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## Distribution and conservation status of the endangered Montagne d'Ambre fork-marked lemur (*Phaner electromontis*)

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1 **Running Head:** Distribution of *Phaner electromontis*

2

3 **Distribution and conservation status of the Endangered Montagne**  
4 **d'Ambre fork-marked lemur (*Phaner electromontis*)**

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27

28 The geographic distribution of a species can provide insights into its population size, ecology,  
29 evolution, and how it responded to past (and may respond to future) environmental change.  
30 Improving our knowledge of the distribution of threatened species thus is a high priority in  
31 assessing their conservation status. However, there are few data available for many recently  
32 described yet understudied and potentially threatened primate taxa, making their conservation  
33 difficult. Here, we investigated the distribution of the Montagne d'Ambre fork-marked lemur,  
34 *Phaner electromontis*, a threatened nocturnal primate endemic to northern Madagascar and  
35 classified as Endangered by the IUCN. As fork-marked lemurs are highly vocal, we used  
36 acoustic surveys to assess species' presence-absence and relative population density within 66  
37 different forest survey sites in northern Madagascar. Further, we compared data among five  
38 forest types within the study area and investigated the relationship between relative  
39 population density and climatic variables. We report the presence of *P. electromontis* in 22  
40 study sites; several of these populations were unknown previously. Although we found *P.*  
41 *electromontis* most frequently in dry-transitional forests, our results suggest that geography  
42 (spatial autocorrelation) rather than environmental variables explains the species' distribution.  
43 We hypothesize that environmental unpredictability and gummivory, combined with the  
44 presence of several distinct *Phaner* species in the studied area, could explain the observed  
45 distribution.

46 **Key words:** acoustic survey; density; geographic range; habitat preference; northern  
47 Madagascar; presence/absence

48 Deforestation and habitat degradation within tropical ecosystems are the primary causes of  
49 species extirpation globally (Myers et al. 2000; Travis 2003; Giam 2017). Because tropical  
50 forest ecosystems host over 65% of the world's terrestrial biodiversity (Gardner et al. 2009),  
51 its high clearing and harvesting rate, for human needs and economic growth, are potentially  
52 catastrophic for global biodiversity (Mittermeier et al. 1998; Jha and Bawa 2006; Bradshaw et  
53 al. 2009). Deforestation in many areas of the tropics has been so severe in the past decades  
54 that only sporadically-dispersed, remote and isolated forest fragments remain of what was  
55 once continuous pristine forest (Zuidema et al. 1996; Fahrig 2003; Wade et al. 2003; Villard  
56 and Metzger 2014). Because many animals are heavily dependent on forest for food, shelter,  
57 and survival, there is grave concern for their conservation (Fahrig 2003; Schwitzer et al.  
58 2011). Primates, in particular, are severely threatened by deforestation because many of them  
59 depend exclusively on the forest for survival (Chiarello and de Melo 2001; Martinez-Mota et  
60 al. 2007; Estrada et al. 2017). However, the distributions of many threatened primate species  
61 remain poorly known (Rylands et al. 2012). Many of the forests within and around their  
62 geographic ranges remain un-surveyed due to their remoteness and difficulty of access  
63 (Turner and Corlett 1996). To protect threatened primate species, *in situ* conservation is  
64 required of their remaining populations and forest habitat (Struhsaker 1981; Dobson & Lyles  
65 1989; Schwitzer et al. 2013), and research is needed to assess their demography and inform  
66 their conservation (Mitani 1990; Strier 1991; Wallace et al. 2006).

67 The necessity for primate distribution assessments may be most applicable to lemurs, a group  
68 endemic to the biodiversity hotspot of Madagascar (Myers et al. 2000; Ganzhorn et al. 2001;  
69 Mittermeier et al. 2008). This is because first, dozens of new lemur species have been  
70 described in the last decades, due to increased fieldwork efforts in remote regions coupled  
71 with advances in genetics (e.g. Yoder et al. 2000; Frasier et al. 2016; Schüßler et al. 2019);  
72 the distributions of many of these new species, particularly the cryptic nocturnal species, are

73 poorly known (e.g. Roos and Kappeler 2006; Hotaling et al. 2016). Second, lemurs are  
74 considered the most threatened group of mammals worldwide, and an understanding of their  
75 geographic ranges is required to conserve their remaining populations (Schwitzer et al. 2013).  
76 The distributions of lemur species within some genera, for example mouse lemurs  
77 (*Microcebus*) and sportive lemurs (*Lepilemur*), have been influenced by certain geographic,  
78 geological or hydrological features (Goodman and Ganzhorn 2004; Wilmé et al. 2006; Craul  
79 et al. 2007; Olivieri et al. 2007). For some of these species, a clear connection with altitude  
80 (*M. Lehilahytsara*: Radespiel et al. 2012), or humidity (*M. arnholdi* versus *M. tavaratra* in  
81 northern Madagascar: Sgarlata et al. 2019) have repeatedly been identified. Furthermore,  
82 some diurnal lemurs, such as the ring-tailed lemur, *Lemur catta* (Goodman et al. 2006), and  
83 the indri, *Indri indri* (Powzyk and Thalmann 2003; Geissman and Mutschler 2006), are  
84 extensively studied and there is a sound understanding of their demography and current  
85 distribution. However, the distributions of most lemurs are much more difficult to study due  
86 to the existence of cryptic species complexes or of ecological peculiarities (e.g. the dwarf and  
87 mouse lemurs; Frasier et al. 2016; Hending et al. 2017a; Sgarlata et al. 2019); there still is a  
88 noticeable paucity of any demographic knowledge of these species.

89 The fork-marked lemurs (*Phaner* sp.) are a group of medium-sized, nocturnal primates that  
90 exhibit primarily-solitary foraging behaviour, yet form cohesive pair-bonds (dispersed pairs,  
91 Schülke and Kappeler 2003). Fork-marked lemurs once were considered a monotypic species  
92 (*P. furcifer*), but were split into four subspecies in 1991, based on morphology and  
93 distribution (Groves and Tattersall 1991). These four subspecies were elevated to species ten  
94 years later by Groves (2001) with opposition from Tattersall (2007; see Groves 2014).  
95 However, the genus *Phaner* remains generally under-studied, with only the pale fork-marked  
96 lemur, *P. pallescens*, having received any significant attention (Petter et al. 1975; Charles-  
97 Dominique and Petter 1980; Schülke 2003a, 2003b, 2005; Schülke and Kappeler 2003;

98 Schülke et al. 2004). The four currently recognized *Phaner* species occupy distinct and  
99 discontinuous geographic ranges (Mittermeier et al. 2010), although few surveys of their  
100 distributions have been conducted (Charles-Dominique and Petter 1980; Hawkins et al. 1990;  
101 Ganzhorn and Kappeler 1996; Salmona et al. 2018). Furthermore, little is known about the  
102 environmental influence on fork-marked lemur distributions in comparison to other lemur  
103 species, whose distributions may sometimes be influenced by abiotic environmental factors  
104 (e.g. Smith et al. 1997; Rendigs et al. 2003; Dunham et al. 2011; Sgarlata et al. 2019). Three  
105 of the four *Phaner* species currently are classified as Endangered (*P. electromontis*, *P.*  
106 *pallescens*, *P. parienti*) while *P. furcifer* is classified as Vulnerable (Andriaholinirina et al.  
107 2014a, 2014b, 2014c, 2014d); a broad and detailed investigation of their demography is  
108 required to assess these classifications (Schwitzer et al. 2013).

109 In this study, we assessed the distribution and the relative population density of fork-marked  
110 lemurs across northern Madagascar (Diana and Sava regions; Figure 1). Although it is unclear  
111 which fork-marked lemur species is present south of the Loky River, Salmona et al. (2018)  
112 suggested that *Phaner* populations further south are closely related to the Montagne d’Ambre  
113 fork-marked lemur (*Phaner electromontis*). We will therefore consider *P. electromontis* as the  
114 focal species of this study and accordingly use its name thereafter, although we are aware that  
115 studies are needed to clarify northern fork-marked lemur taxonomy. We also investigated how  
116 the relative population densities of *P. electromontis* vary according to forest-habitat types,  
117 elevation and climatic conditions. Given the large currently-reported geographic distribution  
118 of *P. electromontis* (Hawkins et al. 1990; Randrianarisoa et al. 1999; Salmona et al. 2018), we  
119 expected to find *P. electromontis* in the sparsely-surveyed forests of northern Madagascar,  
120 which would extend the known geographic distribution of this species. Furthermore, because  
121 habitat characteristics have been reported to influence the population distributions and  
122 densities of other lemurs (Ganzhorn et al. 1997; Jolly et al. 2002; Lehman et al. 2006a;

123 Hending et al. 2017b; Setash et al. 2017), we hypothesized that the relative population density  
124 of *P. electromontis* could vary among forests, depending on forest type, climate and/or  
125 elevation.

## 126 MATERIALS AND METHODS

### 127 *Study Area*

128 Between April of 2011 and August of 2018, we conducted surveys in 66 forest sites spread  
129 over an area of approximately 20,000 km<sup>2</sup> in the Diana and Sava regions of northern  
130 Madagascar (Supplementary Data SD1). Northern Madagascar is a transitional zone between  
131 the dry forests of the west and the humid wet forests of the east (Moat and Smith 2007) and  
132 contains a variety of different forest habitat types (Goodman and Wilmé 2006; Moat and  
133 Smith 2007). We therefore classified the forest habitat type at each of our study sites either as  
134 dry ( $N = 21$ ), dry-transitional ( $N = 16$ ), humid ( $N = 11$ ), humid-transitional ( $N = 16$ ), or  
135 littoral ( $N = 2$ ), using qualitative observations of the site and assessments of the forest's  
136 vegetation species and structure (Hending et al. 2020). The climate throughout the study area  
137 is seasonal, encompassing a hot and wet season from November to April followed by a  
138 slightly-cooler dry season from May to October (Schreurs & Rakotoarisoa, 2011). Mean  
139 annual temperature at our forest sites varied from 19.5 to 26.6 °C and annual precipitation  
140 varied from 1,124 to 1,734 mm for the study period (2011 - 2018; WorldClim dataset). All of  
141 northern Madagascar's forests currently are threatened by agricultural expansion, human  
142 population encroachment, wood exploitation and mineral-mining (Fowler et al. 1989;  
143 Schwitzer et al. 2013).

144 *Phaner electromontis* Presence/Absence Survey

145 We carried out fixed-point acoustic surveys (Thomas et al. 2002) of *Phaner electromontis*  
146 loud calls, 1 – 66 observation points per site, ( $\bar{X} = 16.5$ ,  $\sigma = 15.32$ ); a total of 1,091 points  
147 across all sites (Supplementary Data SD1). Observation points were positioned  $\geq 150$  m from  
148 all other observation points at each study site in a grid; survey number therefore varied among  
149 sites due to differences in site size, which ranged from 5.5 ha (Ampondra; Hending et al.  
150 2020) to 6,248 ha (Bekaraoka; Salmona et al. 2014). In addition, the survey effort at some  
151 sites (Analamanara, Antsoha, and Mahasoia; Supplementary Data SD1) was limited by the  
152 arrival of Cyclone Enawo to our study area (early March 2017). We used acoustic surveys,  
153 instead of visual nocturnal line transect distance sampling because (1) *Phaner* have loud,  
154 species-specific calls that can be heard at a distance of over 30 m from a calling individual,  
155 and distinguished from the calls of hetero-specifics by their acoustic structure (Charles-  
156 Dominique and Petter 1980; Forbanka 2020); and (2) *Phaner* are highly mobile, fast-moving,  
157 and are not particularly attracted by lamplight, making them unlikely to be visually detected  
158 (JS, DH, BLP, ER, pers. obs.). All acoustic surveys were conducted between 17:30 and 21:30,  
159 when *Phaner* are vocally-active (Charles-Dominique and Petter 1980; Schülke 2003a). For  
160 most survey points, we repeated surveys ( $N = 1-8$ ,  $\bar{X} = 2.1$ ) over successive nights. During  
161 each acoustic survey, three observers recorded (1) fauna vocalisations; (2) number of  
162 individuals and approximate direction from which they originated (Geissmann and Mutschler  
163 2006); (3) geographic coordinates (GPS eTrex 10 or 30; Garmin International, Inc., Olathe,  
164 Kansas, USA); and (4) the start and end times of the survey. Calls originating from the same  
165 direction from the survey point during a single fixed-point acoustic survey were deemed to be  
166 the same individual.

167 **Fig. 1 near here**

168

### *Relative Population Density*

169           To estimate relative densities of *P. electromontis*, we calculated the mean number of  
170 individuals per acoustic survey, per survey point, and per study site (including all repeats).  
171 We then estimated relative density of *P. electromontis* for each site to the lowest non-null  
172 average site (i.e. 0.034 ind./survey, Andrafiabe); values of number of individuals/surveys  
173 were used in our calculations of relative site density to control for differences in sampling  
174 effort (number of acoustic surveys) at each survey point and at each site. These estimations  
175 have value for comparison among points and sites (e.g. Butynski 1990; Mutschler et al. 2001)  
176 but are not common densities over a predefined area (e.g. ind/km<sup>2</sup>).

177

### *Elevation and Climatic Variables*

178           For each survey point, we extracted data from the 19 WorldClim recent annual  
179 climatic variables (Bio1-19; resolution ~1 km<sup>2</sup>) commonly used in species distribution models  
180 (Nix 1986; Busby 1991; Booth et al. 2014) using the R package ‘pscl’ (Jackman 2017).  
181 Elevation data were obtained from SRTM 90 m resolution database using the ‘raster’ R  
182 package (R Core Team 2017; Hijmans 2017). We retrieved climate and elevation data for  
183 each survey area by using the GPS point corresponding to the midpoint of all observations  
184 within each site.

185

### *Statistical Analyses*

186           We undertook all statistical analyses in R (R Core Team 2017). We investigated the  
187 influence of forest type, elevation, and climate, on *P. electromontis* presence and relative  
188 population density. We carried out two types of analyses to investigate the relationship  
189 between the presence/absence data gathered on *P. electromontis* and the climate data: i)  
190 Hurdle model analysis (Cragg 1971), which takes into account zero-count-heaviness of our *P.*

191 *electromontis* presence/absence dataset; and ii) Redundancy analysis (RDA), which partitions  
192 and measures the amount of variance explained by climatic variables controlling for other  
193 variables, such as geographic distance. For both analyses, we used the original dataset and a  
194 ‘thinned’ dataset, in which observations were thinned based on geographic distance to reduce  
195 spatial autocorrelation among data. The ‘thinned’ dataset was obtained in R using the  
196 ‘spThin’ package (Aiello-Lammens et al. 2019), setting the thinning parameter (thin.par) to 5  
197 km, that is the minimum distance at which observations have to be separated in order to be  
198 kept in the dataset. We used both Hurdle model and RDA analysis to make our results more  
199 robust.

200 The Hurdle model was fit using the R package ‘pscl’ (Jackman 2017). We tested for the effect  
201 of climate on presence/absence of *P. electromontis* by selecting the climate variables showing  
202 collinearity  $< 0.3$ , ultimately keeping either two or three variables (BIO8: mean temperature  
203 of wettest quarter; BIO12: annual precipitation; BIO19: precipitation of coldest quarter).

204 The RDA analysis was carried out using the R package ‘vegan’ (Oksanen et al. 2019). In this  
205 analysis, we reduced the 19 bioclimatic variables to their most relevant and significant  
206 components by carrying out Principal Components analyses (PCA). To also control for the  
207 effect of geography, geographic distances were transformed in principal coordinates of  
208 neighbor matrices (PCNM) to account for positive spatial autocorrelation among individual  
209 observations (Borcard and Legendre 2002; Dray et al. 2006). Lastly, we repeated the same  
210 analyses with forest type and elevation as predictor variables.

211 We assessed the influence of climate, forest type, or elevation, on the relative population  
212 density of *P. electromontis* (excluding sites with no observations) using generalized linear  
213 modeling (GLM; ‘glm’ function in R). As for the Hurdle model, we selected the climate  
214 variables showing collinearity  $< 0.3$ .

215

### *Ethical Standards*

216 We carried out this study in conformance with the laws of the countries of Portugal, France,  
217 the United Kingdom, and Madagascar (research authorisations [224/11]-[118/11]-[164/12]-  
218 [165/12]-[177/13]-[178/13]-[179/13]-[175/14]-/MEF/SG/DCB.SAP/SCB and [167/16]-  
219 [295/16]-[42/17]-[111/18]-/MEEF/SG/DGF/DSAP/SCB.Re) and with the International  
220 Primatological Society Code of Best Practices for Field Primatology. The research described  
221 in this manuscript followed ASM guidelines (Sikes et al. 2011; Sikes et al. 2016).

222

223

## **RESULTS**

224

### *Calling Activity and Distribution Range*

225 Across the 2,761 point-based acoustic surveys carried out in 66 sites surveyed over an eight-  
226 year period (Fig. 1), we recorded a total of 1,155 *Phaner electromontis* ( $\bar{X} = 0.42$   
227 individuals/survey). This number includes all records of all surveys across all years and  
228 therefore does not represent a population size. *Phaner electromontis* were vocally-active  
229 throughout both the wet and dry seasons but was most vocally-active in the dry season (June-  
230 November; Figure 2A). As previously reported (Charles-Dominique and Petter 1980),  
231 individuals called frequently at the onset of dusk, between 17.30 and 18.30, and at early night,  
232 between 19:00 and 20:00 (Figure 2B).

233

**Fig. 2 near here**

234

235

236

We detected *P. electromontis* in 22 of 66 study sites (33.3%; Fig. 3). Our results confirm the  
occurrence of *P. electromontis* at sites where no *Phaner* previously had been observed, extend  
the distribution of *P. electromontis* 40 km south, to Bezavona-Ankirendrina (BEZ), and report

237 a new isolated population in the Ankarongana forest (ANKA), north of the Irodo River. The  
238 distribution of *P. electromontis* therefore encompasses two National Parks (Montagne  
239 d’Ambre and Ankarana), one Special Reserve (Analamerana), two New Protected Areas  
240 (Andrafiarena-Andavakoera and Loky-Manambato), and several other unprotected areas  
241 (Table 1; Fig. 3).

242 **Table 1 near here**

243 **Fig. 3 near here**

#### 244 *Relative Population Densities*

245 The population density of *P. electromontis* (relative to the site with the lowest density,  
246 Andrafiabe) was highly variable among the 22 presence sites ( $\bar{X} = 32.6$ ,  $\sigma = 30.1$ ). The Station  
247 des Roussettes (Montagne d’Ambre), Bekaraoka, and Bobankora, sites (Loky-Manambato  
248 region) showed the highest relative densities (101.2, 92.1, and 73.5 respectively; Table 1).  
249 The Montagne d’Ambre NP, Manambato-Manambery inter-river system (IRS), and the Loky-  
250 Manambato Protected Area, were the areas with the highest across-sites mean density (Table  
251 1).

#### 252 *Elevation and Forest Type Effects*

253 We recorded *P. electromontis* over a large range of elevations from 18 m (in  
254 Analamerana) to 1,278 m in the Montagne d’Ambre National Park. Presence data and relative  
255 population density showed no clear or significant relationship with elevation, regardless of the  
256 method used (Hurdle, GLM, RDA; Table 2A, C; Fig. 4B, D). We recorded *P. electromontis*  
257 in all forest types, except in littoral forest ( $N = 2$ ; Fig 4A). Presence and relative population  
258 density of *P. electromontis* do not seem affected by forest types (Table 2A, C; Fig. 4C).  
259 However, we found higher presence proportions in ‘Dry/Transition’ than in the other forest

260 types ( $X^2 = 178.33$ ;  $P < 0.001$ ; Fig. 4A). Overall, presence and relative population density  
261 data did not show any significant or relevant relationship either with forest type or elevation;  
262 instead, geography (meant as geographic distances) was the variable explaining the most  
263 variance in the *P. electromontis* presence dataset (18.94% - 36.04%; RDA analysis, Table  
264 2A).

265 **Fig. 4 near here**

#### 266 *Climate Effects*

267 Hurdle and RDA analyses did not identify any evidence of a relationship between  
268 presence probability and climatic variables, whereas a significant amount of variance was  
269 explained by geography, although we used several approaches to account for spatial  
270 autocorrelation (PCNM and spatial thinning). Similarly, relative population density was not  
271 correlated with climate or geography (Table 2C).

272 **Table 2 near here**

### 273 **DISCUSSION**

#### 274 *The Distribution of Phaner electromontis*

275 Across eight years of surveys in 66 sites, our results confirmed the presence of *Phaner*  
276 individuals, most likely *P. electromontis*, in five protected areas, as well as within the isolated  
277 Ankarongana and the unprotected forests of the Manambato-Manambery and Manambery-  
278 Fanambana IRS (Table 1; Fig. 3). We also report the existence of several previously unknown  
279 populations (Fig. 3). In particular, we found *P. electromontis* in several forests south of the  
280 Manambato River, which was considered until recently to constitute the southernmost limit of  
281 the species' distribution (Groves and Tattersall 1991; Mittermeier et al. 2010), and in one

282 small forest patch north of the Irodo River (Ankarongana). These findings extend the  
283 distribution of *P. electromontis* to two inter-river systems further south (Fig. 3) and confirm  
284 its presence between the Manambato and Manambery rivers (Groves and Tattersall 1991;  
285 Hending et al. 2018; Salmona et al. 2018). This represents a significant increase in the known  
286 range of the species, with populations 50 km south of the Manambato river, suggesting the  
287 Fanambana river as its potential southern limit. This new southernmost limit, however, does  
288 not overlap with the northern limit of *P. furcifer* reported in the south of the Sava region  
289 (Groves and Tattersall 1991; Sterling and Rakotoarison 1998). Our results therefore do not  
290 challenge the discontinuous distributions of *Phaner* species without areas of sympatry  
291 suggested by Groves and Tattersall (1991). However, *P. electromontis* also was absent from  
292 66% of our total survey sites, of which 36% were dry forests, 27% humid/transition forests,  
293 18% humid forests, 14% dry/transition forests and 5% littoral forests. The absence of *P.*  
294 *electromontis* from these sites suggests that persistence may not be determined by vegetation  
295 type, but may be more-strongly affected by other habitat characteristics, elevation or climate,  
296 or by other variables (anthropogenic or historical) yet to be quantified.

#### 297 *Forest Type, Elevation, and Climatic Effects*

298 Our results do not show any significant correlation between the presence or relative  
299 population density of *P. electromontis* and the different forest types (Table 2A, C; Fig. 4C),  
300 even though we found a higher proportion of presence sites in ‘dry/transition’ forests (55%)  
301 compared to the other forest types (Fig. 4A). *Phaner* vocalizations have a low frequency  
302 fundamental element (Forbanka 2020) that allows these calls to travel well in densely foliated  
303 habitat types such as humid forest (Forrest 1994). We therefore consider at this point in time  
304 that our higher detection rates in dry forest habitats (and in dryer months, Fig. 2A, Fig. 4) are  
305 not the direct consequence of differences in habitat related call degradation. We do  
306 acknowledge that this hypothesis would need additional studies to be validated. At first

307 glance, the lack of correlation between presence of *P. electromontis* and vegetation types  
308 (Table 2A, C; Fig. 4C) and the high proportion of presences in sites in ‘dry/transition’ forests  
309 may seem contradictory. However, a proportion of presences in sites in ‘dry/transition’ forests  
310 of 55% might not be powerful enough to predict species presence, given that there is a 45%  
311 probability of not having *P. electromontis* observations in ‘dry/transition’ forests. While the  
312 absence of *P. electromontis* in the two visited littoral forests suggests that this forest type  
313 could be unsuitable to its survival, we stress that increasing field effort in littoral forests of  
314 northern Madagascar would be required to confirm this result.

315         We recorded the presence of *P. electromontis* over a wide range of elevations, from 18  
316 m (Analamerana) to an elevation of 1,278 m (Montagne d’Ambre), and our analyses suggest  
317 that *P. electromontis* presence and relative population density both are not significantly  
318 correlated with elevation (Table 2A, C; Figure 4B, D). Similarly, other fork-marked lemur  
319 species also occur over a wide range of elevations (Mittermeier et al. 2010), as well as several  
320 other lemur species such as the indri, *Indri indri* (Glessner and Britt 2005) and the gray-  
321 headed lemur, *Eulemur cinereiceps* (Sterling and Ramaroson 1996), whose population  
322 densities seem little affected by elevation alone. Where relationships between relative  
323 population density and elevation do exist, these likely are caused by elevation-related changes  
324 in temperature or habitat degradation variables (e.g. Sterling and Ramaroson 1996; Goodman  
325 and Ganzhorn 2004; Lehman et al. 2006b). However, in the present study, we did not find a  
326 significant effect of climate on presence or relative population density of *P. electromontis*  
327 (Table 2B, C).

328         Overall, climate, forest type, and elevation, do not explain presence and relative  
329 density of *P. electromontis* in particular sites. Instead, its presence seems explained by  
330 geography (i.e. spatial auto-correlation; Table 2A, B). Recent forest connectivity may have  
331 played a role in the persistence of populations of *P. electromontis* , as has been shown in

332 landscape and movement ecology (e.g. Artzy-Randrup and Stone 2010; Niebuhr et al. 2015).  
333 With regard to recent forest connectivity, the potential role of rivers and open habitat in  
334 limiting connectivity should be formally tested, as has been done in several other primate  
335 species (Lehman 2004; Goossens et al. 2005; Harcourt and Wood, 2012), including lemurs  
336 (e.g. Goodman and Ganzhorn 2004; Quéméré et al. 2012; Aleixo-Pais et al. 2018). The effect  
337 of habitat degradation and disturbance on the relative population density of *P. electromontis*  
338 also should be investigated to better-understand the demography of the species and inform its  
339 conservation, as these parameters often are a profound determinant of lemur population  
340 density (Powzyk and Thalmann 2003; Lehman et al. 2006a; Herrera et al. 2011; Knoop et al.  
341 2018).

342         The disjunct distribution of the other three *Phaner* species, each restricted to certain  
343 forest types (Fig 1; Groves and Tattersall 1991; Mittermeier et al. 2010), suggests strong  
344 habitat preferences in the genus *Phaner*. Surprisingly, we did not find significant relationships  
345 between the presence of *P. electromontis* and environmental variables. Furthermore, *P.*  
346 *electromontis* occurs both in dry and humid forests. *Phaner* species have a gum-specialized  
347 diet (Charles-Dominique and Petter 1980; Génin et al. 2010), and gum trees are known to be  
348 particularly abundant in dry and unpredictable environments (Bearder and Martin 1980; Nash  
349 1986; Génin 2008). Gum tree availability therefore may be an important, or the major,  
350 determinant of the presence of *P. electromontis* in the dry and humid forests of northern  
351 Madagascar, more important than vegetation type, elevation, or climate variables. Testing this  
352 hypothesis would require investigating relationships between gum tree diversity and density,  
353 and the distribution of *P. electromontis*. An alternative hypothesis to explain the lack of a  
354 significant relationship between the presence of *Phaner* and environmental variables might be  
355 that the *Phaner* populations in northern Madagascar belong to more than one species (as  
356 hypothesized by Groves & Tattersall 2001 and Mittermeier et al. 2010). Genetic studies of the

357 *Phaner* populations of northern Madagascar should therefore be conducted to clarify their  
358 taxonomy.

359 *Conservation of Phaner electromontis*

360 Our study allowed us to identify populations beyond the previously known range, with  
361 a significant range increase of 40 km, and a 30% increase of the Extent of Occurrence since  
362 the last IUCN Redlist assessment of this species (Andriaholinirina et al. 2014) (new Extent of  
363 Occurrence = 4,900 km<sup>2</sup>; new Area of Occurrence: 2,400 km<sup>2</sup>). Of the 22 sites where we  
364 found *P. electromontis* to be present, 17 (77.3%) are in protected areas (two National Parks,  
365 two Protected Areas, one Special Reserve). This suggests that *P. electromontis* could benefit  
366 from protection throughout most of its range under the assumption that protection and  
367 conservation are effective (Gardner et al. 2018; Goodman et al. 2018). These new data were  
368 obtained before the last 2018 IUCN assessment of lemurs in Madagascar and thus have been  
369 considered for the assessment of *P. electromontis*' conservation status. Despite the discovery  
370 of new populations, habitat loss remains a concerning threat because deforestation continues  
371 to occur throughout the north of Madagascar (Vieilledent et al. 2018; Goodman et al. 2018).  
372 In particular, some yet unprotected forests hosting populations of *P. electromontis* have  
373 experienced heavy deforestation since our surveys (e.g. Analalava). Our results demonstrate  
374 that if these unprotected forests are not considered urgently for the creation of new protected  
375 areas, unique *Phaner* populations will vanish, likely with other undescribed species sharing  
376 the same habitats. Finally, deforestation rate is increasing throughout all Madagascar,  
377 including the forests of the north where deforestation was low compared to that of the rest of  
378 the island (e.g. Quéméré et al. 2012; Salmona et al., 2017); the forests in the updated  
379 distribution of *P. electromontis* are thus increasingly fragmented (Fig 1-2), thereby reducing  
380 connectivity among *P. electromontis* populations. While our results here focus primarily on

381 environmental variables, more work is needed on anthropogenic factors as a consequence of  
382 human population encroachment to inform and guide conservation.

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405

## SUPPLEMENTARY DATA

406 **Supplementary Data SD1.**—Geographic areas and sites surveyed, their forest type (F.  
407 Type), number of acoustic survey points per site (Points), total number of acoustic surveys  
408 per site, including repeats (Surveys), the mean number of acoustic surveys per point for each  
409 site (Surveys/Point) and *P. electromontis* presence (+) or absence (-). Areas marked with an  
410 asterisk (\*) make up the larger Ramena protected area complex.

411

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708 **FIGURE LEGENDS**

709 **Fig. 1.**—Map of the fixed-point acoustic surveys performed in northern Madagascar between 2011  
710 and 2018. In the top left, we show the currently described distribution of the four *Phaner* species  
711 across Madagascar: blue – *P. pallescens*, orange – *P. parienti*, red – *P. electromontis*, purple – *P.*  
712 *furcifer*. M. d’Ambre: Montagne d’Ambre; ANKA: Ankarongana; BEK: Bekaraoka; BOB:  
713 Bobankora; SAL: Salafaina; BEZ: Bezavona-Ankirendrina; ANALV: Analalava.

714 **Fig. 2.**—Histograms showing (A) the month and (B) the time in which *P. electromontis* individuals  
715 were detected during the acoustic surveys.

716 **Fig. 3.**—Presence and absence of *P. electromontis* over the 66 study sites and four additional sites  
717 from the literature (Hawkins et al. 1990, Randrianarisoa et al. 1999; Salmona et al., 2018) within  
718 northern Madagascar. Shaded polygons show the IUCN distribution of *P. electromontis*  
719 (Andriahonirina et al., 2014). The seven red dots located outside the polygons thus represent new  
720 localities where a *Phaner* species is present, most likely *P. electromontis*. M. d’Ambre: Montagne  
721 d’Ambre; ANKA: Ankarongana; BEK: Bekaraoka; BOB: Bobankora; SAL: Salafaina; BEZ:  
722 Bezavona-Ankirendrina; ANALV: Analalava.

723 **Fig. 4.**—A) Percentages of acoustic points of sites with *P. electromontis* presence, B) elevation  
724 distribution of acoustic points with *P. electromontis* presence or absence, C) relative population  
725 density of sites with *P. electromontis* presence and D) relationship between relative population  
726 density and elevation for the sites with *P. electromontis* presence within five forest types of  
727 northern Madagascar. Forest types: D – dry, D/T – dry-transitional, H – humid, H/T – humid-  
728 transitional, L – littoral.

729

730 **TABLES**

731 **Table 1.**—Results of the *P. electromontis* acoustic surveys - Geographic areas and sites surveyed where *P.*  
 732 *electromontis* was present, the number of *P. electromontis* detections during total surveying effort per site, the mean  
 733 number of *P. electromontis* per survey, and relative population density of *P. electromontis* per site (D) and geographic  
 734 area [D (Area)].

Area	Study site	# ind.	Ind/survey	D	D (Area)
Analamerana Special Reserve	Anteninaomby Ampondrabe	13.0	0.1	3.6	0.6
	Ambohanandramy	10.0	4.1	32.7	
Montagne d'Ambre National Park	Andasibe	4.0	0.6	7.4	56.6
	Station des Roussettes	86.0	4.2	101.2	
Andrafiarena Andavakoera Protected Area	Ampantsogno Anjahankely	13.0	0.1	2.3	
	Antserasera	11.0	0.2	4.9	2.0
	Analamahitsy	66.0	2.2	41.3	
	Andrafiabe	4.0	0.0	1.0	
Ankarana National Park	Mahamasina	160.0	0.6	32.9	28.9
	Marotaolana Ambondromifehy	132.0	2.2	47.4	
	Marovato	130.0	0.6	34.1	
Ankarongana	Ankarongana	2.0	0.1	1.3	1.3
	Antsahabe	11.0	0.4	7.2	
	Antsakay	142.0	4.8	62.3	
Loky-Manambato Protected Area IRS	Bekaraoka	72.0	10.2	92.1	
	Binara	65.0	0.9	31.8	30.7
	Bobankora	20.0	10.5	73.5	
	Bobankora East	85.0	3.3	55.6	
	Analafiana	107.0	1.6	43.7	
Manambato-Manambery IRS	Analamanara	3.0	9.8	29.4	33.1
	Salafaina	10.0	0.4	8.2	
Manambery-Fanambana IRS	Bezavona Ankirendrina	9.0	0.0	2.9	2.8

735  
736

737 **Table 2.**—Relationship between presence or relative population density of *P. electromontis*  
738 and environmental variables. **A)** Results for the presence/absence data of *P. electromontis* in  
739 relation to Forest type (F), Elevation (E), and Geography (G). **B)** Presence/absence data of *P.*  
740 *electromontis* in relation to climatic variables. **C)** Relative population density of *P.*  
741 *electromontis* in relation to Forest type (F), Elevation (E), Geography (G), and Climate (C).  
742 “|” defines the condition in which the effect of the first variable is controlled by the effect of  
743 the second variable. Hurdle: hurdle model; RDA: redundancy analysis; GLM: generalized  
744 linear modeling. ‘not thinned’: original dataset; ‘thinned’: dataset in which records at less  
745 than 5km are removed.  $R^2$ : Adjusted  $R$ -squared, which measures the percentage of variation  
746 explained by a particular variable. Values within parenthesis refer to  $P$  value. BIO var:  
747 Bioclimatic variables.

748 A)

Hurdle	Forest type		Elevation	
	Coeff. ( $P$ value)		Coeff. ( $P$ value)	
not thinned	0 (0.6)		0 (0.31)	
thinned	-0.2 (0.14)		0 (0.12)	
RDA	F   G	G   F	E   G	G   E
not thinned	$R^2 = 0.2\%$ (0.001)	$R^2 = 36\%$ (0.001)	$R^2 = 0.1\%$ (0.12)	$R^2 = 34.6\%$ (0.001)
thinned	$R^2 = 0\%$ (0.89)	$R^2 = 18.9\%$ (0.001)	$R^2 = 0\%$ (0.28)	$R^2 = 18.8\%$ (0.001)

749 B)

Hurdle	BIO var	Coeff. ( $P$ value)
not thinned	BIO8	0 (0.59)
	BIO12	0 (0.19)
thinned	BIO8	0 (0.27)
	BIO12	0 (0.27)
	BIO19	0 (0.06)
RDA	C   G	G   C
not thinned	$R^2 = 0.6\%$ (0.001)	$R^2 = 31.7\%$ (0.001)
thinned	$R^2 = 0\%$ (0.43)	$R^2 = 17.7\%$ (0.001)

751 C)

GLM	BIO var	Coeff. ( $P$ value)
	BIO6	0.2 (0.7)
	BIO12	-0.1 (0.26)
	BIO18	0 (0.78)
	Forest type	Coeff. ( $P$ value)
		-3.9 (0.49)
	Elevation	Coeff. ( $P$ value)
		0 (0.87)

752

RDA	C   G	G   C
	$R^2 = 0\%$ (0.75)	$R^2 = 20.1\%$ (0.34)
	F   G	G   F
	$R^2 = 0\%$ (0.62)	$R^2 = 23.9\%$ (0.26)
	E   G	G   E
	$R^2 = 3.4\%$ (0.25)	$R^2 = 35.6\%$ (0.18)

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