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RESEARCH PAPER

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Broader niches revealed by fossil data do not reduce estimates of range loss and fragmentation of African montane trees

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Aim: The climate tolerances of many species are broader than those estimated from current native ranges. Indeed, the niches of some Afromontane trees are up to 50% larger after incorporation of fossil data. This expansion could reduce estimates of species' future range loss owing to climate change but also implies strong non-climatic limitations on species' current ranges. One such limitation is land use, which fossil data suggest influences Afromontane tree distribution, preventing these trees from occupying warmer conditions than they do currently. We aimed to assess the degree to which the broader climatic tolerances revealed by fossil data buffer projected range loss from climate and land use for Afromontane trees.

Location: Africa.

Time period: Last 21,000 years.

Major taxa studied: Afromontane trees.

Methods: We used species distribution models informed by both current and fossil distributions to project future ranges under climate and land-use projections.

Results: We found that projected range reductions are only slightly ameliorated by incorporation of fossil distributions, and these improvements diminish further under severe land-use or climate change scenarios. Taxa that are less impacted by climate are more impacted by intense land use. Depending on the severity of climate and land use, the geographical extent of Afromontane tree species' ranges will contract by 40–85%, and the trees will be completely lost from large portions of Africa. We projected that the surviving species' ranges will become increasingly fragmented.

Main conclusions: Maintaining Afromontane ecosystems will require mitigation of both climate and land-use change and protection of areas to optimize connectivity. Our findings caution that species with climate tolerances broader than their current range might not necessarily fare better under strong changes in climate or land use.

KEYWORDS

Afromontane, biogeography, niche, palaeoecology, range collapse, species distribution models, tropical climate, tropical forests

1 | INTRODUCTION

Climate change over the 21st century is expected to contribute to species extinctions and turnover (Peterson et al., 2002; Urban, 2015). These risks could be particularly pronounced for montane taxa, because high-elevation species could experience a complete loss of suitable climate conditions on the mountains where they occur (Peterson et al., 2002; Williams, Bolitho, & Fox, 2003). A principal tool for assessing these risks is to construct climatic species distribution models (SDMs), which use the climate conditions that species experience within their modern distributions to assess future potential distributions under climate change (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Lenoir & Svenning, 2015; Pearce & Ferrier, 2000; Urban, 2015). One limitation of this approach is that the realized niche that organisms occupy at present might represent only part of the climatic conditions they can tolerate, and other conditions might also be suitable for species persistence (Araujo & Pearson, 2005). Omitting currently unoccupied conditions that are climatically suitable will underestimate species' "climatic niches" and overestimate the risks posed by climate change. However, including these conditions is difficult because the differences between climatic tolerances and distributions are likely to be species specific and are generally unknown (Sax, Early, & Bellemare, 2013).

Recent work comparing species' native and non-native populations does suggest that some species' native ranges do not fully reflect their climate tolerances (e.g., Early & Sax, 2014; Gallagher, Beaumont, Hughes, & Leishman, 2010). In addition to non-native distribution data, there has been a strong call in the literature for increased use of fossil distribution and palaeoclimate data to improve measurements of species' climate niches (Botkin et al., 2007; Nogues-Bravo, 2009; Veloz et al., 2012). Maiorano et al. (2013) showed how realized niches change through time and that "building a niche" with fossil data altered current and future range projections. Nogues-Bravo et al. (2016) showed that the inclusion of fossil data in SDMs more accurately assessed conservation risk for plant genera and families in Europe and North America. Ivory, Early, Sax, and Russell (2016) used fossil data to show that some Afromontane trees previously occupied warmer conditions than in their current distributions. This is supported by palaeoecological studies which find that anthropogenic impacts since at least the Iron Age have progressively altered East African species' distributions through changing land-use and fire regimes (Hall, Burgess, Lovett, Mbilinyi, & Gereau, 2009).

Climate change and land use have long been appreciated as a dual threat to species persistence, particularly when anthropogenic activities block species range shifts (Barbet-Massin, Thuiller, & Jiguet, 2012; Feeley & Silman, 2010; Hansen et al., 2001). Some work suggests that future changes in land use might be particularly important to species distributions in the tropics (Jetz, Wilcove, & Dobson, 2007). Recent reviews and conceptual considerations of climate and land-use change have concluded that estimates of extinction risk should consider both factors, while acknowledging the challenge of considering dual risks that could interact in complex ways (De Chazal & Rounsevell, 2009; Oliver & Morecroft, 2014).

The Afromontane forest is an excellent example of a system where the interplay between future changes in land use and climate might be particularly important. This region is a globally unique biodiversity hotspot, characterized by a rich endemic flora and a distinctive set of tree species with broad geographical distributions (Ivory et al., 2016; Mittermeier, 2004; Plumptre et al., 2007; White, 1981). Afromontane forests occupy mountaintops across Africa, extending across the tropics and two temperate zones, from the southern Cape of South Africa to the Arabian Peninsula and from West Africa to Madagascar. It is becoming clear that even such extensive systems are at risk from climate change and land use in the future; however, the degree to which each will impact species ranges is currently unknown (Mittermeier, 2004; Niang et al., 2014). Indeed, given current climate conditions and estimated niche requirements, the potential range of certain species, such as *Olea africana*, could be as much as 50% larger than their current realized distributions (Ivory et al., 2016). This expanded tolerance could buffer these species from some extent of future warming. Likewise, the extensive distribution of Afromontane tree species and potential capacity to shift their ranges upslope could also buffer them from a warming climate. Alternatively, Afromontane ecosystems might be disproportionately at risk, because Africa is already one of the warmest places on Earth and is predicted to warm more dramatically than other tropical continents by the end of this century (Dullinger et al., 2012; Gottfried et al., 2012; Niang et al., 2014). Likewise, regional human populations are increasing rapidly (López-Carr et al., 2014), suggesting that land use is likely to intensify. The rate of land conversion is predicted to increase in Africa owing to rapid population growth and intensified agriculture, reducing available habitat and causing extensive disturbance to natural ecosystems (Feeley & Silman, 2010; Niang et al., 2014). If future human land use extends to higher elevations, this could further imperil the Afromontane ecosystem by reducing available habitat. Ultimately, Afromontane forests could provide an excellent system to investigate how species with (a) tolerance to warmer conditions than those currently experienced, (b) the capacity to move upslope, and (c) a broad geographical extent will fare in response to the dual threats posed by future changes in climate and land use.

Here, we use SDMs developed by Ivory et al. (2016) with current and fossil occurrences of eight Afromontane tree taxa to evaluate the risks posed by future changes in climate and land use. We examine low- and high-change scenarios for both climate change and land use to consider the role of these threats individually and together. We evaluate how the relative importance of each varies with the degree of change. We also evaluate the degree to which information on climate tolerances obtained from fossil data reduce range loss relative to predictions based on climate tolerances calculated solely from modern occurrences. We then ask whether the effect of fossil data on any future range loss predictions attenuates with increasing environmental change. Next, we examine whether the patterns observed can be understood better by considering projections in elevational shifts in distribution and changes in geographical extent of these taxa. Finally, we consider the long-term fate of this unique system.

2 | MATERIALS AND METHODS

Afromontane forest covers an area of 98,685 km^2 throughout tropical and southern Africa, beginning at an elevation of *c.* 1,500 m a.s.l. (Bussmann, 2006). Currently, this region is at great risk owing to intensifying land-use pressure from deforestation and agricultural expansion and for use of certain plants as non-timber forest products (Niang et al., 2014). Species distribution models for the eight focal taxa (*Hagenia abyssinica*, *Ilex mitis*, *Juniperus procera*, *Nuxia* spp., *O. africana*, *Olea capensis*, *Podocarpus* spp. and *Prunus africana*) were developed by Ivory et al. (2016), and the methods used are discussed extensively in that manuscript. Vegetation zones vary slightly from mountain to mountain and also by aspect but generally have montane forest or rainforest until *c*. 2,700 m a.s.l., a zone of bamboo until *c*. 3,000 m a.s.l., and are topped by an ericaceous forest or cloud forest until the tree line near 3,900 m a.s.l. (Bussmann, 2006; Hedberg, 1951; White, 1981). *Nuxia* spp. (Stilbaceae), *I. mitis* (Aquifoliaceae), *O. africana* (Oleaceae) and *O. capensis* (Oleaceae) often are found in the mid-elevations from 1,500 to 2,700 m a.s.l. on wetter slopes (Bussmann, 2006; White, 1981). *Prunus africana* (Rosaceae) is an endemic tree that can be found in Afromontane rainforest habitats from 1,500 to 2,300 m a.s.l. (Bussmann, 2006). *Podocarpus* spp. (Podocarpaceae) are the most characteristic tree of the region, and therefore different species can be found in association with other trees or in monodominant stands at many elevations >1,500 m a.s.l. (White, 1981). *Hagenia abyssinica* (Rosaceae) is a characteristic endemic tree occurring between 2,900 and 3,300 m a.s.l. and is a commonly used medicinal plant (Assefa, Glatzel, & Buchmann, 2010; Bussmann, 2006). Above this zone and up to the tree line at 3,500–3,900 m a.s.l., ericaceous forests commonly include *Juniperus procera* (Cupressaceae).

Species occurrence records were acquired from two sources. Observations of modern species occurrences were retrieved from the Global Biodiversity Information Facility (GBIF; www.gbif.org). Modern occurrences were supplemented by modern pollen datasets, which were taken from the African Pollen Database (APD; http://fpd.sedoo.fr/fpd/; Vincens, Lézine, Buchet, Lewden, & Thomas, 2007). Fossil pollen samples were also acquired from the APD and taken from two data-rich periods in the palaeoecological record, which were used by Ivory et al. (2016): the mid-Holocene (MH; 6 ka) and the Last Glacial Maximum (LGM; 21 ka). The taxonomic resolution of all pollen taxa matches the stated descriptions above, with six determined to species level and the remaining two to the genus level (*Nuxia* spp. and *Podocarpus* spp.). All pollen data were converted to relative abundances, then presence or absence of the taxa was determined based on the method developed by Ivory et al. (2016). This method used studies of pollen transport to set a threshold value of abundance that indicates the taxon presence within each climatic grid cell. Four climatic variables (gridded at 10′ resolution) were extracted from Worldclim (www.worldclim.org) to estimate modern and past distributions [mean annual temperature (MAT), mean annual precipitation (MAP), diurnal temperature range (Diurn) and rainfall seasonality (Seas; coefficient of variation)]. The gridded modern climate data were compared with weather station data and found to capture gradients in temperature and precipitation accurately (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Ivory et al., 2016).

For this study, future potential ranges were forecast using climate model output for the end of the century (2061–2080), which were downscaled to 10′ resolution as part of the Worldclim climate dataset (Supporting Information Figure S1; Hijmans et al., 2005) and projected using a Lambert azimuthal equal-area projection for analyses. Higher-resolution climate data were not used because Africa has relatively few weather stations that can be used to downscale climate data spatially, and such data, if used, would have had values with considerable uncertainty (Hijmans et al., 2005). Future climate conditions were predicted using an ensemble of output from the most recent Climate Model Intercomparison Project (CMIP5), integrating output from five climate models: NCAR CCSM4 (Gent et al., 2011), HadGEM2-ES (Collins et al., 2011), MIROC-ESM (Watanabe et al., 2010), IPSL-CM5A-LR (Dufresne et al., 2013) and NorESM1-*M* (Bentsen et al., 2013). We used representative concentration pathways (RCPs) 2.6 and 8.5 to forecast future ranges to evaluate the magnitude of climate change on ranges for each taxon (Supporting Information Figure S1). In 2061–2080, the average MAT at occurrence locations will be 1.4 ± 0.7°C warmer under RCP 2.6 and 3.4 ± 1.1°C warmer under RCP 8.5 (Supporting Information Table S1). All principal analyses in the manuscript used the ensemble model (Supporting Information Table S1). However, we also ran a secondary set of analyses using only output from HadGEM2, which predicts the largest increase in MAT (+4.6°C) and provides a "worst-case scenario" for climate change. Furthermore, to evaluate the impact of extrapolation to no-analogue climate conditions in the future for our taxa of interest, we used the MESS package in R to illustrate that climate forecast under RCP 8.5 has analogous climate in the Afromontane region today, avoiding extrapolation (Elith, Kearney, & Phillips, 2010; Supporting Information Figure S2).

To project the future potential range for each taxon, SDMs were constructed using all regression and machine learning algorithms in BIOMOD2 using R (R Core Team, 2017; Thuiller, Lafourcade, Engler, & Araújo, 2009). We used an area under the receiver operating curve (AUC) threshold of >0.80 to define the best-performing models and constructed a total consensus ensemble of these models. The AUC, a common SDM assessment tool, is a metric of the true number of presences as a function of the number of false positives. These values are presented in the Supporting Information (Table S5), and there is no significant difference between AUC values based on modern-only versus modern and palaeoecological occurrences ($t = -0.803$, $p = 0.4356$). Previous studies have illustrated the application of ensemble forecasts in relationship to individual models (Araújo & New, 2007). To compare the influence of including palaeoecological data in future range projections, we created two sets of SDM ensembles for each taxon: (a) SDMs trained on the modern-only occurrences, and (b) SDMs trained on the modern and palaeoecological occurrences combined. Owing to the lack of information about species' true absences, pseudo-absences (eight times the number of occurrences) were randomly selected from a 400-km radius around occurrences. This follows commonly used methods, such as VanderWal, Shoo, Graham, and Williams (2009), who found that this distance balanced over-fitting SDMs to local distributions versus not including radically different climates in the models. *K*-fold cross-validation was performed for model validation, in which the occurrences were randomly split into training and testing datasets (70–30% split) three separate times. The final models for the modern-only or modern plus palaeoecological datasets were constructed using 100% of the occurrences. A threshold to designate presence versus absence of a species was calculated based on the true skill statistic (TSS) for each model.

We use gridded projections of land-cover change from the integrated assessment models (IAMs; Moss et al., 2010) for the end of the century (2061–2080) to represent the potential impact of future land use. Integrated assessment models are a tool for integrating disparate information from different disciplines (i.e. physical, economic and social processes), which can help scientists and decision-makers to understand the outcomes of complex environmental problems, such as anthropogenic change. To do this, we considered two end-members representing high- and low-intensity land-use scenarios: the model for energy supply strategy alternatives and their general environmental impact (MESSAGE) and the integrated model to assess the global environment (IMAGE), respectively (Moss et al., 2010). We will refer to the MESSAGE scenario as “high land use” and the IMAGE scenario as “low land use”. Species distribution model projections of tree ranges were compared with projections of land use to evaluate the impact of land-use change, and grid cells projected to be unsuitable for natural vegetation were eliminated from SDM forecast ranges for each individual taxon. We considered a grid cell as unsuitable for natural vegetation when the summed area of agricultural land, pasture land and urban areas covered >90% of the grid cell (Supporting Information Figures S2 and S3).

After forecasting potential ranges for each taxon under future climate, we used the PatchStats package in R (McGarigal & Cushman, 2002) to estimate fragmentation of forest populations. This package allowed us to calculate the mean size, number and connectivity of the patches (contiguous grid cells) for each taxon across the forecast ranges for each combination of climate and land use.

We performed a series of sensitivity tests to evaluate how the ranges of Afromontane tree taxa will respond to individual environmental variables at different elevations. For these tests, we projected future ranges using future values of one climate variable but retained modern values of all other variables. We repeated this for all climate variables. The range sizes that resulted from these projections were then compared with those from projections using future values of all climate variables, presented in Figure 1. This allowed us to calculate the proportion of range change at the end of the century that resulted from each climate variable (1 = contributed to range expansion; −1 = contributed to range contraction). We parsed these results for each taxon into 200-m elevational bands (between 1,200 and 3,800 m a.s.l.) to estimate the impact on range sizes of projected future change in each climate variable individually.

3 | RESULTS

3.1 | Geographical range contraction

We forecast that by the end of the 21st century all Afromontane taxa could experience a reduction in range size under all combinations of climate and land-use change (Figure 1; Table 1; Supporting Information Figure S5). However, based on the SDMs constructed from modern and fossil occurrences for our eight focal taxa, range contraction is projected to vary considerably depending on the combination of climate and land-use change. We illustrate this variation by showing range loss associated with the individual and combined effects of RCP 2.6 (moderate climate change; +1.4°C), RCP 8.5 (large climate change; +3.4°C), a low land-use scenario and a high land-use scenario for two exemplar taxa (Figure 1) and for the remaining six taxa (Table 1; Supporting Information Figure S5). The average range loss impacts of RCP 2.6 are more severe than those from a low land-use scenario alone; likewise, the average impacts of RCP 8.5 are more severe than those from a high land-use scenario alone (Figures 1 and 1). However, among taxa there is considerable variation. Some taxa, such as *O. africana*, show a similar magnitude of range loss from both climate and land-use scenarios (Figure 1; Table 1). In contrast, other taxa, such as *P. africana*, show a very high magnitude of range loss from climate but very little impact from even intense land use (Figure 1; Table 1). On average across all taxa, the impacts of even a small change in climate are more severe than those of high-intensity land use (Figure 2; Table 1). Not surprisingly, the strongest impacts on range loss are observed when RCP 8.5 and a high-intensity land-use scenario are combined (Figures 1 and 2; Supporting Information Figure S5), which results in an average range reduction of 79% (Table 1). Considering the impact on this group of taxa as a whole, the extent of area where all representative taxa are lost increases with increasing scenario severity (Figure 3). The combination of these dual impacts results for many individual taxa in the complete extirpation from certain regions (Figure 1; Supporting Information Figure S5). Under high land use and RCP8.5, all studied taxa are lost from Madagascar, tropical western Africa, most of the Arabian Peninsula and much of southern Africa (Figure 3).

Future range forecasts based on both modern and fossil occurrence data decrease range loss on average only slightly relative to range losses calculated using solely modern occurrences (Table 1). For example, the average amelioration in range loss among taxa for RCP 2.6 with and without fossil occurrences is only 7% (Figure 2). Some taxa, particularly those which Ivory et al. (2016) demonstrated to have occupied warmer climates in the past, show a moderate decrease in range loss. These taxa, *O. africana*, *O. capensis* and *Podocarpus* spp., together average 15% lower range loss when fossil data are included (Table 1). Most importantly, the magnitude of the ameliorating effect attenuates with increasing severity of land use and climate change (Figure 2). The average amelioration in range loss with and without the fossil data for RCP 8.5 is only 2%, and this difference is only 9% for the three taxa highlighted above.

In addition to the results described above, we predicted range changes based on the HadGEM2 model output, which forecasts more extreme warming (+4.6°C) than the CMIP5 ensemble. The results are similar, but slightly more severe (Supporting Information Figure S6; Table S2). For example, the potential ranges for all taxa decrease more strongly under RCP 8.5 from HadGEM2 than under the CMIP5 ensemble forecast (5% more range loss on average; Supporting Information

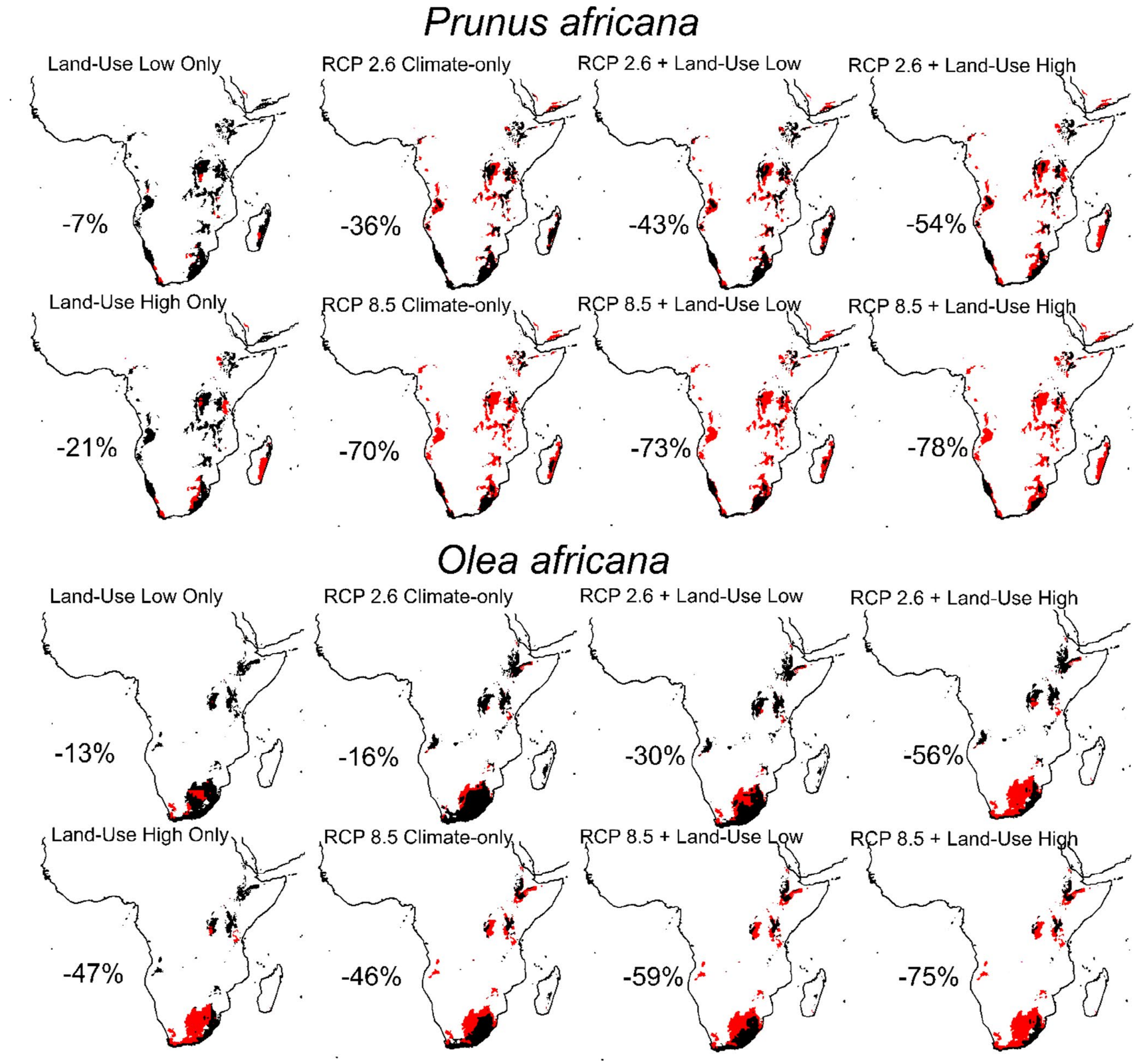

FIGURE 1 Future range forecast (2061–2080) of *Prunus africana* and *Olea africana* from species distribution models including fossil and modern occurrence data and using representative concentration pathways (RCPs) 2.6 and 8.5 and land-use projections of high and low land-use scenarios (MESSAGE and IMAGE). Range forecasts for the six remaining taxa are shown in the Supporting Information (Figure S1). Forecast range retained is shown in black and forecast loss is shown in red (and this percentage of modern range lost is provided as a number below each panel) [Colour figure can be viewed at wileyonlinelibrary.com]

Table S2). Furthermore, the forecast range reduction from the combined effects of RCP 8.5 and the high land use are on average 2% greater under HadGEM2 than those forecast based on the ensemble model (Table 1; Supporting Information Table S2).

3.2 | Elevational range contraction

Future range forecasts using both modern and fossil data predict that the total area occupied at individual elevation bands will be greatly reduced by the end of the century. We illustrate this with two exemplar species (Figure 4), together with the remaining six taxa (Supporting Information Figure S7). There is much variation in the change in geographical extent among taxa. Some taxa (e.g., *O. africana*) lose relatively little suitable habitat under RCP 2.6 (Figure 4), and most lose relatively little suitable habitat under the low land-use scenario (Supporting Information Figure S7). Total reductions in elevational range under RCP 8.5 are universally high (Figure 4; Supporting Information Figure S7). Importantly, the ranges of all taxa, except for *O. africana*, are forecast to contract at lower elevations without a concomitant upward expansion (Figure 4; Supporting

TABLE 1 Proportion of the modern range of eight Afromontane taxa forecast to be lost under future climate change and land-use (LU) scenarios

	Climate only		LU only		LU and climate	
	Palaeo	NO Palaeo	LU Low	LU High	LU Low	LU High
RCP 2.6						
Hagenia abyssinica	0.336	0.348	0.152	0.361	0.489	0.645
Ilex mitis	0.421	0.421	0.081	0.272	0.468	0.610
Juniperus procera	0.387	0.387	0.138	0.337	0.514	0.664
Nuxia spp.	0.361	0.427	0.122	0.315	0.483	0.623
Olea africana	0.156	0.287	0.135	0.472	0.302	0.564
Olea capensis	0.190	0.380	0.060	0.201	0.368	0.475
Podocarpus spp.	0.239	0.366	0.063	0.221	0.309	0.453
Prunus africana	0.364	0.400	0.073	0.208	0.431	0.536
Average	0.307	0.377	0.103	0.298	0.421	0.571
RCP 8.5						
Hagenia abyssinica	0.696	0.705	0.152	0.361	0.766	0.857
Ilex mitis	0.732	0.732	0.081	0.272	0.749	0.812
Juniperus procera	0.664	0.664	0.138	0.337	0.746	0.835
Nuxia spp.	0.684	0.714	0.122	0.315	0.736	0.813
Olea africana	0.437	0.584	0.135	0.472	0.588	0.748
Olea capensis	0.602	0.670	0.060	0.201	0.673	0.732
Podocarpus spp.	0.646	0.719	0.063	0.221	0.664	0.741
Prunus africana	0.701	0.720	0.073	0.208	0.730	0.783
Average	0.645	0.689	0.103	0.298	0.706	0.790

Note. Species distribution models used to generate these forecasts were created using both palaeoecological (Palaeo) and modern occurrences (NO Palaeo) and an ensemble of climate models.

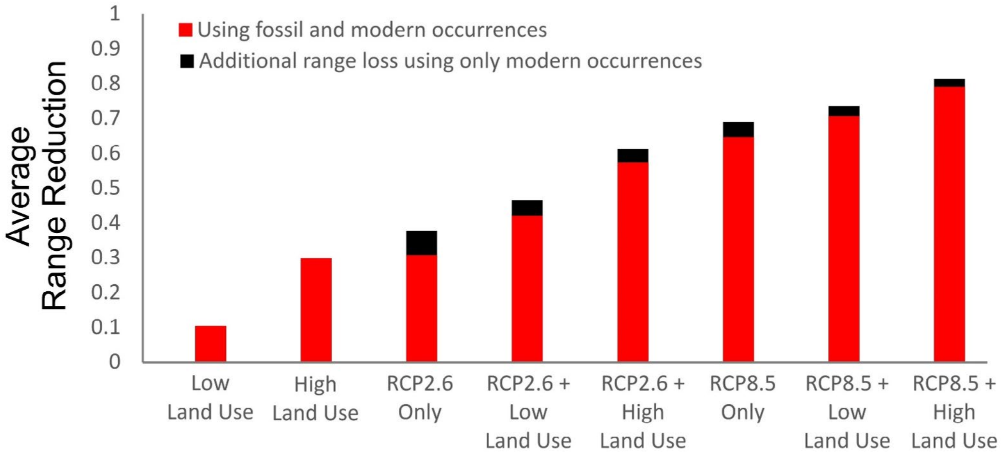

FIGURE 2 Range loss for climate and land-use change combinations forecast to occur on average across species for the end of the century (2061–2080) when species distribution models are based on both modern and fossil occurrences (red) or only on modern occurrences (in which case, the additional forecast loss is shown in black) [Colour figure can be viewed at wileyonlinelibrary.com]

Information Figure S7). Sensitivity analysis of the climate variables used for the SDM range forecasts shows that most lower-elevation range loss is driven by temperature (Figure 4; Supporting Information Figure S7). Future temperature increases result in a particularly notable impact at middle elevations (between 2,000 and 2,800 m a.s.l.); however, projected changes in diurnal temperature and rainfall buffer against reductions in climatic suitability in these elevations (Figure 4; Supporting Information Figure S7).

3.3 | Habitat fragmentation

Our SDM range forecasts based on modern and fossil occurrences show marked reductions in patch size, number and connectivity. This results in fewer, smaller, more isolated patches as climate and land-use change intensifies (Figure 5). Patches of all sizes become less frequent, the largest patches become fragmented, and *c*. 30–50% of the smallest patches disappear (<5,000 km^2; Supporting Information

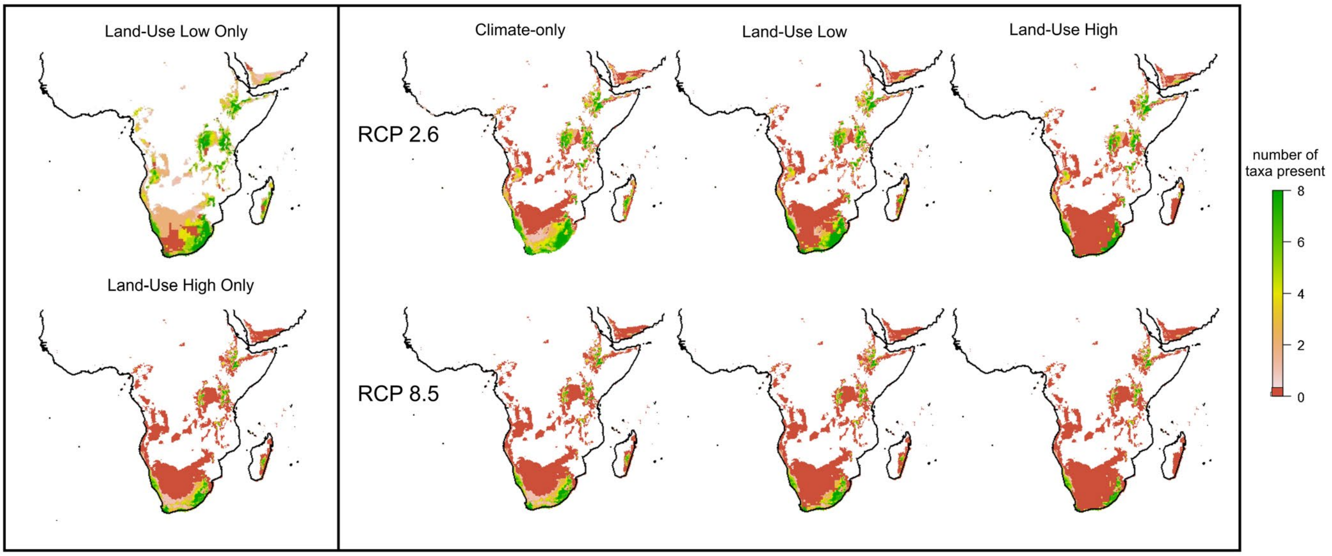

FIGURE 3 Future range forecast (2061–2080) of all studied Afromontane trees from species distribution models including fossil and modern occurrence data and using representative concentration pathways (RCPs) 2.6 and 8.5 and land-use projections of high and low land-use scenarios (MESSAGE and IMAGE). Number of species with forecast ranges retained are shown, and where all forecast range is lost is in red [Colour figure can be viewed at wileyonlinelibrary.com]

Figure S3). Forecasts based solely on RCP 8.5 result in greater reductions in patch size and number than forecasts based on high land use and RCP 2.6. In contrast, patch connectivity is reduced more by high land use together with RCP 2.6 than by RCP 8.5 alone (Figure 5).

4 | DISCUSSION

Across the Afromontane region, future climate and land-use change could result in large-scale collapse of this widespread montane ecosystem. Using palaeoecological data, Ivory et al. (2016) found that Afromontane trees could tolerate warmer climates than they currently occupy, suggesting that they could be less threatened by climate change than one might expect. We show here that although including fossil distribution data does decrease forecast range loss, the amelioration is small and diminishes in importance with increasing severity of climate change. The difference between range loss predicted with and without fossil data becomes almost negligible under RCP 8.5 (Figure 2).

Our findings contrast with other studies, such as those of Nogues-Bravo et al. (2016), who found a strong reduction of range loss when including fossil data for projecting future conservation risks for plants in North America and Europe. Such qualitatively different responses to incorporating fossil data could have many explanations. The results of Nogues-Bravo et al. (2016) might have been influenced by their grouping of species into genera and families, whereas we studied responses at the species level for six of our eight plant taxa. Alternatively, these differences might also be attributable to inherent differences of temperate and tropical species. The thermal niches of tropical species are expected to be narrower than those of temperate species and to show greater conservatism through time. Finally, it is also possible that differences in species diversity and competitive interactions within the tropics might influence this result.

The relatively minor impact of including information about the types of climates occupied in the past on the niches in our study might be attributable to the specific effects of climate change in tropical highlands. It is clear from studies of past vegetation (Dupont et al., 2011; Ivory, Lézine, Vincens, & Cohen, 2018) and previous SDM work (Ivory et al., 2016) that some Afromontane taxa formed continuous forest corridors in the lowlands during past warm periods. Furthermore, in the tropics, changes in rainfall and seasonality are known to have played a strong role in range changes in the past (Vincens, Garcin, & Buchet, 2007). We demonstrate that this is also likely to be true in the future, because projected changes in other climate variables, such as diurnal temperature and rainfall, buffer against reductions in range loss for many taxa at certain elevations. This suggests more complex responses to climate change than would be expected from temperature alone.

Our findings suggest that the magnitude of climate change forecast under RCP 2.6 is large for Afromontane taxa, leading to range loss of up to 42% for certain species, even with niche requirements estimated from modern and fossil occurrences. Africa is expected to warm more than other tropical continents (Niang et al., 2014). This means that even ambitious greenhouse gas reduction targets result in relatively large increases in mean annual temperature (+1.4°C; Supporting Information Table S1) and plant distributions.

These results also differ from work on other regions, such as South America and Europe, where species have shown range contraction at lower elevations and expansion upslope in response to climate warming (Dullinger et al., 2012; Duque, Stevenson, & Feeley, 2015; Feeley & Silman, 2010; Gottfried et al., 2012). In contrast,

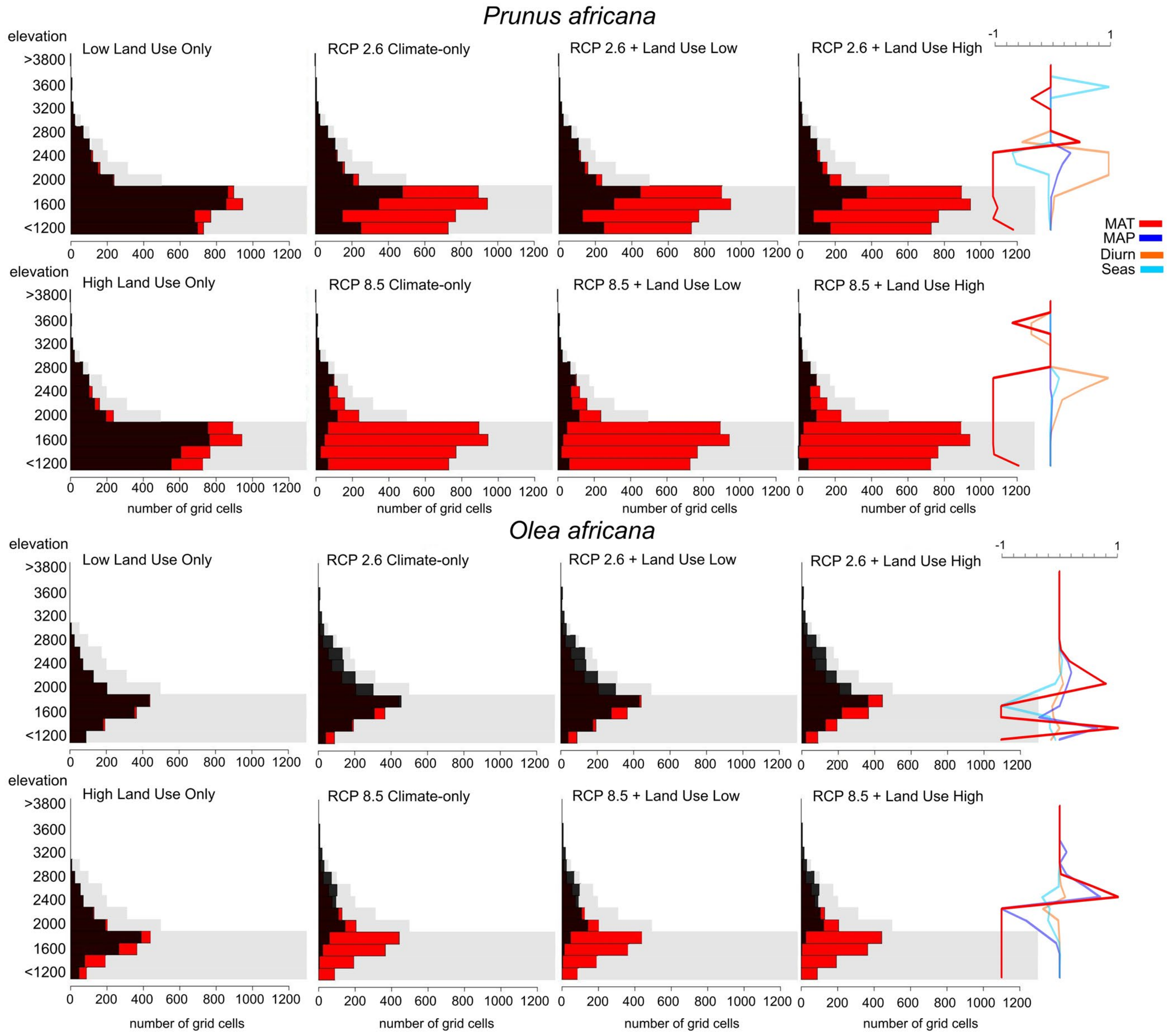

FIGURE 4 Future range forecast (2061–2080) of *Prunus africana* and *Olea africana* by elevation band from species distribution models including fossil and modern occurrence data and using representative concentration pathways (RCPs) 2.6 and 8.5 and land-use projections of high and low land-use scenarios (MESSAGE and IMAGE). Forecast loss is shown in red and future range in black. Light grey represents the total area available in the elevational band. The right-most panel for each RCP shows the range sensitivity in each elevational band to each climate variable: MAT (mean annual temperature, red), MAP (mean annual precipitation, dark blue), Diurn (diurnal temperature, orange) and Seas (rainfall seasonality, light blue). Negative values indicate that a variable contributes to a range contraction, whereas positive values indicate that a variable contributes to a range expansion. The remaining six taxa elevational range forecasts are shown in the Supporting Information (Figure S4) [Colour figure can be viewed at wileyonlinelibrary.com]

these Afromontane taxa are not forecast to expand upslope. This probably results from an important physiographic attribute of this system: that African mountaintops are generally spatially small and discontinuous. Thus, currently there is very little area at higher elevations that is not already occupied by these taxa (Figure 4; Supporting Information Figure S7). In fact, Afromontane trees already occupy >90% of available land area at these elevations, leaving little available for future upslope expansion (Figure 4; Elsen & Tingley, 2015). These species also are not forecast to expand to cooler climates northward or southward, because they already occupy most mountains on the African continent. We therefore suggest that a lack of suitable upslope habitat drastically reduces the capacity of these taxa to adapt to changing climate.

Although the impacts of land-use change alone are smaller than the impacts of climate alone, the combined effects of climate and land-use change can be extremely large (Figures 2 and 2; Table 1). Range reductions can be as much as 26% larger on average when land use is included than from climate alone when RCP 2.6 is used (Table 1). In fact, the impact of RCP 2.6 plus high-intensity land use results in nearly the same magnitude of range loss as for RCP 8.5

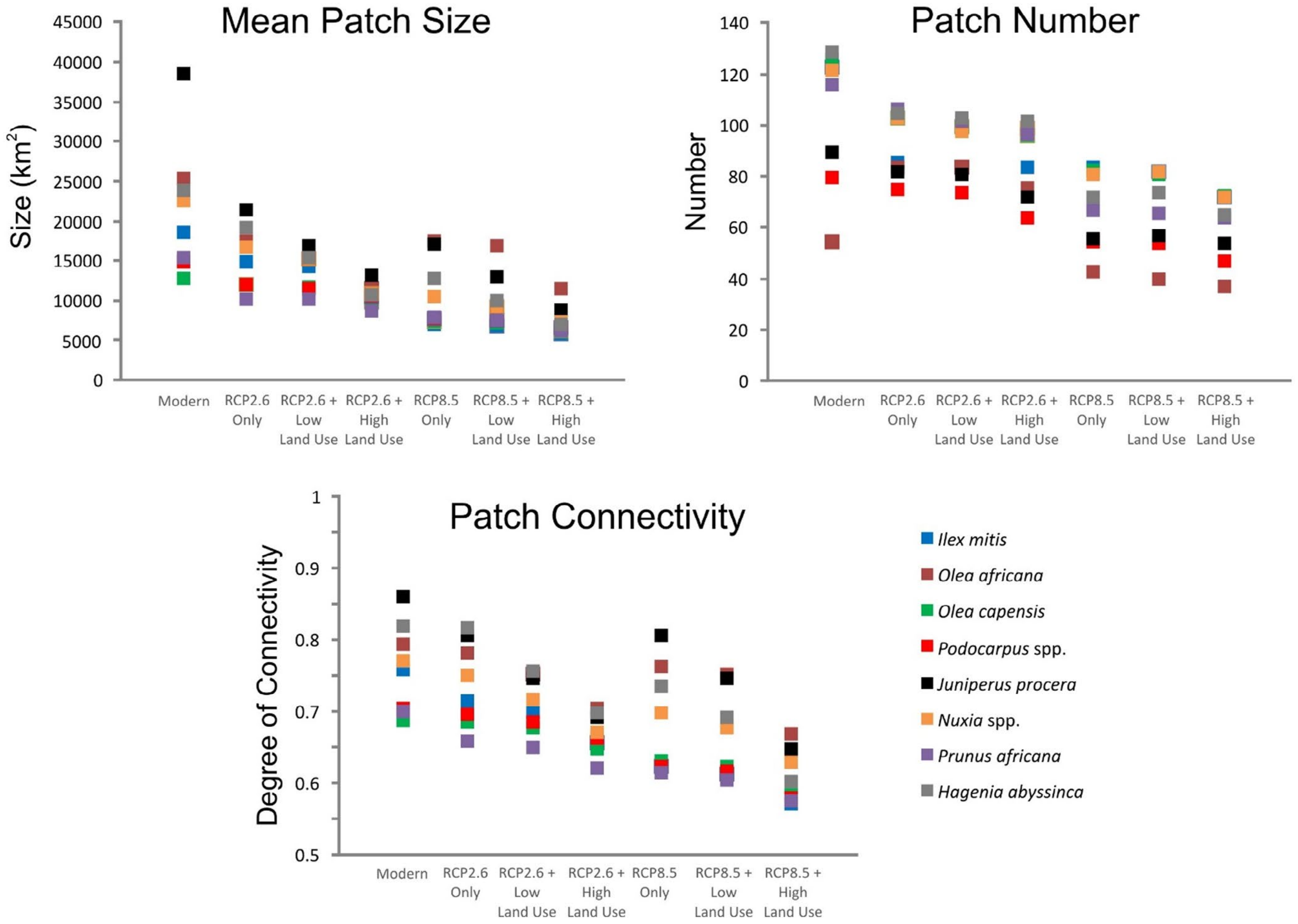

FIGURE 5 Patch statistics for forecast ranges of taxa presented in Figures 1 and Supporting Information Figure S1, derived using species distribution models including fossil and modern occurrence data and using representative concentration pathways (RCPs) 2.6 and 8.5 and land-use projections of high and low land-use scenarios (MESSAGE and IMAGE). Mean patch size is the average of the area of all patches, patch number is the remaining total number of patches, and patch connectivity is a dimensionless index of patch aggregation on the landscape [Colour figure can be viewed at wileyonlinelibrary.com]

climate alone (Figure 2; Table 1). This suggests that even though climate has the strongest single effect on range reduction, intensifying land use will have a powerful secondary effect. Moreover, some species, particularly those shown by Ivory et al. (2016) to be least sensitive to temperature, are disproportionately affected by land-use change. Incorporating both climate change and land-use impacts, *O. africana* could lose almost half its climatically suitable range from land-use change, because its present, low-elevation range is where future land-use changes are forecast to be largest (Figures 2 and 4). Thus, even if species can adapt to a changing climate, range loss at the lower range boundary is still likely, owing to lowland exclusion through anthropogenic activity.

Although the high- and low-intensity land-use scenarios used here can help to give us an understanding of the differential impacts of rapidly growing populations in Africa, the indefinite outcomes of these complex systems injects considerable uncertainty into end-of-century land-use predictions (Pontius & Spencer, 2005). Furthermore, in Africa small-scale land-use changes have impacts beyond those captured in the IAMs, such as harvesting of non-timber forest products (e.g. medicines from *P. africana* and *H. abyssinica*; Cunningham, Anoncho, & Sunderland, 2016; Stewart, 2003). This suggests that the IAMs are likely to be conservative estimates of land-use impacts. Furthermore, many studies investigating the ongoing effects of deforestation in parts of the Afromontane regions suggest massive losses over the last 60 years (Hall et al., 2009) and that land use alone unchecked might result in near total loss of forest (Ngigi & Tateishi, 2004). This is particularly likely given that some of the highlands of Africa are already the most densely human populated lands on the continent, with populations projected to increase faster than anywhere else on Earth (Linard, Gilbert, Snow, Noor, & Tatem, 2012; Plumptre et al., 2007).

The collapse in range size we predict is coupled with forecast changes in the patch size, number and connectivity of populations across the region (Figure 5). Habitat connectivity is crucial to maintaining viable populations (Shoemaker, Breisch, Jaycox, & Gibbs, 2013). In this region, one way this occurs is by maintaining genetic diversity. In Afromontane regions, many tree species are dispersed by animals, such as birds, meaning that geographical barriers and the effects of fragmentation may be overcome by long-distance dispersal (Mairal et al., 2017; White, 1981). However, fragmentation by climate and land-use change leads to small disconnected patches and results in enhanced edge effects, which might lead to regional functional extinctions or extinction debt (population reduction leading to inevitable extinction) long before species completely disappear (Haddad et al., 2015; Jackson & Sax, 2010; Platts, Gereau, Burgess, & Marchant, 2013). Although the quantitative changes we describe here for habitat fragmentation depend on the thresholds used to define land use, the qualitative results themselves do not. For example, we considered a grid cell as unsuitable for Afromontane forest when the summed area of agricultural land, pasture land and urban areas covered >90% of the grid cell. This threshold was chosen because it represented the largest change in land-use distributions with respect to modern within the Afromontane region (Supporting Information Figure S4). However, many of the taxa considered here occur within grid cells projected to undergo complete land-cover conversion, meaning that 100% of land area within a grid cell will exclude natural vegetation (Supporting Information Figure S4). This suggests that regardless of which threshold is chosen as a cut-off for our estimates of grid-cell suitability, anthropogenic activities will have a strong impact.

We did not explicitly consider the role of elevated CO_2 or fire in driving the future distributions of Afromontane taxa. However, by incorporating fossil-informed niches into our models from ancient periods with lower than modern CO_2 (*c*. 180 ppm; LGM) and pre-industrial CO_2 (*c*. 280 ppm; MH), we have some reference on the potential influence that CO_2 might have. Lower atmospheric CO_2 has been cited a driver of tree decline through enhanced water stress in favour of C4-dominated grasslands with higher water-use efficiency (Bragg et al., 2013). Interestingly, we find that during periods with lower CO_2 than today, Afromontane forest species occurred in warmer areas (Ivory et al., 2016). Given the heterogeneity of regional climate change in comparison to CO_2, we suggest that elevated CO_2 will not be a primary driver of vegetation responses to local climate conditions but could modulate responses. Fire is also likely to impact species distributions. Ivory et al. (2018) suggest that the exclusion of highland taxa from the lowlands might, for some species, be related to fire intolerance. Their observation of increased fire activity in lowland East Africa after 80 ka might also play an important non-climatic role in constraining these ranges.

Afromontane forests are ecologically important hotspots of biodiversity, not only for plants, but also for endemic birds, mountain gorillas and other fauna (Dulle et al., 2016; White, 1981). Yet future climate and land-use change could result in large-scale collapse of this now widespread ecosystem. We show that including datasets of fossil distributions can alter range forecasts by counteracting the effect of climate disequilibrium of modern species ranges, but only by a very moderate amount for Afromontane taxa. We show that these taxa will lose a minimum of *c*. 65% of their modern range under high emission and low land-use scenarios (Table 1). Even with large reductions in emissions (RCP 2.6), if land-use change is high, more than half of Afromontane tree taxa modern ranges may be lost. Under higher emissions and land use, much of the geographical footprint of this system (*c*. 80%) may be entirely lost.

In the face of such widespread geographical collapse, it becomes imperative to safeguard patches that will remain. Management strategies that focus on conserving species in situ are unlikely to yield favourable results from many areas at lower elevations in a warming climate, even if we were to achieve the RCP 2.6 trajectory. Furthermore, given that RCP 2.6 is unlikely based on existing emissions, and that few low-elevation regions are forecast to be suitable under higher emissions, management efforts should focus on protecting areas at mid- and upper elevations and across elevational gradients. Likewise, conservation efforts should prioritize the protection of habitat patches forecast to remain largest, such as in southern Africa, because these will minimize potential extinction debts, and to prioritize areas that can provide critical linkages in maintaining connectivity. Ultimately, our study indicates that fossil data used to expand the known niche requirements of extant tropical species may do little to reduce forecast threats from climate change or land use, particularly when there are strong non-climatic constraints on potential shifts in species distributions.

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DATA ACCESSIBILITY

The data supporting the results already exist and are freely available in the Global Biodiversity Information Facility (GBIF) and the African Pollen Database (APD).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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