Are narrow-ranging species doomed to extinction? Dramatic and generalised decline in future climate

suitability of highly threatened species

Running title: Narrow-ranging species and climate change

Nicolas Dubos[1, 2], Frederique Montfort[3], Clovis Grinand[3], Marie Nourtier[3], Gregory Deso[4], Jean-Michel

Probst[5], Julie Hanta Razafimanahaka[6], Raphali Rodlis Andriantsimanarilafy[6], Eddie Fanantenana

Rakotondrasoa[6], Pierre Razafindraibe[6], Richard Jenkins[6,7] and Angelica Crottini[8]

9
10
1 Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Sorbonne Université, MNHN,
55 rue Buffon, 75005 Paris, France.

2 INRAE (UMR TETIS), Maison de la télédétection, 500 rue Jean-François Breton 34093 Montpellier
Cedex 5, France.

3 N'Lab, Nitidæ, Maison de la télédétection, 500 rue Jean-François Breton 34093 Montpellier Cedex 5

4 Association Herpétologique de Provence Alpes Méditerranée, Maison des Associations, 384 route de
Caderousse, F-84100 Orange, France.

5 Association Nature and Patrimoine, 1 rue des amarantes résidence Valeriane 2, Bat C appartement 15.
97490 Sainte Clotilde, Île de La Réunion, France.

6 Madagasikara Voakajy, B.P. 5181, Antananarivo (101), Madagascar.

7 Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, Marlowe
Building, University of Kent, Canterbury, CT2 7NR ; Current address: IUCN Global Species Programme,
219c Huntingdon Road, Cambridge, CB3 0DL, UK.

8 CIBIO, Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus
Agrário de Vairão, Rua Padre Armando Quintas, No 7, 4485-661 Vairão, Portugal.

Abstract

Narrow-ranging species are usually omitted from Species distribution models (SDMs) due to statistical

constraints, which may be problematic in conservation planning. The recently available high-resolution

climate and land use data enable to increase the eligibility of narrow-ranging species for SDMs, provided

their distribution is well known. We modelled the distribution of two narrow-ranging species for which the

distribution of their occurrence records is assumed to be nearly comprehensive and unbiased (i.e., the

Critically Endangered Manapany day gecko *Phelsuma inexpectata* and the Endangered golden Mantella frog

Mantella aurantiaca). We predict a dramatic decline in climate suitability in the whole current distribution

area of both species by 2070, potentially leading to a complete extinction even in the most optimistic

scenario. We identified the areas with the best climate suitability in the future, but these remain largely

suboptimal regarding species climatic niche. The high level of habitat fragmentation suggests that both

species likely need to be at least partly translocated. We propose to consider the use of spatially explicit

guidelines for translocation and habitat restoration in order to leave the species a chance to adapt and persist.

The effect of climate change remains understudied for the extreme majority of rare and highly threatened

species. This study suggests that the level of threats of data-poor and narrow-ranging species already

identified as threatened may be underestimated, especially in heterogeneous tropical environments. We stress

the need to consider the option of implementing proactive actions for threatened narrow-ranging species.

Keywords: Climate change, habitat restoration, Madagascar, *Mantella aurantiaca*, *Phelsuma inexpectata*,

Reunion Island, Species distribution models, translocation

Introduction

Global biodiversity loss has been mainly attributed to human-induced habitat destruction (Sala *et al.*, 2000) but the impact of climate change is predicted to exceed it in the next decades (Bellard *et al.*, 2012). Species Distribution Models (SDMs) are probably the most common approach used to predict the impact of future climate change on species. They are used to predict current and future environmental suitability, and provide guidelines for the identification of priority areas for protection (Leroy *et al.*, 2014), habitat restoration and species (re)introduction/translocations (e.g., Adhikari et al., 2012; Bellis et al., 2020; Draper et al., 2019; Westwood et al., 2020; Wilson et al., 2011). Habitat restoration and translocations are two ecological engineering techniques enabling the restoration of depleted populations. Translocation programs will become increasingly needed in the face of climate change, especially for species with small distribution ranges (Thomas, 2011). In this regard, SDMs help identifying suitable receptor sites that meet the species' habitat requirements while accounting for climate suitability (Bellis et al., 2020). In highly degraded environments a combination of habitat restoration and translocation may be needed to avoid species extinctions. This may be the case in highly fragmented tropical systems, where the number of narrow-ranging species is higher and where climate change effects are expected to be stronger (Deutsch et al., 2008; Tewksbury et al., 2008).

The impact of future climate change is largely understudied in endangered narrow-ranging species. This is mainly due to the difficulty to model their current and future distribution because of low sample sizes and subsequent little spatial replicates when fitted on climate data (Botts *et al.*, 2013; Platts et al., 2014; Breiner et al., 2015; Galante et al., 2018). Both these factors lead to statistical constraints that withdraw these species from eligibility for SDMs. However, the omission of narrow-ranging species in SDMs may be problematic in terms of conservation planning, because the area encompassing their distribution may be downplayed (Platts *et al.*, 2014). Although narrow-ranging species are known to be more vulnerable to climate change (Pearson *et al.*, 2014), few studies have provided quantitative assessment of climate change impacts on these (but see Alamgir *et al.*, 2015; Zhang *et al.*, 2020).

The recent availability of high-resolution climatic data (e.g., Fick & Hijmans, 2017; Karger et al., 2017), along with high-resolution land cover data (e.g., Vieilledent et al., 2018) is offerring new opportunities for

modelling the distribution of these species (Lannuzel et al., 2021). However, despite a probable increase in

statistical power, there is still the possibility for SDMs to produce misleading results due to spatial sampling

bias (Phillips *et al.*, 2009). The effect of sample bias may be particularly strong in rare (or poorly known)

species with small sample sizes, because models are more influenced by each occurrence data that is used

(Pearson *et al.*, 2007). A number of techniques were recently developed to account for sampling bias, but

these often imply the filtering of occurrence or environmental data (Boria *et al.*, 2014; Varela *et al.*, 2014;

Gábor *et al.*, 2019). Data filtering can become problematic for species with low sample sizes (Dubos *et al.*

submitted), and the number of species eligible for SDMs remains limited.

We predicted the current and future distribution of two narrow-ranging, but well studied threatened species:

the Manapany day gecko *Phelsuma inexpectata*, classified as Critically Endangered following the red list

classification (IUCN & MNHN, 2010) and the golden mantella frog *Mantella aurantiaca* formerly classified

as Critically Endangered (Vences & Raxworthy, 2008), now classified as Endangered after the inclusion of

one locality record which increased the extent of occurrence (IUCN SSC Amphibian Specialist Group,

2020). Both species are in continued decline, live in highly fragmented areas (respectively in Reunion Island

and central Madagascar) and are in urgent need for conservation actions. In addition, a recent study of *M.*

aurantiaca populations revealed a severe demographic decline in multiple populations, which seems to have

occurred over the past 1000 years (Crottini et al., 2019). No new locality records that are susceptible to

increase their extent of occurrence were found recently. We therefore assume that the geographic information

for these species is nearly comprehensive and unbiased. Their narrow range, along with high spatial

heterogeneity in the climatic conditions of their region, suggests that their distribution may be highly limited

by climate. We hypothesised that climate change will strongly affect the climate suitability of their current

distribution range. We eventually identify the most suitable areas for habitat restoration and translocation.

Methods

Occurrence data

Phelsuma inexpectata – The Manapany day gecko is endemic to the south of Reunion Island. We retrieved

31 occurrence data from literature (Bour *et al.*, 1995). Since then, the surroundings of the known distribution

range of the species were regularly visited (an 11 km-long costal band). Two localities corresponding to

introduced populations were identified west of the current range, which we added to the data (Deso, 2001;

Porcel *et al.*, 2021). More recent sampling campaigns enabled to find additional occupied habitats (Dubos

2010) but did not add any occurrence point after aggregation at the resolution of the environmental variables

(30 arc seconds). Therefore, we assume that the sample occurrence of the species is nearly comprehensive.

The total number of 30 sec. occupied pixels resulted in 14 presence points.

Mantella aurantiaca – The golden mantella frog is distributed in central-Eastern Madagascar (region of

Moramanga; Fig. 1). We obtained 131 occurrence data from Piludu *et al.* (2015). Those included compiled

published data from surveys conducted between 2001 and 2007 (Bora *et al.*, 2008; Randrianavelona *et al.*,

2010) and new locations from additional surveys conducted between 2008 and 2013. More recent surveys

conducted between 2014 and 2019 enabled to add 39 occurrences. The region has been extensively surveyed

and it is very likely that most occupied habitats were identified. After aggregation to match the resolution of

environmental data, sample size resulted in 101 occurrence points.

The distribution of both these species is highly fragmented as a result of agricultural expansion and invasion

by exotic vegetation, and host their respective species in isolated remnant habitat patches.

Climate data

We used the 19 bioclimatic variables for 30 arc sec (approximately 900m) resolution of the current climate

data and of the 2070 projections from WorldClim Global Climate Data (Fick & Hijmans, 2017; Fig. S1, S2).

We used three Global Circulation Models (GCMs – i.e., BCC-CSM1-1, MIROC5 and HadGEM2-AO) and

two greenhouse gas emission scenarios (the most optimistic RCP26 and the most pessimistic RCP85; Fig.

S3, S4).

Distribution modelling

We modelled and projected species distributions with the Biomod2 R package (Thuiller et al. 2009), using 10

modelling techniques: generalised linear model (GLM), generalised additive model (GAM), classification

tree analysis (CTA), artificial neural network (ANN), surface range envelop (SRE), flexible discriminant

analysis (FDA) and random forest (RF), Multiple Adaptive Regression Splines (MARS), Generalised

Boosting Model (GBM) and Maximum Entropy (MaxEnt). For all models, we generated 8 different sets of

randomly-selected pseudo-absences (Meynard et al. 2019). The remaining model input parameters (i.e., cross

validation partition, number of cross validation runs, number of pseudo-absences) were defined specifically

for variable selection and final model calibration (see below).

Variable selection – We selected one variable per group of inter-correlated variables to avoid collinearity

(Pearson's r > 0.7). We assessed the relative importance of each variable kept (i.e., one per inter-correlated

variable group, plus all non-correlated variables) with 10 permutations. Models were calibrated with 70% of

the data (selected at random). The remaining 30% were used for performance evaluation. This process was

repeated twice. We used 1000 pseudo-absences down-weighted for a 0.5 prevalence (Liu *et al.,* 2019). The

variables included in the final models were those with a relative importance > 0.2 across at least 50% of

model runs. This threshold is conservative and enables to limit model complexity.

Final models – We predicted species distributions with an ensemble of small models approach (ESM;

Breiner et al., 2015). We ran sets of bivariate models, i.e. including all pairwise combinations of the selected

variables, and produced an ensemble model with the mean predictions across all models weighted by their

respective AUC (see Model performance section). This method is advocated for rare species and enables to

reduce model complexity without reducing the explanatory power. We set five runs of cross validation

(except for the jackknife procedure; see below). We tested a range of model input parameters for the number

of pseudo-absences and data partition for cross-validation, and selected those with the highest performance

(see Model performance section). We generated 10 000, 1000 and 10 x n occurrences, down-weighted to

equal presence data (setting prevalence to 0.5). We ran 70%, 80% and 90% calibration subset for cross

validation and a jackknife procedure for *P. inexpectata.* The jackknife procedure is used for small sample

sizes (Pearson *et al.,* 2007; Galante *et al.,* 2018) and was therefore appropriate for *P. inexpectata* (n = 14).

We did not used it for *M. aurantiaca* given that the number of occurrence data was higher (n = 101) and

because it is more demanding in terms of computing effort and data storing capacity. The jackknife consists

in running n iterations corresponding to the number of occurrence data, removing one occurrence for each

run of calibration. Models are evaluated with the withheld occurrence. The method producing the best

performance included 10 x n peudo-absences obtained with the jackknife procedure for *P. inexpectata*, and

1000 pseudo-absences with 80% cross validation subsets for *M. aurantiaca* (Fig S5, S6). The predicted

values were spatially projected (a null value corresponds to the poorest suitability, a value of 1000 represents

the highest suitability).

Model performance – We assessed model performance using the Area Under the Operative Curve (AUC), the

True Skill Statistics (TSS) and the Boyce index (the latter was not computed for the jackknife procedure,

because this index is based on Spearman's coefficients and cannot be estimated on the basis of a single

location). For ensemble models, we excluded models for which the AUC was below 0.9 and for which the

Boyce index was below 0.5 (Gillard et al., 2017). We finally assessed the inter-model variability (as an index

of uncertainty) of our projections by computing the standard deviation of the suitability scores between all

model runs for current and future projections separately (Kujala et al., 2013).

Land use data

We accounted for the habitat requirements of our model species by applying a filter to the projected climate

suitability based on land use and land cover data (e.g., Gillard *et al.,* 2017). This enabled to minimise model

complexity while remaining biologically realistic and relevant for conservation applications.

Reunion Island – We used very high-resolution land cover categories (Urban, agricultural, natural, water) at

1.5m resolution (resampled at 15m for computing purposes) derived from remote sensing (Dupuy and

Gaetano, 2019; Fig S7). Since *P. inexpectata* can be found in both urbanised and natural areas and avoids

agricultural areas (Probst & Turpin, 1997), we excluded the latter land use type only. This is relevant also for

conservation applications because habitat restoration is more difficult to implement in agricultural areas.

Madagascar – *Mantella aurantiaca* is exclusively found in swampy forested areas (Randrianavelona *et al.*,

2010). We filtered our suitability maps to include only cells corresponding to rainforests. We obtained forest

cover data from a a study that combined global tree cover loss data with historical national forest (resolution

30m; Vieilledent et al., 2018; Fig. S8). We used forest cover of the year 2005 for current distribution models

because it corresponds approximately to the period of the oldest occurrence data (some areas were deforested

since then). For future predictions, we used the latest forest cover data available, i.e. 2017.

Results

Variable selection and model performance

Four climatic variables were selected in both cases (Fig. S9, S10, S11, S12). These were annual mean

temperature, yearly isothermality, precipitation of the driest month and precipitation of the wettest quarter for

P. Inexpectata, and mean temperature of the warmest quarter, mean temperature of the coldest quarter,

precipitation of driest month and precipitation of the wettest quarter for *M. aurantiaca*. The current

distribution of both species was well predicted (*P. inexpectata*: mean AUC = 0.96, mean TSS = 0.91; *M.*

aurantiaca: mean Boyce = 0.82, mean AUC = 0.97, mean TSS = 0.94; Fig 1a, 2a). We excluded 874 poorly

performing models out of 8400 for *P. Inexpectata,* and 383 out of 1440 for *M. aurantiaca*. The mean

suitability score at the presence points for *P. Inexpectata* was 863 (911 when removing the two introduced

populations) and 932 for *M. aurantiaca*. Models consistently identified the current distribution range

between all runs for both species, as shown by the uncertainty map (SD intermodel suitability scores at the

presence points of 168 for *P. inexpectata* and 113 for *M. aurantiaca*; Fig. S13, S14, S15, S16).

Future climate suitability

All scenarios indicated an important decrease in climate suitability in the entirety of the current range of both

species by 2070 (Fig. 1B, 2b). On average across scenarios and GCMs, suitability scores decreased by 44%

for *P. Inexpectata* and 94% for *M. aurantiaca* at the presence points (Fig. 3).

In Reunion Island, three ensemble models could not identify any future suitable area (maximum suitability

scores ranging between 186 and 224). Two ensemble models showed the highest suitability (maximum

suitability score: 713 and 725, respectively) about 20km west from the edge of the current distribution of *P.*

inexpectata under the optimistic scenario (RCP26). Surprisingly, the most pessimistic scenario (RCP85)

indicated a higher climate suitability than the most optimistic one with the MIROC5 GCM, distributed along

a band at higher altitudes (maximum suitability score = 916; Fig. 1b).

In Madagascar, none of the ensemble models identified any suitable area in the future (max. suitability score

ranging between 107 and 454), apart from very small areas corresponding to the top of small mountains in

northern Madagascar (HaGem2 – AO, scenario RCP2.6, max. suitability score = 870). However, we

consistently identified the most suitable area across GCMs and scenarios, corresponding to a forest corridor

in central Madagascar encompassing the current range of *M. aurantiaca* and prolonged southward (Fig. 2b).

Fig. 1 Current (a) and projected future (b) environmental suitability for *Phelsuma inexpectata*. Black points

represent the occurrence data. Future projections (2070) were estimated from three Global Circulation

models (GCM) and two RCP scenarios. Left panels represent the most optimistic scenario (RCP26) and right

panels represent the most pessimistic scenario (RCP85).

Fig. 2 Current (a) and projected future (b) environmental suitability for *Mantella aurantiaca*. Black points

represent the occurrence data. Future projections (2070) were estimated from three Global Circulation

models (GCM) and two RCP scenarios. Top panels represent the most optimistic scenario (RCP26) and

bottom panels represent the most pessimistic scenario (RCP85).

Fig. 3 Variation in climate suitability scores at the occurrence points of (a) *Phelsuma inexpectata* and (b)

Mantella aurantiaca under current climate and 2070 climate scenarios.

Discussion

Dramatic and widespread decline in climate suitability

We predict a strong decline of climate suitability in the whole current distribution area of both species by

2070. The subsequent high extinction risk in these species is not surprising, since small occupied areas are

known to be good predictors of vulnerability to climate change (Pearson *et al.,* 2014). In addition, we also

predict that few or no zone will be suitable in the future across the entirety of their respective regions. If

those species are not given the opportunity to adapt.

Depending on the Global Circulation model and the scenario, future predictions still identified areas with

suboptimal climatic conditions. In Reunion Island, the higher suitability found at ca. 20km west from the

current distribution was presumably driven by an increase in precipitation. *Phelsuma inexpectata* is mostly

present where precipitation is the lowest (< 500mm during the wet season, Fig., S10), probably because the

impact of cyclones—a driver of high mortality rates in *Phelsuma* species in the Mascarene (Vinson, 1975)—

is less severe. The identified area coincides with the region with the driest conditions in Reunion Island in

the future, according to these GCMs (Fig. S1). One ensemble model (MIROC5, pessimistic scenario)

showed a higher—but suboptimal—climate suitability around the southern coast of the island, with the

highest suitability along a band following the upper lands. This prediction is likely driven by the increase in

overall temperature, along with reduced precipitation. The species lives under the hottest and driest

conditions of the island, which fits the thermal requirements of the species for reproduction in captivity

(28°C; McKeown, 1993). Climate warming may induce a shift in current climatic conditions towards higher

altitudes in this scenario. Note that this scenario (i.e. RCP 8.5)—which was the least pessimistic for *P.*

inexpectata—is of interest to explore the widest range of possibilities in the future, but is considered unlikely

(Hausfather & Peters, 2020).

In Madagascar, the predicted area of the current distribution of *M. auratiaca* extents northward where the

species is supposedly absent, presumably because of a competitive exclusion with *M. crocea* and *M.*

milotympanum which are known to occupy similar fundamental niche (Bora et al., 2008). Current

distribution is mainly explained by both winter (i.e. the dry season) and summer (i.e., the wet season)

conditions with a short interval of suitability (Fig. S12). An important decline in climate suitability may be

driven by small changes in both winter and summer conditions. During winter, individuals migrate up the

hills to shelter under dead woods and leaves and presumably enter a state of torpor or hibernation

(Randrianavelona *et al.*, 2010; Edmonds *et al.*, 2020). The narrow climatic window may represent optimal

conditions that minimise the risk of desiccation during this period of low activity. The species is also

dependent on summer conditions, with a narrow window of suitable temperature and precipitations (Fig.

S12). This is highly consistent with a field study which recorded a surface temperature of 20-23°C at the

occupied sites (Edwards et al., 2019) and an experimental design which found a decrease in activity when

temperature deviates from 21.5°C (Edwards, 2019) with warm and rainy conditions (Fig. S12). Summer

corresponds to the period of reproduction, where females lay eggs under dead leaves on slopes, which are

likely washed down into temporary pond during heavy rain episodes. This may explain the dependence with

summer high precipitation and temperatures. This combination of climatic conditions is unlikely to be met in

the future, but predictions consistently identified potential suboptimal areas in the central-south of the eastern

forest corridor and in one small area in the north east (corresponding to the top of mountains). For both

species *P. inexpectata* and *M. aurantiaca*, the high level of habitat fragmentation associated to agricultural

areas may limit potential distribution shifts, which calls the need for human intervention.

Sources of uncertainty

We followed a protocol that attempted to mitigate most sources of uncertainty, corresponding to the

recommended standards defined in Araújo *et al.* (2019). The long term, extensive and repeated efforts

dedicated to species sampling enabled to define the current distributions of these two species with high

precision. We chose an exploratory approach for predictor variable selection with the inclusion of the 19

bioclimatic variables, which is not recommended in most cases. However, variable selection followed a

standard protocol and we selected the most straightforward to interpret in terms of biological meaning for

each group of intercorrelated variable. We used the finest resolution available for climate data (i.e. 30 arc

sec) which seems sufficient to discriminate suitable to unsuitable areas at the scale of Reunion Island and

Madagascar. The inclusion of high-resolution land use variables enabled to improve the realism of both

distributions and provide specific guidelines for conservation applications. In addition, we found a causal

interpretation for the selected variables, which, along with the high model performance, brings confidence in

credibility of the models. An important limitation is that we did not use scenarios of future land use. This

may lead to an overestimation of the available habitat in Madagascar, since the country is under important

rates of deforestation (Veilledent et al., 2018). In Reunion Island, most of the natural habitats is incorporated

in private properties or public gardens and in steep zones with limited access for agricultural practices. We

believe that the apparent stability in agricultural areas would maintain the applicability of our results in the

future. The inclusion of a range of different greenhouse-gas emission scenarios and GCMs showed an

important uncertainty in the future suitability for *P. inexpectata*. However, this uncertainty is mostly related

to one scenario (i.e. MIROC5, RCP8.5) and the remaining ones consistently identified the most suitable area

in 2070. Future predictions of *M. aurantiaca* were more consistent between scenarios and GCMs.

Uncertainty related to model design was mitigated by the limitation of model complexity (with the ESM

approach and the post-filtering technique), the removal of collinearity and the testing of a range of input

parameters (number of pseudo-absences sets and coss-validation subsets). Model performance was assessed

by discrimination (AUC and TSS) and reliability (i.e. calibration; Boyce index) metrics, all showing a high

performance overall (Fig. S7, S8). We did not account for species dispersal ability, because the purpose was

not to predict potential shifts, but to assess how suitable will be the climate in the future in order to identify

candidate sites for restoration and translocation. Both species have low dispersal ability and their habitat is

highly fragmented. Therefore, the potential for distributional shifts may be strongly limited and future

projections must not be interpreted as the future distributions of our study species. An important limitation

may be the absence of empirical knowledge on species thermal tolerances or other features of their climatic

niche, adaptability and plasticity, which prevents us from determining whether our future predictions

underestimated the environmental suitability.

A glimmer of hope

Despite the predicted low suitability in climate conditions, it is possible that species persist under changing

conditions through adaptation or plasticity (Chevin *et al.*, 2010; Hoffmann & Sgró, 2011). This hypothesis is

supported by the persistence of two introduced populations of *P. inexpectata* away from their current range in

suboptimal environments (Fig. 1). Their persistence may result either from physiological or behavioural

adaptation while benefiting from a combination of urban island effect and access to microclimate refuges in

anthropogenic structures, as it is the case for *Phelsuma grandis* in Florida (Fieldsend *et al.,* under review). It

is also frequent that the current distribution of a given species represents only a fragment of its climatic niche

(e.g., Guisan *et al.,* 2014). For instance, experimental design on *M. aurantiaca* showed no expression of a

thermal stress during periods of extreme heat (Edmonds *et al.,* 2015). Therefore, predictions of climate

suitability may underestimate the bounds of our model species niches. Further studies are needed to better

characterise their climatic niche, and explore potential adaptive and plastic responses to changing conditions

in these species and, more generally, in other threatened narrow-ranging species. Meanwhile, we encourage

practitioners to implement conservation measures to grant those species a chance to adapt and persist.

Nevertheless, the rate of climate change is generally faster than that of animal adaptive responses (Radchuk

et al., 2019), which stresses the need for urgent actions. In the tropics, extinction risks may be greatly

reduced with the development of land conservation programs provided climate change is mitigated by inter-

governmental actions (Hannah et al., 2020).

Conservation application

In Reunion Island, we identified two potential areas suitable for habitat restoration of *Phelsuma inexpectata*

around the south-western coast and along a mid-altitude band. Despite climate conditions are predicted to be

suboptimal, we believe these might represent the best options to ensure the long-term persistence of the

species. Habitat restoration should be focussed on natural habitats invaded by non-native plants and in

urbanised areas. Habitat restoration will consist in promoting the spread of native species (*Pandanus utilis*,

Latania lontaroides, *Scaevola taccada* and *Psiadia retusa*) for which the species depends on (Bour, 1995).

Finally, given the high level of habitat fragmentation, it is likely that the design of translocation programs

will also represent a relevant aspect to consider for management.

In Madagascar, the area with the highest future climate suitability is located at the south of the current

distribution, along the eastern rainforest corridor between the current distribution area and the north-west of

the Vatovavy-Fitovinany region. The forest cover within the distribution range of *M. aurantiaca* has

experienced a continued decline, regardless of the conservation status of the inhabited area (Piludu *et al.,*

2015; Vieilledent *et al.,* 2018). We recommend to reinforce the level of protection and to improve

governance and management of the Mangabe (Moramanga region) and the Marolambo (Vatovavy-

Fitovinany region) reserves. This can be achieved by promoting the development of alternative economic

solutions through the development of valuable and sustainable activities that mitigate the rate of conversion

of natural areas, the long-term management of soil fertility, and by considering the development of

ecotourism. This species was included into a program that enabled to develop amphibian husbandry

capacities in Madagascar, and that succeeded to establish captive bred colonies for this species

(Rakotonanahary et al. 2017). Efforts of captive husbandry should be maintained (and possibly expanded to

other species) and we encourage the design of translocation programs accounting for both local habitat

characteristics and future climate suitability.

Are all endangered narrow-ranging species doomed to extinction?

Narrow-ranging species usually live under very specific environmental conditions and are the most

vulnerable to climate change (Botts *et al.,* 2013). Not only they are more prone to face distribution shifts and

range contractions, but they might also disappear due to the strong alteration of their climatic envelope

throughout their entire region. This may be the case for most narrow-ranging species with a specialised niche

in regions with heterogeneous climates and high levels of endemism such as Madagascar but also Central

America, South East Asia, tropical islands and more generally in tropical rainforests and mountains (Kier *et*

al., 2009). In such regions, small shifts in climatic conditions may induce important changes in local

environmental suitability for endemic—often specialised—species (e.g., Raxworthy *et al.,* 2008). The risk is

greater in tropical regions where species live closer to the upper bound of their thermal tolerance (Tewksbury

et al., 2008; Şekercioĝlu *et al.,* 2012; Vanderwal *et al.,* 2013; Dubos *et al.,* 2019). Species that are already

under threats are at the greatest risk because of a large array of synergistic effects (Şekercioĝlu *et al.,* 2012).

This might be the case for our two model species, which are threatened by habitat destruction and invasive

species (Dubos, 2013; Piludu *et al.,* 2015). Among the few Critically Endangered species for which the

impact of climate has been investigated, most predict severe reductions in the climate suitability (e.g.,

Alamgir *et al.,* 2015; Zhang *et al.,* 2020), with the suitable range of the giant salamander *Andrias davidianus*

predicted to decrease by more than two thirds by 2050 (Zhang *et al.,* 2020). This species has faced a number

of threats (Turvey *et al.,* 2018) and climate change may be leading to imminent extinction despite a larger

distribution range. Despite recent efforts developed for the monitoring of rare species in the tropics (e.g.,

Dubos et al., 2020), there is still an important lack of species occurrence data in these regions (Feeley &

Silman, 2011). With the newly available high-resolution climate and land use data, the spectre of eligible

species for SDMs has enlarged. We urge filling this data void by starting to assess the effect of climate

change for narrow-ranging species at broader taxonomic scales, promote field investigations, assess species

thermal requirements, and develop proactive conservation actions.

Acknowledgements

We are grateful to all the field workers and their helpers who collected the data. We thank Boris Leroy for

useful discussions and for his continued support.

Conflict of Interest Statement

The authors declare no conflict of interests.

References

Adhikari D, Barik SK, Upadhaya K (2012) Habitat distribution modelling for reintroduction of *Ilex khasiana*

Purk., a critically endangered tree species of northeastern India. *Ecological Engineering,* **40**, 37–43.

Alamgir M, Mukul SA, Turton SM (2015) Modelling spatial distribution of critically endangered Asian

elephant and Hoolock gibbon in Bangladesh forest ecosystems under a changing climate. *Applied*

Geography, **60**, 10–19.

Araújo MB, Anderson RP, Barbosa AM et al. (2019) Standards for distribution models in biodiversity

assessments. *Science Advances*, **5**, 1–12.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the

future of biodiversity. *Ecology Letters*, **15**, 365–377.

Bellis J, Bourke D, Maschinski J, Heineman K, Dalrymple S (2020) Climate suitability as a predictor of

conservation translocation failure. *Conservation Biology*, 1–9.

Bora P, Dolch R, Jenkins R et al. (2008) Geographical distribution of three species of Malagasy poison frogs

of high conservation priority: *Mantella aurantiaca* , *M . crocea* and *M . milotympanum*. *Herpetology*

Notes, 1, 39–48.

Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can

improve the performance of ecological niche models. *Ecological Modelling*, *275*, 73–77.

Botts EA, Erasmus BFN, Alexander GJ (2013) Small range size and narrow niche breadth predict range

contractions in South African frogs. *Global Ecology and Biogeography*, *22*, 567–576.

Bour R, Probst J, Ribes S (1995) *Phelsuma inexpectata* Mertens, 1966, le lézard vert de Manapany-les-Bains

(La Réunion): données chorologiques et écologiques (Reptilia, Gekkonidae). *Dumerilia*, **2**, 99–124.

Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-*

theoretic approach, Springer S edn. New York.

Chevin LM, Lande R, Mace GM (2010) Adaptation, plasticity, and extinction in a changing environment:

Towards a predictive theory. *PLoS Biology*, **8**.

Deso G (2001) Note sur le transport insolite de Geckos verts, le cas du *Phelsuma inexpectata*. *Bulletin*

Phaethon, **13**, 56.

Draper D, Marques I, Iriondo JM (2019) Species distribution models with field validation, a key approach

for successful selection of receptor sites in conservation translocations. *Global Ecology and*

Conservation, **19**.

Dubos, N. (2010). *Analyse des habitats et déclin du Gecko vert de Manapany, Phelsuma inexpectata*

Mertens, 1966 sur l'île de La Réunion: implications pour sa conservation. Muséum national d'Histoire

Naturelle.

Dubos, N. (2013). New locality record for Phelsuma grandis (Sauria: Gekkonidae) in Reunion, in sympatry

with the Critically Endangered Phelsuma inexpectata. *Herpetology Notes*, *6*, 309–311.

Dubos, N., Dehorter, O., Yves, P., & Viol, I. Le. (2019). Thermal constraints on body size depend on the

population's position within the species' thermal range in temperate songbirds. *Global Ecology and*

Biogeography, *28(2)*, 96–106. https://doi.org/10.1111/geb.12805

Dubos, N., Morel, L., Crottini, A., Freeman, K., Honoré, J., Lava, H., Noël, J., Porton, I., Rendryrendry, G.,

Rosa, G., & Andreone, F. (2020). High interannual variability of a climate-driven amphibian

community in a seasonal rainforest. *Biodiversity and Conservation*, *29,* 893–912.

https://doi.org/10.1007/s10531-019-01916-3

Dubos N, Preau C, Lenormand M et al. (Submitted). Assessing the effect of sample bias correction in species

distribution models when independent data is unavailable.

Dupuy S, Gaetano R (2019) *Reunion island - 2017, Land cover map (Pleiades)*.

Edmonds D, Rakotoarisoa JC, Rasoanantenaina S et al. (2015) Captive husbandry, reproduction, and

fecundity of the golden mantella (*Mantella aurantiaca*) at the Mitsinjo breeding facility in Madagascar.

Salamandra, **51,** 315–325.

Edmonds D, Adamovicz L, Rakotoarisoa JC, Soamiarimampionona J, Harris R (2020) Seasonal Activity

Patterns of Golden Mantellas (Mantella aurantiaca). *Journal of Herpetology*, **54**, 325–330.

Edwards, W. M. (2019). *Conservation of the golden mantella in Madagascar : Integrating in situ and ex situ*

research. Kent University.

Edwards, W. M., Griffiths, R. A., Bungard, M. J., Rakotondrasoa, E. F., Razafimanahaka, J. H.,

Razafindraibe, P., Andriantsimanarilafy, R. R., & Randrianantoandro, J. C. (2019). Microhabitat

preference of the critically endangered golden mantella frog in Madagascar. *Herpetological Journal,*

29(4), 207–213. https://doi.org/10.33256/hj29.4.207213

Feeley KJ, Silman MR (2011) The data void in modeling current and future distributions of tropical species.

Global Change Biology, **17**, 626–630.

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.

Fieldsend T, Dubos N, Krysko K, Raxworthy CJ, Malone S (2021) In situ adaptation and ecological release

facilitate the occupied niche expansion of a non-native reptile. *Biodiversity and Conservation*.

Gábor L, Moudrý V, Barták V, Lecours V (2019) How do species and data characteristics affect species

distribution models and when to use environmental filtering? *International Journal of Geographical*

Information Science, **00**, 1–18.

Galante PJ, Alade B, Muscarella R, Jansa SA, Goodman SM, Anderson RP (2018) The challenge of

modeling niches and distributions for data-poor species: a comprehensive approach to model

complexity. *Ecography,* **41**, 726–736.

Gillard M, Thiébaut G, Deleu C, Leroy B (2017) Present and future distribution of three aquatic plants taxa

across the world: decrease in native and increase in invasive ranges. *Biological Invasions,* **19**, 2159–

2170.

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift studies: Insights

from biological invasions. *Trends in Ecology and Evolution,* **29**, 260–269.

Hausfather, Z., & Peters, G. P. (2020). Emissions–the 'business as usual'story is misleading. *Nature* **577**,

618–620.

Hoffmann AA, Sgró CM (2011) Climate change and evolutionary adaptation. *Nature,* **470**, 479–485.

IPCC (2014) Climate Change 2014 Synthesis Report Summary Chapter for Policymakers. *Ipcc,* 31.

IUCN, MNHN (2010) *La Liste rouge des espèces menacées en France. Premiers résultats pour la faune de*

La Réunion. 26pp.

IUCN SSC Amphibian Specialist Group (2020) *Mantella aurantiaca. The IUCN Red List of Threatened*

Species 2020: e.T12776A508612. https://dx.doi.org/10.2305/IUCN.UK.2020-

3.RLTS.T12776A508612.en.

Karger DN, Conrad O, Böhner J et al. (2017) Climatologies at high resolution for the earth's land surface

areas. *Scientific Data*, **4**, 1–20.

Kier G, Kreft H, Tien ML et al. (2009) A global assessment of endemism and species richness across island

and mainland regions. *Proceedings of the National Academy of Sciences of the United States of*

America, **106**, 9322–9327.

Lannuzel G, Balmot J, Dubos N, Thibault M, Fogliani B (2021) High-resolution topographic variables

accurately predict the distribution of rare plant species for conservation area selection in a narrow-

endemism hotspot in New Caledonia. *Biodiversity and Conservation*.

Leroy B, Bellard C, Dubos N et al. (2014) Forecasted climate and land use changes, and protected areas: the

contrasting case of spiders (ed Bradley B). *Diversity and Distributions*, **20**, 686–697.

Liu, C., Newell, G., & White, M. (2019). The effect of sample size on the accuracy of species distribution

models: considering both presences and pseudo-absences or background sites. *Ecography*, *42*(3), 535–

548. https://doi.org/10.1111/ecog.03188

Mckeown S. (1993). The general care and maintenance of day geckos. In: *Advanced Vivarium Systems*.

Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A (2007) Predicting species distributions

from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of*

Biogeography, **34**, 102–117.

Pearson RG, Stanton JC, Shoemaker KT et al. (2014) Life history and spatial traits predict extinction risk

due to climate change. *Nature Climate Change*, **4**, 217–221.

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias

and presence-only distribution models: Implications for background and pseudo-absence data.

Ecological Applications, **19**, 181–197.

Piludu N, Dubos N, Razafimanahaka JH, Razafindraibe P, Christian J, Jenkins RKB (2015) Distribution ,

threats and conservation of a Critically Endangered amphibian (*Mantella aurantiaca*) in eastern

Madagascar. *Herpetology Notes*, **8**, 119–123.

Platts PJ, Garcia RA, Hof C, Foden W, Hansen LA, Rahbek C, Burgess ND (2014) Conservation

implications of omitting narrow-ranging taxa from species distribution models, now and in the future.

Diversity and Distributions, **20**, 1307–1320.

Porcel, X., Deso, G., Probst, J., & Dubos, N. (2021). Sympatrie entre le Gecko vert de Manapany *Phelsuma*

inexpectata endémique de la Réunion et le Gecko vert poussière d'or *P. laticauda* introduits au

Domaine du café grillé : peuvent-ils cohabiter ? *Bulletin Phaethon*, *53*, 36–38.

Probst J-M, Turpin A (1997) Disparition d'une population de Gecko de Manapany dans le secteur littoral de

Saint-Joseph. *Bulletin Phaethon*, **6**, 104.

Radchuk V, Reed T, Teplitsky C et al. (2019) Adaptive responses of animals to climate change are most

likely insufficient. *Nature Communications*, **10**, 1–14.

Randrianavelona R, Rakotonoely H, Ratsimbazafy J, Jenkins RKB (2010) Conservation assessment of the

critically endangered frog *Mantella aurantiac*a in Madagascar. *African Journal of Herpetology*, **59**, 65–

78.

Rakotonanahary, T. F., Dawson, J., Andreone, F., Rakotoarisoa, J. C., Edmonds, D. (2017) Amphibian

Captive Breeding Programs for Madagascar: Where We Are Now and the Road Ahead. *FrogLog, 118*,

37–39.

Raxworthy CJ, Pearson RG, Rabibisoa N et al. (2008) Extinction vulnerability of tropical montane

endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in

Madagascar. *Global Change Biology*, **14**, 1703–1720.

Sala OE, Chapin FS, Armesto JJ et al. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**,

1770–1774.

Şekercioĝlu çaĝan H, Primack RB, Wormworth J (2012) The effects of climate change on tropical birds.

Biological Conservation, **148**, 1–18.

Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the Heat on Tropical Animals The Scale of Prediction.

Science (New York, N.Y.), **320**, 1296–1297.

Thomas CD (2011) Translocation of species, climate change, and the end of trying to recreate past ecological

communities. *Trends in Ecology and Evolution*, **26**, 216–221.

Turvey ST, Chen S, Tapley B et al. (2018) Imminent extinction in the wild of the world's largest amphibian.

Current Biology, **28**, R592–R594.

Vanderwal J, Murphy HT, Kutt AS, Perkins GC, Bateman BL, Perry JJ, Reside AE (2013) Focus on

poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature

Climate Change*, **3**, 239–243.

Varela S, Anderson RP, García-Valdés R, Fernández-González F (2014) Environmental filters reduce the

effects of sampling bias and improve predictions of ecological niche models. *Ecography*, **37**, 1084–

1091.

Vences M, Raxworthy CJ (2008) *Mantella aurantiaca*. The IUCN Red List of Threatened Species.

Vieilledent G, Grinand C, Rakotomalala FA, Ranaivosoa R, Rakotoarijaona JR, Allnutt TF, Achard F (2018)

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.

Vinson JM (1975) Notes on the reptiles of Round Island. *Mauritian Institute Bulletin*, **8**, 49–67.

Westwood R, Westwood AR, Hooshmandi M, Pearson K, LaFrance K, Murray C (2020) A field   validated

species distribution model to support management of the critically endangered Poweshiek skipperling

(*Oarisma poweshiek*) butterfly in Canada. *Conservation Science and Practice*, **2**, 1–15.

Wilson CD, Roberts D, Reid N (2011) Applying species distribution modelling to identify areas of high

conservation value for endangered species: A case study using *Margaritifera margaritifera* (L.).

Biological Conservation, **144**, 821–829.

Zhang Z, Mammola S, Liang Z et al. (2020) Future climate change will severely reduce habitat suitability of

the Critically Endangered Chinese giant salamander. *Freshwater Biology*, **65**, 971–980.