1 Are narrow-ranging species doomed to extinction? Probable dramatic and generalised decline in 2 future climate suitability of highly threatened species

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4 Running title: Narrow-ranging species and climate change

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26 **Abstract**

27 Aim

28 Narrow-ranging species are usually omitted from Species distribution models (SDMs) due to statistical
 29 constraints, while they are predicted to be particularly vulnerable to climate change. The recently available
 30 high-resolution climate and land use data, along with recently developed methods enable to increase the
 31 eligibility of narrow-ranging species for SDMs, provided their distribution is well known. We fill a gap of
 32 knowledge on the effect of predicted climate change on narrow-ranging species.

33 Location

34 Madagascar and Reunion Island.

35 Time period

36 Response to recent climate (1995-2019) and prediction on future climate (2070).

37 Major taxa studied

38 The golden mantella frog *Mantella aurantiaca* and the Manapany day gecko *Phelsuma inexpectata*.

39 Methods

40 We modelled the distribution of two threatened narrow-ranging species for which the distribution of their
 41 occurrence records is well documented. Our modelling scheme included a range of processes susceptible to
 42 address statistical issues related to narrow-ranging species (model complexity, evaluation, background
 43 extent, prevalence, extrapolation).

44 Results

45 We predict an alarming decline in climate suitability in the whole current distribution area of both species by
 46 2070, potentially leading to a complete extinction even in the most optimistic scenarios. We identified the
 47 areas with the best climate suitability in the future, but these remain largely suboptimal regarding species

48 climatic niche. The high level of habitat fragmentation suggests that both species likely need to be at least
49 partly translocated.

50 Main conclusions

51 Climate change may not only drive range contractions or distribution shifts in narrow-ranging species, but
52 may lead to the complete extirpation of suitable environments across their entire region. This study suggests
53 that the level of threats of data-poor and narrow-ranging species already identified as threatened may be
54 underestimated, especially in heterogeneous tropical areas. We stress the need to develop sampling
55 campaigns and implement proactive actions for narrow-ranging species in the tropics.

56

57 Keywords: Climate change, Ensemble of Small Models, Habitat restoration, Jackknife, Madagascar,
58 *Mantella aurantiaca*, *Phelsuma inexpectata*, Reunion Island, Species distribution models, Translocation

59

60 Introduction

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

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

83 The recent availability of high-resolution climatic data (e.g., Fick & Hijmans, 2017; Karger *et al.*, 2017),
84 along with high-resolution land cover data (e.g., Vieilledent *et al.*, 2018) is offering new opportunities for
85 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, often implying the filtering of occurrence or environmental data (Gábor *et al.*, 2019) or non-random pseudo-absence selection (Phillips *et al.*, 2009). However, data filtering can become problematic for species with low sample sizes (Vollering *et al.*, 2019), especially when species distribution is highly localised (Inman *et al.*, 2021) and is not recommended in absence of evidence of bias in occurrence data (Gábor *et al.*, 2019). Similarly, non-random pseudo-absence selection is not always effective (Dubos *et al.*, 2021) and tends to make predictions worse in narrow-niche species (Inman *et al.*, 2021). On the other hand, the reliability of an SDM is more driven by the quality of the data than the implementation of models (Araújo *et al.*, 2019). Therefore, the best option for narrow-ranging SDMs may be to select species for which the distribution is well known.

Given the predicted magnitude of climate change, along with the narrow thermal tolerance of tropical species (Tewksbury *et al.*, 2008), we may not only expect a reduction or a geographical shift in suitable conditions for narrow-ranging species, but the extirpation of suitable conditions across the entirety of their distribution range. Here we fill a gap of knowledge regarding the impact of future climate change on narrow-ranging species using two species for which the distribution is particularly well documented. These were the Manapany day gecko *Phelsuma inexpectata*, classified as Critically Endangered and the golden mantella frog *Mantella aurantiaca* formerly classified as Critically Endangered, now classified as Endangered after the inclusion of one locality record which increased its extent of occurrence. Both species are in continued decline (Probst & Turpin, 1997; Crottini *et al.*, 2019), live in highly fragmented areas (respectively in Reunion Island and central Madagascar) and are in urgent need for conservation actions. Given the important, long-term efforts invested to document their distribution, we assume that the geographic information for these species is nearly comprehensive and unbiased. We tested whether climate change will ‘only’ drive range reductions/shifts, or lead to a total extirpation of their suitable areas. We eventually

112 identify the most suitable candidate areas for habitat restoration and translocation across their respective
113 regions.

114

115 **Methods**

116 *Occurrence data*

117 *Phelsuma inexpectata* – The Manapany day gecko is endemic to the south of Reunion Island. We retrieved
118 31 occurrence data from literature (Bour *et al.*, 1995). Since then, the surroundings of the known distribution
119 range of the species were regularly visited (an 11 km-long coastal band). Two localities corresponding to
120 introduced populations were identified west of the current range, which we added to the data (Deso, 2001;
121 Porcel *et al.*, 2021). Recent sampling campaigns enabled to find additional occupied habitats (Dubos 2010)
122 but did not add any occurrence point after aggregation at the resolution of the environmental variables (30
123 arc seconds). Therefore, we assume that the sample occurrence of the species is nearly comprehensive. The
124 total number of 30 sec. occupied pixels resulted in 15 presence points.

125 *Mantella aurantiaca* – The golden mantella frog is distributed in central-Eastern Madagascar (region of
126 Moramanga; Fig. 1). We obtained 131 occurrence data from Piludu *et al.* (2015). Those included compiled
127 published data from surveys conducted between 2001 and 2007 (Bora *et al.*, 2008; Randrianavelona *et al.*,
128 2010) and new locations from additional surveys conducted between 2008 and 2013. More recent surveys
129 conducted between 2014 and 2019 enabled to add 39 occurrences. The region has been extensively surveyed
130 and it is very likely that most occupied habitats were identified. After aggregation to match the resolution of
131 environmental data, sample size resulted in 101 occurrence points.

132

133 *Climate data*

134 We used the 19 bioclimatic variables for 30 arc sec (approximately 900m) resolution of the current climate
135 data and of the 2070 projections from CHELSA (Karger *et al.*, 2017; Fig. S1, S2). We decided to include all

the 19 variables because both temperature and precipitation are related to the species' biology, including those related to indices of variability (e.g., cyclones drive mortality in *Phelsuma* and heavy rains drive reproduction in *Mantella*; Vinson, 1975; Randrianavelona et al., 2010). 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). We also ran sets of models using the WorldClim Global Climate Data (Fick & Hijmans, 2017), with the same GCMs and scenarios to account for potential effect of the baseline data in our predictions.

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, as known as BIOCLIM), flexible discriminant analysis (FDA) and random forest (RF), Multiple Adaptive Regression Splines (MARS), Generalised Boosting Model (GBM) and Maximum Entropy (MaxEnt). We generated five different sets of randomly-selected pseudo-absences (random generation is recommended for rare and specialised species; Inman et al., 2021). We selected one variable per group of inter-correlated variables to avoid collinearity (Pearson's $r > 0.7$) and assessed the relative importance of each variable kept with 10 permutations per model replicate (total = 500). The variables included in the final models were those with a relative importance > 0.2 across at least 50% of model runs. 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 below). This method is advocated for rare species and enables to reduce model complexity without reducing the explanatory power. We set three runs of cross validation (except for the jackknife procedure; see below). We ran a first set of models (1), hereafter referred to as 'Base' setting, with 1000 pseudo-absences and a background covering the entire respective island of each species. We ran a second set (2) where pseudo-absences were down-weighted to

162 equal presence data for the former two (setting prevalence to 0.5) referred to as ‘equal total weight’ (ETW).
 163 We reperformed the first two model sets but with a background covering the southern part of Reunion Island
 164 and the eastern forested part of Madagascar (see ‘Land use data’ section), without, and with pseudo-absence
 165 down-weighting, respectively referred to as (3) ‘Restricted background’ and (4) ‘ETW-Restricted
 166 background’. Eventually, we ran a (5) Base model set with the Worldclim baseline climate instead of Chelsa,
 167 referred to as ‘Worldclim baseline’. We used a jackknife for *P. inexpectata*, a procedure that is appropriate
 168 for small sample sizes (Pearson *et al.*, 2007; Galante *et al.*, 2018). The jackknife consists in running n
 169 iterations corresponding to the number of occurrence data, removing one occurrence for each run of
 170 calibration. Models are evaluated with the withheld occurrence. We did not used it for *M. aurantiaca* given
 171 that the number of occurrence data was sufficient for a standard procedure, and used an 80% calibration
 172 subset. For both species we present five ensemble models of current distribution (of varying background,
 173 prevalence and baseline climate), and 30 ensemble models of predicted future distribution (of varying
 174 background, prevalence, baseline climate, GCM and RCP).

175

176 *Model evaluations* – Ideally, performance evaluations are based on block-cross validation to limit spatial
 177 autocorrelation at large scales. In our case, species distributions are highly localised and the use of spatial
 178 splits would result in a small number of blocks and strong unbalances between blocks. We therefore used
 179 random splits for *M. aurantiaca* (and a jackknife for *P. inexpectata*). We assessed model performance using
 180 the Area Under the Operative Curve (AUC), the True Skill Statistics (TSS) and the Boyce index (the latter
 181 was not computed for the jackknife procedure, because this index is based on Spearman’s coefficients and
 182 cannot be estimated on the basis of a single location). For ensemble models, we excluded models for which
 183 the AUC was below 0.9 and for which the Boyce index was below 0.5 (Gillard *et al.*, 2017).

184 We performed a multivariate environmental similarity surfaces analysis (MESS) to determine whether
 185 models are well informed for predictions on novel (future) data. We eventually quantified the uncertainty
 186 related to model input parameters (modelling technique, pseudo-absence distribution, number of pseudo-

absences generated, pseudo-absence down-weighting, GCMs, RCPs and baseline climate data) by computing the standard deviation of the suitability scores between model predictions.

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. S5). 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 study that combined global tree cover loss data with historical national forest (resolution 30m; Vieilledent *et al.*, 2018; Fig. S6). We used forest cover of the year 1990 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

Three to four variables were selected in every cases (Table 1; Fig. S7, S8). 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. S9, S10). We excluded 5076 poorly performing

models out of 18750 for *P. inexpectata*, and 343 out of 4140 for *M. aurantiaca*. The median suitability score at the presence points for *P. inexpectata* was 836 (911 when removing the two introduced populations) and 783 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. S11, S12).

Table 1. Selected variables for two narrow-ranging species in Reunion Island and Madagascar. Variables were selected on the basis of 10 permutations per modelling technique and pseudo-absence set (total = 500).

Species	Model set	Selected variables
<i>Phelsuma inexpectata</i>	Base	Bio1, Bio15, Bio18
	Restricted background	Bio1, Bio15, Bio18
	Worldclim baseline	Bio1, Bio3, Bio14, Bio16
<i>Mantella aurantiaca</i>	Base	Bio1, Bio3, Bio4, Bio5
	Restricted background	Bio1, Bio18, Bio19
	Worldclim baseline	Bio10, Bio11, Bio14, Bio16

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. 1–6). On average across scenarios and GCMs, suitability scores decreased by 59% for *P. inexpectata* (Fig. 7) and 73% for *M. aurantiaca* at the presence points (Fig. 8). For *M. aurantiaca*, only one scenario out of 30 showed high suitability values within the current range (i.e. the MIROC5 GCM, RCP85, Chelsa baseline, restricted background).

In Reunion Island, predictions were the most variable between GCMs, but most ensemble models predicted a low climate suitability across the island. The highest suitability was found for the MIROC5 GCM, distributed along a band at higher altitudes (Fig. 1b). However, the MESS analyses indicated novel conditions in the most suitable areas, suggesting model extrapolations in these areas for this GCM (Fig. S13). According to the response curves (Fig. S14) and the predicted decrease in summer precipitations (Fig. S3c-d), climate suitability may have been overestimated.

In Madagascar, predictions varied the most with the background extent. Apart from the restricted background sets, none of the ensemble models identified any suitable area in the future. Nevertheless, we consistently identified a thin forest band in central Madagascar, south the current distribution, as the most suitable area across GCMs and scenarios (Fig. 2b). Models identified clear climatic windows, with no issue related to model extrapolation (Fig. S15, S16).

Fig. 1 Current (a) and projected future (b) environmental suitability for *Phelsuma inexpectata* using Chelsa as baseline climate data, no prevalence setting and the whole island as a background. 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). Models produced similar results when setting prevalence to 0.5 (Equal total weights).

Fig. 2 Current (a) and projected future (b) environmental suitability for *Phelsuma inexpectata* using Chelsa as baseline climate data, no prevalence setting and restricted background. 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). Models produced similar results when setting prevalence to 0.5 (Equal total weights).

Fig. 3 Current (a) and projected future (b) environmental suitability for *Phelsuma inexpectata* using Worldclim as baseline climate data. 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. 4 Current (a) and projected future (b) environmental suitability for *Mantella aurantiaca* using the Chelsa baseline climate, no prevalence setting and the whole island as a background. 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). Models produced similar results when setting prevalence to 0.5 (Equal total weights).

259 Fig. 5 Current (a) and projected future (b) environmental suitability for *Mantella aurantiaca* using the Chelsa
260 baseline climate, no prevalence setting and a restricted background. Black points represent the occurrence
261 data. Future projections (2070) were estimated from three Global Circulation models (GCM) and two RCP
262 scenarios. Top panels represent the most optimistic scenario (RCP26) and bottom panels represent the most
263 pessimistic scenario (RCP85). Models produced similar results when setting prevalence to 0.5 (Equal total
264 weights).

Fig. 6 Current (a) and projected future (b) environmental suitability for *Mantella aurantiaca* using the Worldclim baseline climate. 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).

270

271 Fig. 7 Variation in climate suitability scores at the occurrence points of *Phelsuma inexpectata* under current
272 climate and 2070 climate. We show the variability in model predictions related to the climate scenario (RCP
273 2.6 versus RCP 8.5), the Global circulation model (3 GCMs), the background extent (wide versus restricted),
274 prevalence setting (no setting versus Equal Total Weights, ETW) and baseline climate (Chelsa versus
275 Worldclim).

276

278 Fig. 8 Variation in climate suitability scores at the occurrence points of *Mantella aurantiaca* under current
279 climate and 2070 climate. We show the variability in model predictions related to the climate scenario (RCP
280 2.6 versus RCP 8.5), the Global circulation model (3 GCMs), the background extent (wide versus restricted),
281 prevalence setting (no setting versus Equal Total Weights, ETW) and baseline climate (Chelsa versus
282 Worldclim).

283

284 **Discussion**

285 *Dramatic and widespread decline in climate suitability*

286 We predict a strong decline of climate suitability in the whole current distribution area of both species by
287 2070. The subsequent high extinction risk in these species is not surprising, since small occupied areas are
288 known to be good predictors of vulnerability to climate change (Pearson *et al.*, 2014), but forecasting models
289 were lacking and we contribute to fill this gap. We also predict that few or no zone will be suitable in the
290 future across the entirety of their respective regions. If those species are not given the opportunity to adapt.

291 Depending on the Global Circulation model and the scenario, future predictions still identified areas with
 292 suboptimal climatic conditions. In Reunion Island, the higher suitability found at ca. 20km west from the
 293 current distribution was presumably driven by an increase in precipitation. *Phelsuma inexpectata* is mostly
 294 present where precipitation is the lowest (< 500mm during the wet season, Fig., S10), probably because the
 295 impact of cyclones—a driver of high mortality rates in *Phelsuma* species in the Mascarene (Vinson, 1975)—
 296 is less severe. The identified area coincides with the region with the driest conditions in Reunion Island in
 297 the future, according to these GCMs (Fig. S1). In all model sets, the MIROC5 GCM showed a higher—but
 298 suboptimal—climate suitability around the southern coast of the island, with the highest suitability along a
 299 band following the upper lands. This prediction is likely driven by the increase in overall temperature, along
 300 with reduced precipitation. The species lives under the hottest and driest conditions of the island, which fits
 301 the thermal requirements of the species for reproduction in captivity (28°C; McKeown, 1993). However, we
 302 believe this GCM is questionable because (1) the reduction in precipitation does not reflect the possible
 303 global increase in cyclone risk, and (2) the MESS analysis and response curves suggest an overestimation of
 304 the suitability scores. Note that this scenario (i.e. RCP 8.5)—which was the least pessimistic for *P.*
 305 *inexpectata*—is of interest to explore the widest range of possibilities in the future, but is considered unlikely
 306 (Hausfather & Peters, 2020).

307 In Madagascar, the current distribution is mainly explained by both winter (i.e. the dry season) and summer
 308 (i.e., the wet season) conditions with a short interval of suitability (Fig. S15). An important decline in climate
 309 suitability may therefore be driven by small changes in either winter or summer conditions. During winter,
 310 individuals migrate up the hills to shelter under dead woods and leaves and presumably enter a state of torpor
 311 or hibernation (Randrianavelona *et al.*, 2010; Edmonds *et al.*, 2020). The narrow climatic window may
 312 represent optimal conditions that minimise the risk of desiccation during this period of low activity. The
 313 species is also dependent on summer conditions, with a narrow window of suitable temperature and
 314 precipitations. This is highly consistent with a field study which recorded a surface temperature of 20-23°C
 315 at the occupied sites (Edwards *et al.*, 2019) and an experimental design which found a decrease in activity
 316 when temperature deviates from 21.5°C (Edwards, 2019) with warm and rainy conditions (Fig. S12).

317 Summer corresponds to the period of reproduction, where females lay eggs under dead leaves on slopes,
 318 which are likely washed down into temporary pond during heavy rain episodes. This may explain the
 319 dependence with summer high precipitation and temperatures. This combination of climatic conditions is
 320 unlikely to be met in the future, except for the MIROC5 GCM under the RCP85 scenario (but this scenario is
 321 unlikely, Hausfather & Peters, 2020). However, we consistently identified potential suboptimal areas in the
 322 central-south of the eastern forest corridor and in one small area in the north east (corresponding to the top of
 323 mountains). For both species *P. inexpectata* and *M. aurantiaca*, the high level of habitat fragmentation
 324 associated to agricultural areas may limit potential distribution shifts, which calls the need for human
 325 intervention.

326

327 *Sources of uncertainty*

328 The largest source of uncertainty was related to the GCM for *P. inexpectata*, and to the background extend
 329 for *M. aurantiaca*. We followed a protocol that attempted to mitigate most sources of uncertainty,
 330 corresponding to the acceptable standards defined in Araújo *et al.* (2019). The long term, extensive and
 331 repeated efforts dedicated to species sampling enabled to define the current distributions of these two species
 332 with high precision. Uncertainty map showed a high level of agreement between model replicates for current
 333 projections ()We included the 19 bioclimatic variables for the selection process, which is not recommended
 334 in most cases. However, we selected the most biologically meaningful variables among the groups of
 335 intercorrelated variables. We used the finest resolution available for climate data (i.e. 30 arc sec) which
 336 seems sufficient to discriminate suitable to unsuitable areas at the scale of Reunion Island and Madagascar.
 337 The inclusion of high-resolution land use variables enabled to improve the realism of both distributions and
 338 provide specific guidelines for conservation applications. In addition, we found a causal interpretation for the
 339 selected variables, which, along with the high model performance, brings confidence in credibility of the
 340 models. An important limitation is that we did not use scenarios of future land use. This may lead to an
 341 overestimation of the available habitat in Madagascar, since the country is under important rates of
 342 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 GCM (i.e. MIROC5), which we assume to be doubtful. The remaining ones consistently identified the most suitable area by 2070. 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 cross-validation subsets). Model performance was assessed with random partitions for *M. aurantiaca*, while spatial partitions are recommended. However, we argued that this method is not appropriate for highly localised species due to strong imbalance between spatial blocks. We used multiple evaluation metrics, including discrimination (AUC and TSS) and reliability (i.e. calibration; Boyce index) metrics, all showing a high performance overall. 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. Further study of biotic interaction between *M. aurantiaca* and other amphibians is needed to assess the consequences of its introduction.

407

408 *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; Şekercioğlu *et al.*, 2012; Dubos *et al.*, 2019). Species that are already under threats are at the greatest risk because of a large array of synergistic effects (Şekercioğlu *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 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.

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Conflict of Interest Statement

The authors declare no conflict of interests.

Data availability statement

The dataset and the scripts used in this analysis are available as R objects in the supporting information.

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