Changing climate and geographical patterns of taxonomic richness

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Abstract

The geographic variation of taxonomic richness may be directly determined by climate through contemporaneous/ecological processes, versus other (e.g., historical/evolutionary processes) that happen to be collinear with contemporaneous climate. In Chapter 1 I evaluated hypotheses from both groups of explanations in North America. If contemporaneous climate controls patterns of richness, then richness should vary with climate through time in the same way that richness varies with current climate through space. Over the last *ca.* 11,000 yr, richness-temperature relationships remained reasonably constant. Between 12,000 and 14,000 yr BP, when climate fluctuated rapidly, richness gradients as a function of temperature were significantly shallower. If historical climate over the last 21,000 years determines patterns of richness, then historical climate should be a better predictor of richness than contemporaneous climate. I rejected historical-climate as a better predictor of richness. Contemporaneous climate stands as the most plausible explanation for contemporaneous patterns of richness, at least over the last 11,000 yr. In Chapter two, I tested the prediction that richness of most taxa should increase with temperature in all but the warmest and driest areas. Climate warming during Pleistocene-Holocene transition led richness increases in wet areas, but richness declines in dry regions, as expected from current richness-climate relationships. A decline in small mammal species richness in Northern California since the late Pleistocene was expected from the current richness-climate relationship for this group in North America. These results contest the view that future global warming may lead to species extinction rates that would qualify as the sixth mass extinction in the history of the earth. In chapter three, I first tested the hypothesis that richness gradients mainly reflect the sum of individual species climatic tolerances. I tested this hypothesis for birds, mammals and trees native to eastern North America (ENA, where there are

no major barriers to dispersal). The number of species present in any given area in ENA is usually much smaller than the number of species in the continental pool that tolerate the climatic conditions in that area. Second, I tested several explanations for patterns of unfilled potential richness. Unfilled potential richness is inconsistent with postglacial dispersal lags, climatic variability since the Last Glacial Maximum, or with biotic interactions. In contrast, unfilled richness is highly consistent with a probabilistic model of species climate occupancy. Individual species climatic tolerances is not the process generating the main current patterns of richness, nor are post-glacial dispersal lags, climatic variability since the LGM or biotic interactions. This thesis is consistent with the hypothesis that contemporaneous climate directly controls spatial patterns of richness. Generally, there seems to be little need to invoke historical processes as determinants of current gradients of richness.

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Introduction

There are millions of species on our planet (Mora *et al.* 2011). But why some areas harbor more species than others is perhaps the most addressed question in the fields of ecology and biogeography. Species richness, the number of different species observed or estimated to occur in a given area, is the most common *index* to evaluate how organisms are structured across space. At broad spatial scales (sampling units > 40 km^2), many explanations have been suggested to account for the geographic variation of richness (Willig *et al.* 2003; Brown 2014). Among these, a few hypotheses have attracted serious attention. These hypotheses include habitat heterogeneity: habitats that are spatially heterogeneous can harbor more species (Simpson 1964; Kerr & Packer 1997; Kreft & Jetz 2007); area: habitats that comprise more area support more species (Simberloff 1976; Connor & McCoy 2001; Lomolino 2001); geometric constraints: species ranges tend to overlap most toward the center of bounded biogeographic domains (Colwell & Hurtt 1994); evolutionary processes: region age, coupled with rates of speciation, extinction and immigration (Connell & Orias 1964; Pianka 1989; Rohde 1992; Jablonski *et al.* 2006; Mittelbach *et al.* 2007); evolution and maintenance of climatic tolerances (Janzen 1967; Wiens & Donoghue 2004); historical effects of climate over thousands of years (Montoya *et al.* 2007; Svenning & Skov 2007; Araújo *et al.* 2008) and finally, *contemporaneous* effects of climate (Turner *et al.* 1987; Currie 1991; Obrien 1993; Francis & Currie 2003; Field *et al.* 2009).

Despite the different explanations available, two families of hypotheses dominate most of the current scientific literature. These explanations consider climate as the main determinant of the current geographic variation of richness. One school of thought proposes that there is a direct causal link from contemporary climate to richness (i.e. contemporaneous climate controls richness directly through ongoing ecological processes). Another school of thought suggests that climate influenced richness in the past through historical or evolutionary processes (i.e. processes driven by climate thousands or millions of years ago).

The Richness-Climate Hypothesis (RCH) postulates that contemporaneous climate controls the spatial variation of richness through ecological processes (albeit still unknown). This hypothesis has received much correlative support. For example, at the continental level, climatic related variables account for most of the spatial variation in richness (R^2=0.6-0.9) (Hawkins *et al.* 2003). Similarly, climatic variables explain patterns of richness through annual seasons (H-Acevedo & Currie 2003; Hurlbert & Haskell 2003), among different regions of the globe (Adams & Woodward 1989; Francis & Currie 2003; Kreft & Jetz 2007), insular systems (Kalmar & Currie 2007) and the oceans (Tittensor *et al.* 2010). Overall, richness-climate relationships through space are consistent from regional to global scales (Field *et al.* 2009), through time (H-Acevedo & Currie 2003; Hurlbert & Haskell 2003) and among many taxa, including invertebrates, vertebrates and plants (Currie 1991; Kerr 2001; Francis & Currie 2003; Kreft & Jetz 2007). Few hypotheses have been more extensively tested than the hypothesis that the spatial variation of richness is controlled by a general underlying process mediated by contemporaneous climate.

Historical climate over thousands of years has been hypothesized to affect patterns of richness in different ways. For example, climate stability during the last 21,000 yr could have created suitable areas at lower latitudes where groups of species persisted during and after glaciation times (Araújo *et al.* 2008). In the same line, postglacial dispersal limitation toward the north (i.e. species lags relative to climate), may have resulted in lower richness at higher latitudes (Svenning & Skov 2007). Alternatively, the length of time that land has been available for colonization after the last glacial retreat, which is shorter at higher latitudes, may explain the lower richness observed at these latitudes (Montoya *et al.* 2007).

Evolutionary process mediated by climate over millions of years also may generate gradients of richness. For example, higher richness in tropical environments could have arisen from temperature-dependent rates of diversification (Allen & Gillooly 2006; Allen *et al.* 2006) during the Cenozoic. Similarly, most clades could have originated in tropical climates long ago and conserved their tolerance to warmer environments as they radiated; this evolutionary constraint would prevent species to colonize temperate climates, which would increase richness in tropical environments through time (Wiens & Donoghue 2004; Wiens & Graham 2005; Hawkins & DeVries 2009). Alternatively, species of older, more basal clades that originally adapted to tropical climates of the early Tertiary could have been extirpated from the temperate environments due to global-scale cooling in the Miocene and Oligocene (Hawkins *et al.* 2006).

The relative importance of the *ecological* and the *historical/evolutionary* effects of climate on patterns of richness are subject to debate for several reasons. First, it is argued that both types of effects are not mutually exclusive (Qian and Ricklefs 2004). "Environments differ in their ability to support populations [and therefore species]; they also have different extents and histories that shape the evolutionary diversification of the clades of organisms that fill them in." (Ricklefs, 2004). Second, modern climates and historical climates are collinear (Qian and Ricklefs, 2004). For example, strong latitudinal temperature gradients have existed throughout the Cenozoic; the increase of richness toward the equator could result from either the origin of clades in tropical environments or their inability to colonize areas with lower temperatures, or the latitudinal configuration of contemporary climate (Hawkins 2006). Third, strong predictions from historical/evolutionary hypotheses have been difficult to derive and test (Currie *et al*., 1999; Currie and Francis 2004).

If the relative importance of the *ecological* and the *historical/evolutionary* effects of climate on the geographic variation of richness is to be determined, then hypotheses must generate exclusive predictions that can be tested and potentially falsify or refute the hypotheses (Currie *et al.* 1999).

Karl Popper in the 20th century proposed the criterion of falsifiability or refutability as the way to critically discriminate between available theories and discard the less informative. In Popper's (1959) view, the researcher starts with a theory or hypothesis, deduces predictions from it and then tests the predictions by comparing them with observations and experiments. If empirical observations do not conform to the predictions, then the theory or hypothesis has been falsified (i.e. it has not passed its test). However, if the predictions are verified, then, for the time being, there is no reason to discard the hypothesis from which the predictions were deduced. Currie *et al*. (1999), based on this Popperian perspective, suggested that the failure to establish the primary factors that drive the spatial variation of richness at broad scales may have philosophical foundations: that is, due to the lack of critical tests of the available explanations. Thus, by attempting to refute or falsify the available explanations, we gain critical knowledge about the natural phenomenon of interest and determine the scientific status of a theory (i.e. its importance relative to other theories). In this thesis I apply Popper's falsifiability criterion in an attempt to test the relative importance of the *ecological* and the *historical/evolutionary* effects of climate on the geographic variation of richness.

To test hypotheses in this thesis, I followed a macroecological approach. I assessed the statistical relationships (a pattern/empirical model) between richness and climatic variables at broad spatial and temporal scales (Kerr et al., 2007). Macroecology studies the properties of ecological systems as a whole (in the form of patterns and processes at broad spatial and temporal scales), instead of focusing on specific (local scale) cases (Brown & Maurer 1989; Gaston & Blackburn 2008). If a hypothesis predicts that two variables should be correlated, then the hypothesis can be tested by measuring that correlation. If the correlations hold, for example, in multiple systems (e.g. across taxa, space and time), then multiple tests of the pattern across such systems are consistent with a causal relationship in the phenomenon of interest. In this line, macroecological studies have shown very strong correlations between richness and contemporaneous climatic variables. However, it has rightly been contended that correlation does not imply causation (Qian & Ricklefs 2004). To test causality, it is necessary to manipulate the independent variable in some way and to observe whether the dependent variable changes accordingly. Clearly, it is impossible to manipulate climate experimentally at broad spatial scales, but climate has changed naturally (Kerr *et al.* 2007). Thus, one can use a 'natural experiment' *sensu* Diamond (1986) to determine, in this case, whether natural changes in climate lead to concomitant changes in richness (H-Acevedo & Currie 2003; Kerr *et al.* 2007).

The goal of this thesis is to test prominent hypotheses that suggest either *ecological* or *historical/evolutionary* effects of climate as main drivers of patterns of richness at broad spatial scales. To do this I divide the thesis into three chapters.

Chapter 1 tests competing *ecological* and *historical* hypotheses. First, I test a primary prediction deduced from the *ecological* Richness-Climate Hypothesis: when climate changes, richness should vary with climate through time in the same way that richness varies with contemporaneous climate through space. In other words, changes in climate should lead to concomitant changes in richness. Because this hypothesis predicts a particular statistical relationship between richness and climate, I also assessed the causal link. To do this, I took advantage of a large scale 'natural experiment' in climate that is both temporally extensive (over 14,000 years) and spatially extensive (over much of North America). I observed that the temporal variation in the family richness of woody plants (based on fossilized pollen) was statistically related to the spatio-temporal variation of temperature across North America at 1000 yr intervals over the last 11,000 yr. Between 14,000 yr BP and 12,000 yr BP, temperature accounted for little of the spatio-temporal variation of richness. Second, I tested three hypotheses that suggest that patterns of richness result from historical effects of climate since the last glaciation (last 21,000 years). These effects include a) climate variability, b) postglacial dispersal lags of individual species, and c) the length of time that land has been available for colonization following the Last Glacial Maximum. In all cases, the results indicate that historical climate is not a better predictor of patterns of richness than contemporaneous climate.

Chapter 2 tests a specific case of the Richness-Climate Hypothesis and shows the relevance of richness-climate models to assess potential effects of climate change on diversity, which contrast with the view that future global warming may lead to species extinction rates that would qualify as the sixth mass extinction in the history of the earth. Richness-climate models predict that regional richness of most taxa should increase with temperature in all but the warmest and driest areas. This prediction has been used project patterns of richness of plants and vertebrates under future climate change. However, tests of this prediction against observed changes in richness under natural climate change have never been assessed. In Chapter 2, I assess whether climate warming since the last glaciation led to richness declines across North

America in hot, dry areas. To do this I used temporal changes in both climate and family richness of woody plants (based on fossilized pollen) during the last 18,000 yr, at 1000 yr intervals, at specific sites. I also evaluated to what extent the observed decline of small mammal richness since the late Pleistocene at a single site in northern California conforms with predictions derived from current spatial patterns of small mammal richness of North America based on temperature and water availability. The results show that woody plants richness over the last 18,000 yr tended to increases in wet areas, but to decrease toward areas of increasing water deficit as climate warmed. Similarly, the observation that small mammal richness declined in northern California as a consequence of increasing temperatures is consistent with current spatial patterns of mammals.

Chapter 3 tests the Physiological Tolerance Hypothesis (PTH), which evokes an evolutionary effect of climate on richness gradients. The PTH proposes that current richness varies according to the *evolved* tolerances of individual species for different sets of climatic conditions. It predicts that individual species should occupy climatically suitable areas and that, therefore, the number of species present in any given locality should be essentially the number of species that tolerate the climatic conditions of that locality. To test this prediction I first assume that individual species geographic ranges expand in a region with no physical barriers, to fill 100% of the areas that possess climates the species can physiologically tolerate. Based upon this assumption, I created expected potential individual species ranges, which I used to generate potential patterns of richness. I then compared potential and observed patterns of richness. The hypothesis was tested in birds, mammals and trees natives to eastern North America. I then generated expected distributions of occupied and unoccupied areas for each species in each group to test whether patterns of unfilled potential richness are related to postglacial dispersal

lags, climatic variability since the Last Glacial Maximum (LGM), biotic interactions, or two models that propose that species occupy given areas probabilistically. The first model is conditioned on climate, and the second model on distance and direction from occupied areas (a variant of the Abundant Center Hypothesis). The test of the potential richness showed that, in all groups, when 100% occupancy is considered, the observed number of species in a particular location is lower than the number of species of the continental pool that tolerate the climate of that location. Observed patterns of unfilled richness were inconsistent with predictions from postglacial dispersal lags, climatic variability, and biotic interactions. Patterns of unfilled richness were consistent with the predictions from the distance-dependent model, but highly consistent with the predictions of the climate-dependent probabilistic occupancy model. This is true for birds, mammals and trees.

Chapter 1: Contemporaneous climate directly controls broad-scale patterns of woody plant diversity: a test by natural experiment over 14,000 years.

ABSTRACT

Broad-scale diversity gradients correlate strongly with climate. This correlation may reflect direct control of richness by contemporaneous climate. Alternatively, factors that were collinear with contemporaneous climate may have affected richness (e.g., temperature during the Last Glacial Maximum). We tested the hypothesis that contemporaneous climate directly controls broad scale patterns of richness. If climate directly controls richness, then when climate changes, richness should vary with climate through time in the same way that richness varies with climate through space. We also tested hypotheses arguing that historical climate determines patterns of richness. We found that the spatial and temporal regional variations in richness of woody-plants, observed at 1000 yr intervals and expressed as a function of temperature, remained quite congruent during the changing climate since the end of the Pleistocene (last ca. 11,000 yr). Between 14,000 and 11,000 yr BP, lags occurred during cooling periods, when richness remained anomalously high; however, richness was not anomalously low during the rapid warming preceding the Holocene. Historical climate effects did not explain patterns of richness. We conclude that, in ecological time, contemporaneous climate controls broad-scale patterns of richness. Gradients of diversity, independently of individual species responses, are likely to track current climate change, except when temperature increases are abrupt.

INTRODUCTION

Variation in species richness among biomes is one of the most striking patterns on Earth. Most obviously, the wet tropics are much richer than temperate biomes. More finely resolved geographic variation of species richness (observed at spatial grains of ~10^4 km^2) is remarkably strongly correlated with current climate. This is true in most higher taxa (Currie, 1991; Guegan *et al.*, 1998; Kerr *et al.*, 1998; Hawkins *et al.*, 2003; Field *et al.*, 2009). Richness-climate correlations within biomes are largely congruent with the global pattern among biomes (Francis & Currie, 2003). Current climate is typically by far the strongest predictor of richness (Field *et al.*, 2009).

Explanation of these patterns involves at least two distinct sets of questions. First, what processes gave rise to the particular species that tolerate the strikingly different climates in different biomes? The answer to this question is clearly historical (Wiens & Graham, 2005; Hawkins *et al.*, 2006). It speaks to differences in species *composition* among *biomes*, but less obviously to differences in *richness* (Algar *et al.*, 2009a; Hawkins *et al.*, 2012).

The second question is: why does richness, resolved at a grain of ~10^4 km^2, vary as a continuous function of current climate, both among biomes and within biomes, in which regional species pools are reasonably constant? Why is the richness-climate relationship quite consistent across biome boundaries, which mark dramatic changes in species composition? Why are richness-climate relationships quite similar among continents, despite differences in evolutionary history? For example, climate and area account for 89% of the spatial variation of angiosperm richness in North American and Chinese forests, and inter-continental differences account for an additional 1% (Qian *et al.*, 2007).

The most obvious possible answer is that current climate directly determines regional-scale geographic variation of richness. This might happen in several different ways. Climate may act as a filter for species that can maintain positive net primary productivity in a region (Kleidon & Mooney, 2000). Alternatively, climate might establish a carrying capacity for species richness, as proposed by species-energy theory (Currie, 1991). Similarly, Metabolic theory proposed that environmental temperature could set a carrying capacity for species through its effect on individual metabolic rates (Allen *et al.*, 2002). Alternatively, regional immigration and/or extinction rates could depend upon contemporary climate. For example, species may be better able to persist at lower densities in warm, wet climates (Walker, 2012).

A critical prediction of the hypothesis that current climate directly determines richness is that, when climate changes, richness should change accordingly (H-Acevedo & Currie, 2003; Kerr *et al*., 2007). Predictable *numbers* of species should migrate to, or disappear from, particular regions in response to climatic changes (H-Acevedo & Currie, 2003). In this line, recent studies have associated richness increases to warming temperatures in northern latitudes (Hiddink & Ter Hofstede, 2008), and some have used space-for-time substitution to causally link temporal richness changes and climate (La Sorte *et al.*, 2009; Algar *et al.* 2009a). If there is a causal link between richness and climate, then when climate changes, richness should vary with climate through time in the same way that richness varies with climate through space.

In contrast, contemporary patterns of richness may reflect climatic variation since the last glacial maximum. For example, Araújo *et al.* (2008) argued that climate stability during the last 21,000 yr could have created suitable areas where groups of species persisted during and after glaciation times. Stable suitable climates and species limited colonization ability could have precluded the occupation of new northern areas during interglacial periods (Araújo *et al.*, 2008), and then created a latitudinal gradient of richness. Similarly, slow dispersal from southern suitable areas could have created lags in post-glacial recolonization of individual species climatic potential ranges (Svenning & Skov, 2007), which would result in lower northern richness. Alternatively, lower richness in higher latitudes may result from the length of time that land has been available for colonization since the Last Glacial Maximum (LGM) (Montoya *et al.*, 2007). Areas covered by ice during the LGM (i.e. higher latitudes) would have less time to be colonized and therefore show lower richness. Evolutionary history has also been proposed to be responsible for geographic gradients of richness (e.g., Hawkins et al. 2006). However, we are not aware of any evolutionary hypothesis that predicts the spatial variation in species richness at grains of ~10^4 km^2 within biomes and across continents (e.g. Currie 1991), nor the strong richness–current climate correlation observed at that scale (see also Algar et al., 2009a; Hawkins et al., 2012).

Here, we test the causal link between geographic variation in richness and contemporaneous climate (versus climate at some time in the past). To do this, we treated the climatic fluctuations following the late-Pleistocene deglaciations (last ~14,000 cal. yr) in North America, as a continental-scale "natural experiment", *sensu* (Diamond, 1983). At the end of the Pleistocene, between 14,000 and 11,000 yr BP, the average temperature in North America increased by ~1.3°C/1,000 yr (Fig. 1). Regional temperature anomalies reached ~5°C (Yu, 2007). Later, during the Holocene (last ~11,000 yr), the continental average temperature varied by ~0.2°C (Viau *et al.*, 2006) (Fig. 1). Several cooling and warming events representing up to 3°C shifts in regional temperature occurred at an approximately millennial scale during this period (Viau *et al.*, 2006; Yu, 2007).

What would the richness-climate relationship look like if richness did not track temporal changes in climate? To answer this, we constructed two null-style alternative hypotheses. First, we derive the expected relationship between richness and temperature, assuming that the temporal variation in richness at particular sites over the last 14,000 yr represents white noise (or random sampling variation). Second, we allowed richness to be a constrained random walk from the earliest observed level in our data (14,000 yr BP in many cases), independently of temperature changes.

Finally, we also tested the relationship between richness and historical climate. We evaluated what proportion of the spatial variation of richness could be statistically attributed to: 1) climate stability (or climate variability) over the last 21,000 years, 2) lag effects of historical climate and 3) time since deglaciations (i.e. the length of time that land has been available for colonization since the LGM).

We show that the richness-temperature relationship across North America remained reasonably constant during the last *ca*. 11,000 yr. Before 11,000 yr BP the richness-temperature relationship was weaker. We also show that richness correlated more strongly with temperature when richness was assumed to track climate changes than when richness was assumed to vary randomly through time. Finally, historical climate was a poor predictor of richness in comparison with contemporaneous climate. Our results are consistent with the hypothesis that, at least on ecological time scales, contemporaneous climate directly controls the spatial variation of diversity.

METHODS

To test the hypothesis that richness tracked changes in climate over the last 14,000 yr, we compared the temporal variation in the family richness of fossilized pollen from woody plants (a proxy of woody plant family richness) to the spatio-temporal variation of temperature across North America at 1000 yr intervals.

Temperature data

We used two reconstructions of paleotemperature to obtain temperature values at each sampling site of richness. The first set of temperature data were taken from a general circulation model: the National Center for Atmospheric Research Community Climate System Model ver.3 (CCSM3) (Blois *et al.*, 2013a). From this, we extracted seasonal mean temperature of June-July-August. A second independent reconstruction of mean July temperature was inferred from historic plant assemblage composition using the modern analog technique (MAT) (Viau *et al.*, 2006). Both temperature reconstructions are highly correlated (Appendix S1 Table S1, S2). We estimated temperature in a 50-km radius around each sampling site using both temperature reconstructions. The two methods yielded very similar richness-temperature patterns. We therefore only present the results using the CCSM3 temperature reconstructions.

Richness data

It is currently impossible to reconstruct total historical plant species richness. We therefore used a proxy: the richness of families that are composed mainly of wind-pollinated woody plants using pollen records from the North American Pollen Database (Grimm, 2006). We shall refer to this hereafter as woody plant family richness. Fossilized pollen records in lake sediment samples are available from sampling sites across the parts of North America where lakes occur (i.e. wet areas, mainly in the Northeast) (Fig. 2; Appendix S1 Table S3). We estimated richness at 1,000 yr intervals from standardized samples rarified to 300 pollen counts (Weng *et al.*, 2006). The temporal uncertainty in fossilized pollen data is about 500 yr for the late Pleistocene (Gajewski, 2008; Blois *et al.*, 2013a). The number of sampling sites represented among time periods varied from 45 to 212 sites, unevenly distributed across the continent (Fig. 2; Appendix S1 Table S3).

The spatial grain of this study is similar to that used to construct contemporary continental patterns of gamma diversity (Field *et al.*, 2009). Pollen records from lakes of ~1-150 ha typically represent vegetation within a radius of ~50 km (Bradshaw & Webb, 1985; Prentice, 1987).

Our data included a total of 20 observable families (Appendix S1 Table S4). We used pollen richness at the family level because palynological data permit resolution among families, but not among all genera or all species within families (Gajewski, 2008). To test whether the spatial variation in these 20 observable families is a reasonable indicator of total species richness in extant woody plants, we related the modern spatial variation of species richness of native trees across North America (679 species) to the richness of the 20 families that occur in the pollen data, using 88x88 km quadrats. This spatial grain corresponds to the sampling area used for the analysis with pollen data. Species and family richness were strongly correlated: r^2=0.90 (Appendix S1 Fig. S1). To test how well richness of pollen estimates richness of extant woody plants, we related the spatial variation of modern pollen richness (i.e. pollen in the most superficial layers of sediments) and tree richness at 1780 sampling sites across North America (Appendix S1 Fig. S2a). The correlation between modern pollen family richness (restricted to the 20 families observed in the fossil pollen record) and total extant tree richness (based on the 74 families of North American trees) was r^2=0.66 at the family level and r^2=0.65 at the species level (Appendix S1 Fig. S3). When the analysis was restricted to the 217 fossil pollen sampling sites (Appendix S1 Fig. S2b), the correlations were r^2=0.63 and r^2=0.63, respectively (Appendix S1 Fig. S4). These results indicate that, in the context of variation of tree richness across North

America: a) family richness is a reasonable surrogate for species richness; b) fossilized richness is a reasonable surrogate for extant richness; and c) the sampling sites from which fossilized pollen data are available capture well the variation in richness across North America.

Statistical analysis

We related richness as a sigmoidal function of temperature using least-squares non-linear regressions (Bates & Watts, 1988), according to the following model:

$$WFR = \alpha 2 + (\alpha 1 - \alpha 2) / (1 + \exp((TEMP - \tau) / b))$$

where WFR is the number of woody plant families, and TEMP is the temperature in Kelvins. The remaining terms are fitted parameters: α2, the upper asymptote; α1, the lower asymptote; τ, the value of the abscissa at which the ordinate is halfway between the top and the bottom asymptotes; and *b*, the slope of the ascending portion of the curve. We found that this sigmoidal model provided a significantly better fit to the data than the power or hyperbolic functions used in other studies (as did Currie & Paquin 1987).

Using this model, we determined the proportion of the spatial variance in richness that could be statistically related to temperature at each time period. Next, we asked how much of the spatio-temporal variance in richness can be related to a single relationship that is unchanging through time (model M1). Finally, using an analysis of covariance (Bates & Watts, 1988), we tested whether allowing the shape of the relationship to vary among time periods explained significantly more variance. To do this, we used the entire data set, and we related richness to temperature, time, and temperature x time, where time is a categorical variable distinguishing among time periods at 1,000 yr intervals. This allows each of the model's parameters to vary among periods (model M2). The two models were then compared using an extra-sum-of-squares test (Bates & Watts, 1988) and the Akaike information criterion (AIC).

We evaluated two null-type scenarios that postulate that richness varied temporally independently of temperature. We used the same comparison of models M1 and M2 for each scenario. Scenario A proposes that temporal variation in richness over the last 14,000 yr at individual sites represents white noise (or sampling variation). Here, we calculated the mean and the variance of richness through time at each sampled site. We then generated random richness values, drawn from a normal distribution with the same mean and variance. Scenario B postulates that richness variations over the last 14,000 yr were a constrained random walk. We first determined the range of observed richness changes between adjacent 1,000 year time periods at each site. We then used a uniform random distribution over this range to draw random richness changes. At each site, we added these random changes to the earliest observed richness to generate a constrained random walk at subsequent 1,000 year periods, with the additional constraint that richness could not fall below zero. We simulated each scenario 1,000 times.

To test hypothesized effects of historical climate on richness patterns, we evaluated three different hypotheses using the same sigmoidal model. (1) The Climate stability hypothesis (Araújo *et al.*, 2008), suggests that a measure of climate variability (i.e. difference between current and past climate) is a better predictor of richness than contemporaneous climate. We calculated climate variability for each time period (1,000 yr BP, 2,000 yr BP etc.) as the difference between temperature at that time period and temperature at 21,000 yr BP. (2) The Lag effect hypothesis predicts that the richness-temperature relationship should be stronger when richness is related to the temperature of a previous period (time lag). To test this hypothesis, we related richness in each time period to the temperature 1,000 to 5,000 years earlier. (3) The Time since deglaciation hypothesis predicts that unglaciated areas, having been available longer for colonization, should have higher richness than areas that were covered by ice during the LGM.

To test this hypothesis, we compared the richness-temperature relationships in glaciated and unglaciated portions of North America. If the hypothesis is true, richness should be higher in unglaciated areas, after accounting for temperature.

Note that we did not compare models M1 and M2 as in the initial analysis since the primary goal of testing historical hypotheses was to determine whether different possible effects of historical climate were better predictors of richness than contemporaneous climate at the different time periods.

We tested for spatial autocorrelation in the residuals of models using Moran's I. Moran's I dropped to approximately I <0.16 at *ca*. 500 km. Thus, temperature captures the continental variation of richness, but some spatial structure remains at regional scales.

RESULTS

Individual models at 1,000 yr intervals over the last 14,000 yr show that a sigmoidal function of temperature accounts for 18% to 74% of the spatial variation in woody-plants family richness across North America at any given time period (Fig. 3; Table 1). Richness-temperature patterns are quite consistent through time (Fig. 3; Appendix S1 Fig. S5). In a model that pools over all 14 time periods (Table2 Model M1), a sigmoidal function of temperature explained 54.5% of the spatio-temporal variation in family richness. Allowing the parameters of the richness-temperature relationship to vary among periods increased explained variation to 60.2% (Table2, model M2). Model M2 was significantly stronger than model M1 ($F_{52, 2015} = 6.66$, $P < 10^{-5}$; $\Delta AIC = 221.22$), but the difference in explained variance between the two models was small (5.5%). The greatest differences clearly occurred in the late Pleistocene: 11,000 to 14,000 BP. Richness was not significantly related to time alone between 1,000 and 14,000 yr BP (ANOVA, $F_{13, 2057} = 4.61$, $P = 0.387$). The same analyses carried out using temperatures reconstructed with the MAT technique are qualitatively very similar to, but somewhat stronger than, the ones shown here (Appendix S1 Table S5, Table S6). The observed richness-temperature relationship through time was stronger than would be expected by chance under either of the alternative null-type scenarios we proposed (Appendix S1, Fig. S6). In scenario A, where temporal variation in richness represents white noise, the adjusted R^2 values for both models M1 and M2 are close to observed values. This is not surprising: richness varies among sites more than it does through time, and richness in the white noise scenario is constrained to be close to the mean observed richness at each site. It is therefore necessarily fairly strongly correlated with observed richness. Richness is nonetheless significantly more strongly related to temperature than white noise predicts (Appendix S1, Fig. S6 (a, b), $p<0.0001$). The predictions of the constrained random walk (scenario B) agree very poorly with observed richness (Appendix S1, Fig. S6 (c, d), $p<0.0001$).

Temperature-variability at each time period explained, on average, much less of the spatial variation of richness (26.5%; see Appendix S1, Table S7) than contemporaneous temperature (50.5%). When lags in richness were considered, the mean (over all time periods) of the proportion of the variance in lagged richness explained by temperature was not significantly different among lags (or lag datasets), including no-lags (ANOVA, $F_{5, 63} = 1.046$, $P = 0.398$; Appendix S1, Fig. S7). This is primarily because the continental gradients of temperature were reasonably consistent through time (Appendix S1 Table S1, S2).

Finally, richness observed 1,000 yr BP in glaciated areas was *higher* than richness in unglaciated areas, after controlling for temperature (Fig. 4). A partial regression analysis (Appendix S1, Fig. S8) further shows that age of area alone accounted for a small proportion of the variance (3.4%) in comparison with contemporaneous temperature alone (72.7%).

DISCUSSION

Recent literature has documented many correlations between broad-scale spatial variation in species richness and climate (Field *et al.*, 2009). These correlations, however numerous, leave open the possibility that the relationship may not be directly causal. To test causality, it is necessary to manipulate the independent variable in some way and to observe whether the dependent variable changes (Kerr *et al*., 2007). Clearly, it is impossible to manipulate climate experimentally, but climate has changed naturally. For example, Willis *et al.*(2007) used changes in climate related variables over *ca*. 300,000 years to predict long-term variations in plant richness at a single site in Hungary. Others have used decadal (Algar *et al.*, 2009a) or seasonal (H-Acevedo & Currie, 2003) changes in climate to test causality between richness and climate over broad spatial scales. Our study is the first to test that causal link using a large scale "natural experiment" that is both temporally extensive (over 14,000 years) and spatially extensive (over much of North America) following the last glacial period. The study also tests several hypotheses that suggest that gradients of diversity are the result of historical processes mediated by climate.

Our results are largely consistent with the hypothesis that contemporaneous climate directly controls most of the variation in species richness. First, the relationship between temperature and fossilized woody plant pollen family richness, assessed at millennial intervals, remained reasonably constant between 11,000 yr BP and 1,000 yr BP (Fig. 3; Table 1), under still considerable climate changes (Fig. 1). This suggests that patterns of richness remained close to equilibrium with contemporaneous climate changes, at least at the millennial scale, after the end of the Pleistocene.

Second, our study rejected three different hypotheses suggesting that patterns of richness can be explained by historical climate. Climate variability (or climate stability) explained only half as much of the spatial variation in richness that contemporaneous climate can explain. This is inconsistent with previous studies in amphibians and reptiles arguing that climate stability over the last 21,000 years is a better predictor of species richness than contemporaneous climate (Araújo *et al.*, 2008). Our test of this hypothesis takes a step further than previous work. While others have analyzed current patterns of richness as a function of climate stability, our study tested the effect of this climatic variable on richness at different times in the past. In most cases (Appendix S1, Table S7) climate stability was not a better predictor than contemporaneous climate. Climate variability, however, has been shown to be a good predictor of richness variation at the millennial scale in localized sites (Willis *et al.*, 2007). We also rejected the hypothesis that climate effects are lagged. The richness-temperature relationship assuming lags was not stronger (as the hypothesis predicted) than the richness-climate relationship with no lags. Although individual species ranges do not relate in a constant manner to climate (Williams *et al.*, 2001; Veloz *et al.*, 2012), richness does track changing climate. Finally, the time since deglaciation hypothesis predicted that richness should be higher in the areas that were never covered by ice during the LGM. We found that the opposite was true; richness was higher in areas that were covered by ice during the LGM (Fig. 4). Further, the proportion of the spatial variation explained by age of area alone was very low in comparison with the proportion of the variance explained only by temperature (Appendix S1, Fig. S8). These results are inconsistent with the time since deglaciation hypothesis.

Our results, taken in isolation, cannot exclude at least one historical explanation for richness-climate correlations: the Tropical Conservatism hypothesis (Wiens & Graham, 2005).

Evolutionary radiations of angiosperms during the early Tertiary could have generated sets of species adapted to the climatic conditions that existed at the time, and those tolerances have been strongly conserved to the present (Wiens & Graham, 2005; Hawkins & DeVries, 2009). If dispersal limitation is not an issue, then current climate could filter species according to climatic tolerances established long ago. This explanation is likely to be true at least at very coarse spatial grain: there are no palm trees in the arctic. However, it seems unlikely to account for richness-temperature relationships that are observed at finer scales. Climatic niches are rarely filled: individual species rarely occupy all climatically suitable regions, even when they do occupy climatically similar neighbouring regions (Normand *et al.*, 2009; Boucher-Lalonde *et al.*, 2012). Consequently, the number of tree species present in any given ~10^4 km^2 region in North America is usually much smaller than the number of species in the continental pool that tolerate those climatic conditions (H. Vázquez-Rivera, unpublished data). Thus, if a variant of the Tropical Conservatism hypothesis is to explain contemporary patterns of richness, it must explain why range-filling is incomplete, even in the absence of dispersal barriers. It should additionally explain why realized niches are not fixed relative to climate: over the last 21,000 years, the realized niches of many plant taxa have changed considerably through time (Veloz *et al.*, 2012). Species (or higher taxonomic levels) responses to past and current climate changes also suggest that taxa do not show perfect niche tracking (La Sorte & Jetz, 2012; Veloz *et al.*, 2012). There is growing evidence that niche shift does occur (Gallagher et al. 2010). Moreover, species richness and species composition relate to different climatic variables, in at least some taxa (Algar *et al.*, 2009b; Hawkins *et al.*, 2012). Climatic tolerance, however it arose, seems unlikely to be the prime driver of richness patterns at the spatial grain examined here.

The most divergent spatial richness-temperature relationships we observed were from 14,000 to 12,000 yr BP (Fig. 3; Table 1; Appendix 1 Table S5, Fig. S5). During this period, the sigmoidal model fit was poorer, and richness was higher than expected (relative to the time-invariant model) in areas near the retreating glacial front. Part of the poor fit may be due to uncertainty about temperature during this period. The correlation between our two temperature estimates was weakest during this time (see Appendix S1 Table S1). That said, we suspect that the weak richness-temperature relationships from 14,000 to 12,000 yr BP are not mainly due to errors in the estimates of temperature. Rather, our result is consistent with the conceptual framework of biodiversity dynamics triggered by a forcing event (e.g., climate change) suggested by Jackson & Sax (2010). Their framework proposes that a change in the environment triggers immigration and extinction, which can lead to a transient period of excess or reduced diversity before the diversity of a particular site or region approaches equilibrium again. If extinction is faster than immigration, then diversity deficits are expected; however, if immigration rates are faster than extinction rates, then a diversity surplus can occur (Jackson & Sax, 2010).

We suggest that the anomalously high richness observed between 14,000 to 12,000 yr BP in the coldest parts or North America resulted from relatively rapid colonization, with an extinction lag, during a period of rapidly fluctuating climate. The average temperature in North America between 14,000 and 12,000 yr BP was ~4°C lower than during the Holocene (Fig. 1). However, in eastern North America, during the earlier Bølling–Allerød warm period (~14,500 yr–12,400 yr BP) (Yu, 2007), temperature was only ~1°C lower than in the Holocene. This period was punctuated by three century-long cold events where temperatures decreased by ~3°C: the intra–Bølling (~13,800 yr BP), the Older Dryas (~13,500 yr BP), and the intra-Allerød (~12,700 yr BP) (Yu, 2007). We suggest that sites near the glacial front were colonized by temperate- and warm-temperate taxa (see Appendix S1Table S4) during the warm intervals. However, there was insufficient time for richness *at the family level* to decline at 14,000 - 12,000yr BP (which were cooler than the preceding millennia) to the levels predicted by climate during Holocene. Family-level richness in a region increases when a single species from a new family colonizes the region. However, family richness declines only when all species in a given family drop out of the regional flora. It is not surprising that an extinction debt would develop during periods of rapid climatic fluctuation. In very interesting contrast, we did not observe anomalously low richness during warming periods. Our results suggest that richness at the family level increases during warming more rapidly than it falls during cooling.

The periods and the parts of North America where our richness-temperature relationships are weakest are also the instances where no-analog species assemblages occurred (Williams *et al.*, 2001; Blois *et al.*, 2013a). The presence of no-analog communities (Williams *et al.*, 2001; Blois *et al.*, 2013a), the observation that woody taxa have occupied distinct realized niches at different points in time (Veloz *et al.*, 2012), and the current lack of evidence of massive extinctions of plants during the rapid climate changes of the late Pleistocene (Williams *et al.*, 2011), suggest that individual taxa may fail to track the climates in which they originated. It is possible that species during this period responded to other aspects of climate, such as inter-annual climatic variability (Williams *et al.*, 2001). Therefore, our results suggest that no-analog assemblages may also reflect extinction debt, at least in part. In sum, higher richness and no-analog communities during rapidly changing climate are also inconsistent with the hypothesis that patterns of richness are simply the sum of individual species climatic tolerances that evolved long ago and have been strongly conserved.

Dispersal limitation probably had little effect on our data at the millennial scale. At least over the last 11,000 yr, richness seems to have tracked climate changes fairly well. The analysis on time lags for richness also suggests that individual species lags have no effect on current patterns of richness. Rapid migrations and short-term lags of woody plants during the abrupt climate changes of the last ~16,000 yr are well documented. Estimated response times for migrations in response to climate change vary among species and sites, but most are in the range of ~60-100 yr (Gajewski, 1987; Williams *et al.*, 2002), or faster (Tinner & Lotter, 2001).

Contemporary patterns of plant richness relate statistically to both temperature and precipitation (Currie, 1991; O'Brien *et al.*, 2000; H-Acevedo & Currie, 2003; Hawkins *et al.*, 2003; Hawkins & Porter, 2003). Our historical models did not include precipitation because most sites in our analyses were in areas of relatively high precipitation where contemporary variation in richness depends relatively little on precipitation (Francis & Currie, 2003). In fact, between 1,000 yr BP and 11, 000 yr BP, most of the spatial variation in richness (~45%) is explained only by temperature; precipitation alone explains around 1%; in the late Pleistocene, however, precipitation seems to be a better predictor of richness (H. Vázquez-Rivera, unpublished data).

Finally, our results have important implications for current climate change. Our results suggest that climate is a direct driver of richness patterns, not just an indirect correlate. Thus, diversity shifts due to current human-induced climate change should be predictable from richness-climate models based on contemporary spatial variation of richness and climate (Algar *et al.*, 2009a). These models predict that richness should increase over most of North America, except in dry areas that are forecast to become even drier (Currie, 2001). There are, however, two caveats. First, factors such as anthropogenic fragmentation of landscapes and modified disturbance regimes (e.g., fire) may create barriers to migration (Botkin *et al.*, 2007; Jackson & Sax, 2010) that did not exist in the past. Such barriers may slow or prevent equilibration of richness to climate. Second, if future climate warming is rapid and large, richness may initially overshoot its equilibrium with climate, as apparently happened during the Bølling–Allerød period at the southern front of the Laurentide ice sheet. It should be noted that the time scale of this study is much broader (millennia) than the time scale at which future climate change is expected to happen (decades). Nevertheless, the results obtained here help to improve our knowledge as to the way richness responds to climate changes.

Tables

Table 1. Regressions of woody-plant family richness and temperature, estimated from the CCSM3 climate model, for the last 14,000 cal yr. The same analyses using temperatures estimated using the modern analog technique show somewhat stronger richness-climate correlations, particularly at the earlier time periods (R^2=0.69 – 0.43 at 10000-14000 BP; Appendix S1 Table S5).

Time interval (Years BP)	N	F-test	R^2	Model parameters			
				α1	α2	τ	*b*
1000	212	1449.0	0.733	3.6	9.5	288.1	1.3
2000	198	1272.2	0.733	3.5	9.5	288.2	1.3
3000	193	1260.4	0.731	3.7	9.4	289.0	1.1
4000	184	1056.4	0.738	3.4	10.1	288.3	1.5
5000	191	1065.7	0.719	3.5	9.5	288.7	1.1
6000	191	954.1	0.668	3.6	9.7	289.1	1.5
7000	171	779.3	0.587	3.5	9.7	289.6	2.0
8000	161	689.8	0.518	3.9	9.1	287.8	1.6
9000	133	545.1	0.505	3.6	8.4	288.1	1.3
10000	137	495.2	0.380	3.6	9.1	288.3	2.3
11000	118	380.3	0.207	0.1	9.2	281.4	4.7
12000	78	270.9	0.176	6.6	9.1	290.3	0.4
13000	59	163.9	0.200	5.5	8.9	291.8	1.8
14000	45	101.8	0.181	6.5	10.5	296.8	0.1
1000-14000	2071	8346.3	0.545	4.0	9.2	288.4	1.5

Woody plants family richness (WFR) is fitted as a function of temperature (in Kelvins) at 1,000 yr intervals, according to the following sigmoidal model:

WFR = α2 + (α1 – α2) / (1 + exp((TEMP – τ) / *b*)). N: Number of sampling sites at a given time interval. $P<10^{-5}$ for all regressions. The interval labeled 1000-14000 represent data pooled over all time intervals as described for model M1 in Table 2.

Table 2. Regression models relating richness to a sigmoidal function of temperature covering different time periods. The same analyses using temperatures estimated with the modern analog technique show similar results, but models are somewhat stronger that the ones shown here (R^2=0.72 and R^2=0.75 for model M1 and model M2 respectively; AppendixS1 Table S6).

Model	Source	DF	SS	MS	F-test	P	R^2	AIC
1,000 – 14,000 yr BP								
M1: model parameters identical for all time periods	Regression	4	105231	26943.5	8346	$< 10^{-5}$	0.545	2383
	Residual	2067	6515	3.15				
	Total	2071	111746					
M2: model parameters free to vary among time periods	Regression	56	106186	1896.19	68.	$< 10^{-5}$	0.602	2162
	Residual	2015	5560	2.76				
	Total	2071	111746					

Models are based on data pooled over all time intervals, as shown in Table 1. Model M1 relates the variation in woody-plant family richness among sites and times as a single sigmoidal function of temperature. Model M2 allows the parameters of the sigmoidal function to vary among all time periods.

Figures

Figure 1. Mean July temperature anomaly of North America, relative to current temperature, for the last 14,000 cal yr. Dates expressed as calibrated years before present; redrawn from (Viau et al., 2006).

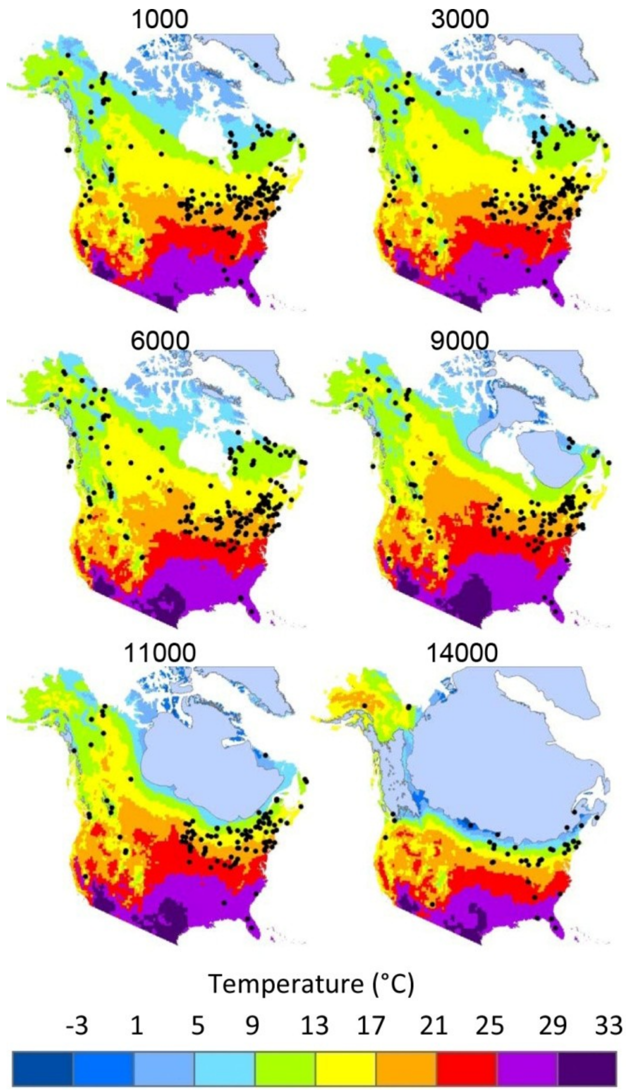
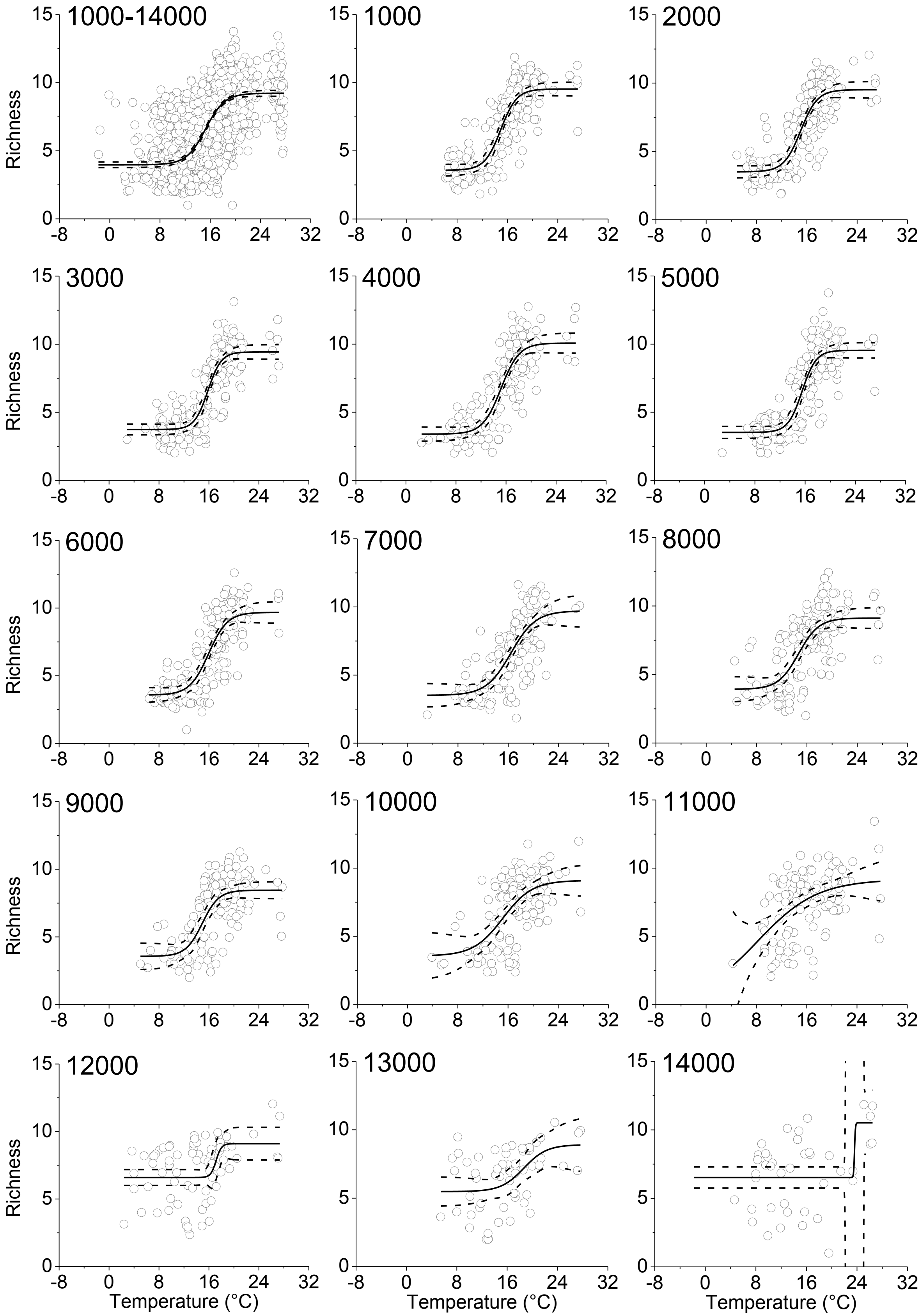


Figure 2. Spatial configuration of sampling sites for pollen in North America. Maps show divergences among six different times during the last 14,000 cal yr. Temperatures correspond to the CCSM3ver.3 (Blois *et al.*, 2012) and represent seasonal mean temperature of June through August. Black dots represent the spatial distribution of sampling sites for temperature and richness at each time period. Ice masses are represented in light blue.

Figure 3. The observed relationships between woody plant family richness and temperature at 1,000 yr interval over the last 14,000 cal yr in North America. Dash lines represent 95% confidence intervals. Relationships estimated with temperatures from the CCSM3 general circulation model. The comparable relationships estimated with temperatures from the MAT are shown in Appendix S1 (Fig. S5).



1000-14000
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
Richness
Temperature (°C)

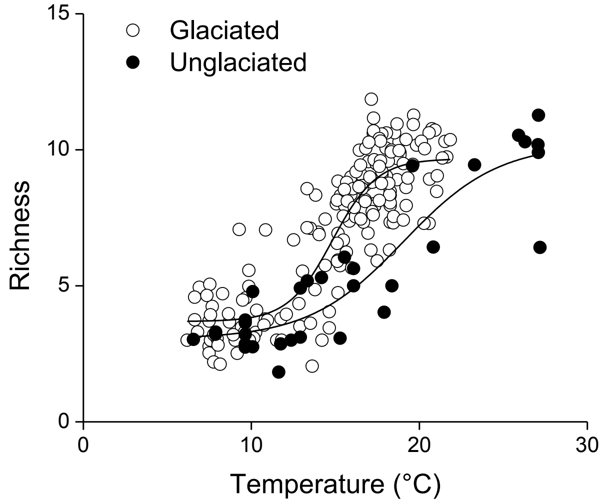


Figure 4. The observed relationship between woody plant family richness and temperature 1,000 yr BP, in areas of North America that were either glaciated or unglaciated during the Last Glacial Maximum.

Chapter 2: Does richness decline when climate warms?

ABSTRACT

Projections of future climate change effects on diversity typically predict potential massive species losses. Moreover, empirical data showing that small mammal diversity declined in Northern California during the global warming at the Pleistocene-Holocene transition suggest that future increasing temperatures will lead to significant loss of species richness. However, richness-climate relationships predict that regional richness of most taxa should increase with temperature in all but the warmest and driest areas. To test this prediction, we contrasted current richness-temperature relationships through space *vs.* temporal richness-temperature relationships over the last *ca.* 18,000 yr, for woody plants of North America. Similarly, we contrasted the current richness-temperature relationship for small mammals of North America, with the temporal pattern of this group observed over the late Pleistocene in Northern California. We found that woody plant family richness did not decline similarly everywhere when climate warmed. In regions of lower water deficit (i.e. wetter areas), richness tended to increase with temperature. In contrast, in regions of higher water deficit (i.e. drier areas), richness tended to decrease. For mammals, the decline of species richness with increasing temperature after the late Pleistocene in Northern California is consistent with the current spatial pattern for this group in hot, dry areas. If richness responds to changing climate in the future in the similar way that it did in the past, then changing climate is more likely to lead to richness declines in areas where increased temperature is accompanied by higher water deficits, than in wetter areas. Massive species extinctions did not occur during the late Pleistocene warming; they seem unlikely during the current warming.

INTRODUCTION

It has been speculated that massive species extinctions may occur as a result of recent climate disruptions (Pimm 2009; Bellard *et al.* 2012). Global warming is the most prominent of these changes. The global average surface temperature has increased about 0.89 [0.69 to 1.08] °C between the years 1901 and 2012, and projections suggest that temperature may increase by 1.7 to 4.8 °C by the end of the 21th century (IPCC 2013). Observed shifts in species ranges across latitude and altitude, and changes in phenological events such as flowering, breeding and arrival of migratory species have been attributed to these climate changes (Parmesan 2006).

Concerns about richness declines have been raised mainly through projections of future global warming effects on individual species climatic niches (Heikkinen *et al.* 2006; Elith & Leathwick 2009). Niche-based models forecast climate change effects by simulating future species distributions under selected climate change scenarios. To do this, niche models relate current species distributions to habitat variables (environmental and/or spatial characteristics), project those correlations on projected future climate, and quantify the mismatch of the two (Heikkinen *et al.* 2006; Elith & Leathwick 2009).

These models predict, for example, that oceanic islands will undergo species extinctions when sea-level rises and species suitable climatic conditions disappear as climate warms (Bellard *et al.* 2014). Species losses in both mountain (Williams *et al.* 2003) and lowland (Colwell *et al.* 2008) ecosystems of tropical areas are also expected to happen under projected warming. Similarly, projections of future climate warming effects on regional diversity distributions often predict potential massive species losses in most biomes of the globe due to the mismatch of species climatic tolerances and shifting patterns of temperature (Peterson *et al.* 2002; Thomas *et al.* 2004).

In contrast, richness-climate models predict that richness is likely to increase in most areas where climate warms, except in areas were warming is accompanied with higher water deficits. Richness-climate models are based on the contemporary geographic variation in species richness in relation to climate. If the empirical relationship between richness and climate is causal (H-Acevedo & Currie 2003; Kerr *et al.* 2007; Algar *et al.* 2009a), then those relationships should make consistent predictions through space and through time. It has been shown that richness-climate models are strong predictors of the number of species across regions (or biomes) of the planet (Francis & Currie 2003), and through time, when climate changes seasonally (H-Acevedo & Currie 2003), or across millennia (Vázquez-Rivera, Chapter 1; Willis *et al*. 2007).

Based on the statistical relationship between current richness and climate (temperature and precipitation), Currie (2001) predicted that species richness of trees and vertebrates would increase with global warming in most regions of the contiguous US, but that they would decreases in the warmest and driest areas. Similarly, Sommer *et al.* (2010) showed that the regional capacity for species richness of plants in the globe is predicted to decrease with increasing temperatures in areas with higher water deficits.

Predictions from richness-climate models regarding changes of richness during periods of climate change can be tested directly with historical data. When climate changes, richness should change through time in the manner predicted by contemporary richness-climate relationships. Algar *et al.* (2009a), using occurrence records of butterflies and climate change of the 20^{th} century in North America, tested the ability of both niche models and richness-climate models to predict shifts in geographic patterns of species richness. They found that patterns predicted from richness-climate models based on historical data (1900-1930), corresponded to patterns observed more recently (1960-1990). They also found that richness-climate models yielded more accurate predictions than niche models.

A similar approach to test richness-climate predictions under climate change is to determine whether observed temporal patterns of richness change in the direction that current spatial patterns predict. La Sorte *et al.* (2009) first related the spatial variation in winter bird richness across North America to temperature. They then showed that terrestrial winter bird richness, averaged over all of North America, changed from 1975 to 2001 in the direction predicted by the spatial relationship between richness and temperature.

Empirical tests of the effect of the environment on compositional turnover through space and through time have been carried out in eastern North America for plants (Blois et al. 2013b). Blois et al. (2013b) estimated compositional dissimilarities through space and through time to calibrate models. Then they predicted compositional dissimilarity through time (temporal turnover) using either a spatial model (space-for-time) or a temporal model (time-for-time). Blois et al. (2013b) found that predictions relying on space-for-time substitution were ~72% as accurate as "time-for-time" predictions during the late Pleistocene, but not during the Holocene, when climate variations where small relative to the late Pleistocene.

In many taxa, richness varies as a function of the interaction between temperature and water availability (e.g. Table 1 in Francis & Currie (2003), and Table 1 in Willis *et al.* (2007)), and one would not expect richness to change with respect to temperature alone in the same manner everywhere. In the case of plants, the interaction of temperature and water deficit is such that richness covaries positively with temperature in areas of low water deficit, and negatively in areas with higher water deficit (Francis & Currie, 2003).

The prediction that richness should increase with temperature in most areas, except in the driest, warmest areas, can be tested with temporal observations from the global warming of the Pleistocene-Holocene transition. During this period, annual mean temperature in North America increased by ~4 °C. The North American Pollen Database (Grimm 2006), which contains fossilised pollen records from sites across much of North America for the last ~18,000 years, provides the opportunity to test predictions for temporal patterns of plants in specific regions. Similarly extensive data are not available for animals. However, the observation that small mammal richness declined at a locality in Northern California during the rapid warming at the Pleistocene-Holocene transition (Blois *et al.* 2010), does allow the prediction to be tested for this site.

In this study we test whether current richness-climate patterns through space correctly predict the direction of the temporal changes of richness during the warming of the Pleistocene-Holocene transition. Specifically, we tested the prediction that when, climate warms through time, richness should increase with temperature in all but the warmest and driest areas (Currie 2001). To do this, we examined changes in woody plant family richness at 362 sites with different water availability across North America over the last 18,000 years. We also examined how small mammal richness currently relates to temperature and water deficit, and whether the decline in small mammals observed by Blois *et al.* (2010) at the Pleistocene-Holocene transition in northern California conforms with this relationship.

METHODS

To test richness-climate predictions under climate change, we examined the contemporary relationships between richness of trees and climate across North America (the US and Canada). We then contrasted the current patterns of richness with temporal trends observed in the fossil richness of this group during the last 18,000 yr at specific sites over the same areas. We carried out the same procedure for small mammals of North America, but the fossil richness was restricted to a single site in Northern California.

Contemporary richness-climate relationships through space

We assembled individual species range maps for trees and terrestrial small mammals of North America. For trees, we used Little's range maps of North American native trees (USGS 1999), and for mammals, we used the range maps from Nature Serve (Patterson *et al.* 2007). We examined small mammals specifically because the fossil richness data were obtained from Blois *et al*. (2010), who observed richness declines in this group during the Pleistocene-Holocene transition. Small mammals are defined here as the species of non-volant mammals with mass <3 kg; however, in some families (Table S1, Appendix S2), some species can reach weights higher than 5kg. For either group, trees or mammals, richness corresponds to the numbers of families or species, respectively, in a grid of 2254 quadrats, each 88 km x 88 km, covering the U.S. and Canada. This spatial grain represents approximately the size of the smallest isolated patch of species presence / absence in either tree or mammal species range maps. We excluded coastal quadrats with less than 50% land to avoid area effects.

For each quadrat we computed two climate-related variables: annual mean temperature (T) and annual total water deficit (WD). WD, the difference between annual potential evapotranspiration and annual actual evapotranspiration, is a measure of absolute water stress that is independent of the actual vegetation of the site. It is considered to be biologically meaningful in ecological studies in comparison with other indexes (Stephenson 1998). We examined richness-temperature relationships in six WD categories (0-250 mm yr^{-1}, 251-500 mm yr^{-1}, 501-750 mm yr^{-1}, 751- 1000 mm yr^{-1}, 1001-1250 mm yr^{-1}, >1250 mm yr^{-1}), following

Francis and Currie (2003). Temperature was obtained from the WorldClim database (Hijmans *et al.* 2005), potential evapotranspiration from the Consortium for Spatial Information (CGIAR-CSI) (http://www.cgiar-csi.org/), and actual evapotranspiration from the FAO GeoNetwork database (http://www.fao.org/geonetwork/srv/en/main.home). All climate variables represent mean annual values over the period 1960-1990.

Temporal trends in richness and climate during the last *ca.* 18,000 yr

It is currently impossible to reconstruct total historical tree species richness per site. We therefore used a proxy: the richness of families that are composed mainly of wind-pollinated, woody plants (i.e. plants that reach a height of 3m or more), using pollen records from the North American Pollen Database (Grimm 2006). We shall refer to this hereafter as woody plant family richness. Our data included a total of 20 observable families (Table S2, Appendix S2). We show elsewhere that pollen richness at the family level is a reasonable indicator of total species richness in extant woody plants (Vázquez-Rivera, Chapter 1). For each site in the North American Pollen Database, we estimated the number of woody-plant families at 1000 yr intervals from standardized samples rarified to 100 pollen counts (Birks & Line 1992). Standardized samples rarified to 300 pollen counts are sometimes recommended (Weng *et al.* 2006). However, using only sites with ≥300 pollen counts led to the loss of many sites, and we considered that the loss of spatial coverage across North America was a more serious problem than the loss of precision in estimating richness. We repeated our analyses using the sites where ≥300 pollen counts were available. The results were qualitatively very similar, but with lower statistical power using 300 pollen counts (n=95 sites) than using 100 counts (n=362 sites).

Fossilized pollen records are available from lake sediment samples across the parts of North America where lakes occur (i.e. wet areas, mainly in the Northeast) (Fig. 1). Pollen records from lakes of ~1-150 ha typically represent vegetation within a radius of ~50 km (Bradshaw & Webb 1985; Prentice, 1987). This spatial grain is similar to the grain we used to construct current continental patterns of mammals and trees.

For each sampling site we calculated the mean annual temperature at the time periods for which richness values were available. We used reconstructions of paleotemperature taken from a general circulation model: the National Center for Atmospheric Research Community Climate System Model ver.3 (CCSM3) (Blois *et al.* 2012).

For small mammals, we digitized the time series of species richness presented by Blois *et al*. (2010) for Samwell Cave, in Northern California. Richness values were linearly interpolated to 1000 yr intervals to match those from temperature data.

We included all sites from the North American Pollen Database for which there were pollen records at a minimum of six dates that incorporate dates of the late Pleistocene–Holocene transition (14,000 – 9,000 yr BP, when temperature increased the most) (Table S3, Appendix S2). Because the prediction we tested suggests different temporal trends (positive or negative) in richness when temperature increases in regions with different water availability, we first determined the temporal trends of richness alone (i.e. richness-time slopes) at each site where temperature increases from the past to the present (Table 1, Table S3 Appendix S2). If changes in climate drive the observed trends in richness, then the relationship between temporal trends of richness and temperature should conform to current spatial patterns of richness and climate (i.e. richness should increase with temperature in wetter areas, but decrease in warmer, drier areas). Thus, we also correlated the temporal variation of richness and temperature at each site (Table 2, Table S4 Appendix S2).

We further distinguished sampling sites by regions with different water availability. However, WD, as currently calculated, was not available in the paleoclimate data. Therefore, as a first approximation, we used current water deficit in North America (Fig. 1). Although climate has changed over the last 18,000 yr, we assumed that the climatic gradients remained broadly similar through time (to a first approximation, a North-South gradient of increasing temperature, and an East-West gradient of increasing water deficit). To test this assumption, we correlated current temperatures with historical temperatures at 1000 yr intervals in sites of North America free of ice since the last 18,000 yr (i.e. present temperature *vs.* temperature values at 1000 yr BP, 2000 yr BP, etc.). The correlations were $r > 0.9$ during the last *ca*. 13,000 yr. Correlations between current temperatures and historical temperatures between 14,000 yr and 18,000 varied from $0.47<r<0.58$. Further, we correlated the current water deficit with current temperature and precipitation. We then used the calibrated model together with historical temperature and precipitation to project historical water deficit at different times (i.e. from 18,000 yr BP to 1000 yr BP at millennial intervals). The correlation between current and historical water deficit ($r = 0.62$; Fig. S1 Appendix S2) shows that, overall, the historically driest areas of North America have remained in the Southwest in the past *ca*. 18,000 yr.

RESULTS

We first examined the spatial variation in contemporary tree family richness in relation to climate so that we could subsequently compare temporal patterns of richness to it. Contemporary tree family richness increases with temperature in most parts of North America, except in areas with the highest water deficit (Fig 2a). This is similar to the pattern that Francis and Currie (2003) observed at the family level in angiosperms.

In the fossilized pollen, the proportion of sites with negative trends (i.e. richness decreased from the past to the present) was higher in regions with higher water deficit (Table 1). In all these sites temperature increased from the past to the present. The correlations between temporal trends of richness and temperature at each site (including statistically and non-statistically significant correlations) are also predominantly negative in regions with high water deficit and predominantly positive in areas with low water deficit (Table 2; Figure 3). Restricting the data to statistically significant correlations shows the same pattern (Table S5, Appendix S2). Consequently, the probability of observing a negative relationship between richness and temperature when climate warms is higher towards the south western region of North America (Figure 4).

Although temperature increased during the Pleistocene-Holocene transition over most of North America, the results presented above include some cases where temperature decreased (Table 1). These sites are mainly in the Yukon Territory and Alaska and near the Continental Divide where the Cordilleran and Laurentide Ice Sheets met (Fig. 2 b, c, Appendix S2). Water deficit is low (0-250 mm) in these areas.

Among contemporary small mammals, the spatial variation of species richness in North America correlates positively with temperature in the wet areas (i.e. water deficit is lowest), and negatively with temperature in the driest areas (Fig. 2b). The negative relationship between small mammal species richness and temperature observed by Blois *et al*. (2010) in Northern California at the end of the late Pleistocene (Fig. 5), corresponds to a relatively dry area with current water deficit of approximately 1000 mm yr^{-1} (areas of Eastern North America, at the same latitude, show water deficits in the range of 250-500 mm).

DISCUSSION

Current richness-climate models allow predictions of richness under future climate change. These predictions are of particular importance because of the possible effects of global warming on species diversity. However, because these predictions of effects of future climate change are essentially untestable, tests with historical data are crucial.

We used temporal trends in both richness and temperature over the last 18,000 yr in sites in North America to test the fundamental assumption of the time-for-space substitution: that when climate warms, richness should increase with temperature in all but the warmest and driest areas, as predicted by contemporary spatial models.

We observed that, as climate warmed during the Pleistocene-Holocene transition, plant richness in North America generally decreased in areas with high water deficit and increased in areas with low water deficit. These results are broadly consistent with contemporary global patterns of richness and climate (Francis & Currie 2003), as well as with current altitudinal patterns in lowlands of subtropical mountains (Liu *et al.* 2007), where water deficit is negatively correlated with plant richness. Our results are also consistent with studies on plants worldwide that suggest that water plays a major role in spatial patterns of richness through warm, dry areas (Hawkins *et al.* 2003; Whittaker *et al.* 2007).

There was clearly considerable variation among sites within macro-climatically similar regions (Tables 1 and 2). Site-specific factors beyond macroclimate (e.g. microclimate, soils, slope and aspect, etc.) probably influenced the variations in richness during the climate change. The most striking departure from the general pattern described above is that richness-temperature relationships are consistently positive immediately south of the Great Lakes, but negative north of the Great Lakes (Fig. 1; Fig. S2 a and b, Appendix S2). Both areas are wet. We do not think that the negative relationships are due to the lakes acting as a dispersal barrier to post-glacial recolonization (Montoya *et al.* 2007), because areas with positive richness-temperature slopes are also found north of Lakes Erie and Ontario (Fig. S2 b, Appendix S2). Richness-temperature slopes become negative farther north. The Holocene climate south of the Great Lakes is relatively warm, and richness is high. We hypothesize that, in this region, which was deglaciated between 18,000 BP and 13,000 BP, the 1000 year time intervals sampled in this study captured the recolonization process. Thus, richness increased as climate warmed. In contrast, areas deglaciated between 13,000 yr BP and 11,000 yr BP, north of Lake Huron and Lake Superior (~46° N), are cooler, and have lower richness. We hypothesize that, within 1000 years post-deglaciation, recolonization overshot the level at which richness eventually stabilized during the Holocene. Consequently, the time slices of 1000 yr did not capture the recolonization. Richness in these areas then declined to the levels observed during the Holocene. This hypothesis is consistent with the observation that richness was considerably higher than temperature would predict in these areas 11,000-13,000 yr BP. Richness then declined through the early Holocene, yielding negative richness-temperature relationships.

Proportions of positive and negative richness-climate relationships are similar within the medium and medium-high water deficits levels. At these levels of water deficit, the slope of the predicted relationship (based on regional macroclimate) flattens, and switches from positive to negative (Table 2; see also Francis & Currie's 2003 Fig. 3). We would expect local variations in microclimate, particularly in mountainous areas in the West, that could lead to wetter or drier sites within regions.

Contemporary relationships between small mammal richness and climate (Fig. 2b) also show that richness correlates negatively with temperature in areas with higher water deficit and positively with temperature in areas of lower water deficit. The Samwell Cave area studied by Blois *et al.* (2010) currently corresponds to a region with medium-high water deficit (~1000 mm; Fig. 1). These patterns predict that, in the area studied by Blois *et al*. (2010), warming would lead to a *decrease* in species richness. The Samwell Cave region became drier from the late Pleistocene to the Holocene. Water deficit changed from an average of ~194 mm yr^{-1} during the late Pleistocene to ~440 mm yr^{-1} during the Holocene. Clearly, there was a substantial decrease in water availability accompanying an increase in temperature of approximately 3 °C (~7 °C in the late Pleistocene to ~10 °C during the Holocene). Declines in small mammal richness over the last *ca.*13,000 yr in the arid western US have been linked to climate change processes evoking moisture reduction and increasing temperature (Grayson 1998, 2006).

We conclude that the results of Blois *et al*. (2010) are consistent with the predictions derived from current richness-climate models. Their suggestion that global change will lead to significant loss of richness appears to be a special case limited to hot, dry areas, whereas the more general pattern is mainly in the opposite direction. For example, current models for mammals and birds predict that higher temperatures for the year 2050 should lead richness to decrease in the southern US and to increase in cold and mountainous areas (Currie 2001). Other studies also suggest that future increasing temperatures will increase extinction probability in lizards (Sinervo *et al.* 2010) and plants and insects (Colwell *et al.* 2008) in warm and dry areas.

Currently, the expected increase of 2–4°C in the global average surface temperature by the end of the 21th century (IPCC 2013) has created concern that climate change can potentially lead to massive species losses everywhere (Deutsch *et al.* 2008; Bellard *et al.* 2012). Some studies based on niche models have estimated substantial species extinctions under different scenarios of future global warming (Peterson *et al.* 2002; Thomas *et al.* 2004; Colwell *et al.*

2008), but these predictions are contentious, because they are based on assumptions about the extent to which species ranges, and their apparent physiological tolerances, will, or will not shift in response to changing climate (Heikkinen *et al.* 2006; Soberón & Nakamura 2009; Wiens *et al.* 2009). Others studies based on empirical negative trends of both species richness (Myers *et al.* 2009; Tingley *et al.* 2012) and species populations (Collen *et al.* 2011; Mair *et al.* 2012) in relation to climate change have also predicted increased species extinction risks. However, evidence of massive species extinctions due to current global warming is still lacking, and extinctions associated with climate change are controversial. For example, Pounds *et al.* (2006) concluded that the extinction of harlequin frogs (*Atelopus sp*.) in the mountains of Costa Rica was caused by the interaction between climate change and a pathogenic fungus. Yet, Rohr *et al.* (2008) showed that other variables that include regional production of bananas and beer are better predictors of these extinctions.

Empirical evidence of massive extinctions of plants during the last natural global warming (~15,000–10,000 yr BP, when global mean temperature increased by ~ 4°C) is also lacking in the fossil record. This lack of evidence has questioned current estimates of species extinction risk under future climate change, particularly because recent studies indicate that the climate changes observed during the Pleistocene Holocene transition may have been even faster than current ones (Hof *et al.* 2011). Only a few cases of species extinctions have been documented in trees (Jackson & Weng 1999; Cole 2010). This is not surprising; in woody plants, richness has tracked changing climate over the last *ca*. 11,000 yr (Vázquez-Rivera, Chapter 1), and species have shifted their climatic niches since the last glacial period (Veloz *et al.* 2012).

Extinctions in the mammals of North America (and other parts of the world) are better known for large species, although the ultimate causes remain controversial (Lima-Ribeiro & Felizola Diniz-Filho 2013). The North American megafauna disappeared during this time, but probably well before the Bølling-Allerød warm period (Gill *et al.* 2009), perhaps related to an extraterrestrial impact (Firestone *et al.* 2007) or to human encroachment (Lorenzen *et al.* 2011). For small mammals, available evidence suggests that species extinctions since the late Pleistocene are due to changing climate (Grayson 2006). Blois *et al.* (2010) attributed regional declines in species richness during the late Pleistocene-Holocene transition to the global warming of this period. They further suggest that future global warming will lead to significant loss of [species] richness (Blois *et al.* 2010). We suggest that losses of species richness are more likely to be observed with drying in warmer, already dry areas. This is consistent with the decrease in small mammal species related to both moisture reductions and increasing temperatures in the western US during the late Pleistocene (Grayson 1998, 2006).

Only a relatively small portion of North America is sufficiently dry for richness to be predicted to decrease with increasing temperature. In the driest part of the US Southwest, the predicted decrease in small mammal species richness with increasing temperature is ~2.7 species per degree C, where regional assemblages contain ~40-60 species (Fig. 2b). In woody plants, the predicted decrease of family richness in the same region is ~0.4 family per degree C, where the regional assemblage contains ~10-20 families. This would correspond to the loss of roughly 2.6 species per degree C. Arguably, the loss of any taxon is never unimportant; however, the reader can judge if these estimates qualify as “significant” or “massive”.

In terms of applicability, we provide empirical evidence that suggests that spatial patterns of richness and climate can be used to predict, to a first approximation, the direction in which temporal patterns of richness would change in specific regions when climate changes. This knowledge can then be used to determine more accurately where species losses are more likely to occur with changing climate, and then advise conservation strategies aiming to integrate climate change into conservation planning (Kerr *et al.* 2007; Heller & Zavaleta 2009).

We conclude that massive species losses due to direct effects of climate change are unlikely to occur everywhere, in contrast to what many studies have suggested. Instead historical changes of richness associated to the abrupt warming of the Pleistocene-Holocene Transition in North America, suggest that species losses with current and future global warming are more likely to be observed in hot, dry areas. Nevertheless, this conclusion should be taken with caution. The observed responses of richness to the climate warming of the Holocene-Pleistocene transition are in a time scale that is much broader (millennia) than the time scale at which future climate change is expected to happen (decades). However, since the predictions derived from current richness-climate models conform well with observations, they could well serve to forecast possible effect of current and future climate changes on richness at the short and mean term, and for specific regions.

Tables

Table 1. The proportion of sites with positive or negative temporal trends in richness of woody plants during the late Pleistocene-Holocene transition in areas of different water deficit (WD) in North America. We distinguish the numbers of sites with negative (Richness↓) and positive (Richness↑) temporal trends in richness at sites with negative (T↓) or positive (T↑) trends in temperature. Sample size (N) includes sites with statistically and non-statistically significant trends.

			Direction of the temporal trends (%)			
			T↑ Richness↓	T↑ Richness↑	T↓ Richness↓	T↓ Richness↑
WD (mm yr^{-1})	Category	N				
0-250	1	119	28	39	8	26
251-500	2	196	28	70	1	2
501-750	3	32	41	59	-	-
751-1000	4	12	75	25	-	-
1001-1250	5	3	67	33	-	-
>1250	6	-	-	-	-	-

Table 2. The proportion of sites with positive or negative correlations between temporal values of richness of woody plants and temperature during the late Pleistocene-Holocene transition in areas of different water deficit (WD) of North America. Negative relationships represent decreasing richness with increasing temperatures through time and positive relationships represent increases in both richness and temperature through time as shown in Fig. 3. Sample size (N) includes cases with both statistically and non-statistically significant correlations. Percentages estimated with statistically significant correlations only, show the same pattern (Table S5, Appendix S2).

			Type of correlation (%)	
WD (mm yr^{-1})	Category	N	Negative	Positive
0-250	1	79	46	54
251-500	2	192	26	74
501-750	3	32	47	53
751-1000	4	12	58	42
1001-1250	5	3	67	33
>1250	6	-	-	-

Figures

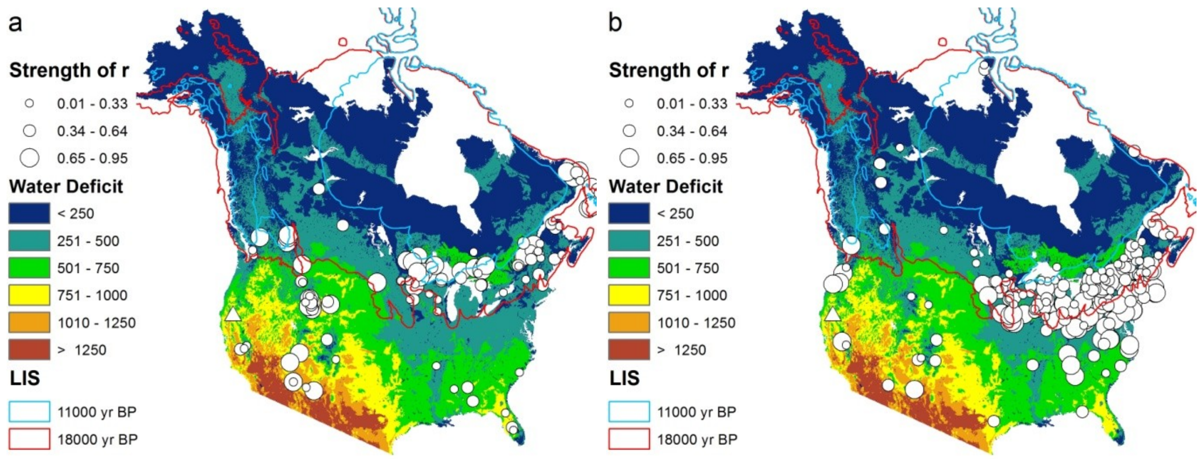


Figure 1. The distribution of sampling sites with a) negative or b) positive temporal trend of richness during the Pleistocene-Holocene transition across different categories of current water deficit in North America. In all cases, temperature increases to the present. Sites for woody plant family richness are indicated as circles. The sampling site for small mammal species richness in Northern California is indicted as a triangle. Circle size indicates the strength of the temporal relationship (Spearman r) for richness. Because dates differ among sites, as indicated in Table S3, the Cordilleran and Laurentide Ice Sheets (LIS) are represented for 18,000 yr BP (red line) and for 11,000 yr BP (blue line) as a reference to locate older and younger sampling sites.

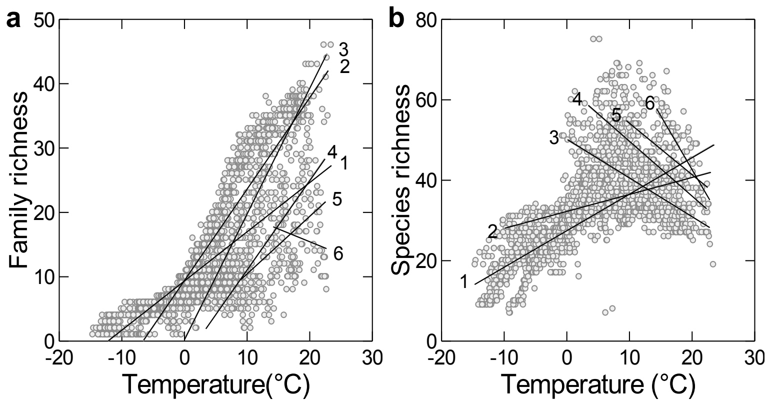
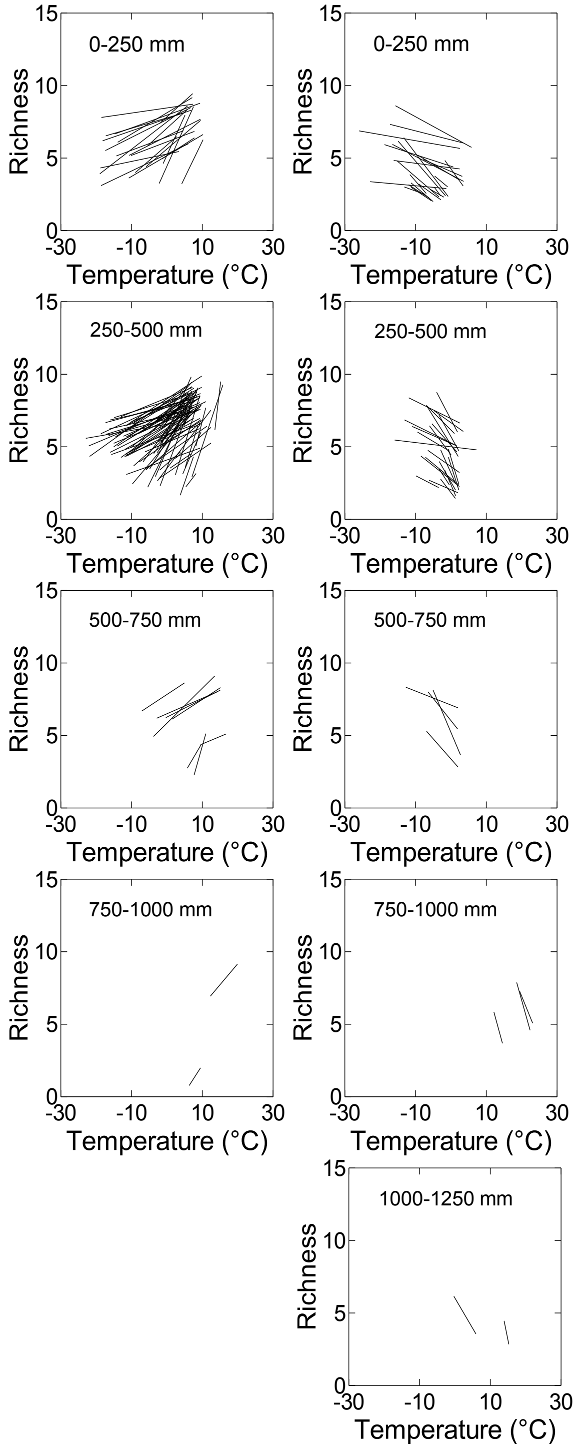


Figure 2. The linear relationships between current temperature and a) woody plant family richness and b) small mammal species richness, over North America, considering quadrats within specified ranges of water deficit: (1) 0-250 mm yr^{-1}, (2) 251–500 mm yr^{-1}, (3) 501–750 mm yr^{-1}, (4) 751–1000 mm yr^{-1}, (5) 1001–1250 mm yr^{-1}, (6) >1250 mm yr^{-1}.

Figure 3. The fitted linear relationships between temporal variation of richness of woody plant families and temperature, observed at n=156 sites across North America. Sites only represent correlations that are statistically significant (Table S4 Appendix S2). Panels indicate regions with different categories of current water deficit. For clarity, relationships with positive slopes are represented on the left and relationships with negative slopes on the right. The relationships all cover the Holocene-Pleistocene transition, but they do not cover identical periods of time (Table S4 Appendix S2). No data showed statistically significant positive relationships in the region with water deficit category 1001-1250 mm yr^{-1}.


0-250 mm
0-250 mm
250-500 mm
250-500 mm
500-750 mm
500-750 mm
750-1000 mm
750-1000 mm
1000-1250 mm
Richness
Temperature (°C)
0
5
10
15
-30
-10
10
30

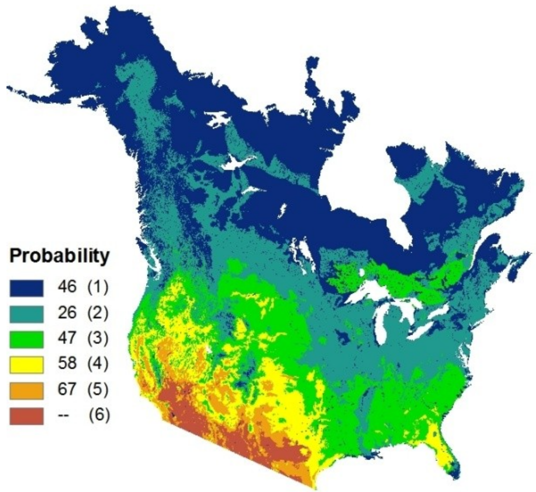


Figure 4. The probability of a negative slope in the temporal richness-temeprature relationships when climate warms. The probability (in percentages) is based on the ratio of negative slopes to the sum of negative and positive slopes across sites of North America over the last 18,000 yr. Probabilities are calculated using both statistically and non-statistically significant correlations, as shown in Table 2. Water deficit level is indicated in parenthesis, following Francis and Currie (2003): (1) 0-250 mm yr^{-1}, (2) 251–500 mm yr^{-1}, (3) 501–750 mm yr^{-1}, (4) 751–1000 mm yr^{-1}, (5) 1001–1250 mm yr^{-1}, (6) >1250 mm yr^{-1}.

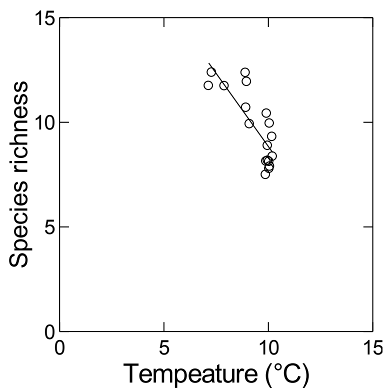


Figure 5. The temporal relationship between small mammal species richness and temperature during the late Pleistocene-Holocene transition at Samwell Cave, northern California, US. (Blois *et al*., 2010). Current water deficit at this sampling site is approximately 1000 mm yr^{-1}.

Chapter 3: Do species richness patterns mainly reflect climatic tolerance?

ABSTRACT

Taxonomic richness is strongly correlated with climate through space. The hypothesis that climate –temperature and precipitation– directly controls gradients of richness has received much correlative support. However, the processes that give rise to these correlations are still debated. Here, we first test the hypothesis that richness gradients mainly reflect the sum of individual species climatic tolerances (potential richness). We found that, for trees, birds, and mammals in eastern North America, the number of species that can tolerate the climate of an area is generally greater than the number whose ranges overlap that area. We then tested whether patterns of unfilled potential richness are related to postglacial dispersal lags, climatic variability since the Last Glacial Maximum (LGM), biotic interactions, or two models that propose that species occupy given areas probabilistically. The first of these models is conditioned on climate, and the second is conditioned on distance from occupied areas (a variant of the Abundant Center Hypothesis). We generated expected distributions of occupied and unoccupied areas for each species under each of these hypotheses. We found that the shape of the relationships between observed richness and expected richness from postglacial dispersal lags, climatic stability, or biological interaction did not correspond to the shape predicted by these hypotheses. In contrast, the shape of the relationship was consistent with the shape of the relationship predicted by the climate-dependent probabilistic occupancy model. This is true for birds, mammals and trees. We conclude that individual species climatic tolerances is not the process generating the main current patterns of richness, nor are post-glacial dispersal lags, climatic variability since the LGM or biotic interactions. we did not observe the expected shape of the relationship predicted by the

INTRODUCTION

Many hypotheses have been proposed to explain gradients of richness (reviewed in Willig *et al.* (2003)). Among them, the hypothesis that current climate –specifically, temperature and precipitation– directly controls geographic gradients of richness has received much correlative support (Adams & Woodward 1989; Kerr *et al.*, 1998; Francis & Currie 2003; Hurlbert & Haskell 2003; Kalmar & Currie 2007; Kreft & Jetz 2007; Algar *et al.*, 2009a; Tittensor *et al.* 2010).

However, the processes that give rise to these correlations are still debated (Francis & Currie 2003; Hawkins *et al.* 2003; Field *et al.* 2009). The most obvious, and probably the oldest, hypothesis is that geographic patterns of richness are determined principally by the tolerances of individual species for climate.

Several processes could underlie species climatic tolerances as the main factor driving diversity gradients. For example, species in widespread, less variable, older climates (e.g. tropical environments) may have developed narrower climatic tolerances, which would limit species dispersal across environmental gradients (Janzen 1967; Terborgh 1973). Limited dispersal and the accumulation of new species through speciation and lower extinction rates in a given stable environment (Terborgh 1973; Kozak & Wiens 2007; Cadena *et al.* 2012) could lead to higher richness. Similarly, groups of taxonomically related species may be limited by intolerance of harsh climatic factors at the poleward edges of their geographic ranges, and biotic interactions at the equatorial edges (Kaufman 1995). In the same line of reasoning, higher species richness at lower latitudes may represent conserved tolerances to ancestral tropical climates, which were widespread when many groups originated. Intolerance of colder climates may then have limited species dispersal into the more recent temperate climates (Wiens &

Donoghue 2004) but cf. (Wiens 2007). Climatic constraints (tolerances) also could affect ecophysiological trade-offs in plants, for example, by decreasing the range of feasible growth strategies in harsher environments (out of the tropics), which ultimately would result in higher richness in more stable environments (within the tropics) (Kleidon & Mooney 2000; Kleidon *et al.* 2009).

All of these hypothesized processes assume that species geographic ranges expand to fill the areas that species can physiologically tolerate. The hypothesis that species climatic tolerances generate patterns of richness predicts that the number of species present in any given locality is essentially the number of species that tolerate the climatic conditions of that locality. Thus, species ranges and contemporaneous climate must be more or less in equilibrium. However, previous studies have shown that plant species (Pither 2003; Boucher Lalonde *et al.* 2012; Sunday *et al.* 2012) and terrestrial ectotherms (Sunday *et al.* 2012; Araújo *et al.* 2013) do not fully occupy the geographic ranges delimited by their climatic tolerances. This observation is apparently inconsistent with tropical niche conservatism (TNC) as an explanation of geographic variations in richness. TNC might be rescued if climatic potential ranges were incompletely filled because of transient historical effects. For example, after the last glaciation, slow dispersal from suitable areas in the south could have left suitable areas unoccupied in northern latitudes (Svenning & Skov 2007). Alternatively, climatic variation since the Last Glacial Maximum could have prevented species from occupying northern areas where climate changed more drastically (Araújo *et al.* 2008).

Alternatively, incomplete climatic niche filling might also occur if geographic areas that fall within a species climatic tolerance are filled probabilistically. Consider two scenarios by which this might happen. First, each species may occupy areas within a biome as a bivariate

Gaussian function of temperature and precipitation (Boucher Lalonde *et al.* 2012). According to this hypothesis, the probability of occurrence of a species is highest at the mean of its climatic range and decreases symmetrically to maximum and minimum values (possibly with respect to transformed climatic variables). Even the most suitable climates may be partially unoccupied, despite being geographically close to occupied areas with the same climate. This might occur if, for example, processes of colonization and extinction at broad scales resemble those associated with metapopulation dynamics at the landscape level, and if species colonization or persistence probability were conditioned on climate according to a Gaussian relationship. Areas with marginal climates would sometimes be occupied, but often not. Similarly, metapopulation models suggest that even highly suitable sites within any given species range maybe temporarily unoccupied, for example, due to environmental stochasticity or habitat modification (Gonzalez *et al.* 1998; Hanski 1998).

A second probabilistic scenario resembles the Abundant Center Hypothesis, according to which population density is highest at the center of species distributions, and declines to the edges (Brown 1984; Brown *et al.* 1995; Sagarin & Gaines 2002). In principle, if extinction were stochastic across a species range, and if colonization of unoccupied areas occurred as a function of proximity to occupied areas within a species range (sources of colonists), then occupied ranges should be surrounded by a ring of unoccupied, but potentially suitable areas. These areas would presumably be quite dynamic, as colonization and extinction occur.

Here, we ask the following questions: a) In a large region with no major barriers to dispersal (eastern North America), if species occupy all areas with climates that they can tolerate, what patterns of richness would result, and how do they differ from observed patterns? b) How does range filling vary spatially? c) Are there geographic areas where species richness is, in a sense, “climatically saturated”: i.e. limited by the number of species that tolerate the climate, while in other places, richness is climatically under-saturated? This might be the case if range limits were mainly determined by climate in cold or dry areas, and by biotic interactions in climatically benign places, d) Why is range filling incomplete? (i.e. what explains unfilled potential richness?) e) Do different taxa (trees, mammals, and birds) have similar patterns in this respect?

METHODS

To test the effect of species climatic tolerances on patterns of richness, we assume that the climates that a species can tolerate are, to a first approximation, the climates observed within the species range. This assumption is the foundation for most studies aiming to project potential species climatic ranges. In principle, species may physiologically tolerate a broader range of climates. A final assumption was that no major physical (geographic) barriers to dispersal would limit species range filling. We therefore limited our study to Eastern North America (ENA), east of the 1000 m elevation cline.

To analyze whether different taxa had similar observed and expected patterns, we assessed birds, mammals and trees natives to eastern North America.

Climatic data

We used annual mean temperature and annual total precipitation. Data were obtained from the WorldClim database (Hijmans *et al.* 2005). Patterns of richness are strongly correlated with those two variables (Francis & Currie 2003). Some might argue that physiological tolerance of climatic extremes is more biologically relevant to species distribution limits (e.g. minimum winter temperature). It can equally be argued that species responses to integrated climate (e.g., growing degree-days, frost-free days, total annual primary productivity) are more important.

However, measures of climates means (temperature and precipitation) have been shown to be important factors in limiting species' geographic range expansion at the regional and global scales (Pigot et al. 2010). Similarly, geographic patterns of richness are often correlated approximately equally strongly to measures of climates means, or variances (Gouveia et al. 2013). Because climatic means and variances are very strongly correlated when examined over broad spatial scales (Boucher Lalonde et al. 2012), it is difficult to resolve this question empirically. Since means can be estimated much more precisely than extremes, we preferred to use means here.

Climates were generated according to Boucher Lalonde *et al*. (2012), with some modifications. Boucher Lalonde *et al*. (2012) created 20 bins at homogeneous intervals for both temperature and precipitation. For this they used the square root values of precipitation (not necessary for temperature) in order to normalize the data.

We created 30 bins for both temperature and precipitation applying Jenks' natural breaks classification method available in ArcGIS. This method minimizes the in-class difference and maximizes the between-class difference of the data, which allows obtaining classes that have, if possible, the same number of continuous values (Casali and Ernst 2012). We also preferred Jenks' method because it allows using the actual values of the variables, which facilitates their biological interpretation.

Observed patterns of richness

To generate observed richness patterns for each group we used current species geographic ranges. We first selected the species according to the following criteria. For birds: a) the species is native to the Americas, and resides or breeds in North America (US and Canada). b) At least 80% of the species mapped range is in eastern North America (ENA). c) If the species breeds in

NA but migrates elsewhere, then at least 80% of the breeding range is observed in ENA. For mammals: a) the species is restricted to NA. b) At least 80% of the species range is observed in ENA. For trees: a) the species is native to NA. b) At least 80% of the species range is observed in ENA.

A total of 100 species of birds, 65 species of mammals and 348 species of trees were included in the analysis. For birds and mammals we used the range maps provided by Nature Serve (Patterson *et al.* 2007). For native trees of NA we used Little's range maps provided by the U.S. Department of Agriculture, Forest Service (USGS 1999).

Range maps were rasterized at 1km for further manipulation, but their grain, based on the smallest isolated patches of presence or absence ranges between 10 and 20 km. Thus, our conclusions apply to observed and/or expected richness within regions of approximately 400 km^2.

Richness maps were assembled for each taxon by tallying individual species ranges.

Expected patterns of richness

The Tolerance hypothesis, in its simplest form, predicts that the species that can tolerate the climate in a given location would be present in that location. To determine potential richness we first determined the climates (combinations of temperature and precipitation) at which each tree, mammal and bird species is observed to occur. We then generated a potential geographic range for each species, based on the assumption of 100% occupancy of those climates in ENA. Next, we tallied the individual potential species ranges to produce potential richness maps for each taxon (Table 1). The extent to which species are observed to occupy these potential ranges can be called "niche filling", as "niche unfilling" is considered to happen when a species only partially expands over an available climate (i.e. partially fills the niche) (Petitpierre *et al.* 2012).

Finally, unfilled potential richness was calculated as the difference between potential richness and observed richness (Table 1, Figure 2).

The Postglacial-dispersal lags hypothesis (Svenning & Skov 2007) suggests that there should be no unfilled niches (and thus no unfilled potential richness) south of the maximum glacial extent at the Last Glacial Maximum (*ca.* 42° N), or at very least that a constant proportion of niches should be unfilled. Above this latitude, the proportion of unfilled potential richness should increase monotonically poleward (Fig. 3a). Unfilled proportional richness was calculated as the ratio between unfilled potential richness and potential richness (Table 1).

The Climate variability hypothesis suggests that unfilled proportional richness should increase monotonically with climate variability since the Last Glacial Maximum (Fig. 3e). We calculated historical climate variability as the difference between temperature 21,000 yr BP and current temperature (Araújo *et al.* 2008). For this hypothesis, we restricted the sampling area to the unglaciated part of eastern North America in order to control for the time that area has been available for recolonization after the retreat of the glaciers. In this area, the temperature anomaly yields negative values only. We used the absolute value of the anomaly in order to facilitate the interpretation of the data.

The hypothesis that species ranges are generally limited by abiotic factors at high latitudes and by biotic interactions at lower latitudes (Kaufman 1995) predicts that the unfilled proportional richness should be high at low latitudes and progressively lower toward high latitudes.

The probabilistic hypothesis of Boucher-Lalonde *et al.* (2012) predicts that each species occupies any given area with a probability that is a function of climate, but that is not dependent upon proximity to other occupied areas. To produce expected climate-dependent richness values, we generated expected occupancy of each species for all areas, based on a probabilistic, bivariate Gaussian model of species climatic occupancy (Boucher Lalonde *et al.* 2012). The probability of occupancy was calculated as the proportion of pixels of a given climate (i.e. the combination of temperature and precipitation) that occur within the species geographic range, relative to the total number of pixels of that climate in ENA. The species expected ranges that we generated were qualitatively similar to those obtained by Boucher Lalonde *et al.* (2012). Bin delineation (i.e. number of bins) does not affect the generation of expected ranges (Boucher Lalonde *et al.* 2012). For each sampling location, we then summed the probabilities of occupancy over all species in the study region. This yields the expected climate-dependent richness (Table 1). We then calculated unfilled expected climate-dependent richness as the difference between potential richness and expected climate-dependent richness. For simplicity, we will refer to this value as unfilled expected richness. If this model is correct, we expect that unfilled potential richness will vary as a function of unfilled expected richness with a slope of 1.0 and an intercept of 0.0 (Fig. 3i). Summing probabilities over all species in a given location to calculate expected richness assumes that the probability of occupancy of the different species incorporates the effect of factors, other than climate, that are found in that location (for example, the presence of other species).

Finally, the Abundant Center Hypothesis predicts that every species is surrounded by a ring of potentially occupiable habitat, independently of the location of the range. The sum of these rings is unfilled potential richness, according to this model. We will refer to this richness as “unfilled surrounding richness”. If unoccupied areas surround occupied ranges, then unfilled potential richness (i.e. the difference between potential richness and observed richness) should vary as a function of unfilled surrounding richness with a slope of 1.0 and an intercept of 0.0

(Fig. 3m). To determine the unfilled surrounding richness, we first created a symmetric buffer area of constant width around each species geographic range. We then overlaid these buffers to produce maps of unfilled surrounding richness (Table 1). We repeated this exercise for buffers of 50 km, 100 km, 200 km and 400km width. Since the strongest relationships were observed using buffers of 200 km, we present only those results.

Data analysis

We sampled each of the variables described above at 1,111 sampling sites (representing $1km^2$ squares) evenly distributed across ENA at 100 km from each other. Sample size for the climate variability hypothesis is N=323 sites because the sampling areas correspond to the unglaciated area of ENA. Then, for each taxonomic group, we correlated the variables according to the predictions from each hypothesis tested.

RESULTS

For the three taxonomic groups (birds, mammals and trees), observed richness in a given geographical area is usually, but not always, lower than the predicted potential richness based on the assumption of 100% occupancy of the climatic niches (Fig. 1). That is, the number of species present in any given location is usually lower than the number of species in the same biome that tolerate the climatic conditions of that location, and that could, at least in principle, disperse to that region.

Observed richness is equal to the potential numbers of species (based on the assumption that species completely fill their climatic niches) in relatively few areas (Fig. 1). The proportion of unfilled potential richness generally increases toward colder areas (higher latitudes) for mammals and trees, as well as in relatively cold and wet areas to the west of the study area (higher elevations) for mammals (Fig. 2). Birds show the opposite pattern; unfilled richness is greatest through the warmer and wetter areas of the southeastern US. That said, there is clearly a great deal of spatial variation in niche filling that is not captured in any simple latitudinal gradient.

The Post-glacial dispersal lag hypothesis predicts that there should be no pattern in the extent of niche filling in parts of the continent that were not glaciated, and that unoccupied potential niches should increase poleward (Fig. 3a). We observe that the shape of the relationship between unfilled potential richness and latitude is not consistent among taxa, that it does not conform to the predicted pattern, and that the scatter around the central trend is very large (Fig. 3b, c, d). Unfilled richness is not constant at latitudes lower than 42° N.

The Historical Climate variability hypothesis predicts that unfilled potential climatic niches should be more abundant in areas where the climate has changed the most between the Last Glacial Maximum and the present (Fig. 3e). The shape of the relationship between unfilled richness and historical climate variability are, in general, inconsistent with the shape of the relationship predicted by this hypothesis. It differs among taxa, and, with the possible exception of mammals, they differ from the pattern predicted by the Climate variability hypothesis (Fig. 3f, g, h).

The biotic-interactions hypothesis predicts higher values of niche unfilling at low latitudes with a monotonic decrease at higher latitudes. The patterns we observe in the unfilled proportional richness (Fig. 3b, c, d) are clearly inconsistent with the predicted pattern from biotic-interactions. Moreover, the mismatch between observed and predicted patterns applies equally to all three taxonomic groups, whereas the patterns we observe among the three groups are very different.

The climate-dependent probabilistic occupancy model predicts that unfilled potential richness should be the same as the summed probabilities of unoccupancy based on climate (i.e. unfilled expected climate-dependent richness) (Fig. 3i). A monotonically increasing linear relationship with a slope 1.0 and intercept 0.0 should be observed. We would expect that there must be some relationship between these two variables, because the probability of occupancy is calculated from observed occupancy. But the observed relationship between the two variables need not conform to the expected slope of 1.0 and intercept of 0.0. Patterns of unoccupied potential niches are well predicted by climate-dependent niche filling in trees (Fig. 3l). However, in birds the residuals tend to show more variation in sites of higher values of expected unfilled richness (Fig. 3j).

The Abundant Center Hypothesis predicts that unoccupied potential niches should be close to potentially occupiable surrounding locations, in a manner that is independent of range location (Fig. 3m). The shape of the relationships show that unfilled potential richness and unfilled surrounding richness are generally well correlated in birds, mammals and trees (Fig. 3n, o, p). In mammals and trees, unfilled potential richness tends to be somewhat higher than predicted by unfilled surrounding richness. Nonetheless, in trees unfilled potential richness is well predicted from unfilled surrounding richness.

Overall, expected potential richness based on a binary model (tolerate *vs.* does not), does not account for the relationship between observed richness and climate. Observed patterns of unfilled potential climatic niches (as measured by the shape of the relationships between observed richness and predicted richness) are generally inconsistent with the predictions from models that postulate post-glacial lags in recolonization and historical climate variability. Instead, predictions from models that suggest that species niche filling is probabilistically climate-dependent and distance-dependent predict potential niche filling reasonably well, the former model being more accurate.

DISCUSSION

Species richness is highly correlated with climate (Currie 1991; Kerr *et al.*, 1998; Francis & Currie 2003; Hurlbert & Haskell 2003; Kalmar & Currie 2007; Kreft & Jetz 2007; Algar *et al.*, 2009a; Field *et al.* 2009; Tittensor *et al.* 2010). We analyzed to what extent species climatic tolerances account for this correlation. If the number of species present in any given locality is essentially the number of species that tolerate the climatic conditions of that locality, then one would expect high correspondence between observed richness and expected richness based on species climatic tolerances.

Our results show that number of observed species in any given location is usually lower than the number of species expected to be there based on their climatic tolerances (Fig. 1). This, in principle, suggests that species climatic tolerances do not account for the number of species in a region with any given climate. Species do not occupy all the areas whose climate they tolerate, even in the absence of dispersal barriers. A divergence between observed and expected richness could be due to physical (geographical) barriers, which may affect the extent of potential ranges based on climatic tolerances. Dispersal barriers could produce expected ranges bigger than the observed ranges. However, there are no obvious physical barriers to prevent dispersal in eastern North America, nor any evidence of barriers in the data. Boucher-Lalonde *et al*. (2012) showed that, for any given species, climatically suitable, but unoccupied, areas occur immediately adjacent to occupied areas. Further, one would expect dispersal barriers to affect multiple taxa. During the late Pleistocene-Holocene transition, richness of woody plants along the front edge of the retreating glaciers indicates that species dispersal was not limited by the presence of the great lakes (Vázquez-Rivera, Chapter 2). Further, in our study, the ratio of observed:expected richness (Fig. 1) is poorly correlated among taxonomic groups ($R^2 < 0.12$). We concluded that it is unlikely that the inclusion of physical barriers could account for the large discrepancy between observed richness and expected richness.

The mismatch between observed and expected richness could also be related to unfilled species climatic ranges due to post-Pleistocene recolonization lags (Hawkins & DeVries 2009). Our results show that the lack of pattern in unfilled niches that the Post-glacial dispersal lag hypothesis (Svenning & Skov 2007) predicts at lower latitudes is not observed. Areas south of 42°N, are expected to have lower, similar proportions of unfilled richness because there have been no barriers for species dispersal during the last 21,000 yr in this area. However, the proportions of unfilled richness generally shows trends within birds, mammals and trees at these latitudes, and the pattern is not consistent among taxa. Similarly, the expected pattern in unfilled richness at latitudes covered by ice during the last glaciation (>42° N) (Fig. 3a), are not consistent among taxa nor with the observed patterns (Fig. 3b, c, d). At these latitudes mammals and trees tend to have lower unfilled richness than it would be expected by lags in niche filling after the LGM.

In birds, the proportion of unfilled potential richness in any given climate relative to the expected potential richness in that climate is more homogeneous through the continent (Fig. 2). It has been suggested that current gradients of bird species richness may reflect the contraction of tropical ancestral species ranges toward areas where the climates persisted (Hawkins *et al.* 2006). This hypothesis also applies to angiosperm trees, which account for the vast majority of tree species in North America, and which also had a tropical origin (Graham 1999). Yet the patterns in Fig. 2 are very different for birds and for trees.

The observed pattern in the proportion of unfilled potential richness as a function of climate variability since the LGM was also inconsistent with the predicted pattern (Fig. 3e, f, g, h). While the Climate variability hypothesis (Araújo *et al.* 2008) predicts lower proportions of unfilled potential richness in areas of lower climate variability, these proportions are generally higher than expected. It could be argued that historical climate is a better predictor among narrow-ranged species, which are expected to occur preferentially in areas with more favorable climates (because colonization of climatically suitable areas is higher) (Araújo *et al.* 2008). Our data do not show strong relationships in the unglaciated part of eastern North America. We reject the Climate variability hypothesis.

The observed patterns of unfilled potential richness are not consistent with the prediction from the Biotic Interactions Hypothesis (Fig. 3 b, c, d). In birds, the proportion of unfilled potential richness increases (not decreases as expected) from lower to higher latitudes (Fig. 3b). In trees, there is a slight trend between 20°N and 50°N that is consistent with the hypothesis. However, in both lower and higher latitudes, the pattern shows much variation in the residuals, and it switches to the opposite direction at higher latitudes (Fig. 3c). The Biotic Interaction Hypothesis was initially proposed in mammals (Kaufman 1995). In this group, there is no observable pattern. Multispecies interactions may generate range limits under low environmental variation (Case *et al.* 2005), yet, the effect of these limits on niche unfilling are not observable in this study. If biotic interactions result in niche unfilling in benign environments (at lower latitudes), it is possible that this niche unfilling simply might not be captured at broad spatial scales. Biotic interactions are generally more related to species richness at medium, lower scales (10-500km^2) (Field *et al.* 2009). Based on our results, we reject the suggestion that biotic interactions limit the physical or niche space of species in more benign climates.

The shape of the relationship between unfilled potential richness and unfilled climate-dependent richness were highly consistent with the shape predicted by the climate-dependent occupancy model (Fig. 3 i, j, k, l). This is consistent with patterns of individual species occupancy based on this model, which suggests that species occupy the climatic space probabilistically (Boucher Lalonde *et al.* 2012; Boucher-Lalonde *et al.* 2014). For example, in trees, a bivariate normal function of temperature and precipitation, averaged over 482 species native of North America, explains 82% of the spatial variation in the probability of occupancy of a given area (Boucher Lalonde *et al.* 2012). For birds (3277 species) and mammals (1659 species) of the Americas, the same model explains around 35% of the deviance in occupancy, but with higher accuracy than models that are based, for example, on climatic tolerances or that include many more parameters (Boucher-Lalonde *et al.* 2014).

It has been suggested that species occupancy would be a peaked (Gaussian) function of climate if fitness and climate followed a Gaussian-like relationship; fitness would decrease from the climatic optimum as the likelihood that other factors make the habitat unsuitable increases (Boucher Lalonde *et al.* 2012). Occupancy also could reflect the probability that a region with a given macroclimate bears microclimates where the species can survive (Boucher Lalonde *et al.* 2012; Boucher-Lalonde *et al.* 2014), for example, through metapopulation-like processes of colonization and extinctions at broad spatial scales. Processes associated with metapopulation dynamics that affect local distributions of individual species seem to “scale up” to modify regional species richness patterns (Desrochers 2011).

The shape of the relationship observed in patterns of unfilled surrounding richness for birds, mammals and trees were in partial agreement with the shape predicted by the Abundant Center Hypothesis. This in principle suggests that beyond the limits of the species ranges, unoccupied, but potentially suitable areas exist where species can persist. Diverse processes may result in lower niche filling in the areas far from the *center* of the species ranges. For example, in the surrounding areas, which are distance-isolated, a species may exhibit negative population growth due to the reductions in the diversity and number of immigrants; a decreased abundance and fitness would then result in increased risk of extinction (Brown *et al.* 1995; Sexton *et al.* 2009). These processes, however, may be constrained by ecological factors that are environment-independent (e.g. allele effects and biological interactions), environment-dependent (e.g. stochastic environmental heterogeneity), or evolutionary factors that suggest species adaptations to the conditions found beyond the central optimum of the species ranges (Sexton *et al.* 2009). In principle, our model assumes that the processes that generate niche unfilling in the surrounding area of the species ranges are environmentally dependent. It is important to recall, however, that the evidence for the Abundant Center Hypothesis is mixed (Sagarin & Gaines 2002; Tuya *et al.* 2008). Yet, this model is not rejected in our study.

The relationship between climate and potential richness based on 100% occupancy is strong ($R^2 \approx 0.88$, $p < 0.0001$) for the three groups studied here. This is consistent with the hypothesis that individual species climatic tolerances is a considerable part of the explanation of richness patterns. However, this relationship shows that tolerance alone is insufficient to account for richness patterns. Recent studies have shown that woody taxa have occupied distinct realized niches since the LGM (Veloz *et al.*, 2012). Furthermore, recent evidence indicates that that species are able to occupy climate niches or biomes in ranges that differ substantially from their native ranges (Beaumont *et al.* 2009; Gallagher *et al.* 2010; Lauzeral *et al.* 2011, but cf. Petitpierre *et al.* 2012).

Whether the possible mechanisms derived from the climate-dependence probabilistic model (Boucher Lalonde *et al.* 2012), and complemented with the metapopulation-like processes as suggested by (Desrochers 2011), can explain richness patterns is unknown. It is possible that the mechanism behind this Gaussian model of occupancy may follow a top-down rather than a bottom-up process of generating patterns of diversity (i.e. climate affects groups of species irrespective of their identities, rather than individual species—as climatic tolerances would do—respectively).

Our results suggest that projections of species geographic ranges, based on the assumption that individual species will occupy climatically suitable areas (i.e. through species tolerances) (Pearson & Dawson 2003; Heikkinen *et al.* 2006; Elith & Leathwick 2009), should be used cautiously. Individual species generally do not fill their climatic niches as expected from species tolerances, even in sites that have been available for colonization since the LGM. Species geographic projection under future climate conditions should put particular attention in models that aim to reduce uncertainty of the projections (Araújo *et al.* 2005; Marmion *et al.* 2009; Guisan *et al.* 2014), if they are, in principle, climate-tolerance based. It would be interesting to assess effects of future climate change by comparing future projections of species geographic ranges based on currently common bioclimatic envelop models (that assume species climatic tolerances) and the projected ranges based on the Gaussian climatic occupancy model proposed by (Boucher Lalonde *et al.* 2012).

In conclusion, we can reject post-glacial dispersal lags and late Pleistocene climatic variation as explanations of the fact that species ranges do not include all areas whose climates the species tolerate, even in the absence of dispersal barriers. Patterns of richness generated with expected richness based on 100% occupancy (climatic tolerances) correlated well with current climate, but substantially over-estimate richness. Patterns of expected unfilled richness based on species climatic occupancy that follow a probabilistic, bivariate Gaussian model make unbiased predictions of richness. This is true for birds, mammals and trees. We conclude that climatic tolerance alone is insufficient to account for current patterns of richness, but it is a large part of the story. Processes that could explain the lack of niche filling would have to explain why unfilled areas surround filled areas, both in geographical and in climatic space.

Tables

Table 1. Summary of the calculation and associated names of the different variables utilized to test the models predicted from the different hypotheses.

ID	Designation	Calculation
O	Observed richness	For a given quadrat, the number of species whose observed ranges overlap the quadrat
P	Potential richness	For a given quadrat, the number of species whose observed ranges include the climate in that quadrat. i.e.: Each species *j* occupies (Y= 1) or does not occupy (Y=0) climate *i*. Potential richness in quadrat with climate *i* is: $$\boldsymbol{P_i = \sum_{j=1}^{n\ species} Y_{ij}}$$
U	Unfilled potential richness	P-O
Up	Unfilled proportional richness	U/P
Ec	Expected climate-dependent richness	The number of species that would be present if species occupied quadrats based on climate-dependent probabilities. i.e.: let X_{ij}= the proportion of quadrats with climate *i* occupied by species *j*. The climate-frequency-dependent expected richness in a quadrat with climate *i* is: $$\boldsymbol{Ec_i = \sum_{j=1}^{n\ species} X_{ij}}$$
Eu	Expected unfilled climate-dependent	P-Ec

	richness	
Sk	Expected unfilled surrounding richness	Su in a given quadrat is the number of species whose buffers include that quadrat. i.e.: for each species j, create a buffer S with a given width around the species range, with S=1 for every quadrat within the buffer, and S=0 outside the buffer. The expected unfilled surrounding richness for quadrat k is: $$\boldsymbol{S_k = \sum_{j=1}^{n\ species} S_j}$$

Figures

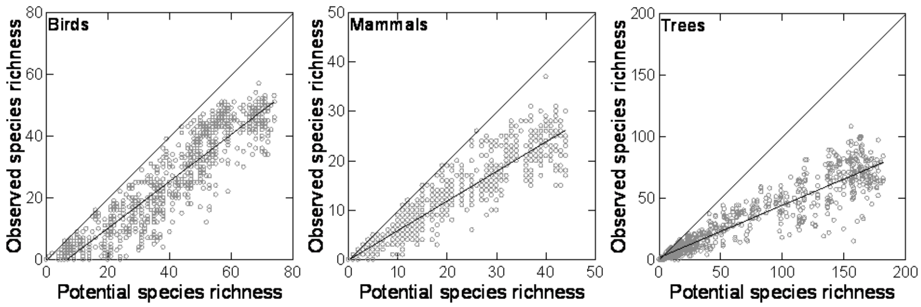


Figure 1. Observed species richness compared to predicted potential species richness for birds, mammals and trees in Eastern North America (ENA). Panels show potential richness assuming 100% of occupancy of all geographic areas in ENA that have a climate that is occupied somewhere within the geographic species range. The upper lines show the predicted 1:1 relationship, while the lower line is the observed relationship. Each point (N = 1,111) represents a 1 km^2 squares within ENA.

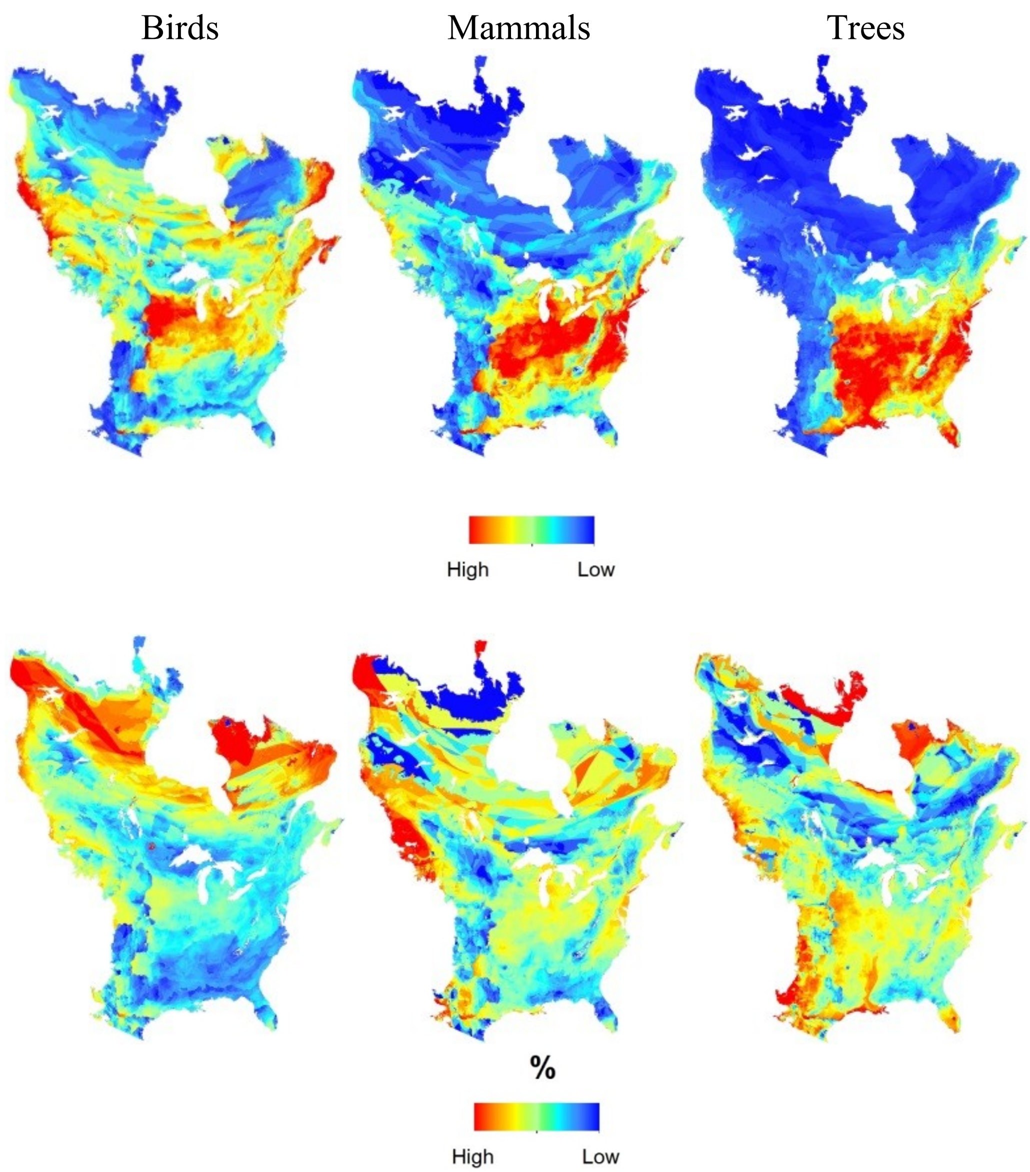
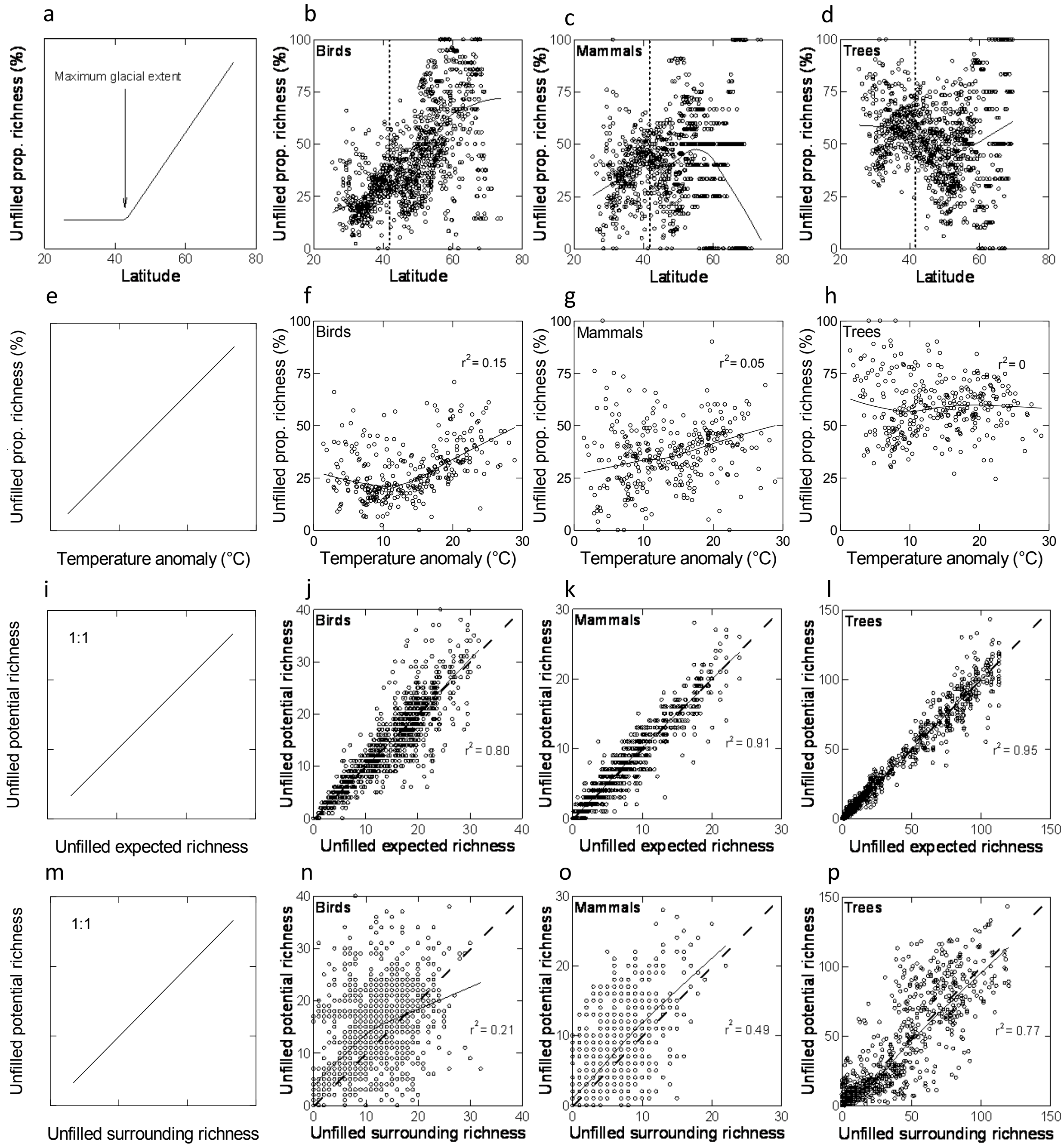


Figure 2. Maps of unfilled potential richness (first row) and unfilled proportional richness (second row) in any given climate for birds, mammals and trees native to Eastern North America (ENA). Unfilled proportional richness is the ratio between unfilled potential richness and potential richness. Potential richness assumes 100% of occupancy of areas in ENA with a climate that is occupied somewhere within the species geographic range.

Figure 3. The relationship among unfilled proportional richness, latitude and temperature anomaly (a measure of climate variability since the LGM), and among unfilled potential richness, unfilled expected richness and unfilled surrounding richness, for birds, mammals and trees in Eastern North America (ENA). Panels in the first column (left) show the expected model derived from each hypothesis, and panels in the subsequent columns show the observed relationships for each group. By row, panels correspond to the Postglacial dispersal lags hypothesis (a, b, c, d), the Historical climate variability hypothesis (e, f, g, h), the Climate-dependent probabilistic occupancy model (i, j, k, l) and the Abundance center hypothesis (m, n, o, p). Solid lines for all the observed relationships represent trends fitted by LOWESS regressions (locally weighted sum of squares), tension = 0.7. Dashed lines, when presented, show the predicted 1:1 relationship. Regression coefficients r^2 are shown for each correlation; $p<0.0001$ for each case, except for trees in panel (h), $p=0.64$. In panel (a), the maximum glacial extend (~21,000 yr BP) is indicated at ~42°N. In panels (b), (c) and (d) the maximum glacial extent (~21,000 yr BP) is indicated with a vertical dashed line. Each point (N = 1,111) in observed relationships represents a 1 km^2 squares within ENA. N = 323 for panels f, g, h.


a
b
c
d
Maximum glacial extent
Birds
Mammals
Trees
Unfilled prop. richness (%)
Latitude
e
f
g
h
Temperature anomaly (°C)
r2 = 0.15
r2 = 0.05
r2 = 0
i
j
k
l
1:1
Unfilled potential richness
Unfilled expected richness
r2 = 0.80
r2 = 0.91
r2 = 0.95
m
n
o
p
Unfilled surrounding richness
r2 = 0.21
r2 = 0.49
r2 = 0.77

Conclusions

This thesis tested two prominent families of hypotheses that postulate climate as the primary factor that drives gradients of diversity. One family proposes that climate directly affects the spatial variation of richness through ecological processes. The other family suggests that gradients of richness are the result of processes driven by climate thousands or millions of years ago.

Patterns of richness are well correlated with climate through space and through time. During the Holocene (~11,000 yr BP), richness-climate patterns were very consistent. However, during the late Pleistocene some other processes, not observed during the Holocene, seem to have affected the richness-climate relationship. It seems that differential rates of recolonization occurred during periods of rapid fluctuations of climate. Richness seems to have increased rapidly during warming, but did not decrease at the same rate during cooling. Although the richness-climate relationship changed consistently during the late Pleistocene, the generality of the Richness-Climate Hypothesis still applies for the Holocene, and indicates that current climate is the main driver of current patterns of richness.

I reject the three historical climate hypotheses. The effect of climate on richness over thousands of years by means of postglacial dispersal lags, climate variability since the Last Glacial Maximum (LGM), or age of area since deglaciations, is not a better predictor than contemporaneous climate. We conclude that contemporaneous climate, but not historical climate, stands as the more plausible explanation for patterns of richness of woody plants, at least during the last 11,000 years.

The global warming of the Pleistocene-Holocene transition increased richness in areas with low water deficit, but lead richness declines mainly in hot, dry regions of North America, as predicted from current richness-climate relationships. Current speculations as to the effect of current and future global warming on richness, which suggest massive species losses in most biomes, should be taken with caution. However, if species richness is expected to decline mainly in areas where increasing temperature is accompanied by higher water deficits, then this knowledge can be used to improve conservation planning. It should be noted that the responses of richness to climate warming that were observed during and after the Holocene-Pleistocene transition are in a time scale that is much broader (millennia) than the time scale at which future climate change is expected to happen (decades). However, the predictions derived from current richness-climate models could well serve to warn possible effects of current and future climate changes on richness at the short and medium term, and for specific regions.

The test of the Physiological Tolerance Hypotheses suggests that species climatic tolerances are, in principle, not enough explanation for current patterns of richness. Patterns of niche unfilling were inconsistent with post-glacial dispersal lags, climate variability since the LGM and biotic interactions. Patterns of unfilling potential richness are particularly well predicted by a probabilistic model of climate-dependence occupancy of species ranges. We reject the post-glacial dispersal lags, the variation in climate over the last 21,000 yr, and biotic interactions at lower latitudes (or benign climates) as possible explanations of the lack of occupancy of areas that include the climates that species tolerate, even in the absence of physical barriers.

In sum, this thesis suggests that contemporaneous climate controls broad-scale patterns of richness and that models based on species tolerances do not account for patterns of richness.

Although this thesis does not consider any specific process for patterns of richness, the results of the different chapters combined offer evidence that is inconsistent with the notion that species climatic tolerances are the main driver of gradients of diversity, the currently most discussed explanation in the family of evolutionary/historical hypotheses for diversity gradients.

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Appendix S1: Supplementary tables and figures accompanying Chapter 1

Table S1. The correlations between the two temperature reconstructions calculated over North America at 1000 yr intervals. Correlations were calculated between the two temperatures observed at the different richness sampling sites at each time period, that is, correlations are spatial not temporal. For temporal correlations by site, see Table S2. Temperature reconstructions correspond to the National Center for Atmospheric Research Community Climate System Model ver. 3 (CCSM3) (Blois *et al*. 2012), and the temperature reconstruction from historic plant assemblages composition based on fossilized pollen using the modern analog technique (MAT: Viau*et al*. (2006)). Number of sites from which temperature values were obtained (N); Pearson correlation coefficient (r).

Time period	N	r
1000	212	0.83
2000	198	0.79
3000	193	0.80
4000	184	0.83
5000	191	0.82
6000	191	0.83
7000	171	0.79
8000	161	0.72
9000	133	0.77
10000	137	0.73
11000	118	0.70
12000	78	0.74
13000	59	0.71
14000	45	0.62

Table S2. The correlations between the two temperature reconstructions calculated at 1000 yr intervals at all sites for which at least 10,000 years of data were available. Temperature reconstructions correspond to the National Center for Atmospheric Research Community Climate System Model ver. 3 (CCSM3) (Blois *et al.* 2012), and the temperature reconstruction from historic plant assemblage composition based on fossilized pollen using the modern analog technique (MAT: Viau*et al*. (2006)). Number of periods of time included in the time series for each sampling site (N); minimum time (Min Time) and maximum time (Max Time) observed in any given time series; Pearson correlation coefficient (r) arranged from higher to lower value. Longitude and Latitude are in decimal degrees.

ID Site	Longitude	Latitude	N	Min Time	Max Time	r
443	-69.41	43.92	13	1000	13000	0.95
99	-85.12	44.88	12	1000	13000	0.94
449	-93.57	44.59	10	1000	11000	0.90
72	-89.73	43.42	14	1000	14000	0.89
82	-80.25	44.37	12	1000	12000	0.89
265	-82.47	40.35	12	1000	14000	0.89
1060	-82.76	41.92	10	3000	12000	0.87
125	-82.00	29.52	11	1000	12000	0.87
105	-73.98	42.24	12	1000	14000	0.85
254	-91.45	45.30	10	1000	12000	0.85
110	-78.67	42.54	13	1000	13000	0.84
439	-80.41	43.24	12	1000	12000	0.83
376	-93.16	44.82	10	1000	14000	0.83
222	-72.12	41.37	12	1000	14000	0.82
1265	-74.04	41.39	13	1000	14000	0.82
1264	-74.20	41.24	12	1000	12000	0.79
247	-76.35	41.67	12	1000	12000	0.77
1332	-131.75	53.42	10	1000	10000	0.73
794	-77.92	44.30	11	1000	11000	0.60
2233	-121.62	48.23	11	1000	14000	0.58
123	-93.13	44.27	10	2000	12000	0.57
847	-122.55	49.31	14	1000	14000	0.55
176	-93.38	47.98	12	1000	12000	0.46

ID Site	Longitude	Latitude	N	Min Time	Max Time	r
1451	-127.62	64.17	10	1000	10000	0.39
771	-94.11	47.08	11	1000	12000	0.33
1969	-112.40	46.53	11	2000	12000	0.22
2234	-122.56	49.33	11	1000	13000	0.19
461	-78.95	33.80	10	1000	14000	0.13
209	-64.80	47.08	10	1000	10000	0.09
3170	-135.40	59.20	11	2000	12000	0.05
268	-81.50	27.58	12	1000	14000	0.03
1331	-68.73	45.04	10	1000	10000	0.02
1450	-128.08	64.65	11	1000	11000	-0.24
1550	-132.02	67.65	11	1000	11000	-0.66
1552	-135.93	65.95	13	1000	13000	-0.74
3500	-133.58	69.28	14	1000	14000	-0.81

Table S3. Sampling sites used in this study from the North American Pollen Database from which data are available at 1000 yr intervals. Time-span for each site is indicated from the most recent date (TMin) to the oldest date (TMax). Number of time-slices for each time-span is indicated (N). Time-span is based upon samples with 300 pollen grains or more. Longitude and Latitude are in decimal degrees.

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
3	-60.583	53.333	6000	6000	1
5	-84.867	47.883	1000	11000	10
7	-78.882	42.251	1000	10000	9
9	-84.9	47.733	9000	11000	3
10	-73.311	45.543	1000	12000	9
11	-85.17	53	2000	6000	5
12	-70.685	47.482	11000	11000	1
13	-74.6	42.5	1000	14000	8
15	-70.05	44.47	1000	1000	1
16	-67.331	45.256	1000	13000	9
17	-81.329	41.144	14000	14000	1
18	-77.917	42.25	1000	14000	6
19	-70.596	46.279	1000	10000	10
20	-76.12	54.047	1000	8000	5
21	-73.317	42.5	1000	10000	6
24	-84.867	47.9	1000	9000	9
27	-95.167	47.183	1000	4000	3
29	-63.2	55.333	1000	7000	6
32	-70.675	45.567	1000	11000	10
33	-74.683	43.917	4000	5000	2
35	-72.15	44.367	1000	11000	3
36	-73.567	42.604	2000	9000	6
37	-86.533	33.5	1000	12000	6
38	-85.017	30.267	4000	14000	4
39	-88.017	46.667	1000	8000	4
41	-63.25	55.667	1000	6000	6
42	-72.999	46.614	3000	12000	10
43	-74.667	41.333	7000	9000	3

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
45	-76.146	54.799	1000	7000	7
46	-76.339	53.091	4000	7000	2
47	-88.343	40.676	10000	11000	2
50	-86.53	41.65	10000	11000	2
52	-93.27	42.02	12000	13000	2
54	-67.883	46.283	1000	1000	1
56	-115.32	67.833	1000	3000	3
57	-80.283	38.2	3000	5000	2
58	-81.267	49.183	1000	10000	10
59	-79.83	43.5	1000	1000	1
61	-84.867	47.9	7000	10000	4
63	-85.958	44.7	1000	9000	9
64	-91.1	36.8	3000	8000	3
65	-105.27	55.267	2000	7000	4
67	-69.4	54.883	1000	7000	7
68	-71.833	44.033	1000	9000	4
69	-69.93	54.424	1000	7000	7
72	-89.732	43.418	1000	14000	14
73	-69.958	60.987	6000	6000	1
74	-76.45	36.583	9000	10000	2
75	-89.167	43.917	10000	13000	4
76	-71.5	46.45	1000	10000	9
77	-70.001	41.933	1000	10000	9
78	-70.35	45.85	2000	11000	3
79	-71.667	44.167	6000	10000	5
80	-58.55	53.233	2000	8000	6
82	-80.25	44.367	1000	12000	12
84	-100.92	61.167	1000	6000	6
86	-78.5	45.5	1000	11000	8
89	-93.75	49.583	2000	12000	10
90	-94.417	44.95	4000	6000	3
91	-73.476	46.276	1000	10000	10
92	-87.733	44.05	8000	8000	1
94	-99.283	49.433	14000	14000	1
95	-86.134	31.721	1000	1000	1
96	-98.25	53	5000	7000	3
98	-62.633	55.033	1000	6000	5
99	-85.117	44.883	1000	13000	12
102	-53.133	47.322	7000	7000	1
103	-72.883	42.567	6000	8000	2
104	-73.968	44.181	1000	4000	3

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
105	-73.979	42.242	1000	14000	12
107	-89.7	46.183	1000	1000	1
109	-60.283	55.467	4000	6000	3
110	-78.67	42.542	1000	13000	13
111	-86.53	41.67	1000	14000	7
113	-90.45	50.917	7000	10000	4
114	-81.767	47.317	1000	11000	11
115	-85.717	37.45	12000	14000	3
117	-93.7	42.26	10000	14000	4
119	-76.644	54.028	1000	8000	8
120	-71.567	48.366	1000	8000	8
122	-71.733	44.133	1000	1000	1
123	-93.125	44.271	2000	12000	10
124	-63.75	56.067	4000	10000	7
125	-92.62	46.72	1000	12000	11
126	-91.8	47.35	10000	14000	5
127	-70.3	46.717	3000	12000	10
129	-79.117	47.288	4000	5000	2
130	-70.376	47.497	11000	11000	1
131	-73.331	45.964	1000	9000	9
132	-65.763	49.158	7000	12000	3
133	-84.317	45.6	3000	8000	6
134	-84.783	45.067	1000	3000	3
138	-89.9	46.25	10000	11000	2
139	-81.317	48.4	1000	8000	8
140	-73.217	46	1000	5000	5
141	-84.867	47.883	10000	10000	1
142	-65.813	49.208	4000	12000	7
143	-92.825	45.05	11000	11000	1
144	-93.6	47.283	1000	6000	4
145	-66.717	45.144	1000	10000	8
148	-56.433	52.45	1000	10000	10
149	-83.258	30.725	1000	9000	8
150	-73.3	45.989	4000	7000	4
151	-73.303	45.992	1000	6000	3
154	-87.97	46.72	1000	8000	6
155	-101.04	56.842	1000	7000	4
156	-70.976	47.597	2000	4000	3
157	-80.66	43.225	2000	11000	8
158	-71.423	47.078	1000	11000	8
159	-94.933	47.183	1000	11000	5

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
160	-64.833	56.783	1000	5000	3
161	-71.433	41.783	2000	3000	2
162	-72.838	46.788	1000	12000	8
164	-97.35	44.817	12000	12000	1
165	-89.417	43.1	6000	6000	1
169	-73.283	41.817	1000	11000	9
170	-69.3	43.767	1000	6000	4
171	-71.175	47.908	1000	10000	9
172	-72.585	45.359	1000	14000	6
173	-58.05	52.267	1000	10000	10
174	-68.639	44.627	5000	14000	3
176	-93.383	47.983	1000	12000	12
177	-61.817	56.533	1000	10000	10
179	-71.65	57.65	3000	6000	4
182	-81.5	46.6	1000	11000	11
185	-79.467	46.45	11000	11000	1
186	-73.05	42.65	3000	12000	9
189	-95.2	43.333	12000	12000	1
194	-71.45	41.517	1000	1000	1
195	-68.5	70.467	3000	7000	4
198	-93.9	42.16	13000	14000	2
200	-75.808	45.469	1000	5000	5
202	-81.25	42.917	1000	9000	9
205	-85.25	41.583	1000	14000	9
206	-84.55	46.567	5000	10000	6
207	-71.936	46.146	10000	11000	2
208	-78.467	42.622	1000	12000	8
209	-64.8	47.075	1000	10000	10
210	-65.167	57.633	1000	6000	6
211	-84.865	34.326	13000	14000	2
213	-76.1	45.6	1000	12000	11
214	-92.7	49.35	7000	12000	5
216	-99.65	50.717	1000	2000	2
217	-84.558	54.306	1000	3000	3
218	-72.067	58.233	3000	6000	4
219	-64.817	56.767	1000	7000	4
222	-72.117	41.367	1000	14000	12
225	-93.87	44.87	1000	1000	1
226	-85.179	46.132	1000	7000	7
227	-72.979	46.654	3000	10000	6
229	-57.717	54.4	3000	3000	1

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
230	-74.467	46.058	1000	11000	11
231	-74.396	46.172	1000	13000	10
234	-87.516	44.45	10000	14000	4
235	-67.132	50.14	1000	7000	7
236	-81.933	36.525	4000	4000	1
237	-91.867	47.917	1000	1000	1
238	-64.183	45.017	5000	10000	4
239	-82	29.517	9000	14000	7
241	-83.8	40.35	1000	7000	3
243	-91.567	49.933	6000	11000	5
245	-63.883	56.633	5000	5000	1
247	-76.35	41.674	1000	12000	12
248	-72.147	48.294	7000	11000	2
249	-74.371	45.946	1000	12000	7
250	-70.933	46.933	2000	4000	3
252	-84.689	40.217	10000	13000	2
253	-71.808	46.892	1000	9000	8
254	-91.45	45.3	1000	12000	10
255	-52.667	47.617	9000	10000	2
259	-75.267	41.033	12000	14000	3
260	-95.771	47.188	1000	4000	4
264	-72.213	42.517	8000	11000	2
265	-82.467	40.35	1000	14000	12
266	-73.317	45.546	1000	12000	6
267	-65.167	55.767	1000	5000	5
268	-81.5	27.583	1000	14000	12
270	-62.05	57.383	2000	12000	11
271	-70.633	45.6	1000	11000	11
272	-84.583	46.55	13000	13000	1
273	-68.9	46.083	1000	5000	5
275	-79.38	44	1000	8000	8
280	-91.66	47.472	8000	11000	4
283	-93.103	46.086	10000	10000	1
285	-71.117	41.967	3000	13000	6
287	-94.117	46.117	11000	14000	3
288	-93.567	45	1000	5000	5
289	-85.661	46.429	3000	11000	8
290	-90.083	45.333	1000	3000	3
291	-73.6	42.633	9000	12000	3
292	-87.95	46.75	3000	10000	3
293	-93.87	43.03	13000	13000	1

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
295	-138.4	64.633	3000	7000	5
312	-72.213	42.517	10000	14000	5
314	-72.183	42.533	11000	14000	4
370	-84.868	34.324	14000	14000	1
376	-93.164	44.822	1000	14000	10
377	-92.717	46.417	12000	12000	1
383	-69.919	54.419	1000	6000	6
384	-70.358	54.356	1000	6000	6
408	-79.638	48.504	1000	9000	5
414	-93.048	45.46	12000	14000	3
418	-71.236	47.64	3000	7000	3
419	-71.163	47.258	1000	8000	8
424	-73.031	46.726	2000	11000	6
425	-69.833	60.783	2000	4000	3
426	-70.616	47.61	1000	10000	10
438	-78.917	46.4	1000	10000	10
439	-80.413	43.237	1000	12000	12
440	-79.45	45.217	1000	10000	10
441	-90.583	36.6	8000	8000	1
443	-69.41	43.921	1000	13000	13
445	-120.88	45.918	1000	7000	5
447	-69.317	44.983	1000	11000	9
448	-70.35	44.033	2000	10000	7
449	-70.35	43.967	1000	11000	10
450	-68.2	45.033	5000	13000	5
451	-114.15	59.25	9000	9000	1
453	-126.12	65.217	1000	7000	7
454	-120.67	57.45	10000	10000	1
455	-119.72	56.717	1000	10000	8
458	-114.6	50.767	4000	9000	2
459	-122.17	59.517	6000	6000	1
461	-78.954	33.799	1000	14000	10
463	-112.1	57.767	1000	11000	10
467	-77.175	44.85	1000	11000	8
473	-99.906	44.836	14000	14000	1
475	-76.378	57.117	1000	8000	7
476	-75.15	58.142	1000	6000	3
477	-75.245	58.578	1000	6000	3
478	-74.583	49.683	1000	8000	8
481	-69.453	47.458	8000	10000	3
482	-64.94	48.198	1000	9000	6

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
483	-65.95	48.967	11000	11000	1
485	-73.342	45.961	5000	8000	4
486	-66.125	48.911	1000	12000	3
487	-71.717	58.867	2000	4000	3
491	-79.513	44.196	1000	4000	4
493	-68.944	47.533	6000	14000	5
494	-69.353	47.844	2000	8000	6
495	-71.95	58.217	2000	6000	3
496	-71.325	45.671	5000	9000	2
497	-72.067	58.233	5000	5000	1
498	-65.267	48.052	7000	8000	2
501	-155.03	67.683	1000	5000	2
502	-146.48	68.333	6000	6000	1
504	-155.03	66.917	6000	8000	3
505	-156.45	66.967	3000	10000	8
509	-154.23	67.067	4000	4000	1
516	-160.43	67.867	8000	8000	1
518	-142.07	67.2	5000	9000	2
520	-149.8	67.417	8000	9000	2
521	-151.42	67.583	7000	13000	3
522	-151.27	64.333	1000	14000	6
523	-151.08	63.483	4000	4000	1
528	-110.6	44.956	10000	10000	1
529	-110.57	64.117	5000	8000	4
530	-110.58	64.133	5000	8000	4
532	-83.254	30.622	1000	6000	6
534	-75.1	56.283	1000	6000	6
535	-75.283	56.1	1000	7000	7
536	-75.25	58.583	1000	7000	5
584	-117.22	52.242	4000	7000	4
585	-71.575	41.158	3000	3000	1
586	-75.617	57.917	3000	7000	3
690	-70.208	41.283	5000	9000	2
695	-119.01	37.596	1000	4000	4
696	-119.07	37.663	1000	11000	2
727	-119.26	37.908	1000	10000	6
731	-93.704	46.128	1000	1000	1
741	-95.558	47.165	1000	2000	2
742	-93.871	44.233	1000	1000	1
755	-93.68	46.068	1000	1000	1
771	-94.113	47.081	1000	12000	11

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
775	-95.008	47.244	1000	3000	3
776	-95.008	47.244	2000	3000	2
777	-95.575	46.922	1000	7000	7
778	-95.575	46.922	1000	4000	4
782	-93.567	44.589	1000	1000	1
789	-78.479	42.545	10000	14000	5
794	-77.917	44.3	1000	11000	11
795	-88.74	48.56	1000	10000	7
799	-80.117	47	1000	7000	7
800	-79.98	44.85	1000	5000	5
802	-79.47	43.64	2000	3000	2
812	-84.883	40.667	10000	14000	5
841	-95.317	46.967	1000	1000	1
844	-73.868	45.961	1000	12000	12
845	-72.983	45.283	6000	9000	3
846	-73.993	45.996	1000	11000	11
847	-122.55	49.308	1000	14000	14
848	-121.5	50.5	1000	7000	7
850	-122.25	46.592	1000	13000	5
853	-55.506	48.936	7000	11000	3
854	-56.196	50.034	1000	7000	7
855	-52.714	47.59	1000	9000	6
856	-55.473	49.471	6000	11000	4
858	-110.6	44.65	1000	9000	5
863	-110.32	43.767	1000	8000	8
864	-110.32	43.767	8000	11000	2
865	-110.23	44.15	11000	11000	1
870	-84.187	35.621	1000	2000	2
871	-50.467	67.05	1000	4000	3
880	-105.5	37.55	9000	9000	1
900	-122.12	48.769	4000	13000	9
906	-95.294	46.206	10000	11000	2
907	-75.833	41.767	1000	2000	2
908	-74.017	43.75	1000	1000	1
910	-93.197	45.411	9000	12000	4
911	-91.117	48	8000	10000	2
924	-83.533	40.1	5000	12000	7
925	-84.75	41.417	3000	13000	7
926	-81.333	41.199	5000	13000	9
927	-82.938	39.668	1000	1000	1
929	-82.933	40.797	10000	12000	2

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
930	-82.063	40.681	11000	11000	1
931	-81.967	41	12000	14000	3
932	-85.742	39.954	13000	13000	1
971	-77.34	46.03	1000	11000	9
1052	-77.925	41.917	2000	5000	3
1056	-81.73	43.22	3000	5000	3
1060	-82.76	41.92	3000	12000	10
1061	-79.38	45.42	3000	3000	1
1070	-80.09	45.05	2000	8000	5
1073	-64.68	56.67	1000	5000	4
1075	-92	49.48	1000	8000	8
1076	-79.98	44.82	3000	3000	1
1080	-116.33	50.75	1000	13000	13
1085	-93.644	47.136	1000	7000	6
1092	-119.53	37.9	1000	3000	3
1094	-119.82	37.95	1000	13000	9
1101	-63.939	44.668	14000	14000	1
1102	-67.331	45.256	11000	11000	1
1103	-66.071	45.303	13000	13000	1
1137	-60.675	45.651	11000	11000	1
1138	-66.079	44.264	11000	11000	1
1144	-107.8	37.483	3000	3000	1
1146	-105.58	39.937	1000	8000	6
1147	-107.81	37.612	7000	7000	1
1152	-116.42	51.65	1000	13000	7
1153	-105.54	40.083	1000	10000	7
1156	-89.117	44.5	11000	11000	1
1157	-87.848	44.238	4000	12000	3
1159	-110.28	44.49	2000	2000	1
1163	-92.017	48.108	1000	11000	4
1164	-92.017	48.108	1000	1000	1
1165	-92.017	48.108	1000	2000	2
1187	-93.688	45.425	10000	12000	2
1259	-138.38	68.383	5000	13000	5
1262	-87.222	41.576	1000	1000	1
1264	-74.204	41.239	1000	12000	12
1265	-74.038	41.391	1000	14000	13
1266	-76.683	44.8	4000	4000	1
1277	-98.158	46.858	12000	13000	2
1281	-116.35	51.36	1000	7000	7
1282	-116.31	51.343	1000	2000	2

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
1307	-123.58	44.168	2000	4000	2
1308	-122.58	44.633	1000	14000	8
1309	-122.04	43.65	10000	10000	1
1317	-144.65	63.711	2000	7000	4
1331	-68.733	45.042	1000	10000	10
1332	-131.75	53.417	1000	10000	10
1336	-108.25	33.867	14000	14000	1
1344	-149.48	61.12	4000	10000	4
1345	-131.91	54.417	6000	7000	2
1346	-132.41	53.267	1000	3000	3
1450	-128.08	64.65	1000	11000	11
1451	-127.62	64.167	1000	10000	10
1452	-127.48	65.017	1000	10000	10
1453	-80.367	43.233	1000	11000	6
1549	-133.47	68.267	1000	12000	7
1550	-132.02	67.65	1000	11000	11
1551	-133.45	69.05	1000	14000	9
1552	-135.93	65.95	1000	13000	13
1969	-112.4	46.531	2000	12000	11
1970	-112.17	46.452	1000	10000	4
2233	-121.62	48.233	1000	14000	11
2234	-122.56	49.325	1000	13000	11
2293	-108.15	37.417	5000	5000	1
2300	-118.37	52.733	8000	11000	4
2301	-117.08	52.783	1000	9000	4
2302	-117.62	52.733	3000	10000	7
2304	-117.12	52.783	8000	9000	2
2339	-77.35	45.183	1000	12000	12
2340	-76.6	44.517	1000	11000	11
2816	-71.033	41.95	2000	13000	9
3170	-135.4	59.2	2000	12000	11
3179	-130.65	61.683	1000	11000	8
3180	-129.02	60.033	1000	10000	9
3181	-87.921	46.833	2000	11000	4
3182	-87.455	45.667	3000	8000	5
3183	-86.958	46.47	1000	13000	7
3184	-71.067	41.9	11000	14000	4
3486	-71.251	44.247	1000	10000	2
3487	-109.96	43.468	1000	5000	5
3488	-109.94	43.45	1000	3000	3
3489	-109.92	43.459	1000	9000	9

Sites at 1000 yr intervals					
Site ID	Longitude	Latitude	TMin	TMax	N
3490	-109.94	43.472	1000	5000	4
3491	-109.95	43.439	1000	9000	5
3497	-74.371	44.309	1000	1000	1
3500	-133.58	69.283	1000	14000	14

Table S4. List of families used to calculate richness of woody plants. Genus, species or family are shown as presented in the North American Pollen Database (NAPD). Arbitrary Thermo-tolerance for the different taxa is based on the plant functional types indicated by Williams *et al*. (2001) –also shown for reference.

Family	NAPD	Thermo-tolerance	Plant functional type
Betulaceae	Alnus crispa	B	BBS, AAS
	Alnus rugosa	B	BBS, AAS
	Alnus sp.	B	BBS, TSG
	Betula sp.	B	BBS, AAS
	Corylus	B	BBS, CTS
Myricaceae	Myrica	B	BBS, TS
Pinaceae	Abies	B	BEC, CTC
	Larix/Pseudotsuga	B	BSC
	Picea glauca	B	BEC, CTC
	Picea mariana	B	BEC, CTC
	Picea sp.	B	BEC, CTC
	Pinus sp.	B	EC
Salicaceae	Populus	B	BBS, TS
	Salix	B	BBS,TS, AAS
Aceraceae	Acer	T	TS
Aquifoliaceae	Aquifoliaceae	T	TS, WTBE, CTBE
Betulaceae	Ostrya/Carpinus	T	TS
Fagaceae	Fagus	T	CTS
	Quercus	T	TS, WTBE
Juglandaceae	Carya	T	TS
Oleaceae	Fraxinus	T	TS
Pinaceae	Pinus strobus	T	CTC
	Tsuga	T	CTC
Tiliaceae	Tilia	T	CTS
Ulmaceae	Ulmus	T	TS
Cornaceae	Nyssa	WT	ITS, WTS
Fabaceae	Prosopis	WT	ITS, AAS
Fagaceae	Castanea	WT	ITS
Hamamelidaceae	Liquidambar	WT	WTS
Juglandaceae	Juglans	WT	ITS
Platanaceae	Platanus	WT	ITS
Rhamnaceae	Rhamnaceae	WT	ITS

Family	NAPD	Thermo-tolerance	Plant functional type
Rubiaceae	Cephalanthus	WT	ITS, WTS
Taxodiaceae	Taxodium	WT	WTC
Ulmaceae	Celtis	WT	ITS, WTS
Cupressaceae	Cupressaceae	B, T, WT	EC
Fagaceae	Chrysolepis	B, T, WT	EC
Magnoliaceae	Magnoliaceae	WT	--

Plant functional types are based on Williams *et al*. (2001). Boreal broadleaved summergreen (BBS), Boreal summergreen conifer (BSC), Boreal evergreen conifer (BEC), Cool temperate conifer (CTC), Warm temperate conifer (WTC), Eurythermic conifer (EC), Temperate summergreen (TS), Cool temperate summergreen (CTS), Intermediate temperate summergreen (ITS), Warm temperate summergreen (WTS), Warm temperate broadleaved evergreen (WTBE), Cool temperate broadleaved evergreen (CTBE), Arctic alpine shrubs (AAS). Some acronyms were renamed to make them easier to follow in the table. Arbitrary classification of plant thermo-tolerance indicated in this study: Boreal (B), Temperate (T), WarmTemperate (WT).

Table S5. Regressions of woody-plant family richness and temperature for the last 14,000calyr using temperatures derived from the Modern Analog Technique (in contrast to the main text, in which analyses based on temperatures from the CCSM ver.3 general circulation model are presented).

Time interval (Years BP)	N	F-test	R^2	Model parameters			
				$\alpha 1$	$\alpha 2$	τ	*b*
1000	212	1924.1	0.797	3.5	9.8	287.9	1.5
2000	198	1770.2	0.806	3.5	10.1	288.4	1.7
3000	193	1691.0	0.798	3.7	9.8	288.6	1.3
4000	184	1469.2	0.809	3.5	10.4	288.7	1.4
5000	191	1467.6	0.794	3.6	9.7	288.3	1.0
6000	191	1406.1	0.771	3.7	9.7	288.2	1.3
7000	171	1216.2	0.731	3.7	9.9	288.0	1.9
8000	161	1387.9	0.754	3.3	10.0	287.7	2.4
9000	133	991.7	0.721	3.7	8.6	287.6	0.9
10000	137	1043.2	0.695	3.5	8.9	286.3	1.4
11000	118	682.6	0.544	3.4	8.9	285.6	1.4
12000	78	541.1	0.574	3.2	9.6	285.7	2.1
13000	59	387.3	0.646	1.5	8.6	282.0	2.6
14000	45	152.2	0.436	0.4	9.7	282.0	3.9
1000-14000	2071	14021.3	0.723	3.3	9.8	287.1	2.1

Woody plants family richness (WFR) is fitted as a function of temperature (TEMP in Kelvins) at 1,000 yr intervals, according to the following sigmoidal model:

$WFR = \alpha 2 + (\alpha 1 - \alpha 2) / (1 + \exp((TEMP - \tau) / b))$. N: Number of sampling sites at a given time interval. $P<10^{-5}$ for all regressions. The interval labeled 1000-14000 represents data pooled over all time intervals as described for model M1 in Table S6. Temperatures correspond to reconstructions based on fossilized pollen in lake sediments (Viau *et al.,* 2006)

Table S6. Two models relating richness to a sigmoidal function of temperature. Temperatures correspond to reconstructions based on fossilized pollen in lake sediments (Viau*et al.,* 2006).

Model	Source	DF	SS	MS	F-test	P	R^2
M1: model parameters identical for all time periods	Regression	4	107773.98	26943.50	14021.33	$< 10^{-5}$	0.723
	Residual	2067	3971.96	1.92			
	Total	2071	111745.94				
M2: model parameters free to vary among time periods	Regression	56	108268.68	1933.37	1120.35	$< 10^{-5}$	0.751
	Residual	2015	3477.27	1.73			
	Total	2071	111745.94				

Models are based on data pooled over all time intervals, as shown in Table 1. Model M1 relates the variation in woody-plant family richness among sites and times as a single sigmoidal function of temperature. Model M2 allows the parameters of the sigmoidal function to vary among the 14 time periods.

Table S7. Regressions of woody-plant family richness and historical temperature-variability, estimated from the CCSM3 climate model as the difference between temperature at a given time period over the last 14,000 yr and temperature at 21,000 yr BP. Calculated mean of the adjusted R^2 over all time periods (0.265).

Time interval (Years BP)	N	F-test	Adj. R^2
1000	212	480.25	0.248
2000	198	449.48	0.291
3000	193	410.22	0.231
4000	184	331.28	0.233
5000	191	372.65	0.255
6000	191	393.09	0.245
7000	171	462.65	0.328
8000	161	572.84	0.426
9000	133	418.79	0.366
10000	137	531.78	0.420
11000	118	373.28	0.193
12000	78	274.32	0.185
13000	59	177.55	0.257
14000	45	84.41	0.032

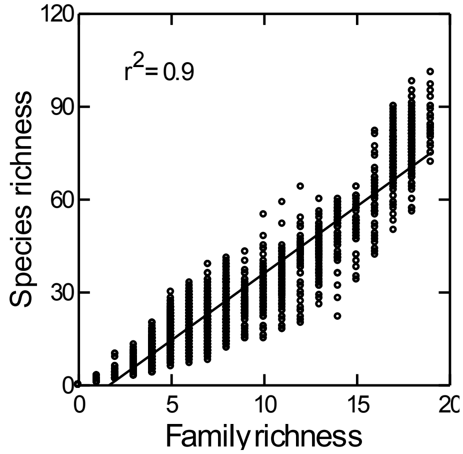


Figure S1. The relationship between family richness and species richness in contemporary trees of North America. The relationship is restricted to the 20 families observed in the fossil data. Data based on Little's range tree maps (US Geological Survey, 1999).

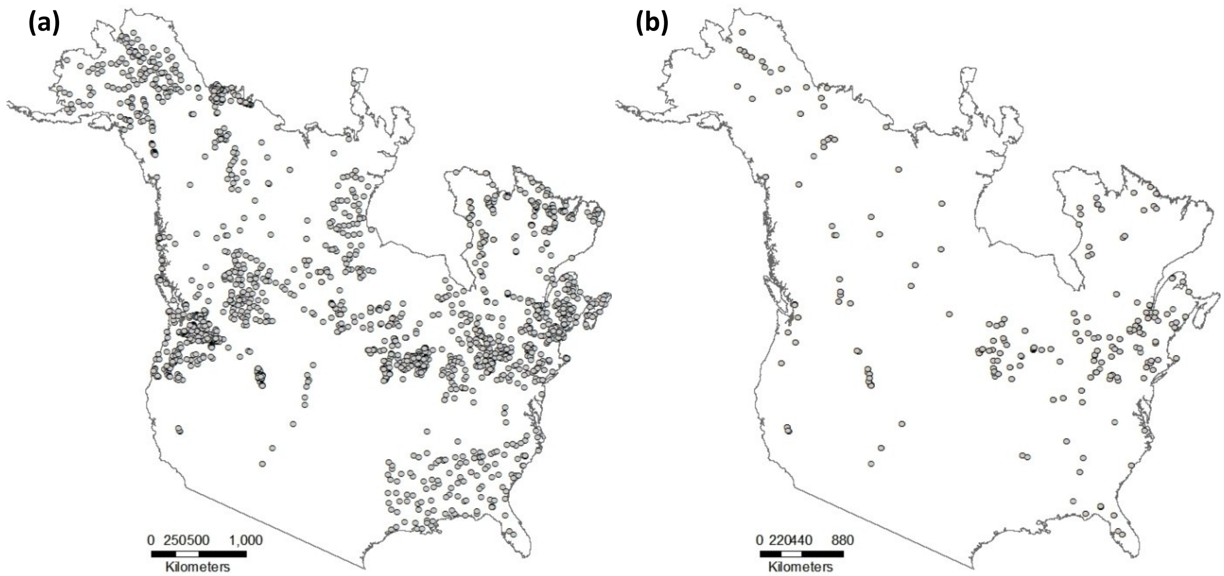


Figure S2. The distribution of modern pollen in North America, across (a) 1780 surface sampling sites and (b) 217 surface sampling sites matching fossil pollen sampling sites at any given time.

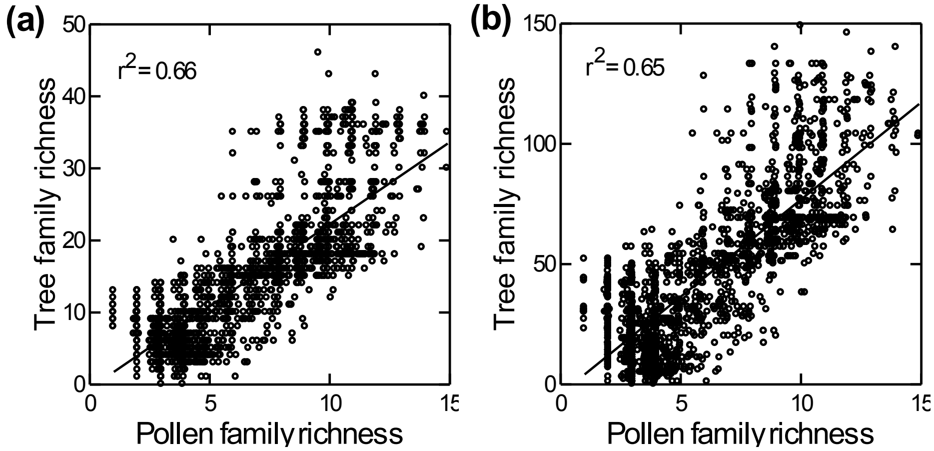


Figure S3. The relationship between modern pollen family richness (based on the 20 families observed in the fossil pollen record) and a) tree family richness and b) tree species richness (based on the 74 families of trees of North America). N = 1780 modern pollen sampling sites. Richness was calculated for samples of 300 or more pollen grains (Weng *et al*., 2006).

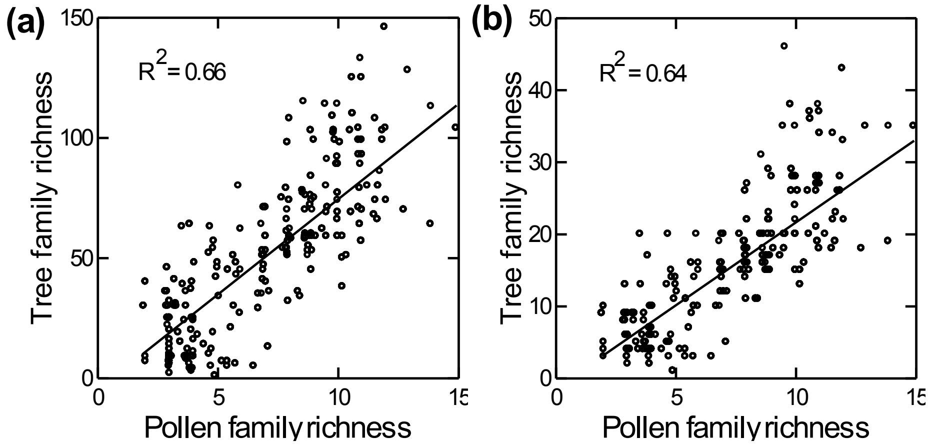
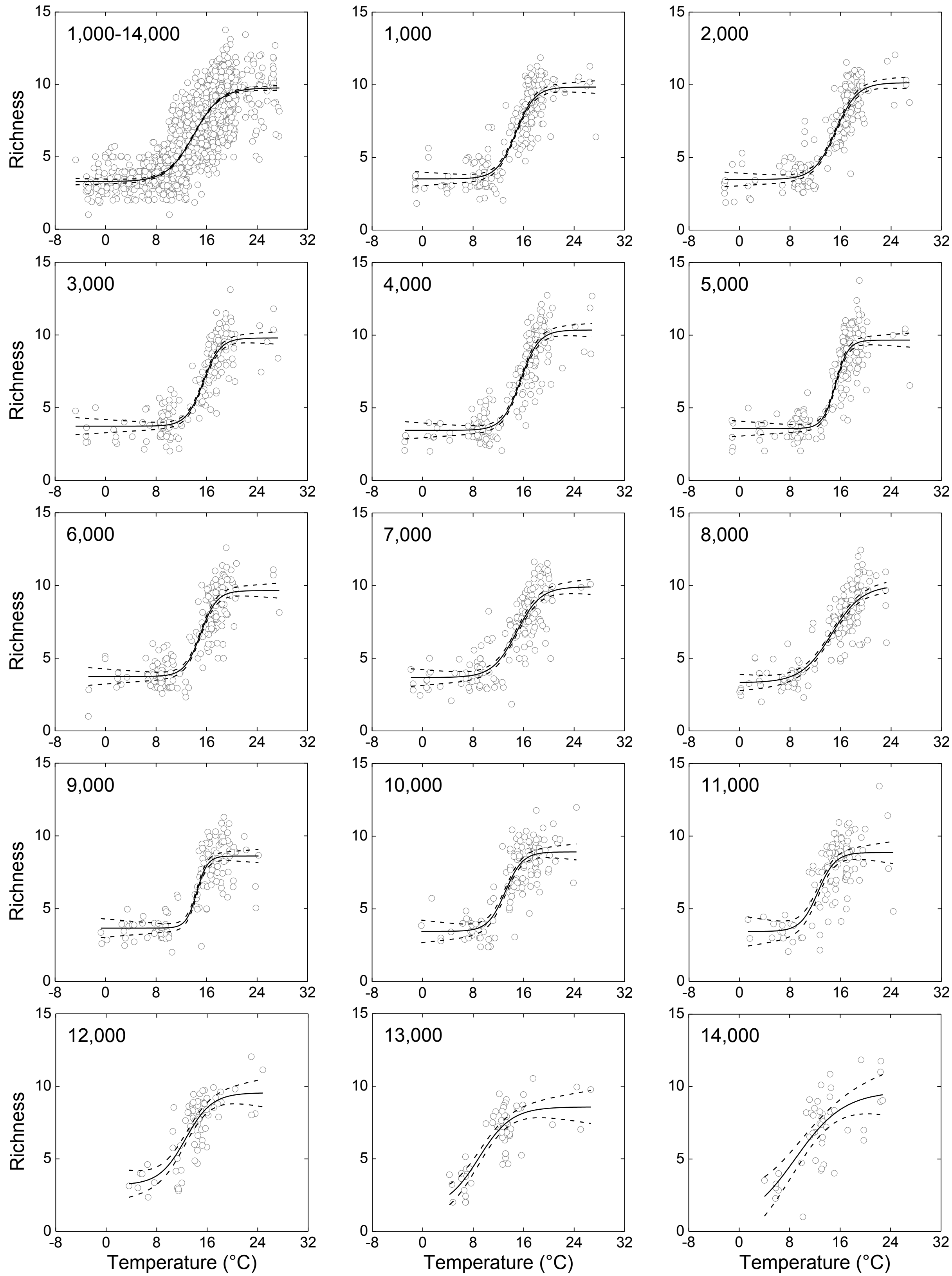


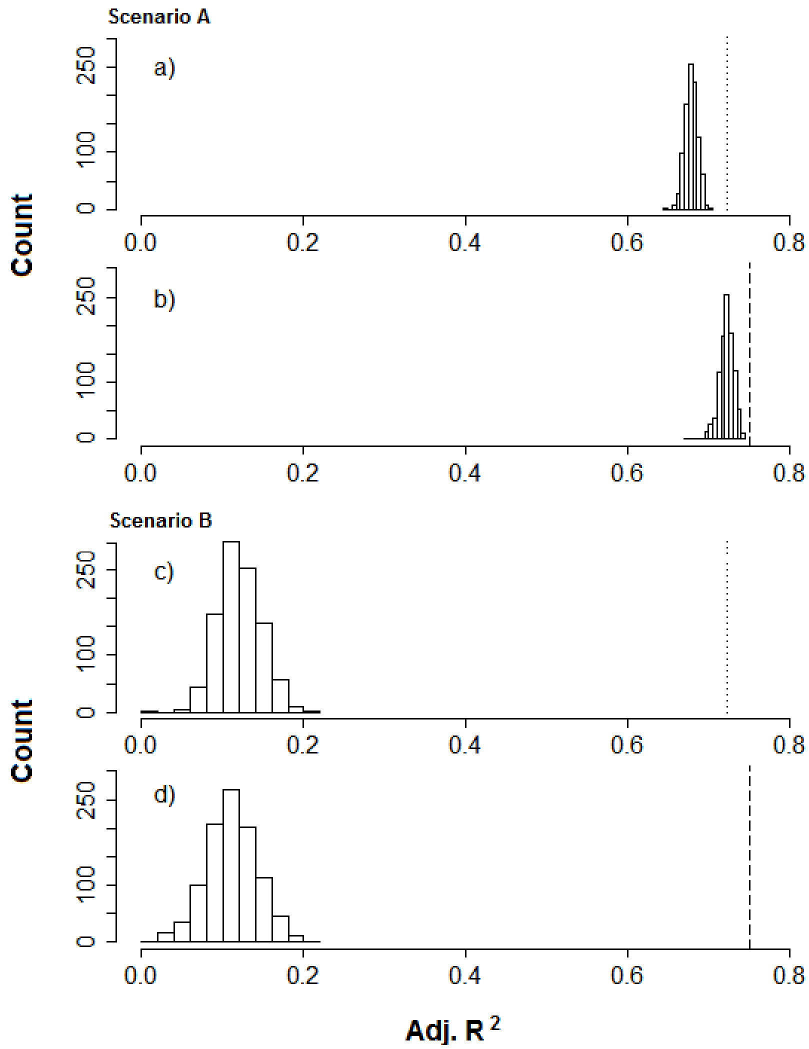
Figure S4. The relationship between modern pollen family richness (based on the 20 families observed in the fossil pollen record) and a) tree family richness and b) tree species richness (based on the 74 families of trees of North America. N = 217 modern sampling sites matching fossil pollen sampling sites. Richness was calculated for samples of 300 or more pollen grains (Weng *et al*., 2006).

Figure S5. Richness of woody plants families as a function of temperature for the last 14,000 yr. Continuous curves represent the individual sigmoidal models fitted at 1,000 yr intervals, beginning at 1000 yr BP. Dash lines represent 95% confidence intervals of the richness-temperature relationships. The curve labeled1000-14,000 represents data pooled over all time intervals as described for model M1. Parameters values and regression coefficients of the sigmoidal model are listed in Table S5. Regressions based on historical temperatures reconstructed with the MAT (Viau*et al.*, 2006).



1,000-14,000
1,000
2,000
3,000
4,000
5,000
6,000
7,000
8,000
9,000
10,000
11,000
12,000
13,000
14,000
Richness
Temperature (°C)

Figure S6. Frequency distributions of adjusted R^2 values from two null-type scenarios correlating richness and temperature. Each scenario was replicated 1,000 times. In scenario A, apparent richness changes represent white noise (or sampling variation). In scenario B, richness is a constrained random walk from its earliest observed value. Panels a) and c) correspond to model M1, which represents a single, sigmoidal richness-temperature relationship invariant over the last 14,000 yr. Panels b) and d) correspond to model M2, which allows the parameters of the sigmoidal relationship to vary through time. See Methods for details. The dotted and dashed lines represent the observed adjusted R^2 values for models M1 and M2 respectively, relating the actual values of richness to temperature.


Scenario A
a)
b)
Scenario B
c)
d)
Count
Count
250
100
0
0.0
0.2
0.4
0.6
0.8
Adj. R 2

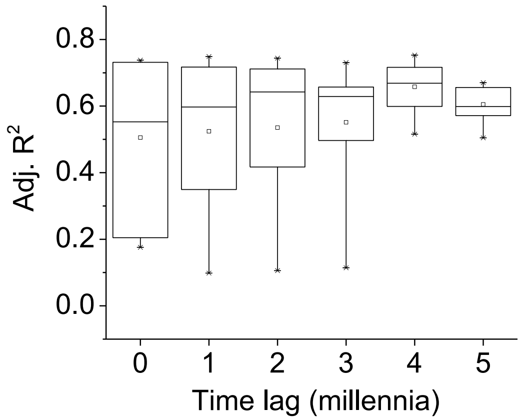


Figure S7. The mean of the adjusted R^2 values, calculated over all time periods in each time lag scenario. Means are not statistically different among time lag (P = 0.398).

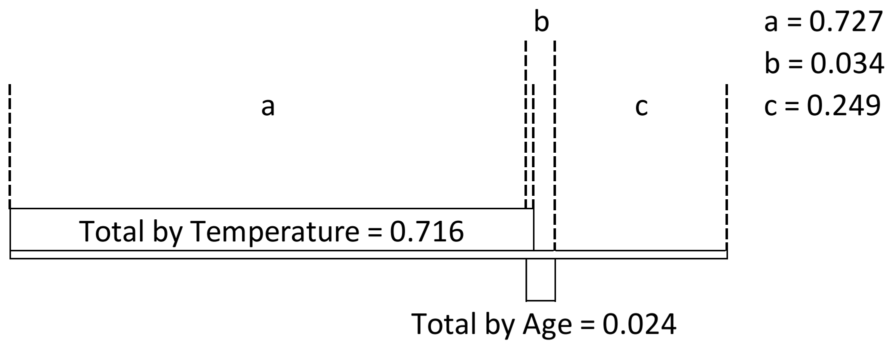


Figure S8. Partial regression analysis partitioning the independent contributions of contemporaneous climate (a) and age of area (b), and the proportion of variation in richness of woody plants family not explained by either factor (c).

References for Appendix S1, Chapter 1

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Appendix S2: Supplementary tables and figures accompanying Chapter 2

Table S1. Families and number of species per family of small mammals utilized to estimate richness in North America. Families that contain species with weights close to or above 5 kg are indicated with an "x".

Family	No. Species	Weight > 5 kg
Aplodontidae	1	
Cricetidae	75	
Dasypodidae	1	x
Didelphidae	1	
Dipodidae	4	
Erethizontidae	1	x
Geomyidae	19	
Heteromyidae	1	
Leporidae	18	x
Mephitidae	5	x
Mustelidae	10	
Ochotonidae	2	
Procyonidae	3	x
Sciuridae	72	
Soricidae	40	
Talpidae	7	

Table S2. List of families used to calculate richness in samples of fossilized pollen of woody plants, in the North American Pollen Database (NAPD). Genus, species or family are shown as they appear in the NAPD.

Family	NAPD
Aceraceae	Acer
Aquifoliaceae	Aquifoliaceae
Betulaceae	Alnus crispa
	Alnus rugosa
	Alnus sp.
	Betula sp.
	Corylus
	Ostrya/Carpinus
Cornaceae	Nyssa
Cupressaceae	Cupressaceae
Fabaceae	Prosopis
Fagaceae	Castanea
	Chrysolepis
	Fagus
	Quercus
Hamamelidaceae	Liquidambar
Juglandaceae	Carya
	Juglans
Magnoliaceae	Magnoliaceae
Myricaceae	Myrica
Oleaceae	Fraxinus
Pinaceae	Abies
	Larix/Pseudotsuga
	Picea glauca
	Picea mariana
	Picea sp.
	Pinus strobus
	Pinus sp.
	Tsuga
Platanaceae	Platanus
Rhamnaceae	Rhamnaceae
Rubiaceae	Cephalanthus

Family	NAPD
Salicaceae	Populus
	Salix
Taxodiaceae	Taxodium
Tiliaceae	Tilia
Ulmaceae	Celtis
	Ulmus

Table S3. Sampling sites where historical records of richness of woody plants and temperature are available for the late Pleistocene–Holocene transition. The number of dates (N), and the minimum (Min.) and maximum (Max.) date observed in each site are presented. Multiple R and slopes for the relationship between Temperature and Time, and for Richness and Time, at each site are shown. Direction indicates the expected slope between richness and temperature given the temporal trends in each variable, not in their actual relationship. Negative direction represents decreasing richness with increasing temperatures through time (from past to present) in a given site. Positive direction represents increases in both temperature and richness through time. Negative direction with the sign '●' indicates positive trends in richness with *negative* trends in temperature. Positive direction with the sign '●' indicates negative trends in both richness and temperature. Sites are deployed in levels of water deficit (WD) following Francis and Currie (2003): (1) 0-250 mm, (2) 250-500 mm, (3) 500-750 mm, (4) 750-1000 mm, (5) 1000-1250 mm. The relationships all cover the Holocene-Pleistocene transition, but they do not cover identical periods of time.

				Dates in sample		Temperature = f (Time)			Richness = f (Time)				
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Multiple R	Slope	p-value	Direction	WD
1	-84.55	46.57	9	5000	13000	0.891	0.001736	0.001	0.362	-0.000111	0.338	Negative	1
2	-84.58	46.55	9	5000	13000	0.891	0.001736	0.001	0.549	-0.000182	0.126	Negative	1
3	-57.30	51.52	11	1000	11000	0.865	0.000612	0.001	0.201	-0.000038	0.553	Negative	1
4	-81.42	45.15	11	1000	11000	0.824	0.000479	0.002	0.452	-0.000081	0.162	Negative	1
5	-55.51	48.94	11	1000	11000	0.877	0.000467	<0.001	0.594	-0.000147	0.054	Negative	1
6	-65.76	49.16	12	1000	12000	0.847	0.001024	0.001	0.08	-0.000012	0.805	Negative	1
7	-93.60	47.28	12	1000	12000	0.713	0.000610	0.009	0.299	-0.000045	0.345	Negative	1
8	-56.43	52.45	12	1000	12000	0.846	0.000861	0.001	0.849	-0.000332	<0.001	Negative	1
9	-58.05	52.27	12	1000	12000	0.84	0.000918	0.001	0.889	-0.000331	<0.001	Negative	1
10	-112.10	57.77	12	1000	12000	0.584	0.000319	0.046	0.597	-0.000001	0.040	Negative	1
11	-69.45	47.46	12	1000	12000	0.84	0.000977	0.001	0.221	-0.000026	0.490	Negative	1
12	-56.20	50.03	12	1000	12000	0.827	0.000773	0.001	0.674	-0.000118	0.016	Negative	1
13	-55.47	49.47	12	1000	12000	0.836	0.000738	0.001	0.629	-0.000099	0.028	Negative	1
14	-87.92	46.83	12	1000	12000	0.752	0.000794	0.005	0.332	-0.000067	0.291	Negative	1
15	-70.60	46.28	13	1000	13000	0.867	0.001033	<0.001	0.344	-0.000057	0.250	Negative	1
16	-81.27	49.18	13	1000	13000	0.867	0.001339	<0.001	0.326	-0.000076	0.277	Negative	1
17	-58.55	53.23	13	1000	13000	0.868	0.000949	<0.001	0.645	-0.000063	0.017	Negative	1
18	-70.30	46.72	13	1000	13000	0.872	0.001060	<0.001	0.157	-0.000036	0.608	Negative	1
19	-66.13	48.91	13	1000	14000	0.87	0.001307	<0.001	0.372	-0.000062	0.210	Negative	1
20	-116.33	50.75	13	1000	13000	0.593	0.000176	0.033	0.91	-0.000098	<0.001	Negative	1
21	-116.35	51.36	13	1000	13000	0.579	0.000178	0.038	0.678	-0.000050	0.011	Negative	1
22	-66.72	45.14	14	1000	14000	0.85	0.001067	<0.001	0.183	-0.000043	0.532	Negative	1
23	-64.94	48.20	14	1000	14000	0.883	0.001167	<0.001	0.228	-0.000029	0.433	Negative	1
24	-65.84	48.24	14	1000	14000	0.882	0.001234	<0.001	0.625	-0.000043	0.017	Negative	1
25	-78.15	43.56	14	1000	14000	0.807	0.001088	<0.001	0.093	-0.000030	0.751	Negative	1
26	-81.32	45.17	14	1000	14000	0.821	0.001253	<0.001	0.538	-0.000159	0.047	Negative	1
27	-58.80	48.26	14	1000	16000	0.861	0.001083	<0.001	0.661	-0.000146	0.010	Negative	1

				Dates in sample		Temperature = f (Time)			Richness = f (Time)				
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Multiple R	Slope	p-value	Direction	WD
28	-93.64	47.14	14	1000	14000	0.785	0.001165	0.001	0.288	-0.000041	0.318	Negative	1
29	-116.42	51.65	14	1000	14000	0.603	0.000456	0.022	0.664	-0.000114	0.010	Negative	1
30	-58.24	48.24	16	1000	17000	0.897	0.001219	<0.001	0.65	-0.000105	0.006	Negative	1
31	-57.03	52.52	17	1000	17000	0.922	0.001352	<0.001	0.603	-0.000036	0.010	Negative	1
32	-91.66	47.47	17	1000	17000	0.883	0.001856	<0.001	0.707	-0.000104	0.002	Negative	1
33	-92.62	46.72	18	1000	18000	0.897	0.001886	<0.001	0.186	-0.000031	0.461	Negative	1
34	-146.48	68.33	12	1000	12000	0.173	-0.000030	0.591	0.143	0.000013	0.656	Negative ●	1
35	-128.08	64.65	12	1000	12000	0.287	-0.000037	0.366	0.311	0.000030	0.325	Negative ●	1
36	-130.65	61.68	12	1000	12000	0.155	-0.000020	0.630	0.549	0.000051	0.064	Negative ●	1
37	-166.27	64.87	12	1000	16000	0.592	-0.000196	0.043	0.529	0.000058	0.077	Negative ●	1
38	-155.05	67.93	13	1000	13000	0.357	-0.000051	0.231	0.732	0.000093	0.004	Negative ●	1
39	-142.07	67.20	13	1000	13000	0.126	-0.000018	0.682	0.654	0.000080	0.015	Negative ●	1
40	-152.60	67.25	13	1000	13000	0.342	-0.000047	0.253	0.517	0.000052	0.071	Negative ●	1
41	-145.70	63.07	13	1000	13000	0.124	-0.000016	0.686	0.42	0.000026	0.153	Negative ●	1
42	-126.42	65.23	13	1000	13000	0.235	-0.000026	0.440	0.835	0.000106	<0.001	Negative ●	1
43	-149.48	61.12	13	1000	13000	0.101	-0.000011	0.743	0.822	0.000098	0.001	Negative ●	1
44	-127.62	64.17	13	1000	13000	0.278	-0.000032	0.358	0.649	0.000061	0.016	Negative ●	1
45	-127.48	65.02	13	1000	13000	0.299	-0.000034	0.320	0.525	0.000073	0.065	Negative ●	1
46	-133.47	68.27	13	1000	13000	0.203	-0.000026	0.505	0.552	0.000093	0.051	Negative ●	1
47	-151.27	64.33	14	1000	14000	0.486	-0.000234	0.078	0.316	0.000024	0.271	Negative ●	1
48	-153.90	67.13	15	1000	15000	0.644	-0.000272	0.010	0.608	0.000074	0.016	Negative ●	1
49	-153.65	67.15	15	1000	15000	0.644	-0.000272	0.010	0.355	0.000035	0.194	Negative ●	1
50	-154.23	67.07	15	1000	15000	0.647	-0.000269	0.009	0.549	0.000048	0.034	Negative ●	1
51	-145.22	68.27	15	1000	16000	0.691	-0.000285	0.004	0.171	0.000017	0.543	Negative ●	1
52	-160.43	67.87	15	2000	16000	0.641	-0.000172	0.010	0.581	0.000053	0.023	Negative ●	1
53	-149.80	67.42	15	1000	15000	0.631	-0.000240	0.012	0.706	0.000074	0.003	Negative ●	1
54	-151.42	67.58	15	1000	15000	0.636	-0.000242	0.011	0.749	0.000083	0.001	Negative ●	1
55	-135.93	65.95	15	1000	15000	0.593	-0.000238	0.020	0.539	0.000058	0.038	Negative ●	1
56	-156.03	68.13	16	1000	16000	0.696	-0.000216	0.003	0.672	0.000064	0.004	Negative ●	1
57	-162.20	63.50	16	1000	16000	0.658	-0.000316	0.006	0.132	0.000009	0.626	Negative ●	1
58	-133.45	69.05	16	1000	16000	0.569	-0.000148	0.021	0.195	0.000022	0.468	Negative ●	1
59	-155.03	66.92	17	1000	17000	0.737	-0.000317	0.001	0.179	0.000018	0.491	Negative ●	1
60	-161.42	68.15	17	1000	17000	0.412	-0.000069	0.100	0.916	0.000072	<0.001	Negative ●	1
61	-157.22	66.77	17	1000	17000	0.739	-0.000298	0.001	0.49	0.000033	0.046	Negative ●	1
62	-146.91	64.44	17	1000	18000	0.733	-0.000446	0.001	0.546	0.000042	0.024	Negative ●	1
63	-132.17	69.12	17	1000	17000	0.29	-0.000062	0.259	0.174	0.000021	0.504	Negative ●	1
64	-138.38	68.38	18	1000	18000	0.602	-0.000168	0.008	0.227	0.000010	0.366	Negative ●	1
65	-64.80	47.08	11	1000	11000	0.888	0.000562	<0.001	0.514	0.000169	0.106	Positive	1
66	-62.05	57.38	11	2000	12000	0.89	0.001204	<0.001	0.387	0.000053	0.239	Positive	1
67	-85.66	46.43	11	1000	11000	0.798	0.000480	0.003	0.187	0.000028	0.581	Positive	1
68	-65.95	48.97	11	1000	11000	0.876	0.000715	<0.001	0.115	0.000031	0.737	Positive	1
69	-87.52	44.45	11	1000	12000	0.786	0.000698	0.004	0.347	0.000094	0.296	Positive	1
70	-95.28	73.13	11	1000	11000	0.738	0.000506	0.010	0.12	0.000010	0.724	Positive	1
71	-87.46	45.67	11	1000	11000	0.8	0.000431	0.003	0.803	0.000300	0.003	Positive	1
72	-73.31	45.54	12	1000	12000	0.81	0.000844	0.001	0.401	0.000081	0.196	Positive	1
73	-84.32	45.60	12	3000	14000	0.861	0.001674	<0.001	0.403	0.000099	0.194	Positive	1
74	-65.81	49.21	12	1000	12000	0.847	0.001024	0.001	0.667	0.000119	0.018	Positive	1
75	-69.30	43.77	12	1000	12000	0.829	0.000631	0.001	0.343	0.000072	0.274	Positive	1
76	-93.38	47.98	12	1000	12000	0.701	0.000651	0.011	0.192	0.000056	0.549	Positive	1
77	-64.08	46.67	12	1000	12000	0.844	0.000727	0.001	0.156	0.000041	0.629	Positive	1
78	-93.60	46.58	12	2000	14000	0.799	0.001202	0.002	0.401	0.000091	0.196	Positive	1
79	-73.32	45.55	12	1000	12000	0.81	0.000844	0.001	0.645	0.000149	0.024	Positive	1
80	-122.17	59.52	12	1000	12000	0.044	0.000009	0.892	0.371	0.000050	0.236	Positive	1
81	-117.22	52.24	12	1000	12000	0.362	0.000089	0.247	0.488	0.000091	0.107	Positive	1
82	-70.06	41.28	12	1000	12000	0.823	0.000400	0.001	0.769	0.000274	0.003	Positive	1
83	-78.67	42.54	13	1000	13000	0.843	0.000698	<0.001	0.075	0.000024	0.808	Positive	1
84	-88.10	43.40	13	1000	13000	0.824	0.000693	0.001	0.512	0.000131	0.073	Positive	1

				Dates in sample		Temperature = f (Time)			Richness = f (Time)				
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Multiple R	Slope	p-value	Direction	WD
85	-88.18	42.35	13	1000	13000	0.83	0.000615	<0.001	0.185	0.000047	0.544	Positive	1
86	-118.70	62.05	13	1000	13000	0.539	0.000163	0.058	0.319	0.000018	0.289	Positive	1
87	-120.67	57.45	13	1000	13000	0.398	0.000108	0.178	0.55	0.000051	0.052	Positive	1
88	-94.11	47.08	13	1000	13000	0.774	0.000735	0.002	0.114	0.000028	0.712	Positive	1
89	-80.86	44.74	13	1000	13000	0.836	0.000907	<0.001	0.151	0.000030	0.623	Positive	1
90	-81.75	43.18	13	1000	13000	0.838	0.000744	<0.001	0.7	0.000367	0.008	Positive	1
91	-78.34	44.10	13	1000	13000	0.843	0.000868	<0.001	0.703	0.000217	0.007	Positive	1
92	-95.07	72.58	13	1000	13000	0.844	0.000691	<0.001	0.469	0.000042	0.106	Positive	1
93	-86.96	46.47	13	1000	13000	0.81	0.000994	0.001	0.329	0.000068	0.272	Positive	1
94	-70.00	41.93	14	1000	14000	0.78	0.000790	0.001	0.79	0.000230	0.001	Positive	1
95	-75.81	45.47	14	1000	14000	0.832	0.001340	<0.001	0.786	0.000138	0.001	Positive	1
96	-70.62	46.58	14	1000	14000	0.86	0.001365	<0.001	0.546	0.000104	0.044	Positive	1
97	-69.41	43.92	14	1000	14000	0.822	0.001009	<0.001	0.679	0.000138	0.008	Positive	1
98	-68.94	47.53	14	1000	14000	0.869	0.001339	<0.001	0.241	0.000040	0.406	Positive	1
99	-76.90	43.51	14	1000	14000	0.807	0.001086	<0.001	0.309	0.000082	0.282	Positive	1
100	-67.33	45.26	15	1000	15000	0.856	0.001369	<0.001	0.064	0.000008	0.822	Positive	1
101	-65.27	48.05	15	1000	15000	0.883	0.001381	<0.001	0.656	0.000094	0.008	Positive	1
102	-93.35	43.15	15	1000	16000	0.837	0.001232	<0.001	0.756	0.000179	0.001	Positive	1
103	-78.10	44.10	15	1000	15000	0.839	0.001501	<0.001	0.88	0.000369	<0.001	Positive	1
104	-87.85	44.24	16	1000	16000	0.863	0.001528	<0.001	0.848	0.000204	<0.001	Positive	1
105	-87.22	41.58	16	1000	16000	0.852	0.001267	<0.001	0.765	0.000180	0.001	Positive	1
106	-87.73	44.05	17	1000	18000	0.89	0.001596	<0.001	0.327	0.000042	0.200	Positive	1
107	-70.21	41.28	17	1000	17000	0.858	0.001295	<0.001	0.801	0.000348	<0.001	Positive	1
108	-78.88	42.25	18	1000	18000	0.897	0.001619	<0.001	0.79	0.000168	<0.001	Positive	1
109	-74.60	42.50	18	1000	18000	0.894	0.001577	<0.001	0.796	0.000191	<0.001	Positive	1
110	-82.76	41.92	18	1000	18000	0.898	0.001533	<0.001	0.821	0.000173	<0.001	Positive	1
111	-119.72	56.72	11	1000	11000	0.476	-0.000064	0.138	0.29	-0.000023	0.387	Positive ●	1
112	-119.48	56.77	11	1000	11000	0.476	-0.000064	0.138	0.227	-0.000025	0.502	Positive ●	1
113	-132.02	67.65	11	1000	11000	0.223	-0.000035	0.510	0.533	-0.000069	0.092	Positive ●	1
114	-118.37	52.73	11	1000	11000	0.393	-0.000039	0.232	0.269	-0.000018	0.424	Positive ●	1
115	-129.02	60.03	11	1000	11000	0.492	-0.000072	0.124	0.376	-0.000065	0.254	Positive ●	1
116	-135.40	59.20	12	1000	12000	0.007	-0.000001	0.983	0.346	-0.000028	0.271	Positive ●	1
117	-126.12	65.22	14	1000	14000	0.437	-0.000055	0.118	0.203	-0.000029	0.485	Positive ●	1
118	-133.58	69.28	14	1000	14000	0.485	-0.000128	0.079	0.184	-0.000024	0.529	Positive ●	1
119	-156.45	66.97	17	2000	18000	0.761	-0.000329	<0.001	0.62	-0.000057	0.008	Positive ●	1
120	-92.72	46.42	6	7000	12000	0.862	0.001692	0.027	0.836	-0.000395	0.038	Negative	2
121	-99.23	47.15	6	4000	13000	0.798	0.000952	0.057	0.84	-0.000471	0.036	Negative	2
122	-92.70	49.35	7	7000	13000	0.913	0.002428	0.004	0.758	-0.000254	0.048	Negative	2
123	-91.57	49.93	8	4000	11000	0.775	0.000644	0.024	0.821	-0.000262	0.012	Negative	2
124	-110.32	43.77	8	7000	14000	0.906	0.000581	0.002	0.867	-0.000394	0.005	Negative	2
125	-71.94	46.15	9	3000	11000	0.883	0.000836	0.002	0.331	-0.000083	0.385	Negative	2
126	-95.17	47.18	11	1000	11000	0.741	0.000240	0.009	0.255	-0.000039	0.449	Negative	2
127	-81.50	46.60	11	1000	11000	0.818	0.000606	0.002	0.016	-0.000003	0.963	Negative	2
128	-72.15	48.29	11	1000	11000	0.854	0.000785	0.001	0.567	-0.000122	0.069	Negative	2
129	-70.62	47.61	11	1000	11000	0.858	0.000736	0.001	0.717	-0.000134	0.013	Negative	2
130	-90.58	36.60	11	8000	18000	0.965	0.001811	<0.001	0.235	-0.000073	0.487	Negative	2
131	-80.70	46.83	11	1000	11000	0.82	0.000614	0.002	0.751	-0.000130	0.008	Negative	2
132	-89.32	48.42	11	1000	11000	0.805	0.000480	0.003	0.528	-0.000138	0.095	Negative	2
133	-88.74	48.56	11	1000	11000	0.805	0.000545	0.003	0.858	-0.000208	0.001	Negative	2
134	-111.18	44.13	11	1000	11000	0.731	0.000051	0.011	0.098	-0.000020	0.775	Negative	2
135	-91.12	48.00	11	1000	11000	0.785	0.000395	0.004	0.724	-0.000213	0.012	Negative	2
136	-79.78	47.23	11	1000	11000	0.827	0.000677	0.002	0.73	-0.000284	0.011	Negative	2
137	-92.02	48.11	11	1000	11000	0.777	0.000374	0.005	0.695	-0.000197	0.018	Negative	2
138	-109.94	43.45	11	1000	11000	0.571	0.000036	0.067	0.877	-0.000089	<0.001	Negative	2
139	-70.68	47.48	12	1000	12000	0.835	0.001002	0.001	0.743	-0.000130	0.006	Negative	2
140	-88.02	46.67	12	1000	12000	0.752	0.000794	0.005	0.461	-0.000083	0.131	Negative	2
141	-71.67	44.17	12	1000	12000	0.821	0.000671	0.001	0.542	-0.000041	0.069	Negative	2

				Dates in sample		Temperature = f (Time)			Richness = f (Time)				
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Multiple R	Slope	p-value	Direction	WD
142	-93.75	49.58	12	1000	12000	0.672	0.000681	0.017	0.809	-0.000147	0.001	Negative	2
143	-106.08	53.80	12	1000	12000	0.588	0.000450	0.044	0.352	-0.000031	0.262	Negative	2
144	-71.42	47.08	12	1000	12000	0.826	0.000977	0.001	0.61	-0.000124	0.035	Negative	2
145	-94.93	47.18	12	1000	12000	0.695	0.000543	0.012	0.07	-0.000013	0.829	Negative	2
146	-72.84	46.79	12	1000	12000	0.82	0.000988	0.001	0.697	-0.000129	0.012	Negative	2
147	-74.47	46.06	12	1000	12000	0.802	0.000959	0.002	0.476	-0.000044	0.118	Negative	2
148	-74.37	45.95	12	1000	12000	0.799	0.000910	0.002	0.002	0.000000	0.996	Negative	2
149	-90.35	45.30	12	1000	12000	0.742	0.000649	0.006	0.272	-0.000090	0.393	Negative	2
150	-84.26	47.31	12	1000	12000	0.786	0.000934	0.002	0.855	-0.000194	<0.001	Negative	2
151	-110.60	44.96	12	1000	12000	0.62	0.000139	0.031	0.011	-0.000002	0.974	Negative	2
152	-121.50	50.50	12	1000	12000	0.374	0.000088	0.231	0.667	-0.000041	0.018	Negative	2
153	-93.69	44.89	12	1000	12000	0.732	0.000502	0.007	0.185	-0.000071	0.566	Negative	2
154	-107.05	40.02	12	1000	12000	0.653	0.000153	0.021	0.628	-0.000149	0.029	Negative	2
155	-109.92	43.46	12	1000	12000	0.593	0.000129	0.042	0.517	-0.000064	0.085	Negative	2
156	-73.97	44.18	13	1000	13000	0.849	0.000860	<0.001	0.016	-0.000003	0.959	Negative	2
157	-89.42	43.10	13	1000	13000	0.819	0.000681	0.001	0.166	-0.000026	0.587	Negative	2
158	-110.26	44.30	13	1000	13000	0.722	0.000184	0.005	0.843	-0.000195	<0.001	Negative	2
159	-68.20	45.03	13	1000	13000	0.873	0.000803	<0.001	0.49	-0.000071	0.089	Negative	2
160	-95.01	47.24	13	1000	13000	0.759	0.000719	0.003	0.039	-0.000016	0.899	Negative	2
161	-112.72	48.55	13	1000	14000	0.642	0.000349	0.018	0.672	-0.000158	0.012	Negative	2
162	-110.23	44.15	13	1000	13000	0.712	0.000188	0.006	0.422	-0.000072	0.151	Negative	2
163	-89.12	44.50	13	1000	13000	0.811	0.000764	0.001	0.205	-0.000033	0.503	Negative	2
164	-110.28	44.49	13	1000	13000	0.722	0.000184	0.005	0.427	-0.000127	0.146	Negative	2
165	-70.35	45.85	14	1000	14000	0.848	0.001278	<0.001	0.183	-0.000040	0.531	Negative	2
166	-93.16	44.82	14	1000	14000	0.796	0.000945	0.001	0.449	-0.000108	0.107	Negative	2
167	-110.23	43.93	14	1000	14000	0.769	0.000245	0.001	0.443	-0.000073	0.112	Negative	2
168	-110.30	44.07	14	1000	14000	0.762	0.000263	0.002	0.471	-0.000095	0.089	Negative	2
169	-122.12	48.77	14	4000	17000	0.867	0.000686	<0.001	0.024	-0.000003	0.934	Negative	2
170	-121.62	48.23	14	1000	14000	0.657	0.000226	0.011	0.22	-0.000025	0.450	Negative	2
171	-71.67	42.83	16	1000	16000	0.848	0.001428	<0.001	0.502	-0.000041	0.047	Negative	2
172	-110.73	44.92	16	1000	16000	0.808	0.000465	<0.001	0.563	-0.000078	0.023	Negative	2
173	-110.60	44.65	18	1000	18000	0.861	0.000607	<0.001	0.831	-0.000149	<0.001	Negative	2
174	-110.60	43.75	18	1000	18000	0.866	0.000514	<0.001	0.685	-0.000101	0.002	Negative	2
175	-147.85	67.43	15	1000	15000	0.612	-0.000272	0.015	0.748	0.000068	0.001	Negative ●	2
176	-144.66	63.94	16	1000	16000	0.672	-0.000389	0.004	0.7	0.000056	0.003	Negative ●	2
177	-143.15	66.58	18	1000	18000	0.729	-0.000341	0.001	0.384	0.000026	0.116	Negative ●	2
178	-80.37	41.55	6	3000	11000	0.872	0.000443	0.024	0.854	0.000302	0.030	Positive	2
179	-93.70	42.26	7	7000	14000	0.917	0.001674	0.004	0.867	0.000638	0.012	Positive	2
180	-78.95	44.62	7	2000	11000	0.863	0.000608	0.012	0.889	0.000220	0.007	Positive	2
181	-98.16	46.86	7	5000	13000	0.838	0.001062	0.019	0.702	0.000240	0.078	Positive	2
182	-97.33	45.50	8	1000	13000	0.756	0.000512	0.030	0.699	0.000269	0.054	Positive	2
183	-99.65	50.72	8	1000	13000	0.745	0.000797	0.034	0.121	0.000037	0.775	Positive	2
184	-96.08	47.20	8	1000	11000	0.78	0.000220	0.022	0.489	0.000068	0.219	Positive	2
185	-94.58	46.28	9	1000	11000	0.827	0.000281	0.006	0.239	0.000041	0.536	Positive	2
186	-105.73	53.24	9	1000	13000	0.87	0.000844	0.002	0.315	0.000030	0.408	Positive	2
187	-93.90	42.16	9	1000	16000	0.868	0.001084	0.002	0.952	0.000297	<0.001	Positive	2
188	-95.28	46.21	9	1000	13000	0.767	0.000632	0.016	0.289	0.000051	0.451	Positive	2
189	-95.31	46.18	9	1000	12000	0.73	0.000464	0.026	0.065	0.000016	0.868	Positive	2
190	-95.29	46.21	9	5000	13000	0.857	0.001109	0.003	0.705	0.000282	0.034	Positive	2
191	-73.60	42.63	10	3000	12000	0.837	0.000742	0.003	0.82	0.000464	0.004	Positive	2
192	-84.87	47.88	11	1000	11000	0.807	0.000601	0.003	0.128	0.000028	0.708	Positive	2
193	-72.15	44.37	11	1000	11000	0.86	0.000484	0.001	0.576	0.000102	0.064	Positive	2
194	-74.67	41.33	11	1000	11000	0.869	0.000288	0.001	0.811	0.000247	0.002	Positive	2
195	-83.24	43.12	11	1000	11000	0.835	0.000385	0.001	0.153	0.000073	0.653	Positive	2
196	-76.45	36.58	11	1000	11000	0.92	0.000143	<0.001	0.901	0.000313	<0.001	Positive	2
197	-99.28	49.43	11	1000	14000	0.814	0.001325	0.002	0.111	0.000030	0.746	Positive	2
198	-74.43	40.38	11	1000	11000	0.88	0.000232	<0.001	0.798	0.000251	0.003	Positive	2

Site	LonDD	LatDD	N	Dates in sample		Temperature = f (Time)			Richness = f (Time)			Direction	WD
				Min.	Max.	Multiple R	Slope	p-value	Multiple R	Slope	p-value		
199	-89.90	46.25	11	1000	11000	0.799	0.000372	0.003	0.451	0.000051	0.164	Positive	2
200	-87.97	46.72	11	1000	11000	0.8	0.000449	0.003	0.282	0.000069	0.401	Positive	2
201	-95.20	43.33	11	1000	17000	0.852	0.001271	0.001	0.831	0.000253	0.002	Positive	2
202	-95.77	47.19	11	1000	11000	0.735	0.000224	0.010	0.411	0.000090	0.209	Positive	2
203	-77.92	44.30	11	1000	11000	0.834	0.000473	0.001	0.669	0.000161	0.024	Positive	2
204	-73.99	46.00	11	1000	11000	0.839	0.000585	0.001	0.504	0.000092	0.114	Positive	2
205	-79.77	44.17	11	1000	11000	0.832	0.000463	0.002	0.408	0.000093	0.213	Positive	2
206	-105.54	40.08	11	1000	11000	0.697	0.000063	0.017	0.569	0.000029	0.067	Positive	2
207	-108.10	37.47	11	1000	11000	0.808	0.000081	0.003	0.487	0.000072	0.128	Positive	2
208	-78.55	39.77	12	1000	12000	0.807	0.000404	0.002	0.373	0.000073	0.233	Positive	2
209	-89.87	43.08	12	1000	12000	0.761	0.000563	0.004	0.609	0.000348	0.036	Positive	2
210	-70.68	45.57	12	1000	12000	0.827	0.000819	0.001	0.064	0.000007	0.844	Positive	2
211	-74.68	43.92	12	1000	12000	0.801	0.000697	0.002	0.881	0.000321	<0.001	Positive	2
212	-93.27	42.02	12	1000	16000	0.82	0.001102	0.001	0.89	0.000254	<0.001	Positive	2
213	-70.38	47.50	12	2000	13000	0.891	0.001229	<0.001	0.03	0.000006	0.925	Positive	2
214	-70.98	47.60	12	1000	12000	0.835	0.001002	0.001	0.357	0.000041	0.255	Positive	2
215	-71.69	43.61	12	1000	12000	0.821	0.000671	0.001	0.277	0.000011	0.384	Positive	2
216	-78.47	42.62	12	1000	12000	0.798	0.000557	0.002	0.723	0.000159	0.008	Positive	2
217	-76.10	45.60	12	1000	12000	0.798	0.000850	0.002	0.086	0.000022	0.790	Positive	2
218	-93.87	44.87	12	1000	12000	0.732	0.000502	0.007	0.639	0.000165	0.025	Positive	2
219	-70.93	46.93	12	1000	12000	0.829	0.000972	0.001	0.681	0.000087	0.015	Positive	2
220	-84.69	40.22	12	7000	18000	0.965	0.002169	<0.001	0.684	0.000331	0.014	Positive	2
221	-91.45	45.30	12	1000	12000	0.737	0.000593	0.006	0.033	0.000007	0.919	Positive	2
222	-70.35	43.97	12	1000	12000	0.827	0.000649	0.001	0.122	0.000026	0.707	Positive	2
223	-77.05	44.48	12	1000	12000	0.798	0.000744	0.002	0.821	0.000180	0.001	Positive	2
224	-79.98	44.85	12	1000	12000	0.792	0.000773	0.002	0.771	0.000228	0.003	Positive	2
225	-73.87	45.96	12	1000	12000	0.806	0.000901	0.002	0.325	0.000058	0.303	Positive	2
226	-93.18	45.43	12	1000	12000	0.731	0.000537	0.007	0.363	0.000182	0.246	Positive	2
227	-93.20	45.41	12	1000	12000	0.731	0.000537	0.007	0.656	0.000143	0.021	Positive	2
228	-79.44	44.18	12	1000	12000	0.794	0.000731	0.002	0.602	0.000301	0.038	Positive	2
229	-93.69	45.43	12	1000	12000	0.729	0.000518	0.007	0.228	0.000063	0.475	Positive	2
230	-76.60	44.52	12	1000	12000	0.798	0.000746	0.002	0.664	0.000133	0.018	Positive	2
231	-71.70	44.14	12	1000	12000	0.821	0.000671	0.001	0.533	0.000103	0.074	Positive	2
232	-73.00	46.61	13	1000	13000	0.861	0.001118	<0.001	0.097	0.000025	0.752	Positive	2
233	-85.00	43.48	13	1000	13000	0.834	0.000727	<0.001	0.758	0.000276	0.003	Positive	2
234	-71.73	44.13	13	1000	13000	0.862	0.000759	<0.001	0.473	0.000056	0.103	Positive	2
235	-93.13	44.27	13	1000	13000	0.799	0.000657	0.001	0.326	0.000075	0.276	Positive	2
236	-73.05	42.65	13	1000	13000	0.854	0.000605	<0.001	0.812	0.000187	0.001	Positive	2
237	-93.63	45.03	13	1000	13000	0.791	0.000649	0.001	0.044	0.000008	0.886	Positive	2
238	-80.13	37.60	13	1000	13000	0.858	0.000357	<0.001	0.615	0.000112	0.025	Positive	2
239	-74.40	46.17	13	1000	13000	0.847	0.001110	<0.001	0.151	0.000028	0.623	Positive	2
240	-93.87	43.03	13	2000	15000	0.824	0.001106	0.001	0.812	0.000253	0.001	Positive	2
241	-80.41	43.24	13	1000	13000	0.841	0.000749	<0.001	0.826	0.000240	0.001	Positive	2
242	-91.50	42.99	13	1000	14000	0.804	0.000841	0.001	0.91	0.000254	<0.001	Positive	2
243	-81.33	41.20	13	1000	13000	0.846	0.000587	<0.001	0.762	0.000121	0.002	Positive	2
244	-82.06	40.68	13	6000	18000	0.956	0.002084	<0.001	0.924	0.000234	<0.001	Positive	2
245	-81.97	41.00	13	5000	17000	0.93	0.001866	<0.001	0.798	0.000288	0.001	Positive	2
246	-80.40	43.90	13	1000	13000	0.84	0.000804	<0.001	0.771	0.000334	0.002	Positive	2
247	-80.40	43.91	13	1000	13000	0.84	0.000804	<0.001	0.618	0.000209	0.024	Positive	2
248	-80.37	43.23	13	1000	13000	0.841	0.000749	<0.001	0.896	0.000340	<0.001	Positive	2
249	-122.56	49.33	13	1000	13000	0.54	0.000129	0.057	0.815	0.000103	0.001	Positive	2
250	-71.03	41.95	13	1000	13000	0.862	0.000523	<0.001	0.874	0.000467	<0.001	Positive	2
251	-83.63	42.33	14	1000	14000	0.803	0.000940	0.001	0.54	0.000128	0.046	Positive	2
252	-72.88	42.57	14	1000	14000	0.793	0.000915	0.001	0.926	0.000366	<0.001	Positive	2
253	-75.67	40.48	14	1000	14000	0.798	0.000659	0.001	0.655	0.000107	0.011	Positive	2
254	-72.58	45.36	14	1000	14000	0.838	0.001288	<0.001	0.406	0.000077	0.150	Positive	2
255	-81.93	36.53	14	1000	14000	0.794	0.000513	0.001	0.456	0.000080	0.101	Positive	2

				Dates in sample		Temperature = f (Time)			Richness = f (Time)				
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Multiple R	Slope	p-value	Direction	WD
256	-72.21	42.52	14	1000	16000	0.836	0.001379	<0.001	0.673	0.000170	0.008	Positive	2
257	-70.63	45.60	14	1000	14000	0.848	0.001278	<0.001	0.084	0.000011	0.774	Positive	2
258	-74.05	44.15	14	1000	14000	0.823	0.001195	<0.001	0.626	0.000076	0.017	Positive	2
259	-93.57	45.00	14	1000	14000	0.793	0.000926	0.001	0.611	0.000123	0.020	Positive	2
260	-79.07	38.00	14	1000	14000	0.8	0.000542	0.001	0.735	0.000145	0.003	Positive	2
261	-71.33	45.67	14	1000	14000	0.846	0.001312	<0.001	0.132	0.000013	0.654	Positive	2
262	-73.32	42.50	15	1000	15000	0.819	0.001262	<0.001	0.814	0.000181	<0.001	Positive	2
263	-88.34	40.68	15	1000	15000	0.812	0.000962	<0.001	0.566	0.000144	0.028	Positive	2
264	-71.83	44.03	15	1000	15000	0.835	0.001361	<0.001	0.227	0.000036	0.415	Positive	2
265	-89.73	43.42	15	1000	15000	0.83	0.001182	<0.001	0.313	0.000068	0.255	Positive	2
266	-85.12	44.88	15	1000	15000	0.84	0.001467	<0.001	0.592	0.000078	0.020	Positive	2
267	-80.66	43.23	15	1000	15000	0.823	0.001291	<0.001	0.821	0.000269	<0.001	Positive	2
268	-76.35	41.67	15	1000	15000	0.82	0.001121	<0.001	0.646	0.000173	0.009	Positive	2
269	-82.47	40.35	15	1000	15000	0.823	0.000993	<0.001	0.076	0.000015	0.789	Positive	2
270	-85.38	42.40	15	1000	15000	0.822	0.001186	<0.001	0.392	0.000045	0.148	Positive	2
271	-90.08	45.33	15	1000	15000	0.837	0.001357	<0.001	0.078	0.000011	0.781	Positive	2
272	-70.35	44.03	15	1000	15000	0.834	0.001317	<0.001	0.774	0.000172	0.001	Positive	2
273	-122.55	49.31	15	1000	15000	0.708	0.000358	0.003	0.799	0.000108	<0.001	Positive	2
274	-110.35	44.93	15	1000	15000	0.787	0.000364	<0.001	0.249	0.000026	0.370	Positive	2
275	-89.68	43.43	15	1000	15000	0.83	0.001182	<0.001	0.513	0.000147	0.050	Positive	2
276	-79.27	39.57	16	1000	16000	0.858	0.000987	<0.001	0.764	0.000117	0.001	Positive	2
277	-89.17	43.92	16	1000	16000	0.86	0.001428	<0.001	0.489	0.000075	0.055	Positive	2
278	-92.83	45.05	16	1000	16000	0.848	0.001441	<0.001	0.343	0.000069	0.193	Positive	2
279	-89.42	43.10	16	1000	16000	0.857	0.001374	<0.001	0.619	0.000100	0.011	Positive	2
280	-77.42	40.80	16	1000	16000	0.854	0.001104	<0.001	0.832	0.000207	<0.001	Positive	2
281	-85.25	41.58	16	1000	16000	0.852	0.001298	<0.001	0.479	0.000068	0.061	Positive	2
282	-71.12	41.97	16	1000	16000	0.837	0.001256	<0.001	0.807	0.000268	<0.001	Positive	2
283	-72.18	42.53	16	1000	16000	0.844	0.001353	<0.001	0.403	0.000105	0.122	Positive	2
284	-69.32	44.98	16	1000	16000	0.873	0.001585	<0.001	0.42	0.000101	0.105	Positive	2
285	-84.75	41.42	16	1000	16000	0.852	0.001243	<0.001	0.879	0.000152	<0.001	Positive	2
286	-89.17	43.92	16	1000	16000	0.86	0.001428	<0.001	0.494	0.000124	0.052	Positive	2
287	-122.58	44.63	16	1000	16000	0.77	0.000174	<0.001	0.81	0.000149	<0.001	Positive	2
288	-71.25	44.25	16	1000	16000	0.868	0.001600	<0.001	0.211	0.000030	0.432	Positive	2
289	-86.53	41.65	17	1000	17000	0.876	0.001341	<0.001	0.804	0.000165	<0.001	Positive	2
290	-80.28	38.20	17	1000	17000	0.88	0.000911	<0.001	0.827	0.000210	<0.001	Positive	2
291	-80.25	44.37	17	1000	17000	0.889	0.001795	<0.001	0.797	0.000270	<0.001	Positive	2
292	-86.53	41.67	17	1000	17000	0.876	0.001341	<0.001	0.673	0.000192	0.003	Positive	2
293	-73.28	41.82	17	1000	17000	0.87	0.001394	<0.001	0.854	0.000234	<0.001	Positive	2
294	-74.33	41.50	17	1000	17000	0.872	0.001277	<0.001	0.62	0.000118	0.008	Positive	2
295	-84.88	43.42	17	1000	17000	0.882	0.001613	<0.001	0.675	0.000146	0.003	Positive	2
296	-122.49	45.80	17	1000	17000	0.796	0.000254	<0.001	0.839	0.000189	<0.001	Positive	2
297	-83.53	40.10	17	1000	17000	0.877	0.001171	<0.001	0.725	0.000129	0.001	Positive	2
298	-77.93	41.92	17	1000	17000	0.877	0.001438	<0.001	0.546	0.000112	0.023	Positive	2
299	-77.92	42.25	18	1000	18000	0.897	0.001616	<0.001	0.802	0.000198	<0.001	Positive	2
300	-77.55	39.97	18	1000	18000	0.899	0.001102	<0.001	0.796	0.000177	<0.001	Positive	2
301	-79.00	37.98	18	1000	18000	0.9	0.000883	<0.001	0.767	0.000160	<0.001	Positive	2
302	-73.98	42.24	18	1000	18000	0.894	0.001577	<0.001	0.711	0.000223	0.001	Positive	2
303	-68.64	44.63	18	1000	18000	0.908	0.001676	<0.001	0.457	0.000079	0.057	Positive	2
304	-76.68	36.17	18	1000	18000	0.906	0.000519	<0.001	0.915	0.000397	<0.001	Positive	2
305	-72.12	41.37	18	1000	18000	0.886	0.001327	<0.001	0.617	0.000125	0.006	Positive	2
306	-83.80	40.35	18	1000	18000	0.897	0.001324	<0.001	0.668	0.000158	0.002	Positive	2
307	-74.48	40.40	18	1000	18000	0.895	0.001072	<0.001	0.713	0.000172	0.001	Positive	2
308	-75.27	41.03	18	1000	18000	0.896	0.001212	<0.001	0.838	0.000283	<0.001	Positive	2
309	-79.38	44.00	18	1000	18000	0.908	0.001859	<0.001	0.853	0.000318	<0.001	Positive	2
310	-122.25	46.59	18	1000	18000	0.834	0.000324	<0.001	0.298	0.000032	0.230	Positive	2
311	-107.68	37.75	18	1000	18000	0.894	0.000460	<0.001	0.092	0.000012	0.716	Positive	2
312	-79.62	38.15	18	1000	18000	0.9	0.000905	<0.001	0.88	0.000323	<0.001	Positive	2

				Dates in sample		Temperature = f (Time)			Richness = f (Time)				
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Multiple R	Slope	p-value	Direction	WD
313	-74.20	41.24	18	1000	18000	0.893	0.001329	<0.001	0.863	0.000156	<0.001	Positive	2
314	-74.04	41.39	18	1000	18000	0.893	0.001329	<0.001	0.794	0.000194	<0.001	Positive	2
315	-114.60	50.77	11	1000	11000	0.046	-0.000003	0.893	0.656	-0.000074	0.028	Positive ●	2
316	-105.50	37.70	6	1000	15000	0.957	0.000407	0.003	0.063	-0.000004	0.906	Negative	3
317	-80.16	47.18	7	5000	11000	0.892	0.001144	0.007	0.821	-0.000702	0.024	Negative	3
318	-73.03	46.73	11	1000	11000	0.845	0.000667	0.001	0.852	-0.000249	0.001	Negative	3
319	-107.47	44.55	11	1000	11000	0.615	0.000042	0.044	0.593	-0.000125	0.054	Negative	3
320	-112.17	46.45	11	1000	12000	0.627	0.000141	0.039	0.21	-0.000029	0.535	Negative	3
321	-88.47	33.56	12	1000	12000	0.833	0.000259	0.001	0.324	-0.000136	0.304	Negative	3
322	-81.77	47.32	12	1000	12000	0.801	0.000981	0.002	0.838	-0.000151	0.001	Negative	3
323	-86.53	33.50	13	1000	13000	0.887	0.000280	<0.001	0.449	-0.000164	0.124	Negative	3
324	-112.40	46.53	13	1000	13000	0.711	0.000182	0.006	0.513	-0.000061	0.073	Negative	3
325	-107.01	44.27	15	1000	15000	0.773	0.000472	0.001	0.758	-0.000157	0.001	Negative	3
326	-119.01	37.60	15	1000	15000	0.814	0.000153	<0.001	0.11	-0.000014	0.697	Negative	3
327	-86.13	31.72	17	1000	17000	0.897	0.000514	<0.001	0.501	-0.000103	0.040	Negative	3
328	-78.95	33.80	18	1000	18000	0.911	0.000454	<0.001	0.016	-0.000005	0.950	Negative	3
329	-78.50	45.50	11	1000	11000	0.824	0.000536	0.002	0.452	0.000064	0.163	Positive	3
330	-79.47	46.45	11	1000	11000	0.816	0.000586	0.002	0.308	0.000069	0.357	Positive	3
331	-78.50	34.50	11	7000	17000	0.965	0.000757	<0.001	0.601	0.000073	0.050	Positive	3
332	-119.07	37.66	11	1000	11000	0.673	0.000023	0.023	0.219	0.000026	0.518	Positive	3
333	-107.26	44.18	11	1000	11000	0.616	0.000043	0.044	0.014	0.000004	0.968	Positive	3
334	-77.34	46.03	11	1000	11000	0.824	0.000607	0.002	0.174	0.000036	0.609	Positive	3
335	-79.50	45.38	11	1000	11000	0.824	0.000530	0.002	0.669	0.000203	0.024	Positive	3
336	-79.38	45.42	12	1000	12000	0.795	0.000829	0.002	0.482	0.000108	0.113	Positive	3
337	-76.68	44.80	12	1000	12000	0.798	0.000796	0.002	0.476	0.000108	0.118	Positive	3
338	-77.18	44.85	14	1000	14000	0.825	0.001277	<0.001	0.327	0.000062	0.254	Positive	3
339	-105.50	37.55	14	1000	14000	0.795	0.000276	0.001	0.633	0.000071	0.015	Positive	3
340	-77.35	45.18	14	1000	14000	0.829	0.001340	<0.001	0.115	0.000025	0.695	Positive	3
341	-85.50	36.03	18	1000	18000	0.891	0.000923	<0.001	0.759	0.000112	<0.001	Positive	3
342	-91.10	36.80	18	1000	18000	0.882	0.001019	<0.001	0.58	0.000101	0.012	Positive	3
343	-85.72	37.45	18	1000	18000	0.891	0.001032	<0.001	0.827	0.000246	<0.001	Positive	3
344	-85.17	34.67	18	1000	18000	0.893	0.000824	<0.001	0.801	0.000156	<0.001	Positive	3
345	-80.78	34.17	18	1000	18000	0.903	0.000599	<0.001	0.157	0.000040	0.533	Positive	3
346	-119.82	37.95	18	1000	18000	0.852	0.000217	<0.001	0.826	0.000114	<0.001	Positive	3
347	-123.58	44.17	18	1000	18000	0.813	0.000166	<0.001	0.697	0.000155	0.001	Positive	3
348	-108.30	33.70	8	7000	18000	0.988	0.000547	<0.001	0.739	-0.000105	0.036	Negative	4
349	-109.43	34.00	8	3000	18000	0.917	0.000455	0.001	0.191	-0.000033	0.650	Negative	4
350	-119.26	37.20	11	1000	11000	0.737	0.000029	0.010	0.094	-0.000013	0.782	Negative	4
351	-111.35	34.46	12	2000	13000	0.82	0.000185	0.001	0.937	-0.000245	<0.001	Negative	4
352	-112.22	36.72	12	1000	12000	0.733	0.000140	0.007	0.662	-0.000112	0.019	Negative	4
353	-111.35	34.46	17	2000	18000	0.909	0.000409	<0.001	0.007	-0.000001	0.978	Negative	4
354	-81.42	27.20	18	1000	18000	0.92	0.000215	<0.001	0.298	-0.000083	0.229	Negative	4
355	-82.00	29.52	18	1000	18000	0.916	0.000322	<0.001	0.008	-0.000002	0.975	Negative	4
356	-81.50	27.58	18	1000	18000	0.92	0.000226	<0.001	0.627	-0.000175	0.005	Negative	4
357	-108.25	33.87	8	7000	14000	0.917	0.000443	0.001	0.823	0.000171	0.012	Positive	4
358	-97.12	30.37	10	6000	18000	0.947	0.000674	<0.001	0.478	0.000214	0.163	Positive	4
359	-85.02	30.27	18	1000	18000	0.924	0.000456	<0.001	0.622	0.000147	0.006	Positive	4
360	-119.83	37.00	13	1000	13000	0.734	0.000084	0.004	0.372	-0.000086	0.210	Negative	5
361	-111.00	38.00	16	1000	17000	0.876	0.000354	<0.001	0.679	-0.000133	0.004	Negative	5
362	-112.00	34.00	10	1000	12000	0.761	0.000146	0.011	0.489	0.000169	0.151	Positive	5

Table S4. The relationship between richness and temperature through time at each sampling site that includes dates of the Holocene-Pleistocene transition. The number of dates (N), and the minimum (Min.) and maximum (Max.) date observed in each site are presented. Multiple R and slopes of the richness-temperature relationships are shown. Temperature increases through time in all relationships, except in the cases identified with the sign '●', which indicates that temperature *decreased* with time. Direction indicates the observed slope of the richness-temperature relationship. Column labelled 'Direction§' indicates the expected slope given the temporal trends in each variable, as described in Table S3. In this column, expected trends that do not match observed trends in the richness-temperature slopes are in italics. Sites are deployed in levels of water deficit (WD) following Francis and Currie (2003): (1) 0-250 mm, (2) 250-500 mm, (3) 500-750 mm, (4) 750-1000 mm, (5) 1000-1250 mm.

				Dates in sample		Richness = f (Temperature)					
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Direction	Direction§	WD
1	-84.55	46.57	9	5000	13000	0.491	-0.077	0.18	Negative	Negative	1
2	-84.58	46.55	9	5000	13000	0.443	-0.076	0.232	Negative	Negative	1
3	-57.30	51.52	11	1000	11000	0.431	-0.115	0.186	Negative	Negative	1
4	-81.42	45.15	11	1000	11000	0.075	-0.023	0.825	Negative	Negative	1
5	-55.51	48.94	11	1000	11000	0.732	-0.341	0.01	Negative	Negative	1
6	-65.76	49.16	12	1000	12000	0.238	-0.031	0.457	Negative	Negative	1
7	-93.60	47.28	12	1000	12000	0.03	-0.005	0.927	Negative	Negative	1
8	-56.43	52.45	12	1000	12000	0.838	-0.323	0.001	Negative	Negative	1
9	-58.05	52.27	12	1000	12000	0.826	-0.281	0.001	Negative	Negative	1
10	-112.10	57.77	12	1000	12000	0.392	-0.001	0.207	Negative	Negative	1
11	-69.45	47.46	12	1000	12000	0.412	-0.042	0.183	Negative	Negative	1
12	-56.20	50.03	12	1000	12000	0.774	-0.145	0.003	Negative	Negative	1
13	-55.47	49.47	12	1000	12000	0.593	-0.106	0.042	Negative	Negative	1
14	-87.92	46.83	12	1000	12000	0.516	-0.099	0.086	Negative	Negative	1
15	-70.60	46.28	13	1000	13000	0.161	-0.022	0.6	Negative	Negative	1
16	-81.27	49.18	13	1000	13000	0.1	0.015	0.744	Positive	*Negative*	1
17	-58.55	53.23	13	1000	13000	0.545	-0.049	0.054	Negative	Negative	1
18	-70.30	46.72	13	1000	13000	0.101	0.019	0.743	Positive	*Negative*	1
19	-66.13	48.91	13	1000	14000	0.713	-0.079	0.006	Negative	Negative	1
20	-116.33	50.75	13	1000	13000	0.56	-0.204	0.047	Negative	Negative	1
21	-116.35	51.36	13	1000	13000	0.587	-0.14	0.035	Negative	Negative	1
22	-66.72	45.14	14	1000	14000	0.422	-0.078	0.133	Negative	Negative	1
23	-64.94	48.20	14	1000	14000	0.451	-0.043	0.105	Negative	Negative	1
24	-65.84	48.24	14	1000	14000	0.635	-0.031	0.015	Negative	Negative	1
25	-78.15	43.56	14	1000	14000	0.526	-0.125	0.053	Negative	Negative	1
26	-81.32	45.17	14	1000	14000	0.688	-0.133	0.007	Negative	Negative	1
27	-58.80	48.26	14	1000	16000	0.723	-0.127	0.004	Negative	Negative	1
28	-93.64	47.14	14	1000	14000	0.646	-0.062	0.013	Negative	Negative	1
29	-116.42	51.65	14	1000	14000	0.924	-0.21	<0.001	Negative	Negative	1
30	-58.24	48.24	16	1000	17000	0.481	-0.057	0.06	Negative	Negative	1
31	-57.03	52.52	17	1000	17000	0.53	-0.022	0.029	Negative	Negative	1
32	-91.66	47.47	17	1000	17000	0.604	-0.042	0.01	Negative	Negative	1
33	-92.62	46.72	18	1000	18000	0.039	-0.003	0.879	Negative	Negative	1
34	-146.48	68.33	12	1000	12000	0.382	0.202	0.22	Positive ●	*Negative* ●	1

				Dates in sample		Richness = f (Temperature)					
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Direction	Direction§	WD
35	-128.08	64.65	12	1000	12000	0.034	-0.025	0.917	Negative ●	Negative ●	1
36	-130.65	61.68	12	1000	12000	0.256	0.184	0.422	Positive ●	*Negative* ●	1
37	-166.27	64.87	12	1000	16000	0.064	-0.021	0.842	Negative ●	Negative ●	1
38	-155.05	67.93	13	1000	13000	0.239	-0.211	0.432	Negative ●	Negative ●	1
39	-142.07	67.20	13	1000	13000	0.142	0.123	0.644	Positive ●	*Negative* ●	1
40	-152.60	67.25	13	1000	13000	0.143	0.103	0.642	Positive ●	*Negative* ●	1
41	-145.70	63.07	13	1000	13000	0.051	0.025	0.869	Positive ●	*Negative* ●	1
42	-126.42	65.23	13	1000	13000	0.153	-0.174	0.618	Negative ●	Negative ●	1
43	-149.48	61.12	13	1000	13000	0.011	0.011	0.973	Positive ●	*Negative* ●	1
44	-127.62	64.17	13	1000	13000	0.147	-0.12	0.632	Negative ●	Negative ●	1
45	-127.48	65.02	13	1000	13000	0.158	-0.196	0.607	Negative ●	Negative ●	1
46	-133.47	68.27	13	1000	13000	0.077	0.101	0.802	Positive ●	*Negative* ●	1
47	-151.27	64.33	14	1000	14000	0.257	-0.04	0.375	Negative ●	Negative ●	1
48	-153.90	67.13	15	1000	15000	0.714	-0.206	0.003	Negative ●	Negative ●	1
49	-153.65	67.15	15	1000	15000	0.329	-0.077	0.231	Negative ●	Negative ●	1
50	-154.23	67.07	15	1000	15000	0.44	-0.092	0.101	Negative ●	Negative ●	1
51	-145.22	68.27	15	1000	16000	0.041	0.01	0.883	Positive ●	*Negative* ●	1
52	-160.43	67.87	15	2000	16000	0.429	-0.147	0.11	Negative ●	Negative ●	1
53	-149.80	67.42	15	1000	15000	0.573	-0.157	0.026	Negative ●	Negative ●	1
54	-151.42	67.58	15	1000	15000	0.551	-0.161	0.033	Negative ●	Negative ●	1
55	-135.93	65.95	15	1000	15000	0.651	-0.174	0.009	Negative ●	Negative ●	1
56	-156.03	68.13	16	1000	16000	0.356	-0.11	0.176	Negative ●	Negative ●	1
57	-162.20	63.50	16	1000	16000	0.063	-0.009	0.817	Negative ●	Negative ●	1
58	-133.45	69.05	16	1000	16000	0.259	-0.111	0.333	Negative ●	Negative ●	1
59	-155.03	66.92	17	1000	17000	0.479	-0.113	0.052	Negative ●	Negative ●	1
60	-161.42	68.15	17	1000	17000	0.415	-0.196	0.097	Negative ●	Negative ●	1
61	-157.22	66.77	17	1000	17000	0.19	-0.032	0.465	Negative ●	Negative ●	1
62	-146.91	64.44	17	1000	18000	0.304	-0.038	0.235	Negative ●	Negative ●	1
63	-132.17	69.12	17	1000	17000	0.016	0.009	0.952	Positive ●	*Negative* ●	1
64	-138.38	68.38	18	1000	18000	0.543	-0.088	0.02	Negative ●	Negative ●	1
65	-64.80	47.08	11	1000	11000	0.142	0.074	0.678	Positive	Positive	1
66	-62.05	57.38	11	2000	12000	0.341	0.035	0.305	Positive	Positive	1
67	-85.66	46.43	11	1000	11000	0.346	-0.087	0.297	Negative	*Positive*	1
68	-65.95	48.97	11	1000	11000	0.258	0.085	0.444	Positive	Positive	1
69	-87.52	44.45	11	1000	12000	0.6	0.182	0.051	Positive	Positive	1
70	-95.28	73.13	11	1000	11000	0.166	-0.02	0.626	Negative	*Positive*	1
71	-87.46	45.67	11	1000	11000	0.781	0.541	0.005	Positive	Positive	1
72	-73.31	45.54	12	1000	12000	0.242	0.047	0.449	Positive	Positive	1
73	-84.32	45.60	12	3000	14000	0.115	0.015	0.722	Positive	Positive	1
74	-65.81	49.21	12	1000	12000	0.435	0.064	0.158	Positive	Positive	1
75	-69.30	43.77	12	1000	12000	0.577	0.158	0.049	Positive	Positive	1
76	-93.38	47.98	12	1000	12000	0.672	0.212	0.017	Positive	Positive	1
77	-64.08	46.67	12	1000	12000	0.109	0.033	0.737	Positive	Positive	1
78	-93.60	46.58	12	2000	14000	0.606	0.092	0.037	Positive	Positive	1
79	-73.32	45.55	12	1000	12000	0.562	0.124	0.057	Positive	Positive	1
80	-122.17	59.52	12	1000	12000	0.28	0.193	0.378	Positive	Positive	1
81	-117.22	52.24	12	1000	12000	0.474	-0.361	0.119	Negative	*Positive*	1
82	-70.06	41.28	12	1000	12000	0.688	0.504	0.013	Positive	Positive	1
83	-78.67	42.54	13	1000	13000	0.391	0.149	0.187	Positive	Positive	1
84	-88.10	43.40	13	1000	13000	0.723	0.22	0.005	Positive	Positive	1
85	-88.18	42.35	13	1000	13000	0.358	0.122	0.229	Positive	Positive	1
86	-118.70	62.05	13	1000	13000	0.398	0.075	0.179	Positive	Positive	1
87	-120.67	57.45	13	1000	13000	0.464	0.16	0.11	Positive	Positive	1
88	-94.11	47.08	13	1000	13000	0.363	0.095	0.223	Positive	Positive	1
89	-80.86	44.74	13	1000	13000	0.295	-0.054	0.328	Negative	*Positive*	1
90	-81.75	43.18	13	1000	13000	0.924	0.545	<0.001	Positive	Positive	1
91	-78.34	44.10	13	1000	13000	0.738	0.222	0.004	Positive	Positive	1

				Dates in sample		Richness = f (Temperature)					
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Direction	Direction§	WD
92	-95.07	72.58	13	1000	13000	0.369	0.04	0.215	Positive	Positive	1
93	-86.96	46.47	13	1000	13000	0.1	0.017	0.746	Positive	Positive	1
94	-70.00	41.93	14	1000	14000	0.722	0.207	0.004	Positive	Positive	1
95	-75.81	45.47	14	1000	14000	0.658	0.072	0.011	Positive	Positive	1
96	-70.62	46.58	14	1000	14000	0.467	0.056	0.092	Positive	Positive	1
97	-69.41	43.92	14	1000	14000	0.562	0.093	0.037	Positive	Positive	1
98	-68.94	47.53	14	1000	14000	0.253	0.027	0.383	Positive	Positive	1
99	-76.90	43.51	14	1000	14000	0.15	0.03	0.609	Positive	Positive	1
100	-67.33	45.26	15	1000	15000	0.077	-0.006	0.784	Negative	*Positive*	1
101	-65.27	48.05	15	1000	15000	0.557	0.051	0.031	Positive	Positive	1
102	-93.35	43.15	15	1000	16000	0.907	0.146	<0.001	Positive	Positive	1
103	-78.10	44.10	15	1000	15000	0.804	0.189	<0.001	Positive	Positive	1
104	-87.85	44.24	16	1000	16000	0.901	0.123	<0.001	Positive	Positive	1
105	-87.22	41.58	16	1000	16000	0.783	0.124	<0.001	Positive	Positive	1
106	-87.73	44.05	17	1000	18000	0.497	0.035	0.043	Positive	Positive	1
107	-70.21	41.28	17	1000	17000	0.497	0.143	0.042	Positive	Positive	1
108	-78.88	42.25	18	1000	18000	0.714	0.084	0.001	Positive	Positive	1
109	-74.60	42.50	18	1000	18000	0.859	0.117	<0.001	Positive	Positive	1
110	-82.76	41.92	18	1000	18000	0.711	0.088	0.001	Positive	Positive	1
111	-119.72	56.72	11	1000	11000	0.514	0.305	0.106	Positive ●	Positive ●	1
112	-119.48	56.77	11	1000	11000	0.081	-0.067	0.812	Negative ●	*Positive* ●	1
113	-132.02	67.65	11	1000	11000	0.258	0.209	0.444	Positive ●	Positive ●	1
114	-118.37	52.73	11	1000	11000	0.458	0.311	0.156	Positive ●	Positive ●	1
115	-129.02	60.03	11	1000	11000	0.318	0.376	0.34	Positive ●	Positive ●	1
116	-135.40	59.20	12	1000	12000	0.585	-0.335	0.046	Negative ●	*Positive* ●	1
117	-126.12	65.22	14	1000	14000	0.138	-0.16	0.638	Negative ●	*Positive* ●	1
118	-133.58	69.28	14	1000	14000	0.579	-0.282	0.03	Negative ●	Positive ●	1
119	-156.45	66.97	17	2000	18000	0.38	0.081	0.133	Positive ●	Positive ●	1
120	-92.72	46.42	6	7000	12000	0.536	-0.129	0.273	Negative	Negative	2
121	-99.23	47.15	6	4000	13000	0.739	-0.347	0.093	Negative	Negative	2
122	-92.70	49.35	7	7000	13000	0.733	-0.092	0.061	Negative	Negative	2
123	-91.57	49.93	8	4000	11000	0.856	-0.328	0.007	Negative	Negative	2
124	-110.32	43.77	8	7000	14000	0.772	-0.548	0.025	Negative	Negative	2
125	-71.94	46.15	9	3000	11000	0.607	-0.161	0.083	Negative	Negative	2
126	-95.17	47.18	11	1000	11000	0.095	-0.045	0.781	Negative	Negative	2
127	-81.50	46.60	11	1000	11000	0.091	0.021	0.789	Positive	*Negative*	2
128	-72.15	48.29	11	1000	11000	0.443	-0.104	0.172	Negative	Negative	2
129	-70.62	47.61	11	1000	11000	0.665	-0.145	0.026	Negative	Negative	2
130	-90.58	36.60	11	8000	18000	0.209	-0.035	0.537	Negative	Negative	2
131	-80.70	46.83	11	1000	11000	0.747	-0.173	0.008	Negative	Negative	2
132	-89.32	48.42	11	1000	11000	0.631	-0.276	0.037	Negative	Negative	2
133	-88.74	48.56	11	1000	11000	0.684	-0.245	0.02	Negative	Negative	2
134	-111.18	44.13	11	1000	11000	0.433	-1.283	0.184	Negative	Negative	2
135	-91.12	48.00	11	1000	11000	0.792	-0.464	0.004	Negative	Negative	2
136	-79.78	47.23	11	1000	11000	0.822	-0.391	0.002	Negative	Negative	2
137	-92.02	48.11	11	1000	11000	0.746	-0.439	0.008	Negative	Negative	2
138	-109.94	43.45	11	1000	11000	0.483	-0.767	0.133	Negative	Negative	2
139	-70.68	47.48	12	1000	12000	0.824	-0.121	0.001	Negative	Negative	2
140	-88.02	46.67	12	1000	12000	0.438	-0.074	0.154	Negative	Negative	2
141	-71.67	44.17	12	1000	12000	0.363	-0.034	0.246	Negative	Negative	2
142	-93.75	49.58	12	1000	12000	0.594	-0.106	0.042	Negative	Negative	2
143	-106.08	53.80	12	1000	12000	0.346	-0.04	0.27	Negative	Negative	2
144	-71.42	47.08	12	1000	12000	0.471	-0.081	0.123	Negative	Negative	2
145	-94.93	47.18	12	1000	12000	0.118	-0.027	0.716	Negative	Negative	2
146	-72.84	46.79	12	1000	12000	0.562	-0.086	0.057	Negative	Negative	2
147	-74.47	46.06	12	1000	12000	0.451	-0.035	0.141	Negative	Negative	2
148	-74.37	45.95	12	1000	12000	0.067	-0.01	0.836	Negative	Negative	2

				Dates in sample		Richness = f (Temperature)					
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Direction	Direction§	WD
149	-90.35	45.30	12	1000	12000	0.343	-0.129	0.275	Negative	Negative	2
150	-84.26	47.31	12	1000	12000	0.632	-0.12	0.027	Negative	Negative	2
151	-110.60	44.96	12	1000	12000	0.397	-0.279	0.202	Negative	Negative	2
152	-121.50	50.50	12	1000	12000	0.12	-0.032	0.71	Negative	Negative	2
153	-93.69	44.89	12	1000	12000	0.295	0.165	0.352	Positive	*Negative*	2
154	-107.05	40.02	12	1000	12000	0.375	-0.379	0.23	Negative	Negative	2
155	-109.92	43.46	12	1000	12000	0.656	-0.377	0.02	Negative	Negative	2
156	-73.97	44.18	13	1000	13000	0.111	-0.022	0.717	Negative	Negative	2
157	-89.42	43.10	13	1000	13000	0.163	0.031	0.596	Positive	*Negative*	2
158	-110.26	44.30	13	1000	13000	0.847	-0.77	<0.001	Negative	Negative	2
159	-68.20	45.03	13	1000	13000	0.288	-0.045	0.339	Negative	Negative	2
160	-95.01	47.24	13	1000	13000	0.409	0.173	0.166	Positive	*Negative*	2
161	-112.72	48.55	13	1000	14000	0.436	-0.189	0.136	Negative	Negative	2
162	-110.23	44.15	13	1000	13000	0.884	-0.576	<0.001	Negative	Negative	2
163	-89.12	44.50	13	1000	13000	0.01	-0.002	0.975	Negative	Negative	2
164	-110.28	44.49	13	1000	13000	0.702	-0.821	0.007	Negative	Negative	2
165	-70.35	45.85	14	1000	14000	0.119	0.017	0.686	Positive	*Negative*	2
166	-93.16	44.82	14	1000	14000	0.091	0.019	0.756	Positive	*Negative*	2
167	-110.23	43.93	14	1000	14000	0.62	-0.319	0.018	Negative	Negative	2
168	-110.30	44.07	14	1000	14000	0.733	-0.427	0.003	Negative	Negative	2
169	-122.12	48.77	14	4000	17000	0.141	0.02	0.631	Positive	*Negative*	2
170	-121.62	48.23	14	1000	14000	0.402	0.133	0.154	Positive	*Negative*	2
171	-71.67	42.83	16	1000	16000	0.601	-0.029	0.014	Negative	Negative	2
172	-110.73	44.92	16	1000	16000	0.713	-0.171	0.002	Negative	Negative	2
173	-110.60	44.65	18	1000	18000	0.758	-0.193	<0.001	Negative	Negative	2
174	-110.60	43.75	18	1000	18000	0.816	-0.202	<0.001	Negative	Negative	2
175	-147.85	67.43	15	1000	15000	0.613	-0.125	0.015	Negative ●	Negative ●	2
176	-144.66	63.94	16	1000	16000	0.76	-0.105	0.001	Negative ●	Negative ●	2
177	-143.15	66.58	18	1000	18000	0.065	0.009	0.797	Positive ●	*Negative* ●	2
178	-80.37	41.55	6	3000	11000	0.956	0.666	0.003	Positive	Positive	2
179	-93.70	42.26	7	7000	14000	0.86	0.347	0.013	Positive	Positive	2
180	-78.95	44.62	7	2000	11000	0.867	0.305	0.012	Positive	Positive	2
181	-98.16	46.86	7	5000	13000	0.74	0.2	0.057	Positive	Positive	2
182	-97.33	45.50	8	1000	13000	0.585	0.332	0.128	Positive	Positive	2
183	-99.65	50.72	8	1000	13000	0.62	0.175	0.101	Positive	Positive	2
184	-96.08	47.20	8	1000	11000	0.751	0.37	0.032	Positive	Positive	2
185	-94.58	46.28	9	1000	11000	0.294	0.149	0.442	Positive	Positive	2
186	-105.73	53.24	9	1000	13000	0.212	0.021	0.585	Positive	Positive	2
187	-93.90	42.16	9	1000	16000	0.905	0.226	0.001	Positive	Positive	2
188	-95.28	46.21	9	1000	13000	0.622	0.134	0.074	Positive	Positive	2
189	-95.31	46.18	9	1000	12000	0.433	0.17	0.244	Positive	Positive	2
190	-95.29	46.21	9	5000	13000	0.581	0.179	0.101	Positive	Positive	2
191	-73.60	42.63	10	3000	12000	0.873	0.557	0.001	Positive	Positive	2
192	-84.87	47.88	11	1000	11000	0.22	-0.064	0.516	Negative	*Positive*	2
193	-72.15	44.37	11	1000	11000	0.674	0.213	0.023	Positive	Positive	2
194	-74.67	41.33	11	1000	11000	0.878	0.807	<0.001	Positive	Positive	2
195	-83.24	43.12	11	1000	11000	0.547	0.562	0.082	Positive	Positive	2
196	-76.45	36.58	11	1000	11000	0.912	2.04	<0.001	Positive	Positive	2
197	-99.28	49.43	11	1000	14000	0.584	0.099	0.059	Positive	Positive	2
198	-74.43	40.38	11	1000	11000	0.791	0.947	0.004	Positive	Positive	2
199	-89.90	46.25	11	1000	11000	0.444	0.109	0.172	Positive	Positive	2
200	-87.97	46.72	11	1000	11000	0.031	-0.014	0.927	Negative	*Positive*	2
201	-95.20	43.33	11	1000	17000	0.809	0.165	0.003	Positive	Positive	2
202	-95.77	47.19	11	1000	11000	0.005	0.003	0.989	Positive	Positive	2
203	-77.92	44.30	11	1000	11000	0.624	0.265	0.04	Positive	Positive	2
204	-73.99	46.00	11	1000	11000	0.322	0.085	0.334	Positive	Positive	2
205	-79.77	44.17	11	1000	11000	0.115	0.047	0.736	Positive	Positive	2

				Dates in sample		Richness = f (Temperature)					
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Direction	Direction§	WD
206	-105.54	40.08	11	1000	11000	0.514	0.292	0.106	Positive	Positive	2
207	-108.10	37.47	11	1000	11000	0.164	0.242	0.63	Positive	Positive	2
208	-78.55	39.77	12	1000	12000	0.364	0.142	0.244	Positive	Positive	2
209	-89.87	43.08	12	1000	12000	0.838	0.647	0.001	Positive	Positive	2
210	-70.68	45.57	12	1000	12000	0.304	0.032	0.337	Positive	Positive	2
211	-74.68	43.92	12	1000	12000	0.805	0.337	0.002	Positive	Positive	2
212	-93.27	42.02	12	1000	16000	0.743	0.157	0.006	Positive	Positive	2
213	-70.38	47.50	12	2000	13000	0.343	0.047	0.276	Positive	Positive	2
214	-70.98	47.60	12	1000	12000	0.301	0.029	0.342	Positive	Positive	2
215	-71.69	43.61	12	1000	12000	0.168	0.008	0.602	Positive	Positive	2
216	-78.47	42.62	12	1000	12000	0.796	0.252	0.002	Positive	Positive	2
217	-76.10	45.60	12	1000	12000	0.114	0.027	0.725	Positive	Positive	2
218	-93.87	44.87	12	1000	12000	0.797	0.3	0.002	Positive	Positive	2
219	-70.93	46.93	12	1000	12000	0.467	0.051	0.126	Positive	Positive	2
220	-84.69	40.22	12	7000	18000	0.719	0.155	0.008	Positive	Positive	2
221	-91.45	45.30	12	1000	12000	0.391	0.105	0.208	Positive	Positive	2
222	-70.35	43.97	12	1000	12000	0.511	0.139	0.089	Positive	Positive	2
223	-77.05	44.48	12	1000	12000	0.556	0.13	0.061	Positive	Positive	2
224	-79.98	44.85	12	1000	12000	0.602	0.182	0.038	Positive	Positive	2
225	-73.87	45.96	12	1000	12000	0.035	0.006	0.915	Positive	Positive	2
226	-93.18	45.43	12	1000	12000	0.821	0.56	0.001	Positive	Positive	2
227	-93.20	45.41	12	1000	12000	0.649	0.193	0.023	Positive	Positive	2
228	-79.44	44.18	12	1000	12000	0.914	0.497	<0.001	Positive	Positive	2
229	-93.69	45.43	12	1000	12000	0.481	0.187	0.113	Positive	Positive	2
230	-76.60	44.52	12	1000	12000	0.45	0.096	0.142	Positive	Positive	2
231	-71.70	44.14	12	1000	12000	0.388	0.092	0.213	Positive	Positive	2
232	-73.00	46.61	13	1000	13000	0.15	0.029	0.624	Positive	Positive	2
233	-85.00	43.48	13	1000	13000	0.864	0.361	<0.001	Positive	Positive	2
234	-71.73	44.13	13	1000	13000	0.533	0.071	0.061	Positive	Positive	2
235	-93.13	44.27	13	1000	13000	0.567	0.158	0.043	Positive	Positive	2
236	-73.05	42.65	13	1000	13000	0.869	0.283	<0.001	Positive	Positive	2
237	-93.63	45.03	13	1000	13000	0.396	0.087	0.181	Positive	Positive	2
238	-80.13	37.60	13	1000	13000	0.527	0.229	0.064	Positive	Positive	2
239	-74.40	46.17	13	1000	13000	0.009	0.001	0.978	Positive	Positive	2
240	-93.87	43.03	13	2000	15000	0.844	0.196	<0.001	Positive	Positive	2
241	-80.41	43.24	13	1000	13000	0.867	0.283	<0.001	Positive	Positive	2
242	-91.50	42.99	13	1000	14000	0.679	0.181	0.011	Positive	Positive	2
243	-81.33	41.20	13	1000	13000	0.816	0.186	0.001	Positive	Positive	2
244	-82.06	40.68	13	6000	18000	0.922	0.107	<0.001	Positive	Positive	2
245	-81.97	41.00	13	5000	17000	0.784	0.141	0.002	Positive	Positive	2
246	-80.40	43.90	13	1000	13000	0.871	0.395	<0.001	Positive	Positive	2
247	-80.40	43.91	13	1000	13000	0.548	0.193	0.052	Positive	Positive	2
248	-80.37	43.23	13	1000	13000	0.761	0.324	0.003	Positive	Positive	2
249	-122.56	49.33	13	1000	13000	0.603	0.32	0.029	Positive	Positive	2
250	-71.03	41.95	13	1000	13000	0.898	0.791	<0.001	Positive	Positive	2
251	-83.63	42.33	14	1000	14000	0.461	0.093	0.097	Positive	Positive	2
252	-72.88	42.57	14	1000	14000	0.841	0.288	<0.001	Positive	Positive	2
253	-75.67	40.48	14	1000	14000	0.736	0.145	0.003	Positive	Positive	2
254	-72.58	45.36	14	1000	14000	0.318	0.039	0.268	Positive	Positive	2
255	-81.93	36.53	14	1000	14000	0.089	0.024	0.761	Positive	Positive	2
256	-72.21	42.52	14	1000	16000	0.531	0.081	0.051	Positive	Positive	2
257	-70.63	45.60	14	1000	14000	0.471	0.04	0.089	Positive	Positive	2
258	-74.05	44.15	14	1000	14000	0.668	0.056	0.009	Positive	Positive	2
259	-93.57	45.00	14	1000	14000	0.879	0.152	<0.001	Positive	Positive	2
260	-79.07	38.00	14	1000	14000	0.733	0.214	0.003	Positive	Positive	2
261	-71.33	45.67	14	1000	14000	0.263	0.017	0.363	Positive	Positive	2
262	-73.32	42.50	15	1000	15000	0.707	0.102	0.003	Positive	Positive	2

				Dates in sample		Richness = f (Temperature)					
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Direction	Direction§	WD
263	-88.34	40.68	15	1000	15000	0.328	0.07	0.233	Positive	Positive	2
264	-71.83	44.03	15	1000	15000	0.089	0.009	0.754	Positive	Positive	2
265	-89.73	43.42	15	1000	15000	0.649	0.099	0.009	Positive	Positive	2
266	-85.12	44.88	15	1000	15000	0.242	0.018	0.386	Positive	Positive	2
267	-80.66	43.23	15	1000	15000	0.722	0.151	0.002	Positive	Positive	2
268	-76.35	41.67	15	1000	15000	0.652	0.128	0.008	Positive	Positive	2
269	-82.47	40.35	15	1000	15000	0.246	0.04	0.377	Positive	Positive	2
270	-85.38	42.40	15	1000	15000	0.367	0.029	0.179	Positive	Positive	2
271	-90.08	45.33	15	1000	15000	0.299	0.026	0.279	Positive	Positive	2
272	-70.35	44.03	15	1000	15000	0.625	0.088	0.013	Positive	Positive	2
273	-122.55	49.31	15	1000	15000	0.322	0.086	0.242	Positive	Positive	2
274	-110.35	44.93	15	1000	15000	0.064	0.014	0.82	Positive	Positive	2
275	-89.68	43.43	15	1000	15000	0.843	0.17	<0.001	Positive	Positive	2
276	-79.27	39.57	16	1000	16000	0.779	0.104	<0.001	Positive	Positive	2
277	-89.17	43.92	16	1000	16000	0.589	0.055	0.016	Positive	Positive	2
278	-92.83	45.05	16	1000	16000	0.556	0.066	0.025	Positive	Positive	2
279	-89.42	43.10	16	1000	16000	0.759	0.076	0.001	Positive	Positive	2
280	-77.42	40.80	16	1000	16000	0.866	0.167	<0.001	Positive	Positive	2
281	-85.25	41.58	16	1000	16000	0.728	0.068	0.001	Positive	Positive	2
282	-71.12	41.97	16	1000	16000	0.586	0.13	0.017	Positive	Positive	2
283	-72.18	42.53	16	1000	16000	0.18	0.029	0.505	Positive	Positive	2
284	-69.32	44.98	16	1000	16000	0.153	0.02	0.571	Positive	Positive	2
285	-84.75	41.42	16	1000	16000	0.833	0.099	<0.001	Positive	Positive	2
286	-89.17	43.92	16	1000	16000	0.802	0.121	<0.001	Positive	Positive	2
287	-122.58	44.63	16	1000	16000	0.873	0.711	<0.001	Positive	Positive	2
288	-71.25	44.25	16	1000	16000	0.549	0.042	0.027	Positive	Positive	2
289	-86.53	41.65	17	1000	17000	0.927	0.124	<0.001	Positive	Positive	2
290	-80.28	38.20	17	1000	17000	0.86	0.211	<0.001	Positive	Positive	2
291	-80.25	44.37	17	1000	17000	0.61	0.102	0.009	Positive	Positive	2
292	-86.53	41.67	17	1000	17000	0.855	0.159	<0.001	Positive	Positive	2
293	-73.28	41.82	17	1000	17000	0.891	0.152	<0.001	Positive	Positive	2
294	-74.33	41.50	17	1000	17000	0.669	0.087	0.003	Positive	Positive	2
295	-84.88	43.42	17	1000	17000	0.64	0.076	0.006	Positive	Positive	2
296	-122.49	45.80	17	1000	17000	0.795	0.561	<0.001	Positive	Positive	2
297	-83.53	40.10	17	1000	17000	0.869	0.116	<0.001	Positive	Positive	2
298	-77.93	41.92	17	1000	17000	0.709	0.089	0.001	Positive	Positive	2
299	-77.92	42.25	18	1000	18000	0.827	0.114	<0.001	Positive	Positive	2
300	-77.55	39.97	18	1000	18000	0.932	0.169	<0.001	Positive	Positive	2
301	-79.00	37.98	18	1000	18000	0.782	0.166	<0.001	Positive	Positive	2
302	-73.98	42.24	18	1000	18000	0.457	0.081	0.057	Positive	Positive	2
303	-68.64	44.63	18	1000	18000	0.315	0.03	0.203	Positive	Positive	2
304	-76.68	36.17	18	1000	18000	0.959	0.726	<0.001	Positive	Positive	2
305	-72.12	41.37	18	1000	18000	0.508	0.069	0.031	Positive	Positive	2
306	-83.80	40.35	18	1000	18000	0.888	0.142	<0.001	Positive	Positive	2
307	-74.48	40.40	18	1000	18000	0.444	0.09	0.065	Positive	Positive	2
308	-75.27	41.03	18	1000	18000	0.871	0.217	<0.001	Positive	Positive	2
309	-79.38	44.00	18	1000	18000	0.96	0.175	<0.001	Positive	Positive	2
310	-122.25	46.59	18	1000	18000	0.607	0.166	0.008	Positive	Positive	2
311	-107.68	37.75	18	1000	18000	0.041	-0.01	0.872	Negative	*Positive*	2
312	-79.62	38.15	18	1000	18000	0.887	0.323	<0.001	Positive	Positive	2
313	-74.20	41.24	18	1000	18000	0.841	0.102	<0.001	Positive	Positive	2
314	-74.04	41.39	18	1000	18000	0.762	0.125	<0.001	Positive	Positive	2
315	-114.60	50.77	11	1000	11000	0.122	-0.21	0.722	Negative ●	*Positive* ●	2
316	-105.50	37.70	6	1000	15000	0.038	-0.005	0.944	Negative	Negative	3
317	-80.16	47.18	7	5000	11000	0.865	-0.577	0.012	Negative	Negative	3
318	-73.03	46.73	11	1000	11000	0.825	-0.306	0.002	Negative	Negative	3
319	-107.47	44.55	11	1000	11000	0.373	-1.149	0.259	Negative	Negative	3

				Dates in sample		Richness = f (Temperature)					
Site	LonDD	LatDD	N	Min.	Max.	Multiple R	Slope	p-value	Direction	Direction§	WD
320	-112.17	46.45	11	1000	12000	0.313	-0.192	0.349	Negative	Negative	3
321	-88.47	33.56	12	1000	12000	0.168	-0.227	0.602	Negative	Negative	3
322	-81.77	47.32	12	1000	12000	0.657	-0.096	0.02	Negative	Negative	3
323	-86.53	33.50	13	1000	13000	0.247	-0.286	0.416	Negative	Negative	3
324	-112.40	46.53	13	1000	13000	0.329	-0.154	0.272	Negative	Negative	3
325	-107.01	44.27	15	1000	15000	0.821	-0.277	<0.001	Negative	Negative	3
326	-119.01	37.60	15	1000	15000	0.213	0.142	0.445	Positive	*Negative*	3
327	-86.13	31.72	17	1000	17000	0.403	-0.145	0.109	Negative	Negative	3
328	-78.95	33.80	18	1000	18000	0.104	0.063	0.681	Positive	*Negative*	3
329	-78.50	45.50	11	1000	11000	0.103	0.022	0.762	Positive	Positive	3
330	-79.47	46.45	11	1000	11000	0.338	0.105	0.309	Positive	Positive	3
331	-78.50	34.50	11	7000	17000	0.665	0.102	0.026	Positive	Positive	3
332	-119.07	37.66	11	1000	11000	0.119	0.409	0.728	Positive	Positive	3
333	-107.26	44.18	11	1000	11000	0.281	-1.191	0.402	Negative	*Positive*	3
334	-77.34	46.03	11	1000	11000	0.241	-0.068	0.475	Negative	*Positive*	3
335	-79.50	45.38	11	1000	11000	0.314	0.148	0.348	Positive	Positive	3
336	-79.38	45.42	12	1000	12000	0.223	0.048	0.485	Positive	Positive	3
337	-76.68	44.80	12	1000	12000	0.709	0.161	0.01	Positive	Positive	3
338	-77.18	44.85	14	1000	14000	0.061	-0.007	0.836	Negative	*Positive*	3
339	-105.50	37.55	14	1000	14000	0.289	0.093	0.317	Positive	Positive	3
340	-77.35	45.18	14	1000	14000	0.158	-0.021	0.59	Negative	*Positive*	3
341	-85.50	36.03	18	1000	18000	0.866	0.123	<0.001	Positive	Positive	3
342	-91.10	36.80	18	1000	18000	0.709	0.107	0.001	Positive	Positive	3
343	-85.72	37.45	18	1000	18000	0.938	0.241	<0.001	Positive	Positive	3
344	-85.17	34.67	18	1000	18000	0.753	0.159	<0.001	Positive	Positive	3
345	-80.78	34.17	18	1000	18000	0.452	0.174	0.06	Positive	Positive	3
346	-119.82	37.95	18	1000	18000	0.766	0.417	<0.001	Positive	Positive	3
347	-123.58	44.17	18	1000	18000	0.793	0.862	<0.001	Positive	Positive	3
348	-108.30	33.70	8	7000	18000	0.675	-0.174	0.066	Negative	Negative	4
349	-109.43	34.00	8	3000	18000	0.445	-0.153	0.27	Negative	Negative	4
350	-119.26	37.20	11	1000	11000	0.082	0.274	0.811	Positive	*Negative*	4
351	-111.35	34.46	12	2000	13000	0.768	-0.89	0.004	Negative	Negative	4
352	-112.22	36.72	12	1000	12000	0.23	-0.203	0.471	Negative	Negative	4
353	-111.35	34.46	17	2000	18000	0.16	0.038	0.539	Positive	*Negative*	4
354	-81.42	27.20	18	1000	18000	0.505	-0.6	0.033	Negative	Negative	4
355	-82.00	29.52	18	1000	18000	0.342	-0.232	0.164	Negative	Negative	4
356	-81.50	27.58	18	1000	18000	0.768	-0.87	<0.001	Negative	Negative	4
357	-108.25	33.87	8	7000	14000	0.882	0.381	0.004	Positive	Positive	4
358	-97.12	30.37	10	6000	18000	0.484	0.304	0.157	Positive	Positive	4
359	-85.02	30.27	18	1000	18000	0.602	0.289	0.008	Positive	Positive	4
360	-119.83	37.00	13	1000	13000	0.6	-1.212	0.03	Negative	Negative	5
361	-111.00	38.00	16	1000	17000	0.856	-0.417	<0.001	Negative	Negative	5
362	-112.00	34.00	10	1000	12000	0.38	0.684	0.279	Positive	Positive	5

Table S5. The proportion of sites with positive or negative correlations between temporal values of both richness of woody plants and temperature during the late Pleistocene-Holocene transition in areas of different water deficit (WD) in North America. Positive relationships represent increases in richness and temperature through time, and negative relationships represent decreasing richness with increasing temperatures through time. Sample size (N) includes cases with statistically significant correlations only.

			Type of correlation (%)	
WD (mm yr^{-1})	Category	N	Negative	Positive
0-250	1	36	42	58
251-500	2	101	22	78
501-750	3	12	33	67
751-1000	4	5	60	40
1251-1500	5	2	100	0
>1500	6	-	-	-

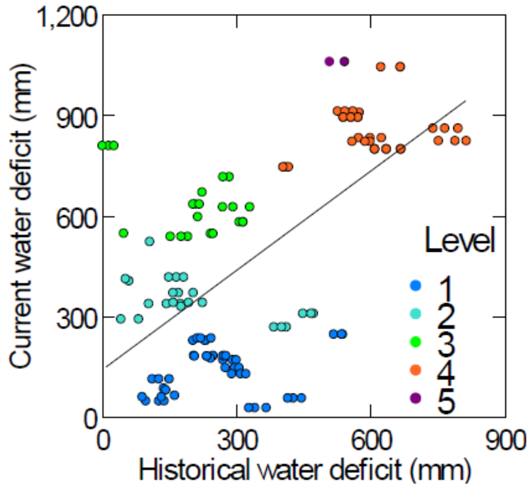

Figure S1. The relationship between historical and current values of water deficit in the non-iced area of North America during the last glaciation. Samples represent sites with time series of both richness and temperature that include dates of the last 18,000, 17,000 and 16,000 yr BP. Level indicates range of water deficit: (1) 0-250 mm, (2) 250–500 mm, (3) 500–750 mm, (4) 750–1000 mm, (5) 1000–1250 mm. Notice that there are no sampling sites in areas with water deficit of level 6 (> 1250 mm).

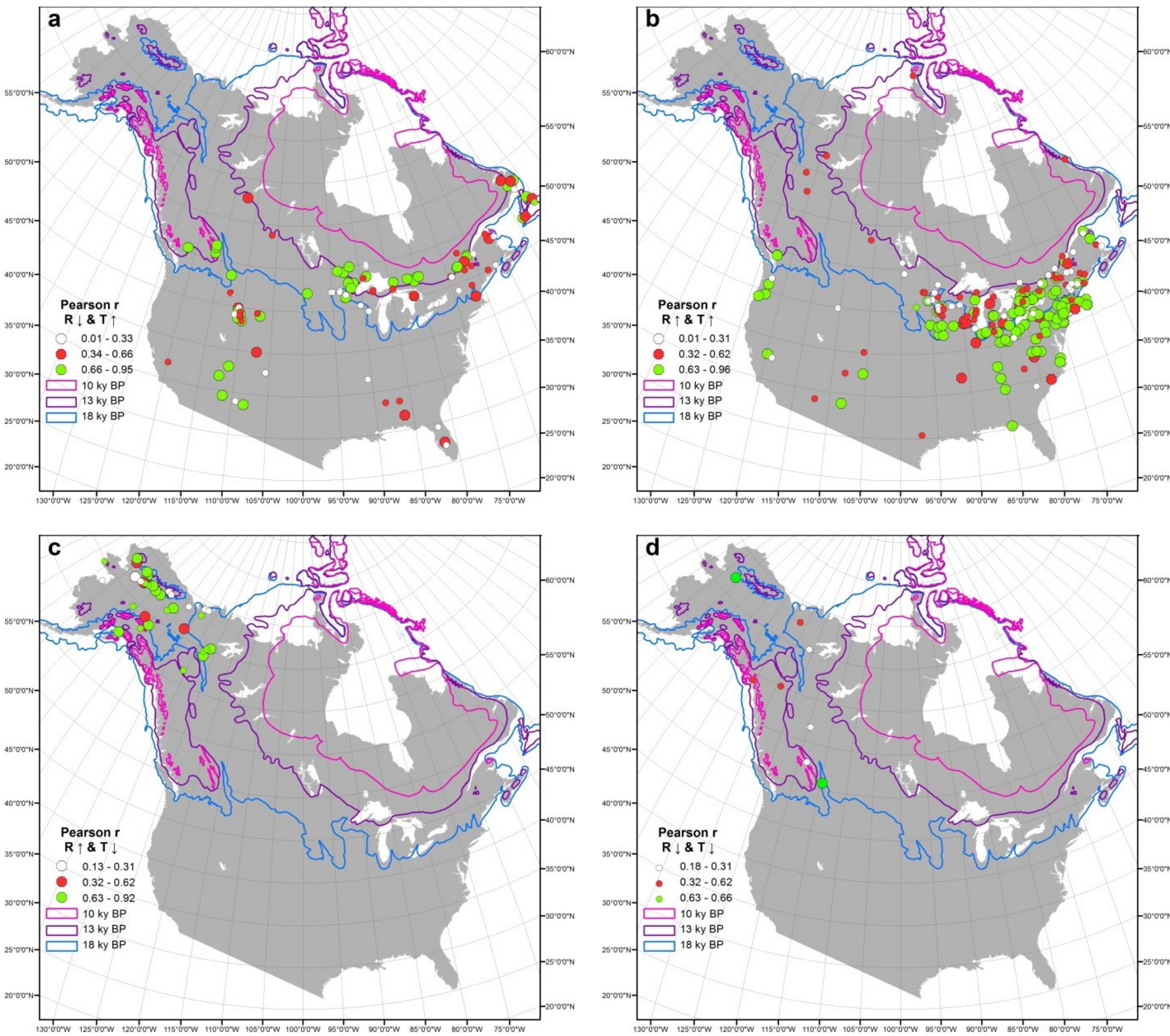

Figure S2. The distribution of sites with negative (a) and positive (b) temporal trends in richness and positive trend in temperature; and negative (c) and positive (d) trends in richness, but negative trend in temperature. Arrows identify negative (↓) or positive (↑) trends in richness (R) or temperature (T). The strength of the richness-time correlation (Pearson r) is shown in each type of trend. Bigger circles identify statistically significant correlations and smaller circles statistically non-significant correlations. The extent of the glaciers at 18,000, 13,000 and 10,000 yr BP are shown in blue, purple, and magenta respectively, as a reference to position sampling sites through time. Sites are always in areas with no ice.