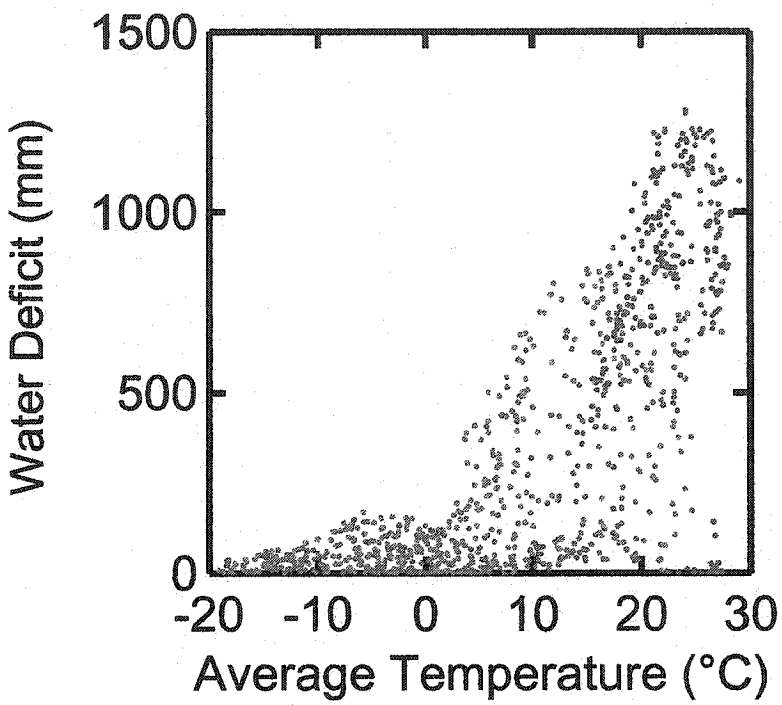


Figure 2.7: North America (red) and Australia (blue) occupy very different climatic areas. North American climate varies more so along the temperature gradient while and Australian climate varies predominantly along the water deficit gradient.

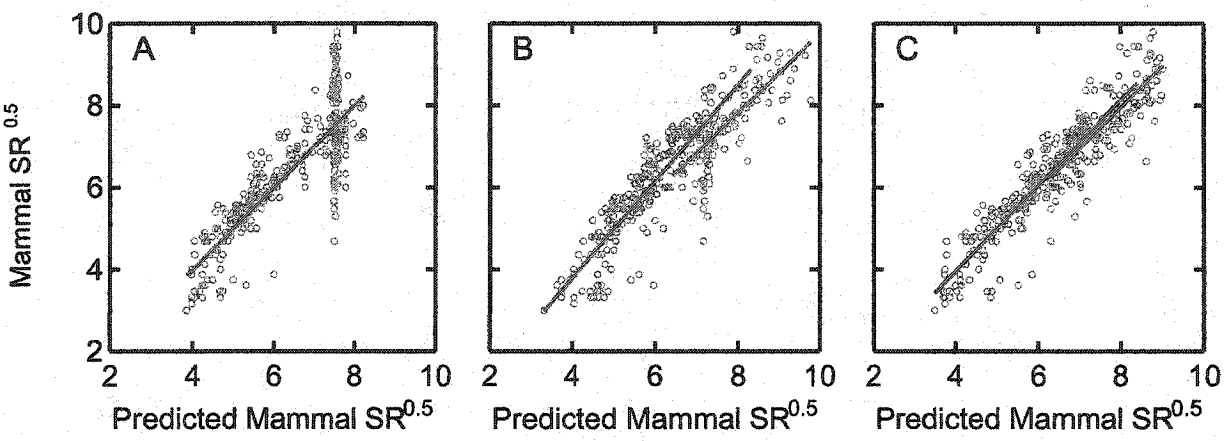


Figure 2.8: North American mammal species richness as predicted by **A** PET alone, **B** temperature and water deficit or **C** PET and water deficit. For all three cases, models regressions were calculated independently for quadrats with PET <1000 mm (blue) and PET≥1000 mm (red).

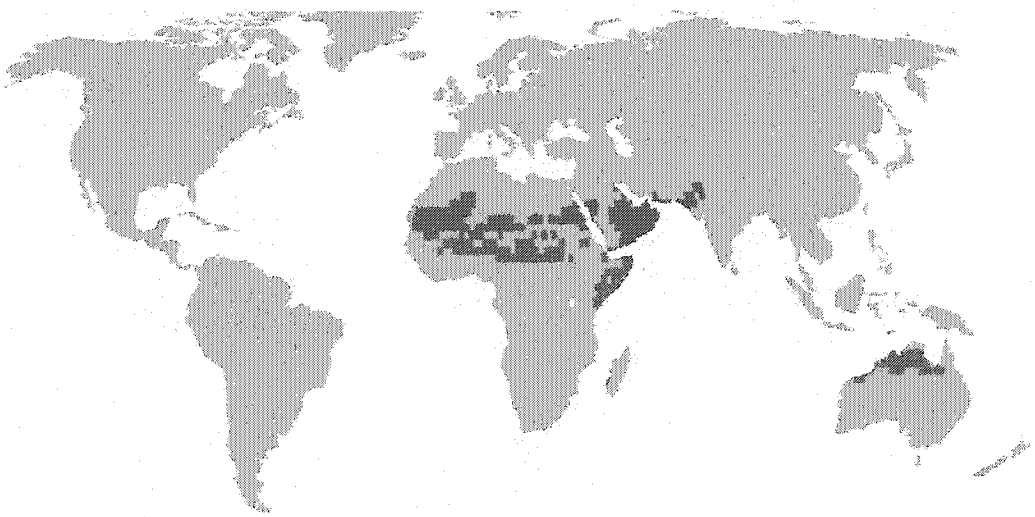


Figure 2.9: Hot (average temperature>25°C) dry (water deficit >900mm) areas of the world with PET < 1350 (blue) or PET >1550 (red).

Chapter 3: Do broad-scale patterns of angiosperm family richness result from climatic tolerances?

Abstract

One possible explaination of broad-scale patterns of species richness is that, by various mechanisms, the number of species that have evolved the adaptations necessary to survive in a given area varies with climatic conditions. Kleidon and Mooney (2000) presented an operationalized form of this climatic tolerance hypothesis by modeling the number of simulated planted species viable along various climatic gradients. It is not clear however, that their simulated gradients richness potential adequately describe real gradients in richness pool size. Using global angiosperm family richness distributions and climatic data, I estimated the climatic tolerances of plant families among various global regions, then examined the relationships of potential family richness patterns to both climatic gradients and observed patterns of family richness. While qualitatively, the spatial pattern of observed family richness loosely resembled that of potential family richness, observed family richness was not strongly related to potential family richness. Potential family richness imposed an upper limit on observed richness levels, but observed richness did not generally approach that limit such that it could explain the functional relationship between observed richness and climate. I reject the angiosperm family pool size as the source of the angiosperm richness patterns.

Introduction

For two hundred years, biologists have noted latitudinal gradients in species plant richness (von Humboldt and Bonpland 1807), and for at least 50 years, ecologists have sought the mechanistic causes of these patterns (Fischer 1960). Studies of richness patterns at broad-scales abound with observations of richness-climate correlations (Mittlebach et al. 2001). However, while the remarkable consistency of these correlations among different regions of the world (Francis and Currie *in press*) suggests a causal connection, the mechanisms that produce these patterns are still contentious.

Probably the simplest mechanism one might hypothesize to explain broad-scale patterns of species richness is that the number of species that have evolved the adaptations necessary to survive in a given area varies with climatic conditions. Accordingly, richness generally decreases towards one or both ends of a given climatic gradient where climatic conditions are harsh (Thiery 1982, Currie 1991). However, conditions are generally defined as harsh when few species are supported. Thus operational predictions of the climatic tolerance hypothesis are not obvious. There is no reason to predict that any particular number of species should have evolved to tolerate a particular set of environmental conditions.

Kleidon and Mooney (2000) recently proposed an operationalized form of the climatic tolerance hypothesis. Using a model of physiological processes involved in carbon balance, they generated a large pool of hypothetical plant species, each having a randomly selected set of physiological parameters governing aspects of metabolism. The hypothetical species that had positive carbon balances, and thus could theoretically

survive, differed under different sets of climatic characteristics. Kleidon and Mooney (2000) calculated that a greater proportion of these simulated planted species would survive in tropical climates. Moreover, they show that this potential richness is at least qualitatively similar to observed richness patterns.

The advantage of Kleidon and Mooney's (2000) approach is that it makes explicit predictions about relative levels of species richness as a function of climatic variables. The disadvantage of Kleidon and Mooney's approach is that it leads to a very weak test (sensu Peters 1991) of the hypothesis that climatic tolerance is the mechanism underlying richness gradients. A strong test would require one to be able to say *a priori* that, if the model predictions were inconsistent with observation, then the hypothesis must be false. Kleidon and Mooney (2000) did not statistically examine the agreement between their model predictions and observed patterns of richness. However, even if they had, any degree of difference between the predictions of their model and observed patterns of richness could indicate either that the hypothesized mechanism is incorrect or incomplete, or that their modeling thereof is incorrect or incomplete. Agreement between model predictions and observed patterns does not mean that the mechanisms in question are true; rather, it means only that they remain plausible, to the extent that they have been tested.

At least one strong prediction can be derived from the hypothesis that climatic tolerance is the mechanism that generates richness patterns: i.e., that the number of species found in a given location is the number that can tolerate the climatic conditions in that place. Moreover, if observed richness varies along climatic gradients, it is because the size of the potential species pool varies along those same gradients (Figure 3.1a). In

this study, I first test these predictions of this unrestricted version of the climatic tolerance hypothesis. I will show that these predictions are not consistent with observed patterns of richness, and therefore the hypothesis is false.

Although some plant families may be able to tolerate the conditions in a particular place, it may be hypothesized that barriers to dispersal have prevented them from reaching those favorable locations. Therefore I also test the predictions that two processes limit richness: physiological tolerance of climatic conditions, and ability to disperse among regions. In other words, richness at a particular location should represent the set of species that occur within a region lacking internal barriers to dispersal, and that can tolerate the climatic conditions at that location (Figure 3.1b).

Finally, it has been hypothesized that environmental heterogeneity increases niche diversity, thus allowing greater species richness (MacArthur 1964, Kerr and Packer 1997). If divisibility of niche space, i.e. niche richness, depends upon climatic stability (Pianka 1966), then high relative levels of richness should be predicted in areas of low climatic variability. Conversely, areas of limited niche variety – due to either low environmental heterogeneity or high climatic variability (Stevens 1989) – should then support low levels of richness. I will test whether patterns of richness are related to a satellite-based measure of environmental heterogeneity or to measures of climatic variability (Figure 3.1c).

Methods

For this study, I used Heywood's global angiosperm family richness distributions and the climatic data set of 4224 quadrats that I had previously assembled (Francis and

Currie *in press*). I began by examining the climatic tolerances of each plant family. Broad scale patterns of plant species richness are generally closely related to some combination of climatic measures of heat and water (Francis and Currie *in press*). I previously constructed richness-climate models using water deficit and either potential evapotranspiration (PET) or temperature. Others have used various combinations of these and other climatic factors such as annual evapotranspiration (AET) (Wright 1983), precipitation (Abramksy and Rosenzweig 1984), or rainfall (O'Brien 2000). To varying degrees, these climatic indices are all collinear. I therefore performed a principal components analysis on my climatic variables and I extracted two independent (orthogonal) "climatic factors" that accounted for 96% of the climatic variation (Table 3.1a).

Using an algorithm scripted in C++, I calculated the potential spatial distribution of each family of angiosperms based on the observed range of climatic variables in which each family occurs. I found the minimum and maximum for each index (i.e. PCA scores) at which it occurred, anywhere in the world. Then, for each quadrat, I calculated the total number of families for which all three climatic ranges intersected the quadrat's average climatic conditions. In other words, I assume (at this step) that each family should occur in every climatically suitable area in the world. Hereafter, I will refer to this as "potential family richness".

Next, I included progressively tighter spatial restrictions on my families when tallying potential richness. I then divided my quadrats first into Wallace's six biogeographic provinces, then further divided each of those into four sub-regions (Brown and Lomolino 1998). Quadrats were categorized according to the province or sub-region

into which they fell. Quadrats crossing zonal boundaries were omitted. I then repeated the protocol described above, determining the minimum and maximum climatic tolerances for each family *within* each province or sub-region. Thus the potential family pool for a given quadrat contained only those families found within that quadrat's province or sub-region.

Using the Global Land Cover Characteristics Data Base V.2. (EROS Data Center), I estimated landscape heterogeneity as the number of ecosystem types per quadrat. This database divides the world into 96 ecosystem categories at a nominal spatial resolution of 1 km^2. To measure climatic variability I conducted a principal components analysis of the within-quadrat annual ranges of all six climatic variables. The first two "climate range factors" accounted for 71% of the variation in the climatic range space (Table 3.1b).

I examined the relationships of potential family richness patterns to both climatic gradients and observed patterns of family richness using multiple regressions. I then compared these relationships with correlative models relating richness directly to climate. If climate determines richness patterns by defining the potential richness pool for a given location, then there should be a causative – and hence correlative – pathway from climate to potential richness to richness. Moreover, the correlation between potential richness and observed richness should be both stronger than, and independent of, the observed richness/climate relationship (Figure 3.1).

In any data set in which sample quadrats fully cover the study region, spatial autocorrelation is bound to be high, leading to an over-estimate of the true number of

degrees of freedom in significance tests. To ascertain the true degrees of freedom of my models, I calculated Moran's I for my model residuals over a series of lags to determine the distance between quadrats at which spatial autocorrelation was minimized. In calculating Moran's I, neighbours were defined using great arc distance between quadrat centroids and successive lags were non-cumulative.

Results

Qualitatively, the spatial pattern of observed family richness (Figure 3.2) loosely resembles that of potential family richness (Figure 3.3). Both exhibit general latitudinal gradients. Both show marked reductions in temperate and tropical desert areas such as the Sahara, the Gobi and the Australian Outback. Moreover, both observed family richness and potential family richness patterns are related to climate (Table 3.2). Generally speaking, potential family richness – like observed family richness – increases along climatic gradients of heat and water (Figure 3.3).

Observed family richness, however, is not strongly related to potential family richness. When potential family distributions are spatially unrestricted, maximum family richness is higher than observed richness in most areas (Figure 3.4a). When potential family distributions are restricted to regions (Figures 3.4b) or sub-regions (Figures 3.4c), observed richness more closely approaches maximum richness, but even with these strong spatial restrictions, most quadrats contain fewer families than could potentially occur in them, given their climatic tolerances. This results in distinctly triangular relationships (Figure 3.4). In areas where few families can potentially tolerate the climatic conditions, few occur (necessarily). However, in areas having climates tolerated

by many families, richness can be either high or low. Thus while maximum potential family richness may impose an upper limit on observed richness levels, observed richness does not generally approach that limit such that potential richness would explain the functional relationship between observed richness and climate.

Both richness and potential richness then are related to climate, but in somewhat different ways. Climate Factor 1 combines AET, PET, precipitation and rainfall – i.e. measures of water and its movement through ecosystems (Table 3.1). Climate Factor 2 is chiefly a measure of water deficit (i.e. stress), but in the negative direction. Thus when Climate Factor is 2 low, stress is high. When no spatial restriction was applied, potential richness peaks at intermediate values of Climate Factor 1– moderate levels of water availability and usage – and generally increases with Climate Factor 2 (Figure 3.5). For observed richness and for potential richness when spatial restriction was used, richness increases more or less linearly with Climate Factor 1 when Climate Factor 2 is low (i.e. high water deficit), but is generally lower and peaked when Climate Factor 2 is high. Compared to observed richness however, potential richness is relatively higher and peaks at higher levels of water availability and usage (Climate Factor 1) when Climate Factor 2 is high (Figure 3.5).

Neither measures of habitat nor climatic heterogeneity greatly improve the ability of potential richness to predict observed richness. Landscape heterogeneity as defined by the number of ecotypes co-occurring within a quadrat accounts for only 1 to 7% of additional variance in observed family richness beyond the limiting effect of the climatic tolerance distribution within the regional species pool (Table 3.3). Annual climatic variance within quadrats did appear to help in terms of variance explained, adding 6 to

23% to the models (Table 3.3). However, examination of the residuals using a Levine's type test shows that variance still increases significantly with the estimate, suggesting that climatic variance does not adequately account for the triangular nature of the richness/potential richness relationship (Table 3.3). Thus neither of these models is as strong as, or provides the stability of variance of the simple observed richness/climate model (Table 3.2) (Levine's test: R2=3.913x10-4, p=0.199, n=4224).

Calculating Moran's I for the residuals of my richness-climate model, I determined that spatial autocorrelation becomes zero when quadrats are separated by a distance of 4080 km (Figure 3.6). This distance allows for a global distribution of 40 statistically independent quadrats. Overlap of species ranges among multiple quadrats is presumably the main cause of autocorrelation (autocorrelation would also result if richness depended upon spatially-structured variables such as temperature). Since families' ranges rarely extend 4080 km, this level of reduction provides for an extremely conservative correction of p. After including all model terms, I am still left with more than 30 degrees of freedom. Models then need only to achieve an F of 1.88 to be significant with a=0.05. Since the F's of all of my models surpass that by upwards of three orders of magnitude, I conclude that spatial autocorrelation does not affect my significance tests.

Discussion

The numbers of angiosperm families with particular climatic tolerances are clearly correlated with climate (Table 3.1): more families tolerate warm wet conditions than cold dry ones. Although I defined the potential geographic range of each family as a

function of climatic variables, there is no necessary reason why potential richness (i.e. the total number of families potentially occurring per site) must also relate to those variables.

This spatial pattern of *potential* richness is consistent with several hypothesized mechanisms. The pattern is consistent with Ricklefs and Schluter's (1993) suggestion that angiosperms first appeared in the humid tropics and took time to develop adaptations to survive climatic conditions elsewhere. It is also consistent with Rosenzweig's (1995) argument that more species evolved in the tropics – and hence are adapted to tropical climatic conditions – because the tropics are geographically large. Similarly, Rohde (1992) suggests that more species evolved to tolerate tropical conditions, but because evolutionary rates are higher in the tropics. Finally, the pattern is consistent with Kleidon and Mooney's (2000) hypothesis that there are more possible physiologies that would be viable in the tropics, which translates to greater evolutionary potential for diversification.

However, the climatic gradient in the potential angiosperm pool does not account for the consistent global relationship between contemporary climate and *observed* angiosperm richness. If climatic tolerance controlled richness, then one would expect a functional relationship between potential and observed richness. Instead I only observed a limiting relationship (Figure 3.4). Further, if climate determines potential richness, and potential richness in turn limits realized richness (Figure 3.1), then the direct correlations must be stronger than the indirect one. I do not observe this (Table 3.2). I reject the angiosperm family pool size as the source of the contemporary angiosperm richness patterns.

My methodology of demarcating the potential climatic niche for each family at

the limits of observed occurrence along each climatic gradient presents two potential problems. Firstly, I may overestimate potential richness. Using rectangular regions of the climatic surface assumes the absence of interaction between climatic constraints. Plant families may in fact not be capable of surviving in the corners of such a climatic space, i.e., simultaneously dealing with extremes of more than one climatic consideration. To reduce this effect, I repeated the entire protocol using a more restrictive elliptical niche space, extending to the upper and lower occurrence limits of each climatic axis. However I found that the elliptical climatic space consistently, and often dramatically, underestimated the real geographic distributions of most plant families. This suggests that many families do exist "in the corners" of rectangular climatic niches, and that I probably have not overestimated potential richness by using rectangular niche spaces.

It is also possible, even probable, that I have underestimated potential richness. Only instances of realized occurrence are used in calculating climatic tolerances. Yet, factors other than tolerance of the observed climatic gradients (e.g., competition) could prevent a given family from occupying otherwise habitable climatic space. This would cause the family's potential climatic range to be underestimated, which would further lead to underestimates of potential richness. Thus, my conclusion that observed richness is often significantly less than climatically determined potential richness is probably very conservative.

Richness deficit – i.e. climatically determined potential richness minus observed richness – may be related to other factors beyond climatic tolerance. For example, factors influencing niche diversity may moderate the ability of a region to sustain the maximum taxonomic compliment. However, habitat heterogeneity (at this scale) added

very little to the richness / richness potential models (Table 3.3) and thus did not contribute significantly to the probability that the maximum potential richness be achieved. This is consistent with my earlier study of richness climate relationships (Francis and Currie *in press*) in which I found the variation in richness attributed to heterogeneity (Kerr and Packer 1997) could be better explained by climatic factors. Although climatic variability did add somewhat to models relating observed to potential richness, this is likely a spurious effect stemming from the collinearity between climatic range and mean climate, given that climatic variability failed to account for the increasing richness deficit (Table 3.4).

The observation that richness varies as a function of climate but is merely bounded by potential richness is consistent with the importance of contemporary climate in determining observed richness patterns (Francis and Currie *in press*). In contrast, Latham and Ricklefs (1993a) argued that angiosperms originated in, and then radiated out from Asia, thereby furnishing Asia with a large potential taxonomic pool leading to general patterns of higher observed richness. Asia as a whole may indeed be home to a higher total number of angiosperm families (Ricklefs and Renner 1994). However, I demonstrated earlier that richness within 35,000 km2 quadrats in Asia is not significantly higher than in other regions (e.g. North America), given climate (Francis and Currie *in press*), despite Eastern sub-tropical Asia having higher potential richness on average than Eastern North America (t=-3.750, d.f.=190.9, p=2.34x10-04). From this study, I can see that this potential for higher diversity is not generally realized in any given region (Figure 3.7). The consistency among regional richness-climate correlations (Francis and Currie *in press*) despite differences in total regional pool sizes (Figure 3.8) may be a

consequence of richness deficit being strongly related to contemporary climatic factors.

Moreover, the importance of climate to observed richness patterns is apparent over the entire range of extant climatic gradients, not just in cold areas, as argued by Kerr and Packer (1997). In very cold or dry climates, the potential angiosperm pool is small (Figure 3.3) and observed richness is also necessarily small (Figure 3.2). It is therefore impossible to distinguish whether contemporary climate directly limits richness in low richness areas, versus whether there only exist few taxa capable of surviving the environmental conditions.

In contrast, as potential richness increases, so does the range of richness deficit. Yet, I have previously demonstrated that richness is also strongly related to climate in high richness areas (Francis and Currie *in press*). Bivariate richness-climate relationships appear to be more variable in tropical areas because richness depends on two climatic variables: heat and water deficit. When both climatic variables are taken into account, the richness-climate relationship is tight and globally consistent. Thus, the effect of contemporary climate on richness is actually most obvious in tropical areas, not cold ones as Kerr and Packer (1997) suggest.

Finally, this study suggests that projecting future geographic distributions based on contemporary climatic tolerance is risky. For example, in an effort to forecast the consequences of global warming, some studies have modeled changes in future species distributions according to species' current climatic tolerance and projected climatic change (e.g. Iverson *et al.* 1999). Since observed richness is often significantly less than potential richness, there is reason to expect that many species will not expand into areas

that appear to be climatically appropriate, even given sufficient time. Total richness may track climate, but composition seems unlikely to do so (cf. Davis 1981).

Conclusions

There is a strong association between the numbers of angiosperm families with particular climatic tolerances and climatic gradients. A potential mechanism is that physiological tolerance leads to a climatic gradient in the potential angiosperm pool. I find, however, that potential richness does not account for the consistent global relationship between contemporary climate and observed angiosperm richness. Climatic tolerances instead provide only an upper bound to richness– one that is usually not reached. Thus I reject the angiosperm family pool size as the source of the angiosperm richness patterns. While it is clear that observed richness patterns vary along climatic gradient, this conclusion suggests that it is unrealistic to predict richness patterns based on projected species ranges.

Tables

Table 3.1: Factor loadings for the four principal components of A) measures of mean annual climate and B) measures annual of local climate range.

A

Climate PCA Factor	1	2	3	4
AET	0.939	0.246	0.236	0.045
PET	0.804	-0.576	0.097	0.113
Precipitation	0.896	0.399	-0.189	0.009
Rainfall	0.932	0.317	-0.166	0.014
Temperature	0.731	-0.651	0.023	-0.205
Water Deficit	-0.056	-0.984	-0.143	0.089
Percent Total Variance Explained	62.26	34.07	2.497	1.082

B

Climate Range PCA Factor	1	2	3	4
AET Range	0.61	0.172	0.669	-0.34
PET Range	-0.527	0.686	0.362	0.007
Precipitation Range	0.958	0.017	0.067	0.251
Rainfall Range	0.953	-0.024	0.12	0.244
Temperature Range	-0.677	-0.222	0.535	0.418
Water Deficit Range	0.126	0.9	-0.27	0.164
Percent Total Variance Explained	49.201	22.671	15.947	7.333

Table 3.2: Multiple regressions of observed family richness (OFR) and potential family richness (PFR) against climate. Potential family richness was calculated using no spatial restriction (PFR_1) as well as by restricting potential richness to regions of provinces (PFR_2) or sub-provinces (PFR_3). All climate models were based on polynomial combinations of Climate Factors 1 and 2 and their interactions (Climate1 + Climate1^2 + Climate2 + Climate2^2 + Climate1*Climate2). For all models $p<10^{-9}$.

Dependant Variable	F	n	R^2
OFR	5090.908	4224	0.858
PFR_1	4930.170	4224	0.854
PFR_2	3493.540	4084	0.811
PFR_3	4023.488	3734	0.844

Table 3.3: Observed family richness as a function of potential family richness (PFR) plus either habitat heterogeneity (H) or climatic variability (CV) – a polynomial combination of Climate Range Factors 1 and 2. Potential family richness was calculated using no spatial restriction (PFR_1) as well as by restricting potential richness to regions of provinces (PFR_2) or sub-provinces (PFR_3). For all models $p<10^{-9}$. Levine Slope is the standardized coefficient (i.e. slope) from a linear regression of the absolute value of model residuals as a function of model estimates. For Levine's tests, all slopes are different from 0 at $p<10^{-4}$. This indicates that the variance in observed family richness increases in the triangular fashion in relation to potential richness (i.e., as shown in Figure 3.4) even after accounting for habitat heterogeneity or climatic variability.

Independent Variables	F	n	R^2	Levine Slope
PFR_1 + H	3022.1	4224	0.589	0.270
PFR_1 + CV	2125.7	4224	0.752	0.077
PFR_2 + H	6583.2	4084	0.763	0.098
PFR_2 + CV	2927.2	4084	0.812	0.063
PFR_3 + H	9053.6	3734	0.829	0.100
PFR_3 + CV	3047.6	3734	0.831	0.124

Table 3.4: The Pearson Correlations between the mean annual value of climate factors and their annual range. For all models $p<1.000x10^{-9}$.

Climate	Climate Range	Pearson R
AET	AET Range	0.410
PET	PET Range	-0.207
Precipitation	Precipitation Range	0.740
Rainfall	Rainfall Range	0.757
Temperature	Temperature Range	-0.859
Water Deficit	Water Deficit Range	0.804

Figures

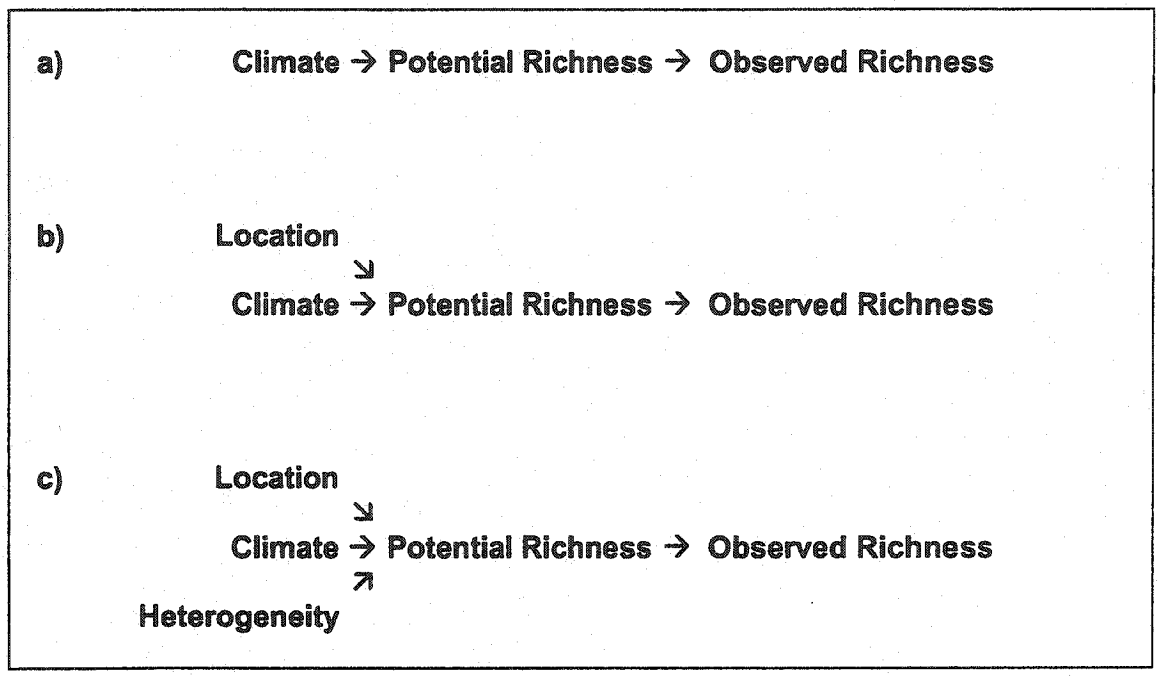


Figure 3.1: Proposed mechanistic pathways of a climatic tolerance hypothesis.

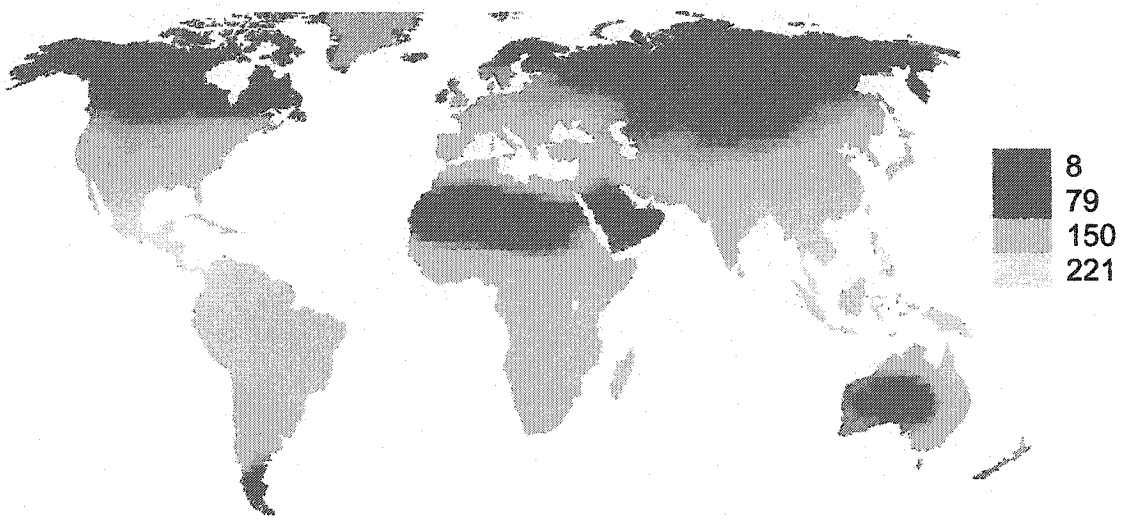
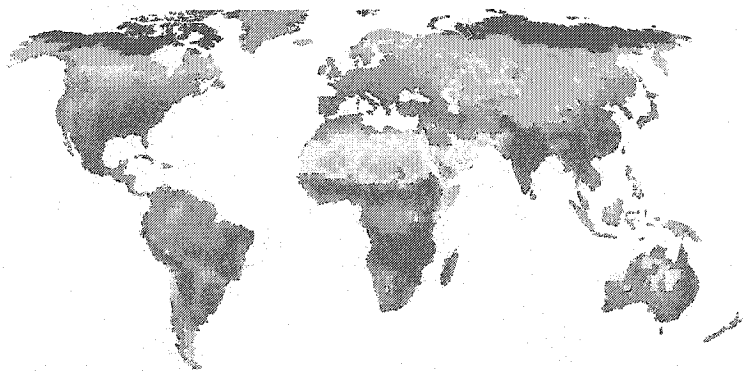


Figure 3.2: Global observed angiosperm family richness.

Figure 3.3: Potential family richness calculated using **A** no spatial restriction as well as by restricting potential richness to regions of **B** provinces or **C** sub-provinces. Gray indicates quadrats situated along boundary areas between regions or missing climatic data (extreme northern areas).

A



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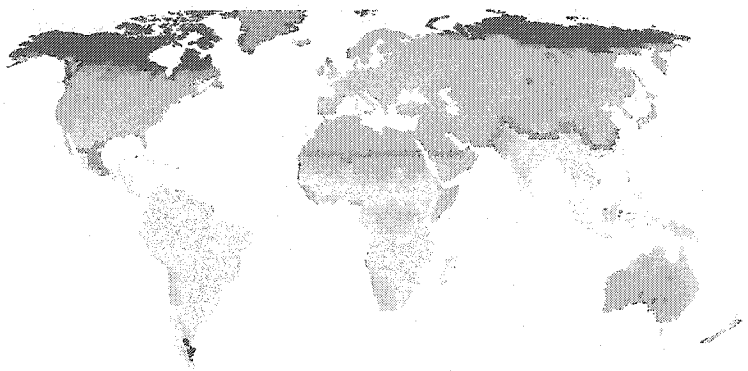

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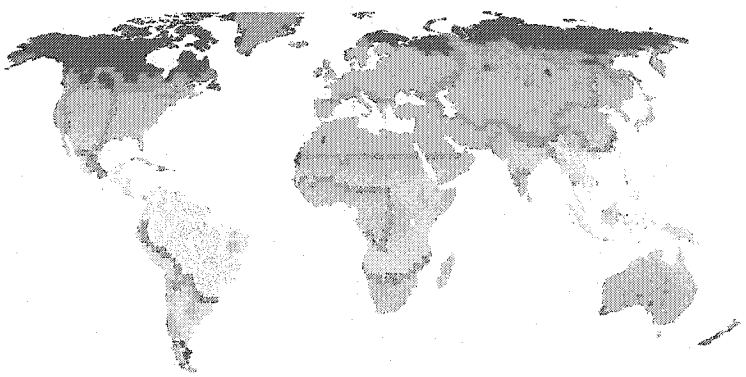
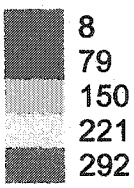




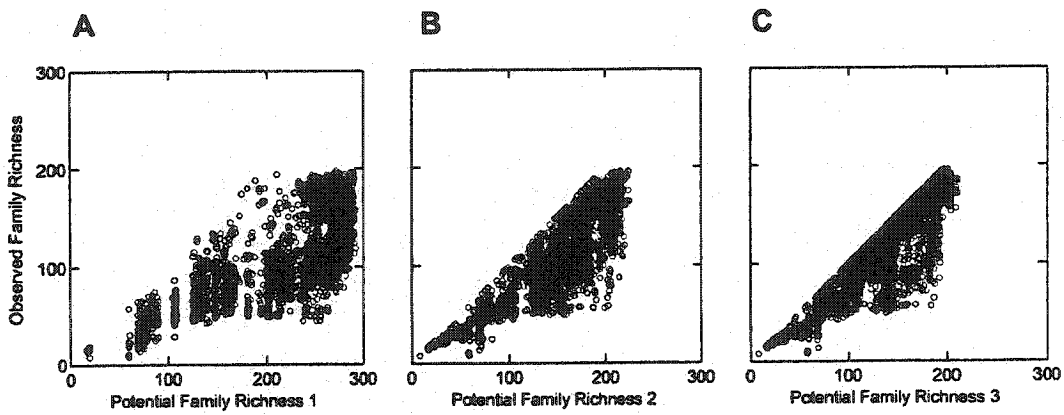


Figure 3.4: Observed Angiosperm Family Richness as a function of **A** Potential Family Richness 1 (no spatial restriction), **B** Potential Family Richness 2 (spatial restricted by province), and **C** Potential Family Richness 3 (spatial restricted by sub-province). Spearman Rank correlations are: **A**($R=0.716$, $n=4224$, $p<1.000\times10^{-15}$), **B** ($R=0.864$, $n=4084$, $p<1.000\times10^{-15}$), **C**($R=0.878$, $n=3734$, $p<1.000\times10^{-15}$).

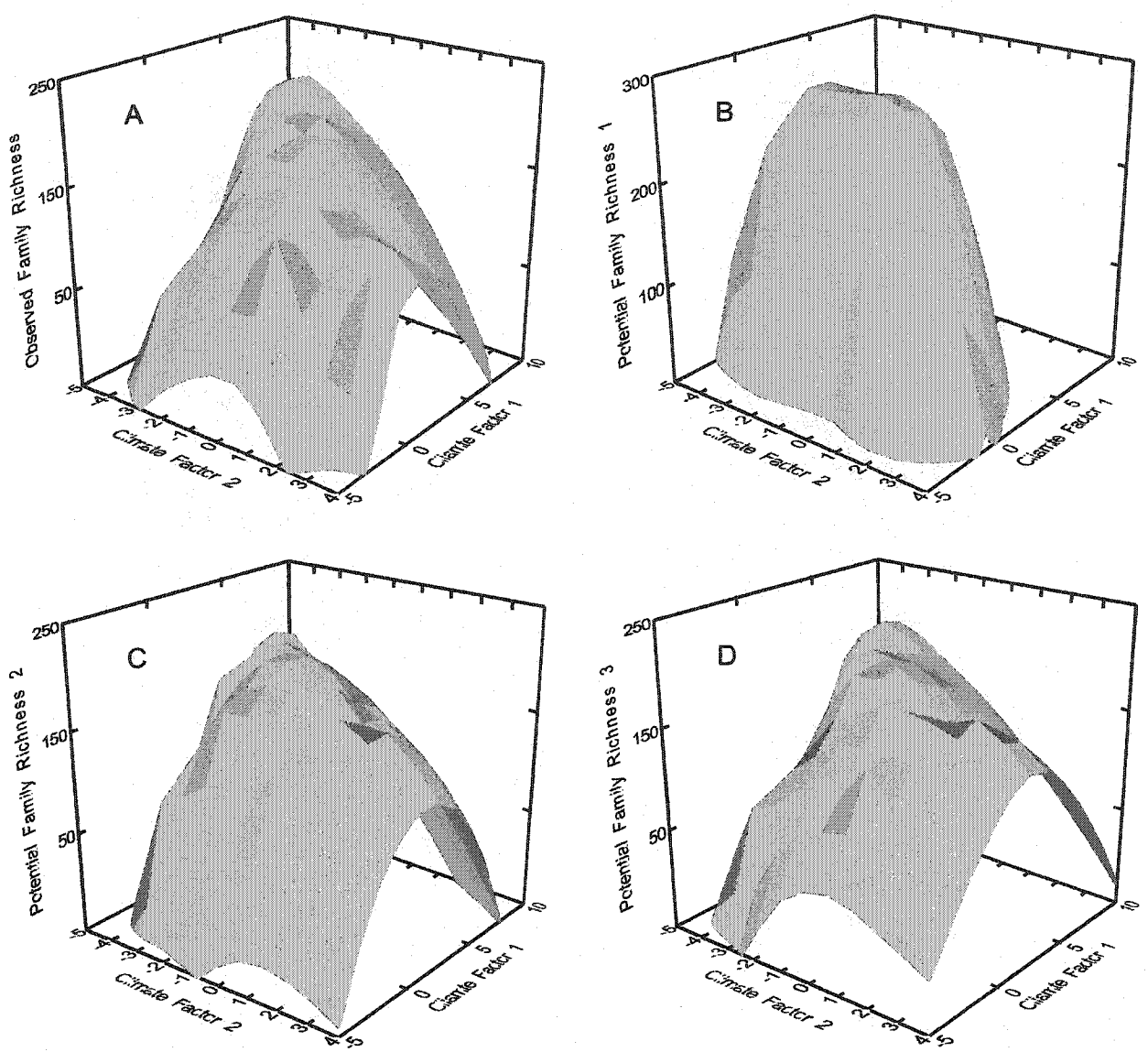


Figure 3.5: Family richness related to climatic factors 1 and 2 where family richness is **A** Observed Family Richness, **B** Potential Family Richness 1 calculated using no spatial restriction, and Potential Family Richness 2 **C** and 3 **D** calculated restricting potential richness to regions of provinces or sub-provinces respectively. Surfaces are fitted using DWLS (distance weight least squares) with a tension of 0.7.

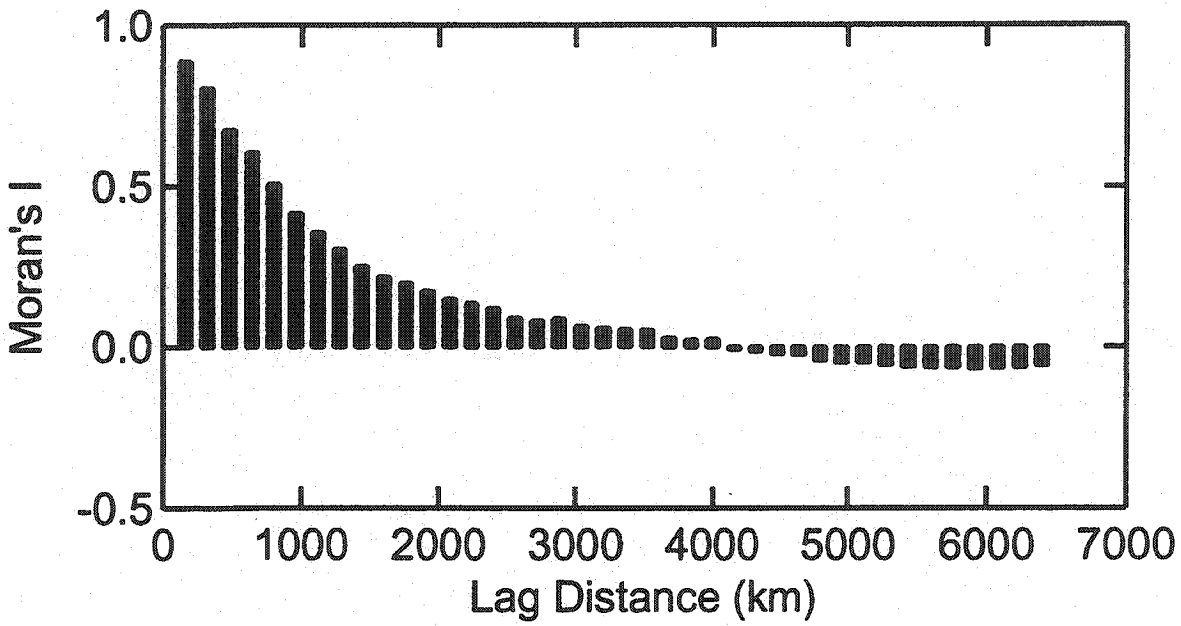
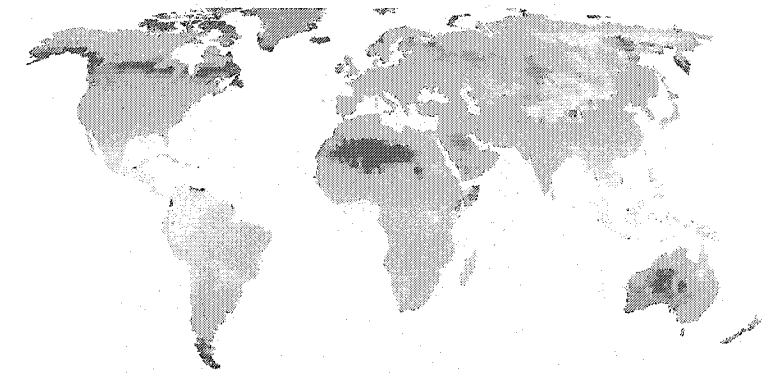


Figure 3.6: Moran's I over successive 160 km lags. Neighbours were defined using great arc distances between quadrat centroids. Successive lags were non-cumulative.

Figure 3.7: Percent realized potential family richness calculated using **A** no spatial restriction as well as by restricting potential richness to regions of **B** provinces or **C** sub-provinces.



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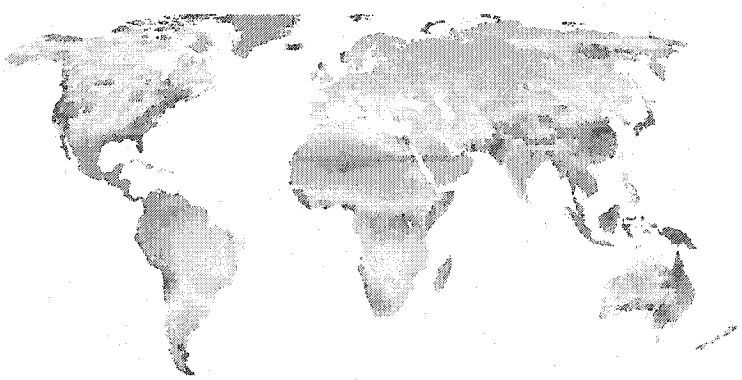

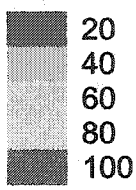

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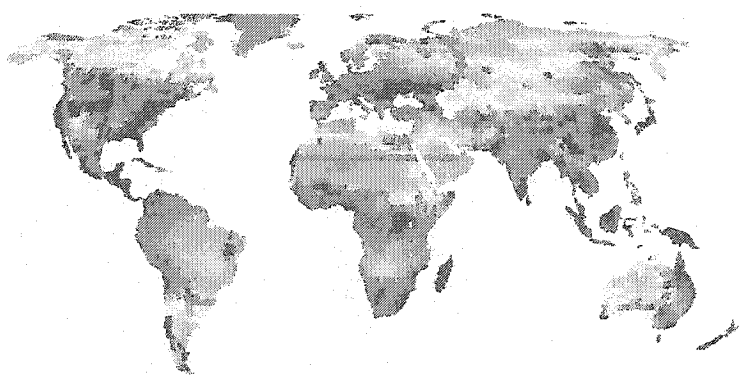


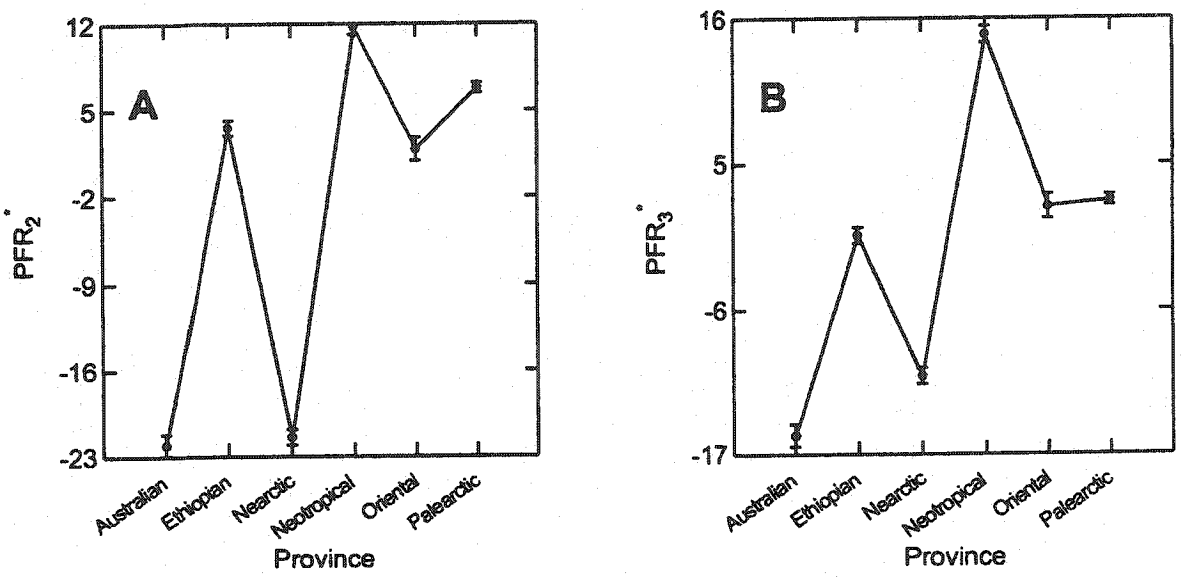


Figure 3.8: Least squares means from ANOVA models of **A** potential family richness spatial restricted by province (PFR_2^*), and **B** potential family richness spatial restricted by sub-province (PFR_3^*) among provinces. In both cases potential family richness is corrected for climate. For both, n=3734 and $p<10^{-11}$.

Chapter 4: Testing the Species-Energy Hypothesis in Forests

Abstract

The Energy-Diversity or Species-Energy theory proposed by Hutchinson (1959) and elaborated by Brown (1981) and Wright (1983), presents a plausible explanation of broad-scale patters of biodiversity. It suggests that, for a given species to persist in an area, there must be sufficient ecosystem energy flux in that area to support enough individuals of that species to maintain a viable population. Thus species richness is postulated to depend upon the number of individuals, which in turn depends upon energy availability. Numerous studies have demonstrated strong correlations between environmentally available energy (usually as indexed by climate) and patterns of richness. The prediction that the number of individuals is proportional to total energy however, has not been tested at broad scales. Using trees counts from 15 forests sites along a latitudinal gradient running from James Bay, Canada to Costa Rica, I tested whether a series of direct correlative links existed from climate to tree density to tree species richness. Despite a positive (but not statistically significant) correlation between AET and richness, the tree density per site was *negatively* correlated with energy. Contrastingly, Alwyn Gentry's global observations of tree density and species richness indicated a positive correlation between AET and tree density for forested areas in the northern hemisphere but no significant correlation at all in the southern hemisphere. However, even where the energy-density correlation was in the predicted direction, path models show that the relationship was not strong enough to explain the richness-energy correlation. At the scale of individual forests (i.e. among distinct sets of tree populations)

energy appears to have little bearing on species richness. Any potential mechanistic influence of environmental energy on richness would likely then operate on a scale larger than that of distinct population clusters. As a bottom up mechanism to explain richness patterns, the energy-diversity theory does not work.

Introduction

For over two centuries, biologists have observed large-scale geographic patterns in the abundance of species for numerous different taxonomic groups (Von Humboldt 1807, Wallace, 1878). In studying these various spatial gradients of richness, particularly at broad scales, biologists have observed correlations between the spatial variation of richness and numerous environmental and climatic factors (Mittlebach *et al.* 2001). There is increasing evidence that the relationship between richness and climate is both strong (Wright *et al.* 1993), and globally consistent (Francis and Currie, in press). However, while these correlations provide useful models for describing and predicting large-scale richness patterns, they do not address the mechanisms underlying the richness climate connection (Rohde 1992).

One such potential mechanism, proposed by Hutchinson (1959) and elaborated by Brown (1981) and others, has come to be known as Energy-Diversity or Species-Energy theory. The energy-diversity hypothesis proposes that an individual needs a positive energy balance to survive. Further, for a species to persist in an area, there must be sufficient energy available in that area to support enough individuals of that species to maintain a viable population (Brown 1981). Thus species richness is postulated to depend upon the number of individuals, which in turn depends upon energy availability.

The forms of the relationships between species richness and individuals were worked out by Preston (1962). Preston first noted that species' population sizes in an assemblage of species are log normally distributed. As a consequence, the total number of species in an assemblage (S) is related to the total number of individuals (I):

$$\log S \propto \log I \quad (1)$$

From this, MacArthur and Wilson (1967) predicted that, since larger areas (A) have more individuals:

$$I \propto A \quad (2)$$

then species richness should also increase with area:

$$S = cA^z \quad (3)$$

where *c* and *z* are empirical constants. Preston derived a theoretical value for z based on what he called "canonical" distributions of population sizes and species richness. The observed value of z varied somewhat from the theoretical value predicted by Preston as heterogeneity and/or isolation of the sample locations changed, but the basic form of the relationship was (MacArthur and Wilson 1967) and has been (Rosenzweig 1995) observed in the great majority of cases. MacArthur and Wilson found, however, that the constant *c* varied tremendously among taxonomic groups and geographic locations.

Wright (1983) attributed the observed variation in the value of *c* to differences in energy availability, thus proposing the link between energy and both population density and species richness. According to Wright,

$$c = k(E/A)^z \quad (4)$$

where *k* is a constant, and *E/A* is energy per unit area. Combining equations 2 and 3:

$$S = k(E/A)^z A^z \quad (5)$$

or

$$S = kE^z \quad (6)$$

Wylie and Currie (1993) found that variation in richness is better described if the

exponents on E (inferring E/A) and A are not forced to be the same.

$$S = kE^{z_1}A^{z_2} \quad (7)$$

Either way, however, richness is hypothesized to vary in proportion to population density, which in turn varies in proportion to energy. Wright used annual evapotranspiration (AET) as an index of energy availability because Rosenzweig (1968) and Leith (1975) had shown that broad-scale variation in primary productivity is strongly correlated with AET. Wright was able to explain 70 - 80% of the variation in species richness of angiosperms and of birds among a set of islands around the world. Thus the two endpoints in the hypothesized causal chain are indeed well correlated (Francis and Currie *in press*). Wright and others however, never tested the assumption implicit in the model that the number of individuals is proportional to total energy:

$$I \propto E \quad (8)$$

The purpose of this study is to test this prediction of energy-diversity theory. Since the mechanism of energy-diversity theory is bottom-up, the effects of energy on richness should be most pronounced at the local scale of individual populations. I chose to test this prediction using trees, as they provide a wide ranging, and diverse group of species that occupy a single trophic level and that potentially interact with each other in the manner proposed by Hutchinson (1959) and subsequent authors. If the energy-diversity hypothesis is correct, there should be a series of direct correlative links from climate to individuals to richness.

Methods

For my study area, I chose 15 forests sites along a latitudinal gradient running

from James Bay, Canada (51.2 °N) to Costa Rica (10.5 °N) (Figure 4.1). Sites were in provincial or state parks, or conservation areas and consisted of relatively undisturbed upland forest typical of the area.

Within each site, I selected ten 10x10m quadrats. I chose quadrats more or less randomly by walking 100m along a trail, and then turning perpendicularly off the trail, and walking 10m farther. If the area was not completely composed of intact forest (e.g. another trail or stream running through it) or was not enumerable (e.g. too steep), I moved another hundred meters down the trail. Subsequent quadrats were chosen by moving 100 m farther along the trail, and 10 m into the woods on the opposite side of the trail. Thus the quadrats followed a transect approximately 1 km long through the site.

Within each quadrat, I identified and measured all trees with a circumference greater than 5cm. Tree species were identitied using field guides (Farrar 1995, Harrar 1962, Petrides 1998, Preston 1989), except in Costa Rica, where trees were identified by Professor P. Sanchez of the Universidad Nacionál de Costa Rica. For each tree, I measured circumference at breast height. I converted this to diameter at breast height (DBH) assuming the trunk to be cylindrical. When, at breast height, a tree had multiple stems, I measured the circumference of each stem, and I calculated the cross-sectional area of each one. I then added the areas and calculated the DBH for a tree with that cross-sectional area.

My study examines patterns of tree species richness and population density at two different scales. At the landscape level, quadrats sample single forest communities. At the regional level, regional species pools integrate species richness over all neighbouring

communities. Estimates of the regional tree species pool for my Canadian and American sites were taken from Currie and Paquin (1987). The regional species pool for my Costa Rican site was taken from Sánchez-Vindas and Poveda Alvarez (1997).

I extracted the rest of my data from various published sources. Following Wright (1983) I used actual evapotranspiration levels (AET) as my measure of available environmental energy. AET values were taken from Ahn and Tateishi's (1994a) digital global water balance maps. For comparative purposes, I also examined Alwyn Gentry's observations of tree density and species richness in 227 small forest sites around the world (Phillips and Miller 2002). After omitting those cases for which I could not obtain AET (small oceanic islands) or for which the total site area was less than 0.1 ha, I was left with data for 199 sites.

I began my statistical analysis by examining the correlations among my variables. Since the predicted model forms I was testing are all monotonic but non-linear, I used Spearman rank correlations. Where I did use regression or multiple regression analysis, I log-transformed my variables to ensure linearity of the models and stable variance in the residuals.

I also examined the distribution of individuals among species. To do this, I divided the species within sites into four abundance categories. Categories covered equal spans on a $\log_{10}$ scale of numbers of individuals per species ranging from one to 160, my highest recorded within site species abundance. Thus species having 1 to 4 individuals per site are considered rare (for that site) while species with 46 to 160 individuals are common.

The density of individuals within a site may change over time due to self-thinning (Ricklefs 1990). Only one of the sites I examined (Temagami, Ontario) appeared to be truly old growth, with very large conifers. The rest of the sites I examined were reasonably mature second growth forests. However, to ensure that varying degrees of self-thinning were not masking some relationship between numbers of individuals and numbers of species among sites, I included DBH as covariate in models using number of trees as an independent variable.

Results

At the landscape scale, the first prediction of the Hutchinson-Brown-Wright formulation of the Energy Richness Hypothesis – that the density of individuals is proportional to energy – was not substantiated. The number of individuals per site was *negatively* correlated with energy as described by AET (Table 4.1, Figure 4.2). Because I examined the same total area for each site, numbers of individuals per site is equivalent to density of individuals. This negative relationship between the number of individuals and energy remained even after controlling for the size of trees (Table 4.2).

Two other important predictions of energy diversity theory also did not hold up at the landscape scale. While there was a nearly five-fold change in richness among sites, I observed no significant correlation between total site tree species richness and the number (density) of individuals per site (Table 4.1). The variation in richness was positively correlated with energy as described by AET (Figure 4.3) but the relationship was not strong enough to be statistically significant (Table 4.1). Thus at the scale of landscapes, a scale at which interactions among individuals may take place and where the

potential for competitive exclusion among populations exists, the energy-diversity hypothesis was not substantiated.

Since richness increases among sites even as numbers of trees diminish, the species assemblages within richer forest sites must be predominantly comprised of less common species. I found that the relative abundances among species did vary among sites. As the richness increased, the absolute number and the proportion of rare species increased while common species decreased. This change in distribution varied slightly with energy, i.e. higher AET sites had more rare species, although the correlation was not quite statistically significant (Table 4.1).

If energy affects richness through local interactions among individuals, then the correlations between climate and local richness, and between local and regional richness, should be stronger than the correlation between regional richness and climate (e.g. in 2.5° X 2.5° quadrats of Currie and Paquin (1987) in Chapter 1). I found that regional richness is positively correlated with site richness, although the relationship was not quite strong enough to be statistically significant (Table 4.3). However, while the relationship between site richness and AET was weak, regional richness was very strongly correlated with AET (Table 4.3). AET statistically explained 84% of the variation in richness among regional species pools. Thus the effect of AET on regional richness goes well beyond any effects on local richness (Table 4.3).

Discussion

The Hutchinson-Brown-Wright formulation of the Energy Richness Hypothesis proposes that increased environmental energy leads to increased numbers of individuals,

which then leads to increased species richness. The model predicts that areas with more energy should have more individuals (Figure 4.4a), which proved not to be true in the upland forest sites I sampled (Table 4.1). This was not simply a case of tropical trees being larger and thus producing lower density stands. The negative relationship between AET and numbers of individuals held, even after controlling for tree size (Table 4.2). Contrary to the energy-diversity theory, my study suggests that upland forests have fewer trees as AET increases.

This same prediction can be tested over a broader spatial scale using Alwyn Gentry's global observations of tree density (Phillips and Miller 2002). Using these data, Enquist and Niklas (2001) found a negative correlation between tree density and latitude. It is odd however, that this relationship is not symmetrical about the equator. Given that AET generally decreases away from the equator (Ahn and Tateishi 1994a), their analysis suggests that population density increases with AET in the northern hemisphere, and decreases in the southern hemisphere. Combining AET extracted from Ahn and Tateishi (1994a) with Gentry's tree data, I confirmed that, oddly enough, this was the case (Figure 4.5a).

Despite the lack of a consistent relationship between AET and tree density (Figures 2 and 5a), species richness still increased with AET (Figure 4.3). Although the correlation was not quite statically significant in my data set (Table 4.1), this may simply be due to the low statistical power inherent in small data sets. Enquist and Niklas (2001) came to the same conclusion in both hemispheres using Gentry's much larger data set (Figures 5b), as did Latham and Ricklefs (1993a) for small forest sites across four continents. The richness-climate correlation is not intermediated by numbers of tree

density. Thus, neither my data nor Gentry's are consistent with the Energy-Richness Hypothesis (Figure 4.4a). Tree density and species richness may be independently correlated with AET (Figure 4.4b), but this arrangement is contrary to the Energy-Richness Hypothesis.

Since the proposed mechanism of the Energy-Richness Hypothesis depends on the competitive interactions of individual population members, a second prediction is that its effects should be most readily observable at scales where competitive interactions occur. i.e., the local scale. This prediction also proved to be inconsistent with my data. AET was strongly correlated with richness at the regional scale (Table 4.2). At the local scale however, the AET richness correlation was too weak to be significant (Table 4.1). While a larger sample size would likely provide statistical significance, based on the data that I do have (Figure 4.3), estimates of the (weak) magnitude of the effect at local scales are unbiased by small sample size. Latham and Ricklefs (1993a) study of richness-climate diversity patterns in forests used quadrats that were intermediate in size between those used here and those at broad scales (Currie & Paquin 1987, Adams & Woodward 1989), and observed an intermediate correlation coefficient is as well. At the scale grain of my regional species pools however, the strength of the richness AET correlation increases markedly (Table 4.3). Likewise, in my re-examination of Latham and Ricklefs' (1993a) study, the richness AET correlations became very strong when I included large forest sites from Currie and Paquin (1989) in the data set (Francis and Currie 1998). As scale grain increases, the strength of the energy richness correlation increases. Again, this is contrary to the Energy Richness hypothesis.

While the observed correlations are not consistent with the mechanism proposed

by the Energy-Richness Hypothesis, the fact remains that climate and regional richness patterns are strongly correlated. Moreover energy explains regional richness beyond the effects of local richness (Table 4.3). This suggests then that energy – or something strongly correlated with energy – impacts regional richness by more than simply affecting local richness. Since the effect of energy increases at as scale grain increases, it seems more likely that energy somehow affects species turnover within regions, i.e., beta diversity.

The potential to observe turnover in this study was low. The study was conducted within essentially one ecotype – i.e. each site represents a reasonably homogeneous community in terms of both species composition and general environmental factors (topography, climatic conditions etc.). The degree of habitat heterogeneity within sites is relatively small. However, as energy increases, the corresponding increase in species richness among small homogeneous forest communities results from the division of individuals into a larger number of less common species rather than an overall increase in the number of individuals (Table 4.1). Forests sites therefore become generally more heterogeneous. If this pattern of heterogeneity is representative of that of other habitat types within regions, or is perhaps even indicative of broad regional trends, it may be that habitat heterogeneity increases along climatic gradients.

I previously found that measures of landscape heterogeneity were unable to explain much significant variance in angiosperm diversity (Chapter Three). Perhaps however, landscape heterogeneity – or others indices like it – do not adequately describe habitat diversity relevant to plants. It may be that climatic constraints determine the relative number of factors defining habitat diversity. For example, when climatic

conditions are benign – warm and moist –many taxa could potentially tolerate the conditions, and it is possible that relatively small microclimatic or edaphic variations may be sufficient to subdivide a region into a large number of subtly differing niches. Conversely, in highly variable or harsh climatic conditions, few species tolerate the climatic conditions, irrespective of local habitat differences. The trend of increasing within-site heterogeneity among ostensibly uniform sites (i.e. consistent general category of site) suggests that I may not perceive relevant changes in plant habitat diversity. The question then remains whether or not this level of heterogeneity is related to AET or other measures of mean climate.

Conclusion

At the scale of individual forests (i.e. among distinct sets of tree populations) energy appears to have only a minor bearing on species richness. Any potential mechanistic influence of environmental energy on richness would likely then operate on a scale larger than that of 100 m^2. As a bottom up mechanism to explain richness patterns, the energy-diversity theory does not work.

Tables

Table 4.1: Spearman rank correlations among 0.1 ha forest sites.

	AET	CAT1	CAT4	I_{Site}	SR_{Site}
AET	1.000				
CAT1	0.504	1.000			
CAT4	-0.637	-0.041	1.000		
I_{Site}	-0.761	-0.169	0.791	1.000	
SR_{Site}	0.405	0.857	-0.011	0.005	1.000

AET = annual evapotranspiration (mm), CAT1 = number of tree species with 1 to 4 individuals per site, CAT4 = number of tree species with 46 to 160 individuals per site, I_{Site} = individual trees per site, SR_{Site} = site tree species richness, ¦ = $p<0.05$.

Table 4.2: Regression models of log(Individual trees per site) among forest sites.

n=15

Model	Independent Variables	Standardized Coefficient	Term p	Model p	R^2
1	log (AET)	-0.791	<0.001	<0.001	0.626
2	log (AET)	-0.463	0.005	<0.001	0.850
	log (DBH)	-0.567	0.001		

AET = annual evapotranspiration (mm), DBH = diameter at breast height (cm)

Table 4.3: Spearman rank correlations among forest sites.

	AET	I_{SITE}	SR_{Site}	SR_{Site}
AET	1.000			
I_{Site}	-0.761	1.000		
SR_{Site}	0.953	-0.754	1.000	
SR_{Site}	0.405	0.005	0.449	1.000

AET = annual evapotranspiration (mm), I_{Site} = individual trees per site, SR_{Site} = site tree species richness, SR_{Site} = regional tree species richness, ¦ = $p<0.05$.

Figures

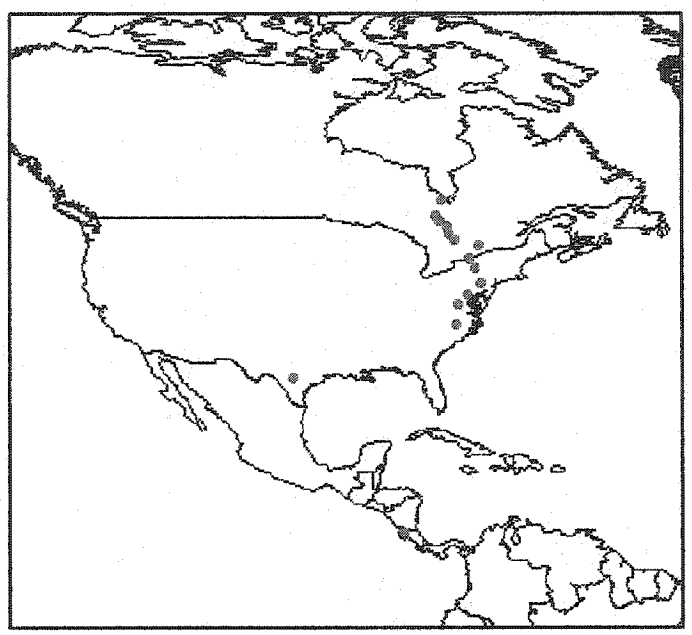


Figure 4.1: Map of 0.1 ha forest sites from James Bay to Costa Rica.

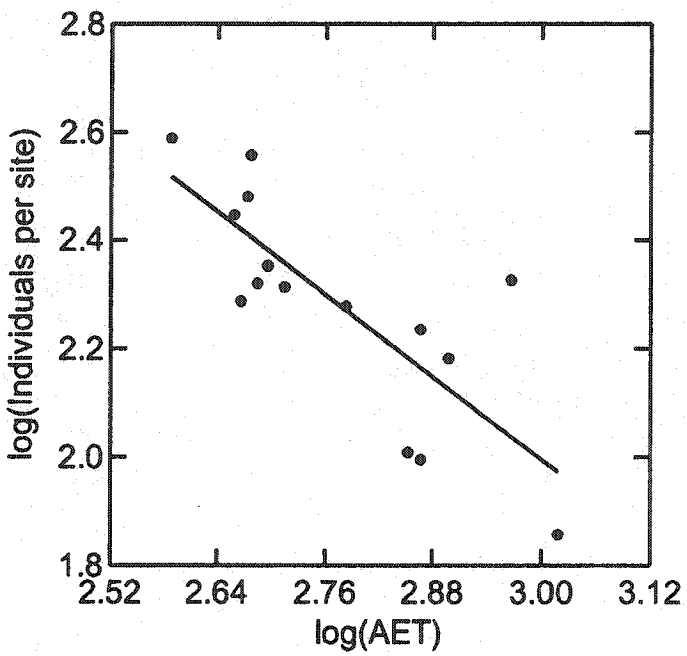


Figure 4.2: Number of individual trees per 0.1 ha forest site decreases with AET (r^2=0.626, n=15 , p<0.001).

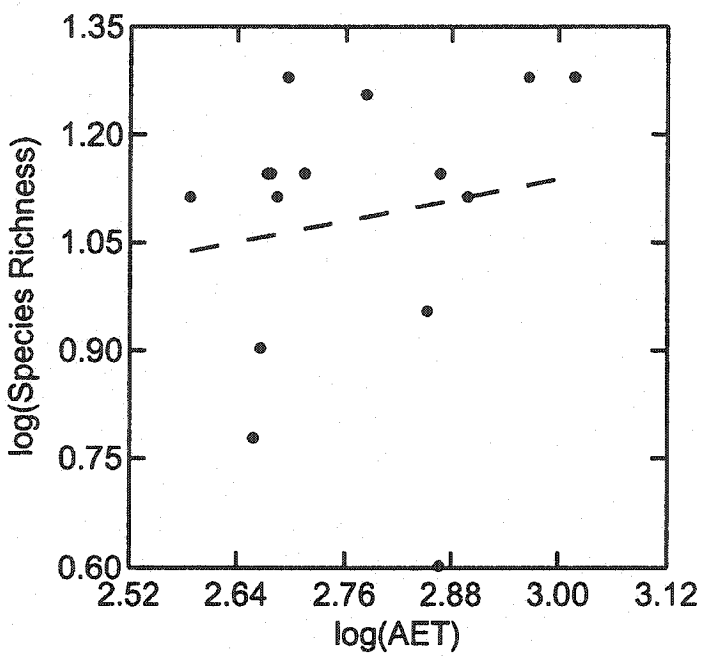


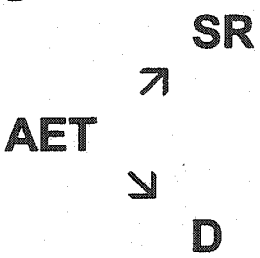
Figure 4.3: The tree species richness per 0.1 ha forest site increase with AET is not statistically significant (r^2=0.026, n=15 , p<0.566).

A

AET → D → SR

Data Set	χ^2	p
North America	7.07925	0.008
Gentry $_{North}$	34.05009	<0.001
Gentry $_{South}$	59.32005	<0.001

B



Data Set	χ^2	p
North America	4.57455	0.032
Gentry $_{North}$	48.09898	<0.001
Gentry $_{South}$	18.06257	<0.001

Figure 4.4: Path models relating AET to tree species richness (SR) and tree density (D). **A.** The AET/species richness correlation is intermediated by tree density. **B.** Species richness and tree density are independently correlated with AET.

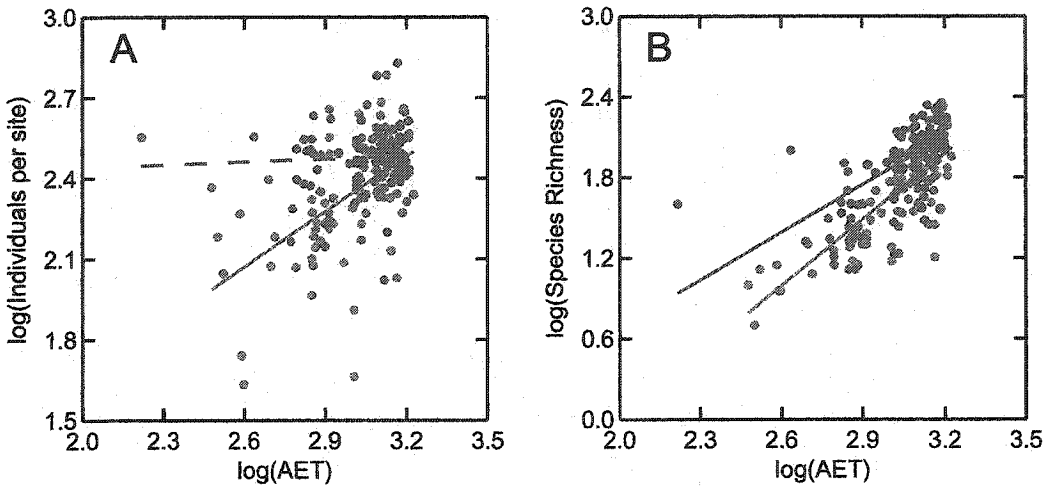


Figure 4.5: **A** Number of individual trees and **B** tree species richness per 0.1 ha forest site from Alwyn Gentry's global data set (Phillips and Miller 2002). Red dots are in the northern hemisphere; blue dots are in the southern hemisphere. The dashed line represents a statistically non-significant relationship.

Conclusions

The first two chapters of this thesis indicate that, on large scales, plant richness varies along climatic gradients in a manner consistent among broad regions. As I discussed in Chapter 1, despite their assertion to the contrary, Latham and Ricklefs's (1993a) study of tree species richness patterns demonstrated strong correlations between AET and tree richness. In Chapter 2, I investigated this pattern more rigorously and determined that, when climate is described by independent descriptors of both heat and water availability (rather than AET), the richness-climate correlation is consistent both among and within global regions. I observed this globally consistent relationship, despite dramatic differences among regions in evolutionary and geological history, edaphic factors, and other regional characteristics.

In Chapter 1, I showed that the problem in Latham and Ricklefs's (1993a) study is the strong collinearity between AET and region in their particular data sets. Since it was impossible to distinguish between the effects of these two variables on species richness, it was entirely ambiguous as to whether richness was responding to climate, or to some other factor that varied among continents. Thus I concluded that the suggestion that richness differences among regions were due to historical factors rather than to contemporary ones was merely speculative. Since climate does generally differ among regions, simple correlations between climate and richness cannot provide unambiguous tests of Latham and Ricklefs's proposed mechanism of richness patterns. To properly test this, or any other hypothesis of diversity patterns requires deduction of specific predictions as I have done in chapters three and four. That being said, since some hypotheses predict that richness should be correlated with climate (e.g. "energy-diversity

theory"), the question of whether of not richness is consistently related to climate is a good starting point.

Much of the confusion in the literature over the consistency of the broad scale patterns among regions stems from incomplete descriptions of relevant climatic gradients. Broad-scale patterns of richness depend mainly on the simultaneous availability of heat and water. If richness depends upon interactions among climatic variables, then bivariate relationships between richness and single variables may have misleading shapes.

For example, both Schall and Pianka's (1978) vertebrate richness-temperature correlations (negative in Australia, positively correlated in the US), and Kerr and Packer's (1997) variable North America mammal richness-PET correlations (strong in cold areas, very weak in warm areas), became strong and consistent when I included measures of water deficit in the models. Even Currie and Paquin's (1987) North American tree richness gradient, for which AET statistically accounted for 76% of the variation in species richness, is better described by models using separate heat and water gradients. The poorer fit of Currie and Paquin's model is due mainly to a group of low AET points from the American Southwest that had much higher richness than the AET model would predict. The southwestern US has AET levels similar to many arctic regions and yet has much higher tree species richness. Using two independent climatic gradients prevents the pooling of areas of such vastly different climatic character.

The dependence of the observed form of the richness-climate relationship upon the choice of climatic variables is a further source of confusion. This may seem an

obvious consideration, but the literature is full of instances where collinear climatic variables are considered as interchangeable. This is not correct. For example, the forms of models relating angiosperm family richness to climate varied tremendously depending on whether temperature or PET was used as a general index of heat. O'Brien (1998) suggested that the plant richness-PET relationship she observed in southern Africa becomes negative at high PET. O'Brien proposed that the pattern resulted from decreased water availability owing to high heat, i.e. implying PET is only a measure of heat. However, many areas of very high PET have no lack of water. Thus for any given level of water deficit (i.e. water availability relative to evaporative demand), richness always covaries positively with PET. Richness is only observed to decrease with heat when heat is described by temperature, and even then only if water deficit is high. PET is related to temperature, but it is also affected by such climatic factors as humidity, cloudiness, and wind patterns, and biotic factors such as plant cover (Sellers 1965). Using PET or temperature interchangeably, without discussing their differences, leads to confusion when comparing models.

Despite dramatic differences among regions in evolutionary and geological history, edaphic factors, and other regional characteristics, there is a globally consistent relationship between richness and climate. For a given richness model to be globally applicable, the description of climate must include both measures of heat and water. However, the apparent form of that richness-climate relationship is highly dependent upon the choice of indices used to describe heat and water.

The observed richness climate patterns, having identified their strength and global consistency, can be used to test which hypothesized mechanisms may play dominant

roles in determining patterns of species richness. Mechanisms cannot be deduced from patterns, nor is it likely that any single mechanism is responsible for these patterns. However, it is possible to test whether proposed mechanisms are consistent with observed patterns. Mechanisms that are statistically unrelated to the observed richness climate patterns are either incorrect or of relatively minor consequence. In the present case, I find little empirical support for the hypotheses that broad-scale angiosperm richness patterns are related to patterns of competition and disturbance (Huston 1979 and 1999), or to regional differences in evolutionary and extinction histories Latham and Ricklefs (1993a). Hypotheses that are potentially consistent with the patterns include the Energy-Richness Hypothesis (Hutchinson 1959, Brown 1984, Wright 1983) and what I have referred to in this thesis as the Physiological Tolerance hypothesis – that greater numbers of physiological configurations (or species) can persist in benign (warm and wet) conditions than in marginal (cold and/or dry) conditions (Hall 1992, Kleidon and Mooney 2000).

The first two chapters may suggest which hypothesized mechanism may be more important to the overall production of extant richness patterns; the second two deduce and test additional predictions from those hypotheses. Under the physiological tolerance hypothesis, large-scale patterns of observed angiosperm richness should have been predicted from the numbers of angiosperm families capable of tolerating the climate in question, given barriers to dispersal. Since this prediction was not corroborated (Chapter 3), I rejected this hypothesis as an important factor in contemporary angiosperm richness patterns.

While the total number of potentially occurring angiosperm families does not

directly control the observed richness level, it does set a logical upper bound (barring any underestimates of the potential richness as discussed in detail in Chapter Three). It is not clear from this study, however, why this upper bound is so closely related to climate. I have suggested that this pattern of potential richness may result from the evolutionary history of angiosperms as a group, rather than realized richness, as proposed by Ricklefs and Schluter (1993), Rosenzweig (1995) and Rohde (1992). Future studies determining which processes are responsible for this relationship may provide useful insight into broad-scale patterns of angiosperm diversity; however, it is not yet clear what specific predictions can be deduced from these hypotheses to allow them to be adequately tested and compared.

The Hutchinson-Brown-Wright formulation of the Energy Richness Hypothesis predicts that areas with more energy should have more individuals. This prediction was also not corroborated (Chapter 4). Among trees in upland forest sites, a negative relationship between AET and numbers of individuals was observed, even after controlling for tree size. Contrary to the energy-diversity theory, my study clearly suggests that upland forests have fewer trees as AET increases. Gentry's data (Phillips and Miller 2002) did indicate a positive correlation between AET and tree density for forested areas in the northern hemisphere. However there was no significant correlation at all in the southern hemisphere. Tree species richness, however was consistently positively correlated with AET despite the lack of any consistent relationship between AET and tree density. Thus I rejected this hypothesis as an important factor in contemporary angiosperm richness patterns.

Since both of the hypotheses tested in this thesis were invalidated as mechanisms

of large-scale patterns of plant diversity, the question of what mechanisms can account for such patterns remains. One strong possibility that is suggested by the results in Chapter Four may be some form of habitat heterogeneity. In Chapter Four I noted that any effect of energy (or climate) potentially influences regional richness much more strongly than does local richness. Since the effect of energy increases as scale grain increases, it seems likely that a significant portion of any influence of energy or climate has on richness is related to increases in beta diversity.

The index of landscape heterogeneity I used in conjunction with the tests of the physiological tolerances hypothesis in Chapter Three was unable to explain much significant variance in angiosperm diversity. However, while this heterogeneity index – or many others like it – may provide measures of landscape variability perceptible to human cognizance it is not necessarily clear that such observed variability is always meaningful to plants. This is conjecture on possible avenues of future research on broad-scale plant diversity patterns.

Since climate is a strong limiter of potential richness (Chapter Three), it may be that poor climate trumps all other factors potentially influencing plant species richness regardless of the strength of their gradients. As an extension of the physiological tolerances hypothesis, gradients of other factors (e.g. edaphic conditions) may only become relevant to plant species as climate improves. However, under highly consistent environmental conditions, plant species may perceive very minor edaphic variations and may subdivide a region into a large number of subtly differing niches. Conversely, plants subjected to rigors of highly variable climatic conditions may be less able to differentiate niches to such a fine degree. Future research may better quantify the

interaction of other factors with climate in determining richness patterns.

Beyond the caveats offered in Chapter 3 regarding the appropriateness of projecting future geographic distributions of specific angiosperm families, the general strength and global consistency of broad scale richness climate correlations tentatively supports their use as important predictors of the future diversity patterns in the face of global climate change (Currie 2001). Specific tests of the mechanisms behind these patterns such as those in this thesis improve our understanding of the diversity relationships. However, given that there is still more to learn, such predictions of the future diversity patterns should be made judiciously.

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Appendix 1: Chapter One Data

Table A1: Tree species richness data for 10 to 10000 km^2 plots from Latham and Ricklefs (1993a)

Region	Area (km^2)	AET (mm)	SR
Continental Asia	17	695	64
Continental Asia	30	836	190
Continental Asia	800	883	217
Continental Asia	350	691	104
Continental Asia	80	686	82
Continental Asia	45	743	70
Continental Asia	47	366	62
Continental Asia	7200	485	93
Eastern North America	34	1061	73
Eastern North America	89	915	80
Eastern North America	24	1001	68
Eastern North America	2000	763	107
Eastern North America	32	510	29
Eastern North America	26	1091	73
Eastern North America	17	599	41
Europe	1000	541	25
Japan	4963	848	203
Japan	7140	740	226
Japan	7401	746	217
Japan	4088	859	216
Japan	2439	862	186
Japan	6109	838	208
Western North America	3600	388	25
Western North America	1000	432	31
Western North America	433	558	35
Western North America	286	322	13

Table A2: Tree species richness for 0.1 ha plots from Latham and Ricklefs (1993a)

Region	AET (mm)	logSPP
Toprical Americas	1697.022	2.433007
Toprical Americas	1512.318	2.236722
Toprical Americas	1519.303	2.05784
Toprical Americas	1585.774	1.940773
Toprical Americas	1523.228	1.857429
Toprical Americas	1512.456	1.39545
Toprical Americas	1460.459	1.83136
Toprical Americas	1419.246	1.920195
Toprical Americas	1314.454	2.190581
Toprical Americas	1219.986	2.23202
Toprical Americas	1083.99	2.040099
Toprical Americas	1032.265	2.003468
South East Asia	1744.393	1.571015
South East Asia	1733.651	1.907352
South East Asia	1734.483	2.0971
South East Asia	1744.772	2.27984
South East Asia	1747.581	2.365802
South East Asia	1730.208	2.387002
South East Asia	1693.019	2.250368
South East Asia	1594.129	2.216559
South East Asia	1466.53	2.289684
South East Asia	1464.679	2.361252
South East Asia	1016.185	2.096286
Africa	1470.084	1.781397
Africa	1484.034	1.83174
Africa	1458.58	1.910088
Africa	1335.395	1.657514
Africa	1334.459	1.897352
Africa	1223.038	1.852601
Africa	1213.063	1.992056
Africa	1179.751	2.070278
Eastern North America	1007.675	1.054401
Eastern North America	734.3286	1.017786
Eastern North America	718.4583	1.056909
Eastern North America	657.6037	1.345902
Eastern North America	666.5651	1.063235
Eastern North America	665.6636	0.891385
Eastern North America	636.8847	1.016219
Eastern North America	602.1264	1.062198
Eastern North America	567.1507	0.760925
Eastern North America	498.7588	0.967458
Japan	829.1536	1.287803
Japan	839.541	1.445485

Region	AET (mm)	logSPP
Japan	798.7054	1.437669
Japan	711.3199	1.275168
Japan	609.8172	1.105281

Appendix 2: Chapter Two and Three Data Processing

A2.1 Sampling Grid Construction Program

This program, written in C++, constructs grids of vector quadrats for sampling digital map data. Coordinates are written in unprojected decimal degrees latitude and longitude. Output is written in ASCII in the Idrisi ".vec" format. Quadrats always cover a constant latitudinal span. Longitudinal span in numbers of degrees may either be constant or may vary proportionally to the inverse of the cosine of the mid quadrat latitude, such that the ground distance of the longitudinal span, and hence quadrat area, remain approximately constant over latitudinal gradients. Quadrats are initially numbered consecutively, however the option exists to identify specific quadrats to drop from the final output using an ASCII text file.

```
//GLOBAL GRID GENERATOR
//*************************************************************************

// #include files
#include <iostream.h>
#include <string.h>
#include <fstream.h>
#include <stdlib.h>
#include <math.h>

// Define Global Constants
const double Pi = 3.14159265358979323846264338327 95;
const int Bitmask = 0xdf;

// Prototypes
void SplashScreen (void);
void EqualAreaGrid (double fMapInfo[]);
void EvenGrid (double fMapInfo[]);
void OutputDvc(char sFileName[], int iProjType, double fMapInfo[]);
double Radians (double fAngle);
void List(int iQuadCounter, int* ReductionList[]);
void OutputFileNames(char sOutput[2][50]);

//Main
//*************************************************************************
void main()
{
        SplashScreen();

        char cRun;
```

```
	int iGridNb=1;
	int iGridType;

	//Define map factors
	//fMapInfo... 0:MinX, 1:MaxX, 2:MinY, 3:MaxY, 4:mX, 5:bX, 6:mY, 7:bY
	//Further elements are use for values specific to each projection
	double fMapInfo[12] = {0, 0, 0, 0, 1, 0, 1, 0, 0, 0, 0, 0};

	do
	{
		WhichGrid:

		cout<< "\n\n\tSelect a grid type:";
		cout<< "\n\t\t1) Equal Area";
		cout<< "\n\t\t2) Equal Degree Span";
		cout<< "\n\n\t\t";
		cin >> iGridType;

		switch(iGridType)
		{
			case(1):
			{
				cout << "\n\nGRID #"<<iGridNb;
				EqualAreaGrid(fMapInfo);
				break;
			}
			case(2):
			{
				cout << "\n\nGRID #"<<iGridNb;
				EvenGrid(fMapInfo);
				break;
			}
			default:
			{
				cout<<"\a";
				goto WhichGrid;
				break;
			}
		}

		cout << "\n\nCreate another grid?";
		cout << "\nY or N: ";
		cin >> cRun;
		cRun = cRun & Bitmask;

		iGridNb++;
	}
	while (cRun == 'Y');
}

//Splash Screen
//*************************************************************************
void SplashScreen()
{
	cout<<"\t\t\xC9\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\
xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xBB\n";
	cout<<"\t\t\xBA                                \xBA\n";
	cout<<"\t\t\xBA        GRID MAKER 2.1        \xBA\n";
	cout<<"\t\t\xBA                                \xBA\n";
	cout<<"\t\t\xC8\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\
xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xBC\n";
}


//Constructs an equal area grid
//*************************************************************************
void EqualAreaGrid(double fMapInfo[])
{

cout << "\n\n\t This program will now construct an equal area grid\n\t     defined in degrees latitude and longitue.\n\n";
```

```
int iGridType = 1;

//Get start points
cout << "\n\nEnter the coordinates of the upper left corner of your grid:";
cout << "\nx = ";
cin >> fMapInfo[0];
cout << "y = ";
cin >> fMapInfo[3];

//Get end points
cout << "\n\nEnter the coordinates of the lower right corner of your grid:";
cout << "\nx = ";
cin >> fMapInfo[1];
cout << "y = ";
cin >> fMapInfo[2];

//Get scaling value
cout << "\n\nEnter the latitudinal span of your quadrats:";
cout << "\nspan = ";
cin >> fMapInfo[8];

//Set the latitude of square quadrats
cout << "\n\nEnter the latitude at which the quadrats are square\n(Do not use 90\xF8!):";
cout << "\nLatidude of square quadrats = ";
cin >> fMapInfo[9];

double fSpan;

//Prepare the output name variable
char sOutput[2][50];
OutputFileNames(sOutput);

//Declare and initialize corner markers
double fX = fMapInfo[0];
double fY = fMapInfo[3];

//Declare Counters
int iLongCounter;
int iLatCounter;
int iQuadCounter;
int iID;

//This loop creates the quadrats
//This first time determines the number of Quadrats produced
iLongCounter=0;
iLatCounter=0;
iQuadCounter=0;
while ((fY-fMapInfo[8]) > fMapInfo[2])
        {

        fY = fMapInfo[3] - (fMapInfo[8]*iLatCounter);
        fSpan     = (fMapInfo[8]*(cos(Radians(fMapInfo[9]))))/(cos(Radians(fY-(fMapInfo[8]/2))));

        while (fX < fMapInfo[1])
                {

                fX = fMapInfo[0] + (fSpan*iLongCounter);

                iQuadCounter++;
                iLongCounter++;

                }

        fX = fMapInfo[0];//reset fX
        iLongCounter = 0;
        iLatCounter++;

        }
```

```
// Declare the pointers that will be use to store the quadrats, do not allocated yet
double* XList;
double* YList;
double* SpanList;

// Allocate the pointers with 'new'
XList = new double[iQuadCounter+5];
YList = new double[iQuadCounter+5];
SpanList = new double[iQuadCounter+5];

//Reset counters and corner markers
iLongCounter=0;
iLatCounter=0;
ilD=0;
fX = fMapInfo[0];
fY = fMapInfo[3];

//This loop creates the quadrats
//This second time writes Quadrats to the QuadratList
while ((fY-fMapInfo[8]) > fMapInfo[2])
        {

        fY = fMapInfo[3] - (fMapInfo[8]*iLatCounter);
        fSpan     = (fMapInfo[8]*(cos(Radians(fMapInfo[9]))))/(cos(Radians(fY-(fMapInfo[8]/2))));

        while (fX < fMapInfo[1])
                {

                fX = fMapInfo[0] + (fSpan*iLongCounter);

                XList[ilD]=fX;
                YList[ilD]=fY;
                SpanList[ilD]=fSpan;

                cout<<"Quadrat "<<ilD+1<<":  ";
                cout<<"Left = "<<XList[ilD]<<"\t";
                cout<<"Top = "<<YList[ilD]<<"\t";
                cout<<"Span = "<<SpanList[ilD]<<"\n";

                iLongCounter++;
                ilD++;

                }

        fX = fMapInfo[0];//reset fX
        iLongCounter = 0;
        iLatCounter++;

        }

//Create .vec file
ofstream VecFilePtr;
VecFilePtr.open(sOutput[0], ios::out);

int iOutCounter;

//Produce Summary File?
char cSummary;
cout << "\n\nDo you want a summary file of the quadrats?";
cout << "\nY or N: ";
cin >> cSummary;
cSummary = cSummary & Bitmask;
char sSummaryFile[50];
if (cSummary=='Y')
{
        cout << "\n\nEnter a full name and path for the summary file:  ";
        cin >> sSummaryFile;
}
```

```
ofstream SummaryPtr;
SummaryPtr.open(sSummaryFile, ios::out);

if (cSummary=='Y')
{
        SummaryPtr <<"Quadrat\tLeftLong\tTopLat\tSpan\n";
}
else
{
        SummaryPtr.close();
}

//Reduce the Quadrat List?
char cReduce;
cout << "\n\nDo you wish to exclude certain quadrats?";
cout << "\nY or N: ";
cin >> cReduce;
cReduce = cReduce & Bitmask;

if (cReduce=='Y')
{
        // Declare the pointer that will be use to store the reduction list, do not allocated yet
        int* ReductionList[2];

        // Allocate the pointer with 'new'
        ReductionList[0] = new int[iQuadCounter+5];
        ReductionList[1] = new int[iQuadCounter+5];

        //Fill the reduction list
        List(iQuadCounter, ReductionList);

        for(iOutCounter=0; iOutCounter<iQuadCounter; iOutCounter++)
        {
                if(ReductionList[1][iOutCounter]==1)
                {
                        VecFilePtr      <<(iOutCounter+1)  <<"\t"<<5 <<"\n";
                        VecFilePtr      <<XList[iOutCounter]        <<"\t"<<YList[iOutCounter]    <<"\n";
                        VecFilePtr      <<XList[iOutCounter]+SpanList[iOutCounter]
        <<"\t"<<YList[iOutCounter]    <<"\n";
                        VecFilePtr      <<XList[iOutCounter]+SpanList[iOutCounter]
        <<"\t"<<YList[iOutCounter]-fMapInfo[8]  <<"\n";
                        VecFilePtr      <<XList[iOutCounter]        <<"\t"<<YList[iOutCounter]-fMapInfo[8]
        <<"\n";
                        VecFilePtr      <<XList[iOutCounter]        <<"\t"<<YList[iOutCounter]    <<"\n";

                        if(ReductionList[0][iOutCounter] != (iOutCounter+1))
                        {
                                cout<<"Error... Your quadrat reduction values file\n";
                                cout<<"      does not match this quadrat set\n";
                                exit(1);
                        }

                        if(cSummary=='Y')
                        {
                                SummaryPtr
<<iOutCounter+1<<"\t"<<XList[iOutCounter]<<"\t"<<YList[iOutCounter]<<"\t"<<SpanList[iOutCounter]<<"\n";
                        }
                }
        }
        // Deallocate memory by destroying pointer
        delete [] ReductionList[1];
        delete [] ReductionList[0];

        // Reset pointer to NULL, unnecessary but makes life easier
        ReductionList[1] = 0;
        ReductionList[0] = 0;
}

else
{
```

```
        for(iOutCounter=0; iOutCounter<iQuadCounter; iOutCounter++)
        {
                VecFilePtr          <<(iOutCounter+1)  <<"\t"<<5 <<"\n";
                VecFilePtr          <<XList[iOutCounter]          <<"\t"<<YList[iOutCounter]     <<"\n";
                VecFilePtr          <<XList[iOutCounter]+SpanList[iOutCounter]        <<"\t"<<YList[iOutCounter]
        <<"\n";
                VecFilePtr          <<XList[iOutCounter]+SpanList[iOutCounter]        <<"\t"<<YList[iOutCounter]-
fMapInfo[8]         <<"\n";
                VecFilePtr          <<XList[iOutCounter]          <<"\t"<<YList[iOutCounter]-fMapInfo[8]   <<"\n";
                VecFilePtr          <<XList[iOutCounter]          <<"\t"<<YList[iOutCounter]     <<"\n";

                if(cSummary=='Y')
                {
                        SummaryPtr
<<iOutCounter+1<<"\t"<<XList[iOutCounter]<<"\t"<<YList[iOutCounter]<<"\t"<<SpanList[iOutCounter]<<"\n";
                }
        }
}

//Finish and close file
VecFilePtr          <<"0\t0";
VecFilePtr.close();
if(cSummary=='Y')
{
        SummaryPtr.close();
}

//Output the vector header
OutputDvc(sOutput[1], iGridType, fMapInfo);

// Deallocate memory by destroying pointers
delete [] XList;
delete [] YList;
delete [] SpanList;

}

//Constructs a rectilinear grid
//*************************************************************************
void EvenGrid(double fMapInfo[])
{

cout << "\n\n\t This program will now construct a rectilinear grid\n\t    defined in degrees latitude and longitue.\n\n";

int iGridType = 2;

//Get start points
cout << "\n\nEnter the coordinates of the upper left corner of your grid:";
cout << "\nx = ";
cin >> fMapInfo[0];
cout << "y = ";
cin >> fMapInfo[3];

//Get end points
cout << "\n\nEnter the coordinates of the lower right corner of your grid:";
cout << "\nx = ";
cin >> fMapInfo[1];
cout << "y = ";
cin >> fMapInfo[2];

//Get lat span
cout << "\n\nEnter the latitudinal span of your quadrats:";
cout << "\nspan = ";
cin >> fMapInfo[8];

//Get long span
cout << "\n\nEnter the longitudinal span of your quadrats:";
cout << "\nspan = ";
cin >> fMapInfo[9];
```

```
//Prepare the output name variable
char sOutput[2][50];
OutputFileNames(sOutput);

//Declare and initialize corner markers
double fX = fMapInfo[0];
double fY = fMapInfo[3];

//Declare Counters
int iLongCounter;
int iLatCounter;
int iQuadCounter;
int iID;

//This loop creates the quadrats
//This first time determines the number of Quadrats produced
iLongCounter=0;
iLatCounter=0;
iQuadCounter=0;
while ((fY-fMapInfo[8]) > fMapInfo[2])
        {

        fY = fMapInfo[3] - (fMapInfo[8]*iLatCounter);

        while (fX < fMapInfo[1])
                {

                fX = fMapInfo[0] + (fMapInfo[9]*iLongCounter);

                iQuadCounter++;
                iLongCounter++;

                }

        fX = fMapInfo[0];//reset fX
        iLongCounter = 0;
        iLatCounter++;

        }


// Declare the pointers that will be use to store the quadrats, do not allocated yet
double* XList;
double* YList;
double* SpanList;

// Allocate the pointers with 'new'
XList = new double[iQuadCounter+5];
YList = new double[iQuadCounter+5];
SpanList = new double[iQuadCounter+5];

//Reset counters and corner markers
iLongCounter=0;
iLatCounter=0;
iID=0;
fX = fMapInfo[0];
fY = fMapInfo[3];

//This loop creates the quadrats
//This second time writes Quadrats to the QuadratList
while ((fY-fMapInfo[8]) > fMapInfo[2])
        {

        fY = fMapInfo[3] - (fMapInfo[8]*iLatCounter);

        while (fX < fMapInfo[1])
                {

                fX = fMapInfo[0] + (fMapInfo[9]*iLongCounter);
```

```
                    XList[ilID]=fX;
                    YList[ilID]=fY;
                    SpanList[ilID]=flMapInfo[9];

                    cout<<"Quadrat "<<ilID+1<<":  ";
                    cout<<"Left = "<<XList[ilID]<<"\t";
                    cout<<"Top = "<<YList[ilID]<<"\t";
                    cout<<"Span = "<<SpanList[ilID]<<"\n";

                    iLongCounter++;
                    ilD++;

                    }

            fX = flMapInfo[0];//reset fX
            iLongCounter = 0;
            iLatCounter++;

            }

//Create .vec file
ofstream VecFilePtr;
VecFilePtr.open(sOutput[0], ios::out);

int iOutCounter;

//Produce Summary File?
char cSummary;
cout << "\n\nDo you want a summary file of the quadrats?";
cout << "\nY or N: ";
cin >> cSummary;
cSummary = cSummary & Bitmask;
char sSummaryFile[50];
if (cSummary=='Y')
{
        cout << "\n\nEnter a full name and path for the summary file:  ";
        cin >> sSummaryFile;
}
ofstream SummaryPtr;
SummaryPtr.open(sSummaryFile, ios::out);

if (cSummary=='Y')
{
        SummaryPtr <<"Quadrat\tLeftLong\tTopLat\tSpan\n";
}
else
{
        SummaryPtr.close();
}

//Reduce the Quadrat List?
char cReduce;
cout << "\n\nDo you wish to exclude certain quadrats?";
cout << "\nY or N: ";
cin >> cReduce;
cReduce = cReduce & Bitmask;

if (cReduce=='Y')
{
        // Declare the pointer that will be use to store the reduction list, do not allocated yet
        int* ReductionList[2];

        // Allocate the pointer with 'new'
        ReductionList[0] = new int[iQuadCounter+5];
        ReductionList[1] = new int[iQuadCounter+5];

        //Fill the reduction list
        List(iQuadCounter, ReductionList);

        for(iOutCounter=0; iOutCounter<iQuadCounter; iOutCounter++)
```

```
	{
		if(ReductionList[1][iOutCounter]==1)
		{
			VecFilePtr		<<(iOutCounter+1)  <<"\t"<<5 <<"\n";
			VecFilePtr		<<XList[iOutCounter]		<<"\t"<<YList[iOutCounter]	<<"\n";
			VecFilePtr		<<XList[iOutCounter]+SpanList[iOutCounter]
	<<"\t"<<YList[iOutCounter]	<<"\n";
			VecFilePtr		<<XList[iOutCounter]+SpanList[iOutCounter]
	<<"\t"<<YList[iOutCounter]-fMapInfo[8]	<<"\n";
			VecFilePtr		<<XList[iOutCounter]		<<"\t"<<YList[iOutCounter]-fMapInfo[8]
	<<"\n";
			VecFilePtr		<<XList[iOutCounter]		<<"\t"<<YList[iOutCounter]	<<"\n";

			if(ReductionList[0][iOutCounter] != (iOutCounter+1))
			{
				cout<<"Error... Your quadrat reduction values file\n";
				cout<<"	does not match this quadrat set\n";
				exit(1);
			}

			if(cSummary=='Y')
			{
				SummaryPtr
<<iOutCounter+1<<"\t"<<XList[iOutCounter]<<"\t"<<YList[iOutCounter]<<"\t"<<SpanList[iOutCounter]<<"\n";
			}
		}
	}
	// Deallocate memory by destroying pointer
	delete [] ReductionList[1];
	delete [] ReductionList[0];

	// Reset pointer to NULL, unnecessary but makes life easier
	ReductionList[1] = 0;
	ReductionList[0] = 0;
}

else
{
	for(iOutCounter=0; iOutCounter<iQuadCounter; iOutCounter++)
	{
		VecFilePtr		<<(iOutCounter+1)  <<"\t"<<5 <<"\n";
		VecFilePtr		<<XList[iOutCounter]		<<"\t"<<YList[iOutCounter]	<<"\n";
		VecFilePtr		<<XList[iOutCounter]+SpanList[iOutCounter]	<<"\t"<<YList[iOutCounter]
	<<"\n";
		VecFilePtr		<<XList[iOutCounter]+SpanList[iOutCounter]	<<"\t"<<YList[iOutCounter]-
fMapInfo[8]		<<"\n";
		VecFilePtr		<<XList[iOutCounter]		<<"\t"<<YList[iOutCounter]-fMapInfo[8]	<<"\n";
		VecFilePtr		<<XList[iOutCounter]		<<"\t"<<YList[iOutCounter]	<<"\n";

		if(cSummary=='Y')
		{
			SummaryPtr
<<iOutCounter+1<<"\t"<<XList[iOutCounter]<<"\t"<<YList[iOutCounter]<<"\t"<<SpanList[iOutCounter]<<"\n";
		}
	}
}

//Finish and close file
VecFilePtr		<<"0\t0";
VecFilePtr.close();
if(cSummary=='Y')
{
	SummaryPtr.close();
}

//Output the vector header
OutputDvc(sOutput[1], iGridType, fMapInfo);

// Deallocate memory by destroying pointers
delete [] XList;
```

```
delete [] YList;
delete [] SpanList;

}


//Write .dvc file
//Writes the new .dvc file to go with the map
//*************************************************************************
void OutputDvc(char sFileName[], int iProjType, double fMapInfo[])
{
ofstream FilePtr;
FilePtr.open(sFileName, ios::out);

switch(iProjType)
{
        case(1):
        {
                FilePtr<<"file title  : Equal area grid - quadrats span "<<fMapInfo[8]<<"° Lat and "<<fMapInfo[8]<<"°
Long at Lat "<<fMapInfo[9]<<"°\n";
                break;
        }
        case(2):
        {
                FilePtr<<"file title  : Rectilinear grid - quadrats span "<<fMapInfo[8]<<"° Lat and "<<fMapInfo[9]<<"°
Long";
                break;
        }
}
                FilePtr<<"id type     : integer\n";
                FilePtr<<"file type   : ascii\n";
                FilePtr<<"object type : polygon\n";
                FilePtr<<"ref. system : latlong\n";
                FilePtr<<"ref. units  : deg\n";
                FilePtr<<"unit dist.  : 1.0000\n";
                FilePtr<<"min. X      : "<<fMapInfo[0]*1.05<<"\n";
                FilePtr<<"max. X      : "<<fMapInfo[1]*1.05<<"\n";
                FilePtr<<"min. Y      : "<<fMapInfo[2]*1.05<<"\n";
                FilePtr<<"max. Y      : "<<fMapInfo[3]*1.05<<"\n";
                FilePtr<<"pos`n error : 0\n";
                FilePtr<<"resolution  : 0\n";

FilePtr.close();
}


//Radians
//*************************************************************************
double Radians(double fAngle)
{
        double RadianValue = (Pi/180)*fAngle;
        return RadianValue;
}


//List - Assembles Quadrat Exclusion List
//*************************************************************************
void List(int iQuadCounter, int* ReductionList[])
{
        char sReductionList[50];
        cout << "\n\nEnter the full name and path of the values file";
        cout << "\nfor the Reduction List: ";
        cin >> sReductionList;

        ifstream FilePtr;
        FilePtr.open(sReductionList, ios::in);

        if(!FilePtr)
        {
```

```
                cout<<"Error opening "<<sReductionList<<"\n";
                exit(1);
        }


        int iCheckQuadCounter=0;

        while(FilePtr)
        {
                FilePtr>>ReductionList[0][iCheckQuadCounter];
                FilePtr>>ReductionList[1][iCheckQuadCounter];
                iCheckQuadCounter++;
        }

        if(iCheckQuadCounter!=(iQuadCounter+1))
        {
                cout<<"Error... Your quadrat reduction values file is an\n";
                cout<<"         inappropriate length for this quadrat set\n";
                exit(1);
        }

        FilePtr.close();
}

//OutputFiles - Prepares the ouput file names
//*************************************************************************
void OutputFileNames(char sOutput[2][50])
{

        int iCheck;

        Name:
        // Declare a pointer
        char* sFileName;

        // Allocate the pointers with 'new'
        sFileName = new char[50];

        //Enter file names
        cout << "\n\nEnter the path and name of the output vector file (no extension): ";
        cin >> sFileName;

        int StringPtr=-1;

        do
        {
                StringPtr++;
                sOutput[0][StringPtr] = sFileName[StringPtr];
                sOutput[1][StringPtr] = sFileName[StringPtr];
        }
        while(sFileName[StringPtr] != '\0');

        // Deallocate memory by destroying pointer
        delete [] sFileName;

        sOutput[0][StringPtr]='.';
        sOutput[0][StringPtr+1]='v';
        sOutput[0][StringPtr+2]='e';
        sOutput[0][StringPtr+3]='c';
        sOutput[0][StringPtr+4]='\0';

        sOutput[1][StringPtr]='.';
        sOutput[1][StringPtr+1]='d';
        sOutput[1][StringPtr+2]='v';
        sOutput[1][StringPtr+3]='c';
        sOutput[1][StringPtr+4]='\0';

        //Check if file already exists
        ifstream TestFilePtr;
        TestFilePtr.open(sOutput[1], ios::nocreate);
```

```
        if(TestFilePtr)
        {
                WarningLoop:

                cout<< "\n\n\tWARNING...";
                cout<< "\n\n\tThe vector file already exists:";
                cout<< "\n\t\t1) Continue";
                cout<< "\n\t\t2) Rename";
                cout<< "\n\t\t3) Quit";
                cout<< "\n\n\t\t";
                cin >> iCheck;

                switch(iCheck)
                {
                        case(1):
                        {
                                TestFilePtr.close();
                                break;
                        }
                        case(2):
                        {
                                TestFilePtr.close();
                                goto Name;
                                break;
                        }
                        case(3):
                        {
                                TestFilePtr.close();
                                exit(1);
                                break;
                        }
                        default:
                        {
                                cout<<"\a";
                                goto WarningLoop;
                                break;
                        }
                }
        }

}
```

A2.2 Sampling Grids

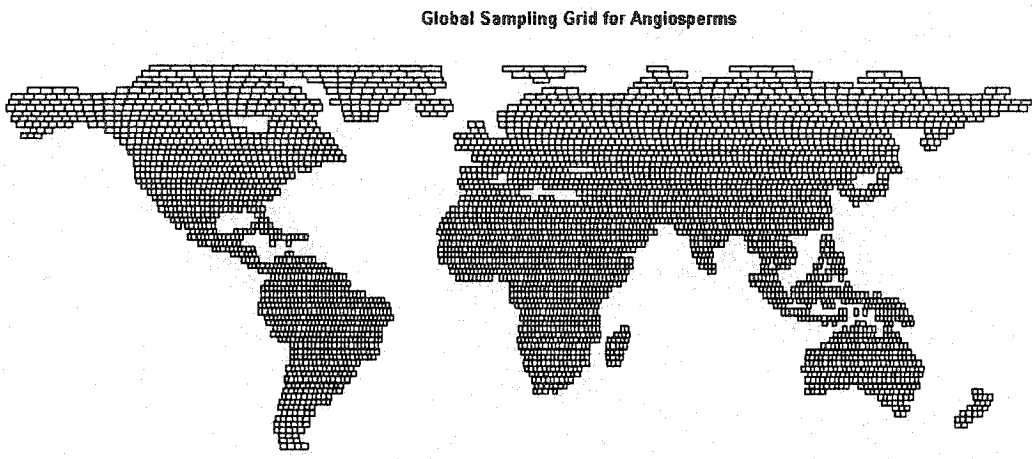

Figure A1: Global grid to sample angiosperm family maps, assembled using the Sampling Grid Construction Program. Note that the map begins on the left at 180°W but continues right beyond 180°E so Siberia remains connected to the rest of Asia, following the map layout in Heywood (1997).

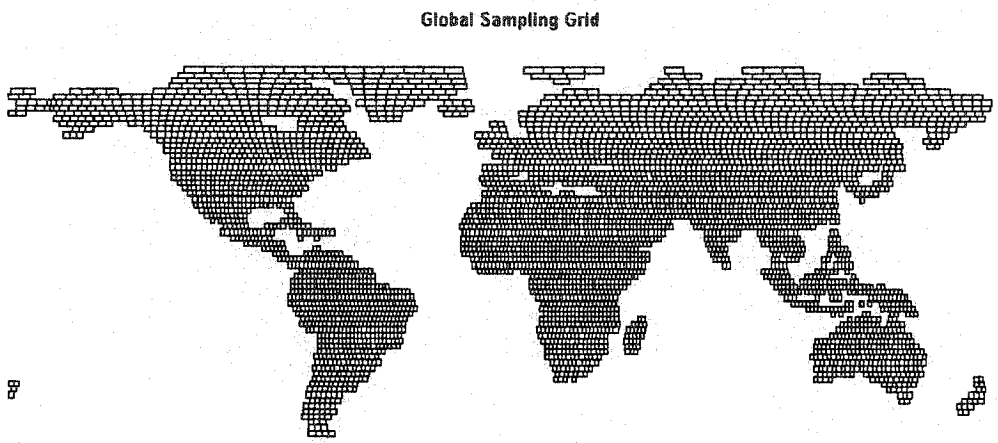

Figure A2: Sampling grid used to extract data from all maps other than angiosperm family distributions. The grid runs from 180°W to 180°E, cutting landforms as necessary. Quadrats lying east of 180°E in the original grid map were moved to the west side, correcting coordinates accordingly. Quadrats lying on 180°W were duplicated and the copy was moved to the left. Rasterizing the grid in Idrisi removed any portions of quadrats west of 180°W or east of 180°E, eliminating the duplication.

A2.3: Vector Map Projection Program

This program, written in C++, takes ASCII Idrisi vector files with coordinates written in unprojected decimal degrees latitude and longitude, and converts them to either Robinson or Mercator projections base on spherical ellipsoid. The program includes the option of including additional rubber sheeting factors allowing the resultant table units to be linearly stretched and translated so that the final vector map may fit over scanned raster maps referenced only in pixel units.

```
// GLOBAL PROJECTIONS PROGRAM
//*************************************************************************

// #include files
#include <iostream.h>
#include <string.h>
#include <fstream.h>
#include <stdlib.h>
#include <math.h>
#include <stdio.h>

//Define Pi
const double Pi = 3.14159265358979323846264338327 95;

//Create Bitmask
const int Bitmask = 0xdf;

// Prototypes
void SplashScreen(void);
void Program(char cStretch, double fMapInfo[]);
void Input(double* fData[], char sFileName[], int iSize);
void Project(double* fData[], int iProjtype, double fMapInfo[]);
void OutputVec(double* fData[], char sFileName[], int iSize);
void OutputDvc(char sFileName[], int iProjType, double fMapInfo[]);
void OutputFileNames(char sOutput[2][50]);
void InputFileNames(char sInput[2][50]);
int Size(char sFileName[]);double Radians (double fAngle);
double MercatorX(double fDegX, double fMapInfo[]);
double MercatorY(double fDegY, double fMapInfo[]);
double RobinsonX(double fDegX, double fDegY, double fMapInfo[]);
double RobinsonY(double fDegY, double fMapInfo[]);

//Main
//*************************************************************************
void main()
{
        SplashScreen();

        char cRun;
        char cStretch='Y';

        //Define map factors
        //fMapInfo... 0:MinX, 1:MaxX, 2:MinY, 3:MaxY, 4:mX, 5:bX, 6:mY, 7:bY
        //Further elements are use for values specific to each projection
        double fMapInfo[12] = {0, 0, 0, 0, 1, 0, 1, 0, 0, 0, 0, 0};
```

```
	do
	{
		cout << "\n\nNEW MAP PROJECTION";

		Program(cStretch, fMapInfo);

		cout << "\n\nDo you want to project another map?";
		cout << "\nY or N: ";
		cin >> cRun;
		cRun = cRun & Bitmask;

		if(cRun == 'Y')
		{
			cout << "\n\nDo you want to change the rubber sheeting coefficients?";
			cout << "\nY or N: ";
			cin >> cStretch;
			cStretch = cStretch & Bitmask;
		}
	}
	while (cRun == 'Y');
}

//SplashScreen
//*************************************************************************
void SplashScreen()
{
	cout<<"\t\t\xC9\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\
xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xBB\n";
	cout<<"\t\t\xBA                          \xBA\n";
	cout<<"\t\t\xBA    VECTOR MAP PROJECTION    \xBA\n";
	cout<<"\t\t\xBA                          \xBA\n";
	cout<<"\t\t\xC8\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\
xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xBC\n";
}

//Main Body of the Program
//*************************************************************************
void Program(char cStretch, double fMapInfo[])
{
	//Gather Info...
	//**************

		//Prepare the input name variable
		char sInput[2][50];
		InputFileNames(sInput);

		//What is the projection type?
		int iProjType;

		RepeatChoice1:

		cout << "\n\nChoose a projection: ";
		cout << "\n\t1) Mercator";
		cout << "\n\t2) Robinson";
		cout << "\n\t3) Not Available";
		cout << "\n\t4) Not Available";
		cout << "\n\n\t";
		cin >> iProjType;
		if(iProjType<1 || iProjType>4)
		{
			cout<<"\a";
			goto RepeatChoice1;
		}

		//Rubber sheeting parameters
		if(cStretch=='Y')
		{
			char cContort;
			cout << "\n\nInclude additional stretch and/or translation parameters (Rubber sheeting)?";
			cout << "\nY or N:  ";
```

```
                cin >> cContort;
                cContort = cContort & Bitmask;
                if(cContort == 'Y')
                {
                        cout << "\n\tm for x = ";
                        cin >> fMapInfo[4];
                        cout << "\n\tb for x = ";
                        cin >> fMapInfo[5];
                        cout << "\n\tm for y = ";
                        cin >> fMapInfo[6];
                        cout << "\n\tb for y = ";
                        cin >> fMapInfo[7];
                }
                else
                {
                        fMapInfo[4]=1;
                        fMapInfo[5]=0;
                        fMapInfo[6]=1;
                        fMapInfo[7]=0;
                }
        }

        //Prepare the output name variable
        char sOutput[2][50];
        OutputFileNames(sOutput);


//What is the size of the file?
//*****************************

        int iTotalPairs = Size(sInput[0]);
        cout<<"\n\n\n\t...entering "<<iTotalPairs<<" data points...\n\n\n";

//Setup the data table
//********************

        //Declare the pointers that will be use to store the input data
        double* fData[2];

        // Allocate the input pointers
        fData[0] = new double[iTotalPairs];
        fData[1] = new double[iTotalPairs];

//Input the vector data
//*********************

        Input(fData, sInput[0], iTotalPairs);

//Project the data
//****************

        Project(fData, iProjType, fMapInfo);

//Output the vector data
//**********************

        cout<<"\n\n\n\t...writing new map...\n\n\n";
        OutputVec(fData, sOutput[0], iTotalPairs);

//Output the vector header
//************************

        OutputDvc(sOutput[1], iProjType, fMapInfo);

// Deallocate memory by destroying pointer
delete [] fData[1];
delete [] fData[0];

// Reset pointer to NULL, unnecessary but makes life easier
fData[1] = 0;
```

```
		fData[0] = 0;
}

//Calculate the size of the vector dat set
//*************************************************************************
int Size(char sFileName[])
{
		int iTotalPairs = 0;
		int iCounter = 0;
		int iTotal = 0;
		double fHold;

		ifstream FilePtr;
		FilePtr.open(sFileName, ios::in);

		if (!FilePtr)
		{
			cout<<"Error opening "<<sFileName<<"\n";
			exit(1);
		}

		do
		{
			FilePtr>>fHold;
			iTotal++;
		}
		while(FilePtr != 0);

		FilePtr.close();

		iTotalPairs = iTotal/2;

		return iTotalPairs;
}

//Input the vector file data
//*************************************************************************
void Input(double* fData[], char sFileName[], int iSize)
{
		int iCounter;

		ifstream FilePtr;
		FilePtr.open(sFileName, ios::in);

		for (iCounter=0; iCounter<iSize; iCounter++)
		{
			FilePtr>>fData[0][iCounter];
			FilePtr>>fData[1][iCounter];
		}

		FilePtr.close();

}

//Projection Funtion
//*************************************************************************
void Project(double* fData[], int iProjType, double fMapInfo[])
{

switch(iProjType)
{
		case(1):
		{
			cout<<"\n\nThe Mercator projection requires the following information...";
			cout<<"\n\n\tR = ";
			cin>>fMapInfo[8];

			cout<<"\n\n\tCentral Longitude = ";
			cin>>fMapInfo[9];
```

```
                break;
        }
        case(2):
        {
                cout<<"\n\nThe Robinson projection requires the following information...";
                cout<<"\n\n\tR = ";
                cin>>fMapInfo[8];

                cout<<"\n\n\tCentral Longitude = ";
                cin>>fMapInfo[9];

                break;
        }
        case(3):
        {
                break;
        }
        case(4):
        {
                break;
        }
}

cout<<"\n\n\n\t...calculating map projection...";

int iFileCounter, iCoordCounter;
int iCoords;

double fX, fY;

iFileCounter=0;

do
{
        iCoords = int(fData[1][iFileCounter]);

        iFileCounter++;

        for (iCoordCounter=0; iCoordCounter<iCoords; iCoordCounter++)
                {
                        switch(iProjType)
                        {
                                case(1):
                                {
                                        fX = MercatorX(fData[0][iFileCounter], fMapInfo);
                                        fY = MercatorY(fData[1][iFileCounter], fMapInfo);
                                        break;
                                }
                                case(2):
                                {
                                        fX = RobinsonX(fData[0][iFileCounter], fData[1][iFileCounter],
fMapInfo);
                                        fY = RobinsonY(fData[1][iFileCounter], fMapInfo);
                                        break;
                                }
                                case(3):
                                {
                                        fX = MercatorX(fData[0][iFileCounter], fMapInfo);
                                        fY = MercatorY(fData[1][iFileCounter], fMapInfo);
                                        break;
                                }
                                case(4):
                                {
                                        fX = MercatorX(fData[0][iFileCounter], fMapInfo);
                                        fY = MercatorY(fData[1][iFileCounter], fMapInfo);
                                        break;
                                }
                        }
```

```
                                fData[0][iFileCounter] = fMapInfo[4]*fX + fMapInfo[5];
                                fData[1][iFileCounter] = fMapInfo[6]*fY + fMapInfo[7];

                                if(iFileCounter==1 && iCoordCounter==0)
                                {
                                        fMapInfo[0] = fData[0][iFileCounter];
                                        fMapInfo[1] = fData[0][iFileCounter];
                                        fMapInfo[2] = fData[1][iFileCounter];
                                        fMapInfo[3] = fData[1][iFileCounter];
                                }

                                if(fData[0][iFileCounter]<fMapInfo[0])
                                {fMapInfo[0] = fData[0][iFileCounter];}

                                if(fData[0][iFileCounter]>fMapInfo[1])
                                {fMapInfo[1] = fData[0][iFileCounter];}

                                if(fData[1][iFileCounter]<fMapInfo[2])
                                {fMapInfo[2] = fData[1][iFileCounter];}

                                if(fData[1][iFileCounter]>fMapInfo[3])
                                {fMapInfo[3] = fData[1][iFileCounter];}

                                iFileCounter++;
                        }
}
while(fData[1][iFileCounter] != 0);
}

//Output the vector file data
//*************************************************************************
void OutputVec(double* fData[], char sFileName[], int iSize)
{

int iFileCounter, iCoordCounter;
int iCoords;

ofstream FilePtr;
FilePtr.open(sFileName, ios::out);

iFileCounter=0;

do
{
        FilePtr<<int(fData[0][iFileCounter])<<"\t"<<int(fData[1][iFileCounter]);
        FilePtr<<"\n";

        iCoords = int(fData[1][iFileCounter]);

        iFileCounter++;

        for (iCoordCounter=0; iCoordCounter<iCoords; iCoordCounter++)
        {
                FilePtr<<fData[0][iFileCounter]<<"\t"<<fData[1][iFileCounter];
                FilePtr<<"\n";

                iFileCounter++;
        }
}
while(fData[1][iFileCounter] != 0);

FilePtr<<"0\t0";

FilePtr.close();
}

//Writes the new .dvc file to go with the map
//*************************************************************************
void OutputDvc(char sFileName[], int iProjType, double fMapInfo[])
{
```

```
ofstream FilePtr;
FilePtr.open(sFileName, ios::out);

switch(iProjType)
{
        case(1):
        {
                FilePtr<<"file title  : Mercator Projection centered at "<<fMapInfo[8]<<"° Longitude\n";
                break;
        }
        case(2):
        {
                FilePtr<<"file title  : Robinson Projection centered at "<<fMapInfo[8]<<"° Longitude\n";
                break;
        }
        case(3):
        {
                FilePtr<<"file title  : Mercator Projection\n";
                break;
        }
        case(4):
        {
                FilePtr<<"file title  : Mercator Projection\n";
                break;
        }
}
FilePtr<<"id type     : integer\n";
FilePtr<<"file type   : ascii\n";
FilePtr<<"object type : polygon\n";
FilePtr<<"ref. system : plane\n";
FilePtr<<"ref. units  : m\n";
FilePtr<<"unit dist.  : 1.0000\n";
FilePtr<<"min. X      : "<<fMapInfo[0]*1.05<<"\n";
FilePtr<<"max. X      : "<<fMapInfo[1]*1.05<<"\n";
FilePtr<<"min. Y      : "<<fMapInfo[2]*1.05<<"\n";
FilePtr<<"max. Y      : "<<fMapInfo[3]*1.05<<"\n";
FilePtr<<"pos'n error : unknown\n";
FilePtr<<"resolution  : unknown\n";

FilePtr.close();
}

//Radians Function
//*************************************************************************
double Radians(double fAngle)
{
        double RadianValue = (Pi/180)*fAngle;
        return RadianValue;
}

//Mercator X Projection
//*************************************************************************
double MercatorX(double fDegX, double fMapInfo[])
{
        double XValue = fMapInfo[8]*(Radians(fDegX) - Radians(fMapInfo[9]));
        return XValue;
}

//Mercator Y Projection
//*************************************************************************
double MercatorY(double fDegY, double fMapInfo[])
{
        double YValue = fMapInfo[8] * log( tan( (Pi/4) + (Radians(fDegY)/2)));
        return YValue;
}

//Robinson X Projection
//*************************************************************************
double RobinsonX(double fDegX, double fDegY, double fMapInfo[])
{
```

```
	double fAbsY=fabs(fDegY);
	double X = (0.99557095+(0.00098604*fAbsY)-(0.00007158*(pow(fAbsY, 2)))+(0.00000007*(pow(fAbsY, 3))));

	double XValue = 0.8487 * X * fMapInfo[8] * (Radians(fDegX) - Radians(fMapInfo[9]));
	return XValue;
}

//Robinson Y Projection
//*************************************************************************
double RobinsonY(double fDegY, double fMapInfo[])
{
	double Y;
	double fAbsY=fabs(fDegY);

	if(fDegY>=0)
	{Y = (0.00433001+(0.01129360*fAbsY)+(0.00004841*(pow(fAbsY, 2)))-(0.00000056*(pow(fAbsY, 3))));}
	else
	{Y = -1*(0.00433001+(0.01129360*fAbsY)+(0.00004841*(pow(fAbsY, 2)))-(0.00000056*(pow(fAbsY, 3))));}

	double YValue =	1.3523 * fMapInfo[8] * Y;
	return YValue;
}

//OutputFiles - Prepares the ouput file names
//*************************************************************************
void OutputFileNames(char sOutput[2][50])
{
	Name:
	// Declare a pointer
	char* sFileName;

	// Allocate the pointers with 'new'
	sFileName = new char[50];

	//Enter file names
	cout << "\n\nEnter the path and name of the output vector file (no extension): ";
	cin >> sFileName;

	int StringPtr=-1;

	do
	{
		StringPtr++;
		sOutput[0][StringPtr] = sFileName[StringPtr];
		sOutput[1][StringPtr] = sFileName[StringPtr];
	}
	while(sFileName[StringPtr] != '\0');

	// Deallocate memory by destroying pointer
	delete [] sFileName;

	sOutput[0][StringPtr]='.';
	sOutput[0][StringPtr+1]='v';
	sOutput[0][StringPtr+2]='e';
	sOutput[0][StringPtr+3]='c';
	sOutput[0][StringPtr+4]='\0';

	sOutput[1][StringPtr]='.';
	sOutput[1][StringPtr+1]='d';
	sOutput[1][StringPtr+2]='v';
	sOutput[1][StringPtr+3]='c';
	sOutput[1][StringPtr+4]='\0';

	//Check if file already exists
	ifstream TestFilePtr;
	TestFilePtr.open(sOutput[1], ios::nocreate);
	if(TestFilePtr)
	{
		WarningLoop:
```

```
                int iCheck;
                cout<< "\n\n\tWARNING...";
                cout<< "\n\n\tThe vector file already exists:";
                cout<< "\n\t\t1) Continue";
                cout<< "\n\t\t2) Rename";
                cout<< "\n\t\t3) Quit";
                cout<< "\n\n\t\t";
                cin >> iCheck;

                switch(iCheck)
                {
                        case(1):
                        {
                                TestFilePtr.close();
                                break;
                        }
                        case(2):
                        {
                                TestFilePtr.close();
                                goto Name;
                                break;
                        }
                        case(3):
                        {
                                TestFilePtr.close();
                                exit(1);
                                break;
                        }
                        default:
                        {
                                cout<<"\a";
                                goto WarningLoop;
                                break;
                        }
                }
        }
}

//InputFileNames - Prepares the input file names
//*************************************************************************
void InputFileNames(char sInput[2][50])
{
        Name:

        // Declare a pointer
        char* sFileName;

        // Allocate the pointers with 'new'
        sFileName = new char[50];

        //Enter file names
        cout << "\n\nEnter the path and name of the input vector file (no extension): ";
        cin >> sFileName;

        int StringPtr=-1;

        do
        {
                StringPtr++;
                sInput[0][StringPtr] = sFileName[StringPtr];
                sInput[1][StringPtr] = sFileName[StringPtr];
        }
        while(sFileName[StringPtr] != '\0');

        // Deallocate memory by destroying pointer
        delete [] sFileName;

        sInput[0][StringPtr]='.';
        sInput[0][StringPtr+1]='v';
        sInput[0][StringPtr+2]='e';
```

```
	sInput[0][StringPtr+3]='c';
	sInput[0][StringPtr+4]='\0';

	sInput[1][StringPtr]='.';
	sInput[1][StringPtr+1]='d';
	sInput[1][StringPtr+2]='v';
	sInput[1][StringPtr+3]='c';
	sInput[1][StringPtr+4]='\0';

	//Check if file exists
	ifstream TestFilePtr;
	TestFilePtr.open(sInput[1], ios::nocreate);
	if(!TestFilePtr)
	{
		WarningLoop:

		int iCheck;
		cout<< "\n\n\tWARNING...";
		cout<< "\n\n\tThis vector does not exist:";
		cout<< "\n\t\t1) Try another file name";
		cout<< "\n\t\t2) Quit";
		cout<< "\n\n\t\t";
		cin >> iCheck;

		switch(iCheck)
		{
			case(1):
			{
				TestFilePtr.close();
				goto Name;
				break;
			}
			case(2):
			{
				TestFilePtr.close();
				exit(1);
				break;
			}
			default:
			{
				cout<<"\a";
				goto WarningLoop;
				break;
			}
		}
	}
	else
	{
		TestFilePtr.close();
	}
}
```

A2.4: Angiosperm Family Richness Calculation Protocol

To extract the angiosperm family richness data, I used the following process.

1. Scanned each map in Heywood's (1993) Flowering Plants Of The World, using the outer boundary of the map as cropping and squaring guide. Maps were scanned at a resolution of 1031 x 719 pixels and stored as two colour (black and white) TIFF files.

2. Made duplicate copies of all map files.

3. "Cleaned" each map in Corel PhotoPaint 5.0. Erased all coastlines and other marks not demarcating zones of family occurrence. Coloured in (black) any points omitted from zones of family occurrence by the scanning process using the original paper maps as a guide.

4. For every map, identified the pixel coordinates of the four points indicated in Figure A3.

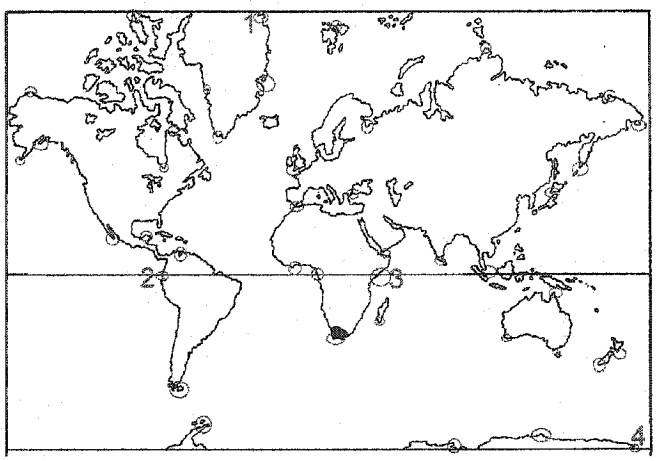

Figure A3: Reference points for rubbersheet type georeferencing of angiosperm family maps. The four numbered points were used to align all angiosperm distribution maps to each other. The full set was used to fit the sampling grid of the distribution maps.

5. For each map, wrote an ASCII ".cor" file comparing the pixel coordinates of those four points to the corresponding locations in the map of Poaceae.

6. Using Idrisi batch files, for each cleaned TIFF map file:

   i. Tifidris –imported the TIFF file to Idrisi

   ii. Convert –set the maps as integer binary format

   iii. Resample – using the .corr files so all maps were aligned

   iv. Assign – converted 0's to 1's and vice versa since Idrisi imports black as 0.

7. Using the Global Projections Program (Appendix x), applied a Mercator projection to

an Idrisi ASCII vector point file containing the degrees latitude and longitude for the 41 points identified on the map in step 4. Regressed the resultant x and y coordinates against the x and y pixel coordinates of the points to determine the appropriate linear rubber sheeting factors to include in the projection program. Applied the same Mercator projection to the Angiosperm Sampling Grid (Appendix x), including the rubber sheeting coordinates. Rasterized the resultant file, fitting it to the angiosperm family presence absence maps.

8. Using an Idrisi batch file, for each cleaned TIFF map file, used "Extract" with the rasterized Angiosperm Sampling Grid to determine presence absence data for all quadrats.

9. Tallied the presence absence data for all families in each quadrat.

A2.5: Potential Family Richness / Climatic Tolerance Program

This program, written in C++, calculates the potential spatial distribution of each family of angiosperms based on the observed range of climatic variables for each family. It has no user interface and so must be recompiled to change any settings. It begins by setting up two arrays: a presence absence table for all families listed in the "DataFile.txt" file, and a table of the levels in each quadrat to the environmental variables listed in the "EnvionFile.txt" file. The two text files are simply lists of other ASCII ".dat" files listing one quadrat value per line. The program inputs one additional ".dat" file identifying the region to which each quadrat belongs. In this file, 0's indicate the quadrat is not used in the analysis.

Within each identified region, the program determines the minimum and maximum for each climatic variable at which each angiosperm family occurs. The environmental levels of each quadrat are then compared to observed environmental tolerances of each family occurring anywhere in the region of the quadrat. If the environmental levels of the quadrat fall within the climatic tolerance hyperspace of the family (defined rectilinearly or ellipsoidally as set under the global variables) the family is considered a potential resident. Total potential residents are then tallied for each quadrat to define potential richness.

```
// CLIMATIC TOLERANCE PROGRAM
//*****************************************************************************

// #include files
#include <iostream.h>
#include <string.h>
#include <fstream.h>
#include <math.h>
#include <stdlib.h>
```

```
// Define Global Constants
const int cLetterLimit=65;              //
const int cTotalQuadrats=5000;          //
const int cTotalMaps = 306;             //# of Maps
const int cEnvironFiles = 3;            //# of Environmental Parameter Files
const int cTotalContinents=2;           //# of regions for spatial restrition + 1 for excluded areas
const int cMaxValue=7000;               //the highest level of any enviro-factor possible plus some ie 6000
const int cErrorPercent=0;              //percent of env range beyond min or max env value possible for occurence
const int cHighestFR=210;               //highest observed FR
const int cToleranceSpace=2;            //1 for rectilinear, 2 for elipsoidal

// Define Global Arrays
float aEnvironTable[cTotalQuadrats][cEnvironFiles];
int aDataTable[cTotalQuadrats][cTotalMaps];
int aContinentList[cTotalQuadrats];
float aMinMaxTable[cTotalMaps][cEnvironFiles*2*cTotalContinents];
int aSRMaxTable[cTotalQuadrats];
float aVolumeList[cTotalQuadrats];
float aVolumeTable[cTotalQuadrats][cHighestFR];

// Prototypes
int EnvironTableFunction(void);
int DataTableFunction (void);
int ContinentListFunction(void);
void MinMaxFunction (int iTotalQuadrats);
void SRMaxRectFunction(int iTotalQuadrats);
void SRMaxElipFunction(int iTotalQuadrats);
void VolumeFunction(int iTotalQuadrats);
void OutputFunction (int &Array, char FileToWrite[cLetterLimit], int iTotalRows, int iTotalColumns);
void OutputFunction (float &Array, char FileToWrite[cLetterLimit], int iTotalRows, int iTotalColumns);

//Main
//*************************************************************************
void main()
{

        int iQuadratCount, iQuadratRecount;

        iQuadratCount=EnvironTableFunction();
        cout<<"The Enviro Table lists "<<iQuadratCount-1<<" quadrats\n\n";

        iQuadratRecount=DataTableFunction();
        cout<<"The Species Table lists "<<iQuadratRecount-1<<" quadrats\n\n";
        if (iQuadratCount!=iQuadratRecount)
        {
                cout<<"Error:  Mismatch in quadrat counts\n";
                exit(1);
        }

        iQuadratRecount=ContinentListFunction();
        cout<<"The Continent Table lists "<<iQuadratRecount-1<<" quadrats\n\n";
        if (iQuadratCount!=iQuadratRecount)
        {
                cout<<"Error:  Mismatch in quadrat counts\n";
                exit(1);
        }

        iQuadratCount--;

        MinMaxFunction(iQuadratCount);
        char MinMaxFile[cLetterLimit];
        strcpy(MinMaxFile, "C:\\MinMax.dat");
        float *pMinMaxTable = &aMinMaxTable[0][0];
        OutputFunction(*pMinMaxTable, MinMaxFile, cTotalMaps, cEnvironFiles*2*cTotalContinents);

        if(cToleranceSpace==1)
        {SRMaxRectFunction(iQuadratCount);}
        if(cToleranceSpace==2)
        {SRMaxElipFunction(iQuadratCount);}
```

```
	char SRMaxFile[cLetterLimit];
	strcpy(SRMaxFile, "C:\\Physlim.dat");
	int *pSRMaxTable = &aSRMaxTable[0];
	OutputFunction(*pSRMaxTable, SRMaxFile, iQuadratCount, 1);

	VolumeFunction(iQuadratCount);
	char VolumeFile[cLetterLimit];
	strcpy(VolumeFile, "C:\\Volume.dat");
	float *pVolumeList = &aVolumeList[0];
	OutputFunction(*pVolumeList, VolumeFile, iQuadratCount, 1);

	char VolumeDistFile[cLetterLimit];
	strcpy(VolumeDistFile, "C:\\VolumeDistribution.dat");
	float *pVolumeTable = &aVolumeTable[0][0];
	OutputFunction(*pVolumeTable, VolumeDistFile, iQuadratCount, cHighestFR);
}

//Output Function:  Outputs a 2D Data Array (Two Parts i.e. overloaded)
//*****************************************************************************

//Integer version
//************************
void OutputFunction(int &Array, char FileToWrite[cLetterLimit], int iTotalRows, int iTotalColumns)
{
int iRowCounter, iColumnCounter;

ofstream OutputFilePtr;
OutputFilePtr.open(FileToWrite, ios::out);

for (iRowCounter=0; iRowCounter<iTotalRows; iRowCounter++)
{
	for(iColumnCounter=0; iColumnCounter<iTotalColumns; iColumnCounter++)
	{
		OutputFilePtr<<*(&Array + iTotalColumns*iRowCounter + iColumnCounter)<<"\t";
	}
	OutputFilePtr<<"\n";
}
OutputFilePtr.close();
}

//FloatingPoint version
//************************
void OutputFunction(float &Array, char FileToWrite[cLetterLimit], int iTotalRows, int iTotalColumns)
{
int iRowCounter, iColumnCounter;

ofstream OutputFilePtr;
OutputFilePtr.open(FileToWrite, ios::out);

for (iRowCounter=0; iRowCounter<iTotalRows; iRowCounter++)
{
	for(iColumnCounter=0; iColumnCounter<iTotalColumns; iColumnCounter++)
	{
		OutputFilePtr<<*(&Array + iTotalColumns*iRowCounter + iColumnCounter)<<"\t";
	}
	OutputFilePtr<<"\n";
}
OutputFilePtr.close();
}
// Set Up Environment Table (Two Parts)
//*****************************************************************************
int EnvironTableFunction()
{

cout<<"Opening Environment Files...\n";

//Open file of file names
//************************
char FileToOpen[]="D:\\Tony\\Programs\\DataFiles\\EnvironFile.txt";
```

```
int iFileNumber=0;

char FileList[cEnvironFiles][cLetterLimit];
char FileName[cLetterLimit];
int iCounter, iCounter2;

ifstream FileListFilePtr;
FileListFilePtr.open(FileToOpen, ios::in);

if (!FileListFilePtr)
{
        cout<<"Error opening "<<FileToOpen<<"\n";
        exit(1);
}

while (FileListFilePtr)
{
        FileListFilePtr.getline(FileName, cLetterLimit);

        if(FileListFilePtr)
        {
                for(iCounter2=0; iCounter2<cLetterLimit; iCounter2++)
                {
                        FileList[iFileNumber][iCounter2]=FileName[iCounter2];
                }
                iFileNumber++;
        }
}

FileListFilePtr.close();

cout<<"The Enviro Table lists "<<iFileNumber<<" constraints\n";

//Enter data from each listed file
//*********************************
for (iCounter = 0; iCounter < iFileNumber; iCounter++)
{
        ifstream FilePtr;
        FilePtr.open(FileList[iCounter], ios::in);

        if (!FilePtr)
        {
                cout<<"Error opening envirofile "<<iCounter<<"\n";
                exit(1);
        }

        iCounter2=0;
        while (FilePtr)
                {
                FilePtr>>aEnvironTable[iCounter2][iCounter];
                iCounter2++;
                }

        FilePtr.close();
}

return iCounter2;
}

// Set Up Data Table (Two Parts)
//*******************************************************************************
int DataTableFunction()
{

cout<<"Opening Species Files\n";

//Open file of file names
//************************
char FileToOpen[]="D:\\Tony\\Programs\\DataFiles\\DataFile.txt";
```

```
int iFileNumber=0;

char FileList[cTotalMaps][cLetterLimit];
char FileName[cLetterLimit];
int iCounter, iCounter2;

ifstream FileListFilePtr;
FileListFilePtr.open(FileToOpen, ios::in);

if (!FileListFilePtr)
{
        cout<<"Error opening DataFile.txt.\n";
        exit(1);
}

while (FileListFilePtr)
{
        FileListFilePtr.getline(FileName, cLetterLimit);

        if(FileListFilePtr)
        {
                for(iCounter2=0; iCounter2<cLetterLimit; iCounter2++)
                {
                        FileList[iFileNumber][iCounter2]=FileName[iCounter2];
                }
                iFileNumber++;
        }
}

FileListFilePtr.close();

cout<<"The Species Table lists "<<iFileNumber<<" species.\n";


//Enter data from each listed file
//*********************************
for (iCounter = 0; iCounter < iFileNumber; iCounter++)
{
        ifstream FilePtr;
        FilePtr.open(FileList[iCounter], ios::in);

        if (!FilePtr)
        {
                cout<<"Error opening specfile "<<iCounter<<"\n";
                exit(1);
        }

        iCounter2=0;
        while (FilePtr)
        {
                FilePtr>>aDataTable[iCounter2][iCounter];
                iCounter2++;
        }

        FilePtr.close();

}
return iCounter2;
}

// Set Up Continent Table
//*****************************************************************************
int ContinentListFunction()
{

cout<<"Opening Continent File\n";

//Set filename to appropriate continent list
char FileToOpen[]="D:\\\\Tony\\Programs\\DataFiles\\AllQuadrats.dat";
```

```
int iCounter;

ifstream FilePtr;
FilePtr.open(FileToOpen, ios::in);

if (!FilePtr)
{
        cout<<"Error opening "<<FileToOpen<<"\n";
        exit(1);
}

iCounter=0;
while (FilePtr)
{
        FilePtr>>aContinentList[iCounter];
        iCounter++;
}

FilePtr.close();
return iCounter;
}


//Caluculate the Min and Max Environment of Each Species
//*************************************************************************
void MinMaxFunction(int iTotalQuadrats)
{
int iContCounter;
int iSpecCounter;
int iGoCounter;
int iCounter1;
int iCounter2;

for (iSpecCounter=0; iSpecCounter<cTotalMaps; iSpecCounter++)//sets intial max min values
{
                for (iGoCounter=0; iGoCounter<(cEnvironFiles*2*cTotalContinents); iGoCounter +=2)
                {
                        aMinMaxTable[iSpecCounter][iGoCounter]=float(cMaxValue);
                        aMinMaxTable[iSpecCounter][iGoCounter+1]=float(-cMaxValue);
                }
}


//go through each continent
for (iContCounter=0; iContCounter<cTotalContinents; iContCounter++)
{
//go to each spec in aMinMaxTable
for (iSpecCounter=0; iSpecCounter<cTotalMaps; iSpecCounter++)
{
        //go across each MinMax env group
        for (iCounter1=0; iCounter1<(cEnvironFiles*2); iCounter1+=2)
        {
                //compare to env and data
                for (iCounter2=0; iCounter2<iTotalQuadrats; iCounter2++)
                {
                        //does data=1 ie is the species present
                        if (aDataTable[iCounter2][iSpecCounter]==1 &&
aContinentList[iCounter2]==(iContCounter+1))
                        {
                                //if env is smaller than envtable
                                //then update min value
                                if
(aEnvironTable[iCounter2][iCounter1/2]<aMinMaxTable[iSpecCounter][iCounter1+(iContCounter*cEnvironFiles*2)] &&
aEnvironTable[iCounter2][iCounter1/2]!=-999)

        {aMinMaxTable[iSpecCounter][iCounter1+(iContCounter*cEnvironFiles*2)]=aEnvironTable[iCounter2][iCounter1
/2];}

                                //if env is larger than envtable
                                //then update max value
```

```
                                        if
(aEnvironTable[iCounter2][iCounter1/2]>aMinMaxTable[iSpecCounter][iCounter1+1+(iContCounter*cEnvironFiles*2)] &&
aEnvironTable[iCounter2][iCounter1/2]!=-999)

        {aMinMaxTable[iSpecCounter][iCounter1+1+(iContCounter*cEnvironFiles*2)]=aEnvironTable[iCounter2][iCount
er1/2];}
                                }
                        }
                }
}
}

}

//Calculate the Max possible SR at each quadrat for the aSRMaxTable Array
//assuming a rectilinear tolerance region
//*************************************************************************
void SRMaxRectFunction(int iTotalQuadrats)
{

int iCont;
int iPossible;

int iQuadCounter;
int iSpecCounter;
int iEnvCounter;

float fTestMin;
float fTestMax;
float fTestRange;

//for each quadrat (going down aSRMaxTable)
for(iQuadCounter=0; iQuadCounter<iTotalQuadrats; iQuadCounter++)
{
        aSRMaxTable[iQuadCounter] = 0;                          // initialize the SR level
        iCont = aContinentList[iQuadCounter]-1; // identify the continent of the quadrat

        //for each species
        for (iSpecCounter=0; iSpecCounter<cTotalMaps; iSpecCounter++)
        {
                //start with a score card for species presence = to 0
                iPossible = 0;

                //for each environmental factor
                for (iEnvCounter=0; iEnvCounter<cEnvironFiles; iEnvCounter++)
                {
                        //prepare test statements
                        fTestMin=aMinMaxTable[iSpecCounter][(2*iEnvCounter)+(iCont*cEnvironFiles*2)];
                        fTestMax=aMinMaxTable[iSpecCounter][(2*iEnvCounter)+(iCont*cEnvironFiles*2)+1];

                        fTestRange=fTestMax-fTestMin;

                        //if environmemtal level of the quadrat is between
                        //the min and max of the species in that iCont,
                        //let the score card iPossible increase by 1
                        if(aEnvironTable[iQuadCounter][iEnvCounter]>=(fTestMin-(cErrorPercent*fTestRange)) &&
aEnvironTable[iQuadCounter][iEnvCounter]<=(fTestMax+(cErrorPercent*fTestRange)))
                        {iPossible++;}
                }

                //if the species can exist in every climate parameter of the quadrat
                //it should have a perfect score card so up the quadrat SR count by 1
                if (iPossible == cEnvironFiles)
                {aSRMaxTable[iQuadCounter]++;}
        }
}
}

//Calculate the Max possible SR at each quadrat for the aOutputTable Array
//assuming an elipsoidal tolerance region
```

```
//*****************************************************************************
void SRMaxElipFunction(int iTotalQuadrats)
{

int iCont;
int iQuadCounter;
int iSpecCounter;
int iEnvCounter;

float fMin, fMax;
float fAxis, fCoordinate;
float fTestCoord, fEPartial;
float iLocationHash;

//for each quadrat (going down aOutputTable)
for(iQuadCounter=0; iQuadCounter<iTotalQuadrats; iQuadCounter++)
{
        aSRMaxTable[iQuadCounter] = 0;                          // initialize the SR level
        iCont = aContinentList[iQuadCounter]-1;// identify the continent of the quadrat

        //for each species
        for (iSpecCounter=0; iSpecCounter<cTotalMaps; iSpecCounter++)
        {
                //reset hash
                iLocationHash = 0;

                //for each environmental factor
                for (iEnvCounter=0; iEnvCounter<cEnvironFiles; iEnvCounter++)
                {
                        //prepare test statements
                        fMin=aMinMaxTable[iSpecCounter][(2*iEnvCounter)+(iCont*cEnvironFiles*2)];
                        fMax=aMinMaxTable[iSpecCounter][(2*iEnvCounter)+(iCont*cEnvironFiles*2)+1];

                        if (fMax>fMin)
                        {
                                fAxis=(fMax-fMin)/2;// e.g. "a" if major axis
                                fCoordinate=(fMax+fMin)/2;    //e.g. "j" if x axis
                                fTestCoord=aEnvironTable[iQuadCounter][iEnvCounter]; //= "x" if x axis
                                fEPartial=pow((fTestCoord-fCoordinate),2)/pow(fAxis,2); //i.e. partial contribution
to ellipsoid = (x-j)^2/a^2
                                iLocationHash+=fEPartial;
                        }

                }

                //if the quadat's climate falls within the climatic tolerance ellipsoid of the species
                //it should support the species... if the species is present (i.e. fMax>fMin), up the quadrat SR count by
1
                if (iLocationHash <=1 && fMax>fMin)
                {aSRMaxTable[iQuadCounter]++;}

        }
}
}


//Calculate the average niche volume per quadrat
//*****************************************************************************
void VolumeFunction(int iTotalQuadrats)
{

int iCont;
int iQuadSR;

int iQuadCounter;
int iSpecCounter;
int iEnvCounter;
int iQuadSpecCounter;

float fEnvMin;
```

```
float fEnvMax;

float fSpecVolume;
float fQuadVolume;

//initialize volume distribution table to -99
for(iQuadCounter=0; iQuadCounter<iTotalQuadrats; iQuadCounter++)
{
        for (iSpecCounter=0; iSpecCounter<cHighestFR; iSpecCounter++)
        {aVolumeTable[iQuadCounter][iSpecCounter]=-99;}
}


//for each quadrat (going down aVolumeList)
for(iQuadCounter=0; iQuadCounter<iTotalQuadrats; iQuadCounter++)
{
        iQuadSR = 0;                            //initialize the SR
        fQuadVolume = 0;            //initialize the volume
        iQuadSpecCounter=0;

        iCont = aContinentList[iQuadCounter]-1;// identify the continent of the quadrat

        //for each species
        for (iSpecCounter=0; iSpecCounter<cTotalMaps; iSpecCounter++)
        {
                fSpecVolume = 0;   //initialize the species volume addition to quadrat total

                if(aDataTable[iQuadCounter][iSpecCounter]==1) //Is the species present in the quadrat?
                {
                        iQuadSR++;
                        fSpecVolume=1; //reinitialize the species volume for mulitplication by environmental
dimensions

                        //for each environmental factor
                        for (iEnvCounter=0; iEnvCounter<cEnvironFiles; iEnvCounter++)
                        {

        fEnvMin=aMinMaxTable[iSpecCounter][(2*iEnvCounter)+(iCont*cEnvironFiles*2)];

        fEnvMax=aMinMaxTable[iSpecCounter][(2*iEnvCounter)+(iCont*cEnvironFiles*2)+1];

                                if(fEnvMax>=fEnvMin) //either multiply
                                {fSpecVolume *= (fEnvMax-fEnvMin);}

                                else //or reset
                                {fSpecVolume = 0;}
                        }

                        if(fEnvMax>=fEnvMin)
                        {
                                aVolumeTable[iQuadCounter][iQuadSpecCounter]=fSpecVolume;
                                iQuadSpecCounter++;
                        }
                }

                fQuadVolume += fSpecVolume;
        }

        if(iQuadSR==0 ) //enter error code
        {aVolumeList[iQuadCounter]=-99;}

        else // or enter average volume
        {aVolumeList[iQuadCounter] = (fQuadVolume/float(iQuadSR));}

}
}
```

A2.6: Moran's I Program

This program, written in C++, calculates Moran's I for a spatial dataset of geographic points (i.e. point data or polygon centroids). Neighbours are determined over successive lags of a set lag distance using great arc distance between points. Arc distance is based on spherical trigonometry, and assumes that one minute of arc is 1.852 km (1 nautical mile). Successive lags may be cumulative, such that neighbours include all points from a centroid or point to the outer lag perimeter, or non-cumulative, such that neighbours include only points between the outer lag perimeter and the previous lag perimeter.

Data is entered using a tab delimited ASCII text file with data in three columns: 1) longitude (in degrees with E positive and W negative), 2) latitude (in degrees with N positive and S negative), and 3) datum values.

```
//MORAN'S I PROGRAM
//*****************************************************************************

// #include files
#include <iostream.h>
#include <string.h>
#include <fstream.h>
#include <stdlib.h>
#include <math.h>

//Define Constants
const int cLetterLimit = 50;
const double Pi = 3.14159265358979323846264338327 95;

//Create Bitmask
const int Bitmask = 0xdf;

// Define Structures
struct Quadrat
{
        double dLong;
        double dLat;
        double dData;
};

// Prototypes
int GetFileSize(char sFileName[]);
void SplashScreen(void);
void DataMatrix(Quadrat* DataArray, int iSize, char sInput[]);
void InputFileName(char sInput[]);
```

```
void OutputFileName(char sOutput[]);
double Radians(double dDeg);
double GeoDistance(double dLong1, double dLong2, double dLat1, double dLat2);
double DataMean(Quadrat* DataArray, int iSize);
double MoranDenominator(Quadrat* DataArray, int iSize, double dDataMean);
double Morans_I(Quadrat* DataArray, int iSize, double dDataMean, double dDenominator, double dStepDistance, int
iLagStep, char cCummulative);


//Main
//*************************************************************************
void main()
{
        SplashScreen();

        //Present basic information
        //*************************
        cout <<"\n\n";
        cout <<"This program calculates Moran's I from geographic points\n";
        cout <<"(i.e. point data or centroids).\n\n";
        cout <<"Enter data using a tab delimited text file.\n";
        cout <<"Data must be in three columns.\n";
        cout <<"\t1) Longitude (in degrees with E positive and W negative)\n";
        cout <<"\t2) Latitude  (in degrees with N positive and S negative)\n";
        cout <<"\t3) Data\n";
        cout <<"\n\n";

        //Prepare the input name variable
        //*******************************
        char sInputFile[cLetterLimit];
        InputFileName(sInputFile);

        //Get the base lag distance in km
        //*******************************
        double dStepDistance;

        Repeat1:

        cout << "\n\nWhat is the base distance for lags (in km)?";
        cout << "\n\n\t";
        cin >> dStepDistance;
        if(!dStepDistance)
        {
                cout<<"\a";
                goto Repeat1;
        }

        //How many lags?
        //**************
        int iLags;

        Repeat2:

        cout << "\n\nHow many lag steps?";
        cout << "\n\n\t";
        cin >> iLags;
        if(!iLags)
        {
                cout<<"\a";
                goto Repeat2;
        }

        //Are lags cummulative or non cummulative?
        //****************************************
        char cCummulative;

        Repeat3:

        cout << "\n\nUse (C)ummulative or (N)on-Cummulative lags?";
        cout << "\nC or N:  ";
```

```
cin >> cCummulative;
cCummulative = cCummulative & Bitmask;
if(!(cCummulative=='C' || cCummulative=='N'))
{
        cout<<"\a";
        goto Repeat3;
}

//Save output to file a file?
//***************************
char cSave;

cout << "\n\nSave your ouput to a file?";
cout << "\nY or N:  ";
cin >> cSave;
cSave = cSave & Bitmask;

char sOutputFile[cLetterLimit];
if(cSave=='Y')
{
        OutputFileName(sOutputFile);
}

//Main Body of Program
//*********************

int iSize=GetFileSize(sInputFile);

Quadrat* DataArray;
DataArray = new Quadrat[iSize];

DataMatrix(DataArray, iSize, sInputFile);

double dDataMean = DataMean(DataArray, iSize);

double dDenominator = MoranDenominator(DataArray, iSize, dDataMean);

ofstream FilePtr;
if(cSave=='Y')
{FilePtr.open(sOutputFile, ios::out);}

int iLagCounter;
double dMoransI;

cout<<"\n\n";
cout<<"*****************************************************";
cout<<"\n\n";

cout<<"Lag Distance = "<<dStepDistance<<" km\n\n";
if(cSave=='Y')
{FilePtr<<"Lag Distance = "<<dStepDistance<<" km\n\n";}

if(cCummulative=='C')
{cout<<"Lags are cummulative\n\n";}
else
{cout<<"Lags are non-cummulative\n\n";}
if(cSave=='Y')
{
        if(cCummulative=='C')
        {FilePtr<<"Lags are cummulative\n\n";}
        else
        {FilePtr<<"Lags are non-cummulative\n\n";}
}

for (iLagCounter=1; iLagCounter<=iLags; iLagCounter++)
{
        dMoransI = Morans_I(DataArray, iSize, dDataMean, dDenominator, dStepDistance, iLagCounter,
cCummulative);

        if(dMoransI==999)
```

```
                {cout<<"For a lag of "<<iLagCounter<<", no neighbours were defined\n";}

                else
                {cout<<"For a lag of "<<iLagCounter<<", I = "<<dMoransI<<"\n";}

                if(cSave=='Y')
                {
                        if(dMoransI==999)
                        {FilePtr<<"For a lag of "<<iLagCounter<<", no neighbours were defined\n";}

                        else
                        {FilePtr<<"For a lag of "<<iLagCounter<<", I = "<<dMoransI<<"\n";}
                }
        }
        if(cSave=='Y')
        {
                FilePtr.close();
        }

        cout<<"\n\n";

        // Deallocate memory by destroying pointer
        delete [] DataArray;
}

//SplashScreen
//*************************************************************************
void SplashScreen()
{
        cout<<"\t\t\xC9\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\
xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xBB\n";
        cout<<"\t\t\xBA                              \xBA\n";
        cout<<"\t\t\xBA        MORAN'S I          \xBA\n";
        cout<<"\t\t\xBA       FOR LAT/LONG        \xBA\n";
        cout<<"\t\t\xBA                              \xBA\n";
        cout<<"\t\t\xC8\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\
xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xCD\xBC\n";
}

//Get File Size
//*************************************************************************
int GetFileSize(char sFileName[])
{
        double dLat, dLong, dData;
        int iCounter=0;

        ifstream FilePtr;
        FilePtr.open(sFileName, ios::in);

        if (!FilePtr)
        {
                cout<<"Error opening "<<sFileName<<".\n";
                exit(1);
        }

        while (FilePtr)
        {
                FilePtr>>dLong;
                FilePtr>>dLat;
                FilePtr>>dData;
                iCounter++;
        }

        FilePtr.close();

        return iCounter-1;
}

//Create Data Matrix
```

```
//*************************************************************************
void DataMatrix(Quadrat* DataArray, int iSize, char sFileName[])
{
        int iCounter;

        ifstream FilePtr;
        FilePtr.open(sFileName, ios::in);

        if (!FilePtr)
        {
                cout<<"Error opening "<<sFileName<<".\n";
                exit(1);
        }

        for(iCounter=0; iCounter<iSize; iCounter++)
        {
                FilePtr>>DataArray[iCounter].dLong;
                FilePtr>>DataArray[iCounter].dLat;
                FilePtr>>DataArray[iCounter].dData;
        }

        FilePtr.close();

}

//Calculate Radians
//*************************************************************************
double Radians(double dDeg)
{
        double dRad;
        dRad = Pi*dDeg/180;
        return dRad;
}


//Calculate Disatance Between Two Points
//*************************************************************************
double GeoDistance(double dLong1, double dLong2, double dLat1, double dLat2)
{
        double dDist;

        double rLong1 = Radians(dLong1);
        double rLong2 = Radians(dLong2);
        double rLat1 = Radians(dLat1);
        double rLat2 = Radians(dLat2);

        dDist = 1.852 * 60 * 180/Pi * acos ( sin(rLat1) * sin(rLat2) + cos(rLat1) * cos(rLat2) * cos(rLong2-rLong1));

        return dDist;
}


//Calculate Average Data Value
//*************************************************************************
double DataMean(Quadrat* DataArray, int iSize)
{
        int iCounter;
        double dData = 0;

        for (iCounter=0; iCounter<iSize; iCounter++)
        {
                dData += DataArray[iCounter].dData;
        }

        return dData/iSize;
}

//Calculate Denominator
//*************************************************************************
double MoranDenominator(Quadrat* DataArray, int iSize, double dDataMean)
```

```
{
	int iCounter;
	double dDenominator = 0;

	for (iCounter=0; iCounter<iSize; iCounter++)
	{
		dDenominator += pow((DataArray[iCounter].dData - dDataMean),2);
	}

	return dDenominator;
}


//Calculate Moran's I
//*************************************************************************
double Morans_I(Quadrat* DataArray, int iSize, double dDataMean, double dDenominator, double dStepDistance, int
iLagStep, char cCummulative)
{
	double dUpperLag = dStepDistance*double(iLagStep);
	double dLowerLag = dStepDistance*double(iLagStep-1);

	//Numerator and W
	//*******************

	int i, j;
	double dGeoDistance;

	long int iW = 0;
	double dNumerator = 0;

	if(cCummulative == 'C')
	{

		for (i=0; i<iSize; i++)
		{
			for (j=i+1; j<iSize; j++)
			{
				dGeoDistance = GeoDistance(DataArray[i].dLong, DataArray[j].dLong,
DataArray[i].dLat, DataArray[j].dLat);

				if(dGeoDistance < dUpperLag)
				{
					dNumerator += (DataArray[i].dData - dDataMean)*(DataArray[j].dLong-
dDataMean);
					iW++;
				}

			}
		}
	}

	else
	{
		for (i=0; i<iSize; i++)
		{
			for (j=i+1; j<iSize; j++)
			{
				dGeoDistance = GeoDistance(DataArray[i].dLong, DataArray[j].dLong,
DataArray[i].dLat, DataArray[j].dLat);

				if(dGeoDistance > dLowerLag && dGeoDistance < dUpperLag)
				{
					dNumerator += (DataArray[i].dData - dDataMean)*(DataArray[j].dLong-
dDataMean);
					iW++;
				}
			}
		}
	}
	//Moran's I
```

```
	//******************

	double dMorans_I;

	if(iW==0)
	{dMorans_I = double(999);}

	else
	{dMorans_I = (iSize*dNumerator)/(iW*dDenominator);}


	return dMorans_I;
}


//InputFileNames - Prepares the input file names
//*************************************************************************
void InputFileName(char sInput[])
{

	Name:

	// Declare a pointer
	char* sFileName;

	// Allocate the pointers with 'new'
	sFileName = new char[cLetterLimit];

	//Enter file names
	cout << "\n\nEnter the full path and name of the input data file: ";
	cin >> sFileName;

	int StringPtr=0;

	do
	{
		sInput[StringPtr] = sFileName[StringPtr];
		StringPtr++;
	}
	while(sFileName[StringPtr] != '\0');

	sInput[StringPtr]='\0';

	// Deallocate memory by destroying pointer
	delete [] sFileName;

	//Check if file exists
	ifstream TestFilePtr;
	TestFilePtr.open(sInput, ios::nocreate);

	if(!TestFilePtr)
	{
		WarningLoop:

		int iCheck;
		cout<< "\n\n\tWARNING...";
		cout<< "\n\n\tThis file does not exist:";
		cout<< "\n\t\t1) Try another file name";
		cout<< "\n\t\t2) Quit";
		cout<< "\n\n\t\t";
		cin >> iCheck;

		switch(iCheck)
		{
			case(1):
			{
				TestFilePtr.close();
				goto Name;
				break;
			}
```

```
                        case(2):
                        {
                                TestFilePtr.close();
                                exit(1);
                                break;
                        }
                        default:
                        {
                                cout<<"\a";
                                goto WarningLoop;
                                break;
                        }
                }
        }

        else
        {
                TestFilePtr.close();
        }
}

//OutputFileNames - Prepares the output file names
//*************************************************************************
void OutputFileName(char sOutput[])
{

        Name:

        // Declare a pointer
        char* sFileName;

        // Allocate the pointers with 'new'
        sFileName = new char[cLetterLimit];

        //Enter file names
        cout << "\n\nEnter the full path and name of the output data file: ";
        cin >> sFileName;

        int StringPtr=0;

        do
        {
                sOutput[StringPtr] = sFileName[StringPtr];
                StringPtr++;
        }
        while(sFileName[StringPtr] != '\0');

        sOutput[StringPtr]='\0';

        // Deallocate memory by destroying pointer
        delete [] sFileName;

        //Check if file already exists
        ifstream TestFilePtr;
        TestFilePtr.open(sOutput, ios::nocreate);
        if(TestFilePtr)
        {
                WarningLoop:

                int iCheck;
                cout<< "\n\n\tWARNING...";
                cout<< "\n\n\tThe file already exists:";
                cout<< "\n\t\t1) Continue";
                cout<< "\n\t\t2) Rename";
                cout<< "\n\t\t3) Quit";
                cout<< "\n\n\t\t";
                cin >> iCheck;

                switch(iCheck)
                {
```

```
                    case(1):
                    {
                            TestFilePtr.close();
                            break;
                    }
                    case(2):
                    {
                            TestFilePtr.close();
                            goto Name;
                            break;
                    }
                    case(3):
                    {
                            TestFilePtr.close();
                            exit(1);
                            break;
                    }
                    default:
                    {
                            cout<<"\a";
                            goto WarningLoop;
                            break;
                    }
            }
        }
}
```

Appendix 3: Chapters Two and Three Data

A3.1: Chapters Two and Three Data Summary

Table A3: Variables used in Chapters Two and Three.

Variable Name	Description
AET	Total annual evapotranspiration (mm)
AETMAX	Highest mean monthly evapotranspiration (mm)
AETMIN	Lowest mean monthly evapotranspiration (mm)
AETRNG	AETMAX-AETMIN (mm)
AETSTD	Standard deviation of mean monthly evapotranspiration
CLIMRNG1	1st PCA loadings for AETRNG, PETRNG, PRERNG, RAINRNG, TEMPRNG, and WDRNG
CLIMRNG2	2nd PCA loadings for AETRNG, PETRNG, PRERNG, RAINRNG, TEMPRNG, and WDRNG
CLIMRNG3	3rd PCA loadings for AETRNG, PETRNG, PRERNG, RAINRNG, TEMPRNG, and WDRNG
CLIMRNG4	4th PCA loadings for AETRNG, PETRNG, PRERNG, RAINRNG, TEMPRNG, and WDRNG
CLIMATE1	1st PCA loadings for AET, PET, PRE, RAIN, TEMP, and WD
CLIMATE2	2nd PCA loadings for AET, PET, PRE, RAIN, TEMP, and WD
CLIMATE3	3rd PCA loadings for AET, PET, PRE, RAIN, TEMP, and WD
ECO-TYPES	Total number of Global Land Cover Characterization classes per quadrat
ELVAVG	Mean elevation (m)
ELVMAX	Highest elevation (m)
ELVMIN	Lowest elevation (m)
ELVRNG	ELVMAX-ELVMIN (m)
FR	Angiosperm family richness
FRMAXAQ	Potential angiosperm richness – no spatial restriction
FRMAXBGR	Potential angiosperm richness – spatial restricted to provinces
FRMAXBGZ	Potential angiosperm richness – spatial restricted to provinces sub-zones
HOLDAG	Holdridge Aggregate Lifezone category
HOLDAGTOTAL	Total number of Holdridge Aggregate Lifezones per quadrat
LANDAREA	Proportion dry land
LAT	Northern quadrat latitude (°)
LONG	Western quadrat longitude (°)

Variable Name	Description
LONGSPAN	Longitudinal span at mid latitude (°)
PET	Total annual potential evapotranspiration (mm)
PETMAX	Highest mean monthly potential evapotranspiration (mm)
PETMIN	Lowest mean monthly potential evapotranspiration (mm)
PETRNG	PETMAX-PETMIN (mm)
PETSTD	Standard deviation of mean monthly potential evapotranspiration
PRE	Total annual precipitation (mm)
PREMAX	Highest mean monthly precipitation (mm)
PREMIN	Lowest mean monthly precipitation (mm)
PRERNG	PREMAX-PREMIN (mm)
PRESTD	Standard deviation of mean monthly precipitation
RAIN	Total annual precipitation for all months with mean temperature > 0°C (mm)
RAINMAX	Highest mean monthly RAIN (mm)
RAINMIN	Lowest mean monthly RAIN (mm)
RAINRNG	RAINMAX-RAINMIN (mm)
RAINSDT	Standard deviation of mean monthly RAIN
SR	Species richness sampled from Barthlott *et al.* (1996)
TEMP	Mean monthly temperature (°K)
TEMPMAX	Highest mean monthly temperature (°K)
TEMPMIN	Lowest mean monthly temperature (°K)
TEMPRNG	TEMPMAX-TEMPMIN (°K)
TEMPSTD	Standard deviation of mean monthly temperature
WD	PET – AET (mm) (using only pixels with both ET data)
WDMAX	Highest mean monthly WD (mm)
WDMIN	Lowest mean monthly WD (mm)
WDRNG	WDMAX-WDMIN (mm)
WDSTD	Standard deviation of mean monthly WD

Table A4: Variables used in Chapters Two and Three summarized for the data set as whole, by biogeographic province, and by provincial sub-zone.

Total Data Set

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	4224	4224	4224	4224	4224	4224	4224	4224	4224	4224
Min	1	0.75	0	0.75	0.281	-1.69	-2.341	-2.323	-3.291	-3.259
Max	1905.667	207	139.667	184	72.16	6.277	2.606	2.521	7.563	7.851
Mean	572.348	93.743	14.012	79.731	29.56	1.09E-11	4.97E-12	2.36E-13	-7.20E-12	4.26E-12
SD	442.273	44.957	28.539	38.611	15.443	1	1	1	1	1.933

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	4224	4224	4224	4224	4224	4224	4224	4224	4224	4224
Min	-4.168	-3.795	1	-26.667	0	-240	0	8	16	0
Max	3.262	1.358	41	5448.917	8840	4880	8780	198	292	225
Mean	4.02E-12	3.55E-12	14.711	604.492	1585.843	246.884	1338.958	116.53	229.27	154.6
SD	1.43	0.387	6.919	783.886	1484.52	490.251	1298.567	43.107	64.679	52.415

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	4224	4224	4224	4224	4224	4224	4224	4224	4224	4224
Min	0	1	1	0.021	-54	-168.161	1.414	34.25	14.75	0
Max	210	14	9	1	80	188.095	7.412	2030	206.083	139.667
Mean	125.104	8.75	1.862	0.877	24.552	19.229	1.98	974.625	135.463	37.69
SD	61.031	3.822	1.029	0.242	30.504	81.677	0.812	489.207	36.052	43.481

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	4224	4224	4224	4224	4224	4224	4224	4224	4224	4224
Min	14.75	5.447	0.083	0.083	0	0.083	0.024	0.083	0.083	0
Max	195.875	72.889	5668.917	1102.75	353	1094.417	445.717	5668.917	1102.75	353
Mean	97.774	36.018	876.939	146.614	24.781	121.833	43.021	816.338	146.17	17.192
SD	41.482	16.312	765.065	123.812	35.386	115.089	42.387	787.993	124.018	35.655

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	4224	4224	4224	4224	4224	4224	4224	4224	4224	4224
Min	0.083	0.024	91	254.055	274.288	221.267	0.45	0.145	0	0
Max	1094.417	445.717	5000	302.859	311.083	300.5	70.383	25.59	1706.167	199.437
Mean	128.978	46.731	1381.91	287.071	296.254	277.369	18.885	6.937	402.276	81.662
SD	112.089	40.842	1180.581	12.238	6.972	18.456	13.844	5.167	396.81	58.184

	WDMIN	WDRNG	WDSTD
n	4224	4224	4224
Min	-53	0	0
Max	111.5	199.437	81.724
Mean	4.494	77.167	28.168
SD	13.386	54.679	20.696

Region: Nearctic

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	675	675	675	675	675	675	675	675	675	675
Min	34.25	14.75	0	14.75	4.82	-1.307	-2.341	-1.836	-2.429	-3.259
Max	1261.5	167.25	44.273	153.75	56.672	1.654	2.513	2.521	1.935	2.245
Mean	379.635	80.076	1.796	78.28	29.539	-0.562	-0.373	0.556	-0.022	-1.268
SD	248.44	35.817	5.437	33.759	12.641	0.388	1.07	0.854	0.878	1.207

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	675	675	675	675	675	675	675	675	675	675
Min	-2.102	-2.809	2	0	0	-120	0	14	16	16
Max	2.752	0.792	34	2949.091	6190	1980	6100	173	289	192
Mean	0.969	0.012	14.677	523.958	1383.659	204.785	1178.874	83.508	196.406	109.089
SD	0.884	0.353	6.703	540.81	1185.098	337.602	1040.083	42.72	86.648	48.921

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	675	675	675	675	675	675	675	675	675	675
Min	0	1	1	0.036	24	-168.161	1.536	34.25	14.75	0
Max	189	13	7	1	80	-21.541	7.412	1355.286	196.437	45.273
Mean	85.83	5.604	1.793	0.826	52.533	-102.033	2.633	535.042	111.282	2.774
SD	50.851	3.336	0.946	0.27	13.417	25.508	1.082	331.917	43.67	7.454

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	675	675	675	675	675	675	675	675	675	675
Min	14.75	5.486	103.875	16.75	0.083	8.667	3.296	42	16.75	0
Max	192	70.79	3106.7	448.75	121.15	345.45	108.846	2889.25	448.75	121.15
Mean	108.508	41.088	643.491	89.569	28.928	60.641	20.359	487.671	88.408	8.428
SD	41.083	15.506	450.54	54.573	26.644	40.838	14.366	420.775	53.911	22.519

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	675	675	675	675	675	675	675	675	675	675
Min	15.417	4.586	91	254.055	275.425	236.719	4.969	1.872	0	0
Max	448.75	131.299	2000	297.44	306.162	292.658	45.563	17.356	1023.333	191.187
Mean	79.981	29.961	733.444	275.471	289.881	260.726	29.156	10.807	155.407	45.955
SD	46.701	17.096	573.888	10.398	7.105	14.196	9.195	3.437	221.522	47.162

	WDMIN	WDRNG	WDSTD
n	675	675	675
Min	-10.313	0	0
Max	17.667	191.187	75.439
Mean	0.074	45.881	16.289
SD	1.291	46.937	17.347

Region: Neotropic

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	603	603	603	603	603	603	603	603	603	603
Min	5.667	1.667	0	1.667	0.607	-1.064	-1.847	-2.27	-3.291	-1.798
Max	1751.333	173.75	125	156.083	62.149	2.919	1.937	1.462	2.956	7.851
Mean	1058.581	127.622	41.958	85.664	31.121	0.782	-0.238	-0.511	-0.398	2.025
SD	405.805	33.968	36.122	34.648	14.296	0.861	0.701	0.842	1.028	1.74

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	603	603	603	603	603	603	603	603	603	603
Min	-2.263	-3.621	4	0	0	-30	0	57	156	72
Max	3.262	1.358	34	4503.889	7070	3660	6800	196	291	225
Mean	0.315	0.111	15.66	537.665	1636.6	147.811	1488.789	161.723	265.794	207.091
SD	0.842	0.523	5.124	796.845	1722.402	327.311	1628.764	25.173	19.511	15.363

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	603	603	603	603	603	603	603	603	603	603
Min	0	1	1	0.069	-54	-106.255	1.414	356.875	82	0
Max	205	14	7	1	26	-36.092	2.466	1829	193.083	129.667
Mean	175.828	12.182	2.053	0.892	-10.133	-64.001	1.519	1330.65	146.605	74.505
SD	56.581	2.512	1.187	0.224	16.861	13.264	0.169	310.293	16.782	40.204

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	603	603	603	603	603	603	603	603	603	603
Min	17.333	5.447	6.25	1.583	0	1.583	0.557	6.25	1.583	0
Max	167.833	61.388	5668.917	593.583	353	542.667	193.175	5668.917	593.583	353
Mean	72.1	25.094	1611.018	244.142	45.152	198.99	70.989	1611.018	244.142	45.152
SD	40.176	15.395	836.158	119.601	45.963	111.232	40.42	836.158	119.601	45.963

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	603	603	603	603	603	603	603	603	603	603
Min	1.583	0.557	100	278.723	282.115	273.456	0.45	0.145	0	0
Max	542.667	193.175	5000	301.036	302.408	300.5	17.5	6.352	1110.083	176.083
Mean	198.99	70.989	2314.907	295.09	297.505	292.328	5.178	1.858	272.069	70.481
SD	111.232	40.42	1326.195	5.08	3.962	6.708	4.258	1.592	231.054	41.322

	WDMIN	WDRNG	WDSTD
n	603	603	603
Min	-12	0	0
Max	63.5	176.083	67.405
Mean	1.875	68.606	24.926
SD	8.418	40.294	15.492

Region: Palearctic

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	1453	1453	1453	1453	1453	1453	1453	1453	1453	1453
Min	1	0.9	0	0.9	0.281	-1.69	-2.266	-1.926	-2.106	-3.057
Max	1085.333	166.167	28.917	150	55.852	1.434	2.606	2.486	3.722	2.943
Mean	295.812	68.915	0.756	68.159	25.38	-0.66	-0.045	0.338	0.369	-1.336
SD	183.381	33.034	2.955	32.05	12.312	0.422	1.109	0.961	0.859	0.839

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	1453	1453	1453	1453	1453	1453	1453	1453	1453	1453
Min	-2.972	-2.012	1	-26.667	60	-240	0	8	19	8
Max	2.308	0.624	38	5448.917	7890	4880	7740	169	291	187
Mean	0.375	-0.053	16.616	672.196	1711.418	287.564	1423.854	93.588	202.719	142.975
SD	1.337	0.243	7.389	930.238	1595.431	652.242	1268.721	27.228	68.97	30.335

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	1453	1453	1453	1453	1453	1453	1453	1453	1453	1453
Min	0	1	1	0.039	24	-26.07	1.536	35.462	15.462	0
Max	179	13	9	1	80	188.095	7.412	1433.667	200.625	52
Mean	108.382	6.192	1.963	0.889	48.6	68.727	2.357	612.316	119.631	4.3
SD	40.841	2.602	1.059	0.23	13.306	46.693	0.831	321.65	37.375	8.99

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	1453	1453	1453	1453	1453	1453	1453	1453	1453	1453
Min	15.462	5.899	0.083	0.083	0	0.083	0.024	0.083	0.083	0
Max	195.875	72.889	2689.625	466.625	119	362.687	116.788	2689.625	466.625	119
Mean	115.331	44.469	497.903	78.778	17.695	61.083	20.706	394.376	78.027	5.19
SD	33.141	12.286	366.861	53.841	20.475	46.277	15.982	355.385	54.004	16.878

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	1453	1453	1453	1453	1453	1453	1453	1453	1453	1453
Min	0.083	0.024	95	256.942	274.288	221.267	4.517	1.789	0	0
Max	362.687	116.788	3750	300.415	310.783	293.658	70.383	25.59	1330.6	199.437
Mean	72.837	27.017	825.06	279.225	294.021	264.036	29.985	11.073	316.505	71.113
SD	47.833	16.83	626.56	10.514	6.919	15.121	11.269	4.19	367.817	62.125

	WDMIN	WDRNG	WDSTD
n	1453	1453	1453
Min	-11.5	0	0
Max	34.571	199.437	81.724
Mean	1.541	69.572	26.107
SD	5.65	60.035	23.389

Region: Ethiopian

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	765	765	765	765	765	765	765	765	765	765
Min	7.083	2.75	0	2.75	1.066	-1.103	-1.754	-2.323	-2.141	-1.576
Max	1611.417	181	121.083	162.5	68.383	5.231	1.954	1.175	6.155	5.28
Mean	685.835	109.17	13.373	95.798	36.106	0.68	0.212	-0.515	-0.492	0.865
SD	424.2	43.14	23.477	40.942	17.898	0.933	0.644	0.729	0.794	1.33

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	765	765	765	765	765	765	765	765	765	765
Min	-4.168	-2.408	1	2.188	60	-150	30	52	129	129
Max	2.086	0.982	21	2278.854	5880	1430	5270	170	291	208
Mean	-1.303	0.072	11.111	651.352	1348.379	341.242	1007.137	131.029	249.689	186.701
SD	1.26	0.377	4.817	441.665	904.32	325.179	880.674	32.201	42.062	18.323

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	765	765	765	765	765	765	765	765	765	765
Min	0	7	1	0.025	-34	-17.442	1.414	837	106.75	2.583
Max	190	14	6	1	24	58.134	1.726	1778.583	200.583	131.833
Mean	150.4	11.294	1.607	0.933	2.51	22.016	1.467	1436.208	152.959	82.902
SD	52.891	1.988	0.771	0.184	15.071	16.536	0.054	166.251	13.552	29.145

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	765	765	765	765	765	765	765	765	765	765
Min	20.083	6.091	7.083	2.75	0	2.75	1.066	7.083	2.75	0
Max	170	61.995	3883.833	916.833	129.25	911.667	328.939	3883.833	916.833	129.25
Mean	70.058	23.624	888.269	180.186	9.835	170.351	61.042	888.269	180.186	9.835
SD	33.741	12.768	666.441	117.657	18.482	113.545	41.562	666.441	117.657	18.482

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	765	765	765	765	765	765	765	765	765	765
Min	2.75	1.066	100	287.776	288.733	280.742	0.625	0.189	3.417	2.417
Max	911.667	328.939	4000	302.859	311.083	300.4	20.758	7.436	1706.167	179.75
Mean	170.351	61.042	1583.667	297.496	300.727	293.618	7.109	2.504	750.373	122.216
SD	113.545	41.562	1046.238	3.337	4.057	4.053	4.228	1.584	387.226	34.802

	WDMIN	WDRNG	WDSTD
n	765	765	765
Min	-15	2.417	0.726
Max	111.5	174.5	68.463
Mean	15.367	106.849	38.583
SD	24.107	34.44	13.507

Region: Oriental

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	284	284	284	284	284	284	284	284	284	284
Min	139.75	46.75	0.6	16.583	5.827	-0.782	-1.936	-2.146	-1.888	-0.776
Max	1905.667	193.75	139.667	157.75	58.993	6.277	1.87	1.761	7.563	6.615
Mean	1083.325	141.891	44.474	97.417	35.909	1.362	0.036	0.02	0.764	2.532
SD	387.355	18.666	44.927	39.602	16.115	1.026	1.098	1.075	1.397	1.603

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	284	284	284	284	284	284	284	284	284	284
Min	-2.622	-3.795	4	2.778	60	-60	60	115	174	124
Max	2.163	0.977	41	4254.083	8840	1980	8780	190	292	217
Mean	0.186	-0.17	17.56	466.517	2010.035	104.859	1905.176	167.842	269.18	199.391
SD	1.116	0.612	7.175	664.839	1519.34	250.883	1432.896	14.076	17.488	16.48

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	284	284	284	284	284	284	284	284	284	284
Min	0	4	1	0.042	-8	67.352	1.414	743.083	107.583	12.167
Max	210	14	9	1	34	124.982	1.686	1914.25	190.5	139.667
Mean	166.746	12.926	1.993	0.801	17.141	95.609	1.499	1428.929	159.99	80.135
SD	56.479	1.51	1.125	0.29	10.178	15.367	0.066	210.243	17.392	32.258

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	284	284	284	284	284	284	284	284	284	284
Min	16.583	5.835	139.75	46.75	0.667	45.917	15.511	139.75	46.75	0
Max	155.75	56.991	4958.833	1102.75	242.5	1094.417	445.717	4958.833	1102.75	242.5
Mean	79.855	26.402	1872.964	346.913	42.98	303.933	110.82	1872.896	346.913	42.967
SD	35.219	12.406	887.689	149.868	60.024	160.273	61.984	887.774	149.868	60.033

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	284	284	284	284	284	284	284	284	284	284
Min	45.917	15.511	458	279.335	288.192	269.258	0.642	0.198	0	0
Max	1094.417	445.717	5000	301.853	308.869	300.408	22.258	8.077	1137.417	178.75
Mean	303.946	110.826	2964.887	297.762	301.767	292.98	8.787	3.056	345.604	84.492
SD	160.262	61.979	1180.789	3.418	3.452	5.801	6.064	2.181	303.28	60.949

	WDMIN	WDRNG	WDSTD
n	284	284	284
Min	-23.5	0	0
Max	32.583	178.75	66.233
Mean	0.307	84.185	30.555
SD	4.437	60.117	22.052

Region: Australian

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	304	304	304	304	304	304	304	304	304	304
Min	145.583	18.667	0	9.333	3.089	-1.247	-1.776	-2.044	-3.086	-1.156
Max	1805.571	185.75	134.25	184	72.16	2.575	2.293	1.427	1.054	6.182
Mean	637.619	98.183	22.665	75.517	26.551	-0.079	0.783	-0.391	-0.413	0.658
SD	467.032	53.344	38.296	50.751	19.894	0.918	0.979	0.904	0.804	1.798

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	304	304	304	304	304	304	304	304	304	304
Min	-2.868	-3.064	4	0	30	-30	30	82	202	94
Max	2.984	0.917	19	1273.333	5030	490	5030	187	291	206
Mean	-0.984	-0.02	9.891	273.05	1015.559	98.125	917.434	122.743	260.362	155.671
SD	1.354	0.384	3.589	211.851	1045.025	133.533	1081.564	33.858	23.369	26.753

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	304	304	304	304	304	304	304	304	304	304
Min	0	7	1	0.021	-44	113.357	1.414	550.25	105	0
Max	196	14	5	1	2	174.852	2	2030	206.083	138
Mean	146.671	10.655	1.589	0.82	-21.993	135.184	1.571	1310.966	170.084	48.496
SD	30.636	2.11	0.766	0.29	10.348	12.694	0.122	323.487	19.427	39.772

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	304	304	304	304	304	304	304	304	304	304
Min	24	7.977	145.583	18.667	0.5	8.417	2.674	145.583	18.667	0.5
Max	174.833	63.292	4045.5	492.667	279.833	428.75	165.994	4045.5	492.667	279.833
Mean	121.588	43.442	906.235	141.337	35.506	105.831	36.921	906.235	141.337	35.506
SD	39.299	14.862	891.753	116.371	55.165	94.791	34.96	891.753	116.371	55.165

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	304	304	304	304	304	304	304	304	304	304
Min	8.417	2.674	145	283.108	287.481	276.781	0.633	0.19	0	0
Max	428.75	165.994	5000	302.209	305.942	300.412	18.2	6.701	1280.5	189.4
Mean	105.831	36.921	1516.901	295.085	300.101	289.175	10.926	4.036	673.347	117.333
SD	94.791	34.96	1292.388	4.567	4.124	5.995	5.361	2.006	387.226	56.247

	WDMIN	WDRNG	WDSTD
n	304	304	304
Min	0	0	0
Max	50	189.4	74.661
Mean	6.144	111.189	39.933
SD	11.23	53.463	19.468

Region: Nearctic Zone: 1

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	17	17	17	17	17	17	17	17	17	17
Min	274.25	66.667	0	60.2	21.227	-0.648	-0.382	-0.663	-0.811	-0.826
Max	462.5	101.5	7	101.5	34.768	1.166	2.513	0.626	0.976	0.81
Mean	362.829	83.273	1.183	82.09	28.472	0.13	1.2	0.061	0.299	-0.263
SD	60.617	9.763	1.876	10.927	3.919	0.553	0.771	0.402	0.492	0.573

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	17	17	17	17	17	17	17	17	17	17
Min	-1.402	-1.629	17	28.667	640	-60	640	93	261	99
Max	1.685	0.014	34	1773.561	4390	60	4330	140	276	178
Mean	0.036	-0.562	27.412	545.47	2630	5.294	2624.706	118.412	273	134.824
SD	1.079	0.484	4.9	459.792	1047.598	26.485	1037.377	14.448	3.518	26.156

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	17	17	17	17	17	17	17	17	17	17
Min	98	7	1	0.107	34	-126.11	1.686	485.067	102	0
Max	140	12	7	1	52	-117.609	2.247	1107.667	196.437	17
Mean	120.353	8.706	3.059	0.763	41.765	-122.678	1.891	834.741	146.94	4.194
SD	12.273	1.532	1.638	0.302	5.826	2.52	0.178	208.047	25.069	5.669

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	17	17	17	17	17	17	17	17	17	17
Min	102	41.328	315.083	62.75	0.083	62	25.092	315.083	62.75	0
Max	192	70.79	2047.313	332.875	52.375	290.312	108.846	2047.313	332.875	46.313
Mean	142.746	53.364	969.659	170.5	12.695	157.805	57.547	945.086	169.746	9.614
SD	22.346	7.37	572.9	88.224	16.352	79.336	27.776	571.297	88.204	12.998

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	17	17	17	17	17	17	17	17	17	17
Min	62	25.092	1053	280.077	288.725	270.644	6.3	2.309	113.733	43.333
Max	290.312	108.846	2000	289.418	298.542	286.2	19.312	6.899	833.417	191.187
Mean	160.132	57.97	1679.471	285.638	292.845	278.87	13.975	5.038	471.912	125.808
SD	78.934	27.632	345.505	2.848	3.303	3.895	4.097	1.434	260.95	43.94

	WDMIN	WDRNG	WDSTD
n	17	17	17
Min	0	43.333	15.101
Max	0	191.187	75.439
Mean	0	125.808	48.442
SD	0	43.94	18.86

Region: Nearctic Zone: 2

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	117	117	117	117	117	117	117	117	117	117
Min	128	22	0	19.286	6.169	-1.271	-0.434	-1.836	-1.273	-1.623
Max	717.5	159.833	25.125	153.75	53.446	0.739	2.058	1.741	0.954	0.469
Mean	386.63	79.952	2.823	77.129	26.74	-0.629	1.068	0.261	-0.006	-0.915
SD	123.484	25.005	4.677	25.387	9.418	0.361	0.523	0.724	0.434	0.467

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	117	117	117	117	117	117	117	117	117	117
Min	-1.966	-0.187	9	24.25	610	0	330	77	216	103
Max	1.053	0.46	25	2949.091	4390	1980	3970	173	287	192
Mean	-0.4	0.15	17.376	1236.703	2525.299	690	1835.299	123.325	263.991	159.085
SD	0.76	0.147	3.612	646.187	1140.075	469.668	931.103	23.09	15.06	22.208

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	117	117	117	117	117	117	117	117	117	117
Min	77	4	1	0.187	24	-120.056	1.536	456.5	114.8	0
Max	189	12	5	1	54	-100.315	2.35	1327.083	188.375	44
Mean	138.077	7.88	2.248	0.938	38.701	-109.095	1.821	888.138	156.915	7.661
SD	29.396	2.213	1.09	0.182	7.345	4.901	0.191	200.882	16.759	11.514

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	117	117	117	117	117	117	117	117	117	117
Min	83	31.308	119	20.125	0.083	8.667	3.296	119	20.125	0
Max	180.083	68.606	721.25	194.083	33.5	193.333	63.964	721.25	194.083	29.812
Mean	149.254	55.889	406.67	71.233	13.37	57.862	19.289	353.557	70.732	4.112
SD	21.397	8.214	127.652	30.22	7.4	31.737	10.949	131.05	30.574	6.88

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	117	117	117	117	117	117	117	117	117	117
Min	15.813	4.586	443	273.804	288.358	254.325	4.969	1.872	91.9	36.3
Max	193.333	63.964	2000	297.44	305.7	292.658	35.92	13.079	970.571	174.562
Mean	66.62	23.051	1279.966	285.073	296.493	273.699	22.795	8.315	501.507	118.789
SD	29.895	10.025	366.451	6.297	3.882	9.267	6.464	2.267	216.794	31.771

	WDMIN	WDRNG	WDSTD
n	117	117	117
Min	-0.667	36.3	12.579
Max	17.667	174.562	64.5
Mean	0.771	118.018	42.403
SD	2.61	31.783	11.651

Region: Nearctic Zone: 3

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	112	112	112	112	112	112	112	112	112	112
Min	474.187	95.875	0	95.875	37.925	-0.666	-1.026	0.649	-2.429	-0.847
Max	1261.5	167.25	44.273	151.778	56.672	0.525	1.085	2.521	-0.413	2.245
Mean	808.392	136.541	6.756	129.785	48.818	-0.281	0.128	1.675	-1.451	0.532
SD	193.637	17.199	10.077	13.508	4.525	0.21	0.395	0.425	0.444	0.798

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	112	112	112	112	112	112	112	112	112	112
Min	0.051	-0.374	10	0	0	0	0	100	255	119
Max	1.528	0.792	29	637.424	2130	300	2010	168	289	179
Mean	0.981	0.229	19.705	188.699	552.679	59.196	493.482	132.42	276.661	157.545
SD	0.27	0.23	4.529	146.092	456.431	78.029	436.222	17.833	7.107	17.064

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	112	112	112	112	112	112	112	112	112	112
Min	101	7	1	0.036	28	-98	1.587	474.187	95.875	0
Max	176	13	4	1	48	-61.803	2.074	1355.286	179.5	45.273
Mean	142.062	9.768	1.437	0.848	39.036	-85.361	1.812	876.485	152.117	6.771
SD	18.153	2.613	0.626	0.252	5.233	8.701	0.129	215.356	18.023	10.134

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	112	112	112	112	112	112	112	112	112	112
Min	95.875	37.925	670.687	83.188	22.937	12.188	3.976	523.937	83.188	0
Max	168.25	63.078	1627.75	222.083	101.583	174.417	66.33	1627.75	222.083	101.583
Mean	145.346	55.159	1202.405	137.508	69.976	67.532	21.809	1083.226	136.848	38.549
SD	15.262	5.458	200.013	29.147	16.282	33.455	11.622	291.588	29.187	37.649

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	112	112	112	112	112	112	112	112	112	112
Min	34.5	11.346	778	276.417	289.9	260.669	9.633	3.693	0	0
Max	174.417	66.33	2000	296.265	302.275	291.225	33.463	12.294	285.75	98.167
Mean	98.3	34.396	1311.545	286.136	297.334	274.472	22.862	8.607	68.093	30.052
SD	30.236	12.977	313.785	5.078	3.105	7.478	5.167	1.805	51.245	18.854

	WDMIN	WDRNG	WDSTD
n	112	112	112
Min	-10.313	0	0
Max	0	98.167	38.089
Mean	-0.36	30.412	10.485
SD	1.511	18.856	6.871

Region: Nearctic **Zone: 4**

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	356	356	356	356	356	356	356	356	356	356
Min	34.25	14.75	0	14.75	5.486	-1.204	-2.341	-1.512	-1.382	-3.259
Max	563	111.5	0	111.5	44.982	1.654	0.48	1.685	1.935	1.426
Mean	229.341	59.639	0	59.639	23.446	-0.667	-1.198	0.255	0.445	-2.073
SD	112.162	22.702	0	22.702	8.994	0.367	0.482	0.675	0.619	0.779

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	356	356	356	356	356	356	356	356	356	356
Min	0.645	-2.809	2	0.889	60	-120	0	14	16	16
Max	2.752	0.261	26	1972.949	6190	790	6100	107	273	157
Mean	1.526	-0.092	10.677	371.325	1181.039	91.882	1089.157	49.045	133.169	70.865
SD	0.272	0.355	5.536	360.323	1048.413	159.537	1012.621	21.878	74.567	31.033

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	356	356	356	356	356	356	356	356	356	356
Min	16	1	1	0.042	48	-168.161	2.074	34.25	14.75	0
Max	113	7	4	1	80	-21.541	7.412	600.5	134.5	0
Mean	66.919	3.16	1.649	0.767	63.039	-103.889	3.31	271.863	76.496	0
SD	26.255	1.603	0.782	0.294	7.833	31.858	1.1	122.743	25.541	0

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	356	356	356	356	356	356	356	356	356	356
Min	14.75	5.486	105.769	24.167	1.583	20.083	6.801	42	18.596	0
Max	134.5	51.61	3106.7	448.75	121.15	345.45	107.995	2889.25	448.75	121.15
Mean	76.496	29.116	521.19	75.648	21.455	54.194	18.293	315.823	74.34	1.041
SD	25.541	10.18	433.554	54.194	21.235	37.244	12.737	333.863	52.854	9.951

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	356	356	356	356	356	356	356	356	356	356
Min	18.596	6.823	91	254.055	275.425	236.719	8.79	3.169	0	0
Max	448.75	131.299	1000	281.316	292.02	275.08	45.563	17.356	243.75	89.4
Mean	73.299	28.909	278.61	267.528	284.497	250.239	34.259	12.746	42.522	19.78
SD	49.122	17.978	197.26	6.198	4.419	8.635	8.109	3.066	42.935	17.026

	WDMIN	WDRNG	WDSTD
n	356	356	356
Min	0	0	0
Max	0	89.4	30.992
Mean	0	19.78	6.691
SD	0	17.026	5.944

Region: Neotropic Zone: 1

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	141	141	141	141	141	141	141	141	141	141
Min	5.667	1.667	0	1.667	0.607	-1.064	-1.178	-2.232	-3.291	-1.798
Max	1237	150	62.833	132	48.389	1.053	1.937	1.45	0.83	2.478
Mean	495.236	82.583	6.657	75.926	28.043	-0.28	0.287	-0.248	-1.036	-0.285
SD	305.701	40.41	9.933	35.066	13.435	0.496	0.638	0.969	0.795	1.053

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	141	141	141	141	141	141	141	141	141	141
Min	-2.263	-2.67	4	3.5	60	-30	60	57	156	72
Max	2.731	0.69	26	4351.944	7070	3660	6800	178	290	220
Mean	-0.044	0.009	15.553	988.68	2617.943	210.496	2407.447	129.809	261.305	194.475
SD	1.05	0.505	5.637	1246.906	2311.546	511.034	2150.076	31.989	26.934	26.587

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	141	141	141	141	141	141	141	141	141	141
Min	67	1	1	0.069	-54	-82.047	1.42	356.875	82	0
Max	193	14	6	1	-4	-51.31	2.466	1447.125	182.583	85.625
Mean	170.199	8.922	2.745	0.843	-30.922	-68.197	1.73	886.17	139.473	18.651
SD	30.564	2.962	1.451	0.251	11.656	6.064	0.238	255.271	24.18	22.291

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	141	141	141	141	141	141	141	141	141	141
Min	45.25	13.305	6.25	1.583	0	1.583	0.557	6.25	1.583	0
Max	167.833	61.388	2973.75	346.25	211.85	293.333	109.938	2973.75	346.25	211.85
Mean	120.822	44.087	725.249	103.294	29.146	74.147	26.32	725.249	103.294	29.146
SD	32.399	12.378	569.922	74.869	34.474	60.458	22.613	569.922	74.869	34.474

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	141	141	141	141	141	141	141	141	141	141
Min	1.583	0.557	100	278.723	282.115	273.456	2.358	0.754	0.25	0.25
Max	293.333	109.938	5000	297.09	301.633	294.208	17.5	6.352	1110.083	176.083
Mean	74.147	26.32	1167.681	287.769	293.05	282.437	10.613	3.899	390.935	77.382
SD	60.458	22.613	1079.389	4.281	4.99	4.514	4.116	1.507	314.613	41.274

	WDMIN	WDRNG	WDSTD
n	141	141	141
Min	-0.187	0.25	0.072
Max	63.5	176.083	67.405
Mean	6.99	70.393	25.191
SD	14.982	38.23	14.288

Region: Neotropic Zone: 2

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	362	362	362	362	362	362	362	362	362	362
Min	661.583	98.333	4	18.583	4.647	-0.174	-1.847	-2.27	-2.643	0.508
Max	1751.333	173.75	125	156.083	59.308	2.919	1.191	1.294	2.956	7.851
Mean	1265.886	141.6	55.104	86.495	31.142	1.177	-0.474	-0.679	-0.108	2.901
SD	217.729	12.482	35.066	34.797	14.811	0.637	0.629	0.767	0.975	1.128

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	362	362	362	362	362	362	362	362	362	362
Min	-1.434	-3.621	4	0	0	0	0	153	180	180
Max	3.262	1.358	30	1847.593	5790	670	5760	191	290	225
Mean	0.483	0.118	15.008	321.389	1039.254	120.884	918.37	169.82	266.961	210.928
SD	0.714	0.517	4.372	298.807	1061.259	125.172	1055.791	8.224	15.305	5.122

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	362	362	362	362	362	362	362	362	362	362
Min	162	10	1	0.083	-26	-80.99	1.414	1108.667	118.75	31.5
Max	205	14	6	1	12	-36.092	1.587	1829	193.083	129.667
Mean	200.199	13.298	1.657	0.94	-5.834	-58.072	1.445	1488.851	148.13	96.35
SD	6.331	0.706	0.811	0.176	9.475	10.807	0.04	152.571	12.833	24.526

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	362	362	362	362	362	362	362	362	362	362
Min	17.333	5.447	664.583	98.5	0.667	62.667	18.264	664.583	98.5	0.667
Max	133.417	48.295	5668.917	593.583	353	542.667	188.747	5668.917	593.583	353
Mean	51.78	17.175	1964.693	298.415	52.194	246.22	87.647	1964.693	298.415	52.194
SD	25.724	9.609	676.808	89.524	50.271	90.291	32.896	676.808	89.524	50.271

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	362	362	362	362	362	362	362	362	362	362
Min	62.667	18.264	907	289.508	290.758	284.808	0.45	0.145	0	0
Max	542.667	188.747	5000	301.036	302.35	300.5	10.492	3.906	814.5	152
Mean	246.22	87.647	2502.812	297.658	298.985	295.927	3.058	1.061	222.965	67.299
SD	90.291	32.896	1098.299	2.216	1.894	3.189	2.139	0.803	174.286	41.876

	WDMIN	WDRNG	WDSTD
n	362	362	362
Min	-11	0	0
Max	12.333	152	62.107
Mean	-0.065	67.364	24.8
SD	1.294	41.803	16.252

Region: Neotropic Zone: 3

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	43	43	43	43	43	43	43	43	43	43
Min	625	94.25	2	40.571	11.248	-0.076	-0.988	-1.422	-1.248	0.105
Max	1455.5	160.5	104.286	153.25	62.149	2.824	0.917	0.515	2.295	4.723
Mean	1113.228	142.897	40.164	102.733	37.54	1.356	0.135	-0.304	0.162	2.428
SD	258.706	15.256	29.153	27.584	12.661	0.626	0.456	0.452	0.841	1.328

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	43	43	43	43	43	43	43	43	43	43
Min	-1.058	-1.231	11	3.889	60	0	60	179	210	206
Max	1.709	1	29	1898.981	4270	300	4270	196	291	224
Mean	0.145	0.03	21.023	478.531	2196.047	18.14	2177.907	191.023	270.767	214.116
SD	0.697	0.54	3.955	475.457	1314.974	64.189	1306.365	3.412	16.798	4.604

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	43	43	43	43	43	43	43	43	43	43
Min	187	12	1	0.146	10	-106.255	1.432	1009.583	119.143	30.417
Max	202	14	5	1	26	-79.771	1.56	1721.667	181	117
Mean	194.907	13.256	2.512	0.716	17.814	-92.643	1.482	1443.801	151.509	84.342
SD	3.715	0.819	0.985	0.268	4.316	7.376	0.034	173.709	10.866	22.522

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	43	43	43	43	43	43	43	43	43	43
Min	45	13.729	652.917	136.833	0.417	115.667	35.08	652.917	136.833	0.417
Max	113	40.962	3331	514.917	107.25	480.833	193.175	3331	514.917	107.25
Mean	67.167	23.814	1755.908	302.848	29.17	273.678	99.753	1755.908	302.848	29.17
SD	18.205	7.048	765.67	96.989	25.542	87.983	34.197	765.67	96.989	25.542

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	43	43	43	43	43	43	43	43	43	43
Min	115.667	35.08	1250	291.172	295.383	285.758	1.158	0.388	58.571	38.571
Max	480.833	193.175	5000	300.582	302.408	299.587	12.875	4.856	666.75	150
Mean	273.678	99.753	3126.163	297.502	299.539	295.042	4.497	1.603	330.573	98.987
SD	87.983	34.197	1160.738	1.964	1.603	3.137	2.798	1.068	160.28	27.856

	WDMIN	WDRNG	WDSTD
n	43	43	43
Min	-12	38.571	11.488
Max	0.6	150	60.826
Mean	-0.378	99.364	36.201
SD	1.919	27.605	11.756

Region: Neotropic Zone: 4

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	7	7	7	7	7	7	7	7	7	7
Min	1204.5	151	44.125	91.5	30.551	0.445	-0.208	-0.457	-1.375	1.931
Max	1291	172	68.5	125	49.507	0.873	0.364	0.23	-0.718	2.4
Mean	1248.958	159.143	52.685	106.458	41.691	0.671	0.055	-0.045	-1.068	2.167
SD	25.892	6.81	8.091	11.805	6.263	0.159	0.21	0.227	0.24	0.167

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	7	7	7	7	7	7	7	7	7	7
Min	-0.405	0.578	8	13.333	670	0	670	167	196	196
Max	0.327	1.069	9	87.315	1710	0	1710	169	272	215
Mean	0.051	0.815	8.571	37.989	1071.429	0	1071.429	167.571	242.571	208.857
SD	0.269	0.195	0.535	28.889	334.087	0	334.087	0.976	32.243	8.194

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	7	7	7	7	7	7	7	7	7	7
Min	167	12	1	0.167	22	-83.21	1.515	1360	151	61
Max	169	13	2	0.604	24	-75.477	1.536	1568	165	80.5
Mean	167.571	12.429	1.571	0.376	22.857	-79.431	1.524	1469.292	158.464	70.042
SD	0.976	0.535	0.535	0.174	1.069	2.665	0.012	76.477	5.244	7.035

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	7	7	7	7	7	7	7	7	7	7
Min	83	30.427	1093.333	171.333	21.5	139.417	41.488	1093.333	171.333	21.5
Max	92.5	34.743	1564.917	245.75	46.667	210.667	82.779	1564.917	245.75	46.667
Mean	88.423	32.777	1355.726	206.857	34.94	171.917	66.738	1355.726	206.857	34.94
SD	3.775	1.652	168.382	23.83	8.536	25.563	15.537	168.382	23.83	8.536

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	7	7	7	7	7	7	7	7	7	7
Min	139.417	41.488	3000	298.558	301.083	295.433	4.208	1.556	142	49.5
Max	210.667	82.779	3000	299.544	301.783	297.358	5.65	2.059	326.5	82.5
Mean	171.917	66.738	3000	299.058	301.373	296.265	5.107	1.84	220.333	68.405
SD	25.563	15.537	0	0.387	0.236	0.727	0.556	0.198	62.159	12.623

	WDMIN	WDRNG	WDSTD
n	7	7	7
Min	-8	49.5	18.812
Max	0	87	29.918
Mean	-2.143	70.548	25.063
SD	3.671	14.851	4.547

Region: Palearctic Zone: 1

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	269	269	269	269	269	269	269	269	269	269
Min	56.583	21.25	0	21.25	8.284	-1.03	-2.007	-1.554	-2.106	-2.64
Max	567.187	113.25	0	113.25	45.781	0.406	0.525	1.272	0.733	0.532
Mean	346.397	80.391	0	80.391	32.418	-0.468	-0.785	0.386	-0.689	-1.236
SD	102.047	16.402	0	16.402	6.909	0.231	0.503	0.586	0.572	0.54

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	269	269	269	269	269	269	269	269	269	269
Min	0.189	-2.012	9	0.179	60	-30	60	17	72	71
Max	2.308	0.283	35	1085.625	4570	300	4450	122	279	186
Mean	1.23	-0.104	19.781	173.046	686.431	44.387	642.045	91.796	230.364	156.059
SD	0.321	0.34	4.417	161.307	651.932	54.273	644.877	20.68	51.597	22.71

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	269	269	269	269	269	269	269	269	269	269
Min	19	1	1	0.039	46	-26.07	2	62.083	25.167	0
Max	124	9	3	1	80	61.634	7.412	661.375	140.875	0
Mean	106.349	5.922	1.662	0.838	57.814	26.775	2.727	396.16	95.361	0
SD	19.709	1.571	0.63	0.268	7.089	19.339	0.685	132.747	24.021	0

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	269	269	269	269	269	269	269	269	269	269
Min	25.167	9.171	338.521	45	9.333	16.687	5.634	78.292	32.208	0
Max	140.875	56.468	2196.25	271.15	98.063	179.65	58.247	2196.25	271.15	97.333
Mean	95.361	38.071	754.026	89.263	41.386	47.877	15.871	556.048	88.401	10.276
SD	24.021	9.826	267.737	31.03	15.491	20.377	7.508	316.159	31.88	23.923

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	269	269	269	269	269	269	269	269	269	269
Min	19.187	6.717	95	266.737	278.066	251.804	7.195	2.747	0	0
Max	189.321	63.215	2000	286.136	298.144	280.505	38.075	14.158	317.25	96.188
Mean	78.125	30.417	680.822	277.733	289.906	266.08	23.826	8.758	49.763	19.359
SD	25.587	9.465	356.442	4.042	3.676	6.666	7.476	2.678	64.353	20.661

	WDMIN	WDRNG	WDSTD
n	269	269	269
Min	-2.8	0	0
Max	0	96.188	36.068
Mean	-0.011	19.37	6.976
SD	0.171	20.655	7.83

Region: Palearctic Zone: 2

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	332	332	332	332	332	332	332	332	332	332
Min	1	0.9	0	0.9	0.281	-1.363	-0.46	-1.926	-2.097	-1.438
Max	644	128	11.313	128	49.507	0.473	2.606	1.462	1.724	0.668
Mean	213.891	44.777	1.01	43.767	14.929	-0.813	1.397	-0.671	0.493	-0.82
SD	174.192	34.543	1.946	33.867	11.592	0.388	0.507	0.819	0.594	0.446

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	332	332	332	332	332	332	332	332	332	332
Min	-2.972	-0.679	1	9	120	-120	120	50	176	108
Max	1.444	0.376	36	2557.833	5580	1370	4970	128	286	187
Mean	-1.559	-0.206	12.714	605.006	1740.241	217.38	1522.861	103.901	246.003	154.361
SD	1.026	0.147	8.9	497.983	1215.014	270.186	1150.417	18.921	31.825	13.578

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	332	332	332	332	332	332	332	332	332	332
Min	92	6	1	0.089	24	-14.93	1.536	642	118	0
Max	150	13	7	1	46	69.566	2	1433.667	200.625	52
Mean	137.979	8.81	1.834	0.862	32.988	23.844	1.681	1067.327	166.125	16.194
SD	8.176	1.426	1.219	0.245	5.36	21.872	0.107	152.156	14.284	11.567

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	332	332	332	332	332	332	332	332	332	332
Min	88	32.723	0.083	0.083	0	0.083	0.024	0.083	0.083	0
Max	195.875	72.889	1484.375	217.625	93.938	207.437	74.2	1484.375	217.625	93.938
Mean	149.931	55.479	315.37	52.63	5.57	47.06	16.536	311.084	52.445	4.945
SD	18.349	6.78	337.972	49.095	13.352	42.975	15.338	334.411	49.01	12.657

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	332	332	332	332	332	332	332	332	332	332
Min	0.083	0.024	100	280.492	292.156	265.894	4.517	1.789	9	4.692
Max	207.437	74.2	2000	300.415	310.783	293.658	30.788	10.517	1330.6	199.437
Mean	47.5	16.703	1005.304	292.823	302.236	282.929	19.308	7.128	853.436	156.881
SD	43.419	15.474	718.871	4.19	4.25	4.703	4.428	1.608	297.803	27.791

	WDMIN	WDRNG	WDSTD
n	332	332	332
Min	-0.75	4.692	1.765
Max	34.571	199.437	81.724
Mean	6.924	149.958	56.969
SD	10.06	28.457	11.961

Region: Palearctic Zone: 3

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	605	605	605	605	605	605	605	605	605	605
Min	17.437	6.937	0	6.937	2.059	-1.69	-2.266	-1.407	-0.626	-3.057
Max	483.125	117.25	2.583	117.25	42.499	0.074	2.233	2.013	3.722	-0.77
Mean	224.411	61.851	0.037	61.815	22.992	-0.845	-0.511	0.497	0.888	-1.985
SD	95.956	22.691	0.241	22.678	9.069	0.297	0.931	0.731	0.636	0.451

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	605	605	605	605	605	605	605	605	605	605
Min	-1.433	-0.44	3	-21.346	60	-240	0	8	19	8
Max	2.052	0.268	31	5448.917	7890	4880	7740	138	274	175
Mean	0.895	0.001	15.046	881.012	1947.091	415.372	1531.719	77.514	146.094	122.929
SD	0.873	0.126	6.001	1152.11	1873.052	839.674	1423.801	23.946	58.058	32.703

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	605	605	605	605	605	605	605	605	605	605
Min	8	1	1	0.075	32	50	1.65	35.462	15.462	0
Max	152	12	9	1	80	188.095	7.412	1073.938	187.562	7.333
Mean	105.873	4.405	2.058	0.935	55.577	101.285	2.729	423.83	101.122	0.094
SD	24.24	2.045	1.077	0.188	11.188	30.432	0.933	199.425	30.805	0.606

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	605	605	605	605	605	605	605	605	605	605
Min	15.462	5.899	17.437	6.937	0	4.812	1.594	16.312	6.937	0
Max	184.187	70.211	1245.125	168.344	49.625	167.25	55.379	843.312	168.344	17.187
Mean	101.028	39.51	361.476	62.905	10.712	52.192	17.498	231.213	61.7	0.122
SD	30.692	12.444	184.144	29.279	9.402	27.838	9.897	115.88	29.038	1.195

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	605	605	605	605	605	605	605	605	605	605
Min	6.937	2.086	97	256.942	274.288	221.267	16.933	6.626	0	0
Max	168.344	65.251	3333	289.938	305.1	278.225	70.383	25.59	822.187	185.687
Mean	61.578	23.969	561.607	271.545	290.655	252.008	38.647	14.353	199.419	55.475
SD	29.193	11.806	487.109	8.362	5.891	11.526	9.317	3.476	215.875	46.667

	WDMIN	WDRNG	WDSTD
n	605	605	605
Min	-7.312	0	0
Max	1	185.687	75.863
Mean	-0.029	55.504	20.753
SD	0.414	46.674	18.518

Region: Palearctic Zone: 4

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	127	127	127	127	127	127	127	127	127	127
Min	216.437	58.375	0	58.375	18.852	-0.845	-1.059	0.186	-1.354	-1.565
Max	1085.333	166.167	28.917	150	55.852	1.434	0.968	2.486	1.576	2.943
Mean	657.877	124.739	5.315	119.425	43.467	0.069	-0.189	1.715	0.036	-0.065
SD	190.019	19.748	7.902	15.327	5.344	0.346	0.467	0.476	0.638	1.032

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	127	127	127	127	127	127	127	127	127	127
Min	-0.281	-1.139	11	7.955	60	0	60	99	239	148
Max	1.865	0.624	38	4406.417	7320	3200	4790	169	285	184
Mean	0.933	0.154	22.78	582.925	1959.843	198.898	1760.945	134.504	269.472	165.173
SD	0.491	0.362	4.175	737.209	1134.364	452.643	882.289	15.291	10.492	8.325

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	127	127	127	127	127	127	127	127	127	127
Min	116	1	1	0.187	28	97.956	1.587	470.45	95	0
Max	179	13	6	1	52	142.927	2.247	1085.833	166.167	28.917
Mean	149.677	8.22	2.063	0.846	38.976	120.875	1.815	761.217	131.294	5.445
SD	12.246	2.182	0.843	0.26	5.817	11.258	0.154	152.587	16.09	7.96

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	127	127	127	127	127	127	127	127	127	127
Min	95	40.421	216.437	58.375	0.375	57.375	18.688	212.125	58.375	0
Max	153.375	58.338	2689.625	466.625	119	362.687	100.322	2689.625	466.625	119
Mean	125.849	48.805	968.621	182.67	27.404	155.266	52.397	920.527	182.611	17.699
SD	12.194	3.884	516.933	63.793	31.184	51.091	16.338	525.799	63.813	31.832

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	127	127	127	127	127	127	127	127	127	127
Min	58.375	19.042	538	271.955	283.992	247.09	18.15	6.539	0	0
Max	362.687	108.362	2710	291.408	303.092	282.281	46.575	17.348	493.375	109.625
Mean	164.912	56.335	1533.78	283.222	297.549	267.39	30.159	10.929	103.341	33.434
SD	50.089	15.196	432.66	5.441	3.479	9.137	7.144	2.659	115.18	30.115

	WDMIN	WDRNG	WDSTD
n	127	127	127
Min	-11.5	0	0
Max	1.75	109.625	39.335
Mean	-0.316	33.75	11.785
SD	1.418	30.462	10.929

Region: Ethiopian Zone: 1

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	464	464	464	464	464	464	464	464	464	464
Min	7.083	2.75	0	2.75	1.066	-1.103	-1.633	-2.323	-1.823	-1.26
Max	1529.167	156.333	112.833	149.417	62.971	1.964	1.331	0.71	1.31	3.715
Mean	543.381	97.89	8.429	89.461	33.562	0.446	0.2	-0.689	-0.647	0.414
SD	393.698	45.223	18.024	43.163	18.701	0.802	0.568	0.709	0.516	1.075

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	464	464	464	464	464	464	464	464	464	464
Min	-4.168	-0.515	1	2.5	90	-150	30	52	129	129
Max	1.142	0.982	21	2278.854	5880	1310	5270	169	291	208
Mean	-1.783	0.034	10.386	725.03	1457.328	372.22	1085.108	119.67	235.828	182.983
SD	1.175	0.316	5.042	454.729	1002.108	322.118	982.188	35.644	47.952	20.271

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	464	464	464	464	464	464	464	464	464	464
Min	79	7	1	0.042	-20	-16.399	1.414	1022	106.75	40.083
Max	190	14	6	1	24	58.134	1.536	1778.583	183.833	131.833
Mean	169.42	10.718	1.591	0.947	7.185	26.468	1.459	1437.312	151.401	82.705
SD	17.9	2.041	0.783	0.161	12.804	15.837	0.033	141.707	12.219	23.589

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	464	464	464	464	464	464	464	464	464	464
Min	20.083	6.091	7.083	2.75	0	2.75	1.066	7.083	2.75	0
Max	120	45.556	2359.25	395	104.417	377.5	135.876	2359.25	395	104.417
Mean	68.695	23.376	643.671	141.453	5.704	135.749	49.131	643.671	141.453	5.704
SD	25.687	10.179	517.387	87.982	12.747	85.245	33.63	517.387	87.982	12.747

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	464	464	464	464	464	464	464	464	464	464
Min	2.75	1.066	100	287.776	288.733	286.108	0.625	0.223	31	10.083
Max	377.5	135.876	3000	302.859	311.083	300.4	20.758	7.436	1706.167	176.667
Mean	135.749	49.131	1250.849	297.935	301.41	293.657	7.753	2.722	893.931	131.615
SD	85.245	33.63	930.742	3.173	4.43	3.147	4.331	1.63	364.797	28.09

	WDMIN	WDRNG	WDSTD
n	464	464	464
Min	-15	10.083	3.408
Max	111.5	174.5	62.795
Mean	22.215	109.399	38.748
SD	27.47	31.061	11.885

Region: Ethiopian Zone: 2

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	134	134	134	134	134	134	134	134	134	134
Min	640.333	120	0.083	26.083	8.133	0.217	-1.754	-2.001	-1.302	0.915
Max	1611.417	168.167	121.083	142.833	61.045	5.231	1.006	0.818	6.155	5.28
Mean	1135.512	138.731	30.409	108.322	39.808	1.625	-0.198	-0.452	0.142	2.52
SD	236.225	7.599	31.753	28.991	13.941	0.749	0.612	0.541	1.257	0.836

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	134	134	134	134	134	134	134	134	134	134
Min	-1.996	-2.408	5	2.188	60	0	60	119	237	152
Max	2.086	0.962	20	1084.722	4080	790	4080	160	290	207
Mean	-0.081	0.088	12.463	376.291	923.358	198.433	724.925	148.522	271.425	190.709
SD	0.863	0.594	3.717	222.398	575.455	167.556	583.435	9.143	12.286	14.187

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	134	134	134	134	134	134	134	134	134	134
Min	120	12	1	0.025	-8	-17.442	1.414	1347.75	129.083	86.083
Max	174	14	3	1	14	21.094	1.451	1698.25	169.833	125.333
Mean	162.037	12.993	1.448	0.921	6.388	5.7	1.426	1525.458	148.726	109.282
SD	10.67	0.751	0.583	0.195	5.005	11.085	0.01	80.706	9.625	9.033

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	134	134	134	134	134	134	134	134	134	134
Min	23.5	7.731	777.5	186.25	0	115.167	36.871	777.5	186.25	0
Max	77.667	24.336	3883.833	916.833	129.25	911.667	328.939	3883.833	916.833	129.25
Mean	39.444	12.567	1726.696	313.411	21.199	292.212	101.248	1726.696	313.411	21.199
SD	11.264	3.383	567.601	122.976	26.855	126.357	44.859	567.601	122.976	26.855

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	134	134	134	134	134	134	134	134	134	134
Min	115.167	36.871	773	295.074	296.433	291.825	0.808	0.246	3.417	2.417
Max	911.667	328.939	4000	301.53	305.65	298.725	7.883	2.567	942.083	162.143
Mean	292.212	101.248	2316.59	298.723	300.565	297.039	3.526	1.179	389.945	97.351
SD	126.357	44.859	952.064	1.309	2.121	1.121	1.636	0.547	255.94	37.975

	WDMIN	WDRNG	WDSTD
n	134	134	134
Min	-0.167	2.417	0.726
Max	0	162.143	65.29
Mean	-0.001	97.352	38.025
SD	0.014	37.974	16.376

Region: Ethiopian Zone: 3

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	68	68	68	68	68	68	68	68	68	68
Min	53	14.6	0	10.857	3.513	-1.083	-0.194	-2.049	-2.141	-1.576
Max	1105.5	181	36.25	160.5	60.972	1.243	1.954	0.964	0.417	1.986
Mean	531.573	89.355	9.412	79.943	29.71	-0.237	0.813	-0.183	-0.797	-0.097
SD	305.993	45.376	7.965	39.776	16.192	0.591	0.548	0.813	0.666	0.897

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	68	68	68	68	68	68	68	68	68	68
Min	-2.392	-0.227	3	9.722	180	0	130	143	222	147
Max	0.644	0.74	20	1838.75	3470	1430	3020	161	289	207
Mean	-0.954	0.198	12.588	807.666	1671.765	438.088	1233.676	152.309	270.559	189.824
SD	0.74	0.289	5.437	524.897	733.774	456.568	716.738	3.767	14.245	13.498

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	68	68	68	68	68	68	68	68	68	68
Min	147	8	1	0.196	-34	13.491	1.479	837	112	2.583
Max	176	13	4	1	-16	38.867	1.726	1657.5	200.583	77
Mean	164.588	10.441	2	0.864	-26.029	24.24	1.594	1165.498	163.153	29.286
SD	6.372	1.832	0.993	0.258	4.168	6.278	0.059	196.827	18.271	18.451

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	68	68	68	68	68	68	68	68	68	68
Min	86.2	30.565	36.833	9.083	0	6.875	2.019	36.833	9.083	0
Max	170	61.995	1360.083	258.5	42.333	242.25	92.084	1360.083	258.5	42.333
Mean	133.868	47.466	555.448	95.743	11.422	84.321	31.808	555.448	95.743	11.422
SD	22.235	8.314	333.799	58.663	9.791	55.351	22.131	333.799	58.663	9.791

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	68	68	68	68	68	68	68	68	68	68
Min	6.875	2.019	100	288.048	292.533	280.742	4.95	1.953	65.833	13.667
Max	242.25	92.084	4000	299.146	301.125	296.175	16.108	5.843	1146.167	179.75
Mean	84.321	31.808	2201.485	292.147	296.95	286.159	10.791	3.983	633.925	111.398
SD	55.351	22.131	1240.22	2.681	2.452	3.725	3.395	1.235	259.492	38.066

	WDMIN	WDRNG	WDSTD
n	68	68	68
Min	0	13.667	4.663
Max	44.167	168.286	68.463
Mean	11.531	99.867	35.274
SD	12.975	38.11	14.802

Region: Ethiopian Zone: 4

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	21	21	21	21	21	21	21	21	21	21
Min	550.5	119.5	1.5	89.833	31.207	0.002	-0.407	-0.221	-1.864	-0.001
Max	1483.5	171.833	77.333	162.5	68.383	2.7	1.584	1.175	1.384	4.28
Mean	976.092	158.584	24.687	133.897	52.36	1.512	0.659	0.641	-0.076	1.923
SD	247.099	12.591	24.447	24.74	11.43	0.74	0.527	0.411	0.994	1.036

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	21	21	21	21	21	21	21	21	21	21
Min	-1.989	-0.485	11	3.611	90	0	90	166	264	188
Max	1.445	0.459	18	1176.759	2870	400	2870	170	288	207
Mean	-0.356	0.036	14.905	440.408	1524.762	40.476	1484.286	168.333	279.095	200.238
SD	0.932	0.301	1.947	392.102	820.613	93.567	784.229	1.197	6.84	5.347

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	21	21	21	21	21	21	21	21	21	21
Min	166	11	1	0.042	-24	42.68	1.451	1175.5	144.429	31.5
Max	170	14	4	1	-12	49.219	1.56	1608.5	183	94.286
Mean	168.571	12.81	2.19	0.718	-18.286	45.603	1.501	1462.145	166.628	66.687
SD	1.207	0.928	0.75	0.338	3.423	1.943	0.032	107.629	10.329	15.626

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	21	21	21	21	21	21	21	21	21	21
Min	50.143	16.767	483.75	89.75	1.833	78.25	28.141	483.75	89.75	1.833
Max	127	44.365	2878.333	477.833	92.167	469.833	172.065	2878.333	477.833	92.167
Mean	99.941	34.877	1474.456	322.535	22.617	299.918	110.993	1474.456	322.535	22.617
SD	19.503	7.507	617.524	111.613	25.206	108.464	39.605	617.524	111.613	25.206

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	21	21	21	21	21	21	21	21	21	21
Min	78.25	28.141	2500	292.423	294.575	288.683	3.192	1.21	52.667	30.333
Max	469.833	172.065	3094	299.772	301.383	297.75	7.581	3.026	956.5	153
Mean	299.918	110.993	2908.429	296.99	299.369	293.556	5.814	2.22	486.053	104.317
SD	108.464	39.605	190.672	2.131	1.928	2.55	1.289	0.525	250.247	30.575

	WDMIN	WDRNG	WDSTD
n	21	21	21
Min	0	30.333	9.728
Max	13.667	153	56.591
Mean	1.622	102.695	35.872
SD	4.121	30.556	12.231

Region: Oriental **Zone: 1**

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	68	68	68	68	68	68	68	68	68	68
Min	139.75	46.75	0.6	45.917	15.511	-0.782	-0.231	-0.64	-0.308	-0.776
Max	988.333	154.333	29.75	147.5	58.993	3.241	1.87	1.586	3.303	2.387
Mean	641.256	129.659	7.749	121.911	47.543	1.148	1.349	0.68	0.946	0.942
SD	206.136	21.394	6.739	19.557	9.219	0.811	0.444	0.436	0.868	0.824

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	68	68	68	68	68	68	68	68	68	68
Min	-2.622	-0.866	8	2.778	60	0	60	115	211	124
Max	0.568	0.434	32	711.75	4750	460	4570	174	290	215
Mean	-1.221	-0.126	15.338	272.301	869.706	111.176	758.529	153.868	276.382	184.647
SD	0.665	0.225	4.589	180.057	635.26	110.122	629.12	14.21	17.264	21.984

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	68	68	68	68	68	68	68	68	68	68
Min	115	8	1	0.187	18	67.352	1.479	1119.438	136.917	18.333
Max	186	14	4	1	34	88.86	1.686	1677.5	190.5	95.75
Mean	171.059	12	1.75	0.936	24.618	77.185	1.547	1372.95	177.578	58.135
SD	16.948	1.281	0.741	0.189	3.477	5.662	0.043	103.706	11.322	18.032

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	68	68	68	68	68	68	68	68	68	68
Min	78.75	24.861	139.75	46.75	0.667	45.917	15.511	139.75	46.75	0.667
Max	155.75	56.991	1959.667	595.917	14.75	594.417	199.452	1959.667	595.917	14.75
Mean	119.442	38.544	997.246	285.693	4.215	281.478	102.609	997.246	285.693	4.215
SD	18.617	7.628	460.545	116.929	2.685	116.053	42.82	460.545	116.929	2.685

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	68	68	68	68	68	68	68	68	68	68
Min	45.917	15.511	458	294.614	301.742	283.208	6.233	2.227	217.167	61.833
Max	594.417	199.452	3000	300.824	308.869	297.067	22.258	8.077	1137.417	178.75
Mean	281.478	102.609	1409.044	298.992	306.014	291.159	14.855	5.037	731.695	155.155
SD	116.053	42.82	716.974	0.929	1.688	2.811	3.866	1.466	186.659	24.92

	WDMIN	WDRNG	WDSTD
n	68	68	68
Min	0	61.833	22.416
Max	32.583	178.75	66.233
Mean	3.016	152.139	53.785
SD	7.368	25.223	8.76

Region: Oriental **Zone: 2**

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	13	13	13	13	13	13	13	13	13	13
Min	734.667	115.25	6.917	34	11.016	0.649	-1.461	-1.458	-0.807	0.939
Max	1573.75	154.75	118.5	117.917	45.755	3.751	0.858	0.279	3.758	4.183
Mean	1023.785	129.421	37.544	91.878	31.155	1.208	0.056	-0.642	0.266	2.095
SD	245.163	13.385	33.788	26.65	10.39	0.836	0.722	0.498	1.162	1.063

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	13	13	13	13	13	13	13	13	13	13
Min	-1.739	-1.258	14	6.389	90	0	90	158	260	185
Max	1.175	0.455	21	738.056	2710	300	2650	163	287	215
Mean	-0.494	0.146	17.308	241.384	1592.308	39.231	1553.077	159.615	277.769	200.538
SD	0.979	0.448	1.932	220.673	761.448	86.068	769.29	1.71	9.347	10.005

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	13	13	13	13	13	13	13	13	13	13
Min	158	11	1	0.292	8	75.001	1.425	1341.667	140.25	82.375
Max	165	14	4	1	16	80.745	1.464	1882.75	180.5	124
Mean	161.231	12.769	2.077	0.708	11.846	77.999	1.441	1514.356	156.52	99.996
SD	2.315	1.092	0.954	0.272	2.641	1.569	0.013	130.773	11.026	11.635

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	13	13	13	13	13	13	13	13	13	13
Min	39.5	11.326	735.333	148.917	6.083	141.833	52.24	735.333	148.917	6.083
Max	77.625	24.897	2770.333	674.583	118.167	659.417	235.547	2770.333	674.583	118.167
Mean	56.524	18.202	1467.292	282.577	31.292	251.285	85.273	1467.292	282.577	31.292
SD	13.372	4.516	678.228	137.584	35.157	134.406	47.648	678.228	137.584	35.157

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	13	13	13	13	13	13	13	13	13	13
Min	141.833	52.24	1000	295.781	298.342	293.4	2.1	0.691	41.75	11.5
Max	659.417	235.547	3012	301.853	306.567	298.883	9.142	2.982	822.25	149.75
Mean	251.285	85.273	2051.769	299.715	302.443	297.075	5.367	1.785	490.571	106.772
SD	134.406	47.648	768.816	1.781	2.582	1.624	2.452	0.787	250.89	43.842

	WDMIN	WDRNG	WDSTD
n	13	13	13
Min	-6.417	11.5	4.389
Max	0	149.75	55.904
Mean	-0.494	107.266	39.382
SD	1.78	43.792	16.475

Region: Oriental **Zone: 3**

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	99	99	99	99	99	99	99	99	99	99
Min	656.333	104	3.417	66.667	25.275	0.091	-0.913	-0.811	-1.888	-0.403
Max	1477.5	184	89	157.75	57.453	5.353	1.171	1.761	7.243	5.107
Mean	1052.836	144.682	27.192	117.489	43.222	1.627	0.014	0.615	0.774	2.264
SD	151.38	16.825	14.7	18.988	6.813	1.042	0.484	0.56	1.532	1.043

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	99	99	99	99	99	99	99	99	99	99
Min	-0.708	-2.714	11	12.5	60	0	60	140	234	167
Max	1.792	0.977	41	4254.083	7800	1980	7650	186	292	217
Mean	0.484	-0.137	22.737	804.559	2602.828	194.545	2408.283	172.111	274.414	206.525
SD	0.571	0.689	6.749	965.624	1646.446	388.246	1423.535	10.366	12.746	10.986

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	99	99	99	99	99	99	99	99	99	99
Min	140	4	1	0.104	10	91.154	1.432	743.083	107.583	12.167
Max	210	14	9	1	32	121.16	1.65	1835.333	188	132
Mean	191.707	12.707	2.354	0.853	22.02	102.847	1.523	1307.192	150.681	65.722
SD	15.591	1.886	1.215	0.269	5.171	7.172	0.052	199.348	16.538	24.782

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	99	99	99	99	99	99	99	99	99	99
Min	43.5	13.018	788.25	157.937	0.833	111.75	42.782	768.833	157.937	0
Max	132.857	48.222	3875.75	990.25	153.5	983.833	366.893	3875.75	990.25	153.5
Mean	84.959	29.356	1819.118	359.149	17.609	341.54	128.747	1818.922	359.149	17.571
SD	20.971	8.573	635.225	159.204	23.098	162.991	63.866	635.549	159.204	23.124

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	99	99	99	99	99	99	99	99	99	99
Min	111.75	42.782	2286	279.335	288.192	269.258	2.467	0.757	0	0
Max	983.833	366.893	5000	300.922	304.033	299.425	21.725	7.848	571.917	156.286
Mean	341.578	128.766	3581.424	295.446	299.972	289.577	10.395	3.739	254.356	72.99
SD	162.949	63.845	684.316	4.406	3.142	6.337	4.254	1.658	166.44	43.867

	WDMIN	WDRNG	WDSTD
n	99	99	99
Min	-16.5	0	0
Max	0	156.286	63.115
Mean	-0.545	73.535	27.508
SD	2.137	43.823	17.385

Region: Oriental **Zone: 4**

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	77	77	77	77	77	77	77	77	77	77
Min	1153	130.9	23	16.583	5.827	-0.05	-1.936	-2.146	-1.171	2.557
Max	1905.667	193.75	139.667	127.5	45.952	3.168	0.365	0.425	2.738	6.085
Mean	1587.916	153.463	110.24	43.223	13.688	0.903	-1.293	-1.437	0.193	4.438
SD	169.214	11.768	26.898	26.079	8.824	0.603	0.609	0.6	0.757	0.807

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	77	77	77	77	77	77	77	77	77	77
Min	-0.286	-1.565	4	5.625	90	-60	120	170	228	175
Max	2.163	0.911	31	863.333	4110	210	4110	190	273	216
Mean	1.227	-0.151	12.091	203.279	2083.636	1.558	2082.078	178.766	254.364	202.442
SD	0.46	0.533	5.914	185.846	930.971	35.059	927.621	5.127	11.669	9.956

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	77	77	77	77	77	77	77	77	77	77
Min	175	12	1	0.042	-8	95.405	1.414	1331	131.1	82.75
Max	197	14	3	1	18	124.982	1.479	1914.25	186.833	139.667
Mean	190.247	13.935	1.429	0.602	3.403	109.908	1.424	1642.813	156.891	117.974
SD	6.306	0.296	0.677	0.307	6.3	8.609	0.014	129.578	12.182	14.736

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	77	77	77	77	77	77	77	77	77	77
Min	16.583	5.835	1607.583	249	11.5	72	20.421	1607.583	249	11.5
Max	77.556	26.754	4067.625	591.417	242.5	556.167	232.614	4067.625	591.417	242.5
Mean	38.917	12.027	2772.784	355.634	124.907	230.727	79.019	2772.784	355.634	124.907
SD	15.589	4.918	517.825	73.6	54.968	93.515	34.854	517.825	73.6	54.968

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	77	77	77	77	77	77	77	77	77	77
Min	72	20.421	2520	293.175	293.65	292.767	0.642	0.198	0	0
Max	556.167	232.614	5000	301.01	302.25	300.408	4.425	1.593	423.5	121
Mean	230.727	79.019	3727.532	299.497	300.236	298.678	1.558	0.498	54.897	22.412
SD	93.515	34.854	551	1.408	1.495	1.383	0.787	0.265	93.263	31.735

	WDMIN	WDRNG	WDSTD
n	77	77	77
Min	-23.5	0	0
Max	0	121	47.1
Mean	-0.389	22.801	7.933
SD	2.727	32.059	11.769

Region: Australian Zone: 1

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	44	44	44	44	44	44	44	44	44	44
Min	1111.5	121.5	10	22.286	7.103	-0.098	-1.776	-2.044	-1.637	2.042
Max	1805.571	182	134.25	140	52.144	1.403	0.879	-0.111	1.054	6.182
Mean	1623.478	157.417	110.429	46.988	15.385	0.627	-1.251	-1.42	-0.388	4.401
SD	149.82	9.666	28.406	26.697	9.721	0.418	0.634	0.448	0.614	0.875

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	44	44	44	44	44	44	44	44	44	44
Min	-0.568	-1.385	7	0	30	0	30	160	232	175
Max	2.161	0.917	17	1273.333	5030	0	5030	187	283	206
Mean	1.154	0.019	13.386	363.86	2837.5	0	2837.5	180.227	253.841	190.909
SD	0.602	0.585	2.325	329.506	1336.065	0	1336.065	6.357	11.678	5.569

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	44	44	44	44	44	44	44	44	44	44
Min	160	12	1	0.062	-8	114.959	1.414	1291	125	82.5
Max	196	14	5	1	2	149.324	1.432	2030	193	138
Mean	188.636	13.932	1.886	0.583	-3.455	134.32	1.42	1679.832	161.78	119.39
SD	7.055	0.334	0.97	0.318	3.031	9.836	0.006	105.794	10.825	10.335

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	44	44	44	44	44	44	44	44	44	44
Min	24	7.977	1399	221.75	12.667	62.75	21.506	1399	221.75	12.667
Max	64	20.277	4045.5	492.667	279.833	319.083	113.246	4045.5	492.667	279.833
Mean	42.389	13.348	2685.95	320.337	139.018	181.319	61.049	2685.95	320.337	139.018
SD	9.351	3.175	609.077	63.314	58.586	62.213	22.439	609.077	63.314	58.586

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	44	44	44	44	44	44	44	44	44	44
Min	62.75	21.506	2395	295.474	296.033	294.525	0.633	0.19	0	0
Max	319.083	113.246	5000	300.807	301.4	300.412	2.75	1.002	483	152
Mean	181.319	61.049	3978.818	299.417	300.022	298.578	1.444	0.51	56.355	21.407
SD	62.213	22.439	717.591	1.421	1.43	1.54	0.667	0.256	119.588	39.559

	WDMIN	WDRNG	WDSTD
n	44	44	44
Min	0	0	0
Max	0	152	59.127
Mean	0	21.407	7.687
SD	0	39.559	14.931

Region: Australian Zone: 2

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	245	245	245	245	245	245	245	245	245	245
Min	145.583	18.667	0	9.333	3.089	-1.247	-0.2	-1.62	-2.689	-1.156
Max	1148.5	185.75	39.143	184	72.16	2.466	2.293	1.237	0.81	2.457
Mean	454.431	85.713	8.083	77.631	27.286	-0.223	1.199	-0.281	-0.318	-0.053
SD	236.358	51.46	7.213	52.474	20.552	0.92	0.38	0.823	0.695	0.862

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	245	245	245	245	245	245	245	245	245	245
Min	-2.868	-0.463	4	0	30	-30	30	82	202	95
Max	1.322	0.596	19	735.917	2230	490	2230	176	291	202
Mean	-1.508	0.017	9.265	257.245	624.286	121.755	502.531	113.269	261.09	148.878
SD	0.855	0.178	3.503	175.488	392.875	138.758	390.235	26.07	24.621	23.632

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	245	245	245	245	245	245	245	245	245	245
Min	95	7	1	0.062	-42	113.357	1.441	692.889	126.889	0
Max	183	14	4	1	-10	151.727	1.934	1872	206.083	120
Mean	142.8	10.18	1.494	0.887	-24.449	133.368	1.582	1272.97	173.682	37.783
SD	23.041	1.689	0.681	0.24	6.617	10.458	0.091	286.468	17.905	28.16

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	245	245	245	245	245	245	245	245	245	245
Min	66	20.728	145.583	18.667	0.5	8.417	2.674	145.583	18.667	0.5
Max	174.833	63.292	1668.25	412.375	71	409.875	155.193	1668.25	412.375	71
Mean	135.898	48.771	529.809	104.531	12.785	91.747	32.434	529.809	104.531	12.785
SD	23.014	8.715	340.188	88.477	14.324	91.256	34.006	340.188	88.477	14.324

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	245	245	245	245	245	245	245	245	245	245
Min	8.417	2.674	145	284.122	287.481	278.506	3.058	1.161	11.75	7
Max	409.875	155.193	3073	302.209	305.942	299.05	18.2	6.701	1280.5	189.4
Mean	91.747	32.434	1100.816	294.795	300.665	287.879	12.786	4.732	818.539	139.973
SD	91.256	34.006	812.965	4.064	3.797	4.645	3.895	1.465	267.101	29.245

	WDMIN	WDRNG	WDSTD
n	245	245	245
Min	0	7	2.252
Max	50	189.4	74.661
Mean	7.624	132.349	47.499
SD	12.053	28.483	10.581

Region: Australian Zone: 4

	AET	AETMAX	AETMIN	AETRNG	AETSTD	CLIMRNG1	CLIMRNG2	CLIMRNG3	CLIMRNG4	CLIMATE1
n	13	13	13	13	13	13	13	13	13	13
Min	498	90.75	0	90.75	35.929	-0.437	-0.518	0.055	-3.086	-0.681
Max	1012	152	19	142	52.663	0.366	0.414	1.427	-1.875	3.451
Mean	708.171	122.764	3.009	119.755	45.088	-0.132	-0.192	0.851	-2.478	1.122
SD	150.294	16.805	5.729	14.078	4.462	0.237	0.309	0.371	0.357	1.159

	CLIMATE2	CLIMATE3	ECO-TYPES	ELVAVG	ELVMAX	ELVMIN	ELVRNG	FR	FRMAX AQ	FRMAX BGR
n	13	13	13	13	13	13	13	13	13	13
Min	0.978	-3.064	8	18.5	640	0	640	94	207	94
Max	2.984	0.141	11	905.417	3750	0	3750	108	285	183
Mean	1.619	-0.767	9.308	304.226	2334.615	0	2334.615	99.154	266.846	159.923
SD	0.636	1.084	0.855	264.488	876.514	0	876.514	4.947	27.163	30.769

	FRMAX BGZ	HOLDAG	HOLDAG TOTAL	LAND AREA	LAT	LONG	LONG SPAN	PET	PETMAX	PETMIN
n	13	13	13	13	13	13	13	13	13	13
Min	94	7	1	0.071	-44	166	1.726	550.25	105	0
Max	109	10	4	1	-34	174.852	2	1100	172	19
Mean	100.154	8.154	2.308	0.476	-40.308	171.293	1.889	731.892	130.929	3.009
SD	5.728	1.519	0.947	0.306	3.146	2.796	0.088	162.86	20.258	5.729

	PETRNG	PETSTD	PRE	PREMAX	PREMIN	PRERNG	PRESTD	RAIN	RAINMAX	RAINMIN
n	13	13	13	13	13	13	13	13	13	13
Min	105	41.355	720.875	76.563	49.625	26.937	7.744	720.875	76.563	49.625
Max	154	56.156	3781.25	375.937	236.875	144.75	41.449	3781.25	375.937	236.875
Mean	127.919	47.654	1839.984	185.962	117.619	68.343	20.625	1839.984	185.962	117.619
SD	15.614	4.744	902.192	89.144	55.76	36.662	10.544	902.192	89.144	55.76

	RAINRNG	RAINSDT	SR	TEMP	TEMPMAX	TEMPMIN	TEMPRNG	TEMPSTD	WD	WDMAX
n	13	13	13	13	13	13	13	13	13	13
Min	26.937	7.744	505	283.108	287.6	276.781	6.769	2.43	0	0
Max	144.75	41.449	1042	289.212	292.925	285.875	11.613	4.162	88	33
Mean	68.343	20.625	765.692	285.179	289.581	280.43	9.15	3.292	23.721	10.392
SD	36.662	10.544	203.651	1.746	1.496	2.525	1.459	0.526	27.648	10.903

	WDMIN	WDRNG	WDSTD
n	13	13	13
Min	0	0	0
Max	0	33	12.033
Mean	0	10.392	3.514
SD	0	10.903	3.78

A3.2: Chapter Two and Three Global Climate and Environment Maps

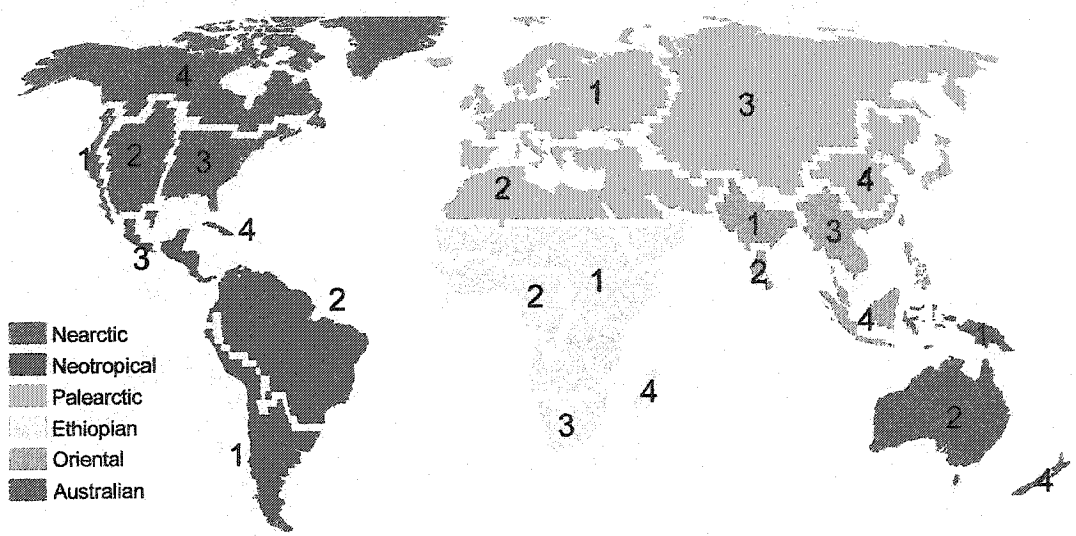

Figure A4: Biogeographic provinces and numbered sub-zones.

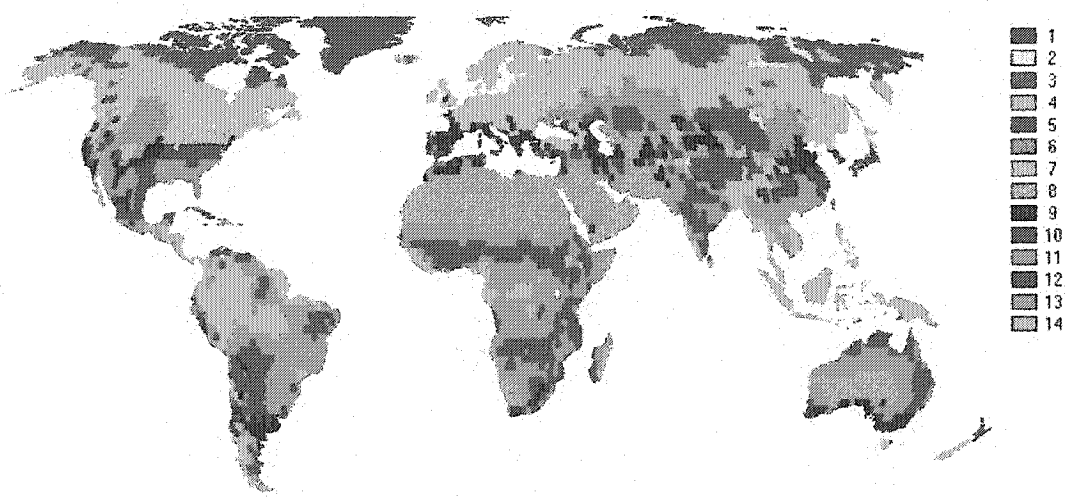

Figure A5: Holdridge aggregate lifezones: 1) tundra, 2) cold parklands, 3) forest tundra, 4) boreal forest, 5) cool desert, 6) steppe, 7) temperate forest, 8)

hot desert, 9) chaparral, 10) warm temperate forest, 11) tropical semi-arid, 12) tropical dry forest, 13) tropical seasonal forest, 14) tropical rain forest.

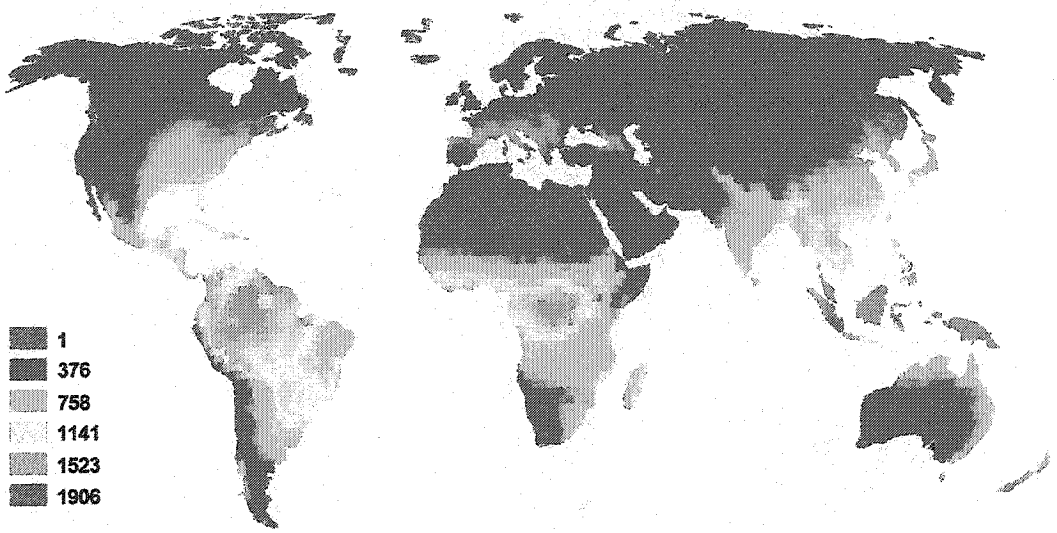

Figure A6: Total annual actual evapotranspiration (mm).

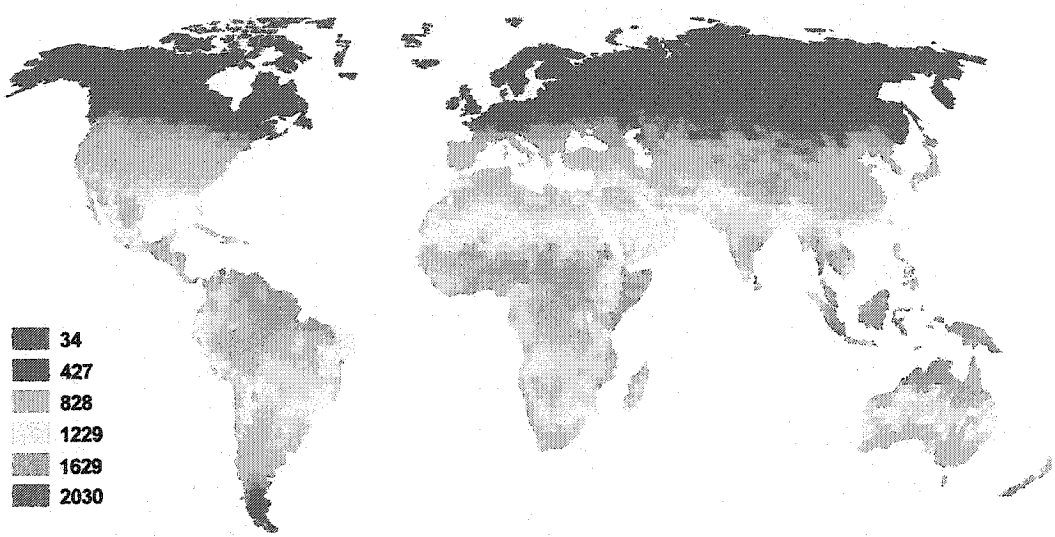

Figure A7: Total annual potential evapotranspiration (mm).

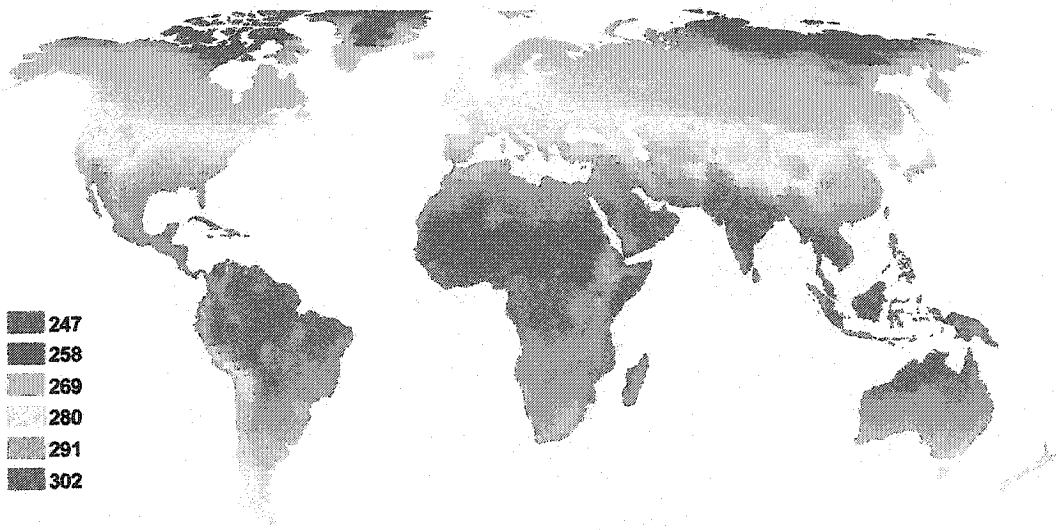

Figure A8: Mean annual temperature (°K).

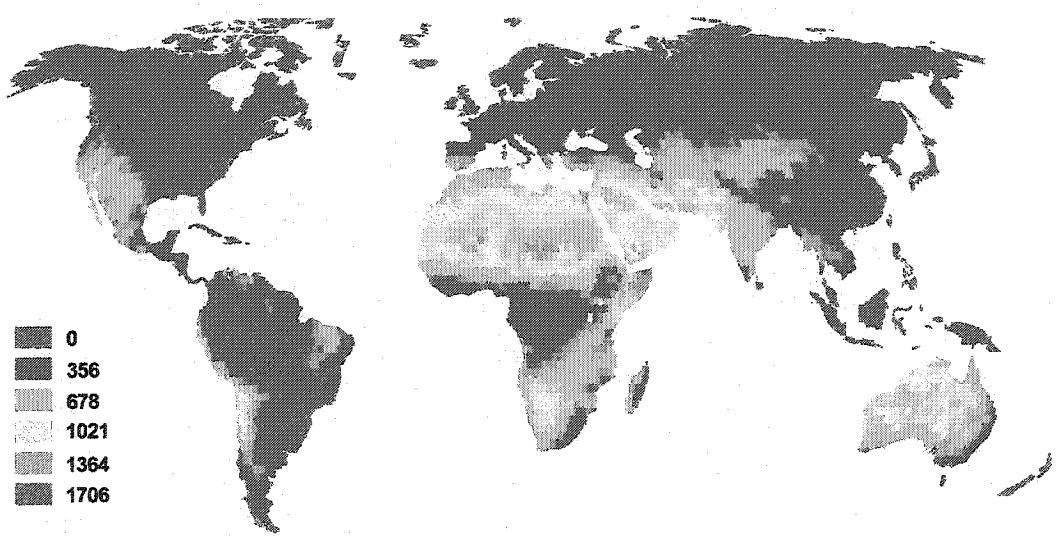

Figure A9: Total annual water deficit (mm).

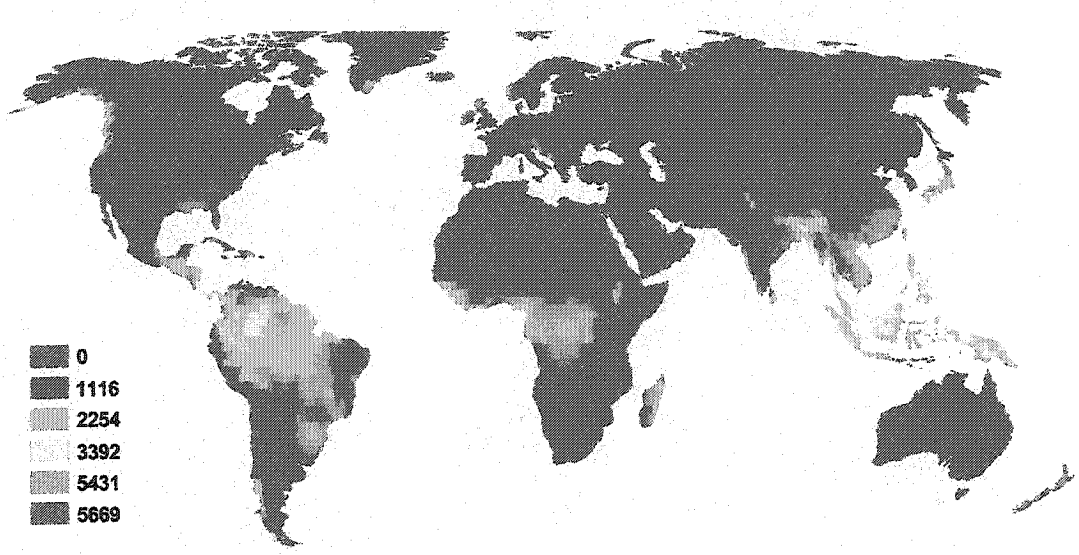

Figure A10: Total annual precipitation (mm).

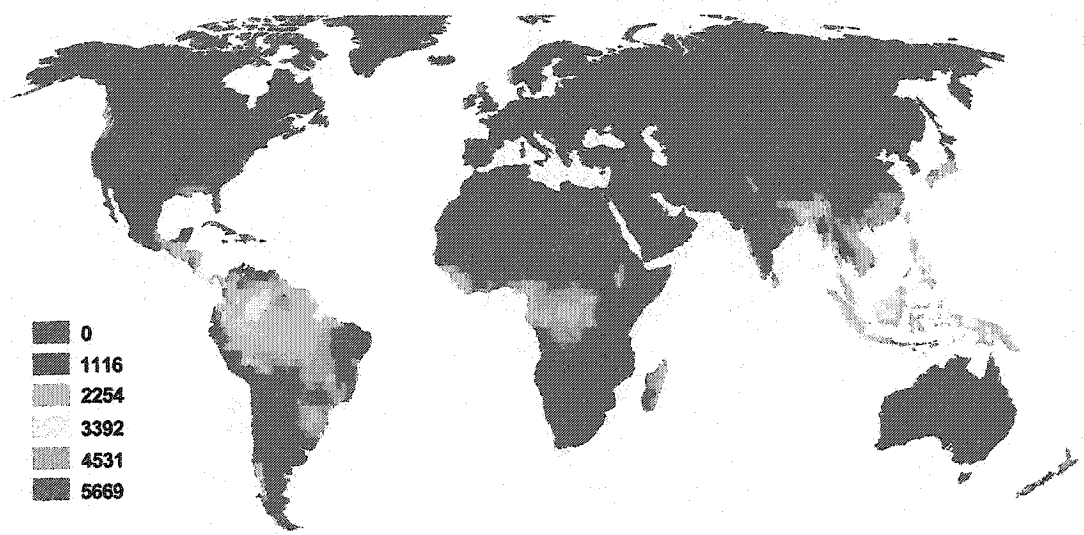

Figure A11: Total annual rainfall (mm).

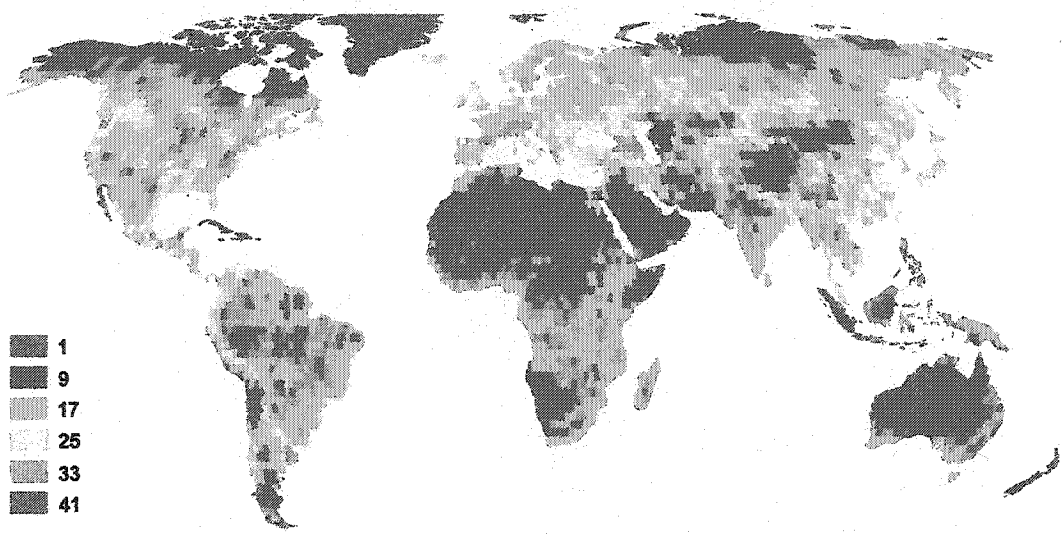

Figure A12: Total number of global land cover classes from the EROS Data Center Global Land Cover Characterization Version 2.

Appendix 4: Chapter Four Data

Table A5: Variables used in Chapter Four.

Variable Name	Description
SITE	Site number
SITE NAME	Name of site park, reseve or state forest
LAT	Latitude (°)
LONG	Longitude (°)
SR_{SITE}	Total tree species richness per site
SR_{QUAD}	Mean quadrat tree species richness per site
SR_{REG}	Sites 1 to 14: Total tree species richness in the Currie and Paquin (1987) quadrat containing the site
	Site 15: Total number of tree species listed by Sánchez-Vindas and Alvarez (1997).
I_{SITE}	Number of individual trees with DBH > 5 cm per site
DBH_{SITE}	Average diameter at breast height of all trees (with DBH greater than 5 cm) per site (cm)
AET	Total annual evapotranspiration (mm)
D_CAT_1	Number of tree species with 1 to 4 individuals per site
D_CAT_2	Number of tree species with 5 to 13 individuals per site
D_CAT_3	Number of tree species with 14 to 45 individuals per site
D_CAT_4	Number of tree species with 46 to 160 individuals per site

Table A6: Data used in Chapter Four.

SITE	SITE NAME	LAT	LONG	SR_{SITE}	SR_{QUAD}	SR_{REG}	I_{SITE}	DBH_{SITE}	AET	D_CAT_1	D_CAT_2	D_CAT_3	D_CAT_4
1	Kettle Lake	48.567	-80.883	8	3.2	39	194	4.862	463	2	2	3	1
2	Greenwater	49.200	-81.283	6	4.2	39	279	4.798	455	0	1	4	1
3	Tidewater	51.217	-80.650	13	6.1	26	388	3.417	387	6	1	3	3
4	Kap-kig-iwan	47.783	-79.883	14	5.7	38	302	3.403	471	4	3	4	3
5	Temagami	47.050	-79.783	14	5.8	62	361	3.525	475	4	4	5	1
6	Champlain	46.300	-78.867	13	5.6	62	209	4.181	483	7	2	2	2
7	Gatineau	45.483	-75.867	14	5.5	80	206	4.277	518	3	5	5	1
8	Fillmore Glen	42.700	-76.417	18	5.2	116	190	5.360	607	9	6	2	1
9	Hickory Run	41.000	-75.667	9	3.5	141	102	6.484	712	3	4	2	0
10	Catoctin Mountain	39.633	-77.450	14	3.7	148	99	7.089	736	9	2	3	0
11	W B Umstead	35.833	-78.750	19	6.6	159	212	3.918	926	11	4	3	1
12	Shenandoah	38.500	-78.450	13	4.3	161	152	5.175	790	6	3	3	1
13	Governor's Canyon	29.333	-98.833	4	2.8	108	172	4.858	735	0	0	3	1
14	McCauley Mountain	43.983	-77.117	19	5.6	116	225	3.511	496	10	4	3	2
15	LaPacifica	10.470	-85.170	19	5.6	423	72	5.527	1042	14	4	1	0

Appendix 5: Measurement Error In The Data

When building general linear models of type used throughout this thesis, measurement error in the both the dependent and independent variables is an important consideration. Throughout this thesis, I have used published data from numerous sources to test my hypotheses. While I have previously outlined the protocols use to calculate the independent variables (i.e. levels of observed and potential richness) from range data, I have commented very little on potential measurement error associated with either these protocols, or the original range maps. Similarly, while I have reported the sources of my independent variables (i.e. climatic gradients) and how I sampled them, I have not described the protocols used to generate in the first place or their associated levels of error. I will do that now.

The measurement error in the dependent variable of family richness comes from two sources: the original estimation of the family range maps and the extraction of presence absence data from those maps. Unfortunately, Heywood (1993) does not provide information on the accuracy of the family range maps. The ranges were extrapolated from hundreds of floras and based on expert opinion, but ultimately, there is no way to determine level of error associated with the final range projections. However, since the many of the ranges are presented with as more or less contiguous regions, it is likely that the ranges have been somewhat over estimated.

It is reasonable to suggest that measurement error arising from my sampling protocol is relatively small compared to any potential error in the range maps. First, the sampling grid was rubber sheeted to the range map using forty test points to generate polynomial stretching models with R2's greater than 0.9999. Second, the resolution of

sampling grid was based on the size of observable gaps in the data ranges. That apparent resolution then was 0.5° over a 360° span, or ± 0.14%.

Of the climatic gradients I used as my independent variables, temperature and precipitation were the only two based on direct observation. The Legates and Willmott (1992) data set Monthly Average Surface Temperature and Precipitation, was compiled from 60 years (1920-1980) of observations from a global network of 24,941 terrestrial air surface temperature stations and 26,858 terrestrial precipitation stations. The data set also included oceanic grid point estimates from a variety of sources (primarily ship board measurements), however, this thesis only examines terrestrial areas. Precipitation measurements were gauge corrected for negative biases caused by splashing and evaporation (negligible effects), and wind deflection (important bias) (Legates and Willmott 1990). Yearly means/totals were calculated from monthly values then averaged for the 60-year period. While the actual measurement errors for these data sets are not available, the natural annual variability likely contributes more to the general uncertainty in the values anyway. Over terrestrial areas, the average standard error per quadrat for temperature was 0.59°. Annual mean temperature has a global range of 60° suggesting an average error of about 1%. Similarly, precipitation has an average standard error of 8.0mm. Annual total precipitation has a global range of about 6600mm suggesting an average error of about 0.1%.

AET and PET are both composite variables based on a number of data sources. PET was estimated using the Preistley-Taylor method, which presents PET as a function of net solar radiation, soil heat flux, water vapor pressure and a psychrometric constant (Ahn and Tateishi 1994b). Ahn and Tateishi (1994a) estimated each of these factors

using four existing global data sets: temperature (Legates and Willmott 1990), albedo (Mathews 1983), cloudiness (Leemans and Cramer 1991), and elevation. Water vapor pressure was calculated directly from temperature using Kotoda's (1986) method. Psychrometric constant was estimated from temperature and elevation, again using Kotoda (1986). In the Priestley-Taylor method, heat flux is subtracted directly from net solar radiation. Unfortunately, calculating heat flux is very difficult (Ahn and Tateishi 1994b). However, heat flux is generally at least an order of magnitude smaller than net solar radiation. Moreover, since daily heat flux for most sites is very close to zero since daytime positive values are counter balanced by negative nighttime values, heat flux can be ignored (Ahn and Tateishi 1994b). Finally, net radiation is total from total radiation (calculated from geographic and astrometric constants) corrected for cloudiness and albedo. Ahn and Tateishi (1994a) calculated mean monthly PET values on a 30-minute global grid, and then produced the mean annual levels for the period from 1920 to 1980.

Monthly AET values were calculated from PET, precipitation levels (Legates and Willmott 1992) and soil water holding capacity (Bouwman et al. 1993). When monthly precipitation was greater than monthly PET, AET was set as equal to PET (Anh and Tateishi 1996). When precipitation was less than PET, AET was estimated as the sum of precipitation and monthly change in soil moisture. Soil moisture in turn was calculated from soil water holding capacity and accumulated potential water loss (based on previous monthly precipitation and PET levels).

Determining the amount measurement error in the AET and PET estimates is not directly possible. While there are data to provide some indication of the confidence interval around the temperature and precipitation data, such data are not presented for

albedo, cloudiness or soil holding capacity. However, in comparisons with other means of calculating AET, Ahn and Tateishi (1994b) demonstrated that their estimates are reasonable. Morton (1983) study 28 river basins in Canada, the USA, Africa, Ireland Australia, and New Zealand and assumed the difference between total precipitation input and total river shed outflow to be equivalent to actual evapotranspiration. Ahn and Tatieshi (1994b) found a root mean square error of 87mm compared to their AET estimates. AET has a range of about 2500mm globally suggesting an average measurement error of 3.5%.

A rigid interpretation of requirement of general linear models that the independent variables be free of measurement error would require the abandonment of type I linear regressions in most ecological studies. However, as with other assumptions, small violations do not necessarily render the statistical test invalid. There are two general rules of thumb regarding permissible levels of measurement error. The first is that measurement error in the independent variable(s) should not exceed five percent of the total range of the variable (Morin and Findlay 2002). The second is that measurement error in the independent variable(s) not exceed one third the measurement error in the dependent variable (Legendre and Legendre 1998).

For my independent climatic variables, temperature and precipitation do not violate the five percent rule. AET and PET are more questionable as the lack of reliable error estimates makes this determination difficult. However, the comparisons to other measures of evapotranspiration suggest that these variables have sufficiently low measurement error avoid rendering my statistical models invalid. Compliance with the one-third rule cannot be adequately determined given the uncertainty in the amount of

error in the dependent variable. It seems likely however, that potential for measurement error in the dependent variable owing to over estimation of ranges would be larger that the generally small measurement error in the climatic variables. Thus the statistical tests presented in this thesis are valid.

If, however, the violation of the assumption of "no measurement error" is too large, there are two potential problems. Measurement error in either dependent or independent variables causes a downward bias in estimation of R2. Moreover the standard error of the slopes will be increased (Berry and Feldman 1985). Thus it becomes more difficult to observe significant effects. All of the relationships presented in this thesis however, demonstrated statistically significant effects. Thus no type two errors were committed.

Measurement error the independent variables may also lead to an upward or downward bias in estimation of the regression coefficients (Berry and Feldman 1985). Thus it becomes difficult to compare regression models. There were two occasions in this thesis where I compared regression models. The first was the selection in chapter two of two richness-climate models from among the many possible contenders. I concluded that it is possible that other combinations of climatic factors may have offered equally good descriptions of the richness patterns. However, as I argued in the chapter discussion, several possible richness climate models were to some degree interchangeable. The purposed of the chapter was to demonstrate that the ostensible form of the models might vary depending on variable selection but, that any combination of heat and water variables provided a globally consistent description of richness patterns. Thus the final model selection was not overly important. The second occasion in which I

compared regression coefficients was in the ANCOVA models of chapter two. However, when slopes are compared in this way, it is only among groups divided from the same data sets, so that any error in estimation of slope should be more or less systematic. Thus, for the purposes of this thesis, measurement error does not significantly affect my conclusions.