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RESEARCH PAPER

Niche expansion and temperature sensitivity of tropical African montane forests

Sarah J. Ivory[1]*, Regan Early[2], Dov F. Sax[3] and James Russell[4]

[1]Institute at Brown for the Study of Environment and Society, Brown University, Providence, RI 02912, USA, [2]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall, Campus, TR10 9FE, UK, [3]Department of Ecology and Evolutionary Biology and Institute at Brown for Study of Environment and Society, Brown University, Providence, RI 02912, USA, [4]Department of Earth, Environment, and Planetary Sciences, Brown University, Providence, RI 02912, USA

ABSTRACT

Aim Climate and land-use change will have a dramatic impact on future ecosystems through alterations to species ranges and community composition. When forming conservation strategies, correlative species distribution models are often created to assess risks for individual species. These models are based on the assumption of climatic equilibrium, such that the modern range is representative of the full range of conditions under which species could thrive. However, the palaeo-ecological record illustrates examples of disequilibrium in species today, and recent studies suggest that many species could occur in much broader climatic settings than previously thought. Montane ecosystems are thought to be at disproportionate risk due to temperature sensitivity and restricted geographical ranges. However, in the Afrotropics the palaeo-ecological record shows that montane forest taxa expanded into the lowlands numerous times, suggesting a possible tolerance to warm temperatures.

Location Africa.

Methods We integrate palaeo-ecological and palaeo-climatic data in order to compare climate conditions in which species are currently found with those in the past. We use species distribution models to construct potential modern ranges for Afromontane species based on modern distributions and distributions in the palaeo-ecological record in order to evaluate the equilibrium of species ranges.

Results We show that many Afromontane trees have occupied warmer climates in the past, which suggests that the current low-elevation boundaries are not set by climate. Interestingly, the species with the largest disequilibrium between palaeo- and modern distributions are those whose modern distributions show the least temperature sensitivity. Mapping of species potential ranges based on modern and palaeo- distributions clearly shows that suitable climate conditions exist today in the lowlands for less temperature-sensitive species.

Main conclusions These results imply that the current range of these forest trees does not necessarily inform risk from climatic change, and that human land use may be the major pressure for many species in the future.

Keywords

Africa, Afromontane, climatic niche, global environmental change, montane ecosystems, palaeo-climate, palaeo-ecology, tropical biogeography, tropical ecology.

*Correspondence: Sarah J. Ivory, Institute at Brown for the Study of Environment and Society, 85 Waterman Street, Brown University, Providence, RI 02912, USA.
E-mail: sarah_ivory@brown.edu

INTRODUCTION

Species distributions are determined by a wide range of factors, of which climate is thought to play a dominant role at large spatial scales. Global climate is currently changing at rates unprecedented in the last 10 000 years (IPCC, 2013), which is likely to result in extinction or massive alteration to species distributions. In order to develop successful conservation practices and assess risk, forecasts of species ranges, combining future climate change scenarios with species

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distribution models (SDMs), are being developed. These statistical models are commonly used with modern distributions of organisms to estimate climatic sensitivities (Pearce & Ferrier, 2000; Guisan & Thuiller, 2005; Elith & Leathwick, 2009).

Despite their potential usefulness, SDMs assume that a species' geographical range fully represents its climate tolerances ('climate equilibrium'). However, a species might only occur in a restricted set of those conditions, the 'realized climatic niche', due to limitations from the non-climatic environment and biotic interactions, creating a climate disequilibrium. It has been suggested that equilibrium is the norm in terrestrial plants (Petitpierre *et al.*, 2012). Recent work, however, suggests that many species apparent climatic tolerances within their native range are much different from those within invasive or naturalized ranges. This is particularly true for species that occupy a narrow set of conditions in their native range (Early & Sax, 2014). Furthermore, evidence from fossil pollen from North America and Europe suggests that through time many species have occupied different climate spaces (Veloz *et al.*, 2012; Maiorano *et al.*, 2013). The potential for climatic disequilibrium poses a problem for the development SDMs and forecasting changes in species distributions. In particular, forecasts for species that can thrive in climatic conditions that are much different from those where they are found today are likely to overestimate risks that occur directly from climate change and ignore other processes that are important for constraining current ranges (Sax *et al.*, 2013).

Assumptions regarding climate equilibrium could be particularly problematic for forecasting extinction risks for species that occupy tropical montane forests. These species are thought to be limited by warm temperatures, preventing them from inhabiting and dispersing through warm lowland environments (Bates *et al.*, 2008). Thus, the prevailing paradigm surrounding the fate of such isolated 'sky-island' populations is that species will undergo range contraction under rising temperatures. Inability to migrate anywhere except upwards is then feared to lead to progressively decreasing ranges and eventual mountaintop extinction (Colwell *et al.*, 2008; Dullinger *et al.*, 2012; Gottfried *et al.*, 2012). However, there is a profound knowledge gap about whether such species are currently in equilibrium with climate or whether their ranges are controlled by non-climatic factors.

Afromontane forests are assumed to be in climatic equilibrium, as compositionally similar modern assemblages occupy all highland areas with similar climatic conditions throughout tropical Africa (*c.* 10° N–35° S; White, 1981, 1983). Despite this, evidence from palaeo-ecological records stretching back into the late Quaternary (*c.* 500 ka) suggest that some of these tree species were once widely expansive in the lowlands during periods when temperatures were warmer than today (Dupont *et al.*, 2000; Ivory, 2013). This suggestion of shifts in occupied climate space through time makes this region an ideal laboratory for testing the climatic equilibrium of montane forests. Further, these iconic tropical forests are considered a biodiversity hotspot currently threatened by climate change as well as pressure from dense human populations (Myers *et al.*, 2000). Ultimately the fate of these forests has important implications not just for plant biodiversity but also for large charismatic mammals like the mountain gorilla, because these forests house the highest vertebrate species diversity in Africa (Advani *et al.*, 2014).

In order to test climate tolerances and equilibrium, we investigated the climate space occupied by species within their modern native ranges and compared this with past ranges from palaeoecological records. Unlike similar studies which use palaeoclimate simulations for past climate data, organic geochemical records, which take advantage of the relationship between temperature and the chemical structure of bacterial membrane lipids, provide independent temperature reconstructions. These records can be used to validate temperature changes generated by climate models at the sites used in this study to represent past species occurrences. Furthermore, in this study we use modern pollen samples to inform our use of fossil pollen samples, providing an important context for our work. Our results shed light on why species exhibit varying degrees of equilibrium with modern climate and the role of non-climatic factors in determining ranges.

METHODS

We consider several tree species which are common in Afromontane forests and in palaeo-ecological records from across the region. *Prunus africana* and *Podocarpus latifolius* are tall trees (>15 m) that occur from 1200–2300 m a.s.l. in Afromontane rain forest habitats. *Nuxia congesta*, *Nuxia floribunda*, *Ilex mitis*, *Olea africana* and *Olea capensis* frequently occur in the mid-elevations from 1500–2700 m a.s.l. on wetter slopes. The area above this zone and to the tree line (*c.* 3500 m a.s.l.) is characterized by forests dominated by *Juniperus procera*, sometimes in conjunction with *Podocarpus falcatus* or *Hagenia abyssinica* (White, 1981; Appendix S1 in Supporting Information).

Tree species were selected based on the availability of large numbers of modern occurrences as well as reliable identification within the pollen records. As the Afromontane region is particularly undersampled (Küper *et al.*, 2006), many endemics were not evaluated due to a lack of field and herbarium occurrence records. Although two species of *Nuxia* and *Podocarpus* occur within the region (*Nuxia congesta* and *Nuxia floribunda*; *Podocarpus falcatus* and *Podocarpus latifolius*), due to morphological similarity of the pollen grains, genus-level identification is the highest taxonomic resolution within the palaeo-records; thus, here we combine modern records for the two species of each genus (Vincens *et al.*, 2007).

We focused our analyses on two data-rich periods in the palaeo-ecological record: the mid-Holocene (MH; 6 ka) and the Last Glacial Maximum (LGM; 21 ka). Modern occurrence records from observational datasets were collected from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/). Both modern and palaeo-ecological occurrence records from pollen data were taken from the African Pollen Database, converted to relative abundances then assessed for presence or absence of our studied species (http://fpd.sedoo.

fr/fpd/; Vincens *et al.*, 2007; Appendices S1 & S4). All occurrences were taken from both data sources for all of sub-Saharan Africa, which is the background region for this study. All occurrences were quality controlled for georeferencing errors, and only observations occurring within the modern climate period (1950–2000) were kept. As some species used in this analysis have long pollen dispersal distances (>100 km), we used studies of pollen transport to set a threshold value of abundance that indicates the presence of a species within area defined by the grid used for our climate data [*c.* 18 km; *Podocarpus* spp. (>5%), *Juniperus* spp. (>1%), *Olea* spp. (>1%); Vincens, 1982; Vincens *et al.*, 2006].

All climate data from the present day (1950–2000) and NCAR CCSM4 (Gent *et al.*, 2011) model output for the MH and LGM were taken from the WorldClim database and validated against palaeo-climate records (http://www.worldclim.org; Hijmans *et al.*, 2005; Appendix S1). All climate data were bioclimatic variables downscaled to a 10 arcmin grid. Data from 30 weather stations in the area were used to verify the downscaled gridded climate data. Residuals of station measurements from the gridded climate data were all within one standard deviation of the station time series for the period 1950–2000. We selected four climatic variables for this study: mean annual temperature, mean annual precipitation, diurnal temperature range and rainfall seasonality. The selection of these variables was based on a principal components analysis (PCA) to best characterize climatic gradients across the Afromontane region as well as the documented sensitivity of some species (Appendix S1; Hedberg, 1969; White, 1981; Hamilton & Taylor, 1992). In this PCA, the first three principal components (PCs) explained 65% of the variance in climate within the Afromontane region. Mean annual precipitation (−0.25) and mean annual temperature (0.3) loaded most strongly on the first PC, rainfall seasonality (−0.3) loaded most strongly on the second PC and diurnal temperature (−0.5) loaded most strongly on the third PC.

We calculated expansion from the modern to the past of the realized climatic niche over time in order to evaluate species equilibrium with modern climate. High climatic niche expansion means that a species occupied climatic conditions in the past that it does not currently occupy, suggesting that the species is not in equilibrium with modern climate. Niche expansion was calculated using a kernel smoother method developed by Broennimann *et al.* (2012) and used for evaluation of native to naturalized range shifts by Petitpierre *et al.* (2012) and Early & Sax (2014). This method calibrates a PCA of the total pooled climate space for the entire study area across all time periods being compared. Based on the first two components of the PCA, a 100 cell × 100 cell gridded climate space is created to represent all climatic conditions over the periods being compared. Species densities are then projected for each cell on the gridded climate space using a kernel density function. Niche expansion from the modern to the past is then equal to the proportion of the density of palaeo-distribution which falls outside the grid cells occupied by the modern distribution. We compared the modern with MH and modern with LGM occurrences separately, then compared the modern occurrences with occurrences in both palaeo-periods combined. Values of expansion can range from zero (indicating that climate conditions in the past are identical to or are a subset of the climate space occupied today) to 100 (no overlap of the climate occupied by the past and modern distributions).

In order to verify how representative of species ranges past pollen data are, we used the niche expansion method to check whether modern pollen data represent species current geographical distributions (Appendices S1 & S5). We calculated expansion between modern pollen data and modern GBIF data. This is necessary validation step, as pollen may be transported over long distances. Modern pollen and GBIF data give very similar values, suggesting that together these data represent species actual distributions well; however, climate space based on GBIF data is bigger than that based on pollen data for all studied species, suggesting that the pollen record is conservative with respect to GBIF.

Additionally, in order to see if climate space occupied in the past is available but unoccupied today, we created SDMs that estimate all potentially suitable areas, i.e. the potential range. This approach allowed us to evaluate how much estimates of species modern potential geographical ranges are influenced by addition of the palaeo-ecological data. We initially constructed SDMs using all regression and machine learning algorithms in BIOMOD2 in R (Thuiller *et al.*, 2009). However, results using the generalized linear model algorithm (GLM) minimized the occurrence of false presences, creating the most reliable models for all species. Thus only SDMs based on GLMs will be presented in this paper. SDMs for each species were created based on two different datasets: (1) the modern distributions alone, and (2) the pooled modern and palaeo-distributions. Due to the lack of true absences in this dataset, pseudo-absences were selected to define background climate. This was conducted by random selection of points (eight times the number of presences for each species) from within a geographical region defined by a 400-km radius around modern presences. These parameters were selected to define the background area following tests where the number of pseudo-absences and geographical extent were varied (from one to ten for number of pseudo-absences and from 50 to 800 km for the radius for geographical extent). The parameters selected maximized predictive ability and correct assessment of presences and absences from the area under the receiver operating curve (AUC) statistic. We employed *k*-fold cross-validation, in which the occurrence data were split into training and testing datasets three times (70:30% split). The final model used all occurrence data but was compared with the three training models. If the evaluation statistics for the final model (AUC, sensitivity, specificity) were within 10% of the evaluation statistic calculated for the testing dataset, the evaluation statistics used with the testing dataset were considered to be representative of the final model. We calculated the sensitivity of each

Table 1 Niche expansion of mid-Holocene (MH) to modern, Last Glacial Maximum (LGM) to modern, and all pooled palaeo-ecological data (All palaeo-data) to modern as a percentage of palaeo-ecological record outside of modern climate.

	MH	LGM	All palaeo-data
Hagenia abyssinica	1.2	18	6.6
Ilex mitis	0.26	NA	5
Juniperus procera	11	4.8	16
Nuxia spp.	10	23	18
Olea africana	20	20	22
Olea capensis	19	28	21
Podocarpus spp.	20	29	24
Prunus africana	12	NA	12

NA indicates insufficient records to perform analysis.

species to each climate variable using a randomization technique in which a series of GLMs is run for each species leaving out one climate variable at a time to quantify sensitivity of the models to that variable. The sensitivity to a specific variable is then the reciprocal of the AUC when that variable is not included (1 – AUC). Further description of sample preparation and analysis can be found in Appendix S1.

RESULTS

Niche expansion was calculated by comparing the proportion of the occurrences in the palaeo-ecological record with modern occurrences. When species occurrences from both palaeo-periods are considered together and compared with the modern distribution, niche expansion ranges from 24% (*Podocarpus* spp.) to 5.0% (*I. mitis*), with a mean expansion across all species of 16% (Table 1). When MH occurrences are compared with modern occurrences, niche expansion ranges from 20% (*Olea africana*/*Podocarpus* spp.) to 0.26% (*I. mitis*), with a mean of 12% across all species. When LGM occurrences are compared with modern occurrences, niche expansion ranges from 29% (*Podocarpus* spp.) to 4.8% (*J. procera*), with a mean of 21%.

During training of the SDMs, species sensitivity to individual climate variables was determined via a leave-one-out randomization process (Table 2). These values range from 0 to 1, indicating no sensitivity and complete sensitivity, respectively. All species showed highest sensitivity to mean annual temperature. However, sensitivity ranges from 0.48 (*O. africana*) to 0.94 (*J. procera*).

The size of the potential range for each species was evaluated using ‘modern only’ occurrences and compared with pooled modern occurrences and occurrences in the palaeo-ecological record. The proportion of the increase in potential range size when the palaeo-ecological data are included was calculated (Table 3). This potential range increase under modern climate conditions varied greatly, with some species showing almost no increase (*H. abyssinica*, 1.1%) while others showed increases of potential range of up to 52% (*O. capensis*).

Table 2 Sensitivity of each species to climate variables used in species distribution models based on randomization.

	MAT	Diurnal temp.	MAP	Seasonality
Hagenia abyssinica	0.92	0.14	0.091	0.25
Ilex mitis	0.84	0.15	0.21	0.076
Juniperus procera	0.94	0.021	0.15	0.17
Nuxia spp.	0.73	0.42	0.16	0.058
Olea africana	0.53	0.25	0.15	0.29
Olea capensis	0.61	0.49	0.054	0.17
Podocarpus spp.	0.61	0.34	0.12	0.24
Prunus africana	0.78	0.33	0.033	0.14

Higher values equal greater sensitivity.
MAT, mean annual temperature; Diurnal temp., diurnal temperature; MAP, mean annual precipitation; Seasonality, rainfall seasonality.

Table 3 Percentage potential range increase with inclusion of the palaeo-ecological data.

	Range increase
Hagenia abyssinica	1.1
Ilex mitis	1.4
Juniperus procera	19
Nuxia spp.	22
Olea africana	20
Olea capensis	52
Podocarpus spp.	45
Prunus africana	14

DISCUSSION

Niche expansion and temperature sensitivity

Although it has been known for decades that widespread changes in the geographical distribution of Afromontane forest have occurred over the late Quaternary and Holocene, we show that most species also occupied widely different climatic space in the past than they do today (White, 1981; Hamilton & Taylor, 1992; Dupont *et al.*, 2000; Ivory, 2013). In general, all eight species occur today in regions with relatively cool mean annual temperatures, low rainfall seasonality and moderate diurnal temperature variability, relative to the full range of climate conditions in sub-Saharan Africa (Figs 1 & 2). Despite the similarity between the modern climate space occupied by the eight species studied here, each species occupied at least some climate space in the past that differs from that today (Table 1). These trees exhibit some degree of climate disequilibrium in their modern native ranges, but there is considerable variation in the degree of niche expansion among species (Table 1). The large amount of expansion through time for species such as *O. africana and Podocarpus*

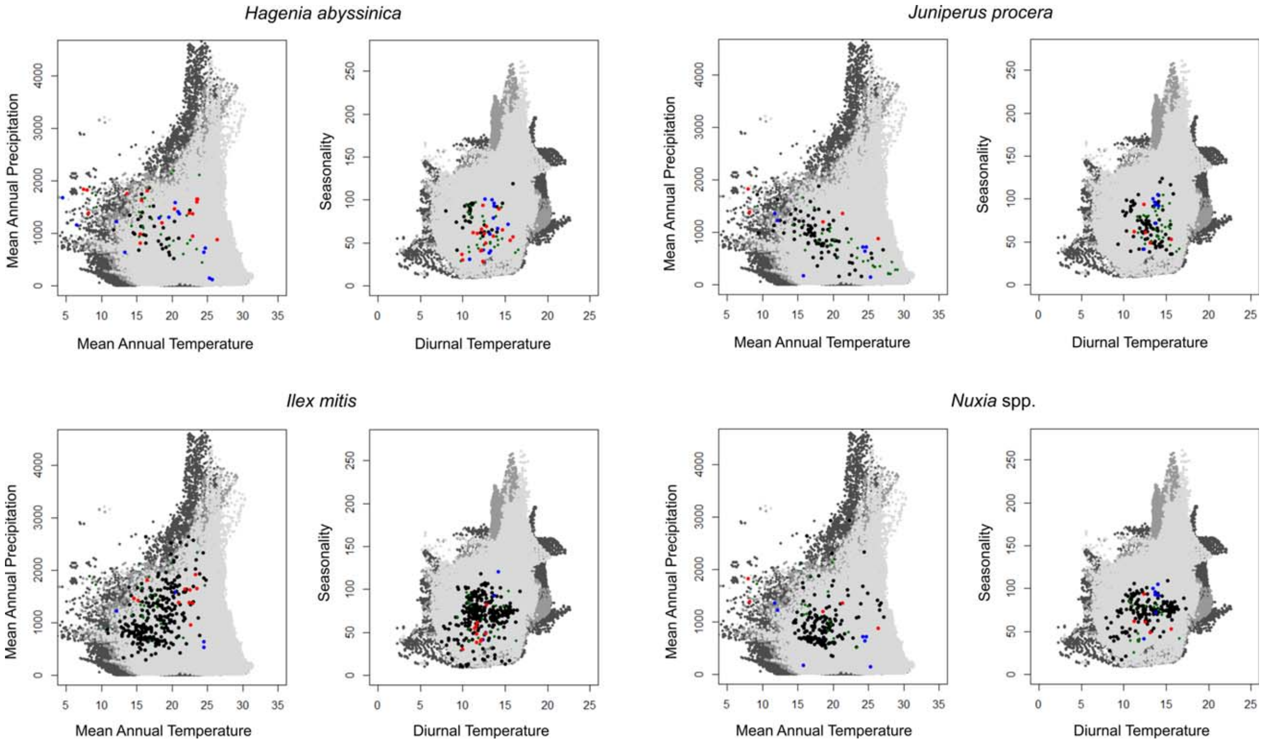

Figure 1 Climate space for all of sub-Saharan Africa (modern = light grey, mid-Holocene = medium grey, Last Glacial Maximum = dark grey). Dots on top of this climate space for the study region are the occurrences for each of the afromontane trees at modern (black), mid-Holocene (MH - grey), and Last Glacial Maximum (LGM - white) for important environmental variables used in this analysis.

spp. implies that the climatic niches of some Afromontane trees may be much broader than previously thought.

Climate models have increased in accuracy over the last decade, and many climate variables have been shown to be quite accurate, in particular mean annual temperature. Despite great improvement, some of the variability in climate space observed using palaeo-climatic simulations may result from model error. However, we have confidence in our results, for two reasons. First, CCSM4 has been used in other similar studies evaluating climate space through time (Veloz *et al.*, 2012) and has been found to reproduce major climatic features with some fidelity, in particular surface air temperature, which is the most sensitive variable for all species. Second, palaeo-climate reconstructions based on organic geochemical proxies were used to evaluate the palaeo-climate simulations (Appendix S1). Although only reconstructions for mean annual temperature and mean annual precipitation were available, the simulated variables from CCSM4 fell within error of the reconstructions for most sites, in particular for the LGM where much of the evidence for increased niche expansion occurs. The uncertainty of the palaeo-temperature reconstructions is about ±2 °C and combines error from instrumental precision as well as calibration error (Loomis *et al.*, 2012). We found that model-simulated LGM temperatures were within instrumental and calibration error of the temperature reconstructions from palaeo-climate data for sites in the highlands and lowlands. For the MH, model-simulated temperatures were within error for lower-elevation sites, but frequently underestimated temperatures by 1–3 °C above 1000 m a.s.l. Underestimation of MH temperatures means that species distributions will underestimate the temperatures occupied in that period, and niche expansion values will be minimum values.

Additionally, as the number of modern records used in this analysis is greater than the number of palaeo-records, this suggests that palaeo-distributions may be undersampled (Appendix S4). In fact, there is a marginally significant positive correlation between the number of palaeo-samples and the amount of niche expansion (MH, $R^2 = 0.47$, $P = 0.058$; LGM, $R^2 = 0.51$, $P = 0.10$; Appendix S3). This implies that our estimates of niche expansion are conservative, and that further sampling of the palaeo-ecological record would be likely to indicate even greater disequilibrium.

Our data show that temperature sensitivity is not equal among Afromontane trees. Interestingly, temperature sensitivity varies even among tree species that form well-established communities. For example, upper montane forest stands are often co-dominated by *J. procera*, *H. abyssinca* and *P. falcatus* (Hamilton, 1975; Bussmann, 2006). Yet *Podocarpus* spp. appear to be much less sensitive to mean annual temperature and more sensitive to diurnal temperature variability and rainfall seasonality than the other taxa (Table 2). This could imply that the community structure and composition of many forests with dominant species of varying sensitivities are probably not fixed. This is supported by the palaeo-ecological records which show individualistic responses of

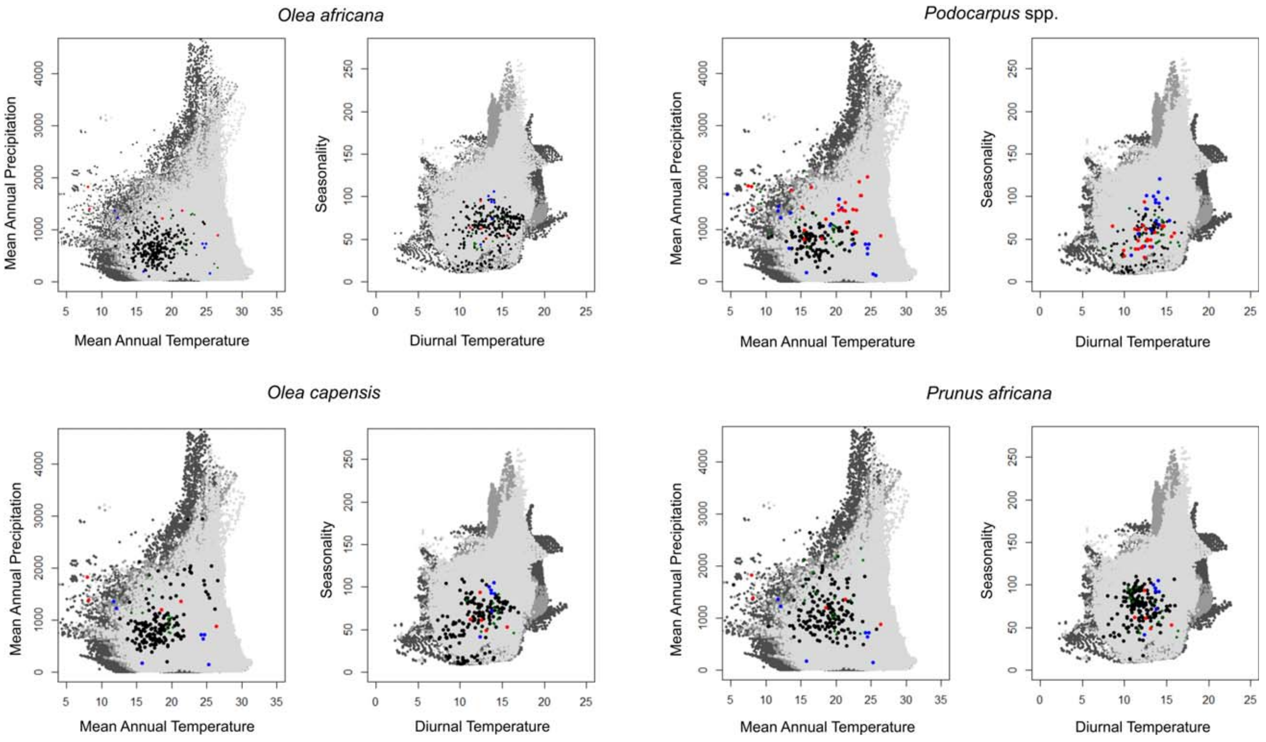

Figure 2 Climate space for all of sub-Saharan Africa (modern = light grey, mid-Holocene = medium grey, Last Glacial Maximum = dark grey). Dots on top of this climate space for the study region are the occurrences for each of the afromontane trees at modern (black), mid-Holocene (MH - grey), and Last Glacial Maximum (LGM - white) for important environmental variables used in this analysis.

species to climate, for example large expansions of *Podocarpus* into the lowlands prior to 100 ka, and therefore changing species associations through time (Dupont *et al.*, 2000; Ivory, 2013).

The high degree of climatic disequilibrium in Afromontane trees is quite remarkable, as it has generally been assumed that the regional homogeneity of these communities indicates equilibrium (White, 1981, 1983; Hamilton and Taylor, 1992). As species show strong co-occurrence patterns, it is assumed that the dominant forest tree species share similar climatic tolerances, in particular a high sensitivity to temperature (Hedberg, 1969; White, 1981). In fact, the assumption of high temperature sensitivity was thought to be supported by palaeo-ecological records, which frequently showed large-scale Afromontane expansion in cooler conditions during the LGM followed by a retreat to high elevations as temperatures warmed in the late Pleistocene (Coetzee, 1964; Livingstone, 1975; van Zinderen Bakker, 1978; Hamilton, 1981). This led many to the conclusion that these trees are restricted to discontinuous sky islands when the world was warm. In contrast, our results show that even during the LGM, many Afromontane trees occupied areas warmer than where they are found today (Figs 1 & 2).

Additionally, the few palaeo-ecological records of vegetation biogeography that extend beyond the LGM support our results. Pollen analyses of marine cores offshore from West and East Africa, as well as a sediment core from Lake Malawi, show repeated large-scale Afromontane expansion into the lowlands during the late Pleistocene (Dupont *et al.*, 2000, 2011; Ivory, 2013). These data indicate that during the Last Interglacial (130–115 ka), when temperatures were at least as warm as today, lowland forests consisted of very different species from today (Cohen *et al.*, 2007; Scholz *et al.*, 2007; Beuning *et al.*, 2011). For example, *Podocarpus* spp. and *Olea* spp. were then common in the lowlands but today are restricted to cool mountains. This is concordant with our findings that these two species are not in equilibrium with modern climate.

Finally, our results suggest that greater temperature sensitivity leads to greater climatic niche conservatism through time. There were significant negative correlations between species mean annual temperature sensitivity and niche expansion in the MH, LGM and both palaeo-periods combined (MH, $R^2 = 0.6933$, $P = 0.011$; LGM, $R^2 = 0.5405$, $P = 0.091$; combined, $R^2 = 0.6374$, $P = 0.015$; Fig. 3). The slopes of these correlations are not significantly different ($t = 0.58$, $P = 0.57$), and this relationship is the same for the MH and LGM, suggesting that it is not an artefact of solely a warmer or cooler global climate.

Our results suggests that although not all montane taxa are temperature sensitive, those that are will be less likely to cope with warming temperatures and more likely show a retreat of their lower range limits upslope. As this relationship is robust across all time periods studied, it may provide a useful tool for assessing the quality of SDMs when no independent data exist to test them. Also, it provides a hypothesis

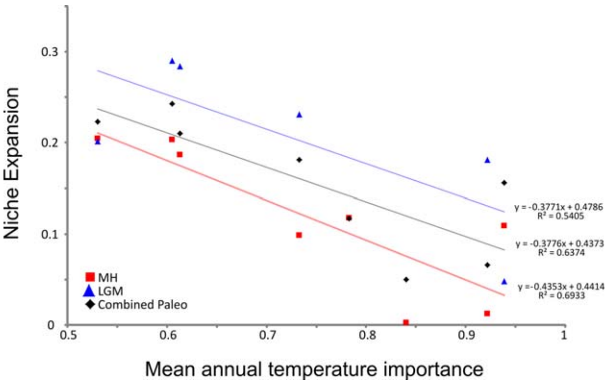

Figure 3 Correlation of sensitivity of afromontane trees to mean annual temperature (from Table 2) with respect to niche expansion (from Table 1). This was conducted comparing mid-Holocene (MH) to modern in light grey squares, Last Glacial Maximum to modern in dark grey triangles, and by pooling all paleoecological data compared to modern in black diamonds. Linear regression formulas are pictured to the side of each line with R2 for correlation of two variables.

that could be tested for generality in other biogeographical regions to evaluate the true climatic tolerances of species which may be at risk in the future.

Non-climatic limitations on the modern potential range

The inclusion of palaeo-ecological occurrences in SDMs increased the estimates of potential range of most species against those based solely on modern distributions. This suggests that many species have not only occupied much different geographical and climatic spaces through time but are currently geographically restricted by non-climatic factors. The magnitude of this mismatch varied strongly among species (Table 3; 0–52%). There is a significant positive correlation between the increase in potential range size and magnitude of past niche expansion ($R^2 = 0.68$, $P = 0.012$; Fig. 4). The negative relationship between niche expansion and temperature sensitivity suggests that the species whose current distributions are most limited by non-climatic factors are those that are least temperature sensitive.

Important non-climatic factors that limit these species distributions could include land use, dispersal barriers like complex topography and large inland lakes, and biotic interactions. Recent increases in historical land use in the lowlands may be particularly important. Our data indicate that *Podocarpus* spp., *O. africana* and *O. capensis* could occur today in many of the lowland areas of East Africa which are also the areas affected by land-use change. Forest conversion to agricultural lands as well as pressure for non-timber forest products are likely to be greatest on the lower slopes of the mountains where people live. Some work suggests that large-scale conversion of natural lands may have begun as early as the mid-Holocene (4800 yr BP), whereas, other studies suggest that impacts on forest were highest less than 3000 yr BP following the introduction of Iron Age smelting due to pressure for charcoal harvesting (Hamilton *et al*., 1986; Mumbi *et al*., 2008; Hall *et al*., 2009). As our analysis focuses on periods that pre-date large-scale land use, human alteration of the landscape is a strong candidate for being one of the major non-climatic factors limiting species current geographical ranges.

Afromontane biogeography and conservation

The potential geographical ranges for less temperature sensitive species indicate continuous lowland corridors that are climatically suitable today for occupation of Afromontane taxa (Fig. 4). This region stretches for thousands of kilometres across the Afrotropics, yet is strikingly discontinuous (White, 1981, 1983; Hamilton & Taylor, 1992). Many have speculated that the founding of these populations, and in particular the high levels of endemism, is related to long-term climate stability in the highlands and expansion into the lowlands during relatively cold periods (Quaternary glacial periods; White, 1981, 1983; Hamilton & Taylor, 1992). Our results suggest that a cold climate dispersal pathway during glacial periods is not necessary, as climates similar to or warmer than today could allow for lowland dispersal. Although modern populations are currently separated by great distances, dispersal of populations in the lowlands may have occurred repeatedly over the last few hundred thousand years, including as recently as 6 ka.

It is clear from palaeo-ecological studies throughout the world that some past climates no longer exist today, leading to no-analogue species assemblages (Williams *et al*., 2001; Williams & Jackson, 2007). This phenomenon has been observed in North America and Europe during the late Pleistocene but has rarely been evaluated in Africa (Veloz *et al*., 2012; Maiorano *et al*., 2013). Although, species with the highest expansion did seem to occupy some past climate spaces that don't exist today, the majority of occurrences observed in the palaeo-ecological record occur in climates that do exist today (Figs 1 & 2, Appendix S2). Thus no-analogue climates are not necessary for large disequilibrium over time. Additionally, the model simulations used here to represent past climate seem to indicate that very little no-analogue climate occurred in Africa over the time periods evaluated in this study (Figs 1 & 2). This suggests that although availability of novel climates results in some range shifts, other range-limiting factors must also be at play.

In contrast to the prevailing paradigm that these species are restricted to high elevations due to long-term climate stability and a high temperature sensitivity (Hedberg, 1969; White, 1981), our results instead suggest that even within communities, environmental sensitivity, particularly to temperature, is quite variable. For example, in the upper montane forest, stands co-dominated by *J. procera*, *H. abyssinca* and *P. falcatus* are common (Hamilton, 1975; Bussmann, 2006). However, despite the close modern association of

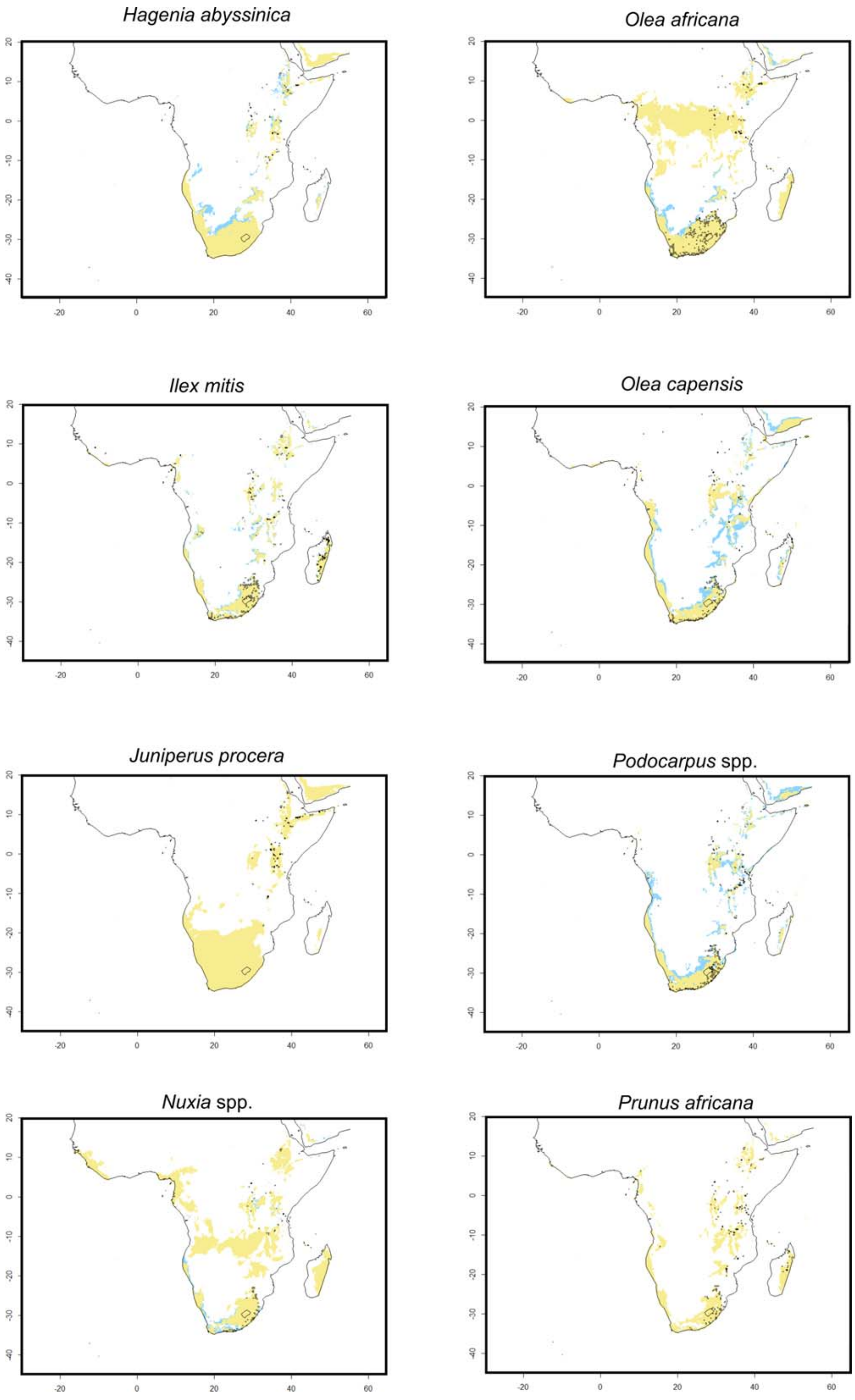

Figure 4 Potential range reconstructions under modern climate from species distribution models based on modern distribution alone (light grey) and based on their modern and paleo distributions combined (dark grey).

these species, *Podocarpus* spp. appear to be much less sensitive to mean annual temperature and more sensitive to diurnal temperature variability and rainfall seasonality (Table 2). This implies that forest community structure and composition are likely very recent and will not be conserved through time. Although conservation efforts within the native range of Afromontane forest have the potential for success in the face of rising temperatures, this will vary from species to species. Furthermore, conservation at the landscape scale of community composition and ecosystem function in these regions may not be realistic given evidence of differential tolerances to warm temperatures.

CONCLUSIONS

We have shown that many important tree species that dominate communities in the tropical African highlands are not currently in climatic equilibrium. Furthermore, despite the long-standing paradigm that Afromontane forest species have similar high sensitivities to warm temperatures, many of these species are much less sensitive to temperature than previously thought. Based on evidence from the palaeo-ecological record of the suitable climate space for Afromontane trees, some of these species could currently occupy extensive continuous ranges within the lowlands based on climate alone.

The differences in the environmental sensitivity among species have important implications for the success of future conservation efforts. While certain species are very likely to respond to rising temperatures by moving upslope, less temperature-sensitive species are likely to be less threatened by increasing temperatures alone. This conclusion could be tempered, however, if strong local adaptation of populations existed in the past, in which case warm-adapted populations might have been lost following their disappearance from the lowlands. Further experimental work on the response of these species to environmental stress may be needed to fully understand this possibility. Furthermore, the most temperature-sensitive species we evaluated are important endemic taxa such as *H. abysinica* and *Prunus africana*. Compositional changes and loss of endemics within the forest are possible due to differences in temperature sensitivity unless we are greatly underestimating the true capacity of these species due to undersampling of the palaeo-ecological record. Further pollen analysis may indicate new areas that were available to important species in the past and allow us to better assess the effect of sample size on niche expansion in the past. Finally, although our results suggest that several Afromontane trees will not be directly negatively affected by climate warming, increasingly dense human populations may have a non-trivial effect on forest composition even within protected areas.

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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 Supplementary methods.
Appendix S2 Kernel density niche expansion plots for all eight species.
Appendix S3 Correlation of fossil sample number and niche expansion.
Appendix S4 Number of species occurrences for each time period.
Appendix S5 Niche expansion of Global Biodiversity Information Facility occurrences as a percentage of the shared environmental space with pollen occurrences.

BIOSKETCH

Sarah Ivory is a post-doctoral fellow in the Institute at Brown for the Study of Environment and Society (IBES). Although she has worked in African palaeoecology for many years, her work focuses on using palaeo-ecological and palaeo-climatic records to better understand and constrain future environmental change. She also has done numerous studies on modern systems in order to better characterize their context in the fossil record. Her website can be found at https://sarahivorypollen.wordpress.com/.

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