RESEARCH PAPER

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

Héctor Vázquez-Rivera and David J. Currie*

Ottawa–Carleton Institute of Biology, University of Ottawa, Ottawa, ON, Canada

ABSTRACT

Aim Broad-scale diversity gradients are strongly correlated 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, LGM). We tested the hypothesis that contemporaneous climate directly controls broad-scale patterns of richness. If climate directly (i.e. causally) 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 that suggest that patterns of richness are primarily determined by processes associated with climate at the LGM.

Location North America, north of Mexico.

Methods We used temperature changes over the last 14,000 years in North America as a 'natural experiment'. We compared a proxy of woody plant family richness (based on fossilized pollen) with two reconstructions of the spatio-temporal variation of temperature across North America at 1000-year intervals.

Results We found that the spatial and temporal regional variations in richness of woody plant families, observed at 1000-year intervals and expressed as a function of temperature, remained quite congruent during the changing climate since the end of the Pleistocene (the last *c.* 11,000 years). 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 in the late Pleistocene. Richness was significantly less strongly related to climate change since the LGM.

Main conclusions Our results provide a strong test of the hypothesis that, in ecological time, contemporaneous climate controls most of the broad-scale variation in patterns of richness. Richness, independently of the responses of individual species, is likely to track current climate change, except possibly when temperature changes are very rapid.

Correspondence: David J. Currie, Ottawa–Carleton Institute of Biology, University of Ottawa, Ottawa, ON, K1N 6N5 Canada. E-mail: david.currie@uottawa.ca

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. Yet richness also varies considerably within biogeographic provinces. Considering quadrats of *c.* 10^4 km² in area, extending over continents, species richness 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).

Moreover, richness–climate correlations within biomes are largely congruent with the global pattern among biomes (Francis & Currie, 2003). At coarse grains and large extents, current climate is typically by far the strongest predictor of richness (Field *et al.*, 2009).

The explanation for 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 gradients of *richness* (Algar *et al.*, 2009a; Hawkins *et al.*, 2012).

The second set of questions is: why does richness, resolved at a grain of *c.* 10^4 km², 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 the logarithm of angiosperm richness in North American and Chinese forests, and intercontinental differences account for only an additional 1% (Qian *et al.*, 2007).

The most obvious possible answer is that regional-scale geographic variation of richness is directly controlled by contemporaneous climate. This might happen in several different ways. Climate may act as a filter for species that can maintain positive net 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 proposes 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 contemporaneous 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 contemporaneous 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 changes in climate. Along these lines, recent studies have associated increases in richness with warming temperatures in northern latitudes (Hiddink & ter Hofstede, 2008), and some have used space-for-time substitution to causally link temporal changes in richness and climate (La Sorte *et al.*, 2009). If there is a strong 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, patterns of richness may reflect the direct influence of variables that happened to be collinear with contemporaneous climate. For example, Araújo *et al.* (2008) argued that climatic stability during the last 21,000 years could have created suitable areas where groups of species persisted during and after

Figure 1 Mean July temperature anomaly across North America, relative to current temperature, for the last 14,000 cal. yr BP. Current temperature (°C) is the monthly mean for July (1961–90) (Climate Research Unit; New *et al.*, 2002). Redrawn from Viau *et al.* (2006).

times of glaciation. Historic climate changes could have precluded the occupation of new northern areas (Araújo *et al.*, 2008) and thereby created latitudinal gradients of richness. Similarly, slow dispersal from suitable southern areas could have created lags in post-glacial recolonization of the climatic potential ranges of individual species (Svenning & Skov, 2007), resulting in lower northern richness. Alternatively, lower richness in higher latitudes may result from the length of time for which land has been available for colonization since the Last Glacial Maximum (LGM) (Montoya *et al.*, 2007). Areas covered by ice during the LGM (primarily higher latitudes) have had less time to be colonized and may 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 *c.* 10^4 km² 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 (the last *c.* 14,000 years) in North America, as a continental-scale 'natural experiment' *sensu* (Diamond, 1983). At the end of the Pleistocene, between 14,000 and 11,000 cal. yr BP, the average temperature in North America increased by *c.* 1.3 °C/1000 years (Fig. 1). Regional temperature anomalies reached *c.* 5 °C (Yu, 2007). Later, during the Holocene (the last *c.* 11,000 years), the continental average temperature varied by *c.* 0.2 °C (Viau *et al.*, 2006) (Fig. 1). Several cooling and warming events representing changes in regional temperature of up to 3 °C occurred at an approximately millennial scale during this period (Viau *et al.*, 2006; Yu, 2007).

What would the richness–climate relationship through time look like if richness did not track temporal changes in climate? To answer this question, we constructed two null-style alternative hypotheses. First, we derived the expected relationship between

richness and temperature, assuming that the temporal variation in richness at particular sites over the last 14,000 years 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 cal. yr BP in many cases), independently of temperature changes.

Finally, we also tested the relationship between richness and aspects of historical climate. We evaluated what proportion of the spatial variation of richness could be statistically attributed to: (1) climate stability (also known as climate variability) over the last 21,000 years (cf. Araújo *et al.*, 2008), (2) lagged effects of historical climate (cf. Svenning & Skov, 2007), and (3) time since deglaciation (i.e. the length of time for which land has been available for colonization since the LGM; cf. Montoya *et al.*, 2007).

We show that the richness–temperature relationship across North America remained reasonably constant during the last *c.* 11,000 years. Before 11,000 cal. yr BP the richness–temperature relationship was weaker. We also show that richness correlated more strongly with temperature than when richness was assumed to change independently of climate 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 years, we compared the temporal variation in the family richness of fossilized pollen from woody plants (a proxy of woody plant family richness) with the spatio-temporal variation of temperature across North America at 1000-year intervals.

Temperature data

We used two reconstructions of palaeotemperature to obtain temperature values at each richness sampling site. The first set of temperature data was taken from a general circulation model, the National Center for Atmospheric Research Community Climate System Model, version 3 (CCSM3) (Blois *et al.*, 2013). From this, we extracted the seasonal mean temperature for June–July–August. A second independent reconstruction of mean July temperature was inferred from historic plant assemblage composition using the Modern analogue technique (MAT) (Viau *et al.*, 2006). The two temperature reconstructions are highly correlated (Tables S1 & S2 in Appendix S1 in Supporting Information). 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 (see below). 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 the richness of families that
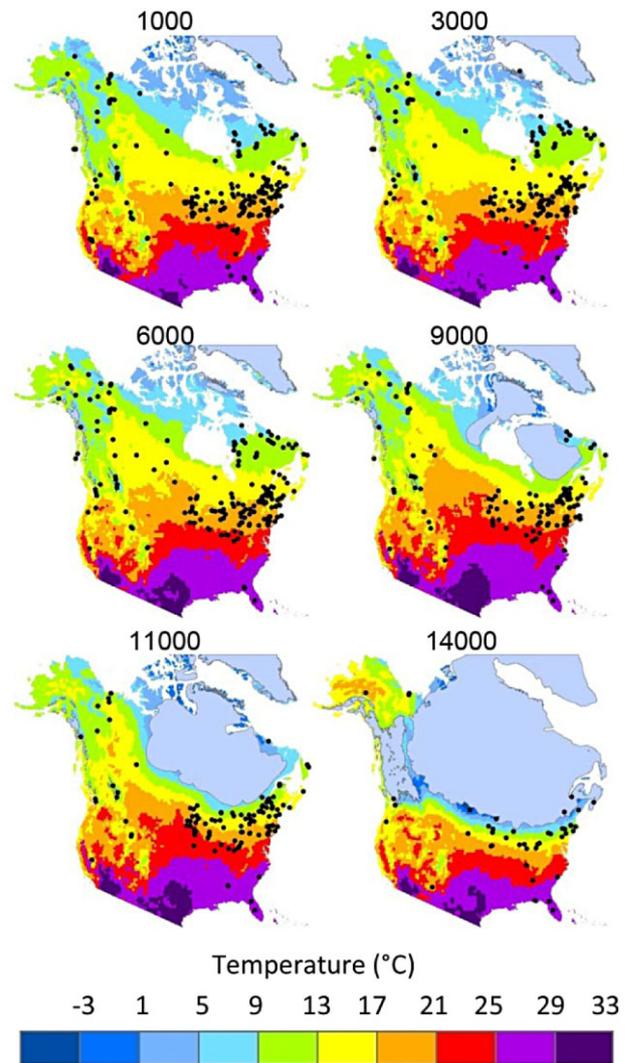
Figure 2 Spatial configuration of sampling sites for pollen in North America. Maps show temperature at six different times during the last 14,000 years. Each panel is labelled with the date in cal. yr BP. Temperature estimates were derived from CCSM3 version 3 (Blois *et al.*, 2013). They represent seasonal mean temperature of June–August. Black dots show the sampling sites for temperature and richness at each time period. The extent of the ice masses at each time period is represented by the light blue-grey areas.

are composed mainly of wind-pollinated woody plants, using pollen records from the North American Pollen Database (Grimm, 2006). We 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, concentrated in the north-east) (Fig. 2, Table S3 in Appendix S1). We estimated richness at 1000-year intervals from standardized samples rarefied to 300 pollen counts (Weng *et al.*, 2006). The temporal uncertainty in fossilized pollen data is about 500 years for the late Pleistocene (Gajewski, 2008; Blois *et al.*, 2013). The number of sampling sites represented per time period varied from 45 to 212,

unevenly distributed across the continent (Fig. 2, Table S3 in Appendix S1). There are 390 independent sampling sites in total.

The spatial grain of this study is similar to that used to construct current continental patterns of gamma diversity (Field *et al.*, 2009). Pollen records from lakes of *c.* 1–150 ha typically represent vegetation within a radius of *c.* 50 km (Bradshaw & Webb, 1985; Prentice *et al.*, 1987). Our data included a total of 20 observable families (Table S4 in Appendix S1). 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 88 km × 88 km quadrats. This spatial grain corresponds to the sampling area used for the analysis with pollen data. Species and family richness of extant trees were strongly correlated ($r^2 = 0.90$, $n = 2312$ quadrats; Fig. S1 in Appendix S1). The richness of modern pollen (based on the 20 families represented in the fossil pollen records) was also strongly correlated with total family richness ($r^2 = 0.74$, $n = 217$ sites; Figs S2a & S3 in Appendix S1), and with species richness ($r^2 = 0.63$, $n = 217$) of extant trees (Fig. S2b in Appendix S1). These results indicate that family richness of fossilized pollen captures well the spatial variation of total species richness of living trees across North America.

All dates presented below are expressed in calibrated years before present (cal. yr BP).

Statistical analysis

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

$$WFR = \alpha2 + (\alpha1 - \alpha2)/\{1 + \exp[(TEMP - \tau)/b]\}$$

where WFR is the number of woody plant families and TEMP is the temperature in K. The remaining terms are fitted parameters: $\alpha2$ is the upper asymptote; $\alpha1$ is the lower asymptote; τ is the value of the abscissa at which the ordinate is half way between the top and the bottom asymptotes; and b is 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 in 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 the interaction between temperature and time, where time is a categorical variable distinguishing among time periods at 1000-year 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).

We tested for spatial autocorrelation in the residuals of models using Moran's *I*. Moran's *I* was always < 0.30, and reaches 0 only at a distance of *c.* 1500 km (Fig. S4 in Appendix S1). This long-distance autocorrelation probably represents an environmental variable not included in the model that is autocorrelated over long distances. Precipitation is the obvious candidate. We did not include precipitation in our models for reasons discussed below.

We evaluated two null-type scenarios that postulate that richness varied temporally independently of temperature. We used the same comparison between models M1 and M2 for each scenario. Scenario A proposes that temporal variation in richness over the last 14,000 years 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 years were a constrained random walk. We first determined the range of observed richness changes between adjacent 1000-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 for subsequent 1000-year periods, with the additional constraint that richness could not fall below zero. We simulated each scenario 1000 times.

To test the hypothesized effects of climate since the LGM 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. the difference between current and past climate) is a better predictor of richness than current climate. We calculated climate variability for each time period (1000 cal. yr BP, 2000 cal. yr BP, etc.) as the difference between temperature at that time and temperature at 21,000 cal. yr BP.

2. The lagged 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 observed 1000 to 5000 years earlier.

3. The time since deglaciation hypothesis predicts that unglaciated areas, having been available for colonization for longer, 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 correct, richness should be higher in unglaciated areas, after accounting for temperature.
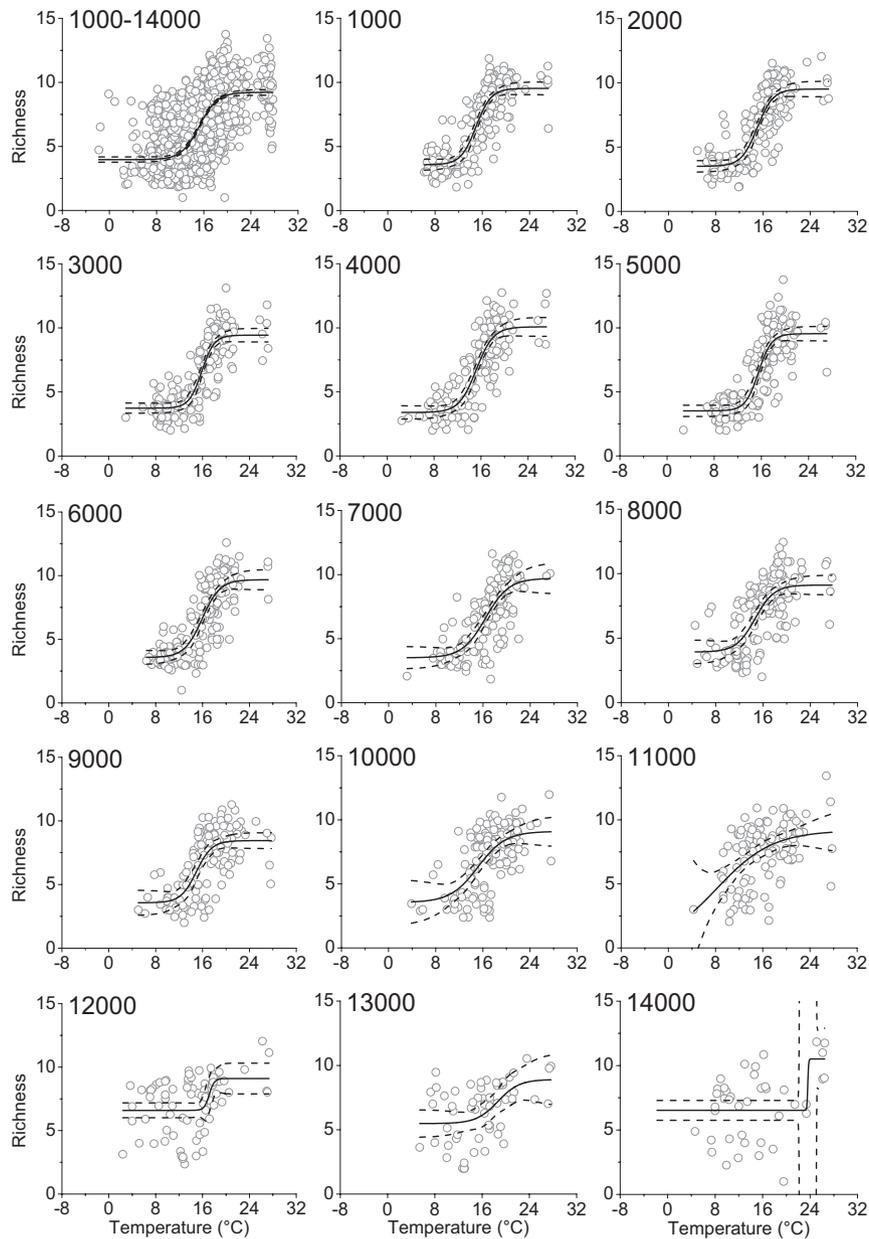
Figure 3 The observed relationships between woody plant family richness and temperature at 1000-year intervals over the last 14,000 years in North America. Dashed lines represent 95% confidence intervals. Each panel is labelled with the date in cal. yr BP. The curve labelled 1000–14,000 represents data pooled over all time intervals as described for model M1. Temperatures were estimated from the CCSM3 general circulation model. Comparable relationships estimated with temperatures from the modern analogue technique are shown in Fig. S5 in Appendix S2.

RESULTS

Individual models at 1000-year intervals over the last 14,000 years show that a sigmoidal function of temperature accounts for 18–74% of the spatial variation in woody plant family richness across North America at any given time period (Fig. 3, Table 1). Richness–temperature patterns are quite consistent through time (Fig. 3 & Fig. S5 in Appendix S2). In a model that pools over all 14 time periods (Table 2, 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 the amount of variation explained to 60.2% (Table 2, model M2). Model M2 was significantly stronger than model M1 ($F_{52, 2015} = 6.66$, $P < 0.0001$), 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 1000 and 14,000 cal. yr BP (ANOVA, $F_{13, 2057} = 4.61$, $P = 0.387$). The same analyses carried out using temperatures reconstructed with the Modern analog technique (Tables S5 & S6 in Appendix S2) are qualitatively

Table 1 Results from the nonlinear regression models of woody plant family richness as a function of contemporaneous temperature for the last 14,000 years. Temperature was estimated from the CCSM3 climate model. The same analyses using temperatures estimated with the Modern analogue technique show somewhat stronger richness–climate correlations, particularly at the earlier time periods ($R^2 = 0.69$–0.43 at 10,000–14,000 cal. yr BP; see Table S5 in Appendix S2).

| Time interval (cal. yr BP) | n | F | 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
10,000	137	495.2	0.380	3.6	9.1	288.3	2.3
11,000	118	380.3	0.207	0.1	9.2	281.4	4.7
12,000	78	270.9	0.176	6.6	9.1	290.3	0.4
13,000	59	163.9	0.200	5.5	8.9	291.8	1.8
14,000	45	101.8	0.181	6.5	10.5	296.8	0.1
1000–14,000	2071	8346.3	0.545	4.0	9.2	288.4	1.5

Woody plant family richness (WFR) is fitted as a function of temperature (in K) at 1000-year 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.
$P < 0.0001$ for all regressions.
The interval labelled 1000–14,000 represents data pooled over all time intervals as described for model M1 in Table 2.

very similar to, but somewhat stronger than, the ones shown here.

The observed richness–temperature relationship through time was stronger than would be expected under either of the alternative null-type scenarios we proposed (Fig. S6 in Appendix S2). 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 (Fig. S6a,b in Appendix S2; $P < 0.0001$). The predictions of the constrained random walk (scenario B) agree very poorly with observed richness (Fig. S6c,d in Appendix S2; $P < 0.0001$).

Temperature variability (i.e. temperature difference since the LGM) at each time period explained, on average, much less of the spatial variation of richness (26.5%; see Table S7 in Appendix S3) than did 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 the no-lag category (ANOVA, $F_{5, 63} = 1.046$, $P = 0.398$; Fig. S7 in Appendix S3). This is primarily because the continental gradients of temperature were strongly correlated through time (Tables S1 & S2 in Appendix S1).

Finally, richness observed 1000 cal. yr BP in glaciated areas was *higher* than richness in unglaciated areas, after controlling for temperature (Fig. 4) and not the reverse as predicted by the time since deglaciation hypothesis. A partial regression analysis further shows (Fig. S8 in Appendix S3) 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 *c.* 300,000 years to assess how well energy and water account for variation in plant richness through time at a single site in Hungary. Others have used decadal (Algar *et al.*, 2009b) or seasonal (H-Acevedo & Currie, 2003) changes in climate to test causal links between richness and climate over broad spatial scales. Our study is the first to test the 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 competing hypotheses that suggest that gradients of diversity are the result of historical processes mediated by climate.

Our results are largely, but not entirely, 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 and 1000 cal. yr BP (Fig. 3, Table 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, the evidence we present is inconsistent with three different hypotheses suggesting that patterns of richness can be explained by historical climate. Climate variability (or climate stability) since the LGM explained only half as much of the spatial variation in richness as contemporaneous climate did. This is inconsistent with previous studies arguing that climate stability over the last 21,000 years is a better predictor of current species richness than current climate (Araújo *et al.*, 2008). Our test of this hypothesis goes a step further than previous work. While others have analysed *current* patterns of richness as a

Table 2 Results from two nonlinear regression models relating richness to a sigmoidal function of contemporaneous temperature over the last 14,000 years. The same analyses using temperatures estimated with the Modern analogue technique show similar results, but models are somewhat stronger that the ones shown here ($R^2 = 0.72$ and 0.75 for models M1 and M2, respectively) (Table S6 in Appendix S2).

Model	Source	d.f.	SS	MS	F	P	R^2
1000–14,000 cal. yr BP:							
M1: model parameters	Regression	4	105,231	26,943.5	8346	< 0.0001	0.545
identical for all time	Residual	2067	6515	3.15			
periods	Total	2071	111,746				
M2: model parameters	Regression	56	106,186	1896.19	687	< 0.0001	0.602
free to vary among	Residual	2015	5560	2.76			
time periods	Total	2071	111,746				

SS, sums of squares; MS, mean squared error.
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.
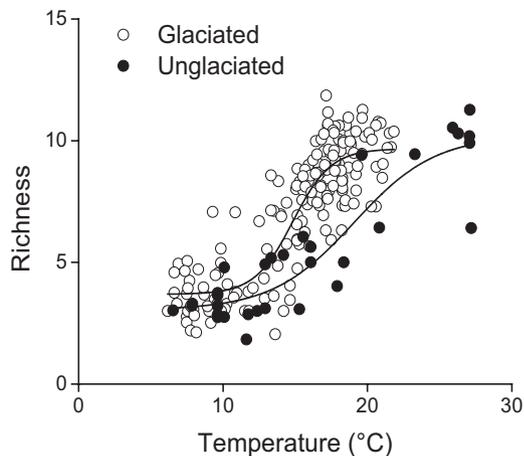
Figure 4 The observed relationship between woody plant family richness and temperature 1000 cal. yr BP, in areas of North America that were either glaciated or unglaciated during the Last Glacial Maximum.

function of climate stability (calculated as the difference between current temperature and temperature at 21,000 cal. yr BP), our study tested the effect of climate stability (calculated as the difference between temperature at a given time and temperature at 21,000 cal. yr BP) on richness at 14 different times in the past. In most cases (Table S7 in Appendix S3) climate stability was not a better predictor than contemporaneous climate.

We also reject the hypothesis that climate effects are lagged. The richness–temperature relationship assuming a consistent lag was not stronger (as the hypothesis predicted) than the richness–climate relationship with no lags. Although the ranges of individual species do not relate in a constant manner to climate (Williams *et al.*, 2001; Veloz *et al.*, 2012), richness apparently did track changing climate, except in the late Pleistocene (see below).

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). This is consistent with the proposition that migration rates into deglaciated areas were faster than subsequent extinction rates – perhaps because family richness declines only when

all species in a given family drop out of the regional flora (we will expand on this below). 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 (Fig. S8 in Appendix S3). These results are inconsistent with the time since deglaciation hypothesis.

Our study does not directly address evolutionary explanations for patterns of richness. For example, our results taken in isolation provide no test for at least one historical explanation for richness–climate correlations: the tropical niche 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 clearly true 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 *c.* 10^4 km² 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 niche conservatism hypothesis is to explain current 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 shifts do occur (Gallagher *et al.*, 2010). Moreover, in at least some taxa, species richness and species composition relate to different climatic variables (Algar *et al.*, 2009a; 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 cal. yr BP (Fig. 3, Table 1; Table S5 & Fig. S5 in Appendix 2). During this period, the sigmoidal model fit was poorer, and richness 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 Table S1 in Appendix S1). That said, we suspect that the weak richness–temperature relationships from 14,000 to 12,000 cal. 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) as 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 immigration rates are faster than extinction rates (which seems likely), then a surplus of diversity can occur (Jackson & Sax, 2010).

We suggest that the anomalously high richness observed between 14,000 and 12,000 cal. yr BP in the coldest parts of North America resulted from relatively rapid colonization following deglaciation, with an extinction lag during subsequent periods of rapidly fluctuating climate. The average temperature in North America between 14,000 and 12,000 cal. yr BP was *c.* 4 °C lower than during the Holocene (Fig. 1). However, in eastern North America, during the earlier Bølling–Allerød warm period (c. 14,500–12,400 yr BP) (Yu, 2007), temperature was only *c.* 1 °C lower than in the Holocene. This period was punctuated by three century-long cold events where temperatures decreased by *c.* 3 °C: the intra-Bølling (*c.* 13,800 yr BP), the Older Dryas (*c.* 13,500 yr BP) and the intra-Allerød (*c.* 12,700 yr BP) (Yu, 2007). We suggest that sites near the glacial front were colonized by temperate and warm-temperate taxa (see Table S4 in Appendix S1) during the warm intervals. However, there was insufficient time for richness at the family level to decline at 14,000–12,000 cal. yr BP (a period which was 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 only declines 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 a 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 historical periods, and the geographical regions, of North America where our richness–temperature relationships are weakest are also the instances where no-analogue species assemblages occurred (Williams *et al.*, 2001; Blois *et al.*, 2013). The presence of no-analogue communities (Williams *et al.*, 2001; Blois *et al.*, 2013), the observation that woody taxa have occu-pied distinct realized niches at different times (Veloz *et al.*, 2012) and the current lack of evidence for 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, during this period, species responded to other aspects of climate such as interannual climatic variability (Williams *et al.*, 2001). Therefore, our results suggest that no-analogue assemblages may also reflect extinction debt, at least in part. In sum, higher richness and no-analogue communities during rapidly changing climate are also inconsistent with the hypothesis that patterns of richness are simply the sum of the climatic tolerances of individual species (fundamental climatic niches) 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 years, richness seems to have tracked climate changes fairly well. The analysis of time lags for richness also suggests that the lags of individual species have no effect on current patterns of family richness. Rapid migrations and short-term lags of woody plants during the abrupt climate changes of the last *c.* 16,000 years 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 *c.* 60–100 years (Gajewski, 1987; Williams *et al.*, 2002) or faster (Tinner & Lotter, 2001).

Current 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). We did not include precipitation in our models, for three reasons. First, we were less confident of the precipitation reconstructions from the CCSM3 model than the temperature reconstructions. Second, the MAT did not furnish precipitation estimates, so we could not compare precipitation reconstructions between the two methods. Finally, we anticipated that any effect of precipitation in our analyses would be small because most sites in our analyses (i.e., lakes) were in areas of relatively high precipitation where current variation in richness depends relatively little on precipitation (Francis & Currie, 2003).

Finally, our results have important implications for the ecological effects of 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 current spatial variation of richness and climate (Algar *et al.*, 2009b). 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, three caveats. First, colonization of unvegetated areas after deglaciation may have happened more quickly than invasion of areas that already have established plant communities, as would happen during future climate changes. Second, 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. Third, 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.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Tables S1–S4 and Figs S1–S4.
Appendix S2 Tables S5 & S6 and Figs S5 & S6.
Appendix S3 Table S7 and Figs S7 & S8.

BIOSKETCHES

David Currie is interested in the predictable properties of the distribution of life on Earth (when he is thinking as a scientist) and the beautiful intricacies of nature (when he is not).

Héctor Vázquez-Rivera is interested in studying spatial and temporal patterns in nature through testable explanations and predictions, in climate change, biodiversity conservation and sustainable development.

Alexandre Felizola Diniz-Filho acted as Editor-in-Chief for the review of this paper.

Editor: Richard Field