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## **Are narrow-ranging species doomed to extinction? Projected dramatic decline in future climate suitability of two highly threatened species**

Nicolas Dubos, Frederique Montfort, Clovis Grinand, Marie Nourtier, Gregory Deso, Jean-Michel Probst, Julie Hanta Razafimanahaka, Raphali Rodlis Andriantsimanarilafy, Eddie Fanantenana Rakotondrasoa, Pierre Razafindraibe, et al.

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1 **Are narrow-ranging species doomed to extinction? Projected dramatic decline in future climate**

2 **suitability of two highly threatened species**

3

4 Running title: Narrow-ranging species and climate change

5

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26

27 **Abstract**

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 environmental predictors, 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. We modelled the  
33 distribution of the golden mantella frog *Mantella aurantiaca* and the Manapany day gecko *Phelsuma*  
34 *inexpectata*, for which the distribution of their occurrence records is well documented. Our modelling  
35 scheme included a range of processes susceptible to address statistical issues related to narrow-ranging  
36 species. We predict an alarming decline in climate suitability in the whole current distribution area of both  
37 species by 2070, potentially leading to a complete extinction in most scenarios. We identified the areas with  
38 the best climate suitability in the future, but these remain largely suboptimal regarding species climatic niche.  
39 The high level of habitat fragmentation suggests that both species likely need to be at least partly  
40 translocated. Climate change may not only drive range contractions or distribution shifts in narrow-ranging  
41 species, but may lead to the complete extirpation of suitable environments across their entire region. This  
42 study suggests that the level of threats of narrow-ranging species already identified as threatened may be  
43 underestimated, especially in heterogeneous tropical areas. We stress the need to develop sampling  
44 campaigns and implement proactive actions for narrow-ranging species in the tropics.

45

46 **Keywords:** Climate change, Ensemble of Small Models, Jackknife, Madagascar, *Mantella aurantiaca*,  
47 *Phelsuma inexpectata*, Reunion Island, Species distribution models, Translocation

## 48 **Introduction**

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

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

71 The recent availability of high-resolution climatic data (e.g., Fick & Hijmans, 2017; Karger *et al.*, 2017),  
72 along with high-resolution land cover data (e.g., Vieilledent *et al.*, 2018) is offering new opportunities for  
73 modelling the distribution of these species (Lannuzel *et al.*, 2021). However, despite a probable increase in

74 statistical power, there is still the possibility for SDMs to produce misleading results due to spatial sampling  
75 bias (Phillips *et al.*, 2009). The effect of sample bias may be particularly strong in rare (or poorly known)  
76 species with small sample sizes, because models are more influenced by each occurrence data that is used  
77 (Pearson *et al.*, 2007). A number of techniques were recently developed for data-poor species. For instance,  
78 jackknife procedures (i.e. leave-one-out; Pearson *et al.* 2007) improves model assessments and Ensemble of  
79 Small Models (ESMs) enable to deal with model complexity while keeping sufficient explanatory power  
80 (Breiner *et al.* 2015). Other techniques are dedicated to sampling bias correction, often implying the filtering  
81 of occurrence or environmental data (Gábor *et al.*, 2019) or non-random pseudo-absence selection (Phillips  
82 *et al.*, 2009). However, data filtering can become problematic for species with low sample sizes (Vollering *et*  
83 *al.*, 2019), especially when species distribution is highly localised (Inman *et al.*, 2021) and is not  
84 recommended in absence of evidence of bias in occurrence data (Gábor *et al.*, 2019). Similarly, non-random  
85 pseudo-absence selection is not always effective (Dubos *et al.*, 2021) and tends to make predictions worse in  
86 narrow-niche species (Inman *et al.*, 2021). However, the restriction of the background area (where pseudo-  
87 absences are generated), i.e. background thickening, can be advantageous for sample bias correction when  
88 data is scarce without discarding presence records (Acevedo *et al.* 2012; Vollering *et al.* 2019). On the other  
89 hand, the reliability of an SDM is more driven by the quality of the data than the implementation of models  
90 (Araújo *et al.*, 2019). Therefore, the best option for narrow-ranging SDMs may be to (1) use all the available  
91 methodological tools to deal with statistical issues, and (2) select species for which the distribution is well  
92 known.

93 Given the predicted magnitude of climate change, along with the narrow thermal tolerance of tropical species  
94 (Tewksbury *et al.*, 2008), we may not only expect a reduction or a geographical shift in suitable conditions  
95 for narrow-ranging species, but the extirpation of suitable conditions across the entirety of their distribution  
96 range. Here we fill a gap of knowledge regarding the impact of future climate change on narrow-ranging  
97 species using two species for which the distribution is particularly well documented. These were the  
98 Manapany day gecko *Phelsuma inexpectata*, classified as Critically Endangered (IUCN & MNHN, 2010)  
99 and the golden mantella frog *Mantella aurantiaca* formerly classified as Critically Endangered (Vences &

100 Raxworthy, 2008), now classified as Endangered after the inclusion of one locality record which increased its  
101 extent of occurrence (IUCN SSC Amphibian Specialist Group 2020). Both species are in continued decline  
102 (Probst & Turpin, 1997; Crottini et al., 2019), live in highly fragmented areas (respectively in Reunion Island  
103 and central Madagascar) and are in urgent need for conservation actions. Given the important, long-term  
104 efforts invested to document their distribution, we assume that the geographic information for these species  
105 is nearly comprehensive and unbiased. We tested whether climate change will ‘only’ drive range  
106 reductions/shifts, or lead to a total extirpation of their suitable areas. We eventually identify the most suitable  
107 candidate areas for habitat restoration and translocation across their respective regions.

108

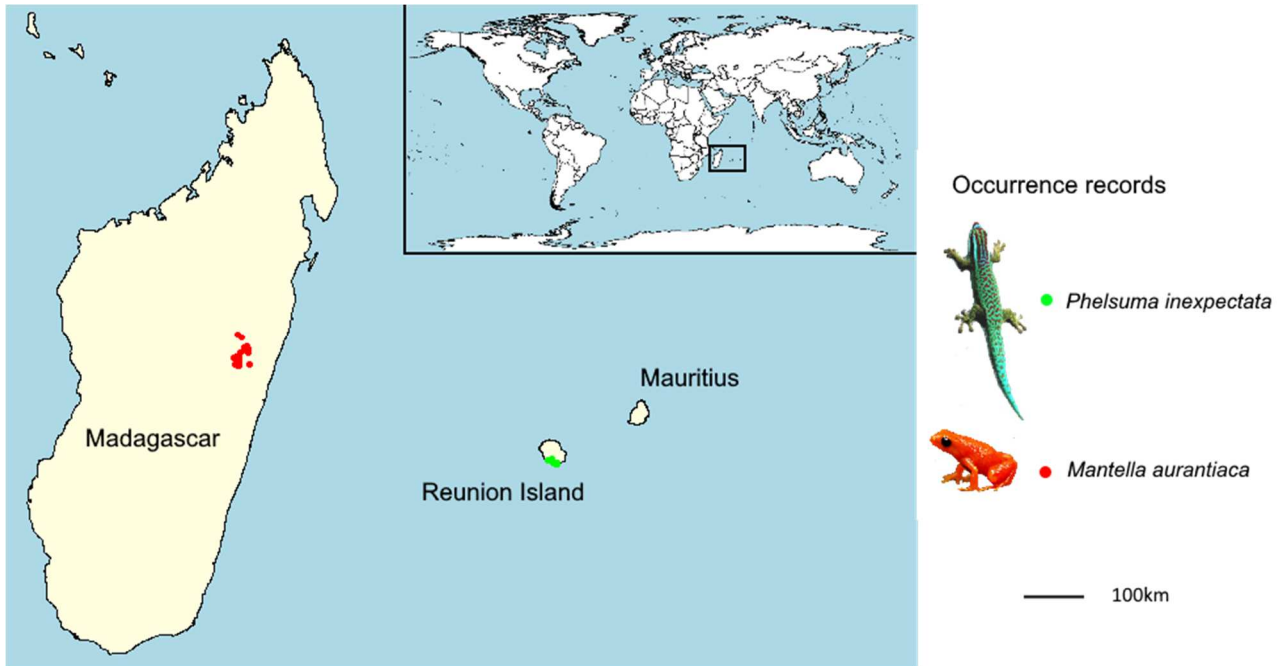
## 109 **Methods**

### 110 *Occurrence data*

111 *Phelsuma inexpectata* – The Manapany day gecko is endemic to the south of Reunion Island. We retrieved  
112 31 occurrence data from literature (Bour *et al.*, 1995). Since then, the surroundings of the known distribution  
113 range of the species were regularly visited (an 11 km-long coastal band; Fig. 1). Two localities corresponding  
114 to introduced populations were identified west of the current range, which we added to the data (Deso, 2001;  
115 Porcel *et al.*, 2021). Recent sampling campaigns enabled to find additional occupied habitats (Dubos 2010)  
116 but did not add any occurrence point after aggregation at the resolution of the environmental variables (30  
117 arc seconds). Therefore, we assume that the sample occurrence of the species is nearly comprehensive. The  
118 total number of 30 sec. occupied pixels resulted in 15 presence points.

119 *Mantella aurantiaca* – The golden mantella frog is distributed in central-Eastern Madagascar (region of  
120 Moramanga; Fig. 1). We obtained 131 occurrence data from Piludu *et al.* (2015). Those included compiled  
121 published data from surveys conducted between 2001 and 2007 (Bora *et al.*, 2008; Randrianelona *et al.*,  
122 2010) and new locations from additional surveys conducted between 2008 and 2013. More recent surveys  
123 conducted between 2014 and 2019 enabled to add 39 occurrences. The region has been extensively surveyed

124 and it is very likely that most occupied habitats were identified. After aggregation to match the resolution of  
125 environmental data, sample size resulted in 101 occurrence points.



126 Fig. 1 Study area and species, with occurrence points.

### 127 *Climate data*

128 We used the 19 bioclimatic variables for 30 arc sec (approximately 900m) resolution of the current climate  
129 data and of the 2070 projections from CHELSA (Karger et al., 2017; Fig. S1, S2). We decided to include all  
130 the 19 variables because both temperature and precipitation are related to the species' biology, including  
131 those related to indices of variability (e.g., cyclones drive mortality in *Phelsuma* and heavy rains drive  
132 reproduction in *Mantella*; Vinson, 1975; Randrianelona et al., 2010). We used three Global Circulation  
133 Models (GCMs; i.e., BCC-CSM1-1, MIROC5 and HadGEM2-AO) and two greenhouse gas emission  
134 scenarios (the most optimistic RCP26 and the most pessimistic RCP85; Fig. S3, S4). We also ran sets of  
135 models using the WorldClim Global Climate Data (Fick & Hijmans, 2017), with the same GCMs and  
136 scenarios to account for potential effect of the baseline data in our predictions.

137

### 138 *Distribution modelling*

139 We modelled and projected species distributions with the biomod2 R package (Thuiller et al. 2009), using 10  
140 modelling techniques: generalised linear model (GLM), generalised additive model (GAM), classification  
141 tree analysis (CTA), artificial neural network (ANN), surface range envelop (SRE, as known as BIOCLIM),  
142 flexible discriminant analysis (FDA) and random forest (RF), Multiple Adaptive Regression Splines (MARS),  
143 Generalised Boosting Model (GBM) and Maximum Entropy (MaxEnt). For machine learning modelling  
144 techniques, hyperparameters were set to their default values implemented in biomod2 (see  
145 [https://www.rdocumentation.org/packages/biomod2/versions/3.5.1/topics/BIOMOD\\_ModelingOptions](https://www.rdocumentation.org/packages/biomod2/versions/3.5.1/topics/BIOMOD_ModelingOptions)). We  
146 generated five different sets of randomly-selected pseudo-absences (random generation is recommended for  
147 rare and specialised species; Inman et al., 2021). We selected one variable per group of inter-correlated  
148 variables to avoid collinearity (Pearson's  $r > 0.7$ ) and assessed the relative importance of each variable kept  
149 with 10 permutations per model replicate (total = 500). The variables included in the final models were those  
150 with a relative importance  $> 0.2$  across at least 50% of model runs (these varied with the baseline climate and  
151 the background extent; Table 1). We show the fitted predicted values for each individual model, and a mean  
152 smoothed response curve. We predicted species distributions with an ensemble of small models approach  
153 (ESM; Breiner et al., 2015). We ran sets of bivariate models, i.e. including all pairwise combinations of the  
154 selected variables, and produced an ensemble model with the mean predictions across all models weighted  
155 by their respective AUC (see below). This method is advocated for rare species and enables to reduce model  
156 complexity without reducing the explanatory power. We set three runs of cross validation (except for the  
157 jackknife procedure; see below). We ran a first set of models (1), hereafter referred to as 'Base' setting, with  
158 1000 pseudo-absences selected from a background covering the entire respective island of each species (i.e.  
159 all island cells). We ran a second set (2) where the 1000 pseudo-absences were down-weighted to equal  
160 presence data (setting prevalence to 0.5) referred to as 'equal total weight' (ETW; Liu et al. 2019). We  
161 reperformed the first two model sets but with a background covering the southern part of Reunion Island and  
162 the eastern forested part of Madagascar (see 'Land use data' section), without, and with pseudo-absence  
163 down-weighting, respectively referred to as (3) 'Restricted background' and (4) 'ETW-Restricted  
164 background'. Eventually, we ran a (5) Base model set with the Worldclim baseline climate instead of Chelsa,



165 referred to as 'Worldclim baseline'. For both species we present five ensemble models of current distribution  
166 (of varying background, prevalence and baseline climate), and 30 ensemble models of projected future  
167 distribution (of varying background, prevalence, baseline climate, GCM and RCP). We did not account for  
168 species dispersal ability, because the purpose was not to predict potential shifts, but to assess how suitable  
169 will be the climate in the future in order to identify candidate sites for restoration and translocation.

170

171 *Model evaluations* – Ideally, performance evaluations are based on block-cross validation to limit spatial  
172 autocorrelation at large scales. In our case, species distributions are highly localised and the use of spatial  
173 splits would result in strong unbalances between blocks. We therefore used a random partitioning for *M.*  
174 *aurantiaca* and a jackknife for *P. inexpectata*. The jackknife procedure is appropriate for small sample sizes  
175 (Pearson *et al.*, 2007; Galante *et al.*, 2018). This approach consists in running  $n$  iterations corresponding to  
176 the number of occurrence data, removing one occurrence for each run of calibration. Models are evaluated  
177 with the withheld occurrence. We did not use it for *M. aurantiaca* given that the number of occurrence data  
178 was sufficient for a standard procedure, and used an 80% calibration subset (random partitioning). We  
179 assessed model performance using the Area Under the Operative Curve (AUC), the True Skill Statistics (TSS)  
180 and the Boyce index (the latter was not computed for the jackknife procedure, because this index is based on  
181 Spearman's coefficients and cannot be estimated on the basis of a single location). Poorly performing models  
182 could result from calibration subsets falling into different conditions than evaluation subsets. For ensemble  
183 models (mean predictions), we excluded models for which the AUC was below 0.9 and for which the Boyce  
184 index was below 0.5 (Gillard *et al.*, 2017).

185 We performed a multivariate environmental similarity surfaces analysis (MESS) to determine whether  
186 models are well informed for projections on novel (future) data. We eventually quantified the uncertainty  
187 related to model input parameters (modelling technique, pseudo-absence distribution, number of pseudo-  
188 absences generated, pseudo-absence down-weighting, GCMs, RCPs and baseline climate data) by computing  
189 the standard deviation of the suitability scores between model predictions.

190

191 *Land use data*

192 We accounted for the habitat requirements of our model species by applying a filter to the projected climate  
193 suitability based on land use and land cover data (e.g., Gillard *et al.*, 2017). This enabled to minimise model  
194 complexity while remaining biologically realistic and relevant for conservation applications.

195 Reunion Island – We used very high-resolution land cover categories (Urban, agricultural, natural, water) at  
196 1.5m resolution (resampled at 15m for computing purposes) derived from remote sensing (Dupuy and  
197 Gaetano, 2019; Fig. S5). Since *P. inexpectata* can be found in both urbanised and natural areas and avoids  
198 agricultural areas (Probst & Turpin, 1997), we excluded the latter land use type only. This is relevant also for  
199 conservation applications because habitat restoration is more difficult to implement in agricultural areas.

200 Madagascar – *Mantella aurantiaca* is exclusively found in swampy forested areas (Randrianelona *et al.*,  
201 2010). We filtered our suitability maps to include only cells corresponding to rainforests. We obtained forest  
202 cover data for two periods (1990 and 2017) from a study that combined global tree cover loss data with  
203 historical national forest (resolution 30m; Vieilledent *et al.*, 2018; Fig. S6). We used forest cover of the year  
204 1990 for current distribution models because it corresponds approximately to the period of the oldest  
205 occurrence data (some areas were deforested since then). For future projections, we used the latest forest  
206 cover data available, i.e. 2017.

207

## 208 **Results**

209 *Variable selection and model performance*

210 Three to four variables were selected in every cases (no change between prevalence settings; see details in  
211 Table 1; Fig. S7, S8). The current distribution of both species was well predicted (across five model sets: *P.*  
212 *inexpectata*: mean AUC = 0.96, mean TSS = 0.91; *M. aurantiaca*: mean Boyce = 0.82, mean AUC = 0.97,  
213 mean TSS = 0.94; Fig. S9, S10). We excluded 5076 poorly performing models out of 18750 for *P.*

214 *inexpectata*, and 343 out of 4140 for *M. aurantiaca*. The median suitability score at the presence points for *P.*  
 215 *inexpectata* was 836 (911 when removing the two introduced populations) and 783 for *M. aurantiaca*.  
 216 Models consistently identified the current distribution range between all runs for both species, as shown by  
 217 the uncertainty map (SD intermodel suitability scores at the presence points of 168 for *P. inexpectata* and 113  
 218 for *M. aurantiaca*; Fig. S11, S12).

219 Table 1. Selected variables for two narrow-ranging species in Reunion Island and Madagascar. Variables  
 220 were obtained from CHELSA (Karger et al., 2017) and Worldclim (Fick & Hijmans, 2017), and selected on  
 221 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

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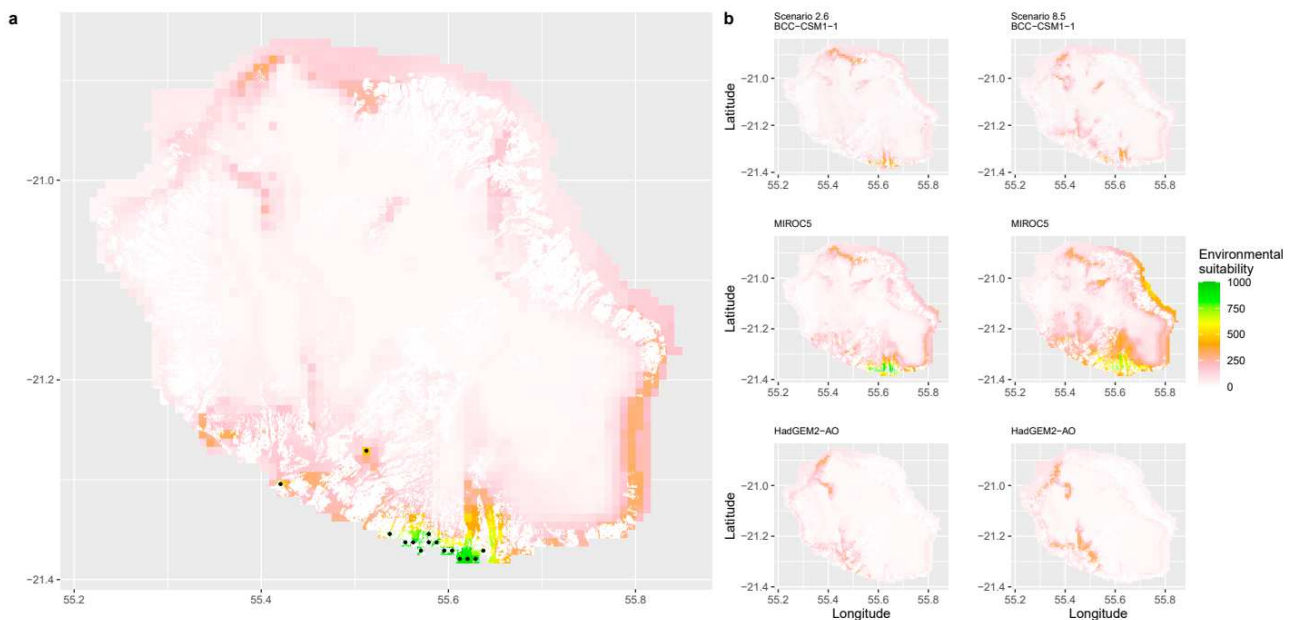
### 223 *Future climate suitability*

224 All scenarios indicated an important decrease in climate suitability in the entirety of the current range of both  
 225 species by 2070 (Fig. 2–7). On average across scenarios and GCMs, suitability scores decreased by 59% for  
 226 *P. inexpectata* (Fig. 8) and 73% for *M. aurantiaca* at the presence points (Fig. 9). For *M. aurantiaca*, only  
 227 one scenario out of 30 showed high suitability values within the current range (i.e. the MIROC5 GCM,  
 228 RCP85, Chelsa baseline, restricted background).

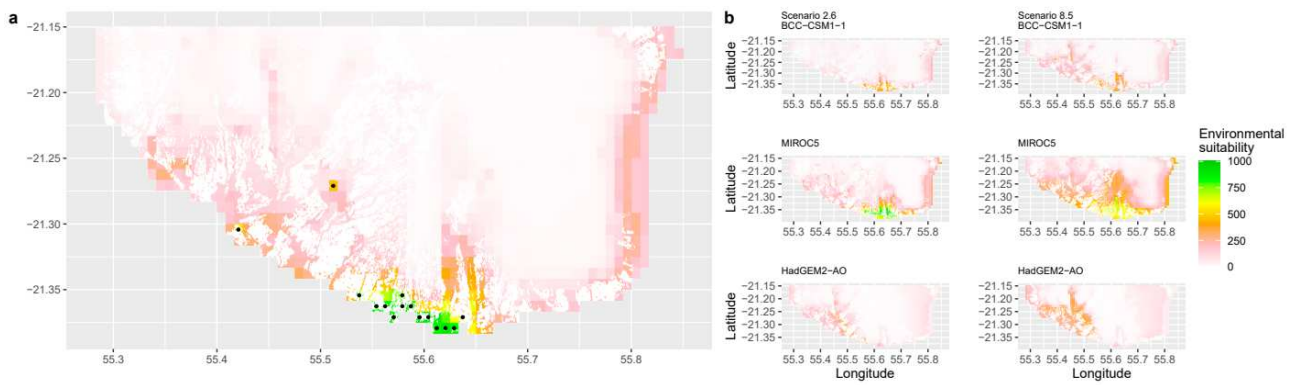
229 In Reunion Island, predictions were the most variable between GCMs, but most ensemble models predicted a  
 230 low climate suitability across the island. The highest suitability was found for the MIROC5 GCM,  
 231 distributed along a band at higher altitudes (Fig. 2b). However, the MESS analyses indicated novel

232 conditions in the most suitable areas, suggesting model extrapolations in these areas for this GCM (Fig. S13).  
 233 According to the response curves (Fig. S14) and the predicted decrease in summer precipitations (Fig. S3c-d),  
 234 climate suitability may have been overestimated.

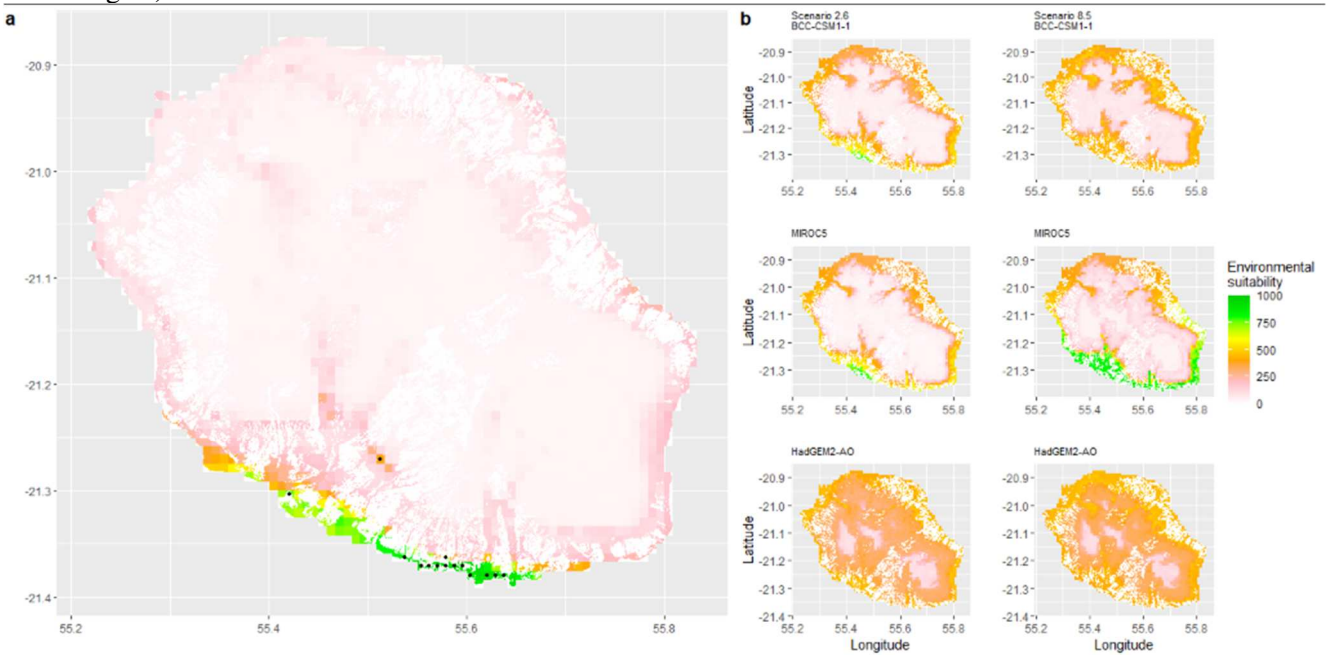
235 In Madagascar, predictions varied the most with the background extent. Apart from the restricted background  
 236 sets, none of the ensemble models identified any suitable area in the future. Nevertheless, we consistently  
 237 identified a thin forest band in central Madagascar, south the current distribution, as the most suitable area  
 238 across GCMs and scenarios (Fig. 3b). Models identified clear climatic windows, with no issue related to  
 239 model extrapolation (Fig. S15, S16).



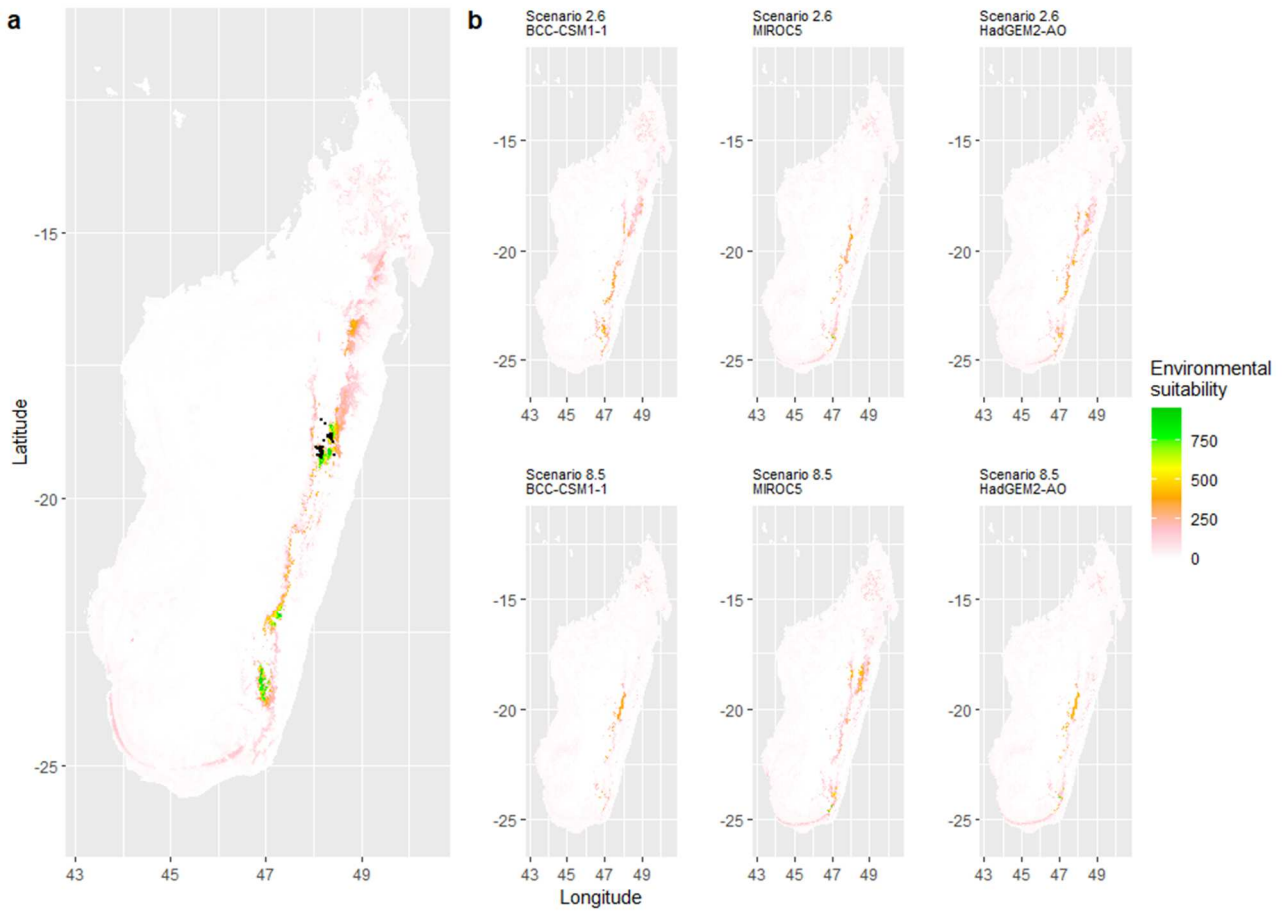
240 Fig. 2 Current (a) and projected future (b) environmental suitability for *Phelsuma inexpectata* using Chelsea  
 241 as baseline climate data, no prevalence setting and the whole island as a background. Predictions were  
 242 filtered to remove agricultural areas. X and Y axes represent the coordinates (WGS84). Black points  
 243 represent the occurrence data. Future projections (2070) were estimated from three Global Circulation  
 244 models (GCM) and two RCP scenarios. Left panels represent the most optimistic scenario (RCP26) and right  
 245 panels represent the most pessimistic scenario (RCP85). Models produced similar results when setting  
 246 prevalence to 0.5 (Equal total weights).



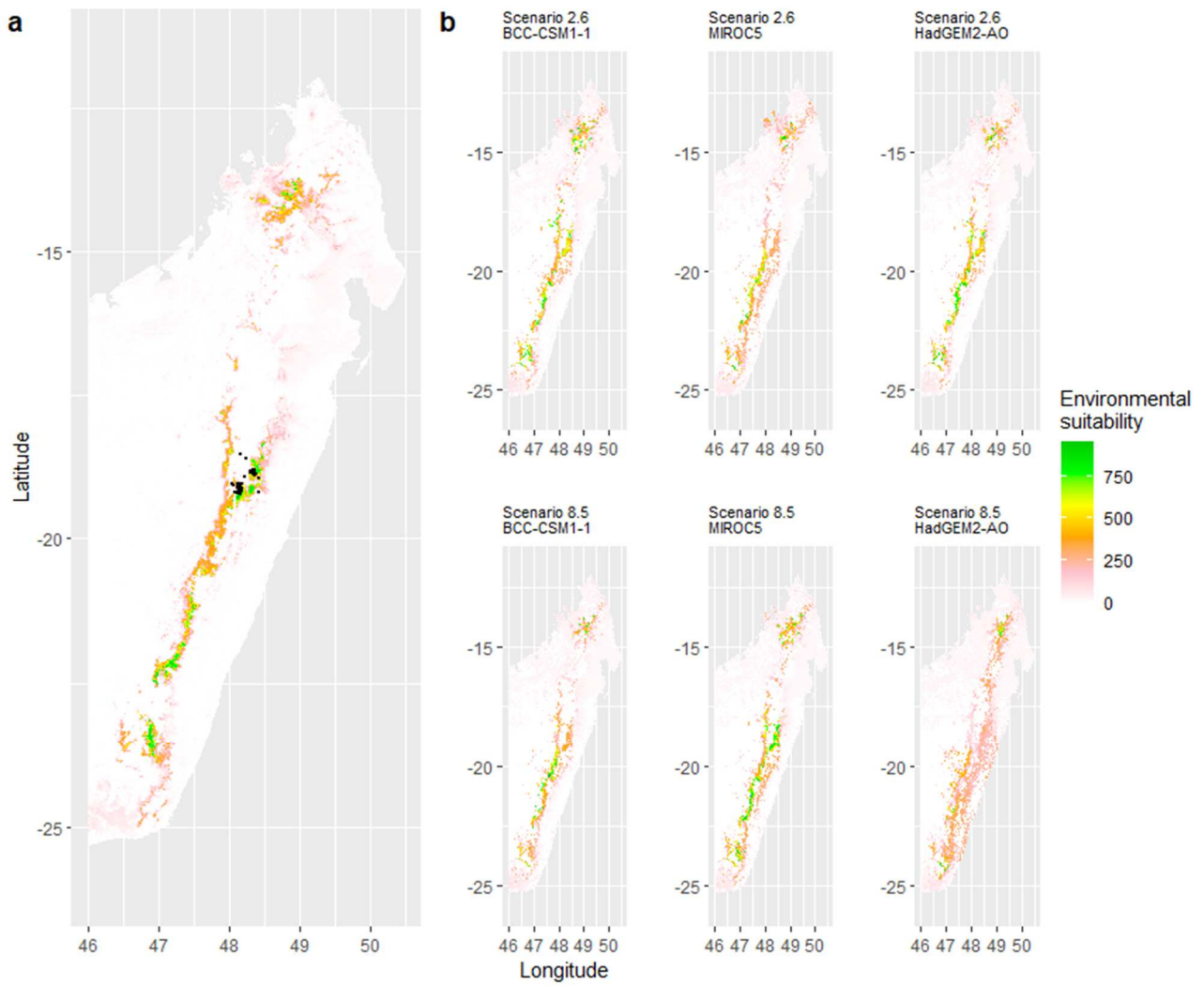
247 Fig. 3 Current (a) and projected future (b) environmental suitability for *Phelsuma inexpectata* using Chelsea  
 248 as baseline climate data, no prevalence setting and restricted background. Predictions were filtered the  
 249 remove agricultural areas. X and Y axes represent the coordinates (WGS84). Black points represent the  
 250 occurrence data. Future projections (2070) were estimated from three Global Circulation models (GCM) and  
 251 two RCP scenarios. Left panels represent the most optimistic scenario (RCP26) and right panels represent the  
 252 most pessimistic scenario (RCP85). Models produced similar results when setting prevalence to 0.5 (Equal  
 253 total weights).



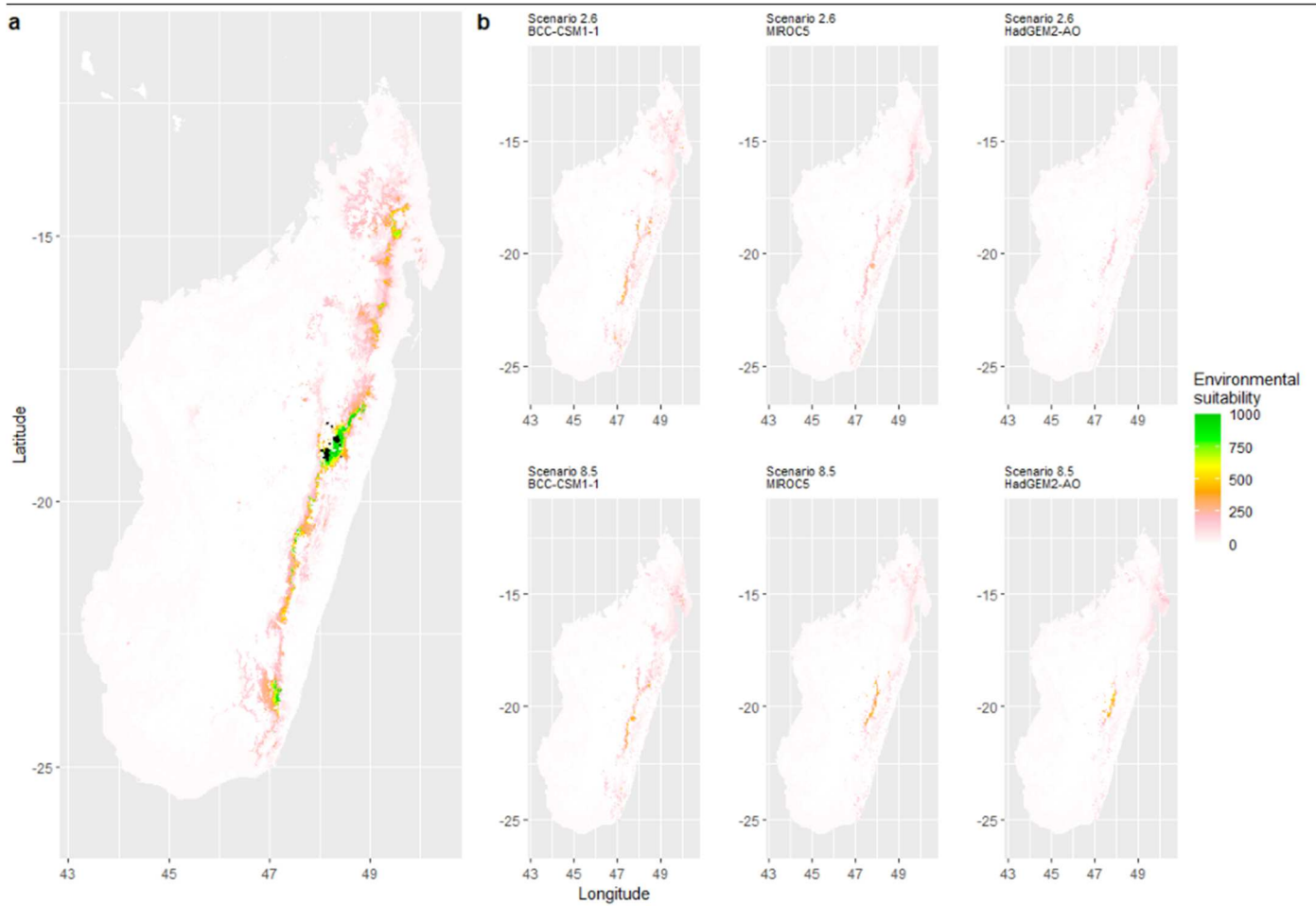
254  
 255 Fig. 4 Current (a) and projected future (b) environmental suitability for *Phelsuma inexpectata* using  
 256 Worldclim as baseline climate data. Predictions were filtered the remove agricultural areas. X and Y axes  
 257 represent the coordinates (WGS84). Black points represent the occurrence data. Future projections (2070)  
 258 were estimated from three Global Circulation models (GCM) and two RCP scenarios. Left panels represent  
 259 the most optimistic scenario (RCP26) and right panels represent the most pessimistic scenario (RCP85).



260 Fig. 5 Current (a) and projected future (b) environmental suitability for *Mantella aurantiaca* using the Chelsa  
 261 baseline climate, no prevalence setting and the whole island as a background. Predictions were filtered to  
 262 include only forested areas. X and Y axes represent the coordinates (WGS84). Black points represent the  
 263 occurrence data. Future projections (2070) were estimated from three Global Circulation models (GCM) and  
 264 two RCP scenarios. Top panels represent the most optimistic scenario (RCP26) and bottom panels represent  
 265 the most pessimistic scenario (RCP85). Models produced similar results when setting prevalence to 0.5  
 266 (Equal total weights).



267 Fig. 6 Current (a) and projected future (b) environmental suitability for *Mantella aurantiaca* using the Chelsa  
 268 baseline climate, no prevalence setting and a restricted background. The background was filtered to include  
 269 only the western rainforest corridor. X and Y axes represent the coordinates (WGS84). Black points represent  
 270 the occurrence data. Future projections (2070) were estimated from three Global Circulation models (GCM)  
 271 and two RCP scenarios. Top panels represent the most optimistic scenario (RCP26) and bottom panels  
 272 represent the most pessimistic scenario (RCP85). Models produced similar results when setting prevalence to  
 273 0.5 (Equal total weights).

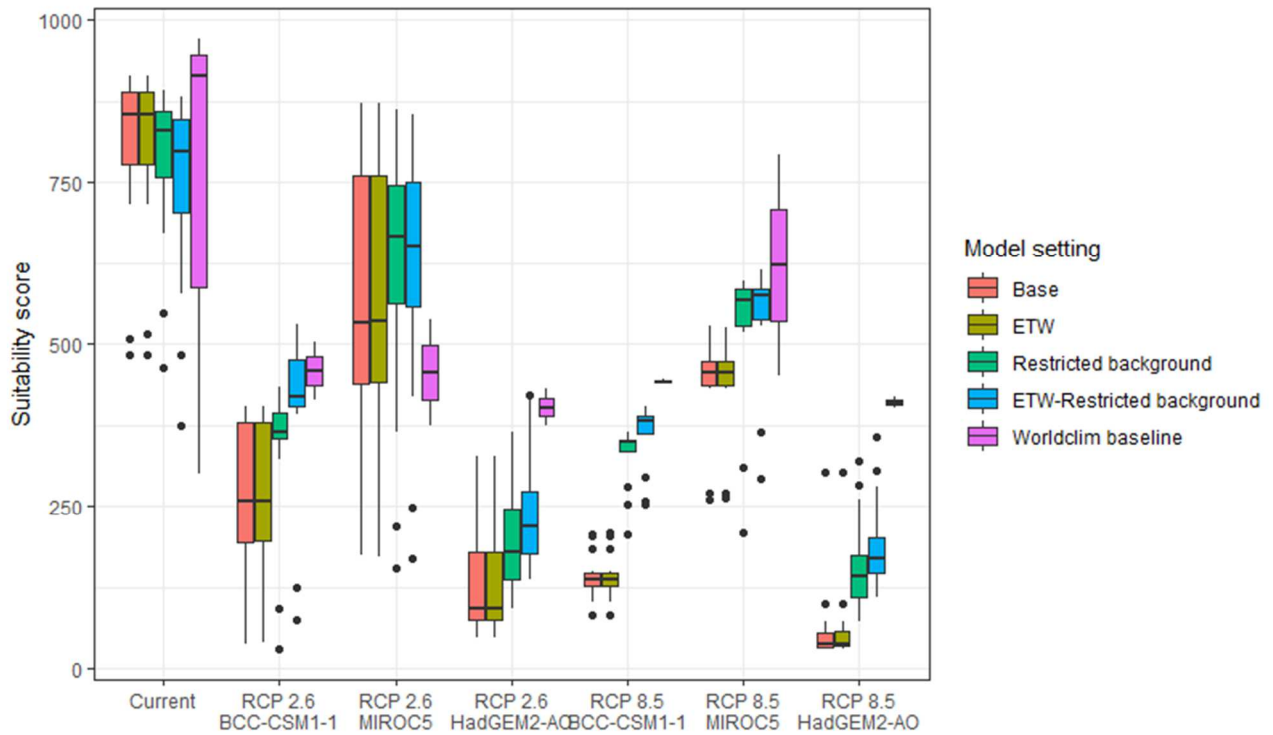


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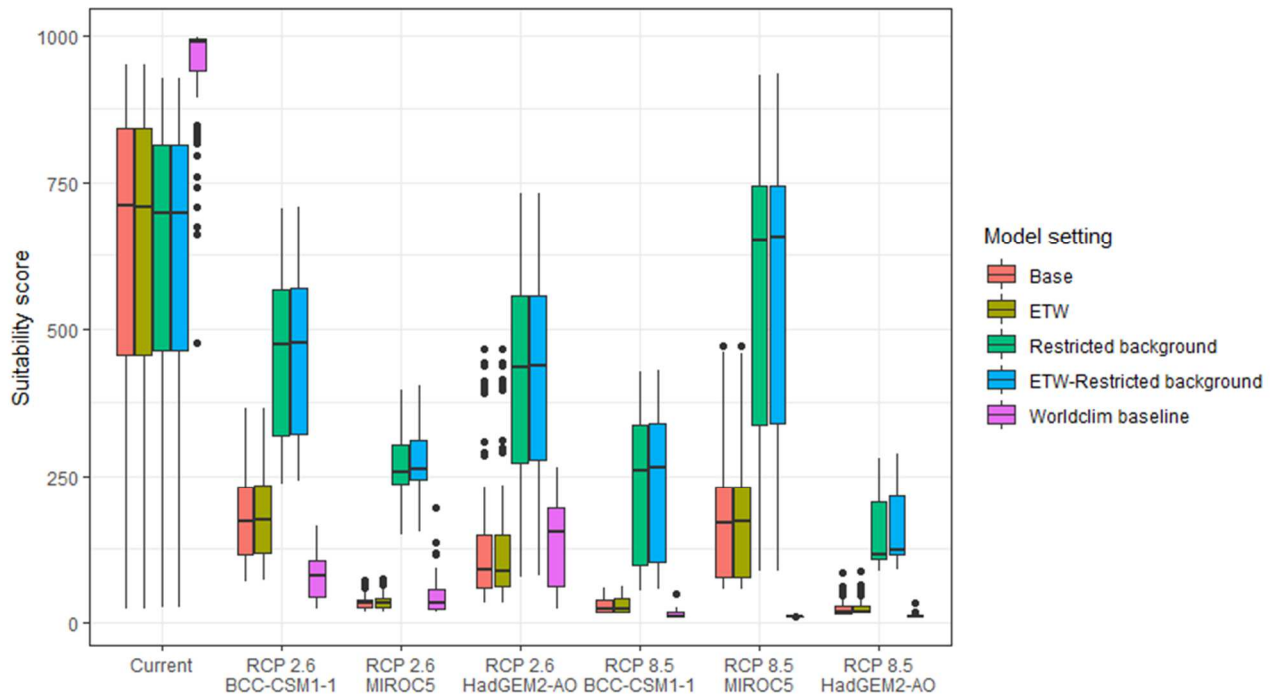
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276 Fig. 7 Current (a) and projected future (b) environmental suitability for *Mantella aurantiaca* using the  
 277 Worldclim baseline climate. Predictions were filtered to include only forested areas. X and Y axes represent  
 278 the coordinates (WGS84). Black points represent the occurrence data. Future projections (2070) were  
 279 estimated from three Global Circulation models (GCM) and two RCP scenarios. Top panels represent the  
 280 most optimistic scenario (RCP26) and bottom panels represent the most pessimistic scenario (RCP85).





282 Fig. 8 Variation in climate suitability scores at the occurrence points of *Phelsuma inexpectata* under current  
 283 climate and 2070 climate. We show the variability in model predictions related to the climate scenario (RCP  
 284 2.6 versus RCP 8.5), the Global circulation model (3 GCMs), the background extent (wide versus restricted),  
 285 prevalence setting (no setting versus Equal Total Weights, ETW) and baseline climate (Chelsa versus  
 286 Worldclim). Each boxplot is composed of the first decile, the lower hinge, the median, the upper hinge and  
 287 the ninth decile.



289

290 Fig. 9 Variation in climate suitability scores at the occurrence points of *Mantella aurantiaca* under current  
 291 climate and 2070 climate. We show the variability in model predictions related to the climate scenario (RCP  
 292 2.6 versus RCP 8.5), the Global circulation model (3 GCMs), the background extent (wide versus restricted),  
 293 prevalence setting (no setting versus Equal Total Weights, ETW) and baseline climate (Chelsa versus  
 294 Worldclim). Each boxplot is composed of the first decile, the lower hinge, the median, the upper hinge and  
 295 the ninth decile.

296

## 297 Discussion

### 298 *Dramatic and widespread decline in climate suitability*

299 We predict a strong decline of climate suitability in the whole current distribution area of both species by  
 300 2070. The subsequent high extinction risk in these species is not surprising, since small occupied areas are  
 301 known to be good predictors of vulnerability to climate change (Pearson *et al.*, 2014), but forecasting models

302 were lacking and we contribute to fill this gap. We also predict that few or no zone will be suitable in the  
303 future across the entirety of their respective regions if those species are not given the opportunity to adapt.  
304 Depending on the Global Circulation model and the scenario, future projections still identified areas with  
305 suboptimal climatic conditions. In Reunion Island, the higher suitability found at ca. 20km west from the  
306 current distribution was presumably driven by an increase in precipitation. *Phelsuma inexpectata* is mostly  
307 present where precipitation is the lowest (< 500mm during the wet season, Fig., S10). The identified area  
308 coincides with the region with the driest conditions in Reunion Island in the future, according to these GCMs  
309 (Fig. S1). In all model sets, the MIROC5 GCM showed a higher—but suboptimal—climate suitability  
310 around the southern coast of the island, with the highest suitability along a band following the upper lands.  
311 This prediction is likely driven by the increase in overall temperature, along with reduced precipitation. The  
312 species lives under the hottest and driest conditions of the island, which fits the thermal requirements of the  
313 species for reproduction in captivity (28°C; McKeown, 1993). However, we believe this GCM is  
314 questionable because (1) the reduction in precipitation does not reflect the possible global increase in cyclone  
315 risk, and (2) the MESS analysis and response curves suggest an overestimation of the suitability scores. Note  
316 that this scenario (i.e. RCP 8.5)—which was the least pessimistic for *P. inexpectata*—is of interest to explore  
317 the widest range of possibilities in the future, but is considered unlikely (Hausfather & Peters, 2020).

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

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

337

#### 338 *Sources of uncertainty*

339 The largest source of uncertainty was related to the GCM for *P. inexpectata*, and to the background extend  
340 for *M. aurantiaca*. We followed a protocol that attempted to mitigate most sources of uncertainty,  
341 corresponding to the acceptable standards defined in Araújo *et al.* (2019). The long term, extensive and  
342 repeated efforts dedicated to species sampling enabled to define the current distributions of both species with  
343 high accuracy. Uncertainty map showed a high level of agreement between model replicates (i.e. modelling  
344 techniques, cross-validation runs and pseudo-absence runs; Fig. S17, S18).

345 In absence of information regarding the dispersal capacity of both species, we used two background  
346 corresponding to past dispersal hypotheses. The background covering the whole respective islands seems the  
347 most appropriate when assuming that only the sea could represent a dispersal barrier and that species could  
348 have dispersed throughout the whole island with regard to past climate and forest cover (Crottini *et al.* 2019),  
349 as assumed in Fieldsend *et al.* (2021). This might be the case for both species, especially *P. inexpectata* since  
350 the island is smaller and mostly occupied by a closely related species (*P. borbonica*; Dubos *et al.* 2021a). The  
351 restricted background corresponds to a hypothesis where *M. aurantiaca* dispersal is limited by current forest

352 cover, and where *P. inexpectata* is limited to the driest part of Reunion Island. This procedure enabled to  
353 encompass the widest range of possibilities with respect to two extreme hypotheses.

354 We included the 19 bioclimatic variables for the selection process, which is not recommended in most cases.  
355 However, we reduced the number of variables by removing the intercorrelated ones, and then selected the  
356 most biologically meaningful variables. We used the finest resolution available for climate data (i.e. 30 arc  
357 sec) which seems sufficient to discriminate suitable to unsuitable areas at the scale of Reunion Island and  
358 Madagascar. The inclusion of high-resolution land use variables enabled to improve the realism of both  
359 distributions and provides specific guidelines for conservation applications. In addition, we found a causal  
360 interpretation for the selected variables, which supports the biological significance of our models (Fourcade  
361 et al. 2018; Dubos et al. 2021b). An important limitation is that we did not use scenarios of future land use.  
362 This may lead to an overestimation of the available habitat in Madagascar, since the country is under  
363 important rates of deforestation (Veilledent et al., 2018). In Reunion Island, most of the natural habitats is  
364 incorporated in private properties or public gardens and in steep zones with limited access for agricultural  
365 practices. We believe that the apparent stability in agricultural areas would maintain the applicability of our  
366 results in the future. The inclusion of a range of different greenhouse-gas emission scenarios and GCMs  
367 showed an important uncertainty in the future suitability for *P. inexpectata*. However, this uncertainty is  
368 mostly related to one GCM (i.e. MIROC5), which we assume to be doubtful. The remaining ones  
369 consistently identified the most suitable area by 2070. Uncertainty related to model design was mitigated by  
370 the limitation of model complexity (with the ESM approach and the post-filtering technique), the removal of  
371 collinearity and the testing of a range of input parameters (number of pseudo-absences sets and cross-  
372 validation subsets). Model performance was assessed with random partitions for *M. aurantiaca*, while spatial  
373 partitions are recommended. However, we argued that this methods is not appropriate for highly localised  
374 species due to strong imbalance between spatial blocks. We used multiple evaluation metrics, including  
375 discrimination (AUC and TSS) and reliability (i.e. calibration; Boyce index) metrics, all showing a high  
376 performance overall. We did not account for species dispersal ability, because the purpose was not to predict  
377 potential shifts, but to assess how suitable will be the climate in the future in order to identify candidate sites

378 for restoration and translocation. Both species have low dispersal ability and their habitat is highly  
379 fragmented. Therefore, the potential for distributional shifts may be strongly limited and future projections  
380 must not be interpreted as the future distributions of our study species. An important limitation may be the  
381 absence of empirical knowledge on species thermal tolerances or other features of their climatic niche,  
382 adaptability and plasticity, which prevents us from determining whether our future projections  
383 underestimated the environmental suitability. Similarly, the extent of the species' fundamental niche is  
384 unknown, and differs from the realised niche as a result of competition, habitat loss and environmental  
385 history, which may particularly important in endemic narrow-ranging species.

386

### 387 *A glimmer of hope*

388 Despite the predicted low suitability in climate conditions, it is possible that species persist under changing  
389 conditions through adaptation or plasticity (Chevin *et al.*, 2010; Hoffmann & Sgró, 2011). This hypothesis is  
390 supported by the persistence of two introduced populations of *P. inexpectata* away from their current range in  
391 suboptimal environments (Fig. 2). Their persistence may result either from physiological or behavioural  
392 adaptation while benefiting from a combination of urban island effect and access to microclimate refuges in  
393 anthropogenic structures, as it is the case for *Phelsuma grandis* in Florida (Fieldsend *et al.*, under review). It  
394 is also frequent that the current distribution of a given species represents only a fragment of its climatic niche  
395 (e.g., Guisan *et al.*, 2014). For instance, experimental design on *M. aurantiaca* showed no expression of a  
396 thermal stress during periods of extreme heat (Edmonds *et al.*, 2015). Therefore, predictions of climate  
397 suitability may underestimate the bounds of our model species niches. Further studies are needed to better  
398 characterise their climatic niche, and explore potential adaptive and plastic responses to changing conditions  
399 in these species and, more generally, in other threatened narrow-ranging species. Meanwhile, we encourage  
400 practitioners to implement conservation measures to grant those species a chance to adapt and persist.  
401 Nevertheless, the rate of climate change is generally faster than that of animal adaptive responses (Radchuk  
402 *et al.*, 2019), which stresses the need for urgent actions. In the tropics, extinction risks may be greatly

403 reduced with the development of land conservation programs provided climate change is mitigated by inter-  
404 governmental actions (Hannah et al., 2020).

405

#### 406 *Conservation application*

407 In Reunion Island, we identified two potential areas suitable for habitat restoration of *Phelsuma inexpectata*  
408 around the south-western coast and along a mid-altitude band. Despite climate conditions are predicted to be  
409 suboptimal, we believe these might represent the best options to ensure the long-term persistence of the  
410 species. Habitat restoration should be focussed on natural habitats invaded by non-native plants and in  
411 urbanised areas. Habitat restoration will consist in promoting the spread of native species (*Pandanus utilis*,  
412 *Latania lontaroides*, *Scaevola taccada* and *Psiadia retusa*) for which the species depends on (Bour, 1995).  
413 Finally, natural colonisation of newly suitable environments will be likely impossible for the species due to  
414 its poor dispersal ability and the high level of habitat fragmentation. We therefore encourage the design of  
415 translocation programs in management schemes.

416 In Madagascar, the area with the highest future climate suitability is located at the south of the current  
417 distribution, along the eastern rainforest corridor between the current distribution area and the north-west of  
418 the Vatovavy-Fitovinany region. The forest cover within the distribution range of *M. aurantiaca* has  
419 experienced a continued decline, regardless of the conservation status of the inhabited area (Piludu *et al.*,  
420 2015; Vieilledent *et al.*, 2018). We recommend to reinforce the level of protection and to improve  
421 governance and management of the Mangabe (Moramanga region) and the Marolambo (Vatovavy-  
422 Fitovinany region) reserves. This can be achieved by promoting the development of alternative economic  
423 solutions through the development of valuable and sustainable activities that mitigate the rate of conversion  
424 of natural areas, the long-term management of soil fertility, and by considering the development of  
425 ecotourism. This species was included into a program that enabled to develop amphibian husbandry  
426 capacities in Madagascar, and that succeeded to establish captive bred colonies for this species  
427 (Rakotonanahary et al. 2017). Efforts of captive husbandry should be maintained (and possibly expanded to

428 other species) and we encourage the design of translocation programs accounting for both local habitat  
429 characteristics and future climate suitability. Further study of biotic interaction between *M. aurantiaca* and  
430 other amphibians is needed to assess the consequences of its introduction.

431

432 *Are all endangered narrow-ranging species doomed to extinction?*

433 Narrow-ranging species usually live under very specific environmental conditions and are the most  
434 vulnerable to climate change (Botts *et al.*, 2013). Not only they are more prone to face distribution shifts and  
435 range contractions, but they might also disappear due to the strong alteration of their climatic envelope  
436 throughout their entire region. This may be the case for most narrow-ranging species with a specialised niche  
437 in regions with heterogeneous climates and high levels of endemism such as Madagascar but also Central  
438 America, South East Asia, tropical islands and more generally in tropical rainforests and mountains (Kier *et al.*,  
439 2009). In such regions, small shifts in climatic conditions may induce important changes in local  
440 environmental suitability for endemic—often specialised—species (e.g., Raxworthy *et al.*, 2008). The risk is  
441 greater in tropical regions where species live closer to the upper bound of their thermal tolerance (Tewksbury  
442 *et al.*, 2008; Şekercioğlu *et al.*, 2012; Dubos *et al.*, 2019). Species that are already under threats are at the  
443 greatest risk because of a large array of synergistic effects (Şekercioğlu *et al.*, 2012). This might be the case  
444 for our two model species, which are threatened by habitat destruction and invasive species (Dubos, 2013;  
445 Piludu *et al.*, 2015). Among the few Critically Endangered species for which the impact of climate has been  
446 investigated, most predict severe reductions in the climate suitability (e.g., Alamgir *et al.*, 2015; Zhang *et al.*,  
447 2020), with the suitable range of the giant salamander *Andrias davidianus* predicted to decrease by more than  
448 two thirds by 2050 (Zhang *et al.*, 2020). This species has faced a number of threats and climate change may  
449 be leading to imminent extinction despite a larger distribution range. Despite recent efforts developed for the  
450 monitoring of rare species in the tropics (e.g., Dubos *et al.*, 2020), there is still an important lack of species  
451 occurrence data in these regions (Feeley & Silman, 2011). With the newly available high-resolution climate  
452 and land use data, the spectre of eligible species for SDMs has enlarged. We urge filling this data void by  
453 starting to assess the effect of climate change for narrow-ranging species at broader taxonomic scales,



454 promote field investigations, assess species thermal requirements, and develop proactive conservation  
455 actions.

456

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460

#### 461 **Conflict of Interest Statement**

462 The authors declare no conflict of interests.

463

#### 464 **Data availability statement**

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

466

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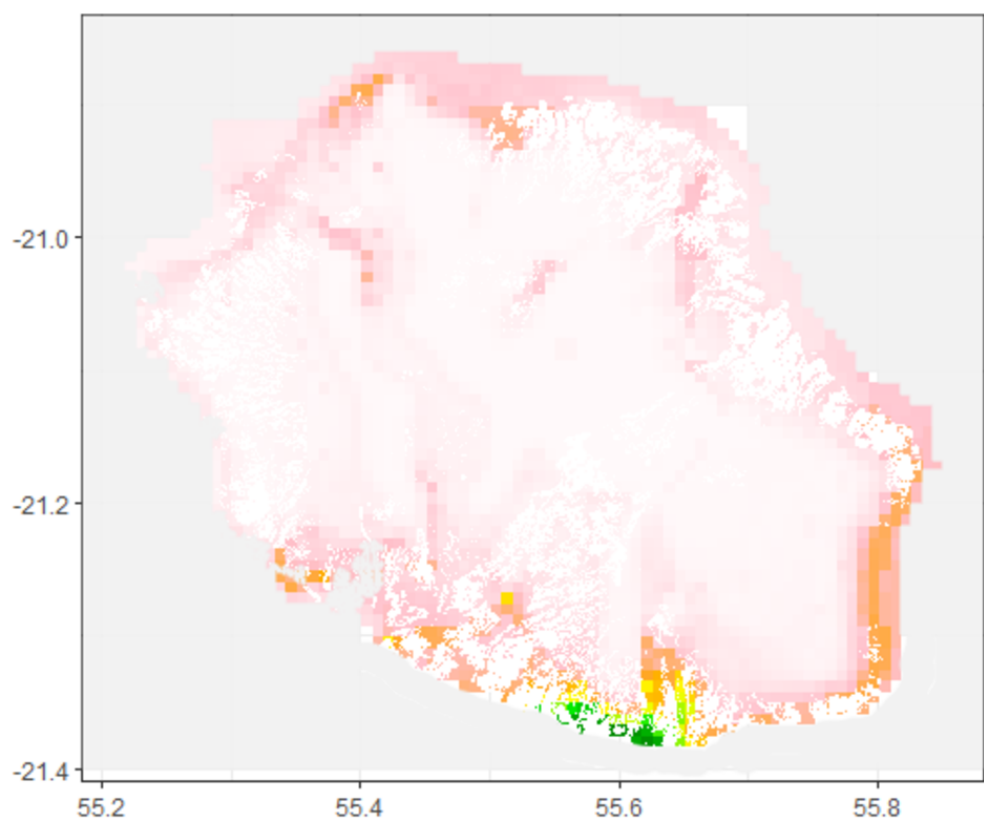
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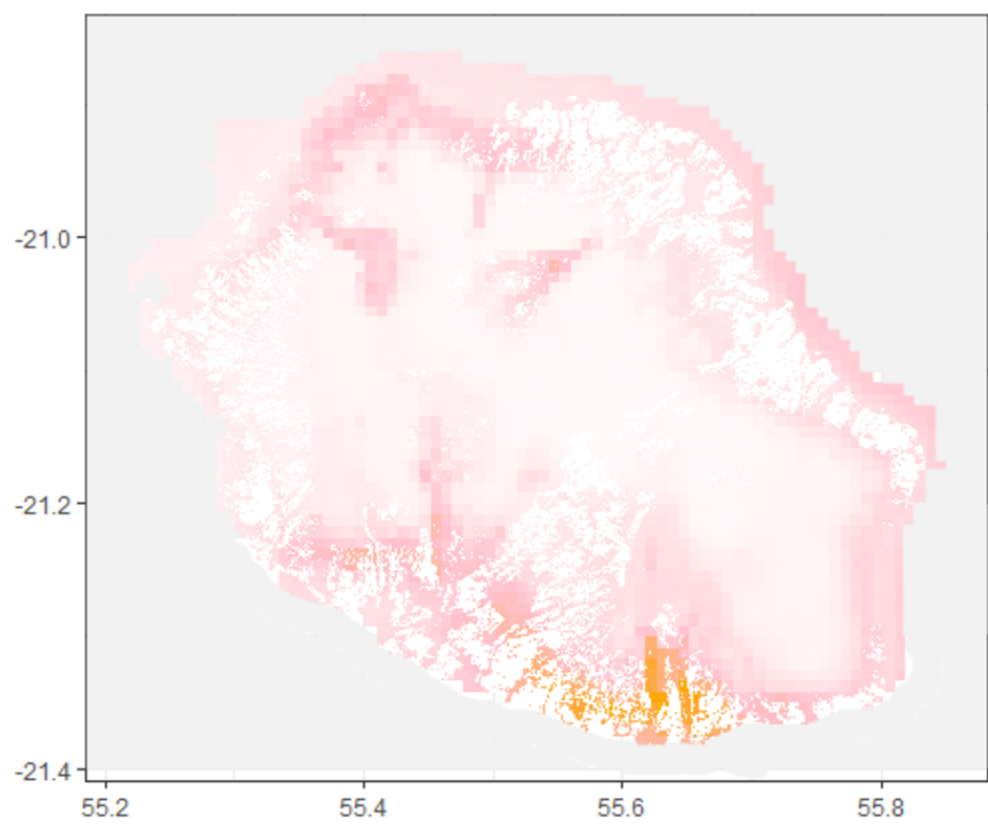
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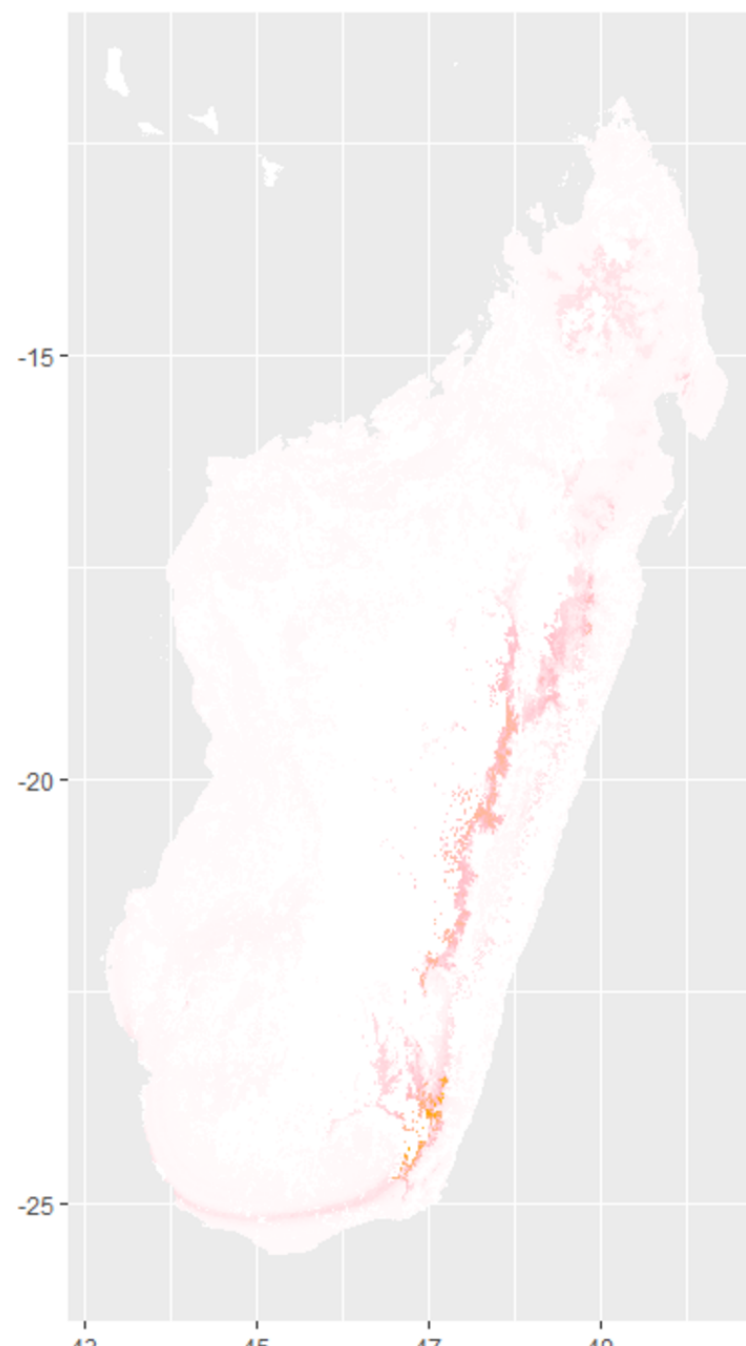
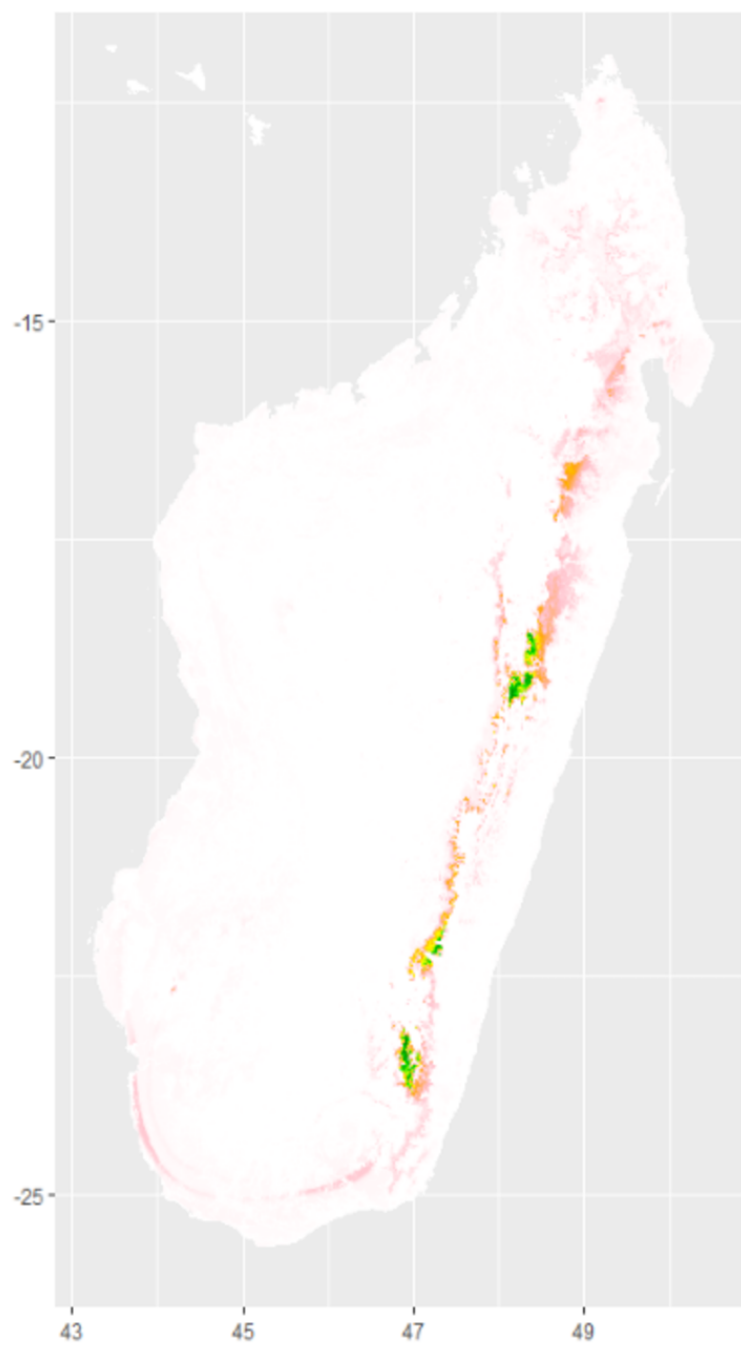
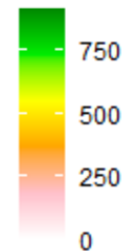
Current



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Suitability



Suitability

