Global Ecology and Biogeography
A Journal of Macroecology

Niche expansion and temperature sensitivity of tropical African montane forests

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4   1   Niche expansion and temperature sensitivity of tropical African montane forests
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31   **Aim:** Climate and land-use change will have a dramatic impact on future ecosystems through alterations

32   to species ranges and community composition. To form conservation strategies, correlative species

33   distribution models are often created to assess individual species risks. These models are based on the

34   assumption of climatic equilibrium, such that the modern range is representative of the full range of

35   conditions under which species could thrive. However, the paleoecological record illustrates examples

36   of disequilibrium in species today, and recent studies suggest that many species could occur in much

37   broader climatic settings than previously thought.   Montane ecosystems are thought to be at

38   disproportionate risk due to temperature sensitivity and restricted geographic ranges. However, in the

39   Afrotropics, the paleoecological record observes montane forest taxa expanded into the lowlands

40   numerous times, suggesting a possible tolerance to warm temperatures.

41   **Location:** Africa

42   **Methods:** We integrate paleoecological and paleoclimatic data in order to compare climate conditions

43   in which species are currently found with those in the past. We use species distribution models to

44   construct potential modern ranges for afromontane species based on modern distributions and

45   distributions in the paleoecological record in order to evaluate equilibrium of species ranges.

46   **Results:** We show that many afromontane trees have occupied warmer climates in the past, which

47   suggests that current low-elevation boundaries are not set by climate. Interestingly, the species with

48   largest disequilibrium between paleo and modern distributions are those whose modern distributions

49   show the least temperature sensitivity. Mapping of species' potential ranges based on modern and

50   paleo-distributions clearly shows that suitable climate conditions exist today in the lowlands for less

51   temperature sensitive species.

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52   **Main Conclusions:** These results imply the current range of these forest trees does not necessarily

53   inform risk from climatic change, and that human land-use may be the major pressure for many species

54   in the future.

55   **Introduction**

56   Species distributions are determined by a wide range of factors of which climate is thought to play a

57   dominant role at large spatial scales. Global climate is currently changing at rates unprecedented in the

58   last 10,000 years (IPCC, 2013), which is likely to result in extinction or massive alteration to species

59   distributions. In order to develop successful conservation practices and assess risk, forecasts of species'

60   ranges, combining future climate change scenarios with species distribution models (SDMs), are being

61   developed. These statistical models are commonly used with modern distributions of organisms to

62   estimate climatic sensitivities (Pearce and Ferrier, 2000; Guisan and Thuiller, 2005; Elith and Leathwick,

63   2009).

64   Despite their potential usefulness, SDMs assume that a species' geographic range fully represents its

65   climate tolerances ('climate equilibrium'). However, a species might only occur in a restricted set of

66   those conditions, the 'realized climatic niche', due to limitations from the non-climatic environment and

67   biotic interactions, creating a climate disequilibrium. It has been suggested that equilibrium is the norm

68   in terrestrial plants (Petitpierre et al., 2012). Recent work, however, suggests that many species'

69   apparent climatic tolerances within their native range are much different than those within invasive or

70   naturalized ranges. This is particularly true for species that occupy a narrow set of conditions in their

71   native range (Early and Sax, 2014). Furthermore, evidence from fossil pollen from North America and

72   Europe suggests that through time many species occupied different climate spaces (Veloz et al., 2012;

73   Maiorano et al., 2013).   The potential for climatic disequilibrium poses a problem for developing SDMs

74   and forecasting changes in species' distributions. In particular, forecasts for species that can thrive in

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75   climatic conditions much different from those where they are found today are likely to overestimate

76   risks that occur directly from climate change and ignore other processes that are important for

77   constraining current ranges (Sax et al., 2013).

78   Assumptions regarding climate equilibrium could be particularly problematic for forecasting

79   extinction risks for species that occupy tropical montane forests. These species are thought to be

80   limited by warm temperatures, preventing them from inhabiting and dispersing through warm lowland

81   environments (Bates et al., 2008). Thus, the prevailing paradigm surrounding the fate of such isolated,

82   "sky-island" populations is that species will undergo range contraction under rising temperatures.

83   Inability to migrate anywhere except upwards is then feared to lead to progressively decreasing ranges

84   and eventual mountaintop extinction (Colwell et al., 2008; Dullinger et al., 2012; Gottfried et al., 2012).

85   However, there is a profound knowledge gap about whether such species are currently in equilibrium

86   with climate or whether their ranges are controlled by non-climatic factors.

87   Afromontane forests are assumed to be in climatic equilibrium, as compositionally similar modern

88   assemblages occupy all highland areas with similar climatic conditions throughout tropical Africa (~10°N-

89   35°S; White, 1981; White, 1983). Despite this, evidence from paleoecological records stretching back

90   into the late Quaternary (~500ka) suggest that some of these tree species were once widely expansive in

91   the lowlands during periods when temperatures were warmer than today (Dupont et al., 2000; Ivory,

92   2013). This suggestion of shifts in occupied climate space through time makes this region an ideal

93   laboratory for testing climatic equilibrium of montane forests. Further, these iconic tropical forests are

94   considered a biodiversity hotspot currently threatened by climate change as well as pressure from dense

95   human populations (Myers et al., 2000). Ultimately the fate of these forests has important implications

96   not just for plant biodiversity, but also for large charismatic mammals, like the mountain gorilla, as these

97   forests house the highest vertebrate species diversity in Africa (WWF, 2014).

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98   In order to test climate tolerances and equilibrium, we investigated the climate space occupied

99   by species within their modern native ranges and compared this with past ranges from paleoecological

100   records. Unlike similar studies which use paleoclimate simulations for past climate data, organic

101   geochemical records, which take advantage of relationship between temperature and the chemical

102   structure of bacterial membrane lipids, provide independent temperature reconstructions. These

103   records can be used to validate temperature changes generated by climate models at the sites used in

104   this study to represent past species' occurrences. Furthermore, in this study we use modern pollen

105   samples to inform our use of fossil pollen samples, providing an important context for our work. Our

106   results shed light on why species exhibit varying degrees of equilibrium with modern climate and the

107   role of non-climatic factors for determining ranges.

108   **Methods**

109   We consider several tree species which are common in afromontane forests and in

110   paleoecological records from across the region. *Prunus africana* and *Podocarpus latifolius* are tall trees

111   (>15m) that occur from 1200-2300m asl in afromontane rainforest habitats. *Nuxia congesta, Nuxia*

112   *floribunda, Ilex mitis, Olea africana*, and *Olea capensis* frequently occur in the mid-altitudes from 1500-

113   2700m asl on wetter slopes. Above this zone and to the tree line (~3500m asl) is characterized by

114   forests dominated by *Juniperus procera* sometimes in conjunction with *Podocarpus falcatus* or *Hagenia*

115   *abyssinica* (White, 1981; Appendix S1 in Supporting Information).

116   Tree species were selected based on availability of large numbers of modern occurrences as well

117   as reliable identification within the pollen records. As the afromontane region is particularly

118   undersampled (Küper et al., 2006), many endemics were not evaluated due to lack of field and

119   herbarium occurrence records. Although two species of *Nuxia* spp. and *Podocarpus* spp. occur within

120   the region (*Nuxia congesta* and *Nuxia floribunda; Podocarpus falcatus* and *Podocarpus latifolius*), due to

121   morphological similarity of the pollen grains, genus level identification is the highest taxonomic

122   resolution within the paleo-records; thus, here we combine modern records for the two species of each

123   genus (Vincens et al. 2007).

124   We focused our analyses on two data-rich periods in the paleoecological record: the mid-

125   Holocene (MH; 6ka), and Last Glacial Maximum (LGM; 21ka).   Modern occurrence records from

126   observational datasets were collected from the Global Biodiversity Information Facility (GBIF;

127   www.gbif.org). Both modern and paleoecological occurrence records from pollen data were taken from

128   the African Pollen Database, converted to relative abundances then assessed for presence or absence of

129   our studied species (APD; http://fpd.sedoo.fr/fpd/; Vincens et al., 2007; Appendix S1 and S4 in

130   Supporting Information). All occurrences were taken from both data sources for all of sub-Saharan

131   Africa, which is the background region for this study. All occurrences were quality controlled for

132   georeferencing errors, and only observations occurring within the modern climate period (1950-2000)

133   were kept. As some species used in this analysis have long pollen dispersal distances (>100km), we used

134   studies of pollen transport to set a threshold value of abundance that indicates the presence of a

135   species within area defined by the grid used for our climate data (~18km; *Podocarpus* spp [>5%]*,*

136   *Juniperus* spp [>1%]*, Olea* spp. [>1%]); Vincens, 1982; Vincens et al., 2006).

137   All climate data from the present day (1950-2000) and NCAR CCSM4 (Gent et al., 2011) model

138   output for the mid-Holocene (MH; 6ka) and Last Glacial Maximum (LGM; 21ka) were taken from the

139   Worldclim database and validated against paleoclimate records (www.worldclim.org; Hijmans et al.,

140   2005; Appendix S1 in Supporting Information). All climate data were bioclimatic variables downscaled

141   to a 10 arc minute grid. Data from 30 weather stations in the area were used to verify the downscaled

142   gridded climate data. Residuals of station measurements from the gridded climate data were all within

143   one standard deviation of the station time series for the period 1950-2000. We selected four climatic

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144   variables for this study: mean annual temperature, mean annual precipitation, diurnal temperature

145   range, and rainfall seasonality.   The selection of these variables was based on a principal components

146   analyses (PCA) to best characterize climatic gradients across the afromontane region as well as

147   documented sensitivity of some species (Appendix S1 in Supporting Information; White, 1981; Hamilton

148   and Taylor, 1992; Hedberg, 1969). In this PCA, the first three principal components explained 65% of the

149   variance in climate within the Afromontane region. Mean annual precipitation (-0.25) and mean annual

150   temperature (0.3) loaded most strongly on the first PC, rainfall seasonality (-0.3) loaded most strongly

151   on the second PC, and diurnal temperature (-0.5) loaded most strongly on the third PC.

152   We calculated expansion from the modern to the past of the realized climatic niche over time in

153   order to evaluate species equilibrium with modern climate.   High climatic niche expansion means that a

154   species occupied climatic conditions in the past that it does not currently occupy, suggesting that the

155   species is not in equilibrium with modern climate. Niche expansion was calculated using a kernel

156   smoother method developed by Broennimann et al. (2012) and used for evaluation of native to

157   naturalized range shifts by Petitpierre et al. (2012) and Early and Sax (2014). This method calibrates a

158   PCA of the total pooled climate space for the entire study area across all time periods being compared.

159   Based on the first two components of the PCA, a 100x100 cell gridded climate space is created to

160   represent all climatic conditions over the periods being compared. Species densities are then projected

161   for each cell on the gridded climate space using a kernel density function. Niche expansion from the

162   modern to the past is then equal to the proportion of the density of paleo-distribution which falls

163   outside of grid cells occupied by the modern distribution. We compared the modern to MH and modern

164   to LGM occurrences separately, then compared the modern occurrences to occurrences in both paleo-

165   periods combined. Values of expansion can range from zero (indicating that climate conditions in the

166   past are identical to or are a subset of the climate space occupied today) to 100 (no overlap of the

167   climate occupied by the past and modern distributions).

168   Also in order to verify representivity of the pollen data in the past of species ranges, we used the

169   niche expansion method to check whether modern pollen data represents the species' current

170   geographic distributions (Appendix S1 and S5 in Supporting Information). We calculated expansion

171   between modern pollen data and modern GBIF data. This is necessary validation step, as pollen may be

172   transported over long distances. Modern pollen and GBIF data give very similar values, suggesting that

173   together these data represent species' actual distribution well; however, climate space based on GBIF

174   data is bigger than for pollen for all studied species, suggesting that the pollen record is conservative

175   with respect to GBIF.

176   Additionally, in order to see if climate space occupied in the past is available but unoccupied

177   today, we created SDMs that estimate all potentially suitable area, the potential range. This approach

178   allowed us to evaluate how much estimates of the species' modern potential geographic ranges are

179   influenced by addition of the paleoecological data. We initially constructed SDMs using all regression

180   and machine learning algorthims in BIOMOD2 in R (Thuiller et al., 2009). However, results using the

181   generalized linear model algorithm (GLM) minimized the occurrence of false presences, creating the

182   most reliable models for all species. Thus only SDMs based on GLMs will be presented in this paper.

183   SDMs for each species were created based on two different datasets: (1) the modern distributions

184   alone, and (2) the pooled modern and paleo- distributions. Due to the lack of true absences in this

185   dataset, pseudo-absences were selected to define background climate. This was conducted by random

186   selection of points (8 times the number of presences for each species) from within a geographic region

187   defined by a 400 km radius around modern presences. These parameters were selected to define the

188   background area following tests where the number of pseudo-absences and geographic extent were

189   varied (1 to 10 for number of pseudo-absences and 50 to 800 km radius for geographic extent). The

190   parameters selected maximized predictive ability and correct assessment of presences and absences

191   from the area under the receiver operating curve (AUC) statistic. We employed k-fold cross-validation,

192   in which the occurrence data were split into training and testing datasets 3 times (70:30% split). The

193   final model used all occurrence data but was compared to the three training models. If the evaluation

194   statistics for the final model (AUC, sensitivity, specificity) were within 10% of the evaluation statistic

195   calculated for the testing dataset, the evaluation statistics used with the testing datasets are considered

196   representative of the final model.   We calculated sensitivity of each species to each climate variable

197   using a randomization technique in which a series of GLMs is run for each species leaving out one

198   climate variable at a time to quantify sensitivity of the models to that variable. The sensitivity to a

199   specific variable then is the reciprocal of the AUC when that variable is not included (1-AUC). Further

200   description of sample preparation and analysis can be found in Appendix S1 in Supporting Information.

201   **Results**

202   Niche expansion was calculated comparing the proportion of the occurrences in the

203   paleoecological record to modern occurrences. When species occurrences from both paleo-periods are

204   considered together and compared to the modern distribution, niche expansion ranges from 24%

205   (*Podocarpus* spp.) to 5.0% (*Ilex mitis*), with a mean expansion across all species of 16% (Table 1). When

206   MH occurrences are compared to modern occurrences, niche expansion ranges from 20% (*Olea*

207   *africana*/*Podocarpus* spp.) to 0.26% (Ilex mitis), with a mean of 12% across all species. When LGM

208   occurrences are compared to modern, niche expansion ranges from 29% (*Podocarpus* spp.) to 4.8%

209   (*Juniperus procera*), with a mean of 21%.

210   During training of the SDMs, species sensitivity to individual climate variables was determined

211   via a leave-one-out randomization process (Table 2). These values range from 0 to 1, indicating no

212   sensitivity and complete sensitivity, respectively. All species showed highest sensitivity to mean annual

213   temperature. However, sensitivity ranges from 0.48 (*Olea africana*) to 0.94 (*Juniperus procera*).

214   The size of the potential range for each species was evaluated using modern only occurrences

215   and compared to pooled modern occurrences and occurrences in the paleoecological record. The

216   proportion of the increase in potential range size when the paleoecological data are included was

217   calculated (Table 3). This potential range increase under modern climate conditions varied greatly, with

218   some species showing almost no increase (*Hagenia abyssinica* – 1.1%) while others showed increases of

219   potential range of up to 52% (*Olea capensis*).

220   **Discussion**

221   *Niche Expansion and Temperature Sensitivity*

222   Although it has been known for decades that wide-spread changes in afromontane forest

223   geographic distribution have occurred over the late Quaternary and Holocene, we show that most

224   species also occupied widely different climatic space in the past than today (White, 1981; Hamilton and

225   Taylor, 1992; Dupont et al., 2000; Ivory, 2013). In general, all eight species occur today in regions with

226   relatively cool mean annual temperatures, low rainfall seasonality, and moderate diurnal temperature

227   variability, relative to the full range of climate conditions in sub-Saharan Africa (Figures 1 and 2).

228   Despite the similarity between the modern climate space occupied by the eight species studied here,

229   each species occupied at least some climate space in the past that differs from today (Table 1). These

230   trees exhibit some degree of climate disequilibrium in their modern native ranges, but there is

231   considerable variation in the degree of niche expansion among species (Table 1). The large amount of

232   expansion through time for species such as *Olea africana and Podocarpus* spp*.* implies that some

233   afromontane trees' climatic niches may be much broader than previously thought.

234   Climate models have increased in accuracy over the last decade and many climate variables

235   have been shown to be quite accurate, in particular mean annual temperature. Despite great

236   improvement, some of the variability in climate space observed using paleoclimatic simulations may

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237   result from model error. However, we have confidence in our results for two reasons. First, CCSM4 has

238   been used in other similar studies evaluating climate space through time (Veloz et al., 2012) and been

239   found reproduce with some fidelity major climatic features and in particular surface air temperature,

240   which is the most sensitive variable for all species. Second, paleoclimate reconstructions based on

241   organic geochemical proxies were used to evaluate the paleoclimate simulations (Appendix S1 in

242   Supporting Information). Although only reconstructions for mean annual temperature and mean annual

243   precipitation were available, the simulated variables from CCSM4 fell within error of the reconstructions

244   for most sites, in particular for the LGM where much of the evidence for increased niche expansion

245   occurs. Uncertainty of the paleo-temperature reconstructions is about +/- 2°C and combines error from

246   instrumental precision as well as calibration error (Loomis et al., 2012). We found that model simulated

247   LGM temperatures were within instrumental and calibration error of the temperature reconstructions

248   from paleoclimate data for sites in the highlands and lowlands. For the MH, model simulated

249   temperatures were within error for sites in the lower altitudes, but frequently underestimated

250   temperatures by 1-3°C above 1000 m asl. Underestimation of MH temperatures means that species

251   distributions will underestimate the temperatures occupied in that period, and niche expansion values

252   will be minimum values.

253   Additionally, as the number of modern records used in this analysis is greater than the number

254   of paleo-records, this suggests that paleo-distributions may be undersampled (Appendix S4 in

255   Supporting Information). In fact, there is a marginally significant positive correlation between number

256   of paleo-samples and the amount of niche expansion (MH: R^2 = 0.47; p = 0.058; LGM: R^2 = 0.51; p = 0.10;

257   Appendix S3 in Supporting Information). This implies that our estimates of niche expansion are

258   conservative, and that further sampling of the paleoecological record would likely indicate even greater

259   disequilibrium.

260   Our data show that temperature sensitivity is not equal among afromontane trees.

261 Interestingly, temperature sensitivity varies even among tree species that form well-established

262 communities. For example, upper montane forest stands are often co-dominated by *Juniperus procera*,

263 *Hagenia abyssinca*, and *Podocarpus falcatus* (Hamilton, 1975; Bussman, 2006). Yet *Podocarpus* spp.

264 appears to be much less sensitive to mean annual temperature and more sensitive to diurnal

265 temperature variability and rainfall seasonality than the other taxa (Table 2). This could imply that

266 community structure and composition of many forests with dominant species of varying sensitivities are

267 likely not fixed. This is supported by the paleoecological records which show individualistic responses of

268 species to climate, for example large expansions of *Podocarpus* into the lowlands prior to 100ka, and

269 therefore changing species associations through time (Dupont et al., 2000; Ivory, 2013).

270   The high degree of climatic disequilibrium in afromontane trees is quite remarkable as it has

271 generally been assumed that the regional homogeneity of these communities indicates equilibrium

272 (White, 1981; White, 1983; Hamilton and Taylor, 1992). As species show strong co-occurrence patterns,

273 it is assumed that the dominant forest tree species share similar climatic tolerances, in particular a high

274 sensitivity to temperature (Hedberg, 1969; White, 1981).   In fact, the assumption of high temperature

275 sensitivity was thought to be supported by paleoecological records, which frequently showed large-scale

276 afromontane expansion in cooler conditions during the LGM followed by a retreat to high elevations as

277 temperatures warmed at the late Pleistocene (Coetzee, 1964; Livingstone, 1975; van Zinderen Bakker,

278 1978; Hamilton, 1981). This led many to the conclusion that these trees were restricted to

279 discontinuous sky islands when the world is warm. In contrast, our results show that even during the

280 LGM, many afromontane trees occupied areas warmer than where they are found today (Figures 1 and

281 2).

282   Additionally, the few paleoecological records of vegetation biogeography that extend beyond

283 the LGM support our results. Pollen analyses of marine cores offshore from West and East Africa, as

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284   well as a sediment core from Lake Malawi, show large-scale afromontane expansion into the lowlands

285   repeatedly during the late Pleistocene (Dupont et al., 2000; Dupont et al., 2011; Ivory, 2013). These

286   data indicate that during the Last Interglacial (130-115ka), when temperatures were at least as warm as

287   today, lowland forests consisted of very different species than today (Cohen et al., 2007; Scholz et al.,

288   2007; Beuning et al., 2011). For example, *Podocarpus* spp. and *Olea* spp. were common in the lowlands,

289   but today are restricted to cool mountains. This is concordant with our findings that these two species

290   are not in equilibrium with modern climate.

291   Finally, our results suggest that greater temperature sensitivity leads to greater climatic niche

292   conservatism through time. There were significant negative correlations between species' mean annual

293   temperature sensitivity and niche expansion in the MH, LGM, and both paleo-periods combined (MH: R^2

294   = 0.6933; p = 0.011; LGM: R^2 = 0.5405; p = 0.091; Combined: R^2 = .6374; p = 0.015; Figure 4). The slopes

295   of these correlations are not significantly different (t = 0.58; p=0.57), and this relationship is the same

296   for the MH and LGM, suggesting that it is not an artifact of solely a warmer or cooler global climate.

297   Our results suggests that although not all montane taxa are temperature sensitive, those that

298   are will be less likely to cope with warming temperatures and more likely show a retreat of their lower

299   range limits upslope. As this relationship is robust across all time periods studied, it may provide a useful

300   tool for assessing the quality of SDMs, when no independent data exist to test them.   Also, it provides a

301   hypothesis that could be tested for generality in other biogeographic regions to evaluate the true

302   climatic tolerances of species which may be at risk in the future.

Non-climatic limitations on the modern potential range

304   Including paleoecological occurrences in SDMs increased potential range estimates of most

305   species against those based solely on modern distributions. This suggests that many species have not

306   only occupied much different geographic and climatic spaces through time but are currently

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307   geographically restricted by non-climatic factors. The magnitude of this mismatch varied strongly

308   among species (Table 3; 0-52%). There is a significant positive correlation between the increase in

309   potential range size and magnitude of past niche expansion (R^2 = 0.68; p = 0.012; Figure 4). The negative

310   relationship between niche expansion and temperature sensitivity suggests that the species whose

311   current distributions are most limited by non-climatic factors are those that are least temperature

312   sensitive.

313   Important non-climatic factors that limit these species distributions could include land-use,

314   dispersal barriers like complex topography and large inland lakes, and biotic interactions. Recent

315   increases in historical land-use in the lowlands may be particularly important. Our data indicate that

316   *Podocarpus* spp., *Olea africana*, and *Olea capensis* could occur today in many of the lowland areas of

317   East Africa which are also the areas affected by land-use change. Forest conversion to agricultural lands

318   as well as pressure for non-timber forest product harvest are likely greatest on the lower slopes of the

319   mountains where people live. Some work suggests that large-scale conversion of natural lands may

320   have begun as early as the mid-Holocene (4800 yr BP), whereas, other studies suggest that impacts on

321   forest were highest less than 3000 yr BP following the introduction of Iron Age smelting due to pressure

322   for charcoal harvesting (Hamilton et al., 1986; Mumbi et al., 2008; Hall et al., 2009). As our analysis

323   focuses on periods that pre-date large-scale land-use, human landscape alteration is a strong candidate

324   for being one of the major non-climatic factors limiting species' current geographic ranges.

325   *Afromontane biogeography and conservation*

326   The potential geographic ranges for less temperature sensitive species indicate continuous

327   lowland corridors that are climatically suitable today for occupation of afromontane taxa (Figure 4). This

328   region stretches for thousands of kilometers across the Afrotropics, yet is strikingly discontinuous

329   (White, 1981; White, 1983; Hamilton and Taylor, 1992). Many have speculated that the founding of

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330   these populations, and in particular the high levels of endemism, is related to long-term climate stability

331   in the highlands and expansion into the lowlands during relatively cold periods (Quaternary glacial

332   periods; White, 1981; White, 1983; Hamilton and Taylor, 1992). Our results suggest that a cold climate

333   dispersal pathway during glacial periods is not necessary, as climates similar to or warmer than today

334   could allow for lowland dispersal. Although modern populations are separated by great distances today,

335   dispersal of populations in the lowlands may have occurred repeatedly over the last few hundred

336   thousand years, including as recently as 6000 years ago.

337   It is clear from paleoecological studies throughout the world that some past climates no longer

338   exist today, leading to no-analog species assemblages (Williams et al., 2001; Williams and Jackson,

339   2007). This phenomenon has been observed in North America and Europe during the late Pleistocene

340   but rarely been evaluated in Africa (Veloz et al., 2012; Maiorano et al., 2013). Although, species with the

341   highest expansion did seem to occupy some past climate spaces that don't exist today, the majority of

342   occurrences observed in the paleoecological record occur in climates that do exist today (Figures 1 and

343   2; Appendix S2 in Supporting Information). Thus no-analog climates are not necessary for large

344   disequilibrium over time. Additionally, the model simulations used here to represent past climate seem

345   to indicate that very little no-analog climate occurred in Africa over the time periods evaluated in this

346   study (Figures 1 and 2). This suggests that although availability of novel climates results in some range

347   shifts, other range-limiting factors must also be at play.

348   In contrast to the prevailing paradigm that these species are restricted to high elevations due

349   long-term climate stability and a high temperature sensitivity (Hedberg, 1969; White, 1981), our results

350   instead suggest that even within communities, environmental sensitivity, particularly to temperature, is

351   quite variable. For example, in the upper montane forest, stands co-dominated by *Juniperus procera*,

352   *Hagenia abyssinca*, and *Podocarpus falcatus* are common (Hamilton, 1975; Bussman, 2006). However,

353   despite the close modern association of these species, *Podocarpus* spp. appears to be much less

354   sensitive to mean annual temperature and more sensitive to diurnal temperature variability and rainfall

355   seasonality (Table 2). This implies that forest community structure and composition are likely very

356   recent and will not be conserved through time. Although conservation efforts within the native range of

357   afromontane forest have the potential for success in the face of rising temperatures, this will vary from

358   species to species. Furthermore, conservation at the landscape-scale of community composition and

359   ecosystem function in these regions may not be realistic given evidence of differential tolerances to

360   warm temperatures.

361   **Conclusions**

362   We show that many important tree species that dominate communities in the tropical African

363   highlands are not currently in climatic equilibrium. Furthermore, despite the long-standing paradigm

364   that afromontane forest species have similar high sensitivities to warm temperatures, many of these

365   species are much less sensitive to temperature than previously thought. Based on evidence from the

366   paleoecological record of the suitable climate space for afromontane trees, some of these species could

367   currently occupy extensive continuous ranges within the lowlands based on climate alone.

368   The differences in the environmental sensitivity among species have important implications for

369   the success of future conservation efforts. While certain species are very likely to respond to rising

370   temperatures by moving upslope, less temperature sensitive species are likely less threatened by

371   increasing temperatures alone. This conclusion could be tempered, however, if strong local adaptation

372   of populations existed in the past, in which case warm-adapted populations might have been lost

373   following their disappearance from the lowlands. Further experimental work of these species to

374   environmental stress may be needed to fully understand this possibility. Furthermore, the most

375   temperature sensitive species we evaluated are important endemic taxa, such as *Hagenia abysinica* and

376   *Prunus africana*. Compositional changes and loss of endemics within the forest are possible due to

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377   differences in temperature sensitivity unless we are greatly underestimating the true capacity of these

378   species due to undersampling of the paleoecological record. Further pollen analysis may indicate new

379   areas available to important species in the past and allow us to better assess the effect of sample size on

380   niche expansion in the past. Finally, although our results suggest that several afromontane trees will not

381   be directly negatively affected by climate warming, increasingly dense human populations may have a

382   non-trivial effect on forest composition even within protected areas.

383   **Acknowledgements**

387   **List of titles in supplementary material**

388   *Appendix S1.* Supplementary Methods

389   *Appendix S2.* Kernel density niche expansion plots for all 8 species.

390   *Appendix S3.* Correlation of fossil sample number and niche expansion.

391   *Appendix S4.* Number of species occurrences for each time period.

392   *Appendix S5.* Niche expansion of GBIF occurrences as a percentage of the shared environmental space

393   with pollen occurrences.

394   **Biosketch**

395   Sarah Ivory is a postdoctoral fellow in the Institute at at Brown for the Study of Environment and Society

396   (IBES). Although she has worked in African paleoecology for many years, her work focuses on using

397   paleoecological and paleoclimatic records to better understand and constrain future environmental

398   change. She also has done numerous studies on modern systems in order to better characterize their

399   context in the fossil record. Her website can be found at https://sarahivorypollen.wordpress.com/.

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528   **Tables**

Table 1. Niche expansion of mid-Holocene (MH) to modern, Last Glacial Maximum (LGM) to modern, and all pooled paleoecological data (All Paleo-Data) to modern as a percentage of paleoecological record outside of modern climate. NA indicates insufficient records to perform analysis.

	MH	LGM	All Paleo-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

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Table 2. Sensitivity of each species to climate variables used in species distribution models based on randomization. Higher values equal more sensitivity. MAT= mean annual temperature, Diurnal Temp. = diurnal temperature, MAP = mean annual precipitation, Seasonality = rainfall seasonality.

	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

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Table 3. Percent potential range increase with inclusion of the paleoecological data.

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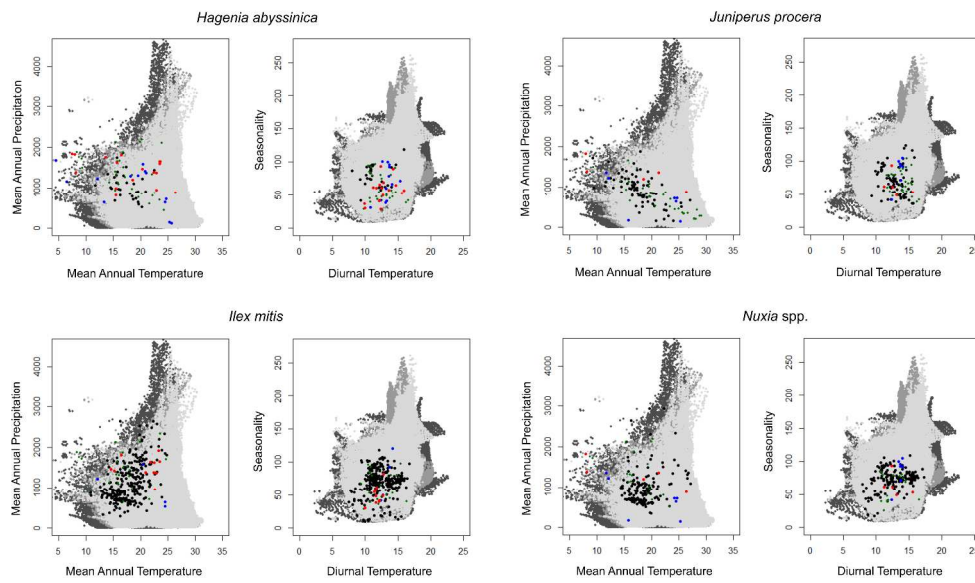|	Range Increase
Hagenia abyssinica	1.1
Ilex mitis	1.4
Juniperus procera	19
Nuxia spp.	22
Olea africana	20
Olea capensis	52
Podocarpus spp.	45
Prunus africana	14

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Figure Legends

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

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

544 Figure 3. Correlation of sensitivity of afromontane trees to mean annual temperature (from Table 2)
545 with respect to niche expansion (from Table 1). This was conducted comparing mid-Holocene (MH) to
546 modern in red, Last Glacial Maximum to modern in blue, and by pooling all paleoecological data
547 compared to modern in black. Linear regression formulas are pictured to the side of each line with R^2
548 for correlation of two variables.

549 Figure 4. Potential range reconstructions under modern climate from species distribution models based
550 on modern distribution alone (yellow) and based on their modern and paleo distributions combined
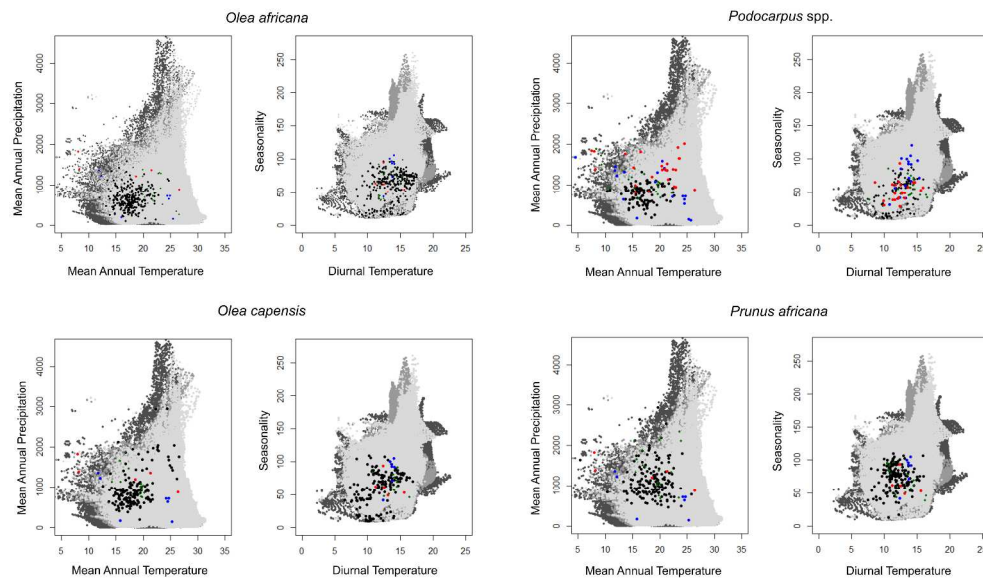551 (blue).

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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 - red), and Last Glacial Maximum (LGM - blue) for important environmental variables used in this analysis.
606x359mm (300 x 300 DPI)

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 - red), and Last Glacial Maximum (LGM - blue) for important environmental variables used in this analysis.
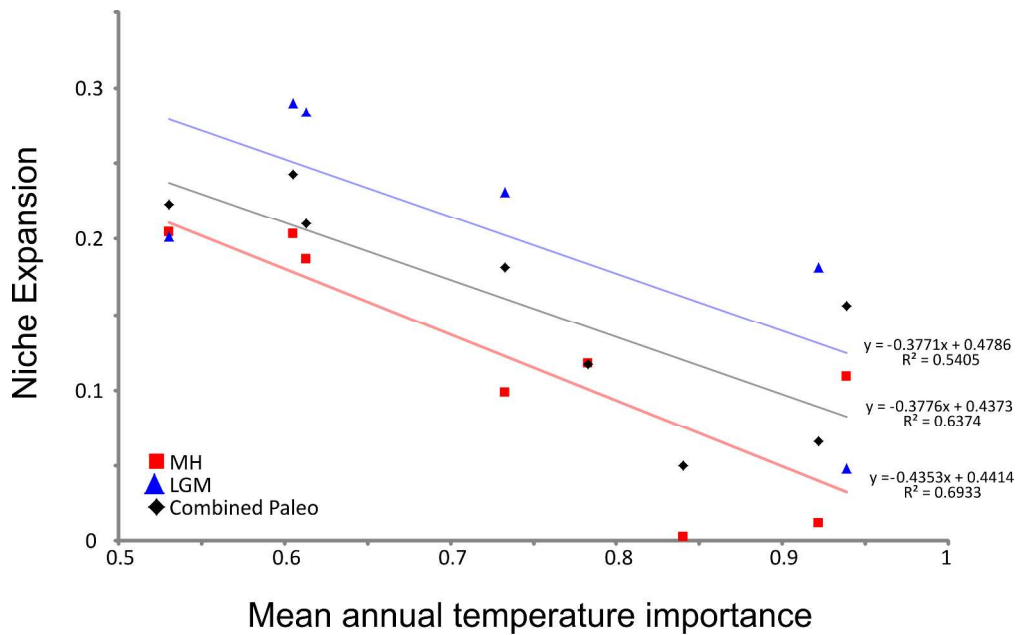607x361mm (300 x 300 DPI)

Figure 2. Correlation of sensitivity of afromontane trees to mean annual temperature (from Table 3) with respect to niche expansion (from Table 1). This was conducted comparing mid-Holocene (MH) to modern in red, Last Glacial Maximum to modern in blue, and by pooling all paleoecological data compared to modern in black. Linear regression formulas are pictured to the side of each line with R2 for correlation of two variables.
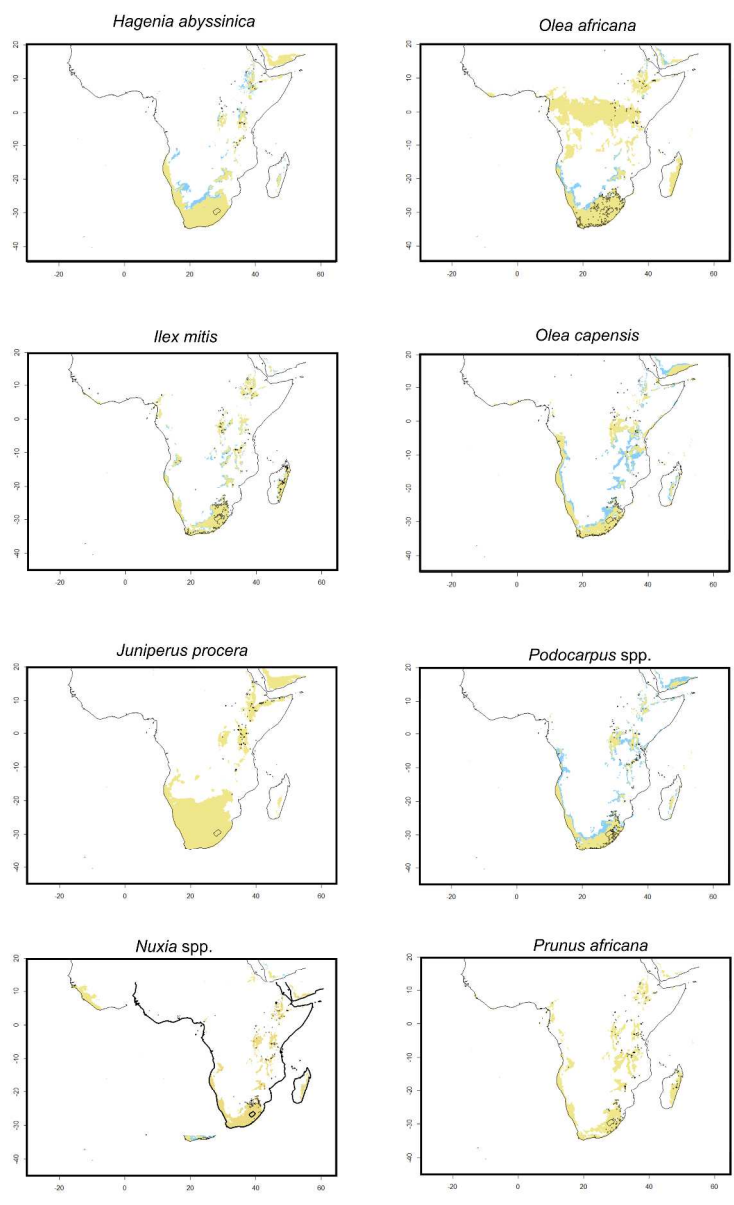375x233mm (300 x 300 DPI)

Figure 3. Potential range reconstructions under modern climate from species distribution models based on modern distribution alone (yellow) and based on their modern and paleo distributions combined (blue).
415x618mm (300 x 300 DPI)

Appendix S1. Supplementary Methods

Climate model accuracy

These climate reconstruction studies were used to validate paleoclimate model out: Powers, 2005; Tierney et al., 2008; Weijers et al., 2007; Berke et al., 2012; Loomis et al., 2012; Loomis et al., 2015

Fossil pollen sample number and niche expansion

A marginally significant positive correlation exists between the number of fossil pollen samples used for each time period for each species and the niche expansion value (MH: $R^2 = 0.47$; $p = 0.058$; LGM: $R^2 = 0.51$; $p = 0.10$; Appendix S1 and S4). These correlations coefficients suggest that almost half of the variance in the niche expansion is explained by the number of fossil pollen samples. Although this indicates some undersampling of the paleo-climate space and minimum estimates of niche expansion for all species, it does not conflict with the interpretation of higher temperature sensitivity leading to less niche expansion. We argue that as temperature sensitivity is calculated without the fossil pollen samples, it is therefore independent of fossil sample number and not causing the relationship with niche expansion. Furthermore, the link made in the manuscript between temperature sensitivity and niche expansion is significant for both time periods and explains much more of the variance (MH: $R^2 = 0.6933$; $p = 0.011$; LGM: $R^2 = 0.5405$; $p = 0.091$; Combined: $R^2 = .6374$; $p = 0.015$; Appendix S3).

Modern pollen to GBIF

We used the niche expansion method to check whether modern pollen data represents the species' current geographic distributions (Appendix 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. Therefore low abundance of a species within a sample may not indicate that a species is actually present within a grid cell, but rather that it occurs in a distant grid cell from which pollen transport has occurred.

Modern pollen and GBIF data give very similar values, suggesting that together these data represent

species' actual distribution well. In all cases the niches represented by the GBIF data are larger than the

pollen data; however, almost all species have very high overlap between modern pollen and GBIF data

(expansion <20%; GBIF data suggest a slightly larger climatic niche than pollen data; Appendix S5). Only

a single species has a niche expansion of greater than 20%. This species, *Hagenia abyssinica,* also has

the lowest number of occurrence records from GBIF (66 occurrences), suggesting that the difference in

pollen- and GBIF-defined environmental space may result from under-recording in the available GBIF

data. This suggests that by adding the modern pollen data, we can correct for the undersampling in the

GBIF dataset to some degree. The low expansion for all other species not only suggests that the pollen

data is representative of the modern vegetation, but also that the GBIF sampling rate is high enough to

accurately represent the climate spaces of these species. Furthermore, the fact that the GBIF data

reconstructs a larger climatic niche than the pollen data, suggests that the niche expansion values when

comparing modern to the past are minimum values.

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Appendix S2. Kernel density niche expansion plots for all 8 species.
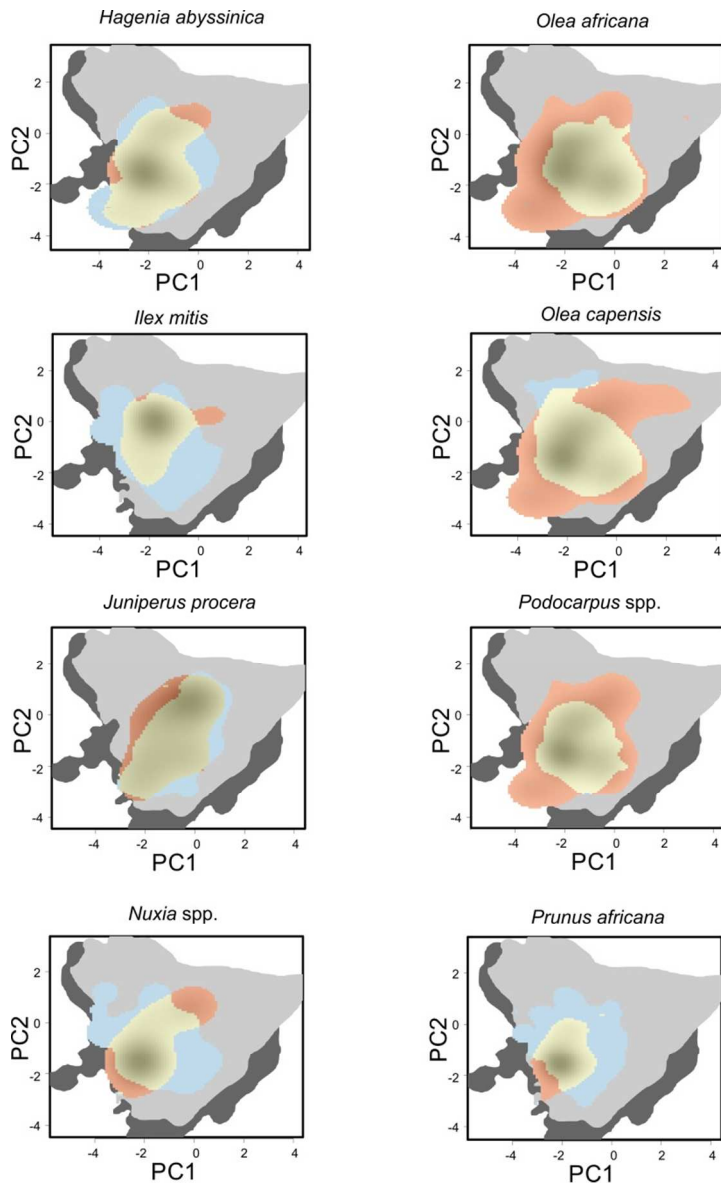
Appendix S2. Kernel density PCA comparing modern climate (light grey) to paleo-climate (dark grey) and suitable climate occupied by each species today (blue), in the combined paleo-periods (brown), and overlapping climate space (yellow).

Appendix S3. Correlation of fossil sample number and niche expansion.
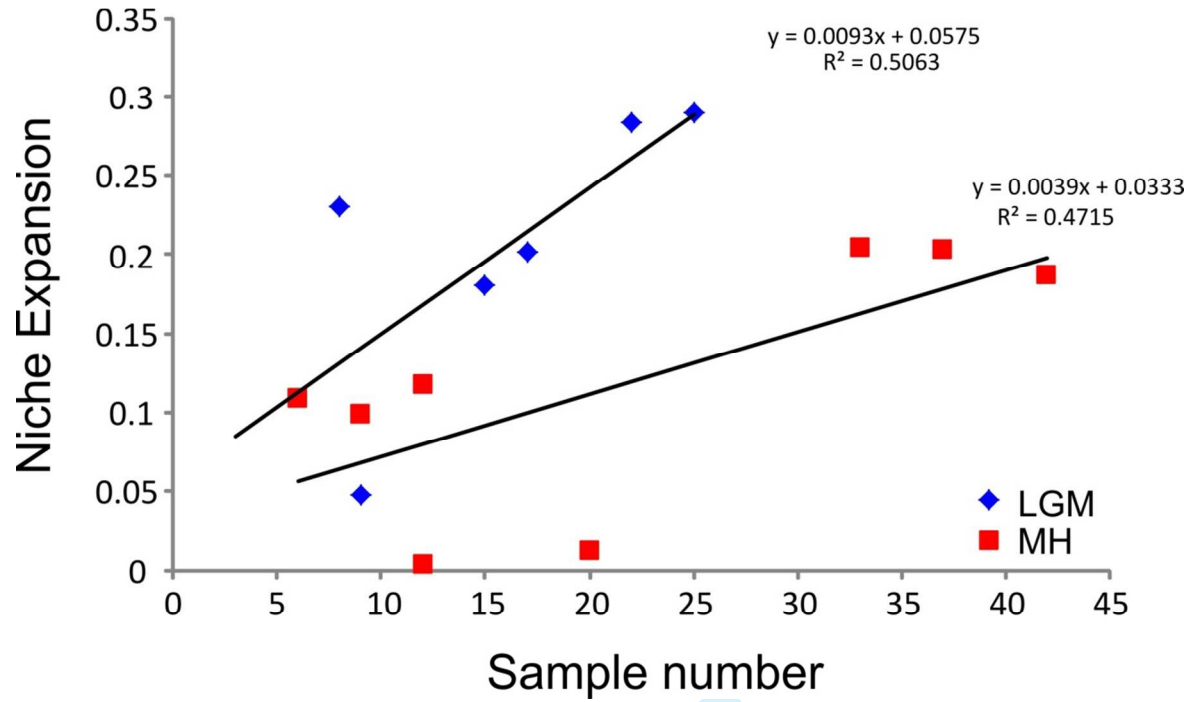
Appendix S3. Correlation of fossil sample number for MH (red) and LGM (blue) and niche expansion

each respective period to modern.

Appendix S4. Number of species occurrences for each time period.

Number of species occurrences for each time period. (MH = Mid-Holocene, LGM = Last Glacial Maximum)

	GBIF	Modern Pollen	MH	LGM
Hagenia abyssinica	66	200	20	15
Ilex mitis	684	55	12	4
Juniperus procera	147	104	6	9
Nuxia spp.	680	56	9	8
Olea africana	632	108	33	17
Olea capensis	382	141	42	22
Podocarpus spp.	804	196	37	25
Prunus africana	295	43	12	3

Appendix S5. Niche expansion of GBIF occurrences as a percentage of the shared environmental space

with pollen occurrences.

Niche expansion of GBIF occurrences as a
percentage of the shared environmental
space with pollen occurrences.

	Expansion
Hagenia abyssinica	34
Ilex mitis	4.5
Juniperus procera	16
Nuxia spp.	0.54
Olea africana	14
Olea capensis	0
Podocarpus spp.	14
Prunus africana	3.7