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4 1 **Title:** Broader niches revealed by fossil data don't reduce estimates of range loss and
5 2 fragmentation of African montane trees

6 3 **Short title:** The future of African montane forests

8 4 **Keywords:** tropical climate, paleoecology, biogeography, species distribution models, niche,
9 5 tropical forests, range collapse, Afromontane

11 6 **Abstract:**

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14 7 *Aim:* Many species' climate tolerances are broader than those estimated from current native
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16 8 ranges. Indeed, some Afromontane trees' niches are up to 50% larger after incorporating fossil
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18 9 data. This expansion could reduce estimates of species' future range loss due to climate change
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20 10 but also implies strong non-climatic limitations on species' current ranges. One such limitation is
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22 11 land use, which fossil data suggest influences Afromontane tree distribution, preventing these
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24 12 trees from occupying warmer conditions than they currently do. We aim to assess the degree to
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26 13 which the broader climatic tolerances revealed by fossil data buffers projected range loss from
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28 14 climate and land use for Afromontane trees.

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33 15 *Location:* Africa

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35 16 *Time period:* Last 21,000 years

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38 17 *Major taxa studied:* Afromontane trees

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41 18 *Methods:* We used species distribution models informed by both current and fossil distributions
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43 19 to project future ranges under climate and land-use projections.

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46 20 *Results:* We found that projected range reductions are only slightly ameliorated by incorporating
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48 21 fossil distributions and these improvements diminish further under severe land use or climate
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50 22 change scenarios. Taxa that are less impacted by climate are more impacted by intense land use.
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52 23 Depending on the severity of climate and land use, the geographic extent of Afromontane tree
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3 24 species' ranges will contract by 40-85% and the trees will completely be lost from large portions
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5 25 of Africa. We projected that the surviving species' ranges will become increasingly fragmented.
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8 26 *Main conclusions:* Maintaining Afromontane ecosystems will require mitigation of both climate
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10 27 and land-use change and protecting areas to optimize connectivity. Our findings caution that
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12 28 species with climate tolerances broader than their current range might not necessarily fare better
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15 29 under strong changes in climate or land use.
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17 30 **Introduction:**

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20 31 Climate change over the 21st century is expected to contribute to species extinctions and
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22 32 turnover (Petersen et al. 2002; Urban 2015). These risks could be particularly pronounced for
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24 33 montane taxa, as high-elevation species could experience a complete loss of suitable climate
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26 34 conditions on the mountains where they occur (Petersen et al. 2002; Williams et al. 2003). A
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28 35 principal tool for assessing these risks is to construct climatic Species Distribution Models
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30 36 (SDMs), which use the climate conditions species experience within their modern distributions
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32 37 to assess future potential distributions under climate change (Pearce and Ferrier 2000; Guisan
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34 38 and Thuiller 2005; Elith and Leathwick 2009; Urban 2015; Lenoir and Svenning 2015). One
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36 39 limitation of this approach is that the realized niche that organisms presently occupy may
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38 40 represent only part of the climatic conditions they can actually tolerate, and other conditions
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40 41 might also be suitable for species persistence (Araujo and Pearson 2005). Omitting currently
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42 42 unoccupied conditions that are climatically suitable will underestimate species 'climatic niches'
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44 43 and overestimate the risks posed by climate change. However, including these conditions is
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46 44 difficult as the differences between climatic tolerances and distributions are likely to be species-
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48 45 specific and are generally unknown (Sax et al. 2013).
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3 46 Recent work comparing species' native and non-native populations does suggest that
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5 47 some species' native ranges do not fully reflect their climate tolerances (e.g., Gallagher et al.
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7 48 2010; Early and Sax 2014). In addition to non-native distribution data, there has been a strong
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9 49 call in the literature for increased use of fossil distribution and paleoclimate data to improve
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11 50 measurements of species' climate niches (Botkin et al. 2007; Nogues-Bravo 2009; Veloz et al.
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13 51 2012). Maiorano et al. (2013) showed how realized niches change through time and that
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15 52 "building a niche" with fossil data altered current and future range projections. Nogues-Bravo et
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17 53 al. (2016) showed that the inclusion of fossil data in SDMs more accurately assessed
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19 54 conservation risk for plant genera and families in Europe and North America. Ivory et al. (2016)
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21 55 used fossil data to show that some Afromontane trees previously occupied warmer conditions
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23 56 than in their current distributions. This is supported by paleoecological studies which find that
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25 57 anthropogenic impacts since at least the Iron Age have progressively altered East African
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27 58 species' distributions through changing land use and fire regimes (Hall et al. 2009).
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34 59 Climate change and land use have long been appreciated as a dual threat to species
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36 60 persistence, particularly when anthropogenic activities block species' range shifts (Hansen et al.
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38 61 2001; Feeley and Silman 2010; Barbet-Massin et al. 2012). Some work suggests that future
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40 62 changes in land use might be particularly important to species distributions in the tropics (Jetz et
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42 63 al. 2007). Recent reviews and conceptual considerations of climate and land-use change have
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44 64 concluded that estimates of extinction risk should consider both factors, while acknowledging
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46 65 the challenge of considering dual risks that could interact in complex ways (De Chazal and
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48 66 Rounsevell 2009; Oliver and Morecroft 2014).
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53 67 The Afromontane forest is an excellent example of a system where the interplay between
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55 68 future changes in land use and climate might be particularly important. This region is a globally
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3 69 unique biodiversity hotspot, characterized by a rich endemic flora, and a distinctive set of tree
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5 70 species with broad geographic distributions (White 1981; Mittermeier 2004; Plumptre et al.
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8 71 2007; Ivory et al. 2016). Afromontane forests occupy mountaintops across Africa, extending
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10 72 across the tropics and two temperate zones - from the southern Cape of South Africa to the
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12 73 Arabian Peninsula and from West Africa to Madagascar. It is becoming clear that even such
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15 74 extensive systems are at risk from climate change and land use in the future; however, the degree
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17 75 to which each will impact species' ranges is currently unknown (Mittermeier, 2004; Niang et al.,
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19 76 2014). Indeed, given current climate conditions and estimated niche requirements, the potential
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21 77 range of certain species, such as *Olea africana*, could be as much as 50% larger than their
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23 78 current realized distributions (Ivory et al. 2016). This expanded tolerance could buffer these
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25 79 species from some extent of future warming. Likewise, Afromontane tree species' extensive
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27 80 distribution and potential capacity to shift their ranges upslope could also buffer them from a
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29 81 warming climate. Alternatively, Afromontane ecosystems might be disproportionately at risk,
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31 82 because Africa is already one of the warmest places on Earth and is predicted to warm more
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33 83 dramatically than other tropical continents by the end of this century (Dullinger et al. 2012;
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35 84 Gottfried et al. 2012; Niang et al. 2014). Likewise, regional human populations are rapidly
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37 85 increasing (Lopez-Carr et al. 2014), suggesting that land use is likely to intensify. The rate of
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39 86 land conversion is predicted to increase in Africa due to rapid population growth and intensified
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41 87 agriculture, reducing available habitat and causing extensive disturbance to natural ecosystems
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43 88 (Feeley and Silman 2010; Niang et al. 2014). If future human land use extends to higher
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45 89 elevations, this could further imperil the Afromontane ecosystem to reduce available habitat.
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47 90 Ultimately, Afromontane forests could provide an excellent system to investigate how species
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49 91 with (i) tolerance to warmer conditions than those currently experienced, (ii) the capacity to
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3 92 move upslope, and (iii) a broad geographic extent, will fare in response to the dual threats posed
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5 93 by future changes in climate and land use.
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8 94 Here we use SDMs developed by Ivory et al. (2016) using current and fossil occurrences
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10 95 of eight Afromontane tree taxa to evaluate the risks posed from future changes in climate and
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12 96 land use. We examine low and high change scenarios for both climate change and land use to
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14 97 consider the role of these threats both individually and together. We evaluate how the relative
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16 98 importance of each varies with the degree of change. We also evaluate the degree to which
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18 99 information on climate tolerances obtained from fossil data reduce range loss relative to
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20 100 predictions based on climate tolerances calculated solely from modern occurrences. We then ask
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22 101 whether the effect of fossil data on any future range loss predictions attenuates with increasing
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24 102 environmental change. Next, we examine whether the patterns observed can be better understood
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26 103 by considering projections in elevational shifts in distribution and changes in geographic extent
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28 104 of these taxa. Finally, we consider the long-term fate of this unique system.
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34 105 **Materials and Methods**

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36 106 Afromontane forest covers an area of 98,685 km² throughout tropical and southern
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38 107 Africa, beginning at an elevation of ~1500 m asl (Bussman, 2006). Currently, this region is at
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40 108 great risk due to intensifying land use pressure from deforestation, agricultural expansion, and
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42 109 for use of certain plants as non-timber forest products (Niang et al. 2014). SDMs for the eight
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44 110 focal taxa (*Hagenia abyssinica*, *Ilex mitis*, *Juniperus procera*, *Nuxia* spp., *Olea africana*, *Olea*
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46 111 *capensis*, *Podocarpus* spp., *Prunus africana*) were developed by Ivory et al. (2016) and the
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48 112 methods used are discussed extensively in that manuscript. Vegetation zones vary slightly from
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50 113 mountain to mountain and also by aspect but generally have montane forest or rainforest until
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52 114 ~2700 m asl, a zone of bamboo until ~3000 m asl, and are topped by an Ericaceous forest or
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3 115 cloud forest until the treeline near 3900 m asl (Hedberg 1951; White 1981; Bussman 2006).
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5 116 *Nuxia* spp (Stilbaceae), *Ilex mitis* (Aquifoliaceae), *Olea africana* (Oleaceae), and *Olea capensis*
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8 117 (Oleaceae) often are found in the mid-altitudes from 1500-2700m asl on wetter slopes (White
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10 118 1981; Bussman 2006). *Prunus africana* (Rosaceae) is an endemic tree that can be found in
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12 119 Afromontane rainforest habitats from 1500-2300m asl m asl (Bussman 2006). *Podocarpus* spp.
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15 120 (Podocarpaceae) are the most characteristic tree of the region, and therefore different species can
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17 121 be found in association with other trees or in monodominant stands at many elevations >1500 m
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19 122 asl (White 1981). *Hagenia abyssinica* (Rosaceae) is a characteristic endemic tree occurring
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21 123 between 2900-3300 m asl and is a commonly used medicinal plant (Bussman 2006; Assefa et al.
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23 124 2010). Above this zone and up to the treeline at 3500-3900 m asl, Ericaceous forests commonly
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25 125 include *Juniperus procera* (Cupressaceae).

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28 126 Species occurrence records were acquired from two sources. Observations of modern
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30 127 species occurrences were retrieved from the Global Biodiversity Information Facility (GBIF;
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32 www.gbif.org). Modern occurrences were supplemented by modern pollen datasets, which were
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34 128 taken from the African Pollen Database (APD; <http://fpd.sedoo.fr/fpd/>; Vincens et al. 2007b).
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36 129 Fossil pollen samples were also acquired from the APD and taken from two data-rich periods in
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38 130 the paleoecological record, which were used in Ivory et al. (2016): the mid-Holocene (MH;
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40 131 6ka), and Last Glacial Maximum (LGM; 21ka). The taxonomic resolution of all pollen taxa
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42 132 matches the stated descriptions above with six determined to species level and the remaining two
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44 133 to the genus level (*Nuxia* spp. and *Podocarpus* spp.). All pollen data were converted to relative
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46 134 abundances, then presence or absence of the taxa was determined based on the method
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48 135 developed by Ivory et al. (2016). This method used studies of pollen transport to set a threshold
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50 136 value of abundance that indicates the taxon presence within each climatic grid-cell. Four
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3 138 climatic variables (gridded at 10' resolution) were extracted from Worldclim
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5 139 (www.worldclim.org) to estimate modern and past distributions (mean annual temperature
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7 140 [MAT], mean annual precipitation [MAP], diurnal temperature range [Diurn], and rainfall
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9 141 seasonality [Seas; coefficient of variation]). The gridded modern climate data was compared to
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11 142 weather station data and found to accurately capture gradients in temperature and precipitation
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13 143 (Hijmans et al. 2005; Ivory et al. 2016).
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17 144 For this study, future potential ranges were forecasted using climate model output for the
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19 145 end of the century (2061-2080), which were downscaled to 10' resolution as part of the
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21 146 Worldclim climate dataset (Fig. S1; Hijmans et al. 2005) and projected using a Lambert
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23 147 Azimuthal equal-area projection for analyses. Higher resolution climate data were not used as
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25 148 Africa has relatively few weather stations that can be used to spatially downscale climate data
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27 149 and such data, if used, would have had values with considerable uncertainty (Hijmans et al.
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29 150 2005). Future climate conditions were predicted using an ensemble of output from the most
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31 151 recent Climate Model Intercomparison Project (CMIP5), integrating output from five climate
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33 152 models: NCAR CCSM4 (Gent et al. 2011), HadGEM2-ES (Collins et al. 2011), MIROC-ESM
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35 153 (Watanabe et al. 2011), IPSL-CM5A-LR (Dufresne et al. 2013), and NorESM1-M (Bentsen et al.
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37 154 2013). We used Representative Concentration Pathways (RCPs) 2.6 and 8.5 to forecast future
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39 155 ranges to evaluate the magnitude of climate change on ranges for each taxon (Fig. S1). In 2061-
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41 156 2080, average MAT at occurrence locations will be $1.4^{\circ}\text{C} + /-0.7^{\circ}\text{C}$ warmer under RCP 2.6 and
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43 157 $3.4^{\circ}\text{C} + /-1.1^{\circ}\text{C}$ warmer under RCP 8.5 (Table S1). All principal analyses in the manuscript use
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45 158 the ensemble model (Table S1). However, we also ran a secondary set of analyses using just
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47 159 output from HadGEM2, which predicts the largest increase in MAT ($+4.6^{\circ}\text{C}$) and provides a
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54 160 “worst case scenario” for climate change. Further, to evaluate the impact of extrapolation to no-
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3 161 analogue climate conditions in the future for our taxa of interest, we used the MESS package in
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5 162 R to illustrate that climate forecast under RCP 8.5 has analogous climate in the Afromontane
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8 163 region today, avoiding extrapolation (Elith et al., 2010; Fig. S7).
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10 164 To project each taxon's future potential range, SDMs were constructed using all
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12 165 regression and machine learning algorithms in BIOMOD2 using R (Thuiller et al. 2009; R Core
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14 166 Team 2017). We used an area under the receiver operating curve [AUC] threshold of >0.80 to
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17 167 define the best performing models and constructed a total consensus ensemble of these models.
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19 168 AUC, a common SDM assessment tool, is a metric of the true number of presences as a function
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21 169 of the number of false positives. These values are presented in the Appendix (Table S5), and
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23 170 there is no significant difference between AUC values based on modern-only versus modern and
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25 171 paleoecological occurrences ($t = -0.803$, $p = 0.4356$). Previous studies have illustrated the
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27 172 application of ensemble forecasts in relation to individual models (Araújo and New 2007). To
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29 173 compare the influence of including paleoecological data in future range projections, we created
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31 174 two sets of SDM ensembles for each taxon: (1) SDMs trained on the modern-only occurrences,
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33 175 and (2) SDMs trained on the modern and paleoecological occurrences combined. Due to the lack
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35 176 of information about species' true absences, pseudo-absences (eight times the number of
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37 177 occurrences) were randomly selected from a 400 km radius around occurrences. This follows
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39 178 commonly used methods, such as VanderWal et al. (2009), who found that this distance balanced
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41 179 over-fitting SDMs to local distributions versus not including radically different climates in the
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43 180 models. K-fold cross validation was performed for model validation in which the occurrences
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45 181 were randomly split into training and testing datasets (70% and 30% split) three separate times.
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47 182 The final models for the modern-only or modern + paleoecological datasets were constructed
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3 183 using 100% of the occurrences. A threshold to designate presence versus absence of a species
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5 184 was calculated based on the True Skill Statistic (TSS) for each model.
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8 185 We use gridded projections of land-cover change from the Integrated Assessment Models
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10 186 (IAMs; Moss et al. 2010) for the end of the century (2061-2080) to represent the potential impact
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12 187 of future land use. IAMs are a tool for integrating disparate information from different
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14 188 disciplines (i.e. physical, economic, and social processes), which can help scientists and
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16 189 decision-makers understand the outcomes of complex environmental problems like
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18 190 anthropogenic change. To do this, we considered two end-members representing high and low
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20 191 intensity land-use scenarios: the Model for Energy Supply Strategy Alternatives and their
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22 192 General Environmental Impact (MESSAGE) and the Integrated Model to Assess the Global
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24 193 Environment (IMAGE), respectively (Moss et al. 2010). We will refer to the MESSAGE
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26 194 scenario as “high land use” and IMAGE scenario as “low land use”. SDM projections of tree
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28 195 ranges were compared to projections of land use to evaluate the impact of land-use change, and
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30 196 grid-cells projected to be unsuitable for natural vegetation were eliminated from SDM forecasted
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32 197 ranges for each individual taxon. We considered a grid-cell as unsuitable for natural vegetation
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34 198 when the summed area of agricultural land, pasture land, and urban areas covered >90% of the
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36 199 grid-cell (Fig. S2 and S3).
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42 200 After forecasting potential ranges for each taxon under future climate, we employed the
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44 201 PatchStats package in R (McGarigal and Cushman 2002) to estimate fragmentation of forest
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46 202 populations. This package allowed us to calculate the mean size, number, and connectivity of the
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48 203 patches (contiguous grid cells) for each taxon across the forecasted ranges for each combination
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50 204 of climate and land use.
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3 205 We performed a series of sensitivity tests to evaluate how the ranges of Afromontane tree
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5 206 taxa will respond to individual environmental variables at different elevations. For these tests, we
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8 207 projected future ranges using future values of one climate variable, but retained modern values of
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10 208 all other variables. We repeated this for all climate variables. The range sizes that resulted from
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12 209 these projections were then compared to those from projections using future values of all climate
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14 210 variables, presented in Figure 1. This allowed us to calculate the proportion of range change at
15
16 211 the end of the century that resulted from each climate variable (1 = contributed to range
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18 212 expansion; -1 = contributed to range contraction). We parsed these results for each taxon into
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20 213 200m elevational bands (between 1200-3800 m asl) to estimate the impact on range sizes of
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22 214 projected future change in each climate variable individually.
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25 26 215 **Results**

27 28 216 *Geographic Range Contraction*

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31 217 We forecast that by the end of the 21st century all Afromontane taxa could experience a
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33 218 range-size reduction under all combinations of climate and land-use change (Fig. 1 and S4; Table
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35 219 1). However, based on the SDMs constructed from modern and fossil occurrences for our eight
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37 220 focal taxa, range contraction is projected to vary considerably depending on the combination of
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39 221 climate and land-use change. We illustrate this variation by showing range loss associated with
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41 222 the individual and combined effects of RCP 2.6 (moderate climate change; +1.4°C), RCP 8.5
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43 223 (large climate change; +3.4°C), a low land-use scenario, and a high land-use scenario for two
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45 224 exemplar taxa (Fig. 1) and for the remaining six taxa (Table 1; Fig. S4). The average range loss
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47 225 impacts of RCP 2.6 are more severe than those from a low land-use scenario alone; likewise, the
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49 226 average impacts of RCP 8.5 are more severe than those from a high land-use scenario alone
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53 227 (Figs. 1 and 2). However, among taxa there is considerable variation. Some taxa, such as *Olea*

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3 228 *africana*, show a similar magnitude of range loss from both climate and land-use scenarios (Fig.
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5 229 1; Table 1). In contrast, other taxa, such as *Prunus africana*, show a very high magnitude of
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8 230 range loss from climate but very little impact from even intense land use (Fig. 1; Table 1). On
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10 231 average across all taxa, the impacts of even a small change in climate are more severe than those
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12 232 of high intensity land use (Fig. 2; Table 1). Not surprisingly, the strongest impacts on range loss
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14 233 are observed when RCP 8.5 and a high intensity land-use scenario are combined (Fig. 1, 2, and
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16 234 S4), which results in an average range reduction of 79% (Table 1). Considering the impact on
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18 235 this group of taxa as a whole, the extent of area where all representative taxa are lost increases
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20 236 with increasing scenario severity (Fig. 3). The combination of these dual impacts results for
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22 237 many individual taxa in the complete extirpation from certain regions (Fig. 1, Fig. S4). Under
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24 238 high land-use and RCP8.5, all studied taxa are lost from Madagascar, tropical western Africa,
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26 239 most of the Arabian Peninsula, and much of southern Africa (Fig. 3).

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31 240 Future range forecasts based on both modern and fossil occurrence data on average decrease
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33 241 range loss only slightly relative to range losses calculated using solely modern occurrences (Table
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35 242 1). For example, the average amelioration in range loss among taxa for RCP 2.6 with and
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37 243 without fossil occurrences is only 7% (Fig. 2). Some taxa, particularly those which Ivory et al.
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39 244 (2016) demonstrated to have occupied warmer climates in the past, show a moderate decrease in
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41 245 range loss. These taxa, *Olea africana*, *Olea capensis*, and *Podocarpus* spp., together average
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43 246 15% lower range loss when fossil data are included (Table 1). Most importantly, the magnitude
44
45 247 of the ameliorating effect attenuates with increasing severity of land use and climate change (Fig.
46
47 248 2). The average amelioration in range loss with and without the fossil data for RCP 8.5 is only
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49 249 2%, and this difference is only 9% for the three taxa highlighted above.

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3 250 In addition to the results described above, we predicted range changes based on the
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5 251 HadGEM2 model output, which forecasts more extreme warming (+4.6°C) than the CMIP5
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7 252 ensemble. The results are similar, but slightly more severe (Fig. S5; Table S2). For example, the
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9 253 potential ranges for all taxa decrease more strongly under RCP 8.5 from HadGEM2 than under
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11 254 the CMIP5 ensemble forecast (5% more range loss on average; Table S2). Further, the forecast
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13 255 range reduction from the combined effects of RCP 8.5 and the high land-use are on average 2%
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15 256 greater under HadGEM2 than those forecast based on the ensemble model (Tables 1 and S2).

19 257 *Elevational Range Contraction*

21 258 Future range forecasts using both modern and fossil data predict that the total area occupied
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23 259 at individual elevation bands will be greatly reduced by the end of the century. We illustrate this
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25 260 with two exemplar species (Fig. 4), together with the remaining six taxa (Fig. S6). There is much
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27 261 variation in the change in geographic extent among taxa. Some taxa, e.g., *Olea africana*, lose
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29 262 relatively little suitable habitat under RCP 2.6 (Fig. 4), and most lose relatively little suitable
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31 263 habitat under the low land-use scenario (Fig. S6). Total reductions in elevational range under
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33 264 RCP 8.5 are universally high (Fig. 4, Fig. S6). Importantly, the ranges of all taxa, except for *Olea*
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35 265 *africana*, are forecast to contract at lower elevations without a concomitant upward expansion
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37 266 (Fig. 4, S6). Sensitivity analysis of the climate variables used for the SDM range forecasts shows
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39 267 that most lower-elevation range loss is driven by temperature (Fig. 4; Fig. S6). Future
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41 268 temperature increases result in a particularly notable impact at middle elevations (between 2000-
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43 269 2800 m asl); however, projected changes in diurnal temperature and rainfall buffer against
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45 270 reductions in climatic suitability in these elevations (Fig. 4; Fig. S6).

51 271 *Habitat Fragmentation*

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3 272 Our SDM range forecasts based on modern and fossil occurrences show marked reductions
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5 273 in patch size, number, and connectivity. This results in fewer, smaller, more isolated patches as
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7 274 climate and land-use change intensifies (Fig. 5). Patches of all sizes become less frequent, the
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9 275 largest patches become fragmented, and ~30-50% of the smallest patches disappear (<5000 km²;
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11 276 Fig. S2). Forecasts based solely on RCP 8.5 result in greater reductions in patch size and number
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13 277 than forecasts based on high land use and RCP 2.6. In contrast, patch connectivity is reduced
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15 278 more by high land use together with RCP 2.6 than by RCP 8.5 alone (Fig. 5).

19 279 **Discussion**

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21 280 Across the Afromontane region, future climate and land-use change could result in large-
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23 281 scale collapse of this widespread montane ecosystem. Using paleoecological data, Ivory et al.
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25 282 (2016) found that Afromontane trees could tolerate warmer climates than they currently occupy,
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27 283 suggesting that they could be less threatened by climate change than one might expect. We show
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29 284 here that although including fossil distribution data does decrease forecasted range loss, the
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31 285 amelioration is small and diminishes in importance with increasing severity of climate change.
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33 286 The difference between range loss predicted with and without fossil data becomes almost
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35 287 negligible under RCP8.5 (Fig. 2).

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37 288 Our findings contrast with other studies, such as Nogues-Bravo et al. (2016), which found
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39 289 a strong reduction of range loss when including fossil data for projecting future conservation
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41 290 risks for plants in North America and Europe. Such qualitatively different responses to
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43 291 incorporating fossil data could have many explanations. The results of Nogues-Bravo et al.
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45 292 (2016) might have been influenced by their grouping of species into genera and families,
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47 293 whereas we studied responses at the species level for 6 of our 8 plant taxa. Alternatively, these
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49 294 differences might also be due to inherent differences of temperate and tropical species. The
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3 295 thermal niches of tropical species are expected to be narrower than temperate species and to
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5 296 show greater conservatism through time. Finally, it is also possible that differences in species
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8 297 diversity and competitive interactions within the tropics may influence this result.
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10 298 The relatively minor impact of including information about the types of climates
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12 299 occupied in the past on the niches in our study might be due to the specific effects of climate
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14 300 change in tropical highlands. It is clear from studies of past vegetation (Dupont et al., 2011;
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16 301 Ivory et al., 2018) and previous SDM work (Ivory et al., 2016) that some Afromontane taxa
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18 302 formed continuous forest corridors in the lowlands during past warm periods. Further, in the
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20 303 tropics, changes in rainfall and seasonality are known to have played a strong role in range
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22 304 changes in the past (Vincens et al., 2007a). We demonstrate that this is also likely true in the
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24 305 future, as projected changes in other climate variables, like diurnal temperature and rainfall,
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26 306 buffer against range loss reductions for many taxa at certain elevations. This suggests more
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28 307 complex responses to climate change than would be expected from temperature alone.
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33 308 Our findings suggest that the magnitude of climate change forecasted under RCP 2.6 is
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35 309 actually quite large for Afromontane taxa, leading to range loss of up to 42% for certain species,
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37 310 even with niche requirements estimated from modern and fossil occurrences. Africa is expected
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39 311 to warm more than other tropical continents (Niang et al. 2014). This means that even ambitious
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41 312 greenhouse gas reduction targets result in relatively large increases in mean annual temperature
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43 313 (+1.4°C; Table S1) and plant distributions.
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47 314 These results also differ from work on other regions, such as South America and Europe,
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49 315 where species have shown range contraction at lower elevations and expansion upslope in
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51 316 response to climate warming (Feeley and Silman 2010; Dullinger et al. 2012; Gottfried et al.
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53 317 2012; Duque et al. 2015). In contrast, these Afromontane taxa are not forecast to expand
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3 318 upslope. This likely results from an important physiographic attribute of this system: that African
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5 319 mountaintops are generally spatially quite small and discontinuous. Thus, currently there is very
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7 320 little area at higher elevations that is not already occupied by these taxa (Fig. 4; S6). In fact,
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9 321 Afromontane trees already occupy over 90% of available land area at these elevations, leaving
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11 322 little available for future upslope expansion (Fig. 4; Elsen and Tingley 2015). These species also
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13 323 are not forecasted to expand to cooler climates northward or southward, as they already occupy
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15 324 most mountains on the African continent. We therefore suggest that a lack of suitable upslope
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17 325 habitat drastically reduces the capacity of these taxa to adapt to changing climate.
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22 326 Although the impacts of land-use change alone are smaller than the impacts of climate
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24 327 alone, the combined effects of climate and land-use change can be extremely large (Figs. 1, 2;
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26 328 Table 1). Range reductions can be as much as 26% larger on average when land use is included
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28 329 than from climate alone when RCP 2.6 is used (Table 1). In fact, the impact of RCP 2.6 plus
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30 330 high intensity land use results in nearly the same magnitude of range loss as for RCP 8.5 climate
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32 331 alone (Fig. 2; Table 1). This suggests that even though climate has the strongest single effect on
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34 332 range reduction, intensifying land use will have a powerful secondary effect. Moreover, some
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36 333 species, particularly those shown by Ivory et al. (2016) to be least sensitive to temperature, are
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38 334 disproportionately affected by land-use change. Incorporating both climate change and land use
39
40 335 impacts, *Olea africana* could lose almost half its climatically suitable range from land-use
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42 336 change, as its present, low-elevation range is where future land-use changes are forecast to be
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44 337 largest (Figs. 1 and 4). Thus, even if species can adapt to a changing climate, range loss at the
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46 338 lower range boundary is still likely due to lowland exclusion through anthropogenic activity.
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51 339 Although the high and low intensity land-use scenarios used here can help give us an
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53 340 understanding of the differential impacts of rapidly growing populations in Africa, the indefinite
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3 341 outcomes of these complex systems injects considerable uncertainty into end-of-century land-use
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5 342 predictions (Pontius and Spencer, 2005). Further, in Africa small-scale land-use changes have
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7 343 impacts beyond those captured in the IAMs, like harvesting of non-timber forest products (e.g.
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9 344 medicines from *Prunus africana* and *Hagenia abyssinica* [Stewart, 2003; Cunningham et al.,
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11 345 2016]). This suggests that the IAMs are likely to be conservative estimates of land-use impacts.
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14 346 Further, many studies investigating the ongoing effects of deforestation in parts of the
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17 347 Afromontane regions suggest massive losses over the last 60 years (Hall et al., 2009) and that
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19 348 land use alone unchecked may result in near total loss of forest (Ngigi and Tateishi, 2004). This
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21 349 is particularly likely given that some of Africa's highlands are already the most densely human
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23 350 populated lands on the continent with populations projected to increase faster than anywhere else
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25 351 on Earth (Plumptre et al., 2004; Linard et al., 2012).

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28 352 The collapse in range size we predict is coupled with forecast changes in the patch size,
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30 353 number, and connectivity of populations across the region (Fig. 5). Habitat connectivity is
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32 354 critical to maintaining viable populations (Shoemaker et al. 2013). In this region, one way this
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34 355 occurs is by maintaining genetic diversity. In Afromontane regions many tree species are
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36 356 dispersed by animals, such as birds, so geographic barriers and the effects of fragmentation may
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38 357 be overcome by long-distance dispersal (White, 1981; Mairal et al., 2017). However,
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41 358 fragmentation leading to small disconnected patches by climate and land-use change result in
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43 359 enhanced edge effects which may lead to regional functional extinctions, or extinction debt
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45 360 (population reduction leading to inevitable extinction) long before species completely disappear
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47 361 (Jackson and Sax 2010; Platts et al. 2013; Haddad et al., 2015). While the quantitative changes
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49 362 we describe here for habitat fragmentation depend on the thresholds used to define land use, the
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51 363 qualitative results themselves are not. For example, we considered a grid-cell as unsuitable for
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3 364 Afromontane forest when the summed area of agricultural land, pasture-land, and urban areas
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5 365 covered >90% of the grid-cell. This threshold was chosen as it represented the largest change in
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7 366 land-use distributions with respect to modern within the Afromontane region (Fig. S3). However,
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10 367 many of the taxa considered here occur within grid cells projected to undergo complete land
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12 368 cover conversion, meaning 100% of land area within a grid cell will exclude natural vegetation
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14 369 (Fig. S3). This suggests that regardless of which threshold is chosen as a cutoff for our estimates
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17 370 of grid-cell suitability, anthropogenic activities will have a strong impact.

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19 371 We did not explicitly consider the role of elevated CO₂ or fire in driving the future
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21 372 distributions of Afromontane taxa. However, by incorporating fossil-informed niches into our
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23 373 models from ancient periods with lower than modern CO₂ (~180ppm; LGM) and pre-industrial
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25 374 CO₂ (~280ppm; MH), we have some reference on the potential influence that CO₂ may have.
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28 375 Lower atmospheric CO₂ has been cited a driver of tree decline through enhanced water stress in
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30 376 favor of C4 dominated grasslands with higher water-use efficiency (Bragg et al., 2013).
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33 377 Interestingly, we find that during periods with lower CO₂ than today, Afromontane forest species
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35 378 occurred in warmer areas (Ivory et al., 2016). Given the heterogeneity of regional climate
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38 379 change in comparison to CO₂, we suggest that elevated CO₂ will not be a primary driver of
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40 380 vegetation responses to local climate conditions, but could modulate responses. Fire is also likely
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43 381 to impact species' distributions. Ivory et al. (2018) suggest that the exclusion of highland taxa
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45 382 from the lowlands may for some species be related to fire intolerance. Their observation of
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47 383 increased fire activity in lowland East Africa after 80ka may also play an important non-climatic
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49 384 role in constraining these ranges.

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51 385 Afromontane forests are ecologically important hotspots of biodiversity, not just for plants,
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53 386 but also for endemic birds, mountain gorillas, and other fauna (White 1981; Dulle et al. 2016).
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3 387 Yet future climate and land-use change could result in large-scale collapse of this now
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5 388 widespread ecosystem. We show that including datasets of fossil distributions can alter range
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7 389 forecasts by counteracting the effect of climate disequilibrium of modern species' ranges, but
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10 390 only by a very moderate amount for Afromontane taxa. We show that these taxa will lose a
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12 391 minimum of ~65% of their modern range under high emission and low land-use scenarios (Table
13
14 392 1). Even with large emissions reductions (RCP 2.6), if land-use change is high, more than half of
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16 393 Afromontane tree taxa modern ranges may be lost. Under higher emissions and land use, much
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18 394 of the geographic footprint of this system (~80%) may be entirely lost.

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21 395 In the face of such widespread geographical collapse, it becomes imperative to safeguard
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23 396 patches that will remain. Management strategies that focus on conserving species *in situ* are
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25 397 unlikely to yield favorable results from many areas at lower elevations in a warming climate,
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27 398 even if we were to achieve the RCP 2.6 trajectory. Further, given that RCP 2.6 is unlikely based
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29 399 on existing emissions, and that few low-elevation regions are forecast to be suitable under higher
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31 400 emissions, management efforts should focus on protecting areas at mid- and upper elevations and
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33 401 across elevational gradients. Likewise, conservation efforts should prioritize protecting habitat
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35 402 patches forecast to remain largest such as is in southern Africa, as these will minimize potential
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37 403 extinction debts, and to prioritize areas that can provide critical linkages in maintaining
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39 404 connectivity. Ultimately, our study indicates that fossil data used to expand the known niche
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41 405 requirements of extant tropical species may do little to reduce forecasted threats from climate
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43 406 change or land use, particularly when there are strong non-climatic constraints on potential shifts
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45 407 in species distributions.

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636 **Data Accessibility Statement:** The data supporting the results already exists and is freely
 637 available in the Global Biodiversity Information Facility (GBIF) and the African Pollen Database
 638 (APD).

639

640 Tables

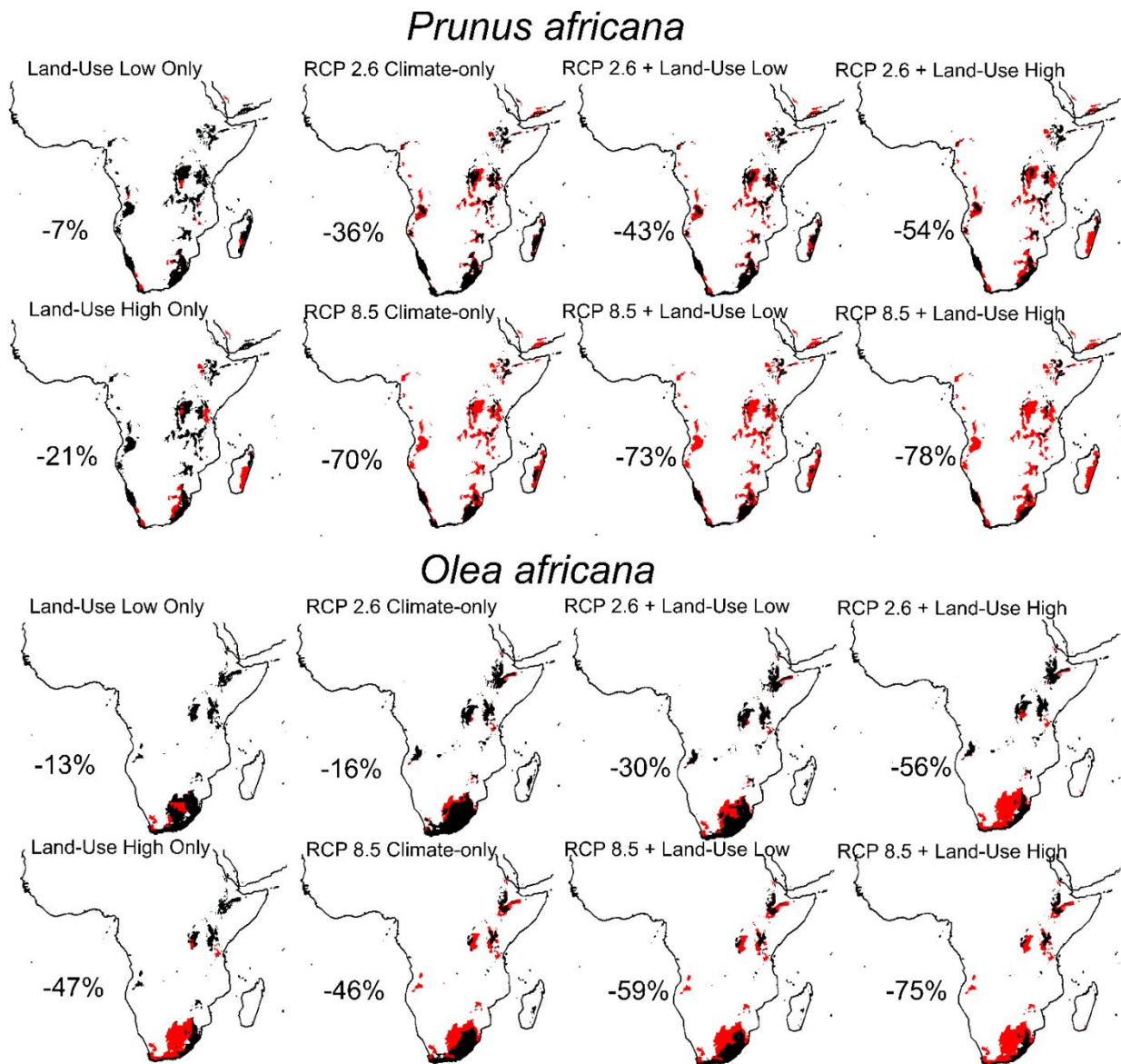
641 **Table 1.** Proportion of the modern range of eight Afromontane taxa forecast to be lost under
 642 future climate change and land-use scenarios. Species distribution models used to generate these
 643 forecasts were created using both paleoecological (Paleo) and modern occurrences (NO Paleo)
 644 and an ensemble of climate models.

		Climate Only		LU-Only		LU and Climate	
RCP 2.6		Paleo	NO Paleo	LU Low	LU High	LU Low	LU High
645	<i>Hagenia abyssinica</i>	0.336	0.348	0.152	0.361	0.489	0.645
647	<i>Ilex mitis</i>	0.421	0.421	0.081	0.272	0.468	0.610
648	<i>Juniperus procera</i>	0.387	0.387	0.138	0.337	0.514	0.664
649	<i>Nuxia</i> spp.	0.361	0.427	0.122	0.315	0.483	0.623
650	<i>Olea africana</i>	0.156	0.287	0.135	0.472	0.302	0.564
651	<i>Olea capensis</i>	0.190	0.380	0.060	0.201	0.368	0.475
652	<i>Podocarpus</i> spp.	0.239	0.366	0.063	0.221	0.309	0.453
653	<i>Prunus africana</i>	0.364	0.400	0.073	0.208	0.431	0.536
654	Average	0.307	0.377	0.103	0.298	0.421	0.571
		Climate Only		LU-Only		LU and Climate	
RCP 8.5		Paleo	NO Paleo	LU Low	LU High	LU Low	LU High
655	<i>Hagenia abyssinica</i>	0.696	0.705	0.152	0.361	0.766	0.857
656	<i>Ilex mitis</i>	0.732	0.732	0.081	0.272	0.749	0.812
657	<i>Juniperus procera</i>	0.664	0.664	0.138	0.337	0.746	0.835
658	<i>Nuxia</i> spp.	0.684	0.714	0.122	0.315	0.736	0.813
659	<i>Olea africana</i>	0.437	0.584	0.135	0.472	0.588	0.748
660	<i>Olea capensis</i>	0.602	0.670	0.060	0.201	0.673	0.732
661	<i>Podocarpus</i> spp.	0.646	0.719	0.063	0.221	0.664	0.741
662	<i>Prunus africana</i>	0.701	0.720	0.073	0.208	0.730	0.783
663	Average	0.645	0.689	0.103	0.298	0.706	0.790

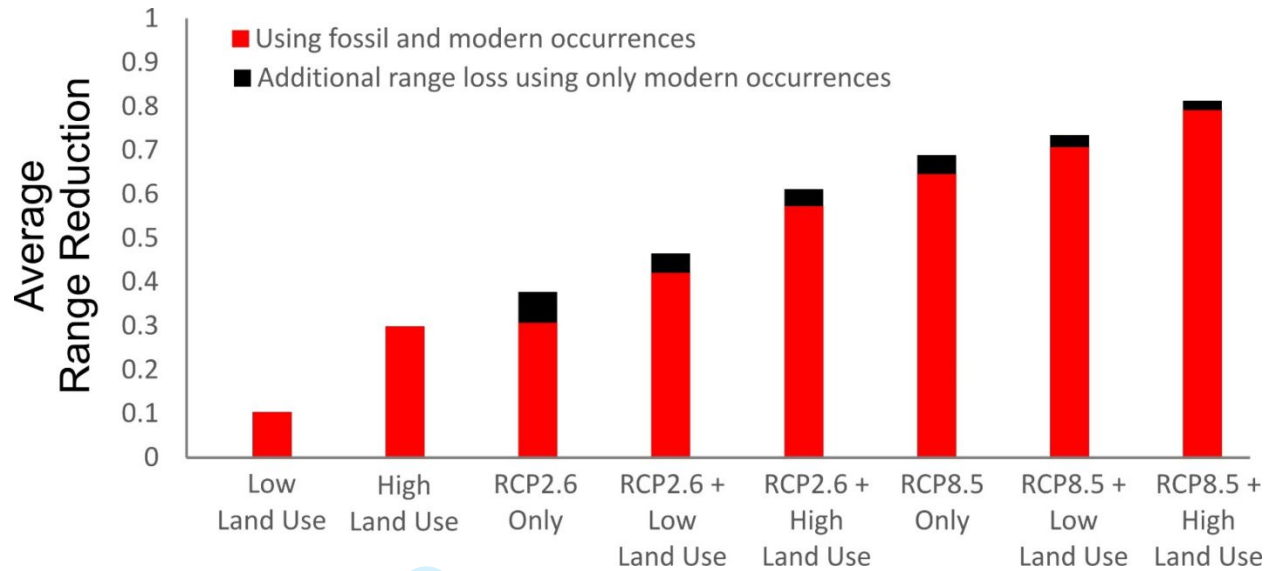
664 Figures

665 **Figure 1.** Future range forecast (2061-2080) of *Prunus africana* and *Olea africana* from species
 666 distribution models including fossil and modern occurrence data and using Representative
 667 Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of high and low land-
 668 use scenarios (MESSAGE and IMAGE). Range forecasts for the six remaining taxa are shown
 669 in Fig. S1. Forecast range retained is shown in black and forecast loss is shown in red (and this
 670 percentage of modern range lost is provided as a number below each panel).

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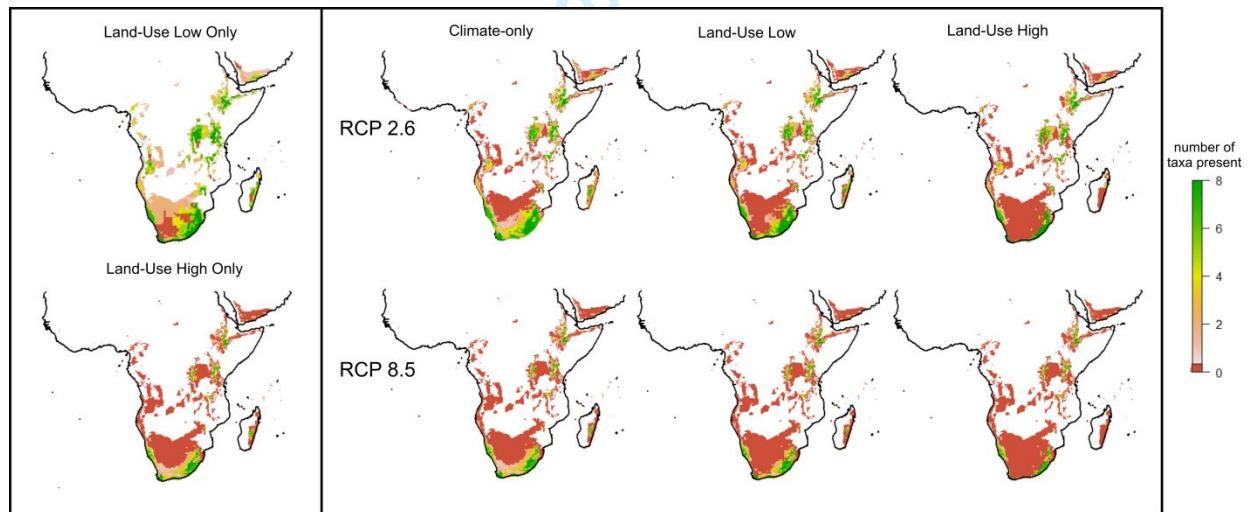


672 **Figure 2.** Range loss for climate and land-use change combinations forecasted to occur on
 673 average across species for the end of the century (2061-2080) when SDMs are based on both
 674 modern and fossil occurrences (red) or just on modern occurrences (in which case the additional
 675 forecasted loss is shown in black).



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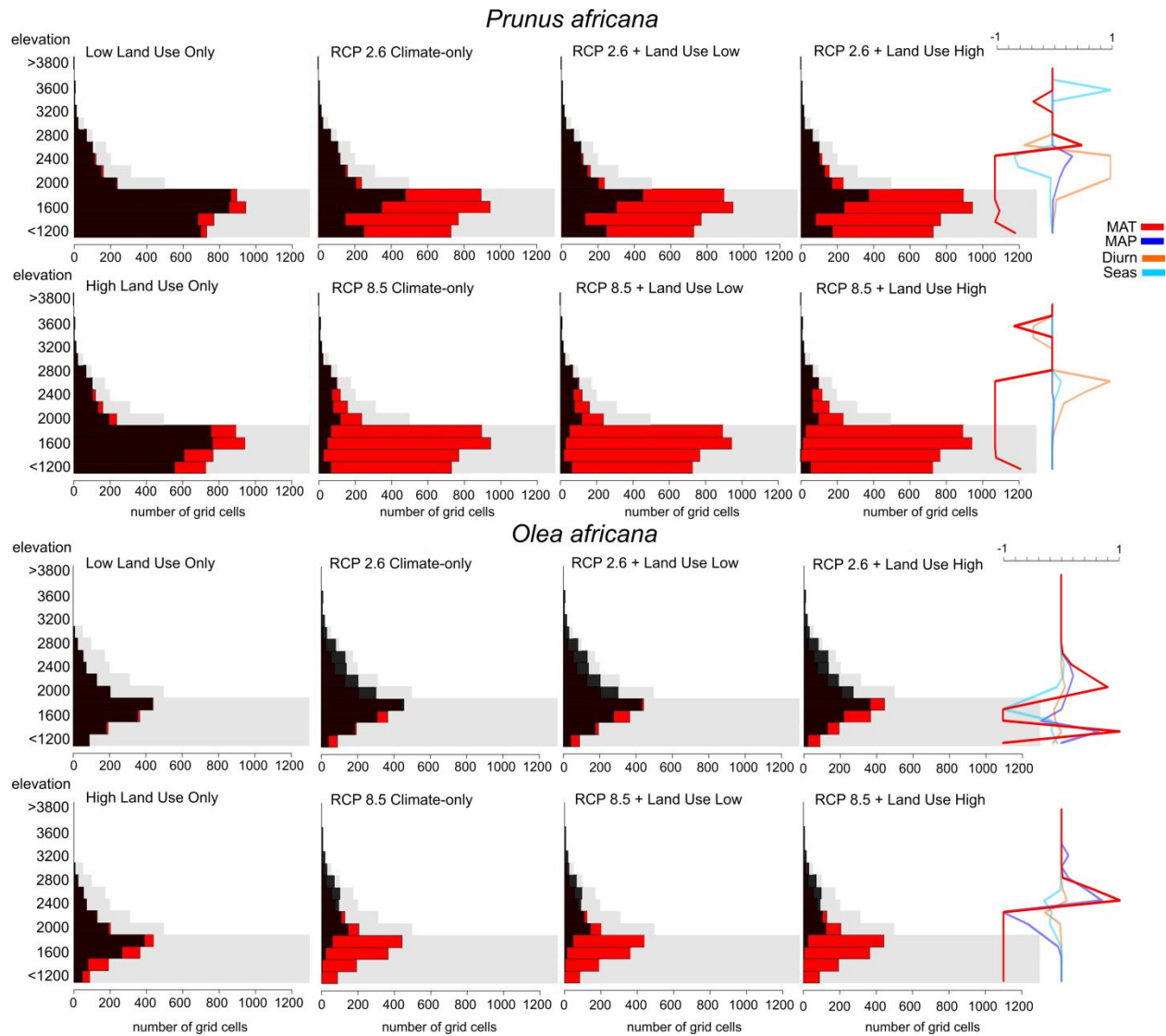
677 **Figure 3.** Future range forecast (2061-2080) of all studied Afromontane trees from species
 678 distribution models including fossil and modern occurrence data and using Representative
 679 Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of high and low land-
 680 use scenarios (MESSAGE and IMAGE). Number of species with forecasted ranges retained are
 681 shown and where all forecasted range is lost is in red.



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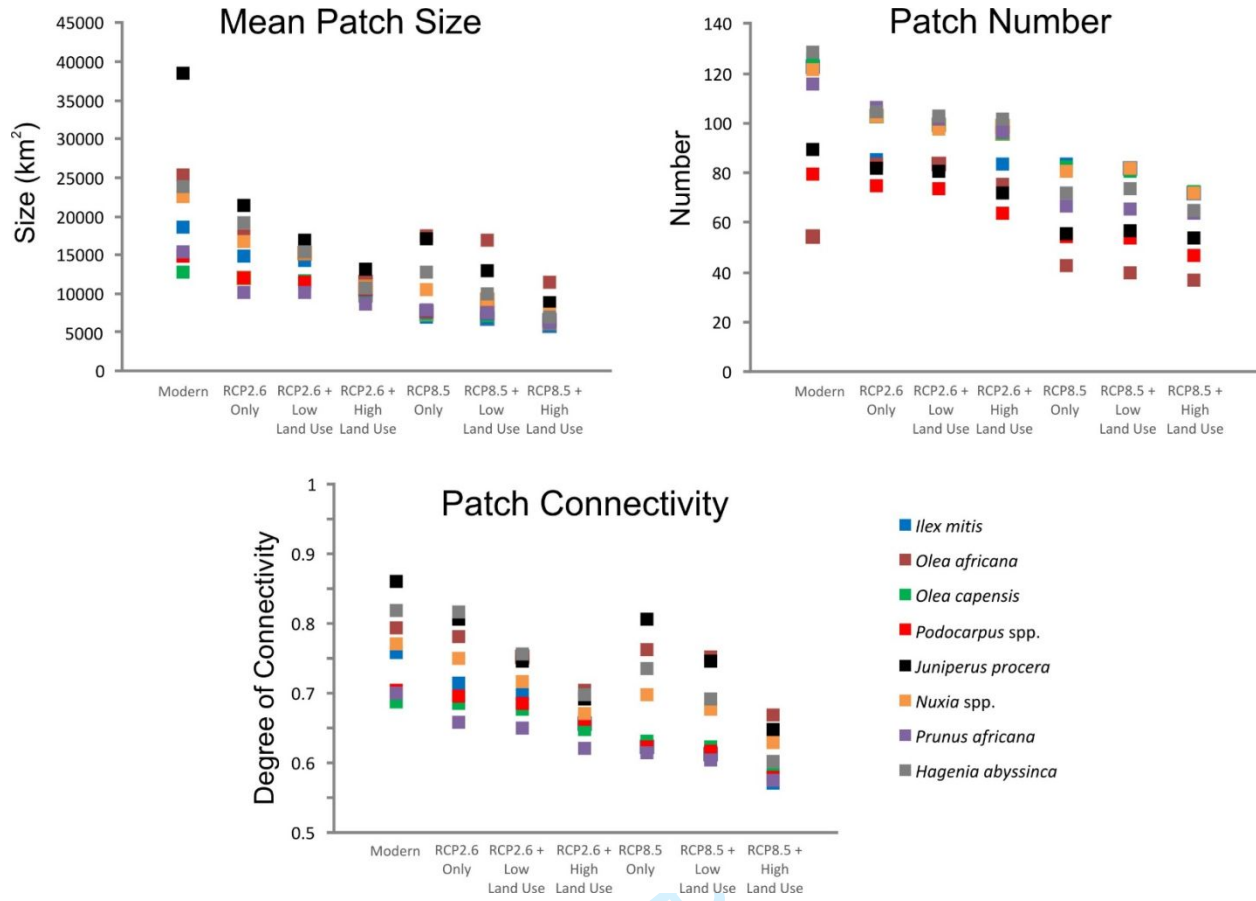
683 **Figure 4.** Future range forecast (2061-2080) of *Prunus africana* and *Olea africana* by elevation
 684 band from species distribution models including fossil and modern occurrence data and using
 685 Representative Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of
 686 high and low land-use scenarios (MESSAGE and IMAGE). Forecasted loss is shown in red and
 687 future range in black. Light grey represents the total area available in the elevational band. The
 688 right-most panel for each RCP shows the range sensitivity to each climate variable in each
 689 elevational band, MAT (mean annual temperature, red), MAP (mean annual precipitation, dark
 690 blue), Diurn (diurnal temperature, orange), Seas (rainfall seasonality, light blue). Negative values
 691 indicate that a variable contributes to a range contraction, positive values indicate that a variable

692 contributes to a range expansion. The remaining six taxa elevational range forecasts are shown in
 693 Fig. S3.



694

695 **Figure 5.** Patch statistics for forecasted ranges of taxa presented in Figures 1 and Fig. S1,
 696 derived using species distribution models including fossil and modern occurrence data and using
 697 Representative Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of
 698 high and low land-use scenarios (MESSAGE and IMAGE). Mean patch size is the average of
 699 the area of all patches, patch number is the remaining total number of patches, and patch
 700 connectivity is a dimensionless index of patch aggregation on the landscape.



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Review

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