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1 **Here be dragons: important spatial uncertainty driven by climate data in**
2 **forecasted distribution of an endangered insular reptile**

3

4 Heading title: High uncertainty driven by climate data in SDMs

5

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21 **Abstract**

22 The effect of future climate change is poorly studied in the tropics, especially in mountainous areas, yet
23 species living in these environments are predicted to be strongly affected. Newly available high-resolution
24 environmental data and statistical methods enable the development of forecasting models, but the uncertainty
25 related to climate models can be strong, which can lead to ineffective conservation actions. Predictive studies
26 aimed at providing conservation guidelines often account for a range of future climate predictions (climate
27 scenarios and global circulation models). However, very few studies consider potential differences related to
28 the source of climate data and/or do not account for spatial information (overlap) in uncertainty assessments.
29 We modelled the environmental suitability for *Phelsuma borbonica*, an endangered reptile native to Reunion
30 Island. Using two metrics of species range change (difference in overall suitability and spatial overlap), we
31 quantified the uncertainty related to the modelling technique ($n = 10$), sample bias correction, climate change
32 scenario, global circulation models (GCM) and data source (CHELSA *versus* Worldclim). Uncertainty was
33 mainly driven by GCMs when considering overall suitability, while for spatial overlap the uncertainty related
34 to data source became more important than that of GCMs. The uncertainty driven by sample bias correction
35 and variable selection was much higher when assessed based on spatial overlap. The modelling technique
36 was a strong driver of uncertainty in both cases. We provide a consensus ensemble prediction map of the
37 environmental suitability of *P. borbonica* to identify the areas predicted to be the most suitable in the future
38 with the highest certainty. Predictive studies aimed at identifying priority areas for conservation in the face
39 of climate change need to account for a wide panel of modelling techniques, GCMs and data source. We
40 recommend the use of multiple approaches, including spatial overlap, when assessing uncertainty in species
41 distribution models.

42

43 **Keywords:** Climate data source, CHELSA, *Phelsuma borbonica*, Reunion Island, Schoener's D overlap,
44 Species distribution models, Uncertainty, Worldclim

45

46

47 **Introduction**

48 Predictive studies of climate change effects on biodiversity are poorly studied in the tropics, especially for
49 rare and endangered species (Pearson et al., 2014). Yet, tropical species are predicted to be more severely
50 impacted by climate change than temperate species because they live closer to their thermal limit
51 (Tewksbury, Huey, & Deutsch, 2008; Jiguet et al., 2010; Dubos et al., 2019). This is particularly true for
52 species with a narrow distribution, a narrow niche, or living in highly heterogeneous environments such as
53 mountainous areas (Raxworthy et al., 2008; Freeman & Class Freeman, 2014; Platts et al., 2014; Tang et al.,
54 2018; Ahmadi et al., 2019; Cordier et al., 2020; Manes et al., 2021). Modelling their responses to climate
55 change (e.g. change in distributional extent) is particularly challenging because species-specific data is often
56 scarce. The most common approach used to assess species response to climate variation is Species
57 Distribution Models (SDMs). These models can be used to forecast species responses to climate change
58 using simulated future climate data. This information is useful in informing conservation management in the
59 face of climate change. Specifically, SDMs enable one to identify priority areas for protection (Leroy et al.,
60 2014; Lannuzel et al., 2021), and suitable conditions for habitat restoration and species (re)introductions and
61 translocations (Minteer & Collins, 2010; Wilson, Roberts, & Reid, 2011; Adhikari, Barik, & Upadhaya,
62 2012; Draper, Marques, & Iriando, 2019; Bellis et al., 2020; Butt et al., 2020; Westwood et al., 2020; Zhong
63 et al., 2021). The recent availability of high-resolution environmental data help to fill the existing gap of
64 knowledge in highly heterogeneous environments such as mountainous islands (e.g., Dubos et al., 2021;
65 Lannuzel et al., 2021).

66 A range of climate data is available for SDMs, including those from sources which are used to predict future
67 change (e.g., Worldclim and CHELSA; Fick & Hijmans, 2017; Karger et al., 2017). Future climate
68 predictions include multiple emission scenarios (Shared Socio-economic Pathways, SPP; also known as
69 Representative Concentration Pathways, RCP) and global circulation models (GCMs). Both emission
70 scenarios and GCMs can produce highly heterogeneous results in terms of predicted future distributions
71 (Buisson et al., 2010; Baker et al., 2016). Most predictive studies included a range of scenarios and GCMs,
72 but very few have considered potential uncertainties related to the source of climate data itself (Baker et al.,
73 2016; Morales-Barbero & Vega-Álvarez, 2019; Datta, Schweiger, & Kühn, 2020; Ocon, 2020; Dubos, et al.,
74 2021). This can induce lead to misidentification of suitable environments, which can affect conservation
75 prioritisation (Kujala et al., 2013; Baker et al., 2016; Muscatello, Elith, & Kujala, 2020) and subsequently

76 ineffective conservation actions (Converse & Sipe, 2021). Despite recent studies emphasising the need to
77 account for multiple climate data sources (Morales-Barbero & Vega-Álvarez, 2019; Datta, Schweiger, &
78 Kühn, 2020; Ocon, 2020), most studies aimed at providing conservation guidelines do not assess the
79 uncertainty related to bioclimatic input data.

80 Uncertainty assessments in SDMs can be made by comparing a range of modalities in model settings or data.
81 These comparisons can be based on differences in performance metrics such as the area under the receiving
82 operating characteristic curve (AUC) or the true skill statistic (TSS; Tessarolo et al., 2021). However, such
83 performance comparisons require independent data to be reliable. In absence of independent data,
84 uncertainty can be assessed based on differences in predicted species range changes between model input
85 parameters, climate scenarios or climate data (e.g., Kujala et al., 2013; Baker et al., 2016; Muscatello, Elith,
86 & Kujala, 2020). Species range change can be estimated using the difference between current and future
87 summed suitability. This approach enables the identification of the parameter that contribute most to
88 uncertainty in the overall suitability across a region. However, it ignores the spatial component in suitability
89 differences. For instance, a difference in shift in distribution with no change in overall suitability would
90 remain undetected. One possible approach to assess each source of uncertainty while accounting for spatial
91 information is the use of overlap metrics such as Pearson's coefficient or similarity indices (Muscatello,
92 Elith, & Kujala, 2020; Dubos, Montfort, et al., 2021). To date, no study has tested for potential differences in
93 uncertainty assessments between these approaches.

94 For conservation applications, it is possible to account for uncertainty when providing guidelines from SDM
95 outputs. An accepted approach is to identify the areas where models are the most in agreement, and consists
96 in discounting the final mean projections with intermodel variability (in other terms: mean – standard
97 deviation; Kujala et al., 2013). This method is highly relevant for conservation purposes since it provides a
98 spatially explicit map of the most consistently identified suitable areas but prevents from disentangling the
99 sources of uncertainty.

100 In our study we generate a set of SDMs for the two subspecies of the Reunion Island day gecko, *Phelsuma*
101 *borbonica borbonica* and *P. borbonica mater* (subsequently referred to as *P. borbonica*), quantify the sources
102 of uncertainty related to the methods and the data, and test potential differences in uncertainty assessments
103 between two different approaches. Reunion Island is located in the western Indian Ocean and has faced a
104 number of alterations over the last century related to agricultural practices (mostly sugarcane cultivation) and

105 invasive species (Strasberg et al., 2005; Dubos, 2013; Fenouillas et al., 2021; Irl et al., 2021). Its
106 herpetofauna has already been strongly modified after multiple local extinctions events and the arrival of
107 allochthonous species (Cheke, 1987; Cheke & Hume, 2010; Sanchez & Probst, 2016). Today only two native
108 reptile species remain, the indigeneous *P. borbonica* and the endemic *P. inexpectata*, while five reptile
109 species having faced extinction in the recent past (Cheke & Hume, 2010). Climate change can facilitate
110 biological invasions and alters habitat suitability for locally adapted species (Mainka & Howard, 2010;
111 Gillard et al., 2017). To date, very few studies have focused on the potential effects of climate change on the
112 future of Reunion Island's biodiversity (but see Legrand et al., 2016). Dubos et al. (2021) predicted the
113 potential extinction of the endemic Reunion Island reptile, *P. inexpectata*, driven by climate change.
114 The Reunion Island day gecko, *P. borbonica* is classified nationally as Endangered due to its narrow
115 distribution (Sanchez 2021). With high rates of land use change in Reunion Island, fire hazards and high
116 pressure related to introduced species (Macdonald & Cedex, 1991; Strasberg et al., 2005; Lagabrielle et al.,
117 2009; Sanchez & Probst, 2016), many populations are isolated and are exposed to local extinctions. This
118 highlights the urgent need to identify priority areas for habitat conservation and restoration.
119 We assess for the first time the climatic niche of *P. borbonica* and the potential effects of climate change on
120 its future distribution. We quantify the uncertainty in species range change (SRC) driven by the statistical
121 methods (modelling technique, sample bias correction, and variable selection) and climate data (RCPs,
122 GCMs and climate data source) using two approaches (difference in summed suitability and spatial overlap)
123 in the predicted future distribution of *P. borbonica*. We then provide a consensus map accounting for
124 uncertainty to guide conservation actions.

125

126 **Methods**

127 *Occurrence data*

128 *Phelsuma borbonica* is distributed in the forested areas of the eastern, southern, and northern parts of
129 Reunion Island, from sea level to 2800 m (Meier, 1995; Sanchez & Probst, 2017). Most observations are
130 made at intermediate altitudes, near trails, on artificial structures or at the edge of pristine or disturbed
131 forested areas (Augros et al., 2017). We obtained 5922 occurrence records (2648 after removing
132 redundancies) from the Système d'information de l'inventaire du patrimoine naturel (SINP ; *Système*
133 *d'information de l'inventaire du patrimoine naturel de La Réunion*. Accessed on 03/06/2021 from

134 www.borbonica.re) provided by the Direction de l'Environnement, de l'Aménagement et du Logement
135 (DEAL) and the Parc National de la Réunion (PNRun) and some additional unpublished occurrence data
136 from various sources (Biotope Océan Indien, Cynorkis, Eco-Med Océan Indien, Nature Océan Indien). These
137 observations were compiled from incidental data and dedicated surveys carried out between 1990 and 2017
138 (Augros et al., 2017 ; Sanchez & Probst, 2017). We removed 171 observations corresponding to single
139 observations with no evidence of persistence (presumably corresponding to individuals transported out of
140 their native range; Deso, 2001), translocated individuals, inaccurate coordinates, or indices of past
141 occurrence (e.g., subfossil clutches). To limit spatial bias, we resampled one occurrence per occupied pixel at
142 the resolution of the environmental data (30 arc seconds, approximately 1000m). The final sample included
143 379 points when resampled either from Worldclim or CHELSA.

144

145 *Climate data*

146 We used 19 bioclimatic variables for 30 arc sec (approximately 900m) resolution for the current climate data,
147 and also for the 2070 projections from CHELSA (Karger et al., 2017) and from Worldclim global climate
148 data (Fick & Hijmans, 2017). We removed isothermality (bio2) from the analysis because of a lack of
149 variability in Reunion Island. We decided to include all the remaining variables because both temperature
150 and precipitation are related to the species' biology, including those representing indices of variability. We
151 used three Global Circulation Models (GCMs; i.e., BCC-CSM1-1, MIROC5 and HadGEM2-AO) and two
152 greenhouse gas emission scenarios (the most optimistic RCP26 and the most pessimistic RCP85; Fig. S1,
153 S2).

154

155 *Land use data*

156 We accounted for the habitat requirements of our model species by applying a filter to model projections. We
157 obtained very high-resolution land cover categories (Urban, agricultural, natural, water) at 1.5m resolution
158 (resampled at 100m for computing purposes) derived from remote sensing (Dupuy, Gaetano, & Le Mézo,
159 2020). We removed agricultural and urbanised areas, because *P. borbonica* is only found in natural and semi

160 natural habitats, which enabled to maximise model parsimony while remaining biologically realistic and
161 relevant for conservation applications.

162

163 *Distribution modelling*

164 We modelled and projected species distributions in R (version 4.0.3; R Core Team, 2020) with the Biomod2
165 R package (Thuiller et al., 2009), using 10 modelling techniques: generalised linear and generalised additive
166 models (GLM and GAM; Guisan, Edwards, & Hastie, 2002), classification tree analysis (CTA; Prasad,
167 Iverson, & Liaw, 2006), artificial neural network (ANN; Manel, Dias, & Ormerod, 1999), surface range
168 envelop (SRE, also known as BIOCLIM; Booth et al., 2014), flexible discriminant analysis (FDA; Manel,
169 Dias, & Ormerod, 1999), random forest (RF; Prasad, Iverson, & Liaw, 2006), multiple adaptive regression
170 splines (MARS; Leathwick et al., 2005), generalised boosting model (GBM; Elith, Leathwick, & Hastie,
171 2008) and maximum entropy (MaxEnt; Phillips & Schapire, 2006).

172 *Pseudo-absence selection and sample bias correction*—We generated five different sets of 1000 pseudo-
173 absences, following Bellard et al. (2016). To quantify the uncertainty related to sample bias correction, we
174 ran both uncorrected and corrected models. In addition, sample bias correction does not always improve the
175 realism of model projections (Dubos, Préau, et al., 2021). In absence of standardised data, it is not possible to
176 reliably assess the effect of sample bias correction with classic performance metrics (Dubos, Préau, et al.,
177 2021). Hence, we assessed the effect of correction by comparing uncorrected and corrected models, and
178 measured the extent to which correction affected predictions relative to the variability between model
179 replicates. For uncorrected models, we ran a first set using a random pseudo-absence selection (Wisz &
180 Guisan, 2009). To account for sample bias, we reperformed all calculations using a weighted random
181 pseudo-absence selection. Following Phillips et al. (2009), we produced five sets of pseudo-absences
182 selected around the presence points to reproduce the spatial bias of the sample. We used a geographic null
183 model generated with the *dismo* R package (Hijmans, 2012) and used it as a probability weight for pseudo-
184 absence selection. Since no independent data were available to assess the effect of sample bias correction, we
185 used the relative overlap index (ROI; Dubos, Préau, et al., 2021) based on Schoener's D overlap. The ROI
186 indicates whether the effect of correction is significant compared to the variability between model runs. It
187 computes (1) the mean overlap between the uncorrected and the corrected predictions (i.e., the absolute

188 effect of correction), and (2) the overlap between every pair of model replicate (between each pseudo-
189 absence and cross validation runs, individually for each modelling technique, i.e. model stochasticity). We
190 computed the ROI as follows:

$$191 \text{ ROI} = \frac{\bar{D}_0 - \bar{D}(p_x, p_y)}{\bar{D}_0}$$

192 Where \bar{D}_0 is the mean overlap between model runs of the corrected group and $\bar{D}(p_x, p_y)$ is the mean
193 overlap between runs of the uncorrected and the corrected models. A value close to 0 represents a perfect
194 match between predictions (i.e. no effect of sample bias correction). A positive value suggests that the effect
195 of sample bias correction was greater than the variability between model replicates. A value close to 1
196 represents a maximal effect of sample bias correction relative to model replicate variability (i.e. strong effect
197 of sample bias correction).

198 For Worldclim and CHELSA individually, we selected one variable per group of inter-correlated variables to
199 avoid collinearity (Pearson's $r > 0.7$, Dormann et al., 2013; See Fig. S3) and assessed the relative importance
200 of each variable kept with 10 permutations per model replicate (total = 500 for each data source). The
201 variables included in the final models were those with a relative importance > 0.2 across at least 50% of
202 model runs (Fig. S4). To determine whether variation in future predictions was driven by climate data *per se*
203 or by differences in the selected variables, we swapped the selected variables between baseline climates and
204 repeated the whole process.

205 *Model evaluation*—We spatially partitioned the data into five folds, with three runs of block cross-validation
206 (i.e., k-fold cross-validation; Fig. S5). We assessed model performance using the Boyce index, assumed to be
207 the best evaluation metric with pseudo-absence data (Leroy et al., 2018). A value of 1 means the models
208 reliably predicted the presence points while a value of 0 means that models did not perform better than
209 random. For ensemble models, we excluded models for which the Boyce index was below 0.5 (Gillard et al.,
210 2017). We verified that models were well informed for predictions on novel (future) data using clamping
211 masks.

212 *Uncertainty analysis*—We assessed the uncertainty in species range change (SRC) related to the modelling
213 technique, sample bias correction, climate scenarios, GCMs, climate data source and variable selection. We

214 quantified SRC following two approaches. Firstly, we computed SRC as the difference between the summed
215 suitability scores of the climate data source and the future predictions. Then we used linear models (LM,
216 assuming Gaussian errors), with SRC as a response variable, and the aforementioned sources of uncertainty
217 as explanatory variables, following Baker et al. (2016). We then assessed the proportion of deviance
218 explained by each source of uncertainty f as follows:

$$219 \quad Pf = \frac{Df - D0}{D1}$$

220 where, Pf = proportion of deviance explained by factor f , $D1$ = deviance of full model, Df = deviance of full
221 model minus factor f , and $D0$ = deviance of null model.

222 Secondly, we quantified SRC using an overlap metric. We computed the Schoener's D overlap between
223 baseline projections and future projections using the ENMTools R package (Warren, Glor, & Turelli, 2010).
224 We repeated the assessment of the proportion of deviance explained by the five aforementioned sources of
225 uncertainty using beta-regression GLM instead of LM, since overlap measures range continuously between 0
226 and 1 (glmmTMB R package; Brooks et al., 2019).

227 In total, we computed 2000 models (10 modelling techniques \times 5 pseudo-absence runs \times 5 block cross-
228 validation runs \times 2 modalities of sample bias correction \times 2 climate data sources \times 2 modalities for variable
229 selection) for the current distribution, and 12000 projections on future climate data (2000 models \times 3 GCMs
230 \times 2 emission scenarios).

231 *Conservation application accounting for uncertainty*—To provide the most certain conservation guidelines,
232 we built a consensus map of the mean predictions across all simulations (of the corrected group and with the
233 original selected variables) after removing poorly performing models, discounting the standard deviation SD
234 (mean – SD; Kujala et al., 2013).

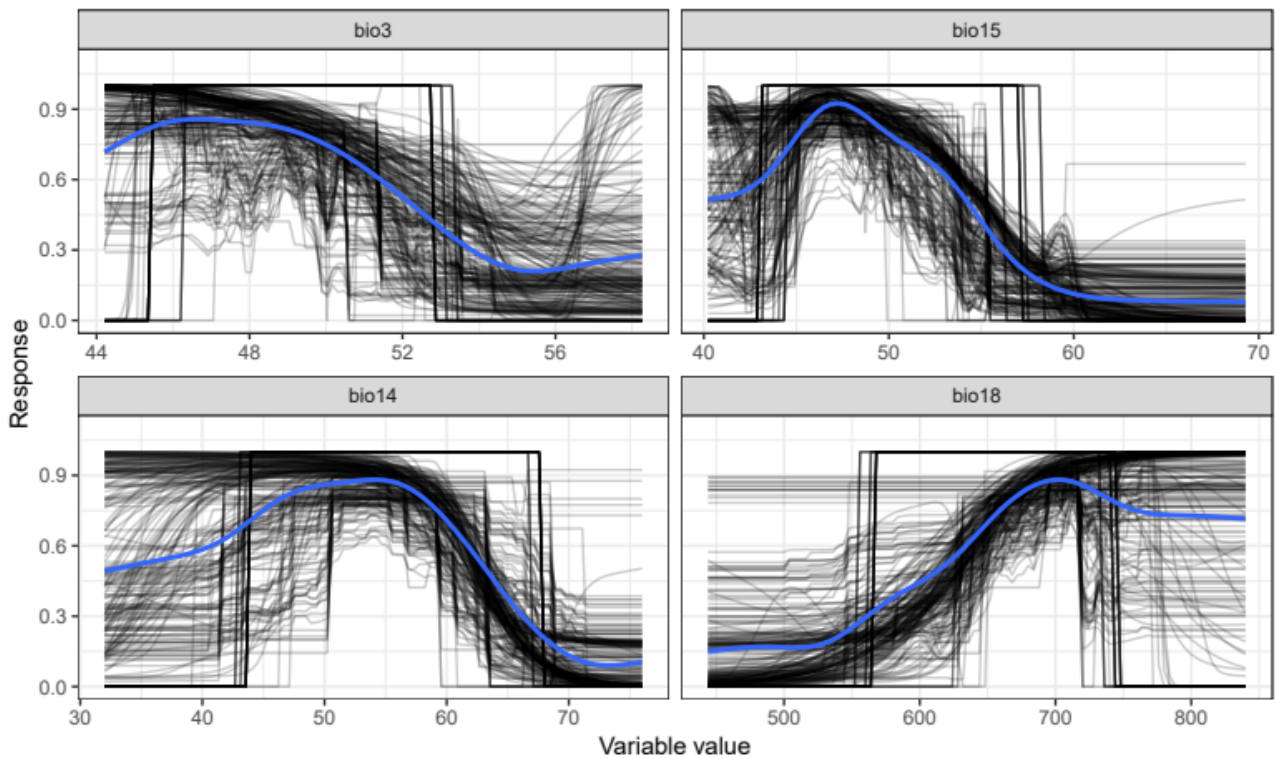
235

236 **Results**

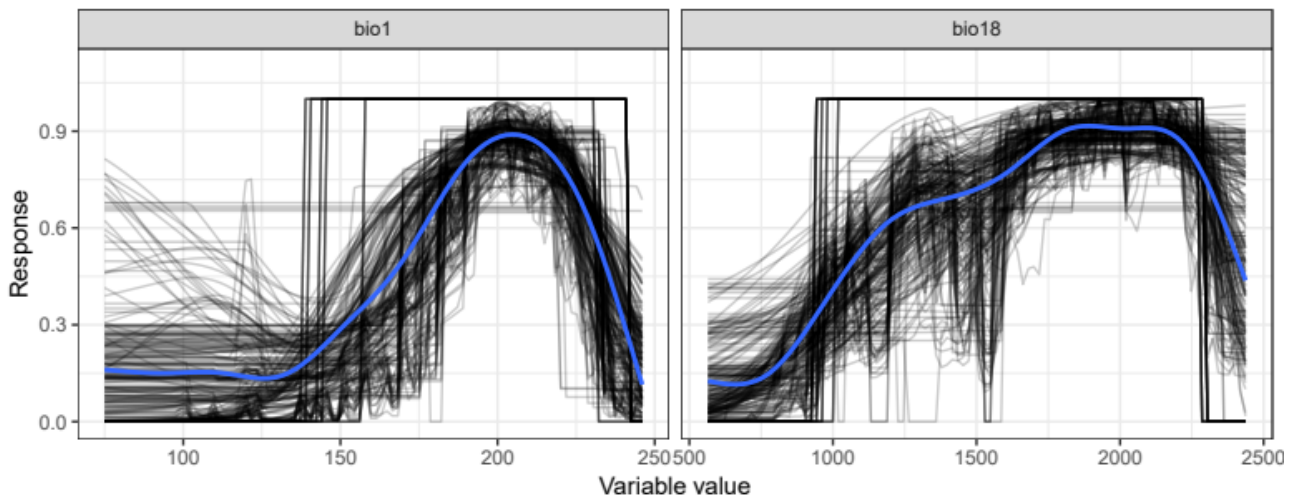
237 *Current distribution*

238 In general, the models did a good job of predicting the presence of *P. borbonica* (median Boyce index
239 (Worldclim) = 0.76; median Boyce index (CHELSA) = 0.77; Fig. S6, S7). A few points, corresponding to

240 isolated populations, fell into areas predicted as moderately suitable. Sample bias correction slightly
 241 increased the predictions of suitable areas, but its effect on projections was low compared to within-model
 242 variation (ROI = 0.006; Fig. S8). With the Worldclim data, the selected variables were isothermality (Bio3),
 243 precipitation of the driest month (Bio14), precipitation seasonality (Bio15) and summer precipitation (Bio18;
 244 Fig. 1, S4). With the CHELSA data, the selected variables were mean annual temperature (Bio1) and summer
 245 precipitation (Bio18; Fig 2, S4).
 246



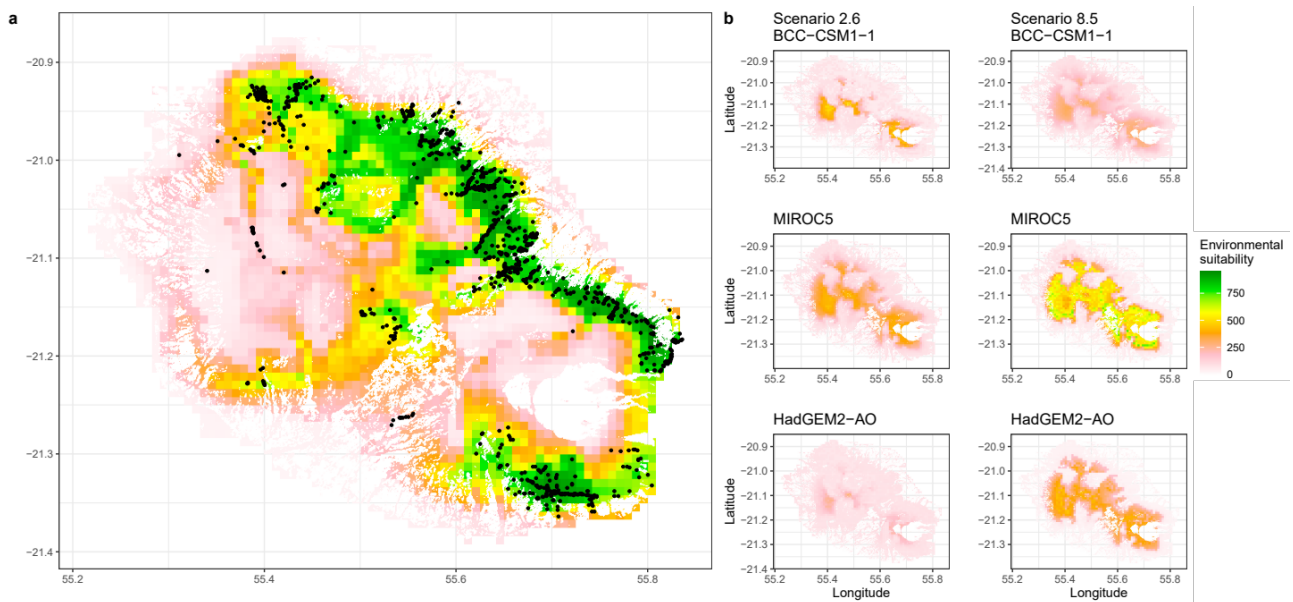
247 Fig. 1 Response of *Phelsuma borbonica* to the selected Worldclim bioclimatic variables. The black lines
 248 represent the individual response curves for each iteration. The blue line represents the smoothed response
 249 across iterations. Bio3: Isothermality; Bio14: Precipitation of driest month (mm); Bio15: Precipitation
 250 seasonality; Bio18: precipitation of warmest quarter (mm).
 251



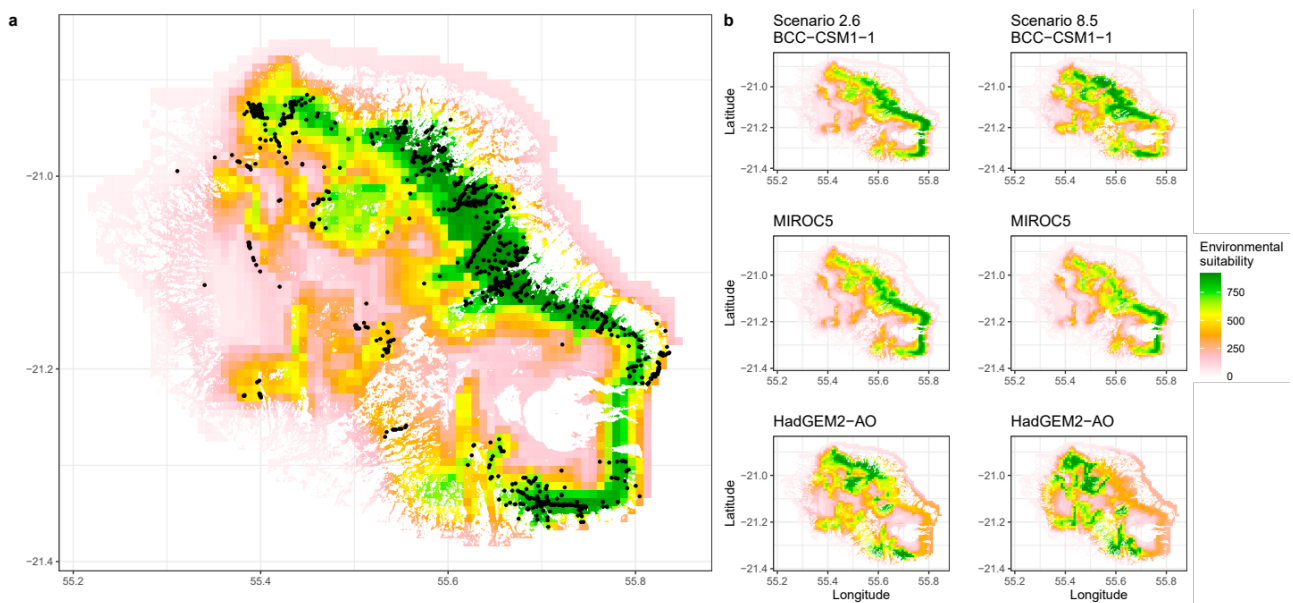
252 Fig. 2 Response of *Phelsuma borbonica* to the selected CHELSA bioclimatic variables. The black lines
 253 represent the individual response curves for each iteration. The blue line represents the smoothed response
 254 across iterations. Bio1: annual mean temperature ($^{\circ}\text{C} \times 10$); Bio18: precipitation of warmest quarter (mm).
 255

256 *Future distribution*

257 Predictions differed strongly between modalities. Predictions derived from Worldclim data indicated a
 258 dramatic decline in climate suitability across the entire island, regardless of the scenario or GCM (Fig. 3).
 259 The best predicted areas would shift upslope, but remain largely unsuitable. When based on CHELSA data,
 260 predictions were more optimistic but highly variable between GCMs (Fig. 4). The ‘BCC-CSM-1-1’ GCM
 261 predicted little effect of climate change, the ‘MIROC5’ GCM indicated a slight decrease in climate
 262 suitability in the north-western part of the current distribution area, while the HadGEM2-AO predicted a
 263 strong decline in the eastern part.



264 Fig. 3 Current (a) and future (b) environmental suitability of *Phelsuma borbonica* in Reunion Island based
 265 on Worldclim climate data.

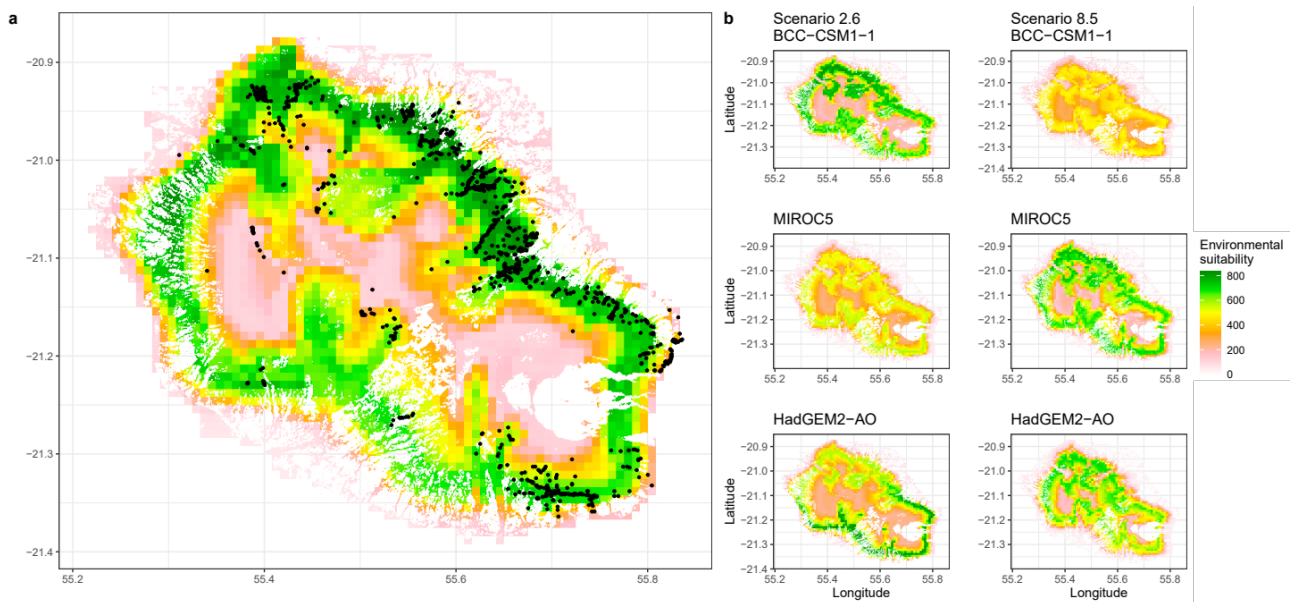


266 Fig. 4 Current (a) and future (b) environmental suitability of *Phelsuma borbonica* in Reunion Island based
 267 on CHELSA climate data.

268

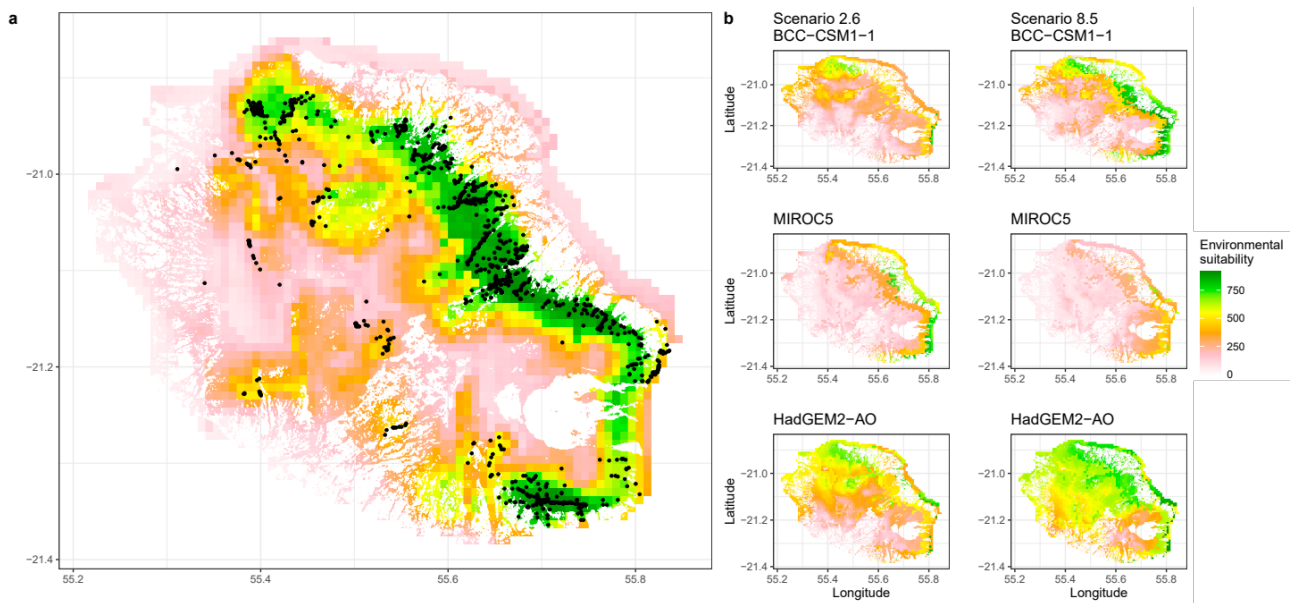
269 *Effect of variable selection*

270 After swapping the selected variables between climate data, the predicted current suitable environments were
 271 extended westwards with Worldclim, but differed little with CHELSA. Projections of future climate
 272 suitability differed greatly after swapping the selected variables for both Worldclim and CHELSA.
 273 Predictions strongly differed between GCMs (Fig. 5, 6).



275 Fig. 5 Current (a) and future (b) environmental suitability of *Phelsuma borbonica* in Reunion Island based
 276 on Worldclim climate data using the selected variables from the CHELSA models.

277



279 Fig. 6 Current (a) and future (b) environmental suitability of *Phelsuma borbonica* in Reunion Island based
 280 on CHELSA climate data using the selected variables from the Worldclim models.

281

282 *Uncertainty analysis*

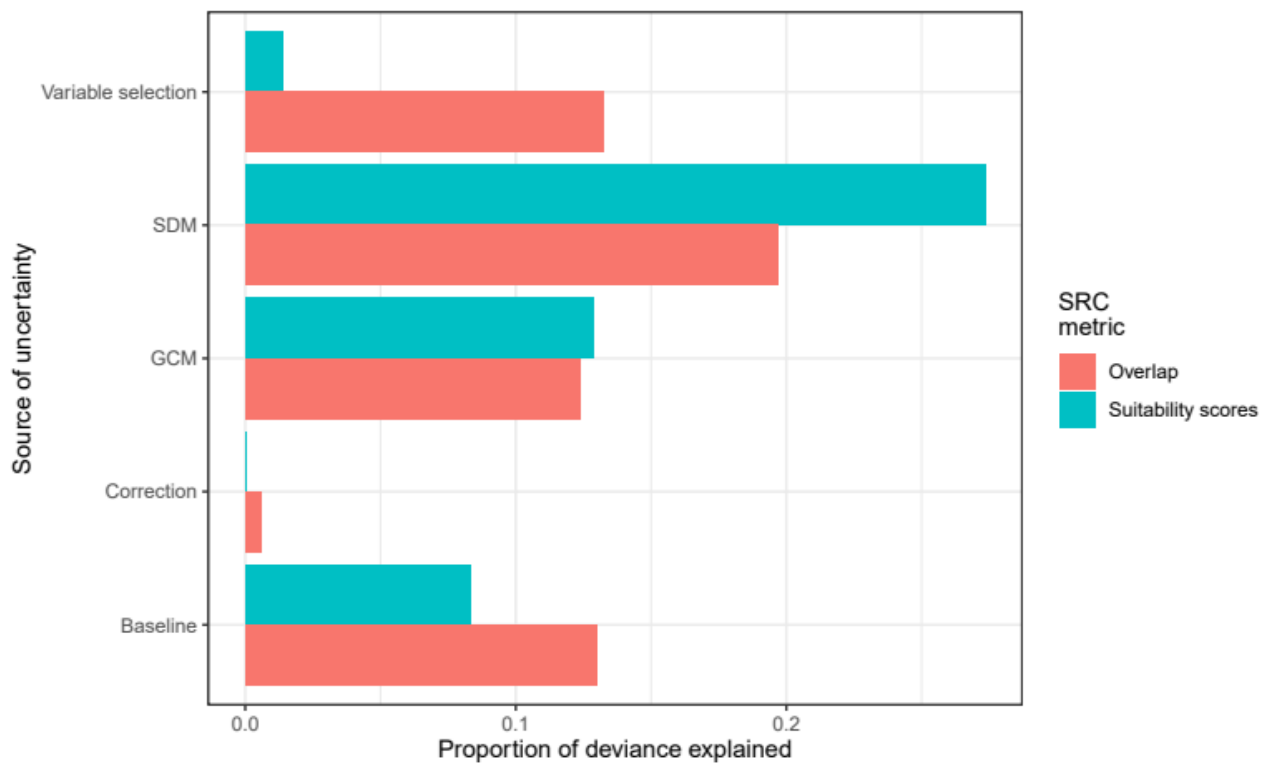
283 The greatest source of uncertainty differed according to the metric of species range change considered (Fig.
284 7). Overall change in suitability scores were most variable between the modelling technique (SDM),
285 followed by the GCM and the climate data source. Uncertainty related to sample bias correction and variable
286 selection were of lower magnitude when considering only suitability scores. Regarding the amount of spatial
287 information shared between current and future predictions (overlap), the highest source of uncertainty was
288 the modelling technique, followed by variable selection and climate data source. The uncertainty related to
289 the GCM was lower than that of climate data source when considering overlaps. Sample bias correction was
290 the lowest source of uncertainty in every case.

291

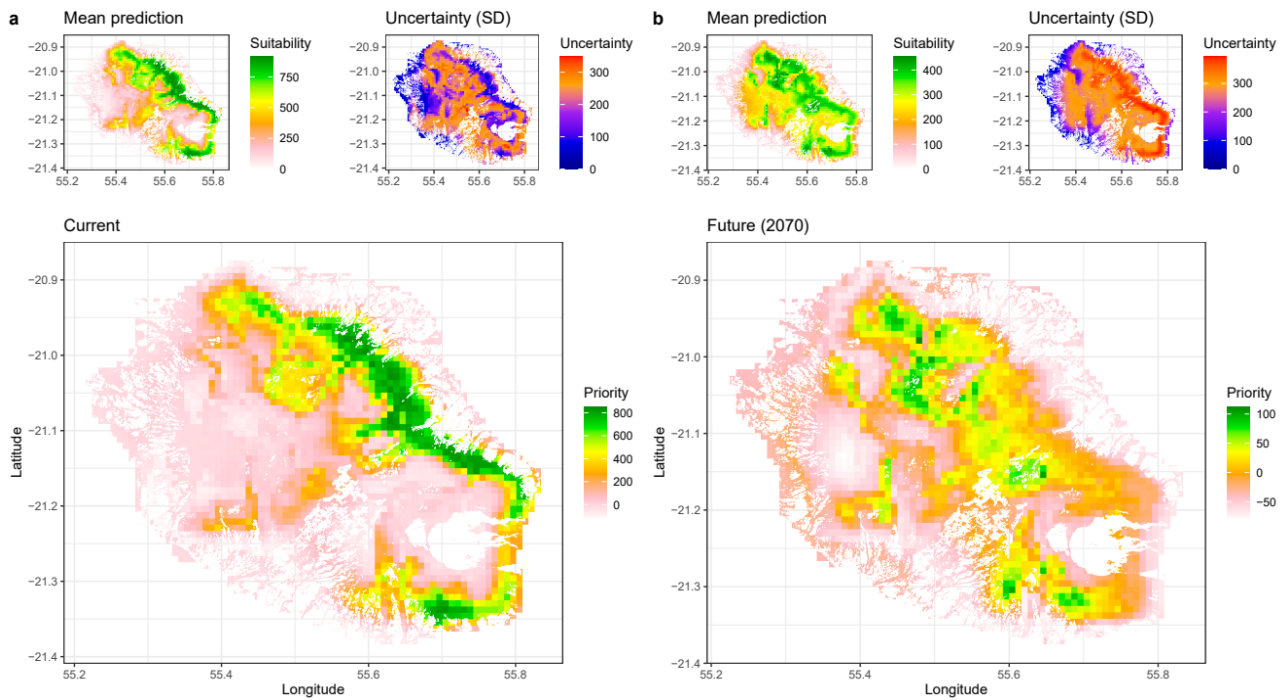
292 *Conservation application*

293 The consensus maps indicate that the climate will become unsuitable at low altitudes, and that the areas with
294 the most consistent suitable conditions will be located at higher altitudes (towards the centre of the island),
295 and eastwards in the future (Fig. 8). These areas are mostly occupied by rainforests (Dupuy et al., 2020),
296 encompassing *la Forêt de Bébour*, *la Plaine des Lianes*, *la Forêt Départementale du Piton Papangue*, *la*
297 *Réserve Naturelle de la Roche Ecrive*, *la Forêt Départemento-domaniale du Textor*, and *la Forêt*
298 *Départemento-domaniale du Volcan Sud*. These are included in the core of the Reunion National Park.
299 Despite this high protection status, most of these forests are occupied by non-native vegetation. The mean
300 prediction maps also indicate that the area currently supporting the best conditions will become largely
301 unsuitable, shifting from a maximum suitability score of 915 under current conditions to 454 by 2070.

302



303 Fig. 7 Proportion of deviance explained by five sources of uncertainty, quantified with two metrics of species
 304 range change (SRC). SDM: modelling technique (species distribution model); GCM: global circulation
 305 model; Correction: sample bias correction (non-random pseudo-absence selection); Baseline: climate data
 306 source (Worldclim versus CHELSA); Overlap: Schoener's D overlap between current and future projections;
 307 Suitability scores: difference between summed suitability scores of current and future predictions.



308 Fig. 8 Consensus maps of current (a) and 2070 (b) priority areas for conservation for *Phelsuma borbonica*,
 309 derived from predicted climate suitability. Current and future predictions (bottom) are the result of mean
 310 projections (top left of each panel) discounted with inter-model variability (top right of each panel).

311

312 Discussion

313 We predicted the future climate suitability of *P. borbonica* while accounting for multiple climate models and
 314 found a strong disagreement between future predictions derived from Worldclim and CHELSA climate data.
 315 The uncertainty related to both methodological aspects and input climate data depended on the approach
 316 used to quantify species range change (summed suitability *versus* overlap). Mean projections indicate an
 317 important decline in climate suitability by 2070.

318

319 Drivers of species distribution

320 The effect of temperature was consistent between simulations, with an optimal suitability estimated around
 321 20°C on average throughout the year (mostly between 15 and 25°C, with a second peak near 10°C for a few
 322 iterations). The identified temperature window corresponds to the overall thermal tolerance of tropical
 323 reptiles (Sunday, Bates, & Dulvy, 2011).

324 *Phelsuma borbonica* was predicted to be more likely to occupy areas with high precipitation, mostly
 325 corresponding to native remnant rainforests. We presume that *P. borbonica* benefits from a higher

326 availability of specific native tree species (e.g., *Arecaceae* and *Pandanaceae*), which provide shelter, food and
327 oviposition sites, as it is also found in other *Phelsuma* species from the Comoros and Seychelles (Noble et
328 al., 2011; Augros et al., 2018; Augros, 2019). These forests may also play a role in the availability of
329 subcanopy micro-climates, favouring the persistence of the geckos (Ineich, 2010; Dubos et al., 2020b).

330 Overall, *P. borbonica* can persist in very different habitats and environmental conditions, from cold and dry
331 rocky slopes near the summits of the island (above 2.000 meters; Sanchez & Probst, 2017) to warm lowland
332 and midland humid forests. We found a bimodality in the response curves to temperature and precipitation
333 for several iterations. These were likely caused by the presence of isolated populations on mountain ridges,
334 since the estimated climate suitability is low in these zones. This may reflect local adaptations to these
335 specific environments. Those bimodalities may also be artefacts of the availability of sites towards the edge
336 of the species distribution. In Reunion, two subspecies have been described, i.e. *P. borbonica borbonica* and
337 *P. borbonica mater* (Meier, 1995; Probst & Deso, 2001). However, the two modalities we found do not
338 correspond to these subspecies, which seem to share the same climatic niche. Preliminary unpublished
339 genetic analyses suggest a strong isolation between these populations (Sanchez et al., 2015; unpubl. Data),
340 but genetic analyses are needed formally characterise a putative genetic structure. Occurrence data which
341 corresponded to isolated observations with no evidence of established populations (i.e., with no individual
342 was observed after further surveys) were from areas that were predicted as unsuitable, a sign that our models
343 identified well the species climatic niche. This highlights the need to carefully select locality records of
344 persisting populations in order to identify well the conditions where a given species is likely to survive and
345 reproduce.

346 Predictions based on Worldclim indicated that suitable conditions can be found around the island at
347 intermediate altitudes. It is possible that *P. borbonica* once occupied this whole area, but was extirpated
348 because of intensive agriculture and habitat fragmentation in the western part of the island. A local extinction
349 of the *P. borbonica* was already documented in Cheke (1987). This depletion was associated with the severe
350 deforestation that occurred in the 18th century at the intermediate and lower belt of the island, and a intense
351 pressure from invasive alien species (i.e., the introduced wolf-snake *Lycodon aulicus*; Cheke & Hume,
352 2010). These combined factors may have dramatically decreased habitat suitability and habitat availability
353 for *P. borbonica* in the past centuries, which may explain its absence in some of the predicted climatically
354 suitable areas. The former presence of *P. borbonica* in the western part of the island is supported by the

355 presence of isolated remnant populations in the southwest (near Les Makes & Le Tampon) and recently
356 extinct populations in the northern lowlands (Cheke, 1987).

357 As shown by the response curves, *P. borbonica* persists over a relatively wide range of climatic conditions.
358 However, its presence remains localised throughout the island. To fully understand and explain the current
359 distribution patterns of *P. borbonica*, there is a need to consider additional key factors such as micro-habitat
360 use and behaviour (Kearney, Shine, & Porter, 2009; Porter & Kearney, 2009). For instance, cold-blooded
361 species can respond to climate change by altering their period of activity and thermoregulation time
362 (Kearney, Shine, & Porter, 2009; Dubos et al., 2020a). Moreover, the availability of suitable oviposition
363 sites, thermoregulation sites with specific exposure to wind, sun or rain is a strong determinant of gecko
364 occupancy (Ineich, 2010; Bungard et al., 2014; Augros et al., 2017, 2018; Roesch et al., 2021). Habitat
365 structure is provided in native forests by tree species from the *Arecaceae* and *Pandanaceae* families and
366 abiotic features, such as sunny-exposed rocks, cliffs, or man-made structures (Petren & Case, 1998; Augros
367 et al., 2017). In addition to climate change, habitat modifications, such as further urbanisation and
368 deforestation will strongly influence the future distribution of *P. borbonica*.

369 Biotic interactions play an important role in shaping species distributions (Araújo et al., 2007). The current
370 distribution of *P. borbonica* is strongly influenced by the occurrence of invasive alien species. While the
371 wolf snake *Lycodon aulicus* is presumed to be the cause of historical local extinctions through predation
372 (Cheke, 1987), the introduced Giant Madagascar day gecko *P. grandis* and the Gold-dust day gecko *P.*
373 *laticauda* are present throughout the island. To date, there is no evidence of local extirpation of *P. borbonica*
374 by these two species. However, *P. grandis* was suspected to be the cause of local extinctions of *Phelsuma*
375 species in Mauritius, presumably through competitive exclusion and/or predation (Buckland et al., 2014). It
376 is also the case for *P. laticauda* in French Polynesia (Lund, 2015). *Phelsuma laticauda* is a rising cause of
377 concern in the south of Reunion Island where it possibly threatens the persistence of the critically
378 endangered *P. inexpectata* (NOI, unpubl. data; but see Porcel et al., 2021). Other introduced species may also
379 affect *P. borbonica* through predation and/or habitat alterations, including other reptiles (*Agama agama*,
380 *Calotes versicolor*, *Furcifer pardalis*), rodents (*Rattus rattus*, *Mus musculus*), ants (*Solenopsis geminata*),
381 birds (*Pycnonotus jocosus*, *Acridotheres tristis*) and plants (*Lantana camara*). The rate of invasion is
382 increasing in Reunion Island (Fenouillas et al., 2021). Further studies will need to account for biotic

383 interactions to better understand the key drivers of the distribution of *P. borbonica* and refine forecasted
384 predictions.

385

386 *Sources of uncertainty*

387 We found a substantial amount of the uncertainty was driven by the chosen modelling technique and GCMs.

388 This is consistent with the findings of Buisson et al. (2010) and Baker et al. (2016) and advocates the use of
389 a wide range of modelling techniques (But see Valavi et al., 2021) and GCMs for conservation planning.

390 However, the uncertainty related to the climate data source was stronger than that of GCM when considering
391 the spatial overlap between current and future predictions. When considering overall suitability, the

392 importance of the climate data source was probably underestimated because it affected the suitability scores
393 to a lower degree than GCMs, however, resulted in higher discrepancies in spatial distribution of the future

394 suitable conditions. The mismatch caused by the climate data source could be due to the differences in

395 temporal coverage, with Worldclim representing the conditions of the 1960–1990 period while CHELSA

396 was computed for 1979–2013. However, temporal coverage cannot fully explain these discrepancies because
397 future predictions (both for 2070) also strongly differed, even when using the same predictors. Alternatively,

398 the differences may be driven by the methodologies used to compute the climatologies, with Worldclim

399 using interpolated data with elevation and distance to the coast as predictors in addition to satellite data (Fick
400 & Hijmans, 2017), and CHELSA using statistical downscaling for temperature, and precipitation estimations

401 incorporate orographic factors (i.e. wind fields, valley exposition, boundary layer height; Karger et al.,

402 2017). These differences led to a higher accuracy in precipitation predictions for CHELSA. This difference

403 in accuracy may be exacerbated in mountainous environments such as Reunion Island. The predicted suitable

404 environments differ the most between Worldclim and CHELSA in steep areas, suggesting that the complex

405 topography—and hence precipitation predictions—may explain the discrepancy. There is an important West-

406 East precipitation gradient for CHELSA while precipitation patterns seem to follow the elevation gradients in

407 Worldclim. The gradient for CHELSA is consistent with the dominant winds in Reunion Island, a parameter

408 that is accounted for in CHELSA climatology only. These results suggest that the spatial component of

409 species range change should not be neglected when the aim is to identify priority areas for conservation.

410 More generally, the importance of drivers of uncertainty may be downplayed when ignoring spatial

411 information. We recommend the use of multiple approaches, including overlap estimations, in uncertainty
412 assessments of species range changes.

413

414 *Conservation considerations*

415 The current distribution of *P. borbonica* is generally consistent with the predicted future suitable areas (see
416 Fig8b, 'Mean prediction' panel). We recommend that the areas identified with the highest certainty should be
417 prioritised for conservation and habitat restoration. In the context of Reunion Island, conservation actions are
418 drastically limited by land use policy as the available land is strongly disputed for by urbanisation and
419 agriculture planning. Overall, conservation efforts should be intensified in the forested uplands, where
420 predictions are favourable and anthropogenic pressure is the lowest. Nevertheless, the conservation of the
421 small, isolated populations of *P. borbonica* along some of the mountain ridges and in the west of Reunion
422 Island is of paramount importance, as these represent remnant populations that possibly form genetically
423 isolated entities (Sanchez et al., 2015; unpubl. data). Being supposedly more adapted to colder conditions,
424 mountain ridge populations may also be at even greater risk due to climate change (Raxworthy et al., 2008;
425 Freeman et al., 2018). We recommend the close monitoring of these populations for early detection of
426 potential signs of population declines.

427 Conservation actions should encompass a range of management strategies, including the protection of native
428 forests, restoration of degraded habitats, creation of artificial oviposition sites and the implementation of
429 sustainable agricultural practices. The control of invasive species represents an additional challenge, for
430 instance with *P. grandis* and *P. laticauda* currently in expansion throughout the island (Dubos, 2013; Porcel
431 et al., 2021).

432 This study stresses the need for proactive conservation actions given the high risk of extinction predicted by
433 some of our models. *Phelsuma borbonica* is already threatened by habitat loss and fragmentation, which will
434 likely increase in the future with human population. Future conservation actions will need to consider socio-
435 economic factors to prevent potential land use conflicts (Lagabrielle et al., 2011). This can be achieved by
436 involving stakeholders from urban and agricultural sectors and conservation practitioners into public
437 decision-making processes.

438 Depending on the climate data considered, our models predicted either a strong decline throughout the entire
439 island, upward, westward, or eastward shifts, or almost no change. Despite the high uncertainty, we

440 identified the areas with the most consistent predictions of suitable climate by 2070. In a context of urgent
441 decision making, we advocate the use of all the available tools to prevent possible extinctions in spite of the
442 apparent uncertainty. Forecasting models need to consider a wide range of methods and data, and assess the
443 variability between them in order to identify and mitigate potential sources of uncertainty and provide
444 relevant conservation guidelines.

445

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450

451 **Data accessibility statement**

452 All R scripts used in this study are available in online supporting information. The occurrence data used in
453 this study are available at www.borbonica.re.

454

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456

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