# *Predicting range shifts for critically endangered plants: is habitat connectivity irrelevant or necessary?*

Article

Published Version

Yesuf, G. U. ORCID: https://orcid.org/0000-0003-0963-2998, Brown, K. A., Walford, N. S., Rakotoarisoa, S. E. and Rufino, M. C. (2021) Predicting range shifts for critically endangered plants: is habitat connectivity irrelevant or necessary? Biological Conservation, 256. 109033. ISSN 0006-3207 doi: https://doi.org/10.1016/j.biocon.2021.109033 Available at https://centaur.reading.ac.uk/99052/

To link to this article DOI: http://dx.doi.org/10.1016/j.biocon.2021.109033

Publisher: Elsevier

Biological Conservation 256 (2021) 109033

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

# Predicting range shifts for critically endangered plants: Is habitat connectivity irrelevant or necessary?

Gabriel U. Yesuf[a,*], Kerry A. Brown[b], Nigel S. Walford[b], Solofo E. Rakotoarisoa[c], Mariana C. Rufino[a]

[a] Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster University, LA1 4YQ, United Kingdom
[b] Department of Geography, Geology and the Environment, Penrhyn Road, Kingston University London, KT1 2EE, United Kingdom
[c] Kew Madagascar Conservation Centre (KMCC), Lot II J 131 B, Antananarivo, Madagascar

## ARTICLE INFO

*Keywords:*
Climate change
Critically endangered plants
Habitat connectivity
Land-cover change
Madagascar
Range shifts

## ABSTRACT

Climate and land-cover change will directly impact future species distributions, leading to range expansions, contractions and local extinctions. However, assessments of future range shifts rarely account for the capacity of the landscape matrix to facilitate species dispersals. Here, we assessed future range shifts for a suite of critically endangered plants in Madagascar. We quantified habitat connectivity using a least cost path model that captured the potential of species to disperse within fragmented landscapes. Next, we constructed three scenarios representing landscapes impacted by climate-only, climate and land-cover change, as well as habitat connectivity. We modelled species distributions using a hierarchical Bayesian framework and measured future range shifts using three spatial indices: net-change, range distance and elevation change. Our results show that the median range shift due to contractions increased by 25% under the climate-only scenario compared with the connectivity scenario. Habitat connectivity is predicted to limit range shifts due to contractions, while increasing shifts due to expansions for many of the endangered and critically endangered plants on Madagascar. However, at least one-third of critically endangered and 50% of endangered plants are expected to experience range contractions and upslope displacement under all scenarios, suggesting that even with habitat connectivity the range of some species may still contract. Despite that finding, our study suggests that including connectivity in range shift models is crucial for developing a relevant connectivity conservation plan, since future climate or climate and land-cover change models do not adequately represent species' potential to reach safe sites.

## 1. Introduction

Climate and land-cover change (LCC) is likely to impact plant habitats leading to range contraction, expansion, upward or downward displacements and, in some places, local extinctions (Kuhn et al., 2016). For most plants, it is predicted that if average global temperatures were to rise above 3 °C then more than one-half of their current habitats would be lost (Warren et al., 2018). Tropical regions are most likely to be severely impacted since future climates in the tropics may create novel environments and possibly facilitate range shifts (Rumpf et al., 2019). For instance, Colwell et al. (2008) determined that tropical lowland biotas may face net habitat loss and elevational range changes due to climate change in Costa Rica. Tropical landscapes are also characterised by increasing rates of species range fragmentation due to LCC, which reduces the size of habitable environments (e.g. forest), threatens critical dispersal pathways and alters species composition (Şekercioğlu et al., 2015). Therefore, when predicting future range shifts it is important to consider active processes (such as habitat fragmentation) and their impact on natural landscapes to determine biological responses to environmental change (Opdam and Wascher, 2004; Record et al., 2018). Considering multiple environmental factors, such as dispersal rates or habitat connectivity may reveal micro-scale patterns that contradict global trends (Zellweger et al., 2019). Measures of connectivity are important as they add an extra layer of realism to range shift predictions and help to determine how localised climate and LCC affect future plant distributions (Corlett and Westcott, 2013).

Plants are unlikely to rapidly evolve the physiological tolerances required to adapt to anthropogenic climate change (Walter et al., 2013)

---

[*] Corresponding author.

*E-mail addresses:* g.yesuf@lancaster.ac.uk (G.U. Yesuf), K.Brown@kingston.ac.uk (K.A. Brown), nwalford@kingston.ac.uk (N.S. Walford), S.Rakotoarisoa@kew.org (S.E. Rakotoarisoa), m.rufino1@lancaster.ac.uk (M.C. Rufino).

https://doi.org/10.1016/j.biocon.2021.109033
Received 13 June 2020; Received in revised form 11 February 2021; Accepted 14 February 2021

and those in the tropics are arguably already adapted to the warmest and wettest parts of their distribution (Laurance et al., 2011). Many species will depend on their dispersal capabilities to survive environmental change (Corlett and Westcott, 2013). Previous assessments of range shifts assume no or restricted dispersal when predicting future plant distributions (Walck et al., 2011), despite suggestions that dispersal syndromes (e.g., anemochory and zoochory), as well as landscape connectivity influence past and current range distributions (Seidler and Plotkin, 2006). Species distribution models (SDMs) can be used to estimate species' potential range shift in response to different environmental factors (Rosenblad et al., 2019). The challenge has always been how to effectively incorporate variables from multiple spatial and-temporal scales within niche-based SDMs (McGarigal et al., 2016).

Process-based distribution models (e.g., hierarchical Bayesian models) may be more robust than niche-based models when using non-climate variables due to the ease of integrating data across multi-scales and quantifying uncertainties (Zurell et al., 2016). Niche-based models tend to overpredict species' extinctions and colonisations (Morin and Thuiller, 2009); while measures of uncertainties could inspire confidence in predictions of process-based models (Boakes et al., 2018). Redding et al. (2017) show that spatial Bayesian modelling is more effective than non-spatial approaches (e.g., boosted regression trees) when using geographically restricted data. Conducting similar assessments based on Bayesian modelling is particularly important for Sub-Saharan Africa (SSA), especially when forest loss and measures of fragmentation are integrated to predicted range shifts (Kreyling et al., 2010). Despite widespread application of SDMs, there is still a lack of ecological assessments that incorporate active processes to explain the complex interactions between species and their environment (Record et al., 2018). Constructing range shift models that include a proxy for dispersal pathways, and are able to measure the capacity for landscapes to facilitate movements (i.e. through habitat connectivity) is likely to result in more reliable predictions of species' response to environmental change (Elith et al., 2010). Some studies showed that habitat connectivity is effective for future migration of plants and animals in North America (Coops et al., 2016; Huang et al., 2020). To our knowledge, there are no similar studies that assess the impact of habitat connectivity for future plant distributions in SSA.

In this study, we use a hierarchical Bayesian model to investigate range shift predictions under scenarios with and without habitat connectivity in Madagascar. We determine the impact of habitat connectivity on predictions of range shift using 87 endangered and critically endangered plants. We implement this assessment in Madagascar – a biodiversity hotspot with high levels of endemism and few range shift studies. Madagascar's plant diversity is expected to be adversely impacted, mainly due to climate and LCC (Brown et al., 2015), range contraction and expansion to some of its endemic species (Hong-Wa and Arroyo, 2012) and extinctions to more than half the species in the genera *Coleeae* (Good et al., 2006). To investigate how future climate and LCC influences plant range shifts, we consider three scenarios and focus on three measures of range shift. First, we consider a climate-only scenario that assumes a 'business as usual' trend in future temperatures and precipitation. This scenario mimics the most common approach used in previous studies and assumes a simplified future natural world that is unaffected by other environmental variables in 2050. Next, we examine a combined climate and LCC scenario. Finally, we use a connectivity scenario to capture species' ability to move through the landscape by including a measure of least cost path between natural habitats.

We test the hypothesis that habitat connectivity will limit range contractions and facilitate range expansions compared with a climate-only scenario (null model) by assessing the following research questions:.

i. How will habitat connectivity affect future range expansion and contraction for plants in the tropics?
ii. How will habitat connectivity affect upslope and downslope range displacements?
iii. To what extent will range shifts under climate land-cover change and connectivity scenarios differ? and
iv. Which geographic locations are more sensitive to predictions of expansion and contraction under different scenarios?

We expect range shift due to contractions to be minimal in the connectivity scenario compared with scenarios without connectivity (Feeley and Silman, 2010). We also expect range expansion and upslope displacement to be dominant under the connectivity scenario and that range shift will vary under all scenarios due to the influence of environmental change (Kubisch et al., 2013). We expect range shifts due to contractions to predominately occur in lowland regions (Colwell et al., 2008). Our assessment of range shift aligns with ongoing conservation efforts in the region – for instance, existing partnerships led by the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) aims to connect evidence-driven policies with biodiversity conservation and could benefit from quantitative measures of the potential changes to plant habitats. We also anticipate that the predicted outcomes of range shifts from this study would form the basis for connectivity conservation planning across the region.

## 2. Materials and methods

### 2.1. Study area

Madagascar covers an area of approximately 585,000 km$^2$ and is inhabited by more than 10,000 endemic plant species (Callmander et al., 2011). Twenty-six percent of its endemic plant genera are closely related, 22% have floristic links with Africa, 9.1% with SE Asia and 6.2% with India (Bevill and Louda, 1999). Despite the high floral diversity, most species are threatened by high rates of deforestation, degradation, habitat fragmentation and biodiversity loss (Vieilledent et al., 2018; Yesuf et al., 2019). The remaining large and intact vegetation formations on the island are grouped into eight categories: lowland evergreen moist forest, medium altitude moist evergreen forest, moist semi-deciduous forest, sclerophyllous woodland, dry deciduous forest, riparian forest and littoral forest (Gautiert et al., 2018). Other natural vegetation types include montane grassland, marshland and montane ericoid thicket; while these are not forested areas, they are equally inhabited by many endemic plant species.

### 2.2. Occurrence records and species selection

All plant species included in this assessment are endemic to Madagascar and their occurrence records sourced from the Global Biodiversity and Information Facility (GBIF) portal (https://doi.org/10.15468/dl.n9k471). Only georeferenced species and those classified either as endangered, critically endangered or vulnerable under the International Union for the Conservation of Nature (IUCN) Red List (IUCN, 2017) were selected. To reduce dense sampling in the observations, spatial thinning was applied resulting in each species having one occurrence per pixel (~1 km$^2$) (Elith et al., 2010). This resolution also represents the pixel sizes of the bioclimatic variables. Additionally, only species with a minimum of 10 occurrence records were selected. In total, 87 species passed the thinning threshold resulting in a total of 2266 presence locations (Appendix A and Table A.1).

### 2.3. Environmental variables

#### 2.3.1. Climate data

For the current and future climate scenarios we selected annual mean temperature, annual precipitation, maximum temperature of the warmest month, minimum temperature of the coldest month, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of the wettest month and precipitation of the driest month (Table A.2). These eight bioclimatic variables are a subset of 19 available from Worldclim (Fick and Hijmans, 2017), and were chosen because they are considered to have high ecological significance for plant survival, and they capture seasonal variations and weather extremes to which plants may have to adapt in the future (Davis et al., 2012; Kuhn et al., 2016). Bayesian process-based models are robust to the effects of collinearity (Golding and Purse, 2016; Stuber et al., 2017) and do not suffer from the effects of highly correlated covariates that often affect semi-parametric models (e.g., generalised additive models). The future climate data were obtained from the Met Office Hadley Centre's coupled *Hadley Global Environment Model 2 – Earth System* (HadGEM-ES) climate model used for the IPCC climate projections (Martin et al., 2011). We used the low and high emission scenarios for the Representative Concentration Pathways (RCP8.5 and RCP2.6). The high emission scenario, predicts future climate conditions defined by no changes in policy to guide practices and development resulting in an average global warming of 1.5–2 °C by 2050 (IPCC, 2018). Recent global warming rates indicate an increase of approximately 0.89 °C in average surface temperature (IPCC, 2014), which suggests that a high emission scenario is more likely by mid-century. As a result, we focus on the business as usual, high emissions climate scenario and provide the alternative outcome under low emission (RCP2.6) in Appendix D (Figs. D.1 – D.5).

### 2.3.2. *Current and future land-cover change*

Landsat TM, ETM and OLI imagery were collected for three dates: 1994, 2002 and 2014 with a spatial resolution of 30 m (https://glovis.usgs.gov/). Individual image scenes were radiometrically corrected and then mosaicked with contiguous scenes to produce island-wide data for each date. Afterwards the images were classified into different land-cover categories namely: forest, exposed surface, cultivated land and vegetation matrix (includes secondary forest, grasslands and shrubland). Subsequently, change detection analysis was implemented to derive two interval datasets representing changes in land-cover categories from 1994 to 2002 (first interval) and 2002–2014 (second interval). The second interval represented the most recent LCC dataset and the basis for predicting LCC to 2050. We also determined the user, producer and overall accuracies for the past and recent land-cover datasets (Appendix B, Tables B.1, B.2).

The future LCC dataset was produced using the land change modeler in IDRISI TerrSet software. The land change modeler is suitable for ecological modelling because it achieves higher allocation and configuration accuracies compared with other spatial explicit models such as GEOMOD (Pickard et al., 2017). Land-cover category transitions to the future (i.e. 2050) were based on second interval change analysis, and include category gains, losses and persistence. The prediction began by developing a transition probability sub-model that accounted for the elevation, and pixel-specific deforestation and forest degradation sizes as drivers of change. The transition probabilities were used to determine pixel suitability before allocating pixels to different land-cover categories using a multi-layer perceptron approach (Atkinson and Tatnall, 1997).

### 2.3.3. *Habitat connectivity: deriving the least cost path model*

The current LCC dataset was used as input for calculating the least cost path (Eq. 1), and to create a layer of connectivity using the GIS Linkage Mapper tool (McRae and Kavanagh, 2011). In this study habitat connectivity is defined by least cost paths and captures species' ability to move through the landscape matrix. Landscape maps classifying vegetation formations into either core (i.e. forest areas) or non-core areas (i.e. exposed surface, cultivated land, vegetation matrix), as well as into their spatial configuration were produced using Morphological Spatial Pattern Analysis (MSPA) (Vogt et al., 2007). Core areas were on average $> 100$ ha in size and had a minimum distance of 100 m to edge areas. These datasets were produced independently for each vegetation formation (i.e. lowland evergreen moist forest, medium altitude moist evergreen forest, moist semi-deciduous forest, sclerophyllous woodland, dry deciduous forest and littoral forest). Vegetation formations consist of both forest and non-forest land-cover types. It should be pointed out that vegetation formations have been referred to as 'eco-regions' by other authors (e.g., Moat and Smith (2007); however, for this study we use the former to remain consistent with more recent publications (Gautiert et al., 2018). Dispersal potentials between core areas were estimated using a cost allocation function and varied according to the resistance between core areas. The resistance surface was developed by assigning thresholds to land-cover categories (Table A.3). With this approach, connected natural features (e.g., forests) are considered enablers of dispersals under environmental change following Gurrutxaga et al. (2011). Therefore, we assume that core areas separated by low resistance pixels correspond to areas with higher probability for species dispersals thereby supporting range shifts. Subsequently, the minimum cost-weighted distance between core pairs was calculated and mapped to create a network of connections in the different vegetation formations (Eq. (1)). To reduce computation time, least cost paths were mapped up to a maximum distance of 5 km, which is greater than recent estimates of dispersal distance from common dispersers (e.g., Lemurs) in Malagasy forests (Razafindratsima et al., 2014). Large mammals are common dispersers of seeds in Madagascar, but a combination of fragmentation and loss of natural habitats due to deforestation also limits dispersal distances to a few hundred metres (Albert-Daviaud et al., 2018; Bodin et al., 2006). Our assumption is that least cost paths are a proxy for seeds' ability to establish in safe sites and for plants to maintain viable populations, which guarantees species dispersals due to range shift.

$$\mathrm{LCP_{AB}} = \mathrm{CWD_A} + \mathrm{CWD_B} - \mathrm{LCD_{AB}} \tag{1}$$

where LCP is the least cost path connecting adjacent habitat areas A and B, $\mathrm{CWD_A}$ is the cost-weighted distance from core A and $\mathrm{CWD_B}$ is the cost-weighted distance from core B and $\mathrm{LCD_{AB}}$ is the least cost distance accumulated moving along an ideal path connecting the core pair.

Finally, least cost paths were calculated using the sum of cost-weighted distance between connected core areas and measured in kilometres (McRae et al., 2012). Least cost paths represent the connection between potential suitable habitats (i.e. habitat connectivity). Because measures of connectivity were implemented within vegetation formations, we used ordinary kriging interpolation technique to obtain values outside these formations and to produce an island-wide layer of connectivity (Fig. A.1). This interpolation technique was used because it accounts for spatial correlation between sample points and was also proposed by Foltête et al. (2012) as a means to facilitate the integration of landscape models in SDMs. Kriging interpolation was implemented using the 3D-analyst tool in ArcGIS to interpolate data points representing measures of least cost paths, while applying a spherical function to progressively decrease the effect of spatial autocorrelation as distance between the points increased.

## 2.4. *Defining the scenarios*

Range shift was predicted based on the differential impact of climate, LCC and habitat connectivity relative to a baseline scenario. The baseline scenario consists of recent climate and land-cover, while future scenarios were defined by adding two environmental variables that define active processes on Madagascar (i.e. LCC and habitat connectivity) to determine how they would impact on future species distributions (Table 1). Therefore, range shift was quantified under **i)** climate-only, where we assume the landscape can facilitate full dispersal (null model), **ii)** climate and LCC and **iii)** climate, LCC and habitat connectivity (hereafter, connectivity scenario). The main steps used to define all scenarios are shown in Fig. A.2.

**Table 1**
Description of scenarios considered in range shift assessment of 87 endangered, critically endangered and vulnerable plant species on Madagascar.

| Scenario | Description | Term used in text |
|---|---|---|
| Current climate and current land-cover scenario | Describes current climate and land- cover variables | Baseline scenario |
| High future climate only scenario | Describes future 'worst case' climatic conditions involving global average temperatures rising by 1.4 °C - 2.6 °C | Climate-only scenario |
| High future climate and land-cover change scenario | Describes future 'worst-case' climatic conditions including average global temperatures rising by 1.4 °C - 2.6 °C and future land- cover | Climate land-cover change scenario |
| High future climate, future land-cover + habitat connectivity scenario | Describes future 'worst-case' climatic conditions including average global temperatures rising by 1.4 °C - 2.6 °C, future land- cover and habitat connectivity | Connectivity scenario |

### 2.5. Species distribution models

Species distribution models were produced using the 'hSDM' package in R programming language v3.2.4 and by performing a binomial logistic regression under a hierarchical Bayesian framework (R Core Team, 2016; Vieilledent et al., 2014). The hierarchical framework allowed presence locations for each species to be integrated with high resolution variables (LCC and habitat connectivity). The modelling process began by using a neighbourhood matrix of observation locations (i.e. presence locations) to ensure that the probability of each pixel suitability is dependent on its surrounding pixels (Lichstein et al., 2002). Neighbourhoods consisted of adjacent pixels (including diagonals) and were used to capture the effect of spatial autocorrelation across all variables. Neighbourhood analysis was also used to correct for undersampling and bias in the species occurrence records. This way, the probability of assigning low suitability pixels in regions with high suitability was minimised. A logit function was then used to modulate the influence of input data (presence location and variables) on the probability of occurrence for each species under different scenarios (Appendix C). Spatial random effects were specified using an intrinsic autocorrelation regression term and to determine the variance of the mean of posterior distributions. Due to lack of previous knowledge for all species, the analysis assumes a normal distribution centred at zero and a fixed large variance of 100 (Rasmussen and Williams, 2006). The outputs are layers of the posterior distribution showing species-specific probability of occurrences as continuous surfaces and ranging from low (0) to high (1) probability. We also quantified the associated uncertainties defined by the variance of the posteriori distribution. The predicted occurrences for all 87 species under all scenarios are provided in the supplementary information (Figs. C.1 - C.7). We used the maximum sum of sensitivity (true positive rate) and the specificity (true negative rate) threshold metrics to transform species-specific probability layers into presence-absence maps. These threshold techniques were selected because they remain consistent under differing ratios of presence and background points (Liu et al., 2016). Presences indicate suitable pixels (i.e. predicted range), while absences indicate unsuitable pixel locations under each scenario.

### 2.6. Quantifying changes in predicted species range

Three spatial indices were modified from Radinger et al. (2017) and Choe et al. (2017) to determine species' range shift. The first range shift metric that was quantified is the *net-change* index, which measures the difference between predicted range gains and losses. Negative net change indicates species' range contractions, while positive net change indicates species' range expansions (Table C.1). The *elevation change* index quantifies the difference between the mean elevation of predicted species' range and the mean elevation of current species' range (Table C.1). Elevation change represents an estimate of upslope or downslope range displacements. *Range distance* index calculates the median distance between the centroid of predicted species' range and the edges of current species range (Table C.1). The range distance metric explicitly quantifies range shift for all species under different scenarios. We used the combination of range expansions, contractions, upslope and downslope displacements to quantify range shift under future scenarios and different IUCN risk classifications. Two-sample Wilcoxon signed-rank tests were used to compare range gain (i.e. range expansion) versus range loss (i.e. range contraction) between the future scenarios. Similarly, the Wilcoxon signed-rank test was used to compare range shifts and range displacements in all scenarios. Generalised linear regression model (GLM) was used to determine the influence of selected variables (e.g., range size) on contraction and expansion in all scenarios and implemented using a binomial distribution in R programming language. The response variable was based on whether species expanded or contracted their ranges, while current range size, dispersal syndromes (Table C.6) and the average elevation of current range were used as predictors. For each scenario, two iterations of GLM were implemented, one without interactions between predictors and the other accounted for interactions between range size and dispersal syndromes. We report the best performing model (i.e. least AIC score).

Using the net change index, regions sensitive to range contraction and expansion were identified. GIS zonal statistical tool was used to determine the number of predicted range contractions and expansions that coincide in each pixel (1km$^2$) by summing the total number of species under each scenario (ESRI, 2015). We designated pixels where more than 50% of the total number of species' experience contractions or expansions as hotspots. However, we expect range changes due to net range losses (i.e. contractions) to drive local extinctions in the future rather than range expansions (Wiens, 2016).

## 3. Results

### 3.1. Range shift due to contractions and expansions across risk classifications

Over a third of critically endangered plants experienced range shifts due to contractions under all scenarios (Table C.2). The median range contractions for critically endangered plants (e.g., *Dypsis brevicaulis*) decreased under climate land-cover change (386 km, Interquartile range, IQR = 60) and connectivity (363, IQR = 38) scenarios compared with the median range contraction (403 km, IQR = 70) under the climate-only scenario (null model) (Fig. 1a). Fifty-five percent of endangered plants (e.g., *Dypsis utilis*) experienced range shift due to contraction under climate-only scenario, while 48% experienced range shift due to contractions under climate land-cover change and connectivity scenarios (Table C.2). The predicted median range contractions for endangered plants under climate-only scenarios was 389 km (IQR = 190) and decreased by 82 km and 98 km under connectivity and climate land-cover change scenarios (Fig. 1b). Only one vulnerable species' range (*Dalbergia baronii*) experienced contraction under climate-only and climate land-cover change scenarios (Fig. 1c). More than 60% of critically endangered plants experienced range expansions in climate land-cover change and connectivity scenarios (Table C.2). Median range expansions for critically endangered plants were highest (337 km, IQR = 151) in the connectivity scenario compared with the climate-only (332 km, IQR = 296) and climate land-cover change (297 km, IQR = 160) scenarios (Fig. 1a). Under the climate-only scenario, the median range expansions for endangered plants were 263 km (IQR = 186) increasing to 283 km (IQR = 160) and 307 km (IQR = 101) under

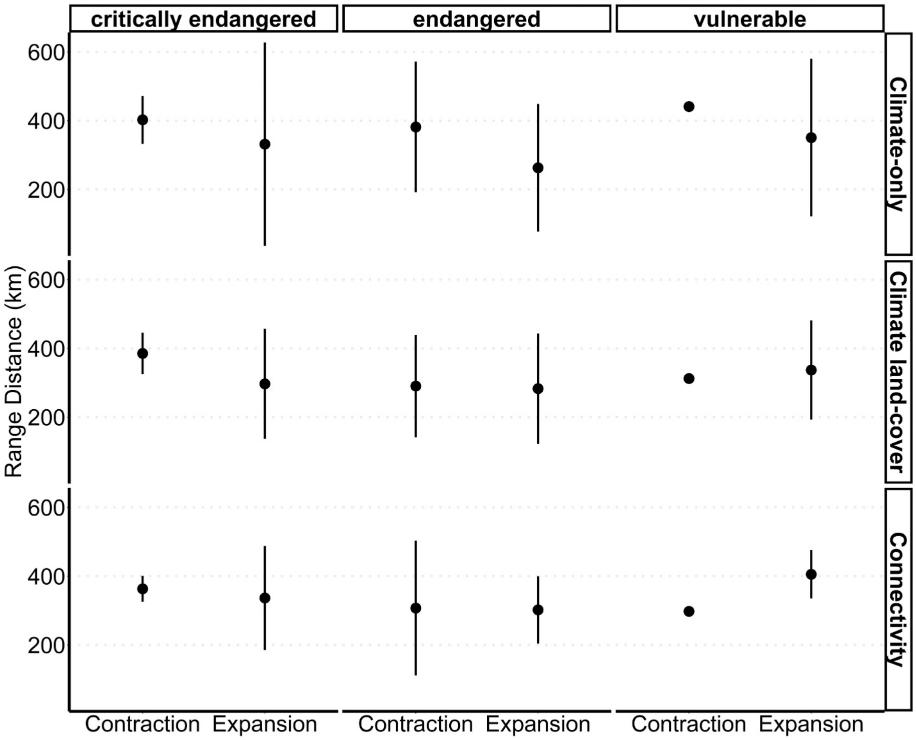

**Fig. 1.** Dot plot showing the median range shift due to contractions and expansions for critically endangered plants (left-panel), endangered plants (middle) and vulnerable plants (right-panel) under climate-only, climate land-cover change and connectivity scenarios. Filled circles indicate the median distance and vertical lines indicate the interquartile range.

climate land-cover change and connectivity scenarios. Over 50% of vulnerable plants experienced range expansions under all scenarios (Table C.2). There was a significant difference ($p \leq 0.05$) between range shift due to contractions and expansions among categories (Fig. C.8). However, there were no significant differences between IUCN categories and scenarios.

### 3.2. *Comparing range shifts under multiple scenarios*

More range contractions were predicted under the climate-only scenario compared with other scenarios (45 contraction and 42 expansion; Fig. 2a). For those species predicted to contract under the climate-only scenario, the median range shift was 397 km (IQR = 155), while for expansions it was 284 km (IQR = 213; Fig. 2a). Fewer range contractions were predicted under climate land-cover change scenario with a median range shift of 319 km (IQR = 139; Fig. 2b), while the median species' range expanded by 304 km (IQR = 154; Fig. 2b). Predictions for the connectivity scenario showed that 40 species would experience range shifts due to contractions (median = 317 km, IQR = 162; Fig. 2c), while 47 species' range would experience shifts from expansions (median = 309 km, IQR = 107; Fig. 2c). On average, range contractions under the climate-only scenario were predicted to be significantly larger than contractions under connectivity and future climate land-cover change scenarios (Wilcoxon signed-rank test, $p \leq 0.05$, Table C.3). This suggests

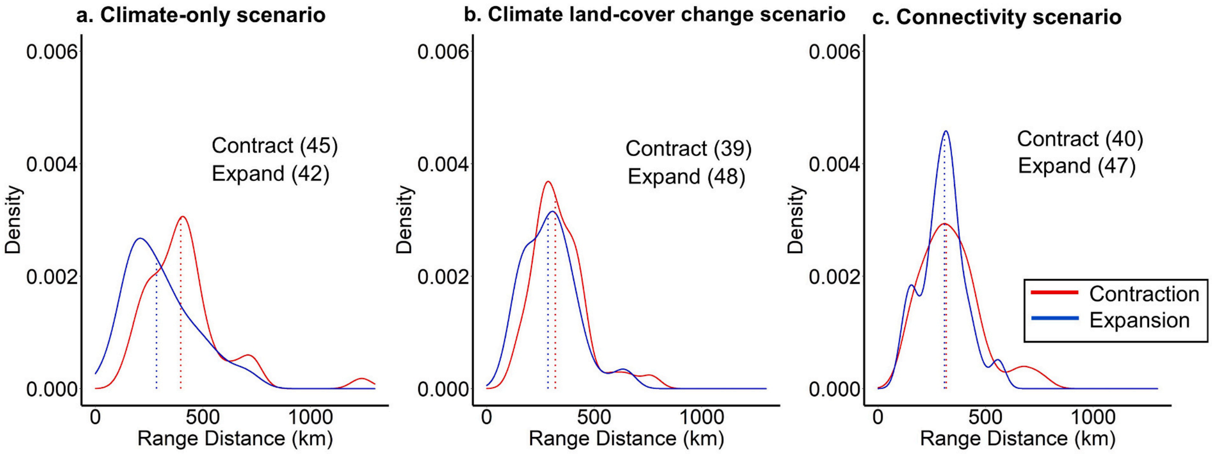

**Fig. 2.** Density plots showing the distribution of predicted range shift due to contractions and expansions for 87 plants under the climate-only, climate land-cover change and connectivity scenarios (a-c). Red curves indicate predicted contraction and blue curves indicate predicted expansions. Numbers in parentheses (a-c) represent the number of species whose range were predicted to either contract or expand in the future. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that inclusion of variables that account for dispersal potentials tends to constrain habitat suitability. There was no significant difference between range contractions and expansions under climate land-cover change and connectivity scenarios (Table C.3). Additionally, there is no strong evidence that dispersal syndromes or average elevation of current range influence contractions and expansions under scenarios (Table C.5). These results also suggest that in the future, connectivity will influence both range expansion and contraction differentially across scenarios (Fig. C.9).

### 3.3. *Comparing range displacements across risk classifications*

Fifty percent of critically endangered plants experienced upslope range displacement under climate land-cover change scenario (median = 92 masl; IQR = 145), while 38% and 62% displaced upslope under connectivity and climate-only scenarios (Fig. 3a, Table C.2). Under the connectivity scenario, 62% of critically endangered plants were predicted to displace downslope (median = −59 masl; IQR = 135). Only 38% of critically endangered plants experienced downslope range displacement (median = −371 masl; IQR = 201) under climate-only scenario. Similar number of endangered plants experienced upslope and downslope range displacements under climate land-cover change and connectivity scenarios the median upslope displacement was lower (16 masl, IQR = 112) under climate land-cover change scenario, increasing to 66 masl (IQR = 223) with connectivity (Fig. 3b). Only one vulnerable plant (*Dalbergia madagascariensis*) was predicted to experience downslope displacement under connectivity and climate land-cover change scenarios (Fig. 3c).

### 3.4. *Comparing range displacements under multiple scenarios*

Irrespective of risk classification, 45 species' ranges were predicted to experience upslope range displacement (median = 47 masl, IQR = 101), while 40 species were predicted to experience downslope displacement (median = −19 masl, IQR = 255, Fig. 4a) in the climate-only scenario. Under the climate land-cover change scenario, 44 species' ranges were predicted to displace upslope (median = 18 masl, IQR = 123), while 41 species' range were predicted to displace downslope (median = −151 masl, IQR = 346, Fig. 4b). In the connectivity scenario, 43 species' range were predicted to displace upslope with a median of 72 masl (IQR = 261) and 42 species would experience downslope range displacement (−97 masl, *IQR* = 155, Fig. 4c). For two species, namely, *Leptolaena pauciflora* and *Asteropeia amblyocarpa* no displacements were predicted.

### 3.5. *Mapping range shift due to contraction and expansion across multiple scenarios*

Zones of range contractions were predicted to be more prevalent under the climate land-cover change scenario compared with the climate-only and connectivity scenarios (Fig. 5, Table C.4). For instance, zones with high number of species' range contractions increased by 229% with climate and LCC relative to the climate-only scenario (Table C.4). Hotspots of range contractions (i.e. locations where more than 50% species' range contract) decreased by 63% under the connectivity scenario compared with climate land-cover change scenario, highlighting the importance of habitat connectivity on range shift assessments. Hotspots of range expansions increased by more than 200% under the connectivity scenario relative to the climate-only scenario (Table C.4). In all scenarios, range contractions and expansions were

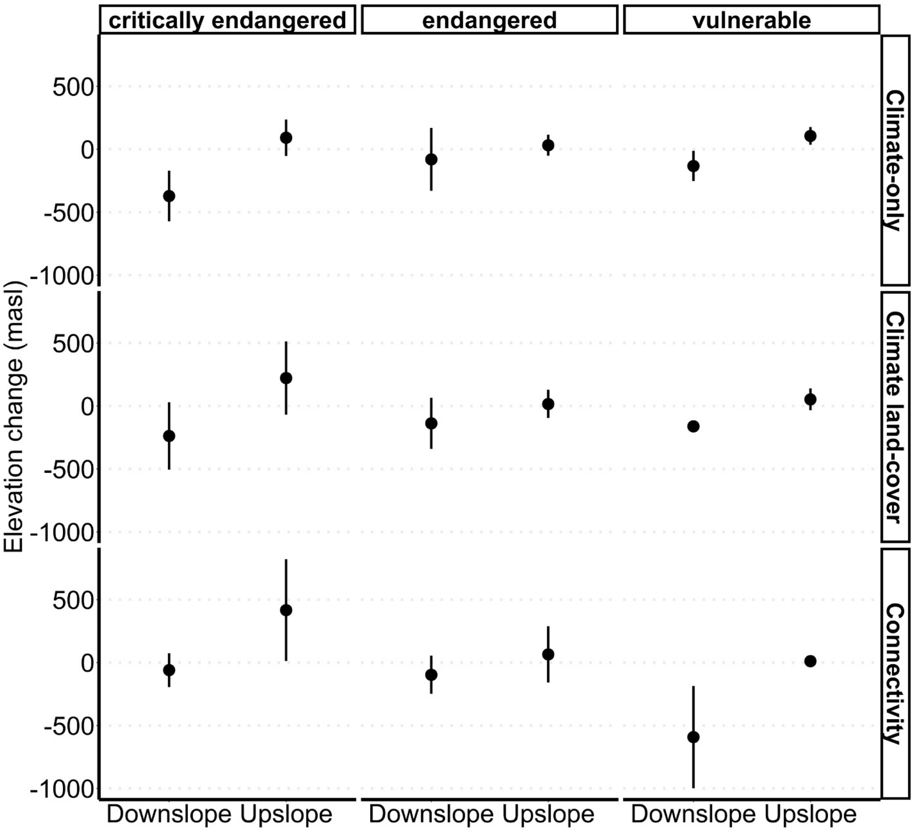

**Fig. 3.** Prediction of median elevation change due to upslope and downslope displacement for critically endangered plants (left-panel), endangered plants (middle) and vulnerable plants (right-panel) under climate-only, climate land-cover change and connectivity scenarios. Filled circles indicate the median distance and the vertical lines indicate the interquartile range.

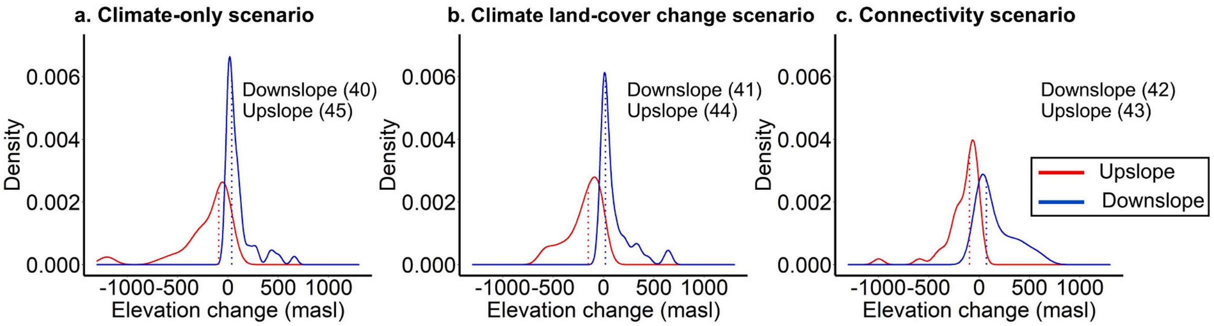

**Fig. 4.** Density plots showing the predicted downslope and upslope displacement in species' range under climate-only (a), climate land-cover change (b) and connectivity (c) scenarios. Dotted lines indicate the median elevation. Red curves indicate upslope displacement and blue curves indicated downslope displacements. Numbers in brackets show the number of species whose ranges were predicted to displace upslope or downslope in future scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

concentrated along the lowland evergreen moist and medium altitude moist evergreen forest formations on the East coast. Range expansion hotspots were also predicted to emerge in the West and South regions of Madagascar.

## 4. Discussion

Our results indicate that LCC and habitat connectivity is expected to limit the number of species experiencing range contractions compared with the climate-only scenario. Across all IUCN risk categories, the median range shift due to expansions were predicted to be higher under the connectivity scenario, which aligns with our expectations, as well as other studies (Mestre et al., 2017). This is also evidenced in the lower median range shifts due to contractions under the connectivity scenario (317 km) compared with climate land-cover change (319 km) and climate-only (397 km) scenarios (cf. Fig. 2). These results suggest that predicting range shift without measures of habitat connectivity and LCC neglects key features of the landscape, even when range shifts (due to expansions and contractions) are predicted, because there is no consideration for whether the landscape can support such movements. Our analysis demonstrate that current connectivity pathways are not only important for future range expansions but may be pivotal in limiting extinction risks that may occur from range contractions. Assessments of range shifts without habitat connectivity or measures of dispersal underestimates species' potential to reach safe sites. It is also possible that some species may adapt to novel environments, especially where human-induced forest loss is minimal thereby increasing ecological resilience under climate change (Spies et al., 2010). Contrary to our expectations, some species' range contracted under the connectivity scenario. This was particularly true for lowland and medium altitude moist evergreen forests, suggesting that connectivity may be inadequate to prevent hotspots of range contractions emerging in those regions. Predictions of multiple range contractions under the connectivity scenario should be taken as an indicator for potential biodiversity erosion. Although biodiversity redistribution is also a possible outcome, that prospect depends on other factors including competition, colonisation and extinction rates under environmental change (Corlett and Westcott, 2013). Nevertheless, conservation initiatives that aim to increase the protected area network and large-scale reforestation programmes on the island may benefit from assessments like ours that determine the role of connectivity on future plant distributions. Conservation planning that is evidence-based and relates to species-specific responses to environmental change is more likely to help develop best-practice and mitigate the impact of habitat loss .

### 4.1. *Significance of land-cover and habitat connectivity*

For some species the threat of extinctions may increase without habitat connectivity. For instance, habitat connectivity is expected to facilitate range expansions for *Angraecum setipes, Asteropeia micraster, Delonix pumila, Dypsis hovomantsina, Euphorbia elliotii, Euphorbia mandravioky, Hildegardia ankaranensis* and *Masoala kona.* Under land cover change scenario and without connectivity their ranges were predicted to contract (Appendix C, Fig. C.9). Suggesting that connectivity may play a vital role in enabling plant dispersals to safe sites. Where connectivity is absent there could be adverse impact on plants, especially for those assessed in this study, because a reasonable proportion (41%) exhibited barochory dispersal syndrome (Table C.6). Meaning that there is a lower probability for long distance dispersal (more common with anemochory) for most of the species considered and a higher probability that future dispersals may depend on the structural integrity of landscape connections (Kubisch et al., 2013). The fact that comparatively fewer focal species exhibit zoochory does not rule out the influence of primates as dispersal agents but highlights the importance of having multiple dispersal agents. Long distance seed dispersals mediated by primates are expected to be constrained due to habitat loss and fragmentation on the island (Albert-Daviaud et al., 2020). Preserving connections between habitat is vital, given our prediction that on average range shifts for the selected species are expected to be between 300 km and 350 km. These predictions are consistent with other assessments of range shifts in South America and demonstrate the likelihood of similar plant responses to environmental change in both regions (Feeley and Rehm, 2012). Some tropical studies suggest that mountaintop species are expected to become vulnerable under climate change (Peters et al., 2019). We find no evidence of this association between species that currently occupy high elevation range (i.e. $\mu > 1000$ masl) and contractions. For instance, *Euphorbia quartziticola* (current mean range = 1746 masl) was predicted to experience range expansion under all scenarios. It should be noted that our results suggest that plant characteristics, such as dispersal syndromes and average elevation of current range, have no impact on the capacity for species to contract or expand their ranges. Future studies could explore whether plant traits affect range shift of Malagasy plants, since there are still knowledge gaps on how most tropical lowland species' trailing and leading edges will respond to climate change (Rumpf et al., 2019).

Despite these gaps, our results indicate that connectivity would facilitate range shifts towards higher elevation for the selected plants . This is evident in the higher median upslope and downslope displacement predicted with connectivity (cf. Fig. 3), which confirm our initial expectation that upslope displacements will be higher with connectivity and increase the capacity for plants to track upward towards suitable climate conditions. There is a high possibility that with upward displacements lowland attrition becomes prevalent, although, this may be tempered by a high proportion of species range displacing downslope. Previous global scale assessments using climate-only variables suggests that range shifts along elevation gradient could increase the risks of

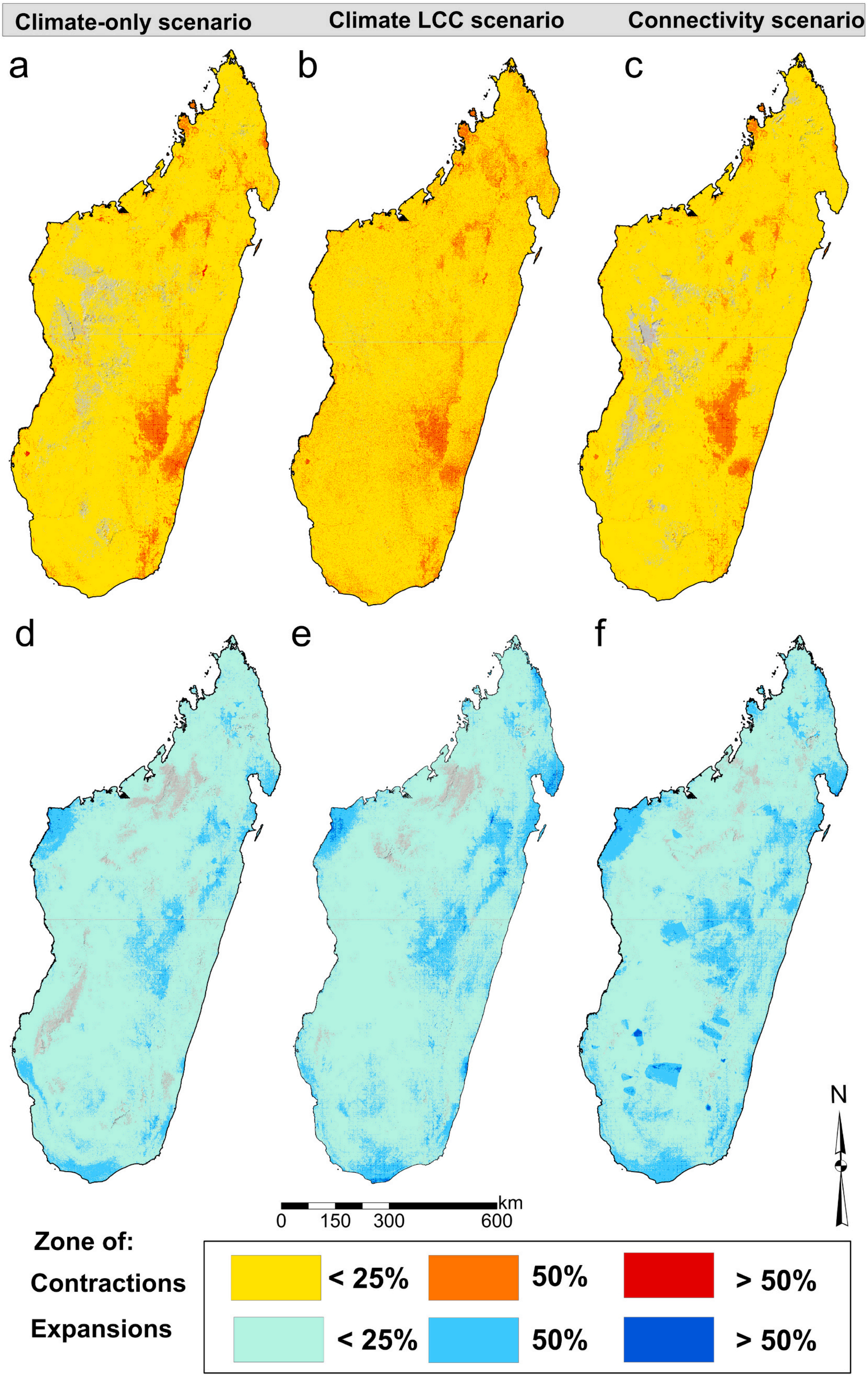

**Fig. 5.** Map showing the proportion of plants predicted to experience range shifts per 1 km$^2$ due to contractions (a, b, c) and expansions (d, e, f) under climate-only, climate land-cover change and connectivity scenarios. Range contraction and expansion hotspots were determined from predicted net losses and gains. Grey areas indicate pixels with no predictions.

extinctions (Chen et al., 2011). The spatial indices used to assess range shift in this study do not explicitly determine extinctions, however, evidence of range contractions and upslope displacements suggests that the risk is very high.

It is important to note that the measure of habitat connectivity used in this study did not account for the effect of common dispersal agents (e.g., wind, primates, birds and bats). In tropical regions, these agents play a crucial role in the success of species colonisation and/or plant community establishments (Carlo and Morales, 2016). Measuring species-specific dispersal rates is beyond the scope of this study and therefore we used structural connectivity as a proxy for dispersal. Using a structural connectivity approach to represent how likely the landscape matrix will support range shift under environmental change was an attempt to circumvent the lack of species-specific data. Although it is not a direct measure of dispersal rates or functional connectivity, we believe it is an improvement over models that fail to include any measure of connectivity. Furthermore, it is worth noting that the impact of environmental change on range shifts was implemented using a singular SDM, however, we assess range shifts using both high (RCP8.5) and low (RCP2.6) climate scenarios. The main results for the low climate emission scenario are provided in Appendix D.

### *4.2. Conservation implications*

Our results suggest that connectivity facilitates range expansions and limits range contractions compared with a LCC scenario for the most at-risk species . We also determine similar influence under a low emission scenario. Since the impact of climate change on plant distributions is inevitable, any hope of preserving Madagascar's unique plant diversity will depend on the response to LCC and the preservation of habitat connectivity. A useful approach could include strategies that target limiting range contractions in the Eastern lowlands while facilitating range expansions in the Western and Southern dry forests. At the national level, there is no evidence of a connectivity conservation plan, despite its successes in other tropical and sub-tropical countries including South Africa (Keeley et al., 2019), and progress in regional efforts aimed at protecting biodiversity and ecosystem services (Bullock et al., 2011).

To ensure that endangered and critically endangered plants respond positively to climate change, conservation strategies should focus on maintaining connectivity pathways. Madagascar has invested heavily in its protected area network (Mansourian and Dudley, 2008), as well as development of corridors connecting protected areas (e.g., Ankeniheny-Zahamena Corridor). Forest corridors do not benefit from the same governance strategy as the national parks they connect (Rakotoson and Razafimahatratra, 2018). By promoting multi-use strategies that allow for sustainable extraction of natural resources within corridors, they are subjected to increased pressures relative to protected areas that are under stricter governance (Ramiadantsoa et al., 2015). Ensuring connectivity between existing protected areas and intact forests is an ideal strategy to promote resilience to climate and LCC. To aid with this approach, we provide a map identifying range contraction and expansion hotspots for these endangered and critically endangered plants. The outcome of our study can guide long-term conservation strategies for many of the threatened plants on Madagascar by prioritising protection of species not established within protected areas or corridors. Although range contractions hotspots are predicted to dominate eastern forest corridors, it is also evident that contractions will be compensated by range expansions elsewhere, suggesting that the eastern corridor may be a hot-bed for range displacements (i.e. upslope and downslope). Such range dynamics across the island requires proactive conservation actions that minimises the threats to IUCN Red Listed species. Some of these actions could benefit from our study, especially if extended to a wider selection of plants to determine their responses to environmental change. More importantly, our study suggests that the use of high resolution, fine-scale, non-climate data focused on habitat connectivity could enable the formulation of conservation management plans that mitigate the impact of range contractions for tropical regions.

## CRediT authorship contribution statement

GUY and KAB conceived the idea; GUY designed and performed the data analysis with input from KAB; GUY and KAB led the writing with inputs from MCR, NSW and SER.

## Declaration of competing interest

We declare that there are no known competing financial interests or personal relationships that could have influenced this study.

## Acknowledgments

The authors acknowledge the HPC team for their technical support. We acknowledge the many contributors to the Global Biodiversity Information Facility (GBIF) from which all the sample of species occurrences were collected for this paper. The manuscript benefitted from the comments of three anonymous reviewers. We also thank Steig Johnson and Jos Barlow for their useful comments and insights on previous drafts of this manuscript. This work was supported by a doctoral research studentship from Kingston University London, UK.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109033.

## References

Albert-Daviaud, A., Perillo, S., Stuppy, W., 2018. Seed dispersal syndromes in the Madagascan flora: the unusual importance of primates Oryx 52, 418–426. https://doi.org/10.1017/S0030605317001600.

Albert-Daviaud A et al. (2020) The ghost fruits of Madagascar: identifying dysfunctional seed dispersal in Madagascar's endemic flora Biol. Conserv. 242:108438 doi:https://doi.org/10.1016/j.biocon.2020.108438.

Atkinson PM, Tatnall AR (1997) Introduction neural networks in remote sensing Int. J. Remote Sens. 18:699–709 doi:https://doi.org/10.1080/014311697218700.

Bevill R, Louda S (1999) Comparisons of related rare and common species in the study of plant rarity Conserv. Biol. 13:493–498 doi:https://doi.org/10.1046/j.1523-1739.1999.97369.x.

Boakes EH, Isaac NJB, Fuller RA, Mace GM, McGowan PJK (2018) Examining the relationship between local extinction risk and position in range Conserv. Biol. 32: 229–239 doi:https://doi.org/10.1111/cobi.12979.

Bodin Ö, Tengö M, Norman A, Lundberg J, Elmqvist T (2006) The value of small size: loss of forest patches and ecological thresholds in southern Madagascar Ecol. Appl. 16: 440–451 doi:https://doi.org/10.1890/1051-0761(2006)016[0440:Tvossl]2.0.Co;2.

Brown KA, Parks KE, Bethell CA, Johnson SE, Mulligan M (2015) Predicting plant diversity patterns in Madagascar: understanding the effects of climate and land cover change in a biodiversity hotspot PLoS One 10:e0122721-e0122721 doi:https://doi.org/10.1371/journal.pone.0122721.

Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities Trends in Ecology & Evolution 26, 541–549. https://doi.org/10.1016/j.tree.2011.06.011.

Callmander MW et al. (2011) The endemic and non-endemic vascular flora of Madagascar updated Plant Ecology and Evolution 144:121-125 doi:https://doi.org/10.5091/plecevo.2011.513.

Carlo TA, Morales JM (2016) Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal Ecology 97:1819–1831 doi: https://doi.org/10.1890/15-2147.1.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming Science 333:1024–1026 doi: https://doi.org/10.1126/science.1206432.

Choe H, Thorne JH, Hijmans R, Kim J, Kwon H, Seo C (2017) Meta-corridor solutions for climate-vulnerable plant species groups in South Korea J. Appl. Ecol. 54:1742–1754 doi:https://doi.org/10.1111/1365-2664.12865.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics Science 322: 258–261 doi:https://doi.org/10.1126/science.1162547.

Coops NC, Waring RH, Plowright A, Lee J, Dilts TE (2016) Using remotely-sensed land cover and distribution modeling to estimate tree species migration in the Pacific Northwest Region of North America Remote Sens. 8:65 doi:https://doi.org/10.3390/rs8010065.

Core Team, R., 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2014.

Corlett, R.T., Westcott, D.A., 2013. Will plant movements keep up with climate change? Trends Ecol. Evol. 28, 482–488. https://doi.org/10.1016/j.tree.2013.04.003.

Davis AP, Gole TW, Baena S, Moat J (2012) The impact of climate change on indigenous Arabica coffee (Coffea arabica): predicting future trends and identifying priorities PLOS ONE 7:e47981 doi:https://doi.org/10.1371/journal.pone.0047981.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species Methods in ecology and evolution 1, 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

ESRI Inc., 2015. ArcGIS Pro1.0. Environmental Systems Research Institute. Redlands, CA. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview. (Accessed 15 July 2017).

Feeley KJ, Rehm EM (2012) Amazon's vulnerability to climate change heightened by deforestation and man-made dispersal barriers Glob. Chang. Biol. 18:3606–3614 doi:https://doi.org/10.1111/gcb.12012.

Feeley KJ, Silman MR (2010) Biotic attrition from tropical forests correcting for truncated temperature niches Glob. Chang. Biol. 16:1830–1836 doi:https://doi.org/10.1111/j.1365-2486.2009.02085.x.

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas International Journal of Climatology 37:4302-4315 doi:https://doi.org/10.1002/joc.5086.

Foltête, J.-C., Clauzel, C., Vuidel, G., Tournant, P., 2012. Integrating graph-based connectivity metrics into species distribution models Landscape Ecology 27, 557–569. https://doi.org/10.1007/s10980-012-9709-4.

Gautiert, L., Tahinarivony, A.J., Ranirison, P., Wohlhauser, S., 2018. Vegetation. In: Goodman, S.M., Raherilalao, M.J., Wohlhauser, S. (Eds.), The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota, vol. 1. Antananarivo, Association Vahatra, pp. 207–242.

Golding, N., Purse, B.V., 2016. Fast and flexible Bayesian species distribution modelling using Gaussian processes Methods in Ecology and Evolution 7, 598–608. https://doi.org/10.1111/2041-210x.12523.

Good, T.C., Zjhra, M.L., Kremen, C., 2006. addressing data deficiency in classifying extinction risk: a case study of a radiation of bignoniaceae from madagascar Conservation Biology 20, 1099–1110. https://doi.org/10.1111/j.1523-1739.2006.00473.x.

Gurrutxaga, M., Rubio, L., Saura, S., 2011. Key connectors in protected forest area networks and the impact of highways: a transnational case study from the Cantabrian Range to the Western Alps (SW Europe) Landscape and Urban Planning 101, 310–320. https://doi.org/10.1016/j.landurbplan.2011.02.036.

Hong-Wa, C., Arroyo, T.P.F., 2012. Climate-induced range contraction in the Malagasy endemic plant genera Mediusella and Xerochlamys (Sarcolaenaceae) Plant Ecology and Evolution 145, 302–312. https://doi.org/10.5091/plecevo.2012.742.

Huang, J.-L., Andrello, M., Martensen, A.C., Saura, S., Liu, D.-F., He, J.-H., Fortin, M.-J., 2020. Importance of spatio–temporal connectivity to maintain species experiencing range shifts Ecography 43, 591–603. https://doi.org/10.1111/ecog.04716.

IPCC (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change IPCC 2014: Climate Change 2014: Synthesis Report 104.

IPCC, 2018. Summary for Policymakers. World Meteorological Organization, Geneva, Switzerland.

IUCN, 2017. The IUCN Red List of Threatened Species. Version 2017-3. https://www.iucnredlist.org/. (Accessed 6 August 2018).

Keeley, A.T.H., Beier, P., Creech, T., Jones, K., Jongman, R.H.G., Stonecipher, G., Tabor, G.M., 2019. Thirty years of connectivity conservation planning: an assessment of factors influencing plan implementation Environmental Research Letters 14, 103001. https://doi.org/10.1088/1748-9326/ab3234.

Kreyling, J., Wana, D., Beierkuhnlein, C., 2010. Potential consequences of climate warming for tropical plant species in high mountains of southern Ethiopia Diversity and Distributions 16, 593–605. https://doi.org/10.1111/j.1472-4642.2010.00675.x.

Kubisch, A., Degen, T., Hovestadt, T., Poethke, H.J., 2013. Predicting range shifts under global change: the balance between local adaptation and dispersal Ecography 36, 873–882. https://doi.org/10.1111/j.1600-0587.2012.00062.x.

Kuhn E, Lenoir J, Piedallu C, Gégout J-C (2016) Early signs of range disjunction of submountainous plant species: an unexplored consequence of future and contemporary climate changes Global Change Biology 22:2094-2105 doi:https://doi.or/10.1111/gcb.13243.

Laurance WF et al. (2011) Global warming, elevational ranges and the vulnerability of tropical biota Biological Conservation 144:548-557 doi:https://doi.org/10.1016/j.biocon.2010.10.010.

Lichstein, J.W., Simons, T.R., Shriner, S.A., Franzreb, K.E., 2002. Spatial autocorrelation and autoregressive models in ecology Ecological Monographs 72, 445–463. https://doi.org/10.1890/0012-9615(2002)072[0445:Saaami]2.0.Co;2.

Liu, C., Newell, G., White, M., 2016. On the selection of thresholds for predicting species occurrence with presence-only data Ecology and Evolution 6, 337–348. https://doi.org/10.1002/ece3.1878.

Mansourian S, Dudley N (2008) Public funds to protected areas.

Martin G et al. (2011) The HadGEM2 family of Met Office Unified Model climate configurations 4:723–757 doi:https://doi.org/10.5194/gmd-4-723-2011.

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook Landscape Ecology 31, 1161–1175. https://doi.org/10.1007/s10980-016-0374-x.

McRae BH, Kavanagh DM (2011) Linkage mapper connectivity analysis software The Nature Conservancy.

McRae, B.H., Hall, S.A., Beier, P., Theobald, D.M., 2012. Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. PLoS One 7, e52604. https://doi.org/10.1371/journal.pone.0052604.

Mestre F, Risk BB, Mira A, Beja P, Pita R (2017) A metapopulation approach to predict species range shifts under different climate change and landscape connectivity scenarios Ecol. Model. 359:406–414 doi:https://doi.org/10.1016/j.ecolmodel.2017.06.013.

Moat, J., Smith, P., 2007. Atlas of the Vegetation of Madagascar Vegetation/Atlas de la Vegetation de Madagascar (Text in English and French). Royal Botanical Gardens, Kew.

Morin, X., Thuiller, W., 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change Ecology 90, 1301–1313. https://doi.org/10.1890/08-0134.1.

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation Biol. Conserv. 117:285–297 doi:https://doi.org/10.1016/j.biocon.2003.12.008.

Peters MK et al. (2019) Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions Nature 568:88-92 doi:https://doi.org/10.1038/s41586-019-1048-z.

Pickard B, Gray J, Meentemeyer R (2017) Comparing quantity, allocation and configuration accuracy of multiple land change models Land 6:52 doi:https://doi.org/10.3390/land6030052.

Radinger J, Essl F, Hölker F, Horký P, Slavík O, Wolter C (2017) The future distribution of river fish: the complex interplay of climate and land use changes, species dispersal and movement barriers Global Change Biology 23:4970-4986 doi:https://doi.org/10.1111/gcb.13760.

Rakotoson, J., Razafimahatratra, P., 2018. Legal, judiciary, and financial aspects of Madagascar protected areas: past, present, and future. In: Goodman, S., Raherilalao, M., Wohlhauser, S. (Eds.), The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota. Association Vahatra, Antananarivo, Madagascar, pp. 105–168.

Ramiadantsoa, T., Ovaskainen, O., Rybicki, J., Hanski, I., 2015. Large-scale habitat corridors for biodiversity conservation: a forest corridor in Madagascar PloS one 10, e0132126. https://doi.org/10.1371/journal.pone.0132126.

Rasmussen, C.E., Williams, C.K., 2006. Gaussian Processes for Machine Learning the MIT Press. MA, Cambridge.

Razafindratsima, O.H., Jones, T.A., Dunham, A.E., 2014. Patterns of movement and seed dispersal by three lemur species American Journal of Primatology 76, 84–96. https://doi.org/10.1002/ajp.22199.

Record, S., Strecker, A., Tuanmu, M.-N., Beaudrot, L., Zarnetske, P., Belmaker, J., Gerstner, B., 2018. Does scale matter? A systematic review of incorporating biological realism when predicting changes in species distributions PLOS ONE 13, e0194650. https://doi.org/10.1371/journal.pone.0194650.

Redding, D.W., Lucas, T.C.D., Blackburn, T.M., Jones, K.E., 2017. Evaluating Bayesian spatial methods for modelling species distributions with clumped and restricted occurrence data PLOS ONE 12, e0187602. https://doi.org/10.1371/journal.pone.0187602.

Rosenblad, K.C., Perret, D.L., Sax, D.F., 2019. Niche syndromes reveal climate-driven extinction threat to island endemic conifers Nature Climate Change 9, 627–631. https://doi.org/10.1038/s41558-019-0530-9.

Rumpf, S.B., Hülber, K., Zimmermann, N.E., Dullinger, S., 2019. Elevational rear edges shifted at least as much as leading edges over the last century Global Ecology and Biogeography 28, 533–543. https://doi.org/10.1111/geb.12865.

Seidler, T.G., Plotkin, J.B., 2006. Seed dispersal and spatial pattern in tropical trees PLoS biology 4, e344. https://doi.org/10.1371/journal.pbio.0040344.

Şekercioğlu, Ç.H., Loarie, S.R., Oviedo-Brenes, F., Mendenhall, C.D., Daily, G.C., Ehrlich, P.R., 2015. Tropical countryside riparian corridors provide critical habitat and connectivity for seed-dispersing forest birds in a fragmented landscape Journal of Ornithology 156, 343–353. https://doi.org/10.1007/s10336-015-1299-x.

Spies, T.A., Giesen, T.W., Swanson, F.J., Franklin, J.F., Lach, D., Johnson, K.N., 2010. Climate change adaptation strategies for federal forests of the Pacific northwest. USA: ecological, policy, and socio-economic perspectives Landscape Ecology 25, 1185–1199. https://doi.org/10.1007/s10980-010-9483-0.

Stuber, E.F., Gruber, L.F., Fontaine, J.J., 2017. A Bayesian method for assessing multi-scale species-habitat relationships Landscape Ecology 32, 2365–2381. https://doi.org/10.1007/s10980-017-0575-y.

Vieilledent G, Merow C, Guélat J, Latimer A, Kéry M, Gelfand A, Silander Jr J (2014) hSDM: hierarchical Bayesian species distribution models vol 1.

Vieilledent, G., Grinand, C., Rakotomalala, F.A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T.F., 2018. Achard F. Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar Biological Conservation 222, 189–197. https://doi.org/10.1016/j.biocon.2018.04.008.

Vogt, P., Riitters, K.H., Estreguil, C., Kozak, J., Wade, T.G., Wickham, J.D., 2007. Mapping Spatial Patterns with Morphological Image Processing Landscape Ecology 22, 171–177. https://doi.org/10.1007/s10980-006-9013-2.

Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K.E.N., Poschlod, P., 2011. Climate change and plant regeneration from seed Global Change Biology 17, 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x.

Walter, J., Jentsch, A., Beierkuhnlein, C., Kreyling, J., 2013. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes Environmental and Experimental Botany 94, 3–8. https://doi.org/10.1016/j.envexpbot.2012.02.009.

Warren R, Price J, Graham E, Forstenhaeusler N, VanDerWal J (2018) The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C Science 360:791-795 doi:https://doi.org/10.1126/science.aar3646.

Wiens, J.J., 2016. Climate-related local extinctions are already widespread among plant and animal species PLOS Biology 14, e2001104. https://doi.org/10.1371/journal.pbio.2001104.

Yesuf, G., Brown, K.A., Walford, N., 2019. Assessing regional-scale variability in deforestation and forest degradation rates in a tropical biodiversity hotspot Remote Sensing in Ecology and Conservation 5, 346–359. https://doi.org/10.1002/rse2.110.

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., Coomes, D., 2019. Advances in Microclimate Ecology Arising From Remote Sensing Trends in Ecology & Evolution 34, 327–341. https://doi.org/10.1016/j.tree.2018.12.012.

Zurell D et al. (2016) Benchmarking novel approaches for modelling species range dynamics Global Change Biology 22:2651-2664 doi:https://doi.org/10.1111/gcb.13251.