

Climate-induced range contraction in the Malagasy endemic plant genera Mediusella and Xerochlamys (Sarcolaenaceae)

Cynthia Hong-Wa^{1,2,*} & Teresa Patricia Feria Arroyo³

¹Department of Biology, University of Missouri–St. Louis, One University Blvd, St. Louis, MO 63121-4000, USA ²Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, USA

³Department of Biology, The University of Texas–Pan American, 1201 West University Drive, Edinburg, TX 78539-2999, USA *Author for correspondence: cynthia.hong-wa@mobot.org

Background and aims – Climate change imposes new challenges on biodiversity conservation, especially in tropical areas where anthropogenic pressures have already increased the vulnerability of many species. New conservation strategies are needed to anticipate the impacts of future climate change and species distribution modeling remains the most useful approach in predicting these impacts and in assisting conservation planning. The objectives of this study were to develop species distribution models for threatened endemic plant species of Madagascar and to assess the impacts of climate change on the species distributions.

Methods – Ten species belonging to the genera *Mediusella* and *Xerochlamys* of Madagascar's endemic plant family Sarcolaenaceae were included in this study. Potential distribution models using 19 climatic variables were developed for the ten species and projected onto the present and future to evaluate the potential distribution of each species. Future distributions of these species were predicted for 2050 using three general circulation models and two climate scenarios. We also assessed the patterns of range shifts by comparing present and future distributions under the different models and scenarios.

Key results – Most species were predicted to undergo major range contraction as a result of climate change. Species in the Central High Plateau of Madagascar were predicted to experience the highest habitat loss, with narrow-range species being the most sensitive. Southward migration was predicted for species distributed in the northwest, whereas upland migration was predicted for some central species.

Conclusions – Future climate change will drastically affect the distribution of our target species, seven of which will experience major range contraction by 2050. Among these, threatened endemic species will face higher risk of extinction due to habitat loss. Range expansion was also predicted for two species. In any case, species' adaptation to a changing climate may not happen soon enough, emphasizing the need to strengthen current conservation efforts, especially in areas where species are most likely to persist.

Key words – Climate change, contraction, endemic, future distribution, Madagascar, *Mediusella*, narrow-range, *Xerochlamys*.

INTRODUCTION

Future climates are expected to change in temperature and precipitation regimes (IPCC 2007). Such changes have already triggered various ecological and evolutionary responses (Parmesan 2006). Increasing evidence suggests that these changes are already affecting species' current geographical distributions (Parmesan 2006, Chen et al. 2011) and will impose new challenges on biodiversity conservation (Pressey et al. 2007, Thuiller et al. 2008). Indeed, one of the most documented responses to climate change is the shifts in the distributions and abundances of species (Parmesan & Yohe 2003, Parmesan 2006, Chen et al. 2011). Yet, despite the worldwide impacts of a changing climate, such studies are still largely lacking for several areas, in particular tropical ones (Cayuela et al. 2009), which may hamper a global effort to address future issues. There is a growing recognition that although the magnitude of global climate change may be stronger in temperate regions, its effects may be more problematic in tropical areas due to increasing climatic variability and cascading effects on species diversity (Bush 2002, Beaumont et al. 2011). There is also a growing recognition that conservation strategies must anticipate the impacts of climate change, and that dynamic strategies are needed to ensure adequate protection of future patterns of biodiversity without compromising current endeavors (Hannah et al. 2002a, Hannah et al. 2008). Although global efforts are necessary to constrain negative effects of future climatic changes, regional approaches are likely to be more successful in addressing specific contextual issues (Hannah et al. 2002b, Galatowitsch et al. 2009), and can be applied to biodiversity hotspots where the stakes are greater but the risks of biodiversity loss are higher (Hannah et al. 2002a, Midgley et al. 2002).

The importance of species distribution modeling in assisting conservation planning has been well emphasized (Araújo & Williams 2000, Ferrier et al. 2002, Thuiller et al. 2005, Urbina-Cardona & Flores-Villela 2010, Araújo et al. 2011). The application of species distribution modeling to investigate the effects of climate change involves characterizing the habitat of a target species (Kearney 2006) based on known occurrence points that provide information on the species climatic environment. These species distribution models can then be projected onto both present and modeled future climates to predict current and future potential distribution (Peterson 2001, Peterson et al. 2004). The validity of species distribution models and their accuracy to forecast future biodiversity patterns and species responses to changing climate and the reliability of projections have been questioned due to uncertainties relating to methodological constraints, ecological theory and climate scenario models (Pearson & Dawson 2003, Thuiller 2004, Guisan & Thuiller 2005, Heikkinen et al. 2006). Nonetheless, species distribution models, despite their limitations, are useful tools providing first approximations on impacts of climate change on species range (Pearson & Dawson 2003, Araújo & Rahbek 2006, Heikkinen et al. 2006), and can be used to identify critical areas of conservation values and to develop strategic conservation planning (Araújo & Rahbek 2006, Hannah et al. 2002a, 2008).

In this study, we focus on Madagascar, a biodiversity hotspot characterized by a high endemism in various groups of organisms (Myers et al. 2000) that have been imperiled by human activities, mainly deforestation (Hanski et al. 2007, Harper et al. 2007). By 2050, Madagascar is expected to have some 1.1-2.6°C increases in mean temperature, have increased summer rainfall and reduced winter precipitation (Hannah et al. 2008, Tadross et al. 2008). The greatest impacts are predicted for the southern part of the island (Ingram & Dawson 2005, de Wit & Stankiewicz 2006, Tadross et al. 2008); however, current patterns of forest fragmentation and vegetation loss (Harper et al. 2007) also put other regions at high risk. Indeed, the most fragmented forest types are the dry forests, woodlands and spiny forests in the western, central and southern parts of Madagascar respectively (Harper et al. 2007). Therefore, species in these regions are expected to be more threatened by climate change. For this study, we selected ten species from the Malagasy endemic plant family Sarcolaenaceae that are mostly narrowly distributed, and occur in areas that are highly fragmented (Harper et al. 2007) and where dramatic changes are expected (Tadross et al. 2008). In particular, the two species of the genus *Medi*usella (M. arenaria and M. bernieri) are both restricted to the northern and north-western part of the island within the dry bioclimatic zone (Schatz 2000), whereas the eight species of the genus Xerochlamys are mostly distributed in the Central High Plateau, with some species in the southern and north-western regions, but all occurring within the arid, dry and subhumid bioclimatic zones. Most species have a narrow range with two, *X. diospyroidea* and *X. itremoensis*, known only from a small geographic area: the Itremo Massif. Six of these ten species have been provisionally evaluated as endangered using IUCN Red List criteria (Hong-Wa 2009). Habitat destruction is the main threat to species of *Mediusella* and *Xerochlamys*, although these species have also been exploited for timber and firewood.

To date, about 14,000 plant species are estimated to occur on Madagascar, of which about 85% are endemic (Callmander et al. 2011). Deforestation at an annual average rate of 1% has already claimed about 90% of the island's natural forest (Harper et al. 2007) and climate change could also inflict an habitat loss of 11-27% under perfect migration and 17-50% without migration (Malcolm et al. 2006). To our knowledge, the only assessment of impacts of climate change on Malagasy plant species predicts mainly a range contraction (42 out of 74 species versus 25 for range expansion; Schatz et al. 2008). Here we present predictions of climate change effects on ten narrowly endemic plant species distributed in areas forecasted to be the most impacted. Our objectives are to (1) develop models of potential distribution for each species to predict their current distribution, (2) apply these models to predict future potential distribution under two scenarios (moderate and severe) of climate change, and (3) assess gain and loss of habitat under different climate scenarios.

METHODS

Species records

Occurrence data used in this study came from field surveys, herbarium specimens and the TROPICOS database of the Missouri Botanical Garden (http://www.tropicos.org). Missing coordinates were assigned post facto using the Gazetteer to Malagasy Botanical Collecting Localities (http://www. mobot.org/MOBOT/Research/madagascar/gazetteer/) and maps. Information on occurrence data can be found in Hong-Wa (2009). In general, our data were characterized by low sample size, with *Xerochlamys elliptica* represented only by six collections. Although denser sampling is generally desirable, different modeling methods can nonetheless perform moderately well to small sample sizes, with Maxent (Phillips et al. 2006) producing the most useful results with sample sizes as small as five occurrences (Hernandez et al. 2006, Pearson et al. 2007). Duplicate occurrence points that fell within the same locality were removed from the analyses.

Environmental data

We obtained the environmental data from the WorldClim database (Hijmans et al. 2005). WorldClim contains a set of global climate layers with a spatial resolution of $\sim 1 \times 1$ km generated through interpolation of climate data (monthly total precipitation, and monthly mean, minimum and maximum temperature) obtained from climate station records from 1950–2000. A set of 19 bioclimatic variables derived from the monthly data were used in this study: BIO1: annual

Table 1 – Performance of present-day species	distribution models a	is measured by the	AUC for the ten s	species of the	Malagasy
endemic genera <i>Mediusella</i> and <i>Xerochlamys</i> .					

AUC: area under the curve of the receiver operating characteristics (ROC).

Species	Training AUC				Test AUC				
	Points	Minimum	Average	Maximum	Points	Minimum	Average	Maximum	
M. arenaria	19	0.9738	0.9805	0.9928	7	0.9176	0.9488	0.9697	
M. bernieri	14	0.9910	0.9931	0.9960	5	0.9737	0.9901	0.9969	
X. bojeriana	46	0.9424	0.9534	0.9692	19	0.8858	0.9367	0.9694	
X. coriacea	11	0.8815	0.9198	0.9767	4	0.8096	0.8799	0.9408	
X. diospyroidea	10	0.9946	0.9958	0.9977	4	0.9912	0.9965	0.9990	
X. elliptica	5	0.9773	0.9857	0.9919	1	0.9111	0.9472	0.9719	
X. itremoensis	8	0.9977	0.9983	0.9993	3	0.9946	0.9979	0.9992	
X. tampoketsensis	8	0.9789	0.9852	0.9978	3	0.8996	0.9679	0.9987	
X. undulata	17	0.9835	0.9869	0.9920	7	0.9595	0.9858	0.9979	
X. villosa	10	0.9911	0.9943	0.9989	4	0.9715	0.9903	0.9996	

mean temperature, BIO2: mean diurnal temperature range, BIO3: isothermality, BIO4: temperature seasonality, BIO5: maximum temperature of warmest month, BIO6: minimum temperature of coldest month, BIO7: temperature annual range, BIO8: mean temperature of wettest quarter, BIO9: mean temperature of driest quarter, BIO10: mean temperature of warmest quarter, BIO11: mean temperature of coldest quarter, BIO12: annual precipitation, BIO13: precipitation of wettest month, BIO14: precipitation of driest month, BIO15: precipitation seasonality, BIO16: precipitation of wettest quarter, BIO17: precipitation of driest quarter, BIO18: precipitation of warmest quarter, and BIO19: precipitation of coldest quarter. We tested for multicollinearity among variables but did not find any significant (p-value < 0.05) strong correlation (Pearson's r > 0.90). Therefore, we did not remove any variable, recognizing that overfitting may thus happen for species with low number of occurrences.

Model building and evaluation

To model the species distribution, we used all 19 bioclimatic variables and the maximum entropy method (Maxent, Phillips et al. 2006) because it is the best-performing method when sample size is small (Hernandez et al. 2006, Pearson et al. 2007). Models were generated by randomly selecting 70% of the occurrence points as training data and were evaluated with the remaining 30% of the species records as test data. We employed this cross-validation procedure on multiple replicate models and generated the species distribution model using the average of the replicates for each species (Mateo et al. 2010). We used the area under the curve (AUC) of the receiver operating characteristic (ROC) to evaluate model performance. The AUC ranges from 0 to 1 and measures the discriminatory ability of a model, where a value of 1 denotes a perfect discrimination between sites where a species is present versus those where it is absent, whereas a value of 0.5 indicates discrimination no better than the null model (Elith et al. 2006). The AUC provides a single measure of overall accuracy of models that is not dependent on a particular threshold (Fielding & Bell 1997). We also

evaluated the importance of each environmental variable in explaining the species distribution with a jack-knife test.

Projection under future scenarios

Future distribution models were developed for 2050 under two climate scenario families: A2 and B2. These scenarios assume a more heterogeneous world, but with B2 being more environmentally focused than A2. We used three general circulations models: the Canadian Centre for Climate Modelling and Analysis (CCCMA), the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Hadley Centre for Climate Change (Hadley).

We estimated potential gain and loss in habitat for each species under the different climate scenarios and general circulation models. We first reclassified the potential distribution models for the present and future to obtain binary maps (presence = 1, absence = 0) using the "Maximum sensitivity plus specificity training" as a threshold (Liu et al. 2005, Jiménez-Valverde & Lobo 2007, Hu & Jiang 2010). The binary maps were then projected onto UTM with a spatial resolution of 1 km². The gain or loss in potential distribution was estimated as the difference between future and current areas occupied by the species.

Authorship of names

Authorship of names used in this study follows Hong-Wa (2009) and Hong-Wa & Schatz (2011): *Mediusella* (Cavaco) Hutchinson *M. arenaria* (F.Gérard) Hong-Wa *M. bernieri* (Baill.) Hutchinson *Xerochlamys* Baker *X. bojeriana* (Baill.) F.Gérard *X. coriacea* Hong-Wa *X. diospyroidea* (Baill.) F.Gérard *X. elliptica* F.Gérard *X. itremoensis* Hong-Wa, G.E.Schatz & Lowry *X. tampoketsensis* F.Gérard

- X. undulata Hong-Wa
- X. villosa F.Gérard

RESULTS

Potential distribution – Present

All species distribution models received high average AUC values (> 0.95), except X. coriacea (table 1), indicating high predictive power of the models. In general, AUC values for the training data were slightly higher than those obtained from the test data, perhaps suggesting over-parameterized models that included too many explanatory variables, some of which may be correlated. However, no strong correlation (Pearson's r > 0.90) was significant at the 0.05 level, and so we did not remove any variables to avoid excluding those with potential ecological relevance. Moreover, overparameterization is less problematic than under-parameterization (Warren & Siefert 2011). The average AUC values were highest for species with restricted distribution such as X. diospyroidea and X. itremoensis, both known only from the Itremo Massif. There was also a good agreement between observed occurrence and occurrence predicted by the models in the present, except for X. coriacea for which distribution was predicted to extend along the eastern escarpment of Madagascar from north to south (fig. 1).

Environmental variables that contributed the most to the models are mostly temperature-related. Interestingly, there was a geographic patterning in the influence of these variables. Indeed, for species distributed in the southern part of the island (*X. coriacea, X. undulata* and *X. villosa*), the predictions were mostly influenced by precipitation of wettest quarter (BIO16) and precipitation of driest quarter (BIO17). Model predictions of species occurring on the Central High Plateau (*X. bojeriana, X. diospyroidea, X. elliptica* and *X. itremoensis*) were mostly influenced by mean temperature of wettest quarter (BIO8) and mean temperature of driest quarter (BIO9) whereas those of the northern species (*M. arenaria, M. bernieri* and *X. tampoketsensis*) were influenced largely either by precipitation of driest month (BIO14) or temperature annual range (BIO7) and mean temperature of coldest quarter (BIO11).

Potential distribution – Future

All general circulation models and scenarios for future climate used in this study predicted substantial changes in the distribution of the ten species belonging to the genera *Mediusella* and *Xerochlamys* by 2050. In particular, all but one species (*M. arenaria*) will experience a considerable loss of habitats under both severe (A2) and moderate (B2) scenarios (figs 2–4; electronic appendices 1 & 2). All models also performed comparably by showing the same patterns of loss or gain. However, in some instances, some contradictions appeared. For example, while the CSIRO and Hadley



Figure 1 – Current potential distribution of species of the genera *Mediusella* and *Xerochlamys*. A, *M. arenaria*; B, *M. bernieri*; C, *X. bojeriana*; D, *X. coriacea*; E, *X. diospyroidea*; F, *X. elliptica*; G, *X. itremoensis*; H, *X. tampoketsensis*; I, *X. undulata*; J, *X. villosa*. White squares are known occurrence points.



Figure 2 – Gain and loss in potential distribution of species of *Mediusella* and *Xerochlamys* by 2050 based on different climate change models (CCCMA, CSIRO, HADLEY) and scenarios (A2 and B2). A–D, *M. arenaria*; E–H, *M. bernieri*; I–L, *X. bojeriana*; M–P, *X. coriacea*.



Figure 3 – Gain and loss in potential distribution of species of *Mediusella* and *Xerochlamys* species by 2050 based on different climate change models (CCCMA, CSIRO, HADLEY) and scenarios (A2 and B2). A–D, *X. diospyroidea*; E–H, *X. elliptica*; I–L, *X. itremoensis*; M–P, *X. tampoketsensis*.

Table 2 – Change in future potential distribution of species of *Mediusella* and *Xerochlamys* and predicted trend by 2050 based on the number of gain and loss exhibited by the models.

Both scenarios A2 and B2 assume a more heterogeneous world but with B2 being more environmentally friendly than A2.

Species	Present		Scenario A2		Scenario B2			<u> </u>	T	Predicted
	(area in km ²)	CCCMA	CSIRO	HADLEY	CCCMA	CSIRO	HADLEY	Gain	Loss	trend
M. arenaria	111740	69.03%	99.50%	112.03%	63.59%	90.97%	27.95%	6	0	Expansion
M. bernieri	40972	57.43%	-33.48%	-49.38%	13.36%	-45.93%	-23.68%	2	4	Contraction
X. bojeriana	129201	-51.15	-63.06%	-47.28%	-47.11%	-62.71%	-21.05%	0	6	Contraction
X. coriacea	223602	-6.90%	-43.40%	-38.98%	-22.14%	-30.49%	4.60%	1	5	Contraction
X. diospyroidea	33669	-74.63%	-100%	-99.48%	65.83%	-94.65%	-65.73%	1	5	Contraction
X. elliptica	207378	-27.35%	-12.58%	-20.58%	-31.32%	-14.14%	-33.44%	0	6	Contraction
X. itremoensis	33306	11.88%	-88.96%	-99.70%	243.14%	-45.82%	-68.59%	2	4	Contraction
X. tampoketsensis	184629	-48.51%	10.56%	26.86%	-26.97%	-10.13%	23.91%	3	3	Ambiguous
X. undulata	32886	-42.33%	-3.95%	12.82%	-62.24%	-40.45%	156.39%	2	4	Contraction
X. villosa	41496	197.65%	-5.92%	-70.75%	8.32%	10.17%	322.1	4	2	Expansion

models for both A2 and B2 scenarios predicted more loss than gain for *M. bernieri*, *X. itremoensis* and *X. villosa*, the CCCMA model showed the opposite (figs 2–4; electronic appendices 1 & 2). Differences also exist between the A2 and B2 scenarios. Except for the CSIRO model, there were more gains than losses under the B2 scenario, but this should be expected given that the B2 scenario is more environmentally friendly.

Our results showed that species could be grouped into three categories based on their predicted trend by 2050. In particular, species exhibited a range expansion, contraction or ambiguous trend as estimated by the number of gain and loss for each of the six models and scenarios (table 2). Species showing range expansion are M. arenaria and X. villosa. The most climate resilient species appeared to be M. arenaria, which exhibited a strong pattern of expansion, with six models predicting more gain than loss in its future distribution. This species is currently distributed in north-western Madagascar and shows major expansion towards the southwest by 2050. By contrast, M. bernieri, X. bojeriana, X. coriacea, X. diospyroidea, X. elliptica, X. itremoensis and X. undulata all showed a range contraction. The most impacted species seemed to be X. bojeriana and X. elliptica, with all six models predicting more loss than gain. Lastly, future trend for X. tampoketsensis appeared ambiguous with the models equally predicting gain and loss.

While the predicted trend suggested that *X. bojeriana* and *X. elliptica* were the most impacted species given the number of models supporting a range contraction, *X. diospyroidea* and *X. itremoensis* exhibited the highest percentage of reduction in terms of areas. Both species were predicted to experience a severe range contraction (\geq 99%) in at least one of the six models (table 2; electronic appendices 1 & 2). These two species have a restricted distribution, occurring only on quartzitic substrates in the Central High Plateau of Madagascar, where habitat loss by anthropogenic fire is also the highest. Similarly, *X. villosa* will experience the greatest expansion based on the area of habitat gained (table 2; electronic appendices 1 & 2).

DISCUSSION

Most of our target species were predicted to undergo major range contraction as a result of climate change. Species in the Central High Plateau of Madagascar were predicted to experience the highest habitat loss, with narrow-range species being the most sensitive. Southward migration was suggested for species distributed in the northwest whereas upland migration was predicted for some, but not all, central species. Our results agreed with other studies in showing that endemic species were the most vulnerable to climate change (Malcolm et al. 2006, Ohlemüller et al. 2008, Morueta-Holme et al. 2010). In particular, we found that the more restrictedly distributed endemics were the most impacted.

In response to a rapidly changing climate, species are predicted to show adaptation, migration or extirpation (Davis & Shaw 2001). Although species of the genera Mediusella and Xerochlamys may adapt to future climate, more studies are required to investigate species' phenological or physiological traits to predict their potential responsiveness to climate change. However, some of the species appeared to be resilient enough to anthropogenic disturbances such as fire (e.g. X. bojeriana; Perrier de la Bâthie 1931, Hong-Wa 2009), hence the same traits might also allow them to adapt to drier and warmer environments predicted for 2050. But the most likely response in many cases will be a range shift. For instance, distributions of M. arenaria and X. tampoketsensis shifted southward in our predictions (figs 2 & 3). At least one model suggested that the species X. bojeriana, X. coriacea and X. elliptica would migrate to the currently more humid habitats in the east (figs 2 & 3), or, in the case of X. undulata, towards higher elevation in the Central High Plateau (fig. 4). Xerochlamys diospyroidea is likely to be extirpated, because its predicted range shift was almost non-existent (fig. 3). Its habitat specificity also puts this species at the highest risk of all species studied here.

The southern part of Madagascar is predicted to become drier and hotter (de Wit & Stankiewicz 2006, Tadross et al. 2008). Our results showed that among the three species in this region, X. coriacea and X. undulata contracted their ranges whereas X. villosa expanded northward in at least one of the six models (figs 2 & 4). Interestingly, patterns of expansion, when predicted by at least one model, differed for the two sympatric species X. undulata and X. villosa. The former will migrate eastward and towards higher elevations whereas the latter will migrate northward and southward but at lower elevations. Similarly, the two closely related species X. coriacea and X. villosa also differed in their response, with the range of X. coriacea mainly contracting, contrary to X. villosa, but possibly migrating northward and to the east of Madagascar as predicted by one model (fig. 2). Possible phylogenetic signal was also absent in the sister species M. arenaria and M. bernieri, with M. arenaria expanding its range southward while *M. bernieri* contracting considerably (fig. 2).

In contrast to previous studies on potential distributions of species in Madagascar (Kremen et al. 2008, Schatz et al. 2008), our study used only climatic variables to build the species' distribution models. The methods we used to model the species distribution do not consider other important factors that influence species distributions such as dispersal capabilities (Pulliam 2000), interactions with other species (Berg et al. 2010), presences of barriers (Soberón & Peterson 2005), or anthropogenic factors (Lippitt et al. 2008). Indeed, although climate change would be one of the most influential drivers of range shift, other ecological and anthropogenic processes could also have great impacts on species distribution, especially at smaller spatial scale. The importance of biotic and anthropogenic factors has been found in regional assessment of climate change (Preston et al. 2008, Melles et al. 2011). In particular, habitat fragmentation can challenge species' dispersal ability (Farhig 2003, Opdam & Wascher 2004). This will likely affect possible migration of the species occurring in the Central High Plateau where only patches of vegetation have remained. Biogeographic barriers may also prevent optimal dispersal of a species. For instance, the current potential distribution of X. coriacea was predicted to occupy much of the eastern escarpment of Madagascar (fig. 1) while biogeographic barriers or other ecological factors could actually constrain its distribution to the currently known range. Accounting for anthropogenic variables, biogeographic and biotic/abiotic limitations in the predictions of species' potential distributions will undoubtedly affect our assessment of future distribution of species of Mediusella and Xerochlamys given that habitat fragmentation is already severe in Madagascar (Harper et al. 2007) and that dispersal ability may be hampered by some biogeographic and abiotic attributes. We suspect that much of the range expansion predicted by the models in our study is optimistic. Nonetheless, our results did not deviate much from those of Schatz et al. (2008). Both showed a general pattern of range contraction, suggesting that climate variability alone could contribute substantially to future habitat loss.



Figure 4 – Gain and loss in potential distribution of species of *Mediusella* and *Xerochlamys* species by 2050 based on different climate change models (CCCMA, CSIRO, HADLEY) and scenarios (A2 and B2). A–D, *X. undulata*; E–H, *X. villosa*.

Even if species can adapt to climate change, it may not happen soon enough to allow the species of Mediusella and Xerochlamvs to maintain viable population sizes over the next 30-40 years. Indeed, among the ten species studied here, six (M. bernieri, X. diospyroidea, X. elliptica, X. itremoensis, X. undulata and X. villosa) have already been evaluated as endangered according to the IUCN Red List Criteria (Hong-Wa 2009). These six species will also experience major range contraction by 2050, and only two of them (X. undulata and X. villosa) occur in protected areas. Moreover, most of our focal species occur in fragmented habitats that are also under increasing human pressure. The coupled effects of anthropogenic activities and climate change will put these species at higher risk of extirpation. Thus, conservation efforts need to focus on areas where populations are likely to maintain, which include areas where the ten species currently occur under relatively low human pressure and areas where future migration is possible in light of the current trends of habitat degradation. We identified the regions of Daraina and Sahafary in the North as critical areas for conservation of *M. bernieri*, as well as Ibity and Itremo in the Central High Plateau for X. bojeriana, X. diospyroidea, X. elliptica and X. itremoensis. These regions also harbor some of Madagascar's most amazing plants (succulents, palms and orchids) and animals (lemurs, reptiles) and some are now being represented among the system of protected areas of Madagascar. It is critical to redouble conservation efforts on these areas and extend conservation initiatives to new ones (e.g. Sahafary). Additionally, species-targeted conservation efforts such as ex situ conservation (e.g. inclusion in botanical gardens and seed banks) may still be required as complementary measure. The effectiveness of ex situ conservation in the context of climate change is, however, still highly debated.

CONCLUSION

This study shows that future climate change will impact the distribution of endemic plant species of Madagascar. Seven of the ten species studied here will experience major range contraction by 2050, two will exhibit some expansion and one will retain an equivocal status. Our results confirm those of Schatz et al. (2008) that contraction will be the predominant pattern exhibited by most endemic species in the island. Small-range species and species occurring in the Central High Plateau will be the most sensitive to climate change. Adequate conservation strategies are needed to ensure the highest persistence of species in their current range as well as to ensure the availability of suitable habitats where future migration is possible.

SUPPLEMENTARY DATA

Supplementary data are available in pdf format at *Plant Ecology and Evolution*, Supplementary Data Site (http://www. ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of:(1) areas (km²) occupied by the 10 species of *Mediusella* and *Xerochlamys* in the present and future (2050, scenario A2); and (2) areas (km²) occupied by the 10 spe-

cies of *Mediusella* and *Xerochlamys* in the present and future (2050, scenario B2).

ACKNOWLEDGEMENTS

We thank T. Distler, J. Dale, Z. Faulkes, E. Robbrecht and two anonymous reviewers for constructive comments that greatly improved the previous version of this manuscript.

REFERENCES

- Araújo M.B., Williams P.H. (2000) Selecting areas for species persistence using occurrence data. Biological Conservation 96: 331–345. http://dx.doi.org/10.1016/S0006-3207(00)00074-4
- Araújo M.B, Rahbek C. (2006) How does climate change affect biodiversity? Science 313: 1396–1397. http://dx.doi.org/10.1126/ science.1131758
- Araújo M.B., Alagador D., Cabeza M., Nogués-Bravo D., Thuiller W. (2011) Climate change threatens European conservation areas. Ecology Letters 14: 484–492. http://dx.doi.org/10.1111/ j.1461-0248.2011.01610.x
- Beaumont L.J., Pitman A., Perkins S., Zimmermann N.E., Yoccoz N.G., Thuiller W. (2011) Impacts of climate change on the world's most exceptional ecoregions. Proceedings of the National Academy of Sciences of the United States of America 108: 2306–2311. http://dx.doi.org/10.1073/pnas.1007217108
- Berg M.P., Kiers E.T., Driessen G., van der Heijden M., Kooi B.W., Kuenen F., Liefting M., Verhoef H.A., Ellers J. (2010) Adapt or disperse: understanding species persistence in a changing world. Global Change Biology 16: 587–598. http://dx.doi. org/10.1111/j.1365-2486.2009.02014.x
- Bush M.B. (2002) Distributional change and conservation on the Andean flank: a palaeoecological perspective. Global Ecology and Biogeography 11: 463–473. http://dx.doi.org/10.1046/ j.1466-822X.2002.00305.x
- Callmander M.W., Phillipson P.B., Schatz G.E., Andriambololonera S., Rabarimanarivo M., Rakotonirina N., Raharimampionona J., Chatelain C., Gautier L., Lowry II P.P. (2011) The endemic and non-endemic vascular flora of Madagascar updated. Plant Ecology and Evolution 144: 121–125. http://dx.doi.org/10.5091/ plecevo.2011.513
- Cayuela L., Golicher D.J., Newton A.C., Kolb M., de Alburquerque F.S., Arets E.J.M.M., Alkemade J.R.M., Pérez A.M. (2009) Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. Tropical Conservation Science 2: 319–352.
- Chen I.C., Hill J.K., Ohlemüller R., Roy D.B., Thomas C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024–1026. http://dx.doi. org/10.1126/science.1206432
- Davis M.B., Shaw R.G. (2001) Range shifts and adaptive responses to quaternary climate change. Science 292: 673–679. http:// dx.doi.org/10.1126/science.292.5517.673
- de Wit M., Stankiewicz J. (2006) Changes in surface water supply across Africa with predicted climate change. Science 311: 1917–1921. http://dx.doi.org/10.1126/science.1119929
- Elith J., Graham C.H., Anderson R.P., Dudık M., Ferrier S., Guisan A., Hijmans R.J., Huettmann F., Leathwick J.R., Lehmann A., Li J., Lohmann L.G., Loiselle B.A., Manion G., Moritz C., Nakamura M., Nakazawa Y., Overton J.M., Peterson A.T., Phillips S.J., Richardson K.S., Scachetti-Pereira R., Schapire R.E., Soberon J., Williams S., Wisz M.S., Zimmermann N.E. (2006)

Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151. http://dx.doi. org/10.1111/j.2006.0906-7590.04596.x

- Farhig L. (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34: 487–515. http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132419
- Ferrier S., Watson G., Pearce J., Drielsma M. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. Biodiversity and Conservation 11: 2275–2307. http://dx.doi. org/10.1023/A:1021302930424
- Fielding A.H., Bell J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38–49. http://dx.doi. org/10.1017/S0376892997000088
- Galatowitsch S., Frelich L., Phillips-Mao L. (2009) Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. Biological Conservation 142: 2012–2022. http://dx.doi.org/10.1016/j.biocon.2009.03.030
- Guisan A., Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters 8: 993–1009. http://dx.doi.org/10.1111/j.1461-0248.2005.00792.x
- Hannah L., Midgley G.F., Lovejoy T., Bond W.J., Bush M., Lovett J.C., Scott D., Woodward F.I. (2002a) Conservation of biodiversity in a changing climate. Conservation Biology 16: 264–268. http://dx.doi.org/10.1046/j.1523-1739.2002.00465.x
- Hannah L., Midgley G.F., Millar D. (2002b) Climate changeintegrated conservation strategies. Global Ecology and Biogeography 11: 485–495. http://dx.doi.org/10.1046/j.1466-822X.2002.00306.x
- Hannah L., Dave R., Lowry II P.P., Andelman S., Andrianarisata M., Andriamaro L., Cameron A., Hijmans R.J., Kremen C., MacKinon,J., Randrianasolo H.H., Andriambololonera S., Razafimpahanana A., Randriamahazo H., Randrianarisoa J., Razafinjatovo P., Raxworthy C.J., Schatz G.E., Tadross M., Wilmé L. (2008) Climate change adaptation for conservation in Madagascar. Biology Letters 4: 590–594. http://dx.doi.org/10.1098/ rsbl.2008.0270
- Hanski I., Koivulehto H., Cameron A., Rahagalala P. (2007) Deforestation and apparent extinctions of endemic forest beetles in Madagascar. Biology Letters 3: 344–347. http://dx.doi. org/10.1098/rsbl.2007.0043
- Harper G.J., Steininger M.K., Tucker C.J., Juhn D., Hawkins F. (2007) Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation 34: 325–333. http:// dx.doi.org/10.1017/S0376892907004262
- Heikkinen R.K., Luoto M., Araújo M.B., Virkkala R., Thuiller W., Sykes M.T. (2006) Methods and uncertainties in bioclimatic envelop modelling under climate change. Progress in Physical Geography 30: 1–27. http://dx.doi. org/10.1177/0309133306071957
- Hernandez P.A., Graham C.H., Master L.L., Albert D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29: 773–785. http://dx.doi.org/10.1111/j.0906-7590.2006.04700.x
- Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. http://dx.doi.org/10.1002/joc.1276

- Hong-Wa C. (2009) Endemic families of Madagascar. XII. Resurrection and taxonomic revision of the genera Mediusella (Cavaco) Hutchinson and Xerochlamys Baker (Sarcolaenacceae). Andansonia 31: 311–339.
- Hong-Wa C., Schatz G.E. (2011) On the correct authorship of three combinations in Xerochlamys Baker (Sarcolaenaceae). Candollea 66: 107–108.
- Hu J., Jiang Z. (2010) Predicting the potential distribution of the endangered Przewalski's gazelle. Journal of Zoology 282: 54–63. http://dx.doi.org/10.1111/j.1469-7998.2010.00715.x
- Ingram J.C., Dawson T.P. (2005) Climate change impacts and vegetation response on the island of Madagascar. Philosophical Transaction of the Royal Society A 363: 55–59. http://dx.doi. org/10.1098/rsta.2004.1476
- Intergovernemental Panel on Climate Change (IPCC) (2007) Synthesis Report: Summary for Policymakers. Fourth Assessment Report, IPCC Plenary XXVII, Valencia Spain, November 2007.
- Jiménez-Valverde A., Lobo J.M. (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. Acta Oecologica 31: 361–369. http://dx.doi. org/10.1016/j.actao.2007.02.001
- Kearney M. (2006) Habitat, environment and niche: what are we modelling? Oikos 115: 186–191. http://dx.doi.org/10.1111/ j.2006.0030-1299.14908.x
- Kremen C., Cameron A., Moilanen A., Phillips S.J., Thomas C.D., Beentje H., Dransfield J., Fisher B.L., Glaw F, Good T.C., Haper G.J., Hijmans R.J., Lees D.C., Louis Jr. E., Nussbaum R.A., Raxworthy C.J., Razafimpahanana A., Schatz G.E., Vences M., Vieites D.R., Wright P.C., Zjhra M.L. (2008) Aligning conservation priorities across taxa in Madagascar with highresolution planning tools. Science 320: 222–226. http://dx.doi. org/10.1126/science.1155193
- Lippitt C.D., Rogan J., Toledano J., Sangermano F., Eastman J.R., Mastro V., Sawyer A. (2008) Incorporating anthropogenic variables into a species distribution model to map gypsy moth risk. Ecological Modelling 210: 339–350. http://dx.doi. org/10.1016/j.ecolmodel.2007.08.005
- Liu C., Berry P.M., Dawson T.P., Pearson R. (2005) Selecting thresholds of occurrence in the predictions of species distributions. Ecography 28: 385–393. http://dx.doi.org/10.1111/j.0906-7590.2005.03957.x
- Malcolm J.R., Liu C., Neilson R.P., Hansen L., Hannah L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. Conservation Biology 20: 538–548. http:// dx.doi.org/10.1111/j.1523-1739.2006.00364.x
- Mateo R.G., Felicísimo A.M., Muñoz J. (2010) Effects of the number of presences on reliability and stability of MARS species distribution models: the importance of regional niche variation and ecological heterogeneity. Journal of Vegetation Science 21: 908–922. http://dx.doi.org/10.1111/j.1654-1103.2010.01198.x
- Melles S.J., Fortin M.J., Lindsay K., Badzinski D. (2011) Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. Global Change Biology 17: 17–31. http://dx.doi.org/10.1111/ j.1365-2486.2010.02214.x
- Midgley G.F., Hannah L., Millar D., Rutherford M.C., Powrie L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Global Ecology and Biogeography 11: 445–451. http://dx.doi.org/10.1046/ j.1466-822X.2002.00307.x
- Morueta-Holme N., Flejgaard C., Svenning J.C. (2010) Climate change risks and conservation implications for a threatened

small-range mammal species. PLoS ONE 5(4): http://dx.doi. org/e10360. 10.1371/journal.pone.0010360

- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G. A. B., Kent J. (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. http://dx.doi.org/10.1038/35002501
- Ohlemüller R., Anderson B.J., Araújo M.B., Butchart S.H.M., Kudrna O., Ridgely R.S., Thomas C.D. (2008) The coincidence of climatic and species rarity: high risk to small-range species from climate change. Biology Letter 4: 568–572. http://dx.doi. org/10.1098/rsbl.2008.0097
- Opdam P., Wascher D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117: 285–297. http://dx.doi.org/10.1016/j.biocon.2003.12.008
- Parmesan C. (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics 37: 637–669. http://dx.doi.org/10.1146/annurev. ecolsys.37.091305.110100
- Parmesan C., Yohe G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37– 42. http://dx.doi.org/10.1038/nature01286
- Pearson R.G., Dawson T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361– 371. http://dx.doi.org/10.1046/j.1466-822X.2003.00042.x
- Pearson R.G., Raxworthy C.J., Nakamura M., Peterson A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34: 102–117. http://dx.doi. org/10.1111/j.1365-2699.2006.01594.x
- Perrier de la Bâthie H. (1931) Remarques sur les Chlaenacées. Bulletin de la Société botanique de France 78: 46–65.
- Peterson A.T. (2001) Predicting species' geographic distributions based on ecological niche modeling. The Condor 103: 599–605. http://dx.doi.org/10.1650/0010-5422(2001)103%5B0599:PSG DBO%5D2.0.CO;2
- Peterson A.T., Martínez-Meyer E., González-Salazar C., Hall P.W. (2004) Modeled climate change effects on distributions of Canadian butterfly species. Canadian Journal of Zoology 82: 851– 858. http://dx.doi.org/10.1139/z04-064
- Phillips S.J., Anderson R.P., Schapire R.E. (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259. http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026
- Pressey R.L., Cabeza M., Watts M.E., Cowling R.M., Wilson K.A. (2007) Conservation planning in a changing world. Trends in Ecology and Evolution 22: 583–592. http://dx.doi. org/10.1016/j.tree.2007.10.001
- Preston K.L., Rotenberry J.T., Redak R.A., Allen M.F. (2008) Habitat shifts of endangered species under altered climate

conditions: importance of biotic interactions. Global Change Biology 14: 2501–2515. http://dx.doi.org/10.1111/j.1365-2486.2008.01671.x

- Pulliam H.R. (2000) On the relationship between niche and distribution. Ecology Letters 3: 349–361. http://dx.doi.org/10.1046/ j.1461-0248.2000.00143.x
- Schatz G.E. (2000) Endemism in the Malagasy tree flora. In: Lourenço W.R., Goodman S.M. (eds) Diversity and endemism in Madagascar. Memoires de la Société de Biogéographie. Société de Biogéographie: 1–9. Paris, ORSTOM.
- Schatz G.E., Cameron A., Raminosoa T. (2008) Modeling of endemic plant species of Madagascar under climate change. Assessing the impact of climate change on Madagascar's livelihoods and biodiversity conference. Antananarivo, Madagascar, 28 January 2008.
- Soberón J., Peterson A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2: 1–10.
- Tadross M., Randriamarolaza L., Rabetafika Z., Yip Z.K. (2008) Climate change in Madagascar, recent past and future. Washington DC, World Bank.
- Thuiller W. (2004) Patterns and uncertainties of species' range shifts under climate change. Global Change Biology 10: 2020–2027. http://dx.doi.org/10.1111/j.1365-2486.2004.00859.x
- Thuiller W., Lavorel S., Araújo M.B., Sykes M.T., Prentice I.C. (2005) Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Science of the United States of America 102: 8245–8250. http://dx.doi.org/10.1073/ pnas.0409902102
- Thuiller W., Albert C., Araújo M.B., Berry P.M., Cabeza M., Guisan A., Hickler T., Midgley G.F., Paterson J., Schurr F.M., Sykes M.T., Zimmermann N.E. (2008) Predicting global change impacts on plant species' distributions: future challenges. Perspectives in Plant Ecology, Evolution and Systematics 9: 137–152. http://dx.doi.org/10.1016/j.ppees.2007.09.004
- Urbina-Cardona J.N., Flores-Villela O. (2010) Ecological niche modeling and prioritization of conservation-area networks for Mexican herpetofauna. Conservation Biology 24: 1031–1041. http://dx.doi.org/10.1111/j.1523-1739.2009.01432.x
- Warren D.L., Siefert S.N. (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological Applications 21: 335–342. http://dx.doi.org/10.1890/10-1171.1

Manuscript received 2 Mar. 2012; accepted in revised version 9 May 2012.

Communicating Editor: Elmar Robbrecht.