



RESEARCH
PAPERS

Late Cenozoic climate and the phylogenetic structure of regional conifer floras world-wide

Wolf L. Eiserhardt^{1*}, Finn Borchsenius¹, Brody Sandel¹, W. Daniel Kissling² and Jens-Christian Svenning¹

¹Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 116, 8000 Aarhus C, Denmark, ²Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, PO Box 94248, 1090 GE Amsterdam, The Netherlands

ABSTRACT

Aim Using conifers as a model system, we aim to test four hypotheses. H1: the processes that shape the phylogenetic structure of regional species assemblages depend on climate. H2: apparent effects of current climate can be equally well explained by past climate. H3: strong Quaternary climate oscillations have led to phylogenetically non-random assemblages, either with few closely related species because isolated populations do not persist long enough to become new species or with many close relatives due to increased allopatric speciation. H4: strong late Cenozoic aridification has led to assemblages with many close relatives due to extinction and adaptive radiation.

Location Global.

Methods We used boosted regression trees to relate the net relatedness index (NRI) of regional conifer assemblages to current climate, past climate (0.021, 3 and 7.3–11.6 Ma), and gradual and cyclic late Cenozoic climate change while simultaneously accounting for habitat and biogeographic covariates.

Results Climate was the most important predictor of NRI, supporting H1. Current and past climate showed similar relationships with NRI, supporting H2. Conifer NRI was further related to Quaternary climate oscillations and gradual late Cenozoic climate trends, but the shape of the relationships supported neither H3 nor H4.

Main conclusions The climate–NRI relationships suggest that late Cenozoic climate consistently influenced the dynamics of conifer speciation, extinction and dispersal, leading to global patterns of phylogenetic assemblage structure. We deduce from the phylogenetic structure that diversification has been highest in warm or dry climates over the last ≥ 11.6 Myr. The fact that phylogenetic structure is related to climate trends and oscillations indicates that climate change plays an important role in addition to climate per se, but the exact underlying mechanisms remain unclear. Our results suggest that past climate needs to be taken into account when aiming to explain the phylogenetic structure of regional assemblages and other related aspects of biodiversity.

Keywords

Araucariaceae, community phylogenetic structure, Cupressaceae, disequilibrium, gymnosperms, macroecology, net relatedness index, palaeoclimate, Pinaceae, Podocarpaceae.

*Correspondence: Wolf L. Eiserhardt, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK.
E-mail: w.eiserhardt@kew.org

INTRODUCTION

Plant diversity and its associated ecosystem functions exhibit tremendous geographic variation. In forests, the world's most diverse and productive ecosystems, vascular plant diversity can differ by several orders of magnitude (Latham & Ricklefs, 1993). Biodiversity is often strongly correlated with the current environment, especially with climate (water and energy; Hawkins *et al.*, 2003), suggesting that current ecological limits to diversity play a role. However, it is clear that diversity patterns also depend on long-term speciation and extinction processes (Swenson, 2011; Wiens, 2011). Those may also be related to climate (e.g. Svenning, 2003; Gillooly & Allen, 2007; Svenning *et al.*, 2008b). Since diversification dynamics generally take millions of years to unfold and the effects of extinction on diversity should consequently also persist for millions of years, currently observed patterns should mainly reflect the cumulative effect of past climate. Correlations between biodiversity and current climate may thus be due to its resemblance to past climate, either because climate itself is stable over extended periods or because species have tracked a suitable climate by dispersal. In cases where climate change outpaces biotic dispersal and diversification, past climate may even be a better predictor of current diversity patterns than current climate, providing strong evidence for historical effects (Svenning *et al.*, 2008a; Rakotoarinivo *et al.*, 2013). Using spatially explicit models of palaeoclimate (e.g. Haywood & Valdes, 2004; Braconnot *et al.*, 2007; Pound *et al.*, 2011), it is now possible to quantitatively explore the extent to which current diversity patterns are legacies of past conditions (Sandel *et al.*, 2011; Blach-Overgaard *et al.*, 2013; Rakotoarinivo *et al.*, 2013). In particular, palaeoclimatic data from different epochs allow us to identify the time-scales at which climate influences diversity patterns through different long-term processes (Kissling *et al.*, 2012b;

Blach-Overgaard *et al.*, 2013). This approach should be particularly powerful in conjunction with time-calibrated molecular phylogenies, which reveal the timing of lineage diversification.

The phylogenetic structure of regional assemblages (sets of species co-occurring in a certain region) integrates current species distributions with time-calibrated phylogenetic history, reflects the dynamics of speciation, extinction and dispersal, and can be related to current and past environments in a spatially explicit manner. Phylogenetic structure can be measured with the net relatedness index (NRI), which quantifies whether the species of an observed assemblage are more closely related ('clustered') or more distantly related ('overdispersed') than expected based on random assembly from a given species pool (Webb *et al.*, 2002). This index was originally developed for community ecology, but its use has recently been extended to explore diversification dynamics at global and regional scales. For example, the NRI of regional palm (*Arecaceae*) assemblages indicates that geographic isolation, past changes in biome area and past climate change have affected speciation, extinction and range dynamics (Kissling *et al.*, 2012a). The regional NRI of African mammal assemblages has been suggested to reflect the interplay of radiation, niche filling and competition (Cardillo, 2011). The NRI of scarabid beetle assembles in previously glaciated parts of Europe has been used to suggest that phylogenetic assemblage structure can be shaped by post-glacial recolonization dynamics, with good dispersers being close relatives (Hortal *et al.*, 2011). Those examples illustrate the ability of the NRI to capture evolutionary and biogeographic dynamics at large spatial scales and their interplay with past environments.

At a global scale, the null expectation of random phylogenetic structure (NRI = 0, Fig. 1a) is unlikely to be met because dispersal among landmasses is limited and climate niche conservatism is influential (Wiens & Donoghue, 2004). Overall, this should lead to phylogenetic clustering (NRI > 0; Fig. 1b). If dispersal is

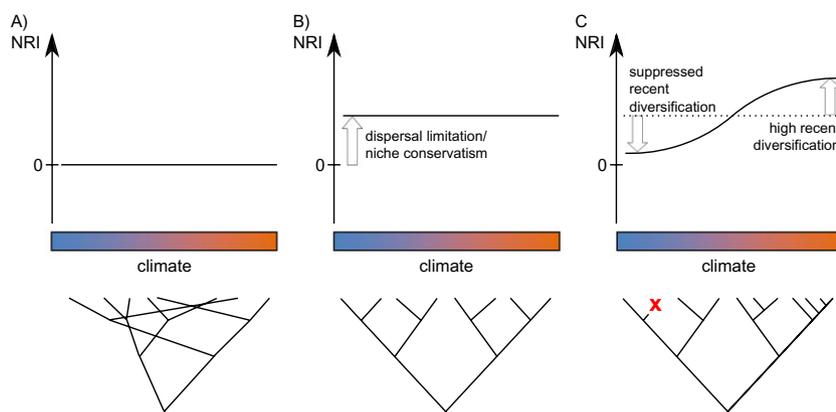


Figure 1 Possible net relatedness index (NRI)–climate relationships and their drivers. (a) The null expectation: diversifying lineages disperse freely and unconstrained by climate, leading to a random phylogenetic structure (NRI = 0) irrespective of climate. (b) The movement of diversifying lineages is constrained by dispersal barriers and/or conservative niche evolution, but diversification is homogeneous in all climates and places, leading to clustered phylogenetic structure (NRI > 0) irrespective of climate. (c) As in (b), the movement of diversifying lineages is constrained by dispersal barriers and/or conservative niche evolution, but recent diversification is increased/suppressed in certain climates, leading to a dependency of NRI on climate. The red 'x' indicates an extinction event.

limited and/or climate niche evolution conservative, different diversification dynamics in different climates can lead to distinct climate–NRI relationships (Fig. 1c). At limited geographic and taxonomic scales, such relationships may emerge by coincidence, if, for example, a key innovation triggers a radiation in a clade that happens to be adapted to a certain climate or happens to inhabit a geographically isolated region of a certain climate. However, when quantified globally across large lineages, and especially if climate–NRI relationships emerge consistently in different parts of the world, a causal role of climate (i.e. stimulation or suppression of diversification by climate) may be inferred.

The effects of climate on the balance of speciation and extinction are an integral part of ecological theory (e.g. Gillooly & Allen, 2007). Certain climatic conditions, mainly high temperature, are thought to increase speciation and decrease extinction (Gillooly & Allen, 2007); this should lead to a relationship between climate and the phylogenetic structure of assemblages (Fig. 1c). In addition, NRI is sensitive to changes in diversification over time (Kissling *et al.*, 2012a). Recent radiations in geologically young climates may cause phylogenetic clustering relative to older climates. However, directional climate change may also cause extinction of species that are maladapted to novel climates (e.g. Svenning, 2003; Sniderman *et al.*, 2013), leading to phylogenetic clustering if climatic tolerances exhibit a phylogenetic signal (Eiserhardt *et al.*, 2015). Fast (10^5 year time-scale), cyclic climate change, such as the glacial–interglacial climate oscillations of the Quaternary, may also cause phylogenetic clustering through extinction (Eiserhardt *et al.*, 2015). Alternatively, rapid climate oscillations may prevent speciation because species ranges are perturbed so frequently that diverging populations come into secondary contact before

they have developed reproductive barriers, or because incipient species go extinct (Dynesius & Jansson, 2000). Strong climate oscillations may select for widespread, generalist lineages that are less prone to extinction, but also less prone to speciation (Jansson *et al.*, 2013), leading to phylogenetically overdispersed assemblages of old, widespread generalist species in climatically unstable regions (Dynesius & Jansson, 2000; Sandel *et al.*, 2011). However, range fragmentation caused by climate change has also been proposed to potentially increase net diversification by causing allopatric speciation (Haffer, 1969). If and how NRI is related to the climate of specific epochs can thus provide important insights into the way diversification – and thus current diversity – is shaped by past climate.

Conifers (Pinophyta), with about 615 species and a subcosmopolitan distribution (Fig. 2a) (Farjon, 2010), are an ideal model group for studying the effect of climate history on the diversification of forest trees. Most conifers are trees; they are frequent in many kinds of forest, the main exception being tropical lowland rain forest, and are dominant canopy trees in many ecosystems (e.g. most boreal forests; Fig. 2b) (Farjon, 2010; Brodribb *et al.*, 2012). Thus, conifers occur across large gradients of climate per se and climate stability, although competition with angiosperms might restrict them to habitats having low productivity or high disturbance (e.g. fire-prone habitats) (Bond, 1989; Brodribb *et al.*, 2012). Within this general ecological strategy, the three large conifer families (Pinaceae, Podocarpaceae and Cupressaceae) show distinct adaptations and distributions (Brodribb *et al.*, 2012). Regional conifer floras can be quite diverse, with up to 88 species per country (Fig. 2a), and multiple conifer species may also co-occur locally (Fig. 2c). Even though the conifer clade dates back to the Carboniferous (Leslie *et al.*, 2012) most of their current diversity originated

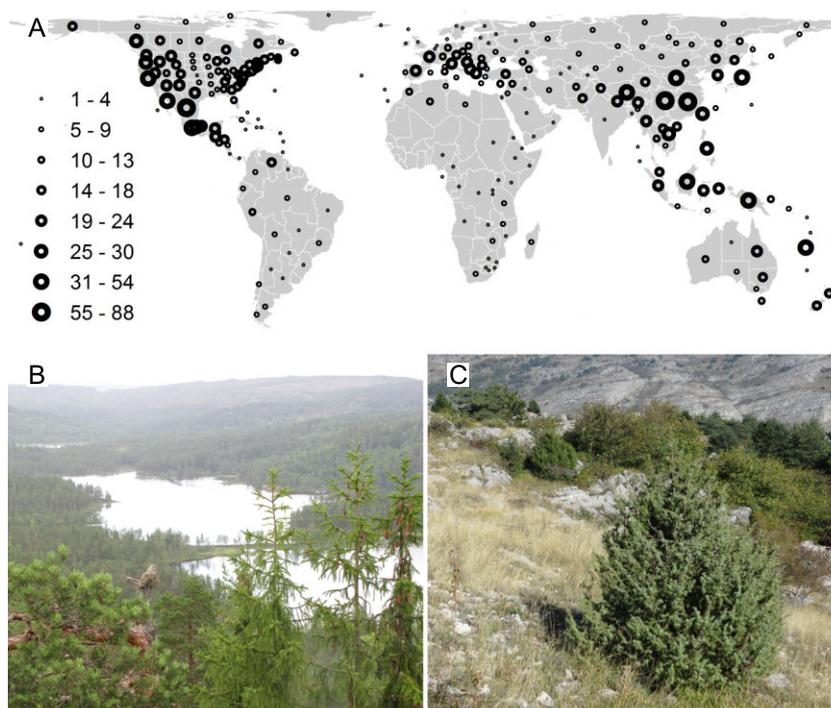


Figure 2 (a) Species richness of regional conifer assemblages (in ‘botanical countries’) world-wide. (b) Coniferous forest in southern Norway in a cold boreal climate, with *Pinus sylvestris* (left) and *Picea abies* (right) in the foreground. (c) Relatively high local diversity of conifer species (*Juniperus communis*, *Juniperus oxycedrus*, *Pinus sylvestris*, *Pinus nigra*) in southern France in a summer-dry climate with moderate winter cold. Photos: Jens-Christian Svenning.

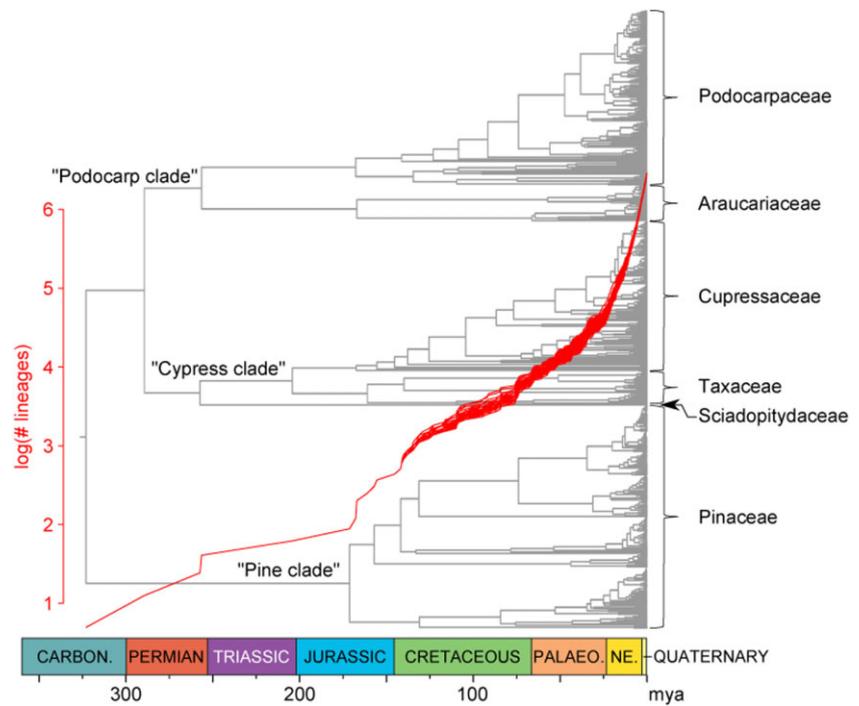


Figure 3 Phylogeny and lineage-through-time plot of conifers. The phylogenetic tree is based on Leslie *et al.* (2012) with the missing species added randomly within their genera (one of the 100 partially random trees used in the analysis). Lineage-through-time plots shown are calculated from the 100 partially random trees.

in the late Cenozoic (Fig. 3). It seems that post-Eocene aridification caused a high turnover of conifer diversity, including massive extinction of mesic and hydric conifer groups and diversification of lineages with vascular or life-history adaptations that allowed them to thrive in the novel, drier climates of the late Cenozoic (Crisp & Cook, 2011; Mao *et al.*, 2012; Pittermann *et al.*, 2012).

Here, we use spatially explicit climate models for the late Miocene (7.3–11.6 Ma), Pliocene (3 Ma) and Last Glacial Maximum (LGM; 21 000 yr BP) to test if the phylogenetic structure of regional conifer assemblages reflects late Cenozoic climate history. Specifically, we address the following four hypotheses.

H1: Climate shapes the phylogenetic structure (NRI) of regional conifer assemblages by affecting speciation and/or extinction (Fig. 1c). Specifically, we expect high positive NRI (phylogenetic clustering) in high-energy climates because of high net diversification. Moreover, we expect high positive NRI in currently dry areas, reflecting diversification of dry-adapted lineages such as junipers (*Juniperus* spp.) and pines (*Pinus* spp.) during the late Cenozoic.

H2: Relationships between current climate and NRI are paralleled by a similar relationship between past climate and NRI. This would reflect the stability of relative climatic differences in space, and suggest that apparent effects of current climate can be equally explained by long-term historical effects.

H3: Quaternary climate oscillations shape NRI because one of the following mechanisms dominates. H3a: Permanently divergent populations are less likely to form in climatically unstable areas, suppressing recent diversification. Thus, areas with strong Quaternary climate oscillations show more nega-

tive NRI than areas with less pronounced oscillations. H3b: Quaternary climate oscillations led to range fragmentation and thus increased allopatric speciation (Pleistocene refuge hypothesis). Thus, areas with strong Quaternary climate oscillations show more positive NRI than areas with less pronounced oscillations.

H4: Areas that have become drier during the late Cenozoic show high positive NRI due to diversification of dry-adapted lineages.

METHODS

Distributional and phylogenetic data

We downloaded occurrence records from the World Checklist of Selected Plant Families (WCSP) for all conifer species accepted in the checklist throughout their natural range (WCSP, 2013). The data included 3001 presences of 662 conifer species in 269 level-three units of the Biodiversity Information Standards (formerly the Taxonomic Databases Working Group, TDWG). The TDWG level three corresponds to geopolitical units such as countries, states or comparable areas, in the following called 'botanical countries' (Fig. 2a). We digitized the dated conifer phylogeny of Leslie *et al.* (2012) using TreeSnatcher (Laubach and von Haeseler 2007). This tree is the maximum clade credibility tree of a time-calibrated Bayesian inference of phylogeny including 489 conifer species. The two data sources followed slightly different taxonomic concepts requiring manual adjustments (for details see Appendix S1 in Supporting Information). The phylogenetic tree lacked 156 species listed by WCSP (24% of the total diversity; see Appendix S2). These were added to the tree in random positions within their genus (100 replicates; see

Appendix S1 for details), resulting in 100 partially random trees, one of which is shown in Fig. 3. The final dataset contained a total of 637 terminal taxa (mostly species, but including some varieties *sensu* WCSF).

Conifer clades

Conifers consist of three large clades of Palaeozoic origin: (1) the 'pine clade' (family Pinaceae), (2) the 'cypress clade' including the cypress (Cupressaceae), yew (Taxaceae s.l., including Cephalotaxaceae) and umbrella pine (Sciadopitydaceae) families, and (3) the 'podocarp clade' including Podocarpaceae s.l. (including Phyllocladaceae) and Araucariaceae (Fig. 3). A preliminary analysis showed that the regional phylogenetic structure (NRI) of conifers as a whole largely reflects which of those three clades are present, and we therefore analysed these three clades separately. This corresponds to cutting the phylogeny at a depth of 289–323 Ma. Choosing a more recent time for cutting the phylogeny into different clades would have resulted in very small groups (e.g. *Sciadopitydaceae*, a single species) with sample sizes too small for statistical analysis. Thus, using the three aforementioned clades allowed us to analyse all conifers while avoiding a disproportionate influence of the deepest divergences. At the same time, it provided us with three replicate groups, allowing us to assess the consistency of our results across major evolutionary lineages.

Phylogenetic assemblage structure

We quantified the phylogenetic structure of regional assemblages, i.e. the sets of species co-occurring in botanical countries, using the NRI (Webb *et al.*, 2002). The NRI quantifies how much the relatedness of co-occurring species (measured as the mean pairwise distance or mean nearest taxon distance; Webb *et al.*, 2002) deviates from a null expectation, in our case a null model where taxon labels were permuted 999 times on the phylogeny. The index is defined as a negative standardized effect size, i.e. $NRI = -[MPD_{obs} - \text{mean}(MPD_{null})]/SD(MPD_{null})$, where MPD_{obs} is the mean pairwise divergence time among co-occurring species and MPD_{null} is the mean pairwise divergence time among species in the null assemblages. We used the computationally efficient *R*-function of Brundberg *et al.* (2014) to calculate the NRI. The NRI was calculated separately for the three major clades (cf. Fig. 3). Assemblages with only one species were excluded since the NRI is only defined for sets of two or more species. We calculated NRI separately for each of the 100 partially random trees, and used the mean NRI of each botanical country across the 100 replicates for further analysis. This approach is justified since the variation caused by the random placement of taxa was very small compared with the variation among botanical countries.

Current and past climate

Mean annual temperature (TEMP) and annual precipitation (PREC) data were obtained from WorldClim ([http://](http://www.worldclim.org)

www.worldclim.org; Hijmans *et al.*, 2005) at 10' resolution for the present and at 2.5' resolution for the LGM. We used the mean values of the CCSM and MIROC models of LGM climate distributed by the PIMP2 project (Braconnot *et al.*, 2007). Middle Pliocene (c. 3 Ma) TEMP and PREC were obtained at 1° resolution from Haywood and Valdes (2004). Late Miocene (Tortonian, 11.61–7.25 Ma) TEMP and PREC were obtained at 1.25° resolution from Pound *et al.* (2011). For each of the four points in time we calculated mean TEMP and mean PREC for each botanical country using the Zonal Statistics tool in ArcGIS 10.1 (ESRI, Redlands, CA, USA). Palaeoclimate layers were resampled to 10' resolution using bilinear interpolation prior to calculating the botanical country means.

Palaeoclimate change

In addition to the absolute values of current and past climate, we also calculated several measures to represent temporal climate variation at different time-scales. To capture the effect of Quaternary climatic oscillations we calculated the difference ('anomaly') between current and LGM climate, separately for temperature and precipitation. We assumed that the magnitude of climate change between the LGM and the present is representative of the strength of glacial–interglacial climate oscillations throughout the Pleistocene (Sandel *et al.*, 2011). Anomalies were calculated at 2.5' resolution and subsequently resampled to 10' and averaged for each botanical country as described above.

To represent the gradual long-term climate trend during the late Cenozoic (here defined as approximately the last 10 Myr), we used the ordinary least squares regression slope of climate regressed on time in Myr, separately for temperature and precipitation. This measure integrates the climate values from all four points in time (current, LGM, Pliocene and Miocene) into one measure of overall climate trend. To improve interpretation, we inverted the time scale so that positive slopes indicate increases in precipitation or temperature. All measures were calculated for a 10' grid using resampled versions of the coarser layers (bilinear interpolation), and subsequently averaged for botanical countries.

Alternative drivers of phylogenetic structure

In addition to climate and climate change, we also included a range of habitat and biogeographic variables as covariates in our models (see below). To represent habitat heterogeneity, we measured the elevational range of each botanical country on a 30" resolution digital elevation model obtained from WorldClim (Hijmans *et al.*, 2005). In addition, we calculated the number of soil types present in each botanical country based on a 30" raster obtained from the Harmonized World Soil Database (Fischer *et al.*, 2008). We used the biogeographic realm of each botanical country as a surrogate variable for any factor causing divergent diversification in different realms, including plate tectonics, broad-scale environmental differences and possible differences in intrinsic diversification rates of different realm-

endemic clades (see Appendix S1 for details). Finally, we used current TEMP and PREC to calculate climate rarity (i.e. the area of similar climate within a 1000-km radius) as described in Sandel *et al.* (2011), and averaged this measure for each botanical country. We include climate rarity here as it represents isolation rather than climate per se.

Maps of all predictor variables are shown in Fig. S1.

Analyses

We tested for overall trends towards phylogenetic clustering or overdispersion using intercept-only simultaneous autoregressive models (Kembel & Hubbell, 2006; Kissling & Carl, 2008). This approach is equivalent to a *t*-test, but takes spatial autocorrelation into account (see Appendix S1 for details). To rule out potential biases introduced by differences in the size of botanical countries, we checked for correlations between country area and NRI, species richness and all predictor variables, respectively (Fig. S3). We then explored the relationship between the climate, habitat and biogeographic variables and NRI in our three conifer clades, using boosted regression trees (BRT) as implemented in the R-package 'dismo' (Hijmans *et al.*, 2013). BRT is a machine learning method that can identify complex nonlinear responses of a variable (here NRI) to a set of predictors without constraining the functional form of the response or the possible kinds of interactions a priori (Elith *et al.*, 2008). In our basic model, we included current climate (temperature and precipitation), Pleistocene climatic oscillations (temperature and precipitation) and the gradual long-term climate trend of the late Cenozoic (temperature and precipitation) as well as the habitat and biogeographic variables (elevation range, number of soil types, biogeographic realm and climate rarity) as predictor variables. This model allowed us to identify the relative contribution of each variable to explaining NRI, and the strength, direction and shape of the relationships. We used the stepwise model simplification procedure of Elith *et al.* (2008) to identify redundant predictor variables based on predictive deviance.

To test our second hypothesis, we replaced current climate with LGM, Pliocene or Miocene climate (one after another). This allowed us to compare the ability of current climate with the ability of past climate at different points in time to explain NRI while simultaneously accounting for the effect of the gradual long-term climatic trend of the late Cenozoic, the climatic oscillations of the Pleistocene, biogeographic factors and habitat variables.

To explore whether the inferred NRI–environment relationships were general or tied to certain geographic areas, we divided our dataset into a New World (North and South America) and an Old World (all other realms) half and repeated the BRT analysis. Note that we did not recalculate NRI, i.e. the NRI values were still based on a global species pool. To explore whether our results were biased by the averaging of climate within botanical countries (some of which are climatically very heterogeneous), we repeated our global analysis 100 times, each time using the climate conditions at a random geographic location within each

botanical country instead of the mean. In all BRT analyses, we used a tree complexity of five and a learning rate of 0.001, which were inferred using the procedures recommended by Elith *et al.* (2008).

All analyses were performed in R v.3.0.1 (R Development Core Team, 2010) unless stated otherwise.

RESULTS

The phylogenetic structure of conifer assemblages showed strong geographic variation in all three clades (Fig. 4). Values for the pine clade ranged from moderate overdispersion to extreme phylogenetic clustering (NRI -2.17 to 8.00), but were not significantly different from random on average (mean NRI = 0.86 , $P = 0.26$). The two other clades exhibited a smaller range of NRI values (podocarp clade, -2.30 to 2.66 ; cypress clade, -2.70 to 4.04), but a significantly positive mean NRI indicating phylogenetic clustering (podocarp clade, mean NRI = 1.08 , $P < 0.001$; cypress clade, mean NRI = 1.08 , $P < 0.001$).

In the BRT analysis, climate variables per se (represented by either current, LGM, Pliocene or Miocene values of temperature or precipitation) were by far the most influential predictors in all three clades (Fig. 5, Table S2). They contributed half of the model performance in the pine and cypress clades and about a third in the podocarp clade (Fig. 5). However, different aspects of climate were important in different clades (Tables 1 & S2, Figs 6 & S4): in the pine and podocarp clades, NRI was strongly related to temperature while the effect of precipitation was weak, while the cypress clade showed the opposite pattern with a strong response to precipitation, but not to temperature. The pine clade showed a steep increase of NRI between *c.* 10 and 15 °C; this pattern was found in both hemispheres, but was far more pronounced in the New World. The podocarp clade also showed a steep increase of NRI with TEMP, albeit at higher temperatures (20–25 °C), in both hemispheres. The cypress clade showed the strongest clustering in dry areas below *c.* 500 mm of annual precipitation and a very steep decrease of NRI between *c.* 500 and 1000 mm in both hemispheres.

In all three clades, NRI showed an independent, strong signal of historical climate change as measured by Pleistocene climatic oscillations and the gradual late Cenozoic climate trend (Fig. 5). Together these historical climate change variables accounted for up to 49.8% of the model performance (for the pine clade when combined with LGM climate; Table S2). Again, the different clades showed different responses (Tables 1 & S2, Figs 7 & S4). Precipitation change had the clearest and most consistent effect on NRI. The pine and cypress clades showed similar responses to Pleistocene precipitation oscillations, with higher NRI values in areas that have become drier during post-glacial warming (Fig. 7a). This pattern was present in both hemispheres for the pine clade, but restricted to the New World for the cypress clade (Fig. S4e,f). The podocarp clade did not show a clear response to Pleistocene precipitation oscillations (Fig. 7a), although this variable was not dropped in model simplification (Table 1). Pleistocene temperature oscillations were identified as redundant in all clades (Table 1). All three clades showed the same

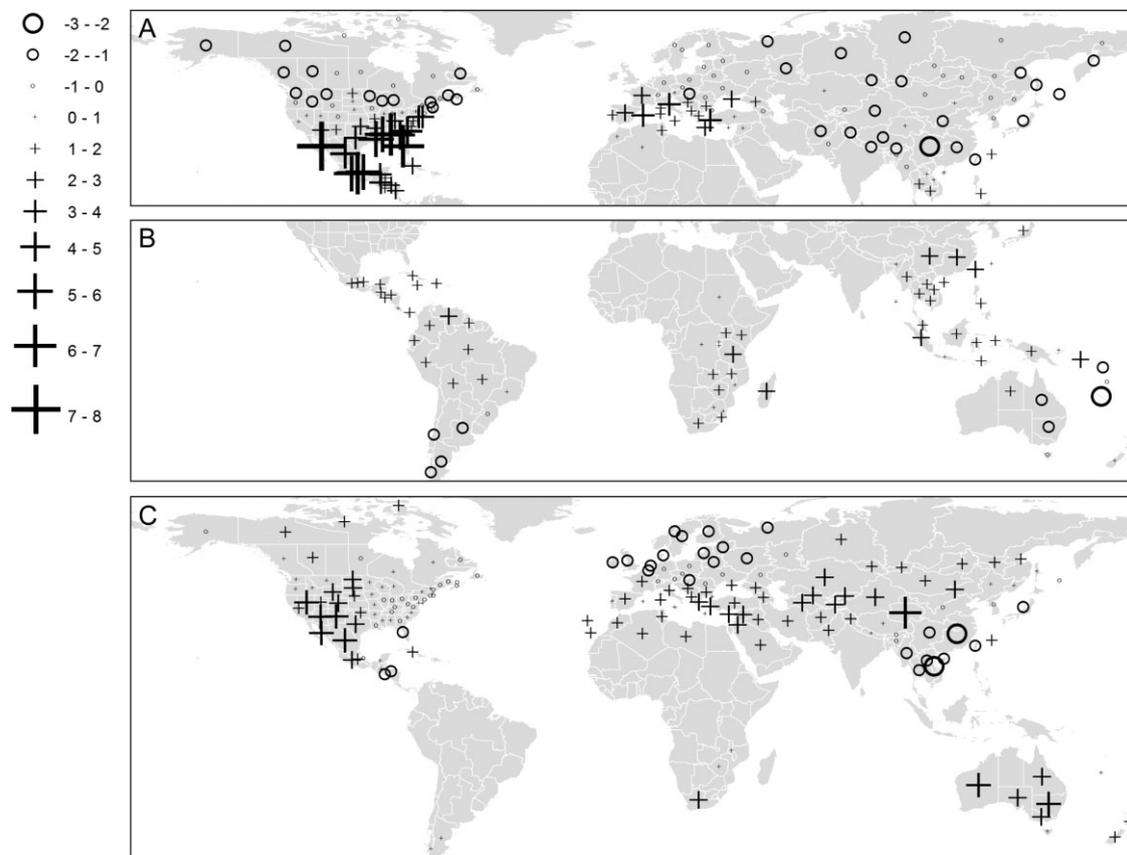


Figure 4 Geographic variation in phylogenetic community structure (net relatedness index, NRI) in three conifer clades: (a) pine clade, (b) podocarp clade, (c) cypress clade (see Fig. 2). Positive NRI values indicate coexistence of close relatives, whereas negative values indicate coexistence of distant relatives. White lines indicate the botanical countries for which the NRI was computed.

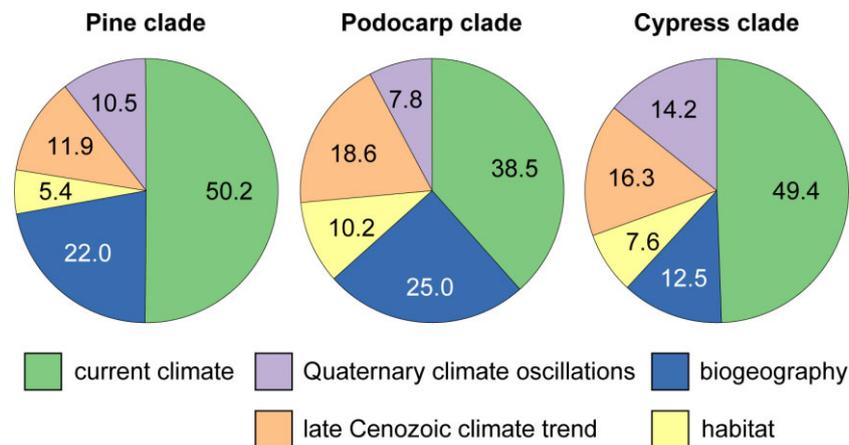


Figure 5 Relative importance of predictor categories in boosted regression tree models explaining the phylogenetic structure of regional assemblages in three major conifer clades. The importance value of each group is the sum of the importance values of its constituent variables [current climate: mean annual temperature, annual precipitation; Quaternary climate oscillations: Last Glacial Maximum (LGM) temperature anomaly, LGM precipitation anomaly; late Cenozoic climate trend: late Cenozoic temperature trend, late Cenozoic precipitation trend; biogeography: biogeographic realm, climate rarity; habitat: altitudinal range, number of soil types]. Similar results were obtained when current climate was replaced with the LGM, Pliocene and Miocene climate (Table S2).

qualitative response to the gradual late Cenozoic precipitation trend (Fig. 7c): higher NRI in areas where precipitation has increased over the late Cenozoic compared with areas where precipitation has decreased. This pattern also emerged in the

Old World analysis but not in the New World (Fig. S4i,j). The long-term temperature trend was retained in the model for the podocarp and cypress clades, but the responses appeared idiosyncratic across clades and hemispheres (Figs 7d & S4k,l).

Table 1 Variables retained in a stepwise model simplification procedure based on predictive deviance (Elith *et al.*, 2008). All variables were included in the initial model; variables retained in the simplified model are marked 'x'. For clades see Fig. 3.

	Annual precipitation (current)	Mean annual temperature (current)	LGM precipitation anomaly	LGM temperature anomaly	Long-term precipitation trend	Long-term temperature trend	Elevational range	Number of soil types	Climate rarity	Biogeographic realm
Pine clade		x	x		x					
Podocarp clade		x	x		x	x				x
Cypress clade	x		x		x	x				x

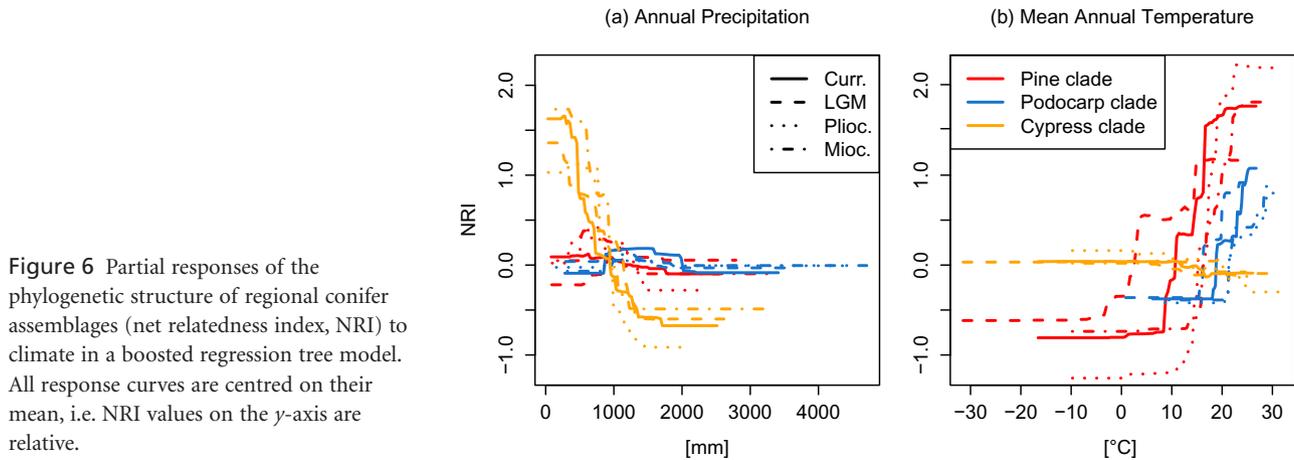


Figure 6 Partial responses of the phylogenetic structure of regional conifer assemblages (net relatedness index, NRI) to climate in a boosted regression tree model. All response curves are centred on their mean, i.e. NRI values on the y -axis are relative.

Covariates related to habitat explained up to 12% of the variation in NRI (Table S2). Soil diversity was essentially irrelevant, whereas elevation range showed idiosyncratic responses in the NRI of the three clades (Fig. S5). Biogeographic variables contributed up to 25% of the overall predictive power (Table S2). This contribution depended heavily on the biogeographic realm. While some differences among realms appeared to be clade specific, there were also systematic patterns, for example a consistently higher NRI in the New World than in the Old World (except Australasia) in the pine and cypress clades (Fig. S5d).

DISCUSSION

In conifers, temperature and precipitation have clearly influenced speciation, extinction and dispersal, the three fundamental processes by which spatial patterns of species diversity can change (Wiens, 2011). The phylogenetic structure of floras and faunas strongly reflects those processes at the regional scale (Cavender-Bares *et al.*, 2009); this allowed us to demonstrate the impact of climate by statistically linking the phylogenetic structure of regional conifer assemblages to a range of climatic and non-climatic variables, including palaeoclimate, at a high spatial resolution.

Our first hypothesis predicted clustered phylogenetic structure in high-energy climates as well as in dry areas, a pattern that was partly confirmed by the results. As predicted, the pine and podocarp clades showed a positive relationship between temperature and NRI (Fig. 6b), which is in line with the prediction

of metabolic theory (Gillooly & Allen, 2007) that net diversification should be higher in high-energy environments due to a high mutation rate and large population sizes. Alternatively, the relationship may be due to allopatric speciation; in the warm low latitudes, Pinaceae and Podocarpaceae/Araucariaceae tend to occur in montane habitats or on poor soils that are geographically fragmented and thus conducive to allopatric speciation. Interestingly, the same qualitative response of Pinaceae NRI is found in both hemispheres, but it is quantitatively about eight times stronger in the New World than the Old World (Fig. S4c,d). This pattern is presumably driven by the radiation of a limited number of pine clades (e.g. ponderosa pines, pinyon pines and south-eastern pines in Section Australes) in Mexico and the south-eastern United States. This suggests that while there is some generality to the NRI–temperature relationship, region-specific factors (possibly including the representation of certain subclades) are also important. In the podocarp clade, negative NRI values are concentrated in the far south of South America and Australasia; this pattern may be due to high extinction in the cool high-latitude climates (Palazzesi *et al.*, 2014), leaving assemblages with distantly related survivors and thereby creating a positive NRI–temperature relationship. In contrast to the pine and podocarp clades, the cypress clade did not show any relationship between temperature and NRI (Fig. 6b). Instead, it showed a negative relationship between NRI and precipitation (Fig. 6a), indicating that the diversification of this clade was controlled by a different mechanism, probably late Cenozoic aridification. Trends of habitat area over time can potentially

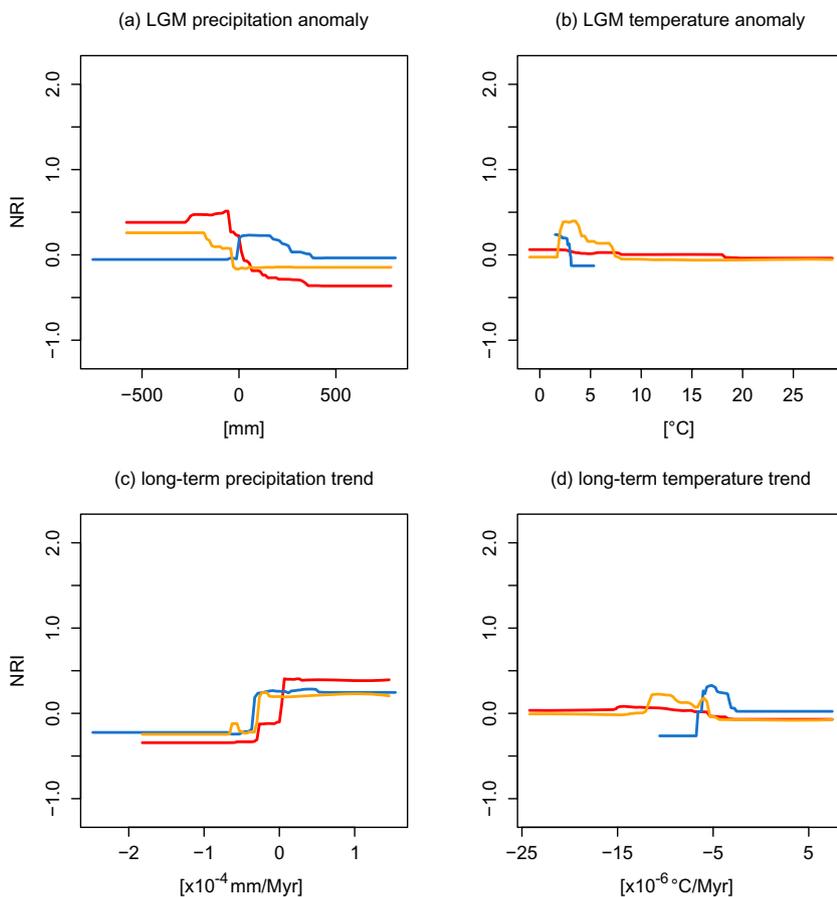


Figure 7 Partial responses of the phylogenetic structure of regional conifer assemblages (net relatedness index, NRI) to past climate change in a boosted regression tree model. All response curves are centred on their mean, i.e. NRI values on the y -axis are relative. Red, pine clade; blue, podocarp clade; yellow, cypress clade.

influence the phylogenetic structure of assemblages (Kissling *et al.*, 2012a). In Cupressaceae, lineages retaining the ancestral mesic–hydric niche contracted into relictual distributions during the Neogene, while the evolution of drought tolerance allowed extensive diversification within the crown groups of Cupressoideae and Callitroideae (Pittermann *et al.*, 2012). This mechanism may have caused a higher NRI in the expanding xeric habitats compared with the contracting mesic habitats. The heterogeneity among the three conifer clades in their response to temperature and precipitation (Fig. 6) underlines that they are distinct in ecology and biogeographic history, despite sharing important ecological attributes (Brodribb *et al.*, 2012). Despite those differences, our results support the idea that the overall pattern of more recent diversification of Northern Hemisphere conifers compared with the Southern Hemisphere was influenced by Neogene climate change (Leslie *et al.*, 2012).

Strong correlations between biodiversity and current climate (e.g. Hawkins *et al.*, 2003) are often thought to prove that biological communities are in equilibrium with the environment. According to this view, history is mainly reflected in patterns of species composition, while the environment dictates how the species combine into communities and thus controls species richness. However, even strong correlations can be misleading if potential predictor variables are collinear (Dormann *et al.*, 2013). Macroecological studies regularly account for this

problem by considering as many aspects of the current environment as possible, but past environments are much more rarely taken into account. We hypothesized that if the relative climatic differences between different points in space are stable through time, every relationship between current climate and NRI would be paralleled by a similar relationship between past climate and NRI (hypothesis H2). This was supported by our results; in fact, the observed climate–NRI relationships may have originated at any time since the late Miocene (Fig. 6a,b), or even earlier, if the (unknown) climatic patterns at earlier points in time were also similar. It is impossible that an inherently historic measure such as the NRI can be entirely shaped by current processes; however, a relationship between NRI and current *but not* past climate would indicate different diversification dynamics in clades of different climatic preference that move freely to track climate, a scenario that requires climatic niche conservatism but not dispersal limitation. Our result is compatible with a scenario of dispersal limitation restricting different clades to different regions that consistently differ in climate, and thus in their effect on diversification. This neither requires nor precludes niche conservatism. Disentangling the relative influences of niche evolution and dispersal constraints requires a different approach (Eiserhardt *et al.*, 2013).

The rapid climate oscillations of the Quaternary apparently had a distinct effect on the phylogenetic structure of conifers (Fig. 7a,b), but there was no support for our hypothesis H3,

which predicted a decrease (H3a) or increase (H3b) of NRI with the magnitude of climate oscillations. Instead, the pine and cypress clades showed a *directional* response to Quaternary precipitation oscillations, with a higher NRI in areas with a negative LGM precipitation anomaly (Fig. 7a). This pattern may reflect the selective survival and diversification of the drought-adapted conifer lineages that had diversified during the Neogene in response to long-term aridification (Pittermann *et al.*, 2012). We suggest that the survival and further diversification of those lineages during the Quaternary depended on conditions with relatively wet glacial periods and relatively dry interglacial periods, as indicated by a negative LGM precipitation anomaly. Even drought-tolerant conifers do not tolerate conditions which are too arid (e.g. Adams *et al.*, 2009); thus, a relatively high precipitation would be needed for their survival during glacial periods, which were characterized by low CO₂ levels (Sigman & Boyle, 2000) and thus relatively high drought stress. During interglacial periods, the survival of those lineages would require relatively dry conditions, allowing them to escape competition from angiosperms, which is known to limit the ecological niche of conifers (Brodrick *et al.*, 2012). Numerous diversification events in drought-tolerant lineages such as *Juniperus*, *Hesperocyparis* and *Pinus* date to the Quaternary (Leslie *et al.*, 2012), indicating that those lineages not only survived but also diversified. According to our results, this survival and diversification was spatially structured by the balance of glacial and interglacial precipitation, confirming our expectation that Quaternary climatic oscillations are a strong driver of phylogenetic assemblage structure.

In all three clades, the effect of late Cenozoic climate trends was quantitatively important (Fig. 5), supporting our expectation that gradual long-term climate change is an important driver of diversification processes. However, the direction of the effect – higher NRI in areas where precipitation has increased since the late Miocene (Fig. 7c) – runs opposite to our hypothesis H4 which predicts more clustering in environments with a negative precipitation trend due to radiations in areas that have become more arid. Interestingly, this trend seems to be absent in the New World (Fig. S4j). The origins of this relationship remain unclear, but the spatial patterns of NRI (Fig. 4) and the temperature trend (Fig. S11) indicate that it may be driven by parts of the Mediterranean region. The Mediterranean as a whole underwent strong aridification during the late Cenozoic; however, according to our palaeoclimatic data, in some parts of it (notably the Iberian and Italian peninsulas) precipitation increased on average since the late Miocene. Those parts also show high NRI, possibly due to radiation of drought-tolerant lineages followed by relatively low Quaternary extinction. Increased precipitation might have alleviated extinctions, but this conjecture requires further testing.

The recent availability of high-resolution climate models reaching as far back as the Miocene (Pound *et al.*, 2011) now allows us to test the influence of palaeoclimate on evolutionary processes with unprecedented spatial detail, but incorporating those variables into biodiversity models remains a challenge. Ideally, one would wish to reconstruct the movement of diver-

sifying lineages across space and environments explicitly, i.e. model the dispersal and niche shifts of lineages along the branches of the phylogenetic tree at high resolution. However, models of niche evolution and range evolution are still insufficiently integrated (Lawing & Matzke, 2014), and while our ability to incorporate palaeoclimate into such models has improved substantially (Condamine *et al.*, 2013) this is not yet possible at a high spatial resolution. Analysing the phylogenetic structure of regional assemblages enables us to let spatial patterns of diversification emerge from the data (Fig. 4) instead of relying on coarse a priori area definitions. Moreover, it allows us to use environmental data at the resolution of our distributional data (here botanical countries) instead of using global average palaeoclimate (Condamine *et al.*, 2013) and approximating species climate niches by summary statistics such as means or extremes. However, the contribution of individual lineages to the NRI patterns is generally unknown (but sometimes obvious) and macroevolutionary rates are not measured directly, although their variation can be qualitatively inferred from variation in the patterns of NRI (Fig. 1). The integration and improvement of macroevolutionary and biogeographic models is an active research field (Lawing & Matzke, 2014) and many of the limitations will soon be overcome, but for the time being important complementary insights into the geography of lineage diversification can be gained by analysing NRI patterns.

Our results suggest that the current distribution of conifer phylogenetic diversity is strongly driven by late Cenozoic climate history. We have demonstrated that statistical relationships between current climate and biodiversity cannot be taken as evidence for current processes without testing for a possible historical background. This applies to studies of spatial biodiversity patterns in general. In the specific case of conifers, it has proved statistically impossible to discriminate the effects of current and past climate. This situation may be common, because relative climatic differences in space depend strongly on features that change slowly even on geological time-scales, such as topography and the distribution of land and water; relative differences thus often persist in spite of global climate trends. However, in our study system the historical explanation is more convincing because both fossil and phylogenetic evidence suggests that late Cenozoic climate change was a driver of both extinction and diversification in conifers (e.g. Crisp & Cook, 2011; Mao *et al.*, 2012; Pittermann *et al.*, 2012). This illustrates the importance of considering long-term evolutionary and historical mechanisms for explaining diversity patterns as well as their relations to the current environment, as previously suggested (e.g. Wiens & Donoghue, 2004; Ricklefs, 2006). We have also shown that not just past and present climate per se, but also the rate of past climate change can play an important role in current biodiversity patterns. This idea is not new (e.g. Dynesius & Jansson, 2000), but spatially explicit palaeoclimatic models have only recently allowed empirical studies to demonstrate this relationship with palaeoclimatic change (see also Sandel *et al.*, 2011; Kissling *et al.*, 2012a; Blach-Overgaard *et al.*, 2013). Effects of either past climate as such or changes in past climate require time lags in biodiversity–environment relationships, i.e. that

biodiversity is not in perfect equilibrium with current climate. As in the present case, an explicit historical approach can reveal such time lags, which appear to be relevant at time-scales of up to tens of millions of years. We suggest that the quantitative, spatially explicit historical approach developed here should be applied more widely when investigating the determinants of biodiversity to avoid misleading conclusions from an exclusive or predominant focus on present-day factors.

ACKNOWLEDGEMENTS

We thank the Danish Council for Independent Research | Natural Sciences for economic support (STABFOR, grant 12-125079 to J.-C.S.). W.D.K. acknowledges a University of Amsterdam (UvA) starting grant. We are grateful to Andrew Leslie for very helpful comments on a previous version of the manuscript and to Peder K. Bøcher for valuable advice on GIS methods. We thank the Royal Botanic Gardens, Kew for providing the World Checklist of Selected Plant Families online, and Alan M. Haywood and Matthew J. Pound for providing climate reconstruction data for the Pliocene and the late Miocene epochs. We further acknowledge the international modelling groups for providing the LGM data, and the Laboratoire des Sciences du Climat et de l'Environnement (LSCE) for collecting and archiving them.

REFERENCES

- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A. & Huxman, T.E. (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences USA*, **106**, 7063–7066.
- Blach-Overgaard, A., Kissling, W.D., Dransfield, J., Balslev, H. & Svenning, J.C. (2013) Multimillion-year climatic effects on palm species diversity in Africa. *Ecology*, **94**, 2426–2435.
- Bond, W.J. (1989) The tortoise and the hare – ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society*, **36**, 227–249.
- Braconnot, P., Otto-Bliesner, B., Harrison, S. *et al.* (2007) Results of PMIP2 coupled simulations of the mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features. *Climate of the Past*, **3**, 261–277.
- Brodribb, T.J., Pittermann, J. & Coomes, D.A. (2012) Elegance versus speed: examining the competition between conifer and angiosperm trees. *International Journal of Plant Sciences*, **173**, 673–694.
- Brunbjerg, A.K., Cavender-Bares, J., Eiserhardt, W.L., Ejrnæs, R., Aarssen, L.W., Buckley, H.J., Forey, E., Jansen, F., Kattge, J., Lane, C., Lubke, R.A., Moles, A.T., Monserrat, A.L., Peet, R.K., Roncal, J., Wootton, L. & Svenning, J.-C. (2014) Multi-scale phylogenetic structure in coastal dune plant communities across the globe. *Journal of Plant Ecology*, **7**, 101–114.
- Cardillo, M. (2011) Phylogenetic structure of mammal assemblages at large geographic scales: linking phylogenetic community ecology with macroecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2545–2553.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Condamine, F.L., Rolland, J. & Morlon, H. (2013) Macroevolutionary perspectives to environmental change. *Ecology Letters*, **16**, 72–85.
- Crisp, M.D. & Cook, L.G. (2011) Cenozoic extinctions account for the low diversity of extant gymnosperms compared with angiosperms. *New Phytologist*, **192**, 997–1009.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquez, J.R.G., Gruber, B., Lafourcade, B., Leitao, P.J., Munkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schroder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27–46.
- Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA*, **97**, 9115–9120.
- Eiserhardt, W.L., Borchsenius, F., Plum, C.M., Ordonez, A. & Svenning, J.-C. (2015) Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. *Ecology Letters*, **18**, 263–272.
- Eiserhardt, W.L., Svenning, J.C., Baker, W.J., Couvreur, T.L.P. & Balslev, H. (2013) Dispersal and niche evolution jointly shape the geographic turnover of phylogenetic clades across continents. *Scientific Reports*, **3**, 1164.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.
- Farjon, A. (2010) *A handbook of the world's conifers*. Brill, Leiden.
- Fischer, G., Nachtergaele, F., Prieler, S., van Velthuisen, H.T., Verelst, L. & Wiberg, D. (2008) *Global agro-ecological zones assessment for agriculture (GAEZ 2008)*. IIASA, Laxenburg and FAO, Rome.
- Gillooly, J.F. & Allen, A.P. (2007) Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. *Ecology*, **88**, 1890–1894.
- Haffer, J. (1969) Speciation in Amazonian forest birds. *Science*, **165**, 131–137.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Haywood, A.M. & Valdes, P.J. (2004) Modelling Pliocene warmth: contribution of atmosphere, oceans and cryosphere. *Earth and Planetary Science Letters*, **218**, 363–377.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

- Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2013) Dismo. Available at: <http://cran.r-project.org/web/packages/dismo/index.html>.
- Hortal, J., Diniz, J.A.F., Bini, L.M., Rodriguez, M.A., Baselga, A., Nogues-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741–748.
- Jansson, R., Rodríguez-Castañeda, G. & Harding, L.E. (2013) What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution*, **67**, 1741–1755.
- Kemmel, S.W. & Hubbell, S.P. (2006) The phylogenetic structure of a Neotropical forest tree community. *Ecology*, **87**, S86–S99.
- Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59–71.
- Kissling, W.D., Eiserhardt, W.L., Baker, W.J., Borchsenius, F., Couvreur, T.L.P., Balslev, H. & Svenning, J.-C. (2012a) Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences USA*, **109**, 7379–7384.
- Kissling, W.D., Baker, W.J., Balslev, H., Barfod, A.S., Borchsenius, F., Dransfield, J., Govaerts, R. & Svenning, J.C. (2012b) Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography*, **21**, 909–921.
- Latham, R.E. & Ricklefs, R.E. (1993) Continental comparisons of temperate-zone tree species diversity. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 294–314. University of Chicago Press, Chicago.
- Laubach, T. & von Haeseler, A. (2007) TreeSnatcher: Coding trees from images. *Bioinformatics*, **23**, 3384–3385.
- Lawing, A.M. & Matzke, N.J. (2014) Conservation paleobiology needs phylogenetic methods. *Ecography*, **37**, 1109–1122.
- Leslie, A.B., Beaulieu, J.M., Rai, H.S., Crane, P.R., Donoghue, M.J. & Mathews, S. (2012) Hemisphere-scale differences in conifer evolutionary dynamics. *Proceedings of the National Academy of Sciences USA*, **109**, 16217–16221.
- Mao, K., Milne, R.I., Zhang, L., Peng, Y., Liu, J., Thomas, P., Mill, R.R. & Renner, S. (2012) Distribution of living Cupressaceae reflects the breakup of Pangea. *Proceedings of the National Academy of Sciences USA*, **109**, 7793–7798.
- Palazzesi, L., Barreda, V.D., Cuitino, J.I., Guler, M.V., Telleria, M.C. & Santos, R.V. (2014) Fossil pollen records indicate that Patagonian desertification was not solely a consequence of Andean uplift. *Nature Communications*, **5**, 3558.
- Pittermann, J., Stuart, S.A., Dawson, T.E. & Moreau, A. (2012) Cenozoic climate change shaped the evolutionary ecophysiology of the Cupressaceae conifers. *Proceedings of the National Academy of Sciences USA*, **109**, 9647–9652.
- Pound, M.J., Haywood, A.M., Salzmann, U., Riding, J.B., Lunt, D.J. & Hunter, S.J. (2011) A Tortonian (Late Miocene, 11.61–7.25 Ma) global vegetation reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **300**, 29–45.
- R Development Core Team (2010) *R: a language and environment for statistical computing*. R Development Core Team, Vienna, Austria.
- Rakotoarinivo, M., Blach-Overgaard, A., Baker, W.J., Dransfield, J., Moat, J. & Svenning, J.C. (2013) Palaeo-precipitation is a major determinant of palm species richness patterns across Madagascar: a tropical biodiversity hotspot. *Proceedings of the Royal Society B: Biological Sciences*, **280**: 20123048.
- Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, **87**, S3–S13.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.C. (2011) The influence of late Quaternary climate-change velocity on species endemism. *Science*, **334**, 660–664.
- Sigman, D.M. & Boyle, E.A. (2000) Glacial/interglacial variations in atmospheric carbon dioxide. *Nature*, **407**, 859–869.
- Sniderman, J.M.K., Jordan, G.J. & Cowling, R.M. (2013) Fossil evidence for a hyperdiverse sclerophyll flora under a non-Mediterranean-type climate. *Proceedings of the National Academy of Sciences USA*, **110**, 3423–3428.
- Svenning, J.C. (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters*, **6**, 646–653.
- Svenning, J.C., Normand, S. & Skov, F. (2008a) Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography*, **31**, 316–326.
- Svenning, J.C., Borchsenius, F., Bjorholm, S. & Balslev, H. (2008b) High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. *Journal of Biogeography*, **35**, 394–406.
- Swenson, N.G. (2011) The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *American Journal of Botany*, **98**, 472–480.
- WCSP (2013) World checklist of selected plant families. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; Available at: <http://apps.kew.org/wcsp/> (accessed 23 April 2013).
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Wiens, J.J. (2011) The causes of species richness patterns across space, time, and clades and the role of ‘ecological limits. *Quarterly Review of Biology*, **86**, 75–96.
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, **19**, 639–644.

SUPPORTING INFORMATION

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

Appendix S1 Supplementary methods.

Appendix S2 Species not included in the molecular phylogenetic tree.

Table S1 Taxonomic matching of the molecular phylogenetic tree and the World Checklist of Selected Plant Families.

Table S2 Relative importance of predictor variables in models of conifer phylogenetic structure.

Figure S1 Maps of predictor variables used to predict the phylogenetic structure of regional conifer assemblages.

Figure S2 Moran's *I* correlograms of the residuals of ordinary least squares and spatial autoregression models used to calculate the average phylogenetic structure of regional conifer floras world-wide.

Figure S3 Relationships between geographic area and conifer phylogenetic structure, conifer species richness and environmental variables across all 'botanical countries' with conifers.

Figure S4 Partial responses of conifer phylogenetic structure to climate variables in the Old World and the New World.

Figure S5 Partial responses of conifer phylogenetic structure to habitat and biogeographic variables.

Figure S6 Partial responses of conifer phylogenetic structure to climate variables, taking into account climatic variation within 'botanical countries' – pine clade.

Figure S7 Partial responses of conifer phylogenetic structure to climate variables, taking into account climatic variation within 'botanical countries' – podocarp clade.

Figure S8 Partial responses of conifer phylogenetic structure to climate variables, taking into account climatic variation within 'botanical countries' – cypress clade.

BIOSKETCH

The authors are broadly interested in geospatial ecology, mainly of plants, and the spatial and temporal scaling of processes that determine biodiversity patterns (taxonomic, phylogenetic and functional). They share a particular interest in long-term biodiversity dynamics, and the interplay of ecological and evolutionary processes. To find out more, please visit www.wolfeiserhardt.net, <http://pure.au.dk/portal/en/svenning@bios.au.dk>, <http://pure.au.dk/portal/en/finn.borchsenius@sm.au.dk>, brodysandel.wordpress.com and www.danielkissling.de.

Editor: Jeremy Kerr