

Spatial heterogeneity of climate change in an Afrotropical centre of endemism

Philip J. Platts, Roy E. Gereau, Neil D. Burgess and Rob Marchant

P. J. Platts (*philip.platts@york.ac.uk*), *The York Inst. for Tropical Ecosystem Dynamics (KITE), Environment Dept, Univ. of York, Heslington, York, YO10 5DD, UK, and Conservation Science Group, Zoology Dept, Univ. of Cambridge, Cambridge, CB2 3EJ, UK.* – R. E. Gereau, *Missouri Botanical Garden, PO Box 299, St Louis, MO 63166-0299, USA.* – N. D. Burgess, *Conservation Science Group, Zoology Dept, Univ. of Cambridge, Cambridge, CB2 3EJ, UK, and Centre for Macroecology, Evolution and Climate, Dept of Biology, Copenhagen Univ., Universitetsparken 15, DK-2100, Copenhagen, Denmark, and WWF-US Conservation Science Program, 1250 24th Street NW, Washington DC 20037, USA.* – R. Marchant, *The York Inst. for Tropical Ecosystem Dynamics (KITE), Environment Dept, Univ. of York, Heslington, York, YO10 5DD, UK.*

Broad-scale assessments of how climate change might impact mountain ecosystems, especially in areas of high biodiversity and endemism, are compromised by the lack of localised climate feedback in global circulation models. Here, we use regionally downscaled climate models to highlight how spatial variation in forecast change could impact rare plant distributions differentially across the Eastern Arc Mountains of Tanzania and Kenya, part of the Eastern Afrotropical Biodiversity Hotspot. Concordant with the theory that climatic stability facilitates the accumulation of rare species, we find significant positive correlations between endemic plant richness and future climatic persistence within the dispersal-limiting sky islands of this mountain archipelago. Further, we explore the hypothesis that mountain plants will move upslope in response to climate change and find that, conversely, some species are predicted to tend downslope, despite warmer annual conditions, driven by changes in seasonality and water availability. Importantly, two thirds of the modelled plant species are predicted to respond in different directions in different parts of their ranges, exemplifying the potential for individualistic responses of species and disjunct populations to environmental change, and the need for regional focus in climate change impact assessment. Conservation planners, and more broadly those charged with developing climate adaption policy, are advised to take caution in inferring local patterns of change from zoomed perspectives of broad-scale models. Moreover, a preoccupation with mean annual temperature as the principal driver of ecosystem change is misguided and could compromise efforts to make conservation plans resilient to future climate change. Faced with spatially complex and inherently uncertain future conditions, sensible priorities are to restore forest connectivity and to underpin adaption strategies with knowledge of how ecosystems and people have adapted to previous episodes of rapid change.

Global and continental-scale modelling assessments warn of climate-induced range contraction and potential extinction for many species by the end of the 21st century (Thomas et al. 2004, McClean et al. 2005, Pereira et al. 2010). With respect to globally important but locally complex mountain systems, these studies have limited potential to guide ground-level adaption. The datasets employed are too coarse-grained to detect accurately changes in niche-space or potential refugia for all but the most generalist and wide-ranging of species, risking a bias in climate-sensitive priorities toward the least vulnerable components of biodiversity. Spatially downscaled, high-resolution climate projections are therefore in great demand for conservation planning, especially in tropical Africa where species data and observational time-series are scarce (Wilby et al. 2004).

Addressing this need, a recently popularised technique is change-factor downscaling, whereby anomalies forecast

by global circulation models (GCMs) are added to higher-resolution contemporary baselines (Ramirez and Jarvis 2008, Tabor and Williams 2010, Kou et al. 2011). The resulting surfaces convey locally important detail such as orographic rainfall, affording investigations of ecological impacts at scales more relevant to management (e.g. 1 km). A serious shortcoming, however, is that spatial heterogeneity in change is crudely approximated by interpolation of GCM squares (typically of side 200–600 km). Governments, conservation organisations and other bodies concerned with climate change adaption are therefore provided with seemingly high-resolution scenarios of change, upon which policy is developed, but that omit key regional dynamics that are fundamental to the conservation of species, habitats and associated natural resources. Incorporation of more localised climate feedback is especially critical in highly heterogeneous landscapes and areas

with strong land-ocean climate gradients, both of which are exemplified in east Africa.

An increasingly accessible means to minimise this spatial uncertainty is through the use of dynamically downscaled forecasts, obtained from regional climate models (RCMs). RCMs employ thermodynamic processes, interactions and feedbacks similar to those of large-scale coupled atmosphere-ocean models, but operate on horizontal resolutions of tens rather than hundreds of kilometres. Although not currently available for all parts of the world, the derivation of change factors from regional models is likely to become increasingly feasible within the timeline of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC-AR5, scheduled for 2014). In this paper, we

combine dynamic and change-factor downscaling to investigate patterns of change forecast for the Eastern Arc Mountains (EAMs) of Tanzania and Kenya (Fig. 1a), part of the Eastern Afromontane Biodiversity Hotspot (Mittermeier et al. 2004). Of the 26848 vascular plant species indigenous to tropical Africa, a remarkable 3834 (14%) have been documented in the EAMs (Gereau unpubl.) – habitats representing just 0.24% of the land area (Platts et al. 2011). The assessment of climate change impacts on these species is, per unit area of investment, one of the most important and cost effective foci for biodiversity conservation and adaption planning globally (Brooks et al. 2002), but has to date been hindered by a lack of data and analytical methods at spatial scales relevant for conservation decision making.

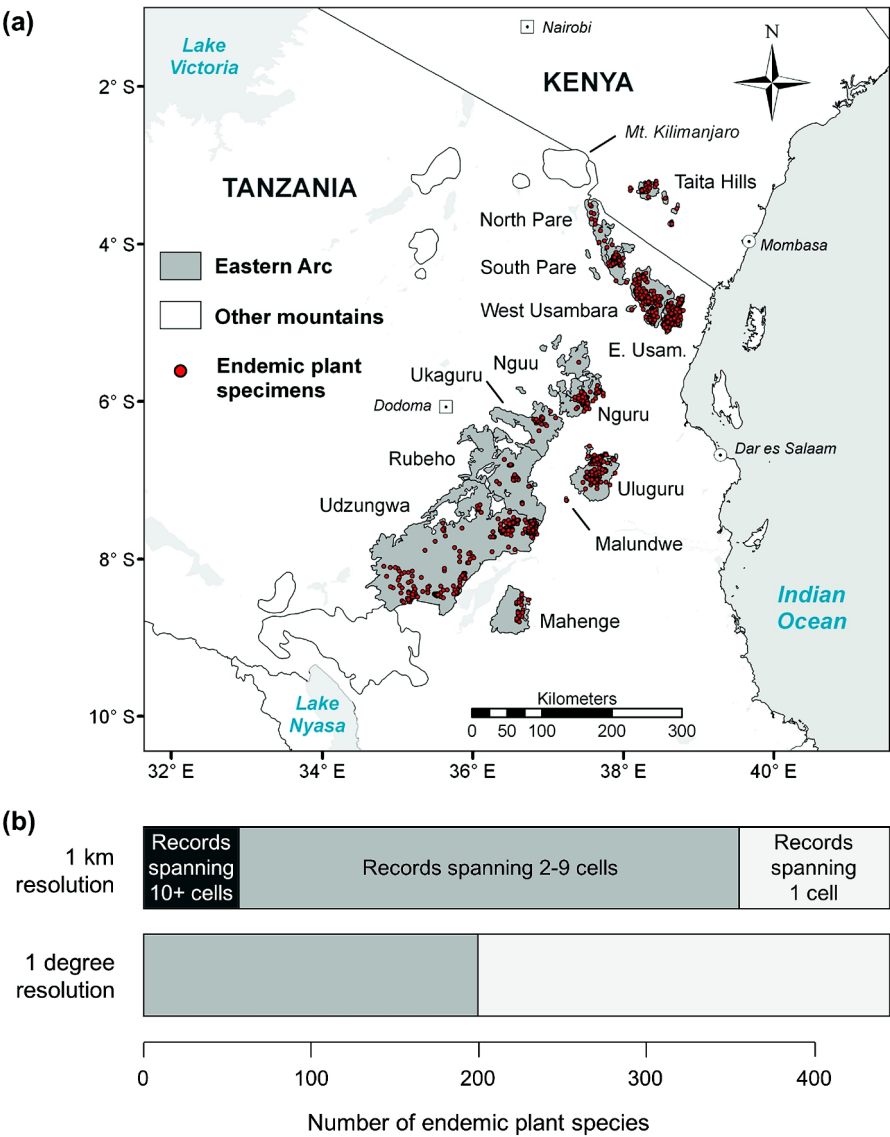


Figure 1. (a) The Eastern Arc Mountains, spanning 5.2 million ha (10% forest) and 13 distinct blocs. Volcanoes to the north and highlands to the south are floristically distinct and contain fewer species of restricted distribution, attributed to geological age and climatic influence (Lovett 1990). Red dots locate the origins of endemic plant specimen data used in this study. (b) Bar plot summarises sample prevalence at resolutions suitable for species distribution modelling at local (1 km) and continental/global (1° ~ 111 km) scales. Simple envelope models are possible for 354 and 198 species at the higher and lower resolutions, respectively. For more sophisticated kinds of distribution model (e.g. statistical regression), records of occurrence in at least ten cells are required (Stockwell and Peterson 2002). At 1 km resolution, 56 species satisfy this condition; no species has sufficient coverage at 1° resolution.

The EAMs encapsulate many characteristics that confound site-scale inference from broad-scale assessments: they are topographically complex, fragmented across a series of 'sky islands' and historically dependent upon maritime climatic influence for species persistence (Lovett 1990, Marchant et al. 2007, Platts et al. 2011). Using an RCM already available for the region, we identify sites where baseline climates might be lost and where novel conditions could emerge. Implications for conservation are discussed in relation to plant species strictly endemic to the mountain ecoregion, revealing how spatially diverse shifts in seasonality and rainfall have potential to drive ecosystem change in directions unforeseen by broader-scale models. With this new level of spatial detail, it is possible for the first time to question whether future change may be indicative of past ecosystem stability in this globally important centre of endemism.

Methods

Selection of study region

The EAMs (Fig. 1a) harbour remnants of a pan-African forest belt, which prior to the uplift of the Central Tanganyika Plateau (25 MY BP) periodically extended to the Guineo-Congolian forests in west and central Africa (Couvreur et al. 2008). Even older possible links to Madagascar and southeast Asia indicate speciation events dating back over 100 MY to the breakup of Gondwana (Dinesen et al. 1994). Species persistence is attributed to long-term moisture stability under the influence of the Indian Ocean, coupled with potential for populations to 'cling on' in topoclimatic refugia or else track transient conditions up or down slope (Fjelds  et al. 1997, Lovett et al. 2005). In the language of Williams et al. (2007), familiar conditions may have been slow to 'disappear' despite more pronounced climate change at broader scales, giving species longer to adapt via selection or dispersal. The pollen record, although incomplete, appears to support relatively low climate velocities in the EAMs during the Late Quaternary period (Mumbi et al. 2008, Finch et al. 2009). Similarly, analysis of macroclimatic shifts since the last glacial maximum suggests low climate velocities in centres of endemism more generally (Sandel et al. 2011). These deeper time perspectives link to key questions for biogeography and conservation planning, such as which sites might remain buffered under the present warming trend, and whether linking past and future change through theory could help planners to mitigate biodiversity loss.

Plant data

Point distributions for plant species currently understood to be endemic to the EAMs were downloaded from TROPICOS (<www.tropicos.org/>). The raw data consisted of 3526 herbarium specimens spanning 471 endemic species in 80 vascular plant families, of which 262 species (56%) are endemic to a single mountain bloc. Due to narrow ranges and threats to habitat, the majority of these species are being assessed for possible inclusion on the IUCN Red List of Threatened Species (Gereau et al. 2010, IUCN

2011). Botanical identifications were verified at the Royal Botanic Gardens Kew (UK), the Missouri Botanical Garden (USA) and the Univ. of Dar es Salaam (Tanzania). Discrepancies between recorded (specimen labels) and remotely-sensed (SRTM ver. 4; Jarvis et al. 2008) elevations were investigated alongside field notes, ensuring that each specimen was reliably georeferenced to the correct 100 m altitudinal band. Unambiguous errors were corrected (e.g. confusion between UTM zones or between eastings and northings); unresolved records were discarded. This resulted in a dataset spanning 444 species, of which 354 had records of occurrence in at least two distinct 1 km grid squares and 56 in at least ten distinct grid squares (Fig. 1b).

Climate data

Regional climate forecasts were obtained from the REMO RCM (Potsdam Inst. for Climatic Impacts Research), which operates at a horizontal resolution of 55 km (0.5 ). Boundary conditions were from the ECHAM5 GCM (210 km horizontal resolution, 1.9 ), which shows good agreement with observed 20th century climate in east Africa (Doherty et al. 2010). As for other GCMs, ECHAM5 predicts hotter and wetter conditions in east Africa (17% increase in both annual mean temperature and annual rainfall by 2090). Two IPCC-AR4 scenarios were available for REMO. The first, scenario A1B, describes a world in which economic growth and globalisation prevail, and where energy sources are balanced across fossil-intensive and no-fossil technologies. Global population peaks mid-century and declines thereafter. The second scenario, B1, assumes similar population and convergence among regions as A1B, but with more rapid improvements in public services and economic structures – the emphasis is on clean and resource-efficient technologies, leading to reduced warming trend (IPCC 2007). Given recent patterns in global energy consumption and sluggish rates of decarbonisation, both of these SRES storylines may now be considered optimistic (Peters et al. 2012).

Regional anomalies for the years 2055 (mean of 2046–2065) and 2090 (2081–2100) were calculated relative to present-day conditions before being spatially interpolated to 1 km using regularised splines with tension (Mitasova and Mitas 1993). These smoothed surfaces were then added to high-resolution baseline grids (Fig. 2). For temperature baselines, we used 1 km monthly interpolations of records from the period 1950–2000 (mean 1975; WorldClim, Hijmans et al. 2005). Rainfall baselines were from the Tropical Rainfall Measuring Mission (1997–2006, mean 2001), post-processed to obtain 1 km monthly grids of surface-received orographic rain (Mulligan 2006). Mist- and fog-affected zones could not be identified directly, but might to some extent reflect patterns in the rainfall grids, which include corrections for wind velocity, slope aspect and topographic exposure (Mulligan 2006).

From the monthly grids, we derived five climatic gradients known to correlate well with plant distributions in the study region (Platts et al. 2010, Greve et al. 2011): mean annual temperature and temperature seasonality (annual range); mean annual rainfall and dry season water stress; and a moisture index, which provides a parsimonious

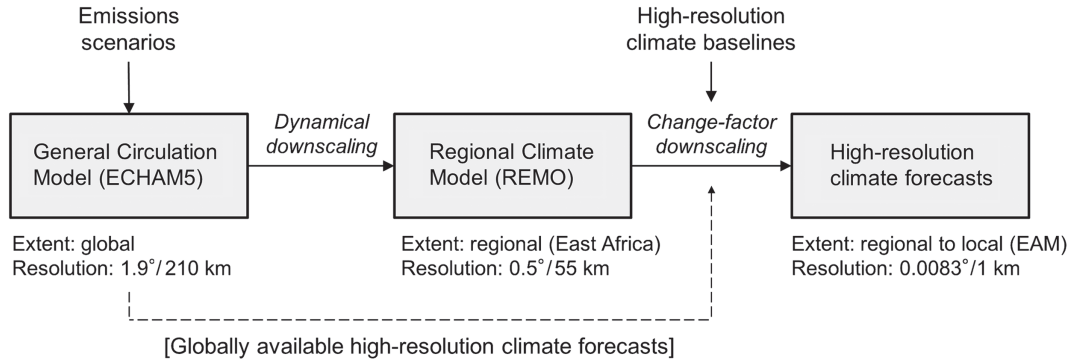


Figure 2. Two-step climate downscaling procedure exploits mechanistic models to their spatial limits, beyond which fine-scale variation is inferred from contemporary estimates. Step 1: parameterise a regional climate model using boundary conditions from a subset of GCM squares. Step 2: calculate 21st century anomalies, interpolate and add to higher-resolution baseline grids.

measure of annual conditions (ratio of annual rainfall to potential evapotranspiration, according to Thornthwaite 1948). Water stress is defined as the cumulative deficit in mean monthly rainfall throughout the longest dry season, where a deficit is $< 10 \text{ mm month}^{-1}$.

Climates lost and gained

Sites were identified where future conditions might extend beyond climate-space accessible to species in the present (climates ‘gained’), as well as the reciprocal: areas where current climates may no longer be accessible in the future (climates ‘lost’). The search for climate analogues extended to all grid cells within, but not beyond, each of the 13 mountain blocs that comprise the EAM chain: lowland habitats and large rivers are significant barriers to dispersal. Results were mapped according to the proportional ‘distance’ of climates gained, or lost, beyond present or future extremes, respectively (Williams et al. 2007, Platts et al. 2008). These values were summed over four of the five summary variables described above (moisture index was omitted to provide an equal balance between temperature and rainfall, and between annual and seasonal conditions):

$$Gain_{i,b} = \sum_{X \in S} \frac{\max\{F_{X,b,i} - \max(P_{X,b}), \min(P_{X,b}) - F_{X,b,i}, 0\}}{\max(P_{X,b}) - \min(P_{X,b})}$$

$$Loss_{i,b} = \sum_{X \in S} \frac{\max\{P_{X,b,i} - \max(F_{X,b}), \min(F_{X,b}) - P_{X,b,i}, 0\}}{\max(F_{X,b}) - \min(F_{X,b})}$$

where S is the set of four climate variables, $P_{X,b,i}$ and $F_{X,b,i}$ are present and future values of variable X in cell i of mountain bloc b , and $P_{X,b}$ and $F_{X,b}$ are the sets of present and future values of X across all cells in the same bloc.

Overlaying the plant data with maps of climate loss revealed how many species will be forced to adapt their climatic niche during the 21st century, or else persist in refugia at the sub-1 km scale, regardless of forest connectivity or dispersal capacity within their current mountain bloc distributions. Under the ecoclimatic stability hypothesis, areas with historically stable climates are thought to

contain higher levels of endemism (Fjeldsø et al. 1997, Lovett et al. 2005). By extension, one might expect climates lost in the 21st century to exhibit some negative correlation with patterns of endemic plant richness, a possibility we investigated by plotting the former against the latter at known endemism sites.

Endemism vs altitude

Univariate response

The popular application of temperature lapse-rate models in preference to spatially explicit, multivariate climate projections, particularly in mountain regions (Colwell et al. 2008, Kreyling et al. 2010, La Sorte and Jetz 2010), carries an implicit assumption that seasonality and rainfall are less important than annual mean temperatures in limiting species’ altitudinal (latitudinal) distributions, or at least that changes in these variables will act upon distributions in a similar way. Accordingly, we tested the null hypothesis that peak plant endemism would shift upslope in response to forecast changes in seasonality and rainfall, as well as to warming along the altitudinal gradient. For each of the 354 species with two or more spatially distinct populations recorded (on a 1 km grid; Fig. 1b), we inferred continuous climatic suitability, subject to forest and bloc distributions, within the range of conditions at collection sites. Postulating that each climate variable, in turn, is solely important for determining species’ range limits, these one-dimensional envelopes were forced under climate scenarios and then summed over species to reveal net changes in the altitudinal distribution of endemism.

Multivariate response

For 56 species with ten or more spatially distinct occurrence records (Fig. 1b), we used generalised additive modelling to investigate the relative importance of temperature, seasonality and moisture in determining range limits. For each species, performance-weighted multi-models were obtained using stepwise selection (Platts et al. 2008). Highly correlated variables (annual rainfall vs moisture index, Pearson’s $r = 0.92$) were separated prior to selection based on univariate model performance. Where possible,

statistical normality was improved using power transforms (Supplementary material Appendix 1). Each predictor was allowed between one and four effective degrees of freedom, optimised according to a cross-validation of the sum of squared residuals (Yee and Mitchell 1991). Linear fits were preferred where smooth terms did not improve predictive performance under cross-validation. Background data were distributed within the same mountain blocs as the presence data (prevalence = 0.2), and specifically at locations where other endemic plant species have been recorded. Thus, absences exhibited similar spatial, environmental and taxonomic bias as presences (Phillips et al. 2009, Ahrends et al. 2011). Each regression model was iterated ten times using different realisations of background data. The final model for a given grid square was the median prediction across these ten runs. Post-model analysis was restricted to those species for which robust predictive fits were achieved (five-fold cross-validation of the area under the ROC curve, $AUC_{CV} \geq 0.7$). We recorded which climate variables were most often retained during selection and the extent to which species-specific contractions/expansions and altitudinal shifts varied between populations on different mountain blocs.

Results

Spatial variation in change

Annual mean temperature is forecast to increase similarly across the study region (Supplementary material

Appendix 2), reaching a median 21.3°C (scenario B1) or 22.5°C (A1B) by 2090 (interquartile range [IQR] in percentage change from baseline conditions: B1 [12, 15] %; A1B [18, 22] %). Forecasts for other important determinants of species distributions were not so readily anticipated (Fig. 3 and Supplementary material Appendix 2). For example, in West Usambara forests, temperatures become less seasonal (B1 [-4, -3] %; A1B [-5, -4] %) and annual rainfall is predicted to increase (B1 [9, 16] %; A1B [14, 33] %), resulting in a stable moisture index and little change in dry season water stress, despite the rising temperatures. In Uluguru forests, seasonality in temperature and rainfall remain constant, whilst increased potential for evapotranspiration tips the moisture index toward drier conditions by the end of the century. In Udzungwa forests, farther south and more distant from the coast, temperature seasonality is predicted to increase (IQR 2090: B1 [3, 4] %; A1B [8, 10] %) and annual rainfall to decrease (IQR 2090: B1 [-16, 0] %; A1B [-23, 2] %), resulting in a lower moisture index and an increasingly harsh dry season.

Climates lost and gained

Under both emissions scenarios, cool summit conditions are lost to rising temperatures (Fig. 4). Contemporary conditions on the highest peaks of West Usambara, Uluguru and, to a lesser extent, South Pare and Nguru, have no climate analogue anywhere in the EAM chain by 2090. Some such sites are grassland, lacking forest cover and associated levels of endemism due to factors such as frost,

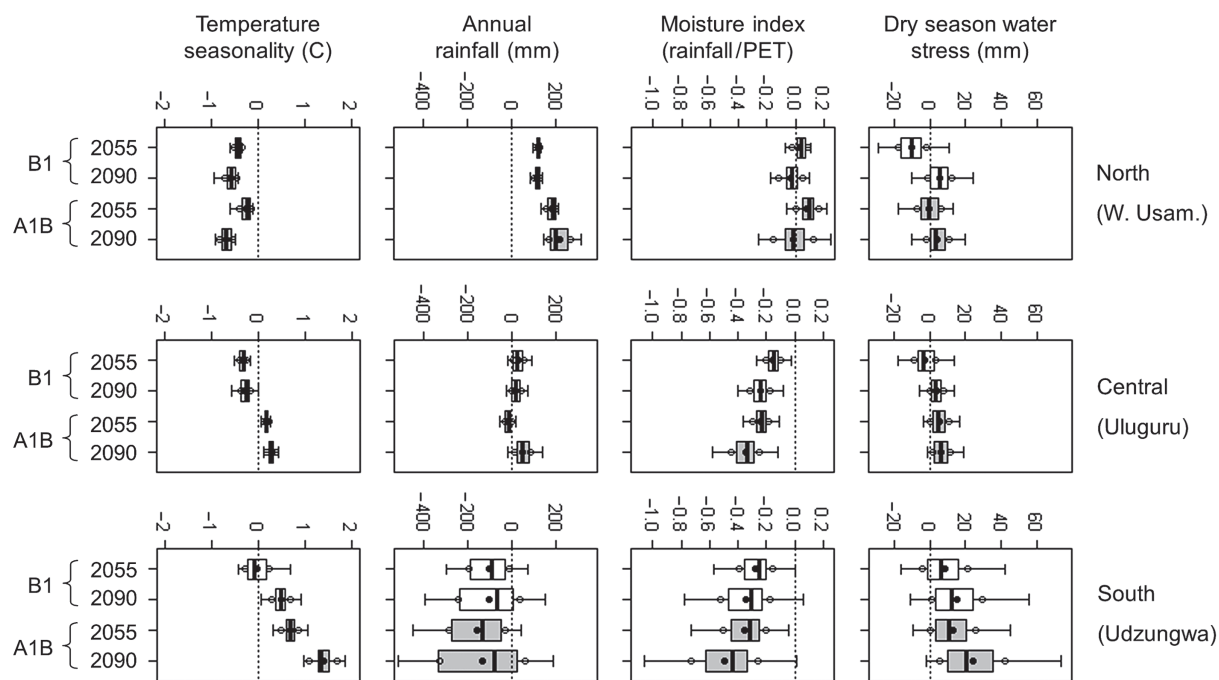


Figure 3. Spatial variation in climate anomalies at sub-regional scales (future minus present, IPCC-AR4 emissions scenarios B1 [white] and A1B [grey]), focussing on forests in three of the best studied and most biologically important mountain blocs: West Usambara, Uluguru and Udzungwa. Dotted lines correspond to baseline conditions. Whiskers extend up to 1.5 times the interquartile range. Filled and open circles show means \pm standard deviations, respectively. Forecasts for mean annual temperature are similar across all mountain blocs (Supplementary material Appendix 2), whereas measures of seasonality and moisture vary considerably from north to south and with distance from the coast.

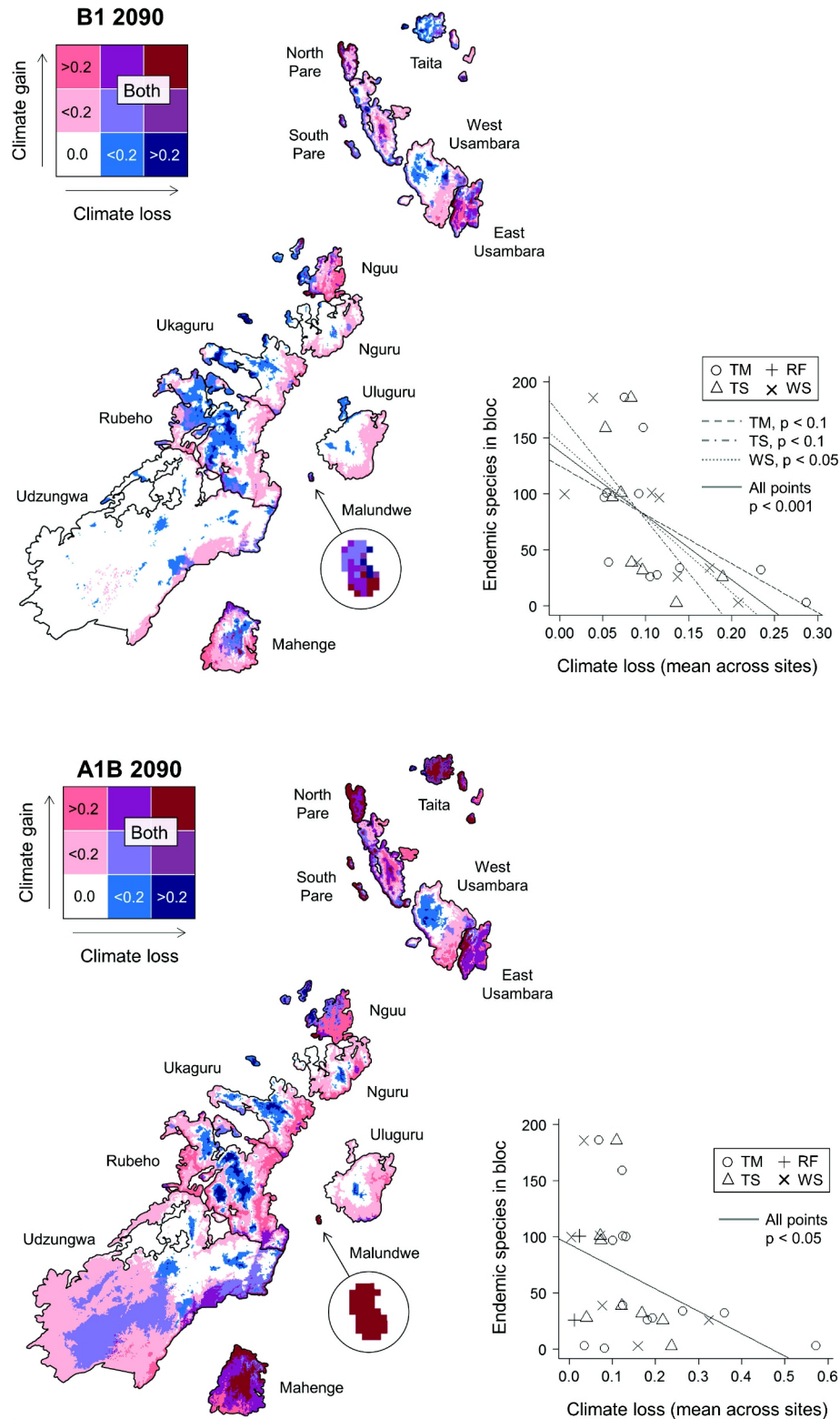


Figure 4. Climatic conditions lost and gained in the EAMs under scenarios B1 and A1B by the year 2090. Search for climate analogues is restricted to individual mountain blocs, reflecting the range-restrictions of many endemic plant species (median recorded range = 1 bloc). Climate loss is scaled by the dissimilarity of present-day conditions compared with future climatic extremes within the same mountain bloc, with respect to: mean annual temperature (TM), temperature seasonality (TS), mean annual rainfall (RF) and dry season water stress (WS). Climate gain is the proportional dissimilarity of future conditions beyond present-day bloc extremes. Scatter plots compare no-zero loss (mean across known endemism sites) with endemic plant richness. Regression lines and corresponding p-values (F-tests) show significant relationships. Results for 2055 are presented in Supplementary material Appendix 3.

fire and lower incidence of mist (Finch and Marchant 2011). In some cases, higher temperatures could potentially lead to more forest cover due to reduced chance of frost, whilst other areas could maintain or expand grassland habitat through increased fire frequency.

The coincidence of climates lost and gained (purple shades in Fig. 4) indicates that not only will a species in situ be subject to conditions currently found nowhere else within the bloc (climate gain), but that it may also have no opportunity to colonise sites with familiar climate analogues by way of within-bloc dispersal (climate loss). Such conditions are predictably extreme in Malundwe (an isolated peak with just 2 km² of forest) due to its small extent and present lack of climatic heterogeneity. However, especially under A1B, such a forecast is also apparent for Taita, North and South Pare, East Usambara, Nguu, Udzungwa and Mahenge. For the first five, higher annual temperatures coincide with reduced seasonality and, in the case of East Usambara, increased dry season water stress on lower slopes (despite higher annual rainfall; Supplementary material Appendix 2). Increased annual rainfall (loss of dry annual conditions) contributes to purple shading in the Pares and Nguu. In Mahenge and on the high plateaus of Udzungwa, higher temperature seasonality is gained, coupled with the loss of cooler mean annual conditions, whilst high temperature seasonality is lost in Matundu forest (lower slopes of east Udzungwa).

Of the 719 distinct 1 km sites where endemic plant species have been sampled, 22% (B1) or 17% (A1B) are forecast to experience climate loss by 2055, and 29% (B1) or 51% (A1B) by 2090. A climate lost means that an endemic species must migrate to an entirely different

mountain bloc in order to avoid extinction, assuming it cannot adapt in situ. Concentrating on locations where loss is non-zero, we found that endemism sites in mountain blocs with greater endemic richness (> 50 species) are generally less susceptible to extreme change (Fig. 4). The most significant relationship is for climates lost by 2090 under the B1 scenario ($p < 0.001$, $R^2 = 0.38$; F-test on 25 DF), which is arguably more representative of past change than A1B, but also evident for the latter ($p < 0.05$, $R^2 = 0.17$; F-test on 27 DF). The observed relationship, of lower endemic richness at sites where scope for within-bloc persistence via dispersal is least likely, is consistent with the ecoclimatic stability hypothesis, especially with respect to dry season water stress (B1 scenario; $p < 0.05$, $R^2 = 0.57$; F-test on 6 DF). Relationships between climate loss and endemic richness were also significant for the year 2055 under both emissions scenarios. Climate gain, less directly associated with species persistence (suitable conditions may be accessible elsewhere in the bloc) although still indicative of extreme change, was significant only for A1B 2090 (Supplementary material Appendix 3).

Endemism vs altitude

Univariate response

Documented plant endemism exhibits an altitudinal peak between 1000 and 1700 m above mean sea level. Constructing one-dimensional climate envelope maps for 354 species and forcing these under scenarios of change shows peak endemism shifting upslope in response to mean annual warming and, to a lesser extent, the annual moisture index (Fig. 5).

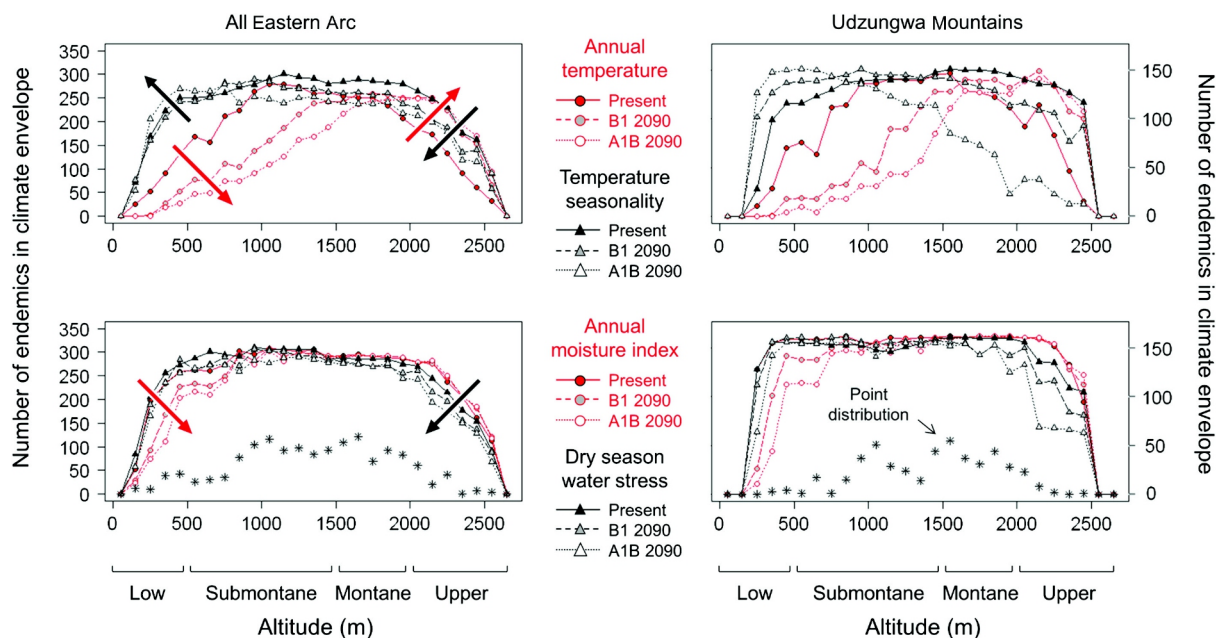


Figure 5. Altitudinal distribution of endemism, now and in the future, according to one-dimensional climate envelopes for 354 plant species. Arrows emphasise directions of change. If mean annual conditions (red) are most important for limiting species' distributions, then peak endemism is expected to shift upslope in response to warming. Conversely, if seasonality (black) is more important, then peak endemism could shift downslope. Patterns are stronger for temperature gradients (upper) than for moisture gradients (lower), the latter being more variable within a given altitudinal band. Patterns are broadly consistent across mountain blocs, but especially clear in Udzungwa forests (right panel) where forecast change is most pronounced.

The latter is perhaps a conservative estimate of the potential for downslope movement, given that Thornthwaite PET is insensitive to forecast changes in humidity, which could offset a rise in temperature (moisture index = annual rainfall/PET). A similar analysis focussed on seasonal measures illustrates the opposite trend, with species limited in their distributions by temperature seasonality and/or dry season rainfall expected, on average, to migrate downslope in order to maintain their climatic niches (Fig. 5). With annual and seasonal forces acting in opposite directions at the extremes of the altitudinal gradient, it seems that mid-altitude forests will maintain (and possibly further develop) high concentrations of endemic species into the future, although floristic composition at these sites will undoubtedly be different and subject to uncertain outcomes from novel biotic interactions.

Multivariate response

Of the 56 endemic plant species eligible for multivariate regression, 34 were modelled with sufficient accuracy for further analysis (median AUC = 0.84, range [0.76, 0.96]; median AUC_{CV} = 0.75, range [0.70, 0.86]; median D² = 0.45, range [0.19, 0.66]). On average, each climate variable was selected a similar number of times and contributed similarly to model performance, although there was considerable variation among species (Supplementary material Appendix 4). Temperature seasonality was selected marginally more often (55% of model runs, cf. 53% annual temperature, 52% water stress, 49% rainfall or moisture index), and explained more deviance when selected (mean over species = 15%, cf. 13% annual temperature, 12% water stress, 11% rainfall or moisture index). Up to nine of the 34 species, depending on the emissions scenario, were forecast to undergo a net increase in climatic suitability across occupied mountain blocs during the 21st century. Around twice as many were forecast with increasing suitability in one part of their range, but decreasing suitability in another, especially under scenario B1 by 2055 (Table 1 and Supplementary material Appendix 4).

As suggested by univariate analysis (Fig. 5), multivariate species models did not predict ubiquitous upslope shifts in species' altitudinal optima. Of the 34 species, 10–14 were projected to undergo upslope shifts, 6–10 downslope, and 10–16 no net change. In order to maintain their current

climatic niches, around two thirds of the species are required to migrate upslope in some parts of their range, but downslope in others (Table 1 and Supplementary material Appendix 4). A spatially explicit illustration of how directions of change could vary both within and between species is provided in Fig. 6, which maps the contrasting responses of *Tricalysia aciculiflora* and *Danais xanthorrhoea* (both Rubiaceae) in Udzungwa, whilst both species maintain relatively stable ranges in Nguru.

Discussion

Progress in bridging the gap between coarse-resolution global datasets and the high-resolution, regionally focussed information necessary for the development of practical climate change adaption strategies has, to date, exhibited bias toward lowland regions and temperate biomes (Wilby et al. 2004). The highly biodiverse and habitat-heterogeneous tropical zone could experience climate change impacts sooner than temperate regions (Beaumont et al. 2011), but many countries, particularly in Africa, lack the species information, climate data and monitoring systems necessary to guide environmental policy (IPCC 2007). Since much of the rapidly growing African population depends directly on natural resources for fuel, building materials, medicine and food, such a data gap and lack of fundamental understanding on the possible impacts of climate change on the natural world is a major concern. The local, national and global goals of poverty reduction, sustainable development, biodiversity conservation and climate change mitigation are highly interwoven (Rapport et al. 1998), and predicting outcomes for any and all is strongly hampered by a scarcity of meaningful data at the relevant spatial scales, especially in mountainous regions.

GCM forecasts are the backbone of climate change assessment, but at their native or interpolated resolutions they provide limited insight into the spatial heterogeneity of change important for site-scale conservation. As RCM predictions become more widely available through initiatives such as CORDEX (Coordinated Regional Climate Downscaling Experiment; <http://wcrp.ipsl.jussieu.fr/>), more studies can take account of the unique regional forcings that underpin species persistence and ecosystem change in their study areas. In this paper, we have shown that climate change impacts on endemic mountain plants could vary considerably from site to site and from species to species. Further, by looking at variation in endemic species richness between the dispersal-limiting island systems of a mountain archipelago, it has been possible to correlate an uncertain future with hypotheses of past ecosystem stability. Our findings demonstrate that, despite the plethora of global climate impact assessments in the scientific literature, conservation planners working on the ground would be ill advised to base adaption strategies on zoomed perspectives of these broad-scale models. Overlooking fine-scale variation, regional climate dynamics or other factors relevant to historical stability, especially in the highly biodiverse tropical mountains of Africa, could result in misguided policy and wasted conservation/adaption investment.

Table 1. Directions of change in climatic suitability and altitudinal optima (100 m bands) summarised for 34 multivariate species models. Numbers show how many endemic plant species are predicted to experience a net increase or decrease in suitability/altitude across all EAM blocs, and how many respond in opposite directions on different blocs within their range. Species-specific results are presented in Supplementary material Appendix 4.

		Climatic suitability			Optimum altitudinal band			
		▲	▼	▲▼	▲	◄►	▼	▲▼
B1	2055	9	25	20	12	16	6	23
	2090	6	28	11	11	15	8	23
A1B	2055	6	28	13	10	15	9	21
	2090	6	28	11	14	10	10	22

▲ net increase; ▼ net decrease; ◄► no net change, ▲▼ varies by mountain bloc.

In the downscaling methodology presented here, we obtained high-resolution forecasts from a RCM by applying change-factors to contemporary climate grids. In regions with sufficient observational time-series data, an alternative to change-factor downscaling would be to correlate large-scale atmospheric variables with local climatic conditions (statistical downscaling). However, the statistical downscaling of climatic change in mountain regions is a complex and data-hungry procedure (Dobrowski et al. 2009) and few, if any, such studies exist for the tropics (Wilby et al. 2004). Change-factor analysis applied to regionally focussed climate models is therefore a more realistic goal for the near term. At local scales, it is important to note that both procedures are insensitive to changes in land-surface feedback. Anecdotal evidence from residents and long-term researchers in the EAMs tells of the cloud line shifting upslope during the 20th century, as forest at lower elevations has been cleared (see also Fairman et al. 2011). In East Usambara, predicted here to experience higher annual temperatures but lower temperature seasonality, and increased annual rainfall but harsher dry seasons, there are reports of reduced regeneration of some tree species, attributed to a lower incidence of mist in recent decades (Hamilton and Bensted-Smith 1989). In anticipation of how socio-economic forces might play out across landscapes, there is scope to embed

detailed scenarios of land use change within sub-national climate downscaling projects. There exists a wealth of local knowledge on vegetation-climate feedbacks in mountain regions, which should not be overlooked in such a process. In particular, greater understanding is needed on how micro-climatic variation responds to broader-scale change, especially with regard to fog, mist and conditions beneath the forest canopy.

Some previous studies have minimised downscaling complications by reducing the forcing mechanism in species' distributions to a monotonic relationship between altitude and temperature, which predicts upward range-shifts, mountaintop extinction and lowland biotic attrition in accord with broader-scale warming trends (Colwell et al. 2008). We caution, however, that findings based solely on annual temperature are confounded by changes in seasonality and rainfall (Knapp et al. 2008, McCain and Colwell 2011), shown here to be equally important for explaining observed patterns of occurrence, if not spatial and temporal variation in the lapse rates themselves (Peyron et al. 2000). We find that two thirds of multivariate species models predict populations of endemic flora to decrease in elevation in at least one mountain bloc, and that any population whose range is predominantly governed by water stress or low temperature seasonality might be expected to tend downslope rather than up.

(a) *Tricalysia aciculiflora* Robbr.

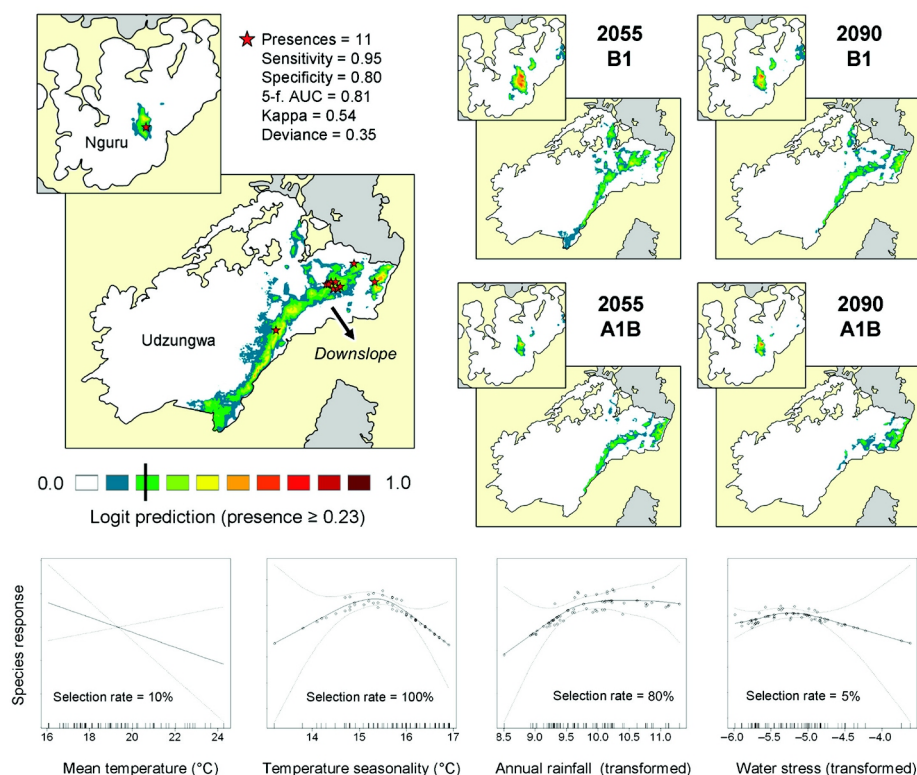


Figure 6. Present day distribution of *Tricalysia aciculiflora* (a) is best explained by temperature seasonality and annual rainfall. Climatic suitability is stable (A1B) or increasing (B1) in Nguru. In Udzungwa, increased seasonality and less rainfall may push the species downslope toward the north-east of the bloc. Conversely, *Danaïx xanthorrhoea* (b) is predicted to have a similar Udzungwa range to *T. aciculiflora* at present but climate suitability tends in the opposite direction over time (upslope to the south-west). Suitability for *D. xanthorrhoea* is stable in Nguru, expands upslope in South Pare, West Usambara and Uluguru, but contracts in East Usambara.

(b) *Danais xanthorrhoea* (K. Shum.) Bremek.

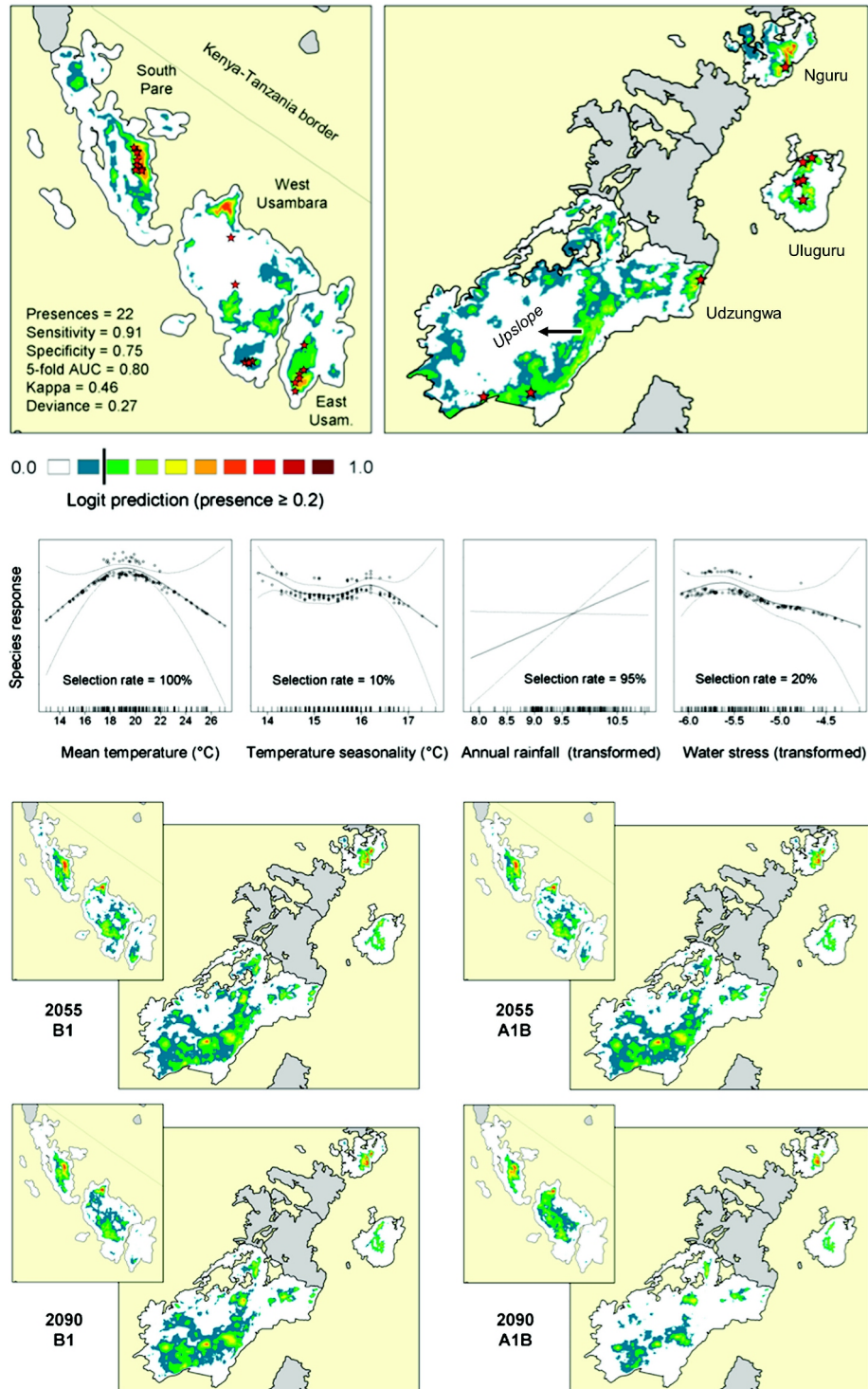


Figure 6. (Continued).

Tropical species, subject to lesser seasonal overlap in thermal regimes between low and high altitudes, are thought to be especially sensitive to temperature change (Janzen 1967; see also Ghalambor et al. 2006, Cadena et al. 2012), but empirical studies do not necessarily support upward shifts at the magnitude forecast by warming models (Forero-Medina et al. 2011, Scherrer and Koerner 2011). Whilst

there exist numerous examples of upslope migration in response to climate change in the 20th century (Lenoir et al. 2008, Jump et al. 2012), it would be premature to suppose this pattern will hold true for all species in all regions (Lenoir et al. 2010). Alongside upward shifts for 118 plant species in Europe, Lenoir et al. (2008) also report downward shifts for 53 species, suggesting that climatic factors other than

mean annual temperature may be mediating their distributions. Similarly in California, coastal flora have shifted their altitudinal optima downhill, despite warming along the gradient, due to changes in the water balance (Crimmins et al. 2011) – phenomena that cannot be explained by adiabatic lapse rates alone. Most fundamentally, when anticipating climate change impacts on species, it is preferable that predictor variables have direct, or at least physiologically relevant, influence over observed patterns of occurrence: relations to proximal measures such as altitude are mediated by factors beyond the model's scope, which themselves could be subject to change (Austin 2007).

At continental scales, low seasonality correlates with higher species richness and rarity (Jetz et al. 2004). Here we find this variable to be an important predictor of intra-specific distribution at the landscape scale. Simple climate envelope models suggest that the downslope influence of changes in seasonality, combined with the upslope forces of warming, could maintain, if not accentuate, a mid-altitudinal peak in endemic species richness. This pattern has parallels with the mid-domain effect, whereby hard boundaries at opposite ends of the altitudinal gradient are said to promote greater species overlap at intermediate elevations (McCain and Colwell 2011). The past contraction of species range limits toward mid-elevations, leading to novel vegetation assemblages composed of both high and low altitude taxa, has been recorded in the pollen record, for example on Mt Kenya following the last glacial maximum (Rucina et al. 2009). Further, the predicted accumulation of plant species at mid-altitudes coincides with a peak in the richness of ancient bird species (Fjeldsø et al. 2010). Based on these findings, we suggest that submontane refugia, and the migration pathways to and from them, be given high priority in conservation plans.

For clarity in assessing climate change impacts on rare mountain flora, we have focussed on species strictly endemic to the EAMs proper (as delimited in Platts et al. 2011). The possibility of currently low-elevation flora migrating upslope in response to warming, or otherwise, was not considered explicitly. In today's human-dominated landscape, the lower forest edge is defined both by climatic factors and by reserve boundaries and challenging terrain, which limit agricultural encroachment and production. Opportunities for gradual migration from lowland to mountain habitats, or vice versa, are therefore limited mainly to species capable of long distance dispersal. Since we restricted our analysis to accurately georeferenced, and therefore mostly recent, collections, some putative mountain endemics may in fact be persisting at the upper altitudinal limits of previously more extensive distributions, curtailed at lower elevations by land use change (especially forest loss). Warming might conceivably benefit such species by restoring their thermal optima, a possibility missed by climatic regression against post-clearance species distributions.

Macroclimatic shifts during the Late Quaternary suggest that extreme episodes of past climate change impacted species in some regions less severely than in others (Sandel et al. 2011), promoting accumulation of now relictual taxa in centres of endemism such as the EAMs. Concordant with hypotheses of long-term ecoclimatic stability (Fjeldsø et al. 1997, Lovett et al. 2005), we find that endemic

richness in the EAMs is significantly higher where species have the potential to maintain familiar conditions throughout the 21st century by within-bloc dispersal, suggesting that spatial heterogeneity in future climatic change could be similar to that of the past. The current rate of climate change, although exacerbated by anthropogenic effects, is not without precedent (McInerney and Wing 2011). For example, the Younger Dryas (ca 11000 yr BP) was characterised by a very rapid warming episode, with temperatures in some regions increasing by as much as 7°C in just 50 yr (Dansgaard et al. 1989). However, on a Quaternary time-scale there has never been a change in climate from a warm to warmer state concomitant with high concentrations of atmospheric CO₂, such as that which is currently being experienced. Above all, the ability of narrow-ranged mountain plants to respond to future change will be very different to that of the past: the processes by which organisms were previously able to adapt, adjust and migrate have been massively curtailed in a landscape dominated by people and agricultural/pastoral land (Fjeldsø and Lovett 1997).

Migration speeds of long-lived tropical trees, which define the forest canopy and mediate fog-capture and micro-climatic conditions in the understory, are relatively slow. Even for species with reproductive cycles in accord with future climate velocities, anthropogenic fragmentation of the forest mosaic has compromised migration pathways and agents for dispersal (e.g. birds; Cordeiro and Howe 2003). In the EAMs, there has been a peak in deforestation at low- to mid-altitudes (Hall et al. 2009), presenting a serious obstacle to the patterns of within-bloc movement considered here. In favour of in situ persistence, the forests that remain occupy significantly more complex terrain (altitudinal range within 1 km squares) than the background mountain area ($p < 0.001$; Wilcoxon rank sum), suggesting the potential for small populations to be maintained in topoclimatic refugia, at least in the short term (Randin et al. 2009, Austin and Van Niel 2011). The upper montane zone, characterised by complex micro-habitat mosaics, has more often survived agricultural encroachment, again providing narrow-ranged species with the possibility of localised refuge from thermal shifts (Scherrer and Koerner 2011).

RCM ensemble forecasts, anticipated to become more widely available in time for IPCC-AR5 (which will convey a revised set of emissions scenarios; Rogelj et al. 2012), should help to quantify uncertainty in the REMO/ECHAM5 models presented here. In the meanwhile, sensible priorities for management are to protect all remaining forest, regardless of patch size, and to seek to establish migration corridors between isolated fragments, especially in the submontane zone. Where available, information at the genetic level could help to ensure that natural variation is maintained, facilitating species' adaption to uncertain future conditions (Kahindo et al. 2007). At the heart of any successful conservation strategy will be the need to find ways to manage sustainably, and where possible restore, forest ecosystems, whilst addressing the resource needs of increasingly numerous human populations. Solutions to the huge challenges of climate change, biodiversity loss, population growth and pressure on ecosystem services will require further targeted research on both the spatial and temporal character of environmental change, and how this impacts

ecosystems and associated livelihoods. It is not sufficient to apply models that are too coarse, or to apply scientific understanding that is not rooted in the ecosystem under investigation.

Acknowledgements – We thank the many providers of plant data to the Missouri Botanical Garden's TROPICOS database, Jon Newell for heroic amounts of specimen data entry, and Stefan Hagemann and Daniela Jacob (Max Planck Inst. for Meteorology, Hamburg) for providing REMO climate forecasts for east Africa. Thanks to Colin McClean for useful discussion. This work was funded by the Marie-Curie programme of the European 6th Framework (MEXT-CT-2004-517098), with additional support from the Leverhulme Trust (<www.valuingthearc.org/>), the Ministry for Foreign Affairs of Finland (<www.chiesa.icipe.org/>) and the British Inst. in Eastern Africa (<www.biea.ac.uk/>).

References

- Ahrends, A. et al. 2011. Conservation and the botanist effect. – *Biol. Conserv.* 144: 131–140.
- Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. – *Ecol. Model.* 200: 1–19.
- Austin, M. P. and Van Niel, K. P. 2011. Improving species distribution models for climate change studies: variable selection and scale. – *J. Biogeogr.* 38: 1–8.
- Baumont, L. J. et al. 2011. Impacts of climate change on the world's most exceptional ecoregions. – *Proc. Natl Acad. Sci. USA* 108: 2306–2311.
- Brooks, T. M. et al. 2002. Habitat loss and extinction in the hotspots of biodiversity. – *Conserv. Biol.* 16: 909–923.
- Cadena, C. D. et al. 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. – *Proc. R. Soc. B* 279: 194–201.
- Colwell, R. K. et al. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. – *Science* 322: 258–261.
- Cordeiro, N. J. and Howe, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. – *Proc. Natl Acad. Sci. USA* 100: 14052–14056.
- Couvreur, T. L. P. et al. 2008. Molecular phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees. – *BMC Biol.* 6: 10.
- Crimmins, S. M. et al. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. – *Science* 331: 324–327.
- Dansgaard, W. et al. 1989. The abrupt termination of the Younger Dryas climate event. – *Nature* 339: 532–534.
- Dinesen, L. et al. 1994. A new genus and species of perdicine bird (Phasianidae, *Perdicini*) from Tanzania – a relict form with Indo-Malayan affinities. – *Ibis* 136: 3–11.
- Dobrowski, S. Z. et al. 2009. How much influence does landscape-scale physiography have on air temperature in a mountain environment? – *Agric. For. Meteorol.* 149: 1751–1758.
- Doherty, R. M. et al. 2010. Implications of future climate and atmospheric CO₂ content for regional biogeochemistry, biogeography and ecosystem services across east Africa. – *Global Change Biol.* 16: 617–640.
- Fairman, J. G. et al. 2011. Land use change impacts on regional climate over Kilimanjaro. – *J. Geophys. Res. Atmos.* 116: 24.
- Finch, J. and Marchant, R. 2011. A palaeoecological investigation into the role of fire and human activity in the development of montane grasslands in east Africa. – *Veg. Hist. Archaeobot.* 20: 109–124.
- Finch, J. et al. 2009. Late Quaternary vegetation dynamics in a biodiversity hotspot, the Uluguru Mountains of Tanzania. – *Quat. Res.* 72: 111–122.
- Fjelds , J. and Lovett, J. C. 1997. Biodiversity and environmental stability. – *Biodivers. Conserv.* 6: 315–323.
- Fjelds , J. et al. 1997. Are biodiversity 'hotspots' correlated with current ecoclimatic stability? A pilot study using the NOAA-AVHRR remote sensing data. – *Biodivers. Conserv.* 6: 401–422.
- Fjelds , J. et al. 2010. Distribution of highland forest birds across a potential dispersal barrier in the Eastern Arc Mountains of Tanzania. – *Steenstrupia* 32: 1–43.
- Forero-Medina, G. et al. 2011. Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. – *PloS One* 6: e28535.
- Gereau, R. E. et al. 2010. Plant conservation assessment in the Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya. – <www.mobot.org/MOBOT/Research/tanzania/cepf.shtml/>.
- Ghalambor, C. K. et al. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. – *Integr. Comp. Biol.* 46: 5–17.
- Greve, M. et al. 2011. Environmental and anthropogenic determinants of vegetation distribution across Africa. – *Global Ecol. Biogeogr.* 20: 661–674.
- Hall, J. et al. 2009. Conservation implications of deforestation across an elevational gradient in the Eastern Arc Mountains, Tanzania. – *Biol. Conserv.* 142: 2510–2521.
- Hamilton, A. C. and Bensted-Smith, R. 1989. Forest conservation in the East Usambara Mountains, Tanzania. – International Union for the Conservation of Nature.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- IPCC 2007. Climate change 2007: synthesis report. – Intergovernmental Panel on Climate Change.
- IUCN 2011. IUCN Red List of Threatened Species. – Version 2011.2 <www.iucnredlist.org/>.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – *Am. Nat.* 101: 233–249.
- Jarvis, A. et al. 2008. Hole-filled seamless SRTM data. Version 4. – International Centre for Tropical Agriculture (CIAT), <http://srtm.csi.cgiar.org/>.
- Jetz, W. et al. 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. – *Ecol. Lett.* 7: 1180–1191.
- Jump, A. S. et al. 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. – *Ecography* 35: 204–210.
- Kahindo, C. et al. 2007. The relevance of data on genetic diversity for the conservation of Afro-montane regions. – *Biol. Conserv.* 134: 262–270.
- Knapp, A. K. et al. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. – *Bioscience* 58: 811–821.
- Kou, X. et al. 2011. High-resolution bioclimatic dataset derived from future climate projections for plant species distribution modeling. – *Ecol. Inform.* 6: 196–204.
- Kreyling, J. et al. 2010. Potential consequences of climate warming for tropical plant species in high mountains of southern Ethiopia. – *Divers. Distrib.* 16: 593–605.
- La Sorte, F. A. and Jetz, W. 2010. Projected range contractions of montane biodiversity under global warming. – *Proc. R. Soc. B* 277: 3401–3410.
- Lenoir, J. et al. 2008. A significant upward shift in plant species optimum elevation during the 20th century. – *Science* 320: 1768–1771.
- Lenoir, J. et al. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. – *Ecography* 33: 295–303.

- Lovett, J. C. 1990. Classification and status of the moist forests of Tanzania. – *Mitt. Inst. Bot. Hamburg* 23a: 287–300.
- Lovett, J. C. et al. 2005. The oldest rainforests in Africa: stability or resilience for survival and diversity? – In: Purvis, A. et al. (eds), *Phylogeny and conservation*. Cambridge Univ. Press, pp. 198–229.
- Marchant, R. et al. 2007. The Indian Ocean dipole – the unsung driver of climatic variability in east Africa. – *Afr. J. Ecol.* 45: 4–16.
- McCain, C. M. and Colwell, R. K. 2011. Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. – *Ecol. Lett.* 14: 1236–1245.
- McClean, C. J. et al. 2005. African plant diversity and climate change. – *Ann. Missouri Bot. Gard.* 92: 139–152.
- McInerney, F. A. and Wing, S. L. 2011. The Paleocene-Eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. – *Annu. Rev. Earth Planetary Sci.* 39: 489–516.
- Mitasova, H. and Mitas, L. 1993. Interpolation by regularized spline with tension. 1. Theory and implementation. – *Math. Geol.* 25: 641–655.
- Mittermeier, R. A. et al. 2004. Hotspots revisited. – *CEMEX*.
- Mulligan, M. 2006. Global gridded 1 km TRMM rainfall climatology and derivatives. – Version 1, <www.ambiotek.com/1kmrainfall>.
- Mumbi, C. T. et al. 2008. Late Quaternary vegetation reconstruction from the Eastern Arc Mountains, Tanzania. – *Quat. Res.* 69: 326–341.
- Pereira, H. M. et al. 2010. Scenarios for global biodiversity in the 21st century. – *Science* 330: 1496–1501.
- Peters, G. P. et al. 2012. CORRESPONDENCE: rapid growth in CO₂ emissions after the 2008–2009 global financial crisis. – *Nat. Clim. Change* 2: 2–4.
- Peyron, O. et al. 2000. Climate of east Africa 6000 C-14 yr BP as inferred from pollen data. – *Quat. Res.* 54: 90–101.
- Phillips, S. J. et al. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. – *Ecol. Appl.* 19: 181–197.
- Platts, P. J. et al. 2008. Predicting tree distributions in an east African biodiversity hotspot: model selection, data bias and envelope uncertainty. – *Ecol. Model.* 218: 121–134.
- Platts, P. J. et al. 2010. Can distribution models help refine inventory-based estimates of conservation priority? A case study in the Eastern Arc forests of Tanzania and Kenya. – *Divers. Distrib.* 16: 628–642.
- Platts, P. J. et al. 2011. Delimiting tropical mountain ecoregions for conservation. – *Environ. Conserv.* 38: 312–324.
- Ramirez, J. and Jarvis, A. 2008. High resolution statistically downscaled future climate surfaces. – International Centre for Tropical Agriculture (CIAT), <www.ccafs-climate.org/>.
- Randin, C. F. et al. 2009. Climate change and plant distribution: local models predict high-elevation persistence. – *Global Change Biol.* 15: 1557–1569.
- Rapport, D. J. et al. 1998. Assessing ecosystem health. – *Trends Ecol. Evol.* 13: 397–402.
- Rogelj, J. et al. 2012. Global warming under old and new scenarios using IPCC climate sensitivity range estimates. – *Nat. Clim. Change* 2: 248–253.
- Rucina, S. M. et al. 2009. Late Quaternary vegetation and fire dynamics on Mount Kenya. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 283: 1–14.
- Sandel, B. et al. 2011. The influence of Late Quaternary climate-change velocity on species endemism. – *Science* 334: 660–664.
- Scherrer, D. and Koerner, C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. – *J. Biogeogr.* 38: 406–416.
- Stockwell, D. R. B. and Peterson, A. T. 2002. Effects of sample size on accuracy of species distribution models. – *Ecol. Model.* 148: 1–13.
- Tabor, K. and Williams, J. W. 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. – *Ecol. Appl.* 20: 554–565.
- Thomas, C. D. et al. 2004. Extinction risk from climate change. – *Nature* 427: 145–148.
- Thorntwaite, C. W. 1948. An approach toward a rational classification of climate. – *Geogr. Rev.* 38: 55–94.
- Wilby, R. et al. 2004. Guidelines for use of climate scenarios developed from statistical downscaling methods. – Intergovernmental Panel on Climate Change, <www.ipcc-data.org/guidelines/dgm_no2_v1_09_2004.pdf>.
- Williams, J. W. et al. 2007. Projected distributions of novel and disappearing climates by 2100 AD. – *Proc. Natl Acad. Sci. USA* 104: 5738–5742.
- Yee, T. W. and Mitchell, N. D. 1991. Generalized additive models in plant ecology. – *J. Veg. Sci.* 2: 587–602.

Supplementary material (Appendix E7805 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.