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1 BARATA et al.

2 **Overcoming the lack of distribution data for range-restricted habitat specialist frogs**

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18 **Abstract:** With over 40% of species threatened with extinction, the distributional range of most
19 amphibians is still unknown, generating uncertainty whether species are naturally rare, under-
20 sampled or difficult to detect. We implemented a modelling approach that uses bromeliads as
21 surrogates to predict the distribution of habitat specialist frogs that lack distributional data. We
22 aimed to predict and survey potential new sites for occurrence of a rare and microendemic
23 bromeliad-dwelling frog from the Atlantic Rainforest of Brazil. We used Maxent to predict
24 suitable areas based on climate and topographic profiles, combined with 21 occurrence records
25 of bromeliads within which our target frog species (*Crossodactylodes itambe*) is strictly
26 restricted. The bromeliad-based models identified four areas potentially suitable and subsequent
27 surveys revealed an entirely new species of a rare bromeliad-dwelling frog in one of the areas.
28 We demonstrate that using easy-to-survey surrogate species that have a strong relationship with
29 species that are hard to detect has enormous potential to reveal crucial information on potential
30 ranges and distribution of cryptic taxa. Such surrogate modelling approach could be extended to
31 other habitat specialist species that lack distribution data such as amphibians restricted to specific
32 refugia and/or reproduction sites. This could improve the targeting of surveys and increase
33 understanding of the patterns of rarity and the drivers of species distribution, especially for areas
34 with high endemism and range-restricted frogs.

35 **Keywords:** bromeligenous frogs, distribution models, few occurrence data, Maxent, new
36 species, rare species.

37 **1. INTRODUCTION**

38 Most range-restricted species are rare, concentrated in tropical areas and threatened with
39 extinction (Pimm & Jenkins, 2010; Morais et al., 2012). These species are of high conservation
40 concern, but the absence of reliable distribution data means there is uncertainty concerning their
41 conservation status (Mace et al., 2008). A quarter of amphibians in the world have very small
42 geographical ranges ($<10^3$ km²) (Pimm et al., 2014) and 41% of species are at risk of extinction
43 (Luedtke et al., 2023) with the great majority living in the tropics (Stuart et al., 2008). Equally,
44 amphibians are often habitat specialists and have reduced dispersal capabilities. Bromeliad-
45 dwelling frogs are a case in point. Out of 99 species of bromeligenous frogs, 35% are either data
46 deficient or not evaluated, and 41% are threatened with extinction (Sabagh et al., 2017).

47 Restricted to South America, bromeligenous frogs are known from very few locations and spend
48 their entire life cycle within bromeliads. In extreme cases, these frogs are restricted to a single
49 species of plant, with one known population recorded at a high-elevation site that can be
50 challenging to survey (MacCulloch & Lathrop, 2005; Barata et al., 2013; Kok et al., 2013).

51 Understanding how range-restricted species are distributed and where new populations are likely
52 to be found can indicate whether these species are indeed naturally rare or simply under-
53 sampled. Species distribution modelling (SDM) can be used to identify under-sampled locations
54 to prioritize surveys of range-restricted species (Raxworthy et al., 2003) – an approach that has
55 been successfully applied across different geographic regions and taxa (Pearson et al., 2007;
56 Marini et al., 2010; Chunco et al., 2013; Sarkinen et al., 2013; McCune, 2016). However, the
57 substantial lack of information in tropical areas (Collen et al., 2008) hampers further application
58 of the method which relies on species occurrence records. When there are limited data on the

59 target species, SDMs can be generated by using information from a species that is more abundant
60 yet associated with a rare species. In such cases, a strong association and similar habitat
61 requirements between a lesser common species and the targeted rare species can be beneficial
62 (Edwards et al., 2005). With very limited distribution data available, bromeligenous frogs are
63 challenging for modelling, however, their unique life history traits create an exceptional
64 opportunity for modelling species distribution. We used bromeliads as surrogates for frog
65 occurrence, and even though there was little information on the target frog species, we produced
66 models using occurrence records of bromeliads that are more widely available.

67 We built SDMs using bromeliad distribution data to predict new potential areas for a range-
68 restricted habitat specialist, the Itambe's bromeliad frog (*Crossodactylodes itambe*). The species
69 extent of occurrence is less than 0.5 km² in a single location at 1700 m a.s.l., in the Atlantic
70 Rainforest of Brazil (Barata et al., 2013). Species is Critically Endangered under the criteria of
71 geographic range, quality of habitat and population number (IUCN/SSC/ASG, 2023a; Barata et
72 al., 2018a). To understand species distribution and investigate its patterns of rarity, we aimed to
73 a) predict and map areas of high suitability for plants and describe environmental requirements
74 for plant occurrence; and b) search for new populations of the target frog in areas of high
75 suitability located inside and outside protected areas. As such, our results focused not only on the
76 geographical extent of bromeligenous frogs and their levels of threat, but also to the general
77 implications of survey effort of montane endemic species and habitat specialist amphibians in
78 tropical areas. We demonstrate that the success of our modelling approach can lead to promising
79 applications of SDM to endemic habitat specialist species allowing us to understand patterns of
80 rarity of many elusive frogs for which we have no data and that are otherwise difficult to survey.

81 2. METHODS

82 2.1 Study system and modelling approach

83 Tank bromeliads are large arboreal or terrestrial plants with a central tank that collects water, leaf
84 litter and detritus, providing a wide range of microhabitats for numerous species (Lehtinen,
85 2004). Bromeligenous frogs are strictly dependent on bromeliads, where they lay their eggs and
86 complete their life cycle without leaving the plant (Peixoto, 1995). Half of these 99
87 bromeligenous frogs are restricted to montane areas higher than 1000 m a.s.l. (Sabagh et al.,
88 2017), and their ecology and natural history are poorly known. The genus *Crossodactylodes*
89 comprises seven small-sized bromeligenous frogs which are range restricted, rare and occur in
90 specific species of bromeliads in montane areas of the Atlantic Forest of Brazil. Our target
91 species, *Crossodactylodes itambe*, is known to occur on one mountaintop in the Espinhaço
92 Mountain Range of Brazil (Barata et al., 2013) – a 1200 km biodiversity-rich mountain chain
93 that divides the Atlantic Rainforest to the east, and the Cerrado to the west. *Crossodactylodes*
94 *itambe* lives in a single species of tank bromeliad, *Vriesea medusa* (Santos et al., 2017), which is
95 also endemic to two locations in the Espinhaço Range (Versieux et al., 2008; Versieux et al.,
96 2010). Despite the cryptic nature of all *Crossodactylodes* spp., there is information available on
97 the taxonomy (Barata et al., 2013; Santos et al., 2020), reproduction (Santos et al., 2017; Santos
98 et al., 2021), behaviour (Barata et al., 2018b) and ecology (Barata et al., 2017; Barata et al.,
99 2018a) of our targeted species *C. itambe*, serving as a good candidate to investigate species
100 distribution base on habitat requirements.

101 In Maxent, model outcome can be strongly affected by the background points chosen (Elith et al.
102 2010). Our goal was to identify areas where our targeted species could potentially occur, in the

103 vicinities of current known extent of occurrence. We therefore restricted the geographical scale
104 of our models to the southern portion of the Espinhaço Range – a UNESCO Biosphere Reserve
105 that also comprises a mosaic of protected areas of different sizes and shapes (hereafter,
106 Espinhaço Mosaic). Since *C. itambe* is a small-sized frog with limited dispersal capabilities,
107 drawing background points from a smaller scale enabled projections to be made without
108 extrapolating to areas outside the likely range of our targeted species. Hence, our goal was to
109 predict suitable areas for bromeliads and ground-truth likely areas for new populations of *C.*
110 *itambe* within the limits of the Biosphere Reserve and the Espinhaço Mosaic (Figure 1A). Since
111 *C. itambe* is known from a single site, we used bromeliads as a surrogate for species presence
112 and we therefore modelled not our target species, but the environmental requirements for
113 occurrence of bromeliads. *Vriesea* is one of the most diverse genera of bromeliads in our study
114 area (Versieux & Wendt, 2006) and contains some of the largest species. Considering that the
115 structure of the bromeliad such as size, number of leaves, volume of the central tank and number
116 of neighbouring plants are important predictors of abundance for *C. itambe* (Barata et al., 2018a),
117 at least five other species of *Vriesea*, with similar size and structure (i.e., larger plants with larger
118 water tanks), were used to generate our models. We therefore used occurrence records of the
119 genus *Vriesea*, assuming the structure of the plant – rather than plant species – would be
120 important for frog occurrence.

121 **2.2 Occurrence and environmental data**

122 To obtain occurrence records of the bromeliads, we searched for *Vriesea* species in nine
123 locations between 1029 m - 1592 m a.s.l. within our study area. We selected these locations
124 using Google Earth images at 100 m resolution, by comparing images with similar outcrops

125 where bromeliads can potentially occur. We used the method validated by Silva & Alves-Silva
126 (2013) and identified similar areas based on vegetation cover and substrate type, comparing the
127 surrounding landscape with the Itambé summit, where *C. itambe* originally occurs. Although we
128 acknowledge this method might introduce some bias by sampling similar outcrops, we aimed at
129 maximising the number of records that could be used in our models.

130 In 2015, we surveyed these areas gathering occurrence records of *Vriesea* spp. Over 6-days we
131 had a total of 133 occurrences recorded in GPS, but these records were, inevitably, very close to
132 each other (on some occasions <100 m), which could increase the chances of model overfitting
133 by including records that are not spatially independent (Shcheglovitova & Anderson, 2013).
134 Therefore, we only used records of bromeliads that were at least 1 km apart from each other. We
135 filtered these records with ArcGIS version 10.5.1, creating a 1 km buffer around every
136 occurrence, and identifying overlapping occurrences that were later excluded. Consequently, we
137 had a total of 21 unique records that could be used in our distribution models (Figure 1B).

138 For environmental data we downloaded 19 bioclimatic variables and altitude from WorldClim
139 Global Climate Data version 2 (Fick & Hijmans, 2017; at 30 seconds resolution, ~1 km²), and
140 soil type (1:650.000) from the Department of Soils and AgroSciences at the Federal University
141 of Viçosa, in Brazil (available at <https://dps.ufv.br/software/>). Elevation is an important factor
142 for the occupancy and abundance of *C. itambe* (Barata et al., 2017; Barata et al., 2018a).

143 Additionally, the bromeliads we modelled have rupicolous life form, growing on rocky fields
144 characterized by shallow and sandy soils (Versieux and Wendt, 2006).

145 Using ArcGIS, we standardized all environmental variables, using the same extent and cell size,
146 and defined their geographical boundaries accordingly to the study area. We built distribution
147 models by combining climatic variables, altitude, and soil type. We selected climatic variables
148 by performing a Principal Component Analysis (PCA) in ArcGIS and selecting variables that
149 contributed most to the first and second axes of principal components and that were not
150 correlated according to the correlation matrix output from the PCA (values <0.5). Outputs from
151 PCA provide the variance explained by Eigenvector coefficients (indicating the relative weight
152 of each variable in the component), percentage Eigenvalues and accumulative Eigenvalues,
153 which we interpreted as the contribution of each axis as the principal components of our analysis
154 (see Supplementary Information for details).

155 **2.3 Model settings and validation**

156 We used Maxent version 3.4.1 (Phillips et al., 2006) to identify suitable areas based on climate
157 and topographic profiles, combined with 21 (presence-only) occurrence records of at least five
158 species of bromeliads from the genus *Vriesea*. Small sample sizes may compromise the power of
159 predictions (Stockwell & Peterson, 2002) but Maxent performs well compared to other
160 algorithms (Elith et al., 2006; Wisz et al., 2008), even with sample sizes below 20 records
161 (Hernández et al., 2006; Papeş & Gaubert, 2007; Pearson et al., 2007; Williams et al., 2009; Le
162 Lay et al., 2010; Marini et al., 2010; Chunco et al., 2013). We built 12 different models with
163 Maxent using slightly different settings (details available as Supplementary Information). For all
164 models we created response curves and predictions using a Jackknife to measure variable
165 importance, with a logistic output, and set the number of maximum iterations to 5000. The area
166 under the receive-operator curve (AUC) is usually used to evaluate models, however, AUC

167 values should be used with caution for presence only methods (Merow et al., 2013). To test the
168 predictive performance of our models we used a Jackknife approach described by Pearson et al.
169 (2007), which is reliable for small sample sizes. The test compares success-failure for each
170 model to the proportion of the study area predicted present i.e., performance is assessed based on
171 the ability of each model to predict the single locality excluded from the training data in the
172 leave-one-out procedure (Pearson et al., 2007). A P-value was calculated based on the
173 predictions of our models (R script available at <http://www.ucl.ac.uk/cber/pearson>).

174 Although we fitted 12 models for parametrisation using different Maxent settings (details
175 available as Supplementary Information), here we present a final model that contained a layer of
176 soil type, altitude, and the selected climatic variables. For this final model, we modified Maxent
177 settings following recommendations for small samples: we applied a Jackknife cross-validation
178 (or leave-one-out procedure, Pearson et al., 2007), using the minimum training presence
179 threshold, regularization multiplier of 2 and a hinge feature (Shcheglovitova & Anderson, 2013;
180 Radosavljevic & Anderson, 2014).

181 Finally, to validate our final model we surveyed areas indicated in our projections. Areas were
182 selected based on a combination of high suitability for bromeliad occurrence and low standard
183 deviations (≤ 0.05) predicted in the models, the predictive performance of models (given by the
184 Jackknife approach), and we also considered expert knowledge (I. M. Barata, personal
185 observation). We selected areas both inside and outside protected areas (PA) to compare
186 differences in plant numbers and plant structure (i.e., tank size). We assumed that areas inside
187 PA were well preserved and more likely to contain good quality habitat, whereas areas outside
188 PA were presumed to be impacted by human activities, such as fire and cattle grazing. We

189 collected data on bromeliad tank size (height and width of central tank, in centimetres) and total
190 number of bromeliads recorded. We performed a t-test to evaluate significant differences on tank
191 size of bromeliads inside and outside PA. If bromeliads were verified during daytime surveys
192 they were resurveyed after dusk to search for *C. itambe*. Each area was intensively surveyed
193 during 2-4 consecutive days during the rainy season, between January and March 2017.

194 **3. RESULTS**

195 **3.1 Predicting environmental suitability for plant occurrence**

196 Fitted models identified similar areas of high suitability, showing consistency in predictions
197 across different settings (Supplementary Information). The model presented here (with selected
198 bioclimatic variables, altitude and soil type) gave us broader predictions but also higher *SD* when
199 compared to other models, expanding predictions to the south of study area (Figure 2).

200 Projections in the north-east were consistent across all models, which falls within the limits of
201 the Atlantic Rainforest. Results from Jackknife showed a high and significant success rate for
202 our model ($r = 0.9$, $P < 0.05$). Low *SD* were associated with areas to the east, especially when
203 compared to areas on the south where predictions were less precise (Figure 2).

204 Overall, suitable areas for bromeliad occurrence are high elevational sites with appropriate soil
205 type (i.e., outcrop with shallow soil and quartz gravels, low in nutrient content), with reduced
206 seasonal variation in temperature (response curves and output summaries available in
207 Supplementary Information). Temperature seasonality was an important variable for bromeliad
208 occurrence with reduced tolerance in seasonality, daily fluctuations, and extreme conditions.
209 Temperature seasonality and annual precipitation explained 97% of variation according to the

210 PCA (and were therefore the selected as climatic variables for modelling, details available in
211 Supplementary Information). While temperature seasonality represents change over the year and
212 had a negative influence in our predictions, annual precipitation is the sum of all monthly rainfall
213 and can be used to interpret the importance of water availability to a species distribution – in our
214 case it was positive for the bromeliad. Nonetheless, the selected climatic variables (temperature
215 seasonality and annual precipitation) contributed to less than 15% of predicted area and
216 projections were mostly influenced by altitude and soil type.

217 **3.2 Searching for new populations of frogs**

218 Bromeliads were present in every area predicted by the models that we surveyed. Areas to the
219 east not only had a high predicted suitability with lower *SD* but are also under the domains of the
220 Atlantic Rainforest, which is the same biome where original population of *C. itambe* is currently
221 recorded. We therefore opted to survey areas within the domains of the Atlantic Rainforest and
222 located in the north-east of our study area (Figure 2). Due to financial and logistic constraints
223 (limited manpower, reduced time, and poor road access), we selected four different areas to be
224 surveyed, two inside PA (12,184 ha and 13,6541 ha) and two outside PA. These areas are on
225 average 38.4 km from each other and located within the Espinhaço Mosaic, which covers an area
226 of approximately two million hectares.

227 We recorded a total of 541 bromeliads. The areas differed in the total number of bromeliads
228 available (inside PA = 462, outside PA = 79) and elevational range (varying from 1029 m to
229 1592 m a.s.l.). Bromeliad had larger tanks inside PAs (mean = 79 cm², *SD* = 36.1, *N* = 112) than
230 outside PAs (mean = 37.9 cm², *SD* = 13.1, *N* = 55; *P* < 0.005, t-value = 10.7, *df* = 155). Although

231 every recorded bromeliad was resurveyed during the night, we only found frogs in one of the
232 four predicted areas: a forested patch inside a PA (Figure 3), about 60 km from the original
233 population. Further examination of sampled individuals in the lab revealed that our new record
234 was not a new population of *C. itambe*, but in fact a new species of the genus *Crossodactylodes*
235 (recently described by Santos et al., 2023). This PA has high altitude (1519–1620 m a.s.l.) and
236 falls completely within the domains of the Atlantic Rainforest (Figure 3). Different from other
237 areas we surveyed, the forest patch where frogs were found contained a high density of plants
238 and the PA had bromeliads with the largest tanks (mean = 88.6 cm²; SD = 42.5; N = 63).

239 **4. DISCUSSION**

240 We generated distribution models for a widely distributed genus of bromeliad to predict the
241 occurrence of a habitat specialist amphibian for which data are limited, prioritising survey areas
242 highly suitable for plants where our target plant-dependent species was, consequentially, more
243 likely to be found. Our modelling approach is suitable for species that have a strong dependency
244 on their host plant but for which there is otherwise limited information on determinants of
245 distribution (and therefore no other parameter can be modelled). The method could be broadly
246 extended to range-restricted habitat specialist species that require further investigation on their
247 extent of occurrence, such as other threatened and data deficient bromeligenous frogs (c.75% of
248 species, Sabagh et al., 2017) and other amphibians species that are presumed to occur more
249 widely and are constrained to specific refugia and/or breeding sites, such as tree buttresses,
250 waterfilled tree holes, bamboo stumps, nut husks, leaf axils, and other such habitats.

251 Overall, our models yielded consistent predictions despite the use of a small dataset,
252 compensating for the lack of data on our target species. Valuable occurrence data for bromeliads
253 could also be obtained from open access digital herbariums (Besnarda et al., 2018; Heberling et
254 al., 2019). For instance, we found over 3000 records from the last 10 years of *Vriesea* species
255 available on the Global Biodiversity Information Facility, contrasting with the poor data on
256 *Crossodactylodes* species distribution, demonstrating the potential of digital databases in
257 contributing to modelling plant-dependent species. When fieldwork is needed, obtaining
258 presence data for plants can be less time consuming and more cost effective than searching for
259 the targeted animal species. For example, to collect bromeliad occurrence, we covered an
260 extensive area in six days of survey, resulting in more than 130 records. On the other hand, at
261 least four nocturnal visits are needed to reliably detect our target frog (Barata et al., 2017),
262 requiring greater logistical and financial support. Modelling bromeliad data, collected either in
263 the field or from online databases, is therefore a feasible and cost-effective alternative approach
264 for other species in the genus. At least four *Crossodactylodes* species are expected to occur more
265 widely, one of which is threatened with extinction with decreasing population (VU
266 *Crossodactylodes izeckshoni* IUCN/SSC/ASG, 2023b) and other that has not been recorded since
267 its first collection in 1909 (DD *C. pintoii* IUCN/SSC/ASG, 2023c), and further intensive surveys
268 should be conducted to define species extent of occurrence, habitat restrictions and patterns of
269 rarity. This is also a good opportunity for developing a true test of the performance of the
270 suggested modelling approach by comparing the occurrence of bromeliads and frogs between
271 sites with both high and low suitability, according to the models.

272 Noteworthy, bromeliads can determine the distributional ranges of plant-dependent animals
273 under the assumption that their environmental and climatic requirements will encompass those of
274 the target species. Our results give further support that our target species is indeed restricted to
275 high altitude, possibly occupying bromeliads that tolerate environments with low temperature
276 variation and higher water availability. Consequently, these strict environmental conditions for
277 plant distribution might also restrict species range resulting in species being microendemic and
278 having low tolerance to habitat disturbance. Furthermore, the abundance of bromeligenous frogs
279 can be highly dependent on the bromeliad structure and the presence of water in bromeliad tanks
280 (Barata et al., 2018a). Frogs were only recorded inside PA and our results shed light on the
281 impacts of environmental change on the occurrence of habitat specialist amphibians. Although
282 we recorded bromeliads in every area we visited, they varied in number, quality, and size.
283 Outside PA the number of plants was lower, and size of bromeliad was significantly reduced. In
284 these locations, we observed that the structure of plants was damaged, either by fire and or cattle
285 trampling. Considering the high rate of deforestation recorded in the Atlantic Rainforest of Brazil
286 (Ribeiro et al., 2009), it is more likely that discoveries of new populations (or even new species)
287 will fall inside areas where potential threats are expected to be reduced, such as remote locations
288 and PA that held more pristine habitats.

289 Finally, our results reinforce the need for additional survey effort, especially in tropical areas that
290 remain insufficiently represented in amphibian conservation studies (Ficetola, 2015). Species
291 with restricted ranges might be naturally rare or suffer from insufficient survey effort but
292 distinguishing between these two can be difficult. Ecological observations are uneven throughout
293 South America (Martin et al., 2012) where all bromeligenous frogs are known to occur, and in

294 Brazil survey effort is unequally distributed (Oliveira et al., 2016), including in our study area
295 (Barata, Correia and Ferreira, 2016). The discovery of a new species demonstrates that montane
296 regions still need increased sampling effort to uncover their full biodiversity. Despite our survey
297 effort we only found frogs in one new area, indicating that both targeted and newly discovered
298 species are naturally rare with a genuinely restricted distribution. This might be true for many
299 other range-restricted taxa that are constrained to high altitudes and depend on bromeliads
300 thriving on specific environmental and climatic conditions. We conclude that the use of
301 surrogates for habitat specialist species can enhance the potential of SDM, allowing a wise
302 allocation of survey effort to substantially improve our knowledge on the distribution of rare and
303 range-restricted amphibians that are currently under threat. Additional case-studies will improve
304 our understanding on the geographical extent of poorly known amphibian species, however, such
305 pattern of rarity (with restricted habitat requirements and small distributional range) is likely true
306 for other bromeligenous frogs.

307

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316 locations and for assistance during expeditions and night surveys.

317 **Conflict of interest**

318 The authors declare no conflicts of interest.

319 **Author contribution statement**

320 IMB and RAG contributed to study concept and design. Fieldwork and data collection was
321 delivered by IMB. Data analysis was done by IMB with input from VMU and LGC and FF
322 produced the maps. IMB led on the writing of the article with equal contributions from each of
323 the other authors.

324 **Supplementary Information**

325 Details of different settings and predictive maps for 12 models built using Maxent is available
326 online, including plotted standard deviation and bioclimatic variables used in the final model
327 discussed in this manuscript. A summary table of explanatory variables, Principal Components
328 Analysis results and response curves and output summary for models' performance from Maxent
329 are also available online.

330

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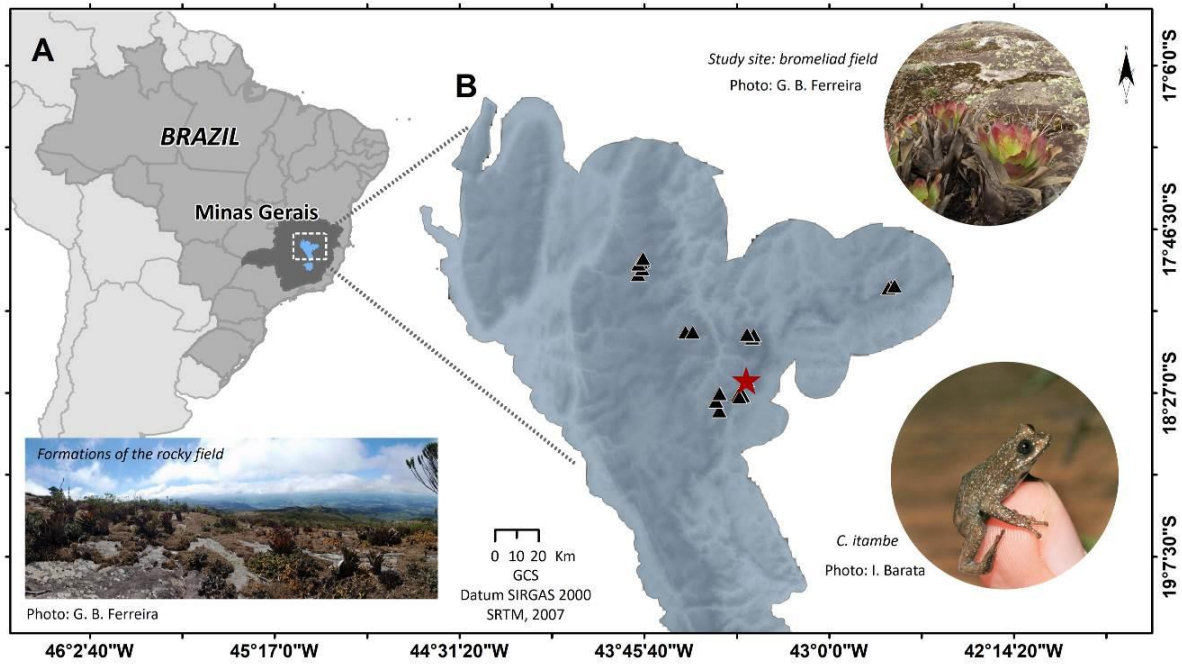
468 **Figure captions**

469 **Figure 1.** Study area with (A) the location of the Biosphere Reserve and the Espinhaço
470 Mosaic (blue area) in the state of Minas Gerais, in south-eastern Brazil; and (B) filtered
471 occurrence records (triangles, N = 21) of the bromeliad *Vriesea* spp. used in our models. Star
472 shows the known population of our target species *Crossodactylodes itambe*.

473 **Figure 2.** Suitable areas predicted for bromeliad occurrence and associated standard
474 deviations (*SD*) from customised model. Value represents habitat suitability on a scale from 1
475 to 0 (on prediction) and standard deviations on a scale of 0 to 0.05 (on *SD*). Prediction
476 warm/darker colours indicating high suitability and *SD* warm/darker colours indicates high
477 standard deviation. Dashed circles indicate areas with both high suitability and low *SD*.

478 **Figure 3.** Areas of high suitability based on the reduced model and the original occurrence of
479 *Crossodactylodes itambe*, showing the four visited locations. Detailed map shows the limits
480 of the Cerrado (CE) and the Atlantic Rainforest (AF) with bromeliad records and the
481 occurrence of the new *Crossodactylodes* species.

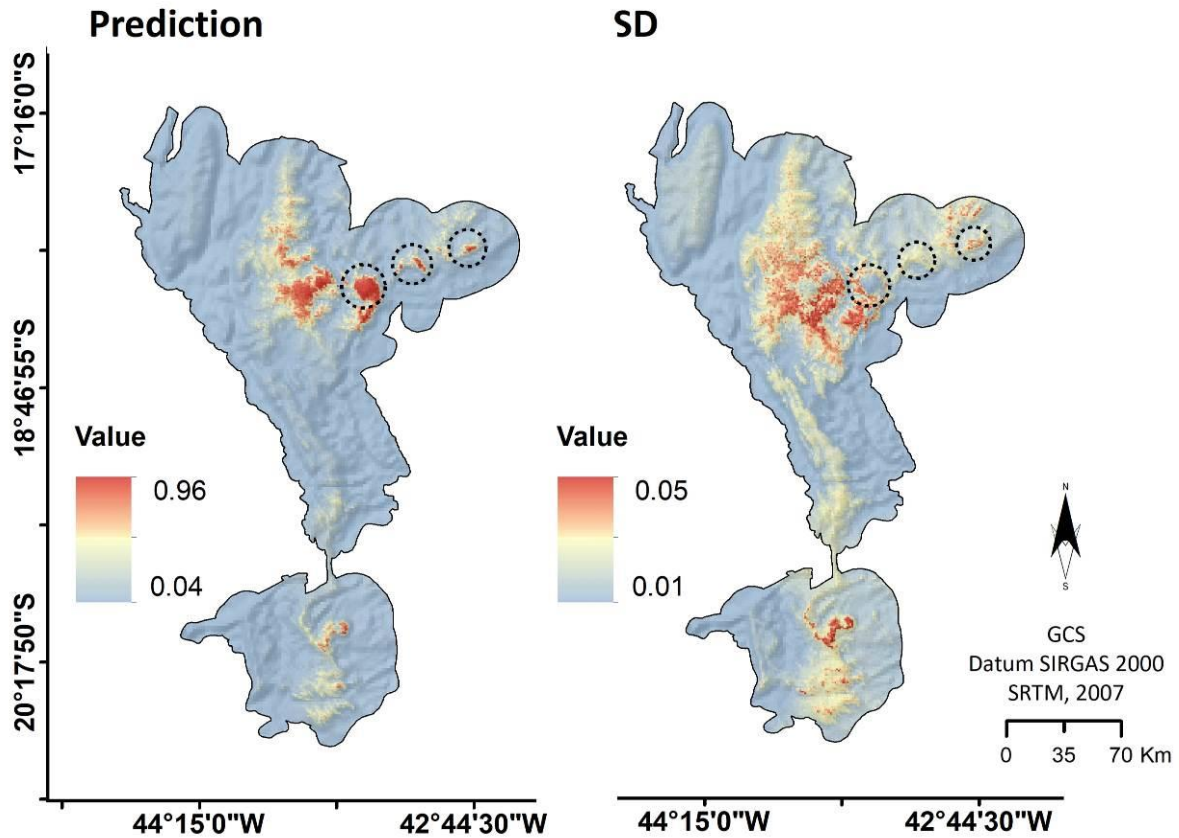
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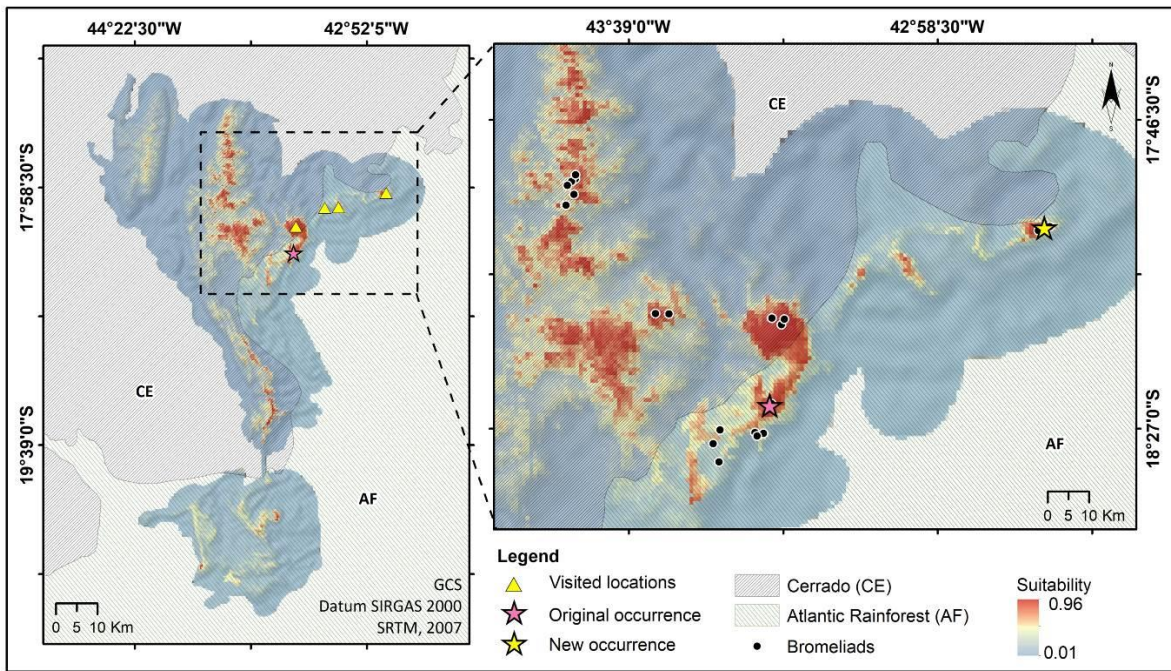
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