

1 **REVIEW**

2 **Elevation gradients of lemur abundance emphasise the importance of Madagascar's**  
3 **lowland rainforest for the conservation of endemic taxa**

4

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25 **ABSTRACT**

26 1. Elevation gradients correlate with changes in several environmental conditions and are  
27 known to influence animal abundance. Animals in regions with a naturally limited extent of  
28 lowland rainforest are expected to have evolved adaptations to intermediate elevations that  
29 provided a stable environment during their evolution.

30 2. Since the lowland rainforest of Madagascar has a limited extent and suffers from  
31 increasing anthropogenic pressure, it is essential to understand how well species tolerate  
32 intermediate and high elevations. In this study, we aim to quantify the relationship between  
33 lemur abundance and elevation in the eastern rainforest of Madagascar.

34 3. We correlated abundance data on 26 lemur species (10 genera), including 492 records from  
35 26 studies, with elevation. We analysed the consistency of correlations across species with a  
36 meta-analytical approach. We assessed the relationship between species' body mass and  
37 elevational gradients of abundance, and controlled for species' elevational range and median  
38 elevation. We then ran generalised linear mixed models to determine whether encounter rates  
39 were influenced by elevation, body mass, plant productivity, and anthropogenic disturbance.

40 4. Overall, the abundance of lemur species in Malagasy rainforests was negatively correlated  
41 with elevation, and species occupying broader elevational ranges showed stronger  
42 correlations. Body mass did not influence species' tolerance of high elevations. Even though  
43 several lemur species showed tolerance to the elevation gradient, the few remaining large  
44 patches of lowland rainforests host lemur species at greater abundances than other sites.  
45 Abundance across species was negatively related to body mass, elevation and seasonality in  
46 plant productivity, and positively related to plant productivity and anthropogenic disturbance.

47 5. Despite the ecological flexibility of many lemur species, the largest remnant patches of  
48 lowland rainforests host the highest levels of lemur abundance and are key to lemur

49 conservation. It is crucial to preserve this priority habitat both for biodiversity conservation  
50 and for our understanding of lemur adaptations.

51

52 **Keywords:** altitude, lowland rainforest, Madagascar, meta-analysis, primate

53

## 54 **INTRODUCTION**

55 The study of elevation gradients in relation to biodiversity patterns has received renewed  
56 interest in ecology, biogeography, and climate change research (Lomolino 2001, Körner  
57 2007, McCain 2007, Malhi et al. 2010). High-elevation tropical ecosystems are of particular  
58 interest, since they may have represented essential refugia during drier periods in the tropics  
59 (Wilmé et al. 2006, Colwell et al. 2008, Malhi et al. 2010). Studying the effects of elevational  
60 gradients on animal distribution and populations can unveil species' niche tolerance and help  
61 us to understand their abilities to cope with environmental changes (Körner 2007). Many  
62 studies have been focused on species' diversity patterns along elevational gradients (e.g.  
63 Brown 2001, Heaney 2001, Lomolino 2001, Rahbek 2005, McCain 2007), while only few  
64 comparative studies have explored patterns of abundance in relation to elevation (e.g. Silva et  
65 al. 2001, Bateman et al. 2010). This relationship needs further investigation, since abundance  
66 is related to extinction risk, and understanding geographic patterns of animal abundance is  
67 key to informing conservation strategies (Brown et al. 1995, Sanderson 2006). Patterns of  
68 abundance are mainly the result of interactions between species' biological traits (e.g. those  
69 related to energetics), intra- and inter-specific interactions (e.g. territoriality and competition,  
70 respectively), environmental factors (e.g. resource availability and weather), and  
71 anthropogenic disturbance (Silva et al. 1997, Lomolino 2001, Benítez-López et al. 2017,  
72 Novosolov et al. 2017, Santini et al. 2018). Among species-specific characteristics, body  
73 mass and diet have been identified as major drivers of abundance in terrestrial vertebrates

74 (Silva et al. 1997, Santini et al. 2018), with large species and those at higher trophic levels  
75 living at lower abundance due to their higher energetic requirements and lower resource  
76 availability (Blackburn et al. 1993, Silva et al. 1997, Santini et al. 2018).

77 High elevation habitats tend to be more isolated than low elevations, and therefore  
78 generally suffer lower anthropogenic disturbance (Lomolino 2001). Furthermore, several  
79 environmental conditions are associated with elevational gradients (Brown 2001, Lomolino  
80 2001, Körner, 2007, McCain 2007). Ambient temperature, atmospheric pressure and partial  
81 pressure of biologically important gases (e.g. oxygen and carbon dioxide) gradually decrease  
82 with an increase in elevation (Brown 2001, Körner 2007). Other environmental conditions,  
83 such as precipitation and plant productivity, do not follow a specific elevation trend but vary  
84 in different regions (Brown 2001, Körner 2007). In the tropics, optimal conditions for plant  
85 productivity and precipitation generally reach their maximum at intermediate elevations  
86 (around 800-1000 m above sea level - a.s.l.; Körner 2007, Propastin 2011, but the elevation  
87 varies among regions, e.g. it is 1500 m a.s.l. in the Philippines; Heaney 2001). Therefore,  
88 tropical species are usually expected to reach their peak abundance at intermediate elevations  
89 (Lomolino 2001).

90 Madagascar is a major hotspot of biodiversity and endemic species (Myers et al.  
91 2000), many of which are now threatened with extinction (Schwitzer et al. 2014). Around  
92 50% of Madagascar's eastern rainforests have been lost since the 1950s. Deforestation has  
93 increased rapidly in recent decades (Vieilledent et al. 2018), and lowland rainforests are  
94 particularly affected (Scales 2014). The lowland rainforest has a naturally limited extent in  
95 Madagascar since large portions of the eastern floodplains drifted away as a consequence of  
96 the break-up of the Indo-Madagascar subcontinent between 90 and 80 million years ago  
97 (Krause 2003, Wells 2003). Thus, lemurs have been hypothesised to have evolved  
98 adaptations to cope with intermediate elevations that represented a more stable environment

99 and a larger expanse of forest than lowland rainforests during the Pleistocene (Messmer et al.  
100 2000, Goodman & Ganzhorn 2004). In support of this hypothesis, the average intermediate  
101 elevation point for lemur species diversity (around 900 m a.s.l.) is higher than that for  
102 primates outside Madagascar (around 400 m a.s.l.; Goodman & Ganzhorn 2004, Lehman  
103 2014). The large data set accumulated over the last decade on lemur abundance and  
104 distribution at rainforest sites and the easy access to contextual ecological data offer the  
105 opportunity to explore this hypothesis with more robust analyses. The eastern rainforest in  
106 Madagascar occupies a continuum from low to high elevations, and several lemur species  
107 occur over the entire elevational range while others are restricted to narrow geographic  
108 ranges (Goodman & Ganzhorn 2004, Wilmé et al. 2006). Considering the reduced area of  
109 lowland rainforest left on the island (Schwitzer et al. 2014), identifying the lemur species that  
110 have high abundance in lowland rainforest is imperative both for their conservation and for  
111 our understanding of their adaptations.

112 In this study, we aimed to quantify responses of lemur abundance to elevational  
113 gradients in the eastern rainforests of Madagascar. We considered different threats and  
114 constraints to make our predictions: surface effect and plant productivity for intermediate  
115 elevations, metabolic effects for small lemur species, and human impact for large lemur  
116 species. Considering that the optimal conditions for plant productivity usually occur at  
117 intermediate elevations in the tropics and lemur diversity is known to be higher at  
118 intermediate elevations, we hypothesised that the maxima of population abundance for most  
119 lemur species also occur at intermediate elevations (600-1200 m a.s.l.; Lehman 2014). We  
120 also hypothesised that small lemur species would show their maxima of abundance in  
121 lowland rainforests, since the ratio between energy expenditure and nutrient intake is  
122 disadvantageous for them at high elevations due to the increased costs of thermoregulation  
123 and locomotion in cool and harsh habitats (Caldecott 1980). Conversely, larger species,

124 generally more threatened by anthropogenic activities, may show their maxima of abundance  
125 at high elevations which are less accessible to humans (Lomolino 2001, Körner 2007).

126 To test these hypotheses, we determined the effect sizes of the correlation coefficients  
127 between species encounter rates (a proxy of abundance) and elevation. This determination  
128 was achieved via a meta-analysis to identify the overall effect across all species and genera,  
129 and how these relationships are influenced by body mass. To investigate in more depth  
130 whether the species reached a peak of abundance at intermediate elevations, and test the  
131 influence of body mass, plant productivity and its seasonality, and anthropogenic disturbance,  
132 we also ran a linear model with both linear and quadratic terms. Specifically, we predicted:

133 1) No monotonic relationship between abundance and elevation for the lemur species  
134 that occur over the entire elevational range, since the best conditions for their survival are  
135 expected to be at intermediate elevations.

136 2) A positive effect of body mass on the correlation coefficient between abundance  
137 and elevation, reflecting the expectation that larger species with higher volume/surface ratios  
138 cope better with low temperatures due to the increase in heat conservation.

139 3) An effect of median elevation and elevational range on the effect sizes, because the  
140 relationship between elevation and abundance can be influenced by the elevational  
141 distribution of the species. In particular, species occupying broader elevational ranges were  
142 expected to show a weaker relationship between elevation and abundance than species  
143 showing limited elevational variation.

144 4) A positive influence of plant productivity; a negative influence of body mass,  
145 seasonality in plant productivity, and anthropogenic disturbance.

146

## 147 **METHODS**

### 148 **Data collection**

149 We collected population abundance estimates from the literature (including peer-reviewed  
150 and grey literature) for lemur species inhabiting the eastern rainforest of Madagascar. We  
151 excluded the littoral forests on sandy soil, since these habitats differ from rainforests (Bollen  
152 & Donati 2006). We used Google Scholar and Web of Science as search engines with the  
153 following research terms: abundance OR encounter rate OR density, AND lemur OR primate  
154 AND Madagascar, AND rainforest. We then excluded rainforest from the search in case any  
155 publications on lemur abundance in rainforests had been missed. We then inspected the  
156 papers and retained those that contained relevant data. We also searched other sources such  
157 as dissertations, book chapters, the International Union for Conservation of Nature's Species  
158 Survival Commission Primate Specialist Group newsletter (Lemur News), and the Fieldiana  
159 Zoology series (that included a large dataset on lemur encounter rates at different elevations).

160 We included a total of 26 publications in the meta-analysis. We used encounter rates  
161 (observed individuals per transect length) and not density estimates (estimated individuals per  
162 area) for analysis, since the former were more frequent in the literature. We excluded  
163 *Daubentonia madagascariensis* from the analysis since this lemur is very difficult to detect  
164 with line transects, and encounter rates are likely to be underestimated. Using the geographic  
165 coordinates of the 26 studies, we extracted average values for the Normalised Difference  
166 Vegetation Index (NDVI; proxy of plant productivity), the seasonality in plant productivity  
167 (NDVI<sub>sd</sub>), and the Human Influence Index (HII; proxy of anthropogenic disturbance; Venter  
168 et al. 2016). NDVI variables were calculated starting from monthly layers between 1990 and  
169 2015 with a resolution of 0.1 degree (~11 km) downloaded from  
170 <https://neo.sci.gsfc.nasa.gov/>. HII is a composite variable with a resolution of 30 arc-seconds  
171 (~1km) that integrates human population density, human land use and infrastructure, and  
172 human access.

173

174 **Data analysis**

175 We estimated the relationship between encounter rate and elevation for each lemur species  
176 using Spearman rank correlations. We transformed correlation coefficients to Fisher's  $z$   
177 scores using the correlation sample size to obtain the effect size  $z$  [1] and variance  $V_z$  [2] for  
178 each correlation:

179 
$$z = 0.5 \times \ln\left(\frac{1+r}{1-r}\right) \quad [1]$$

180 
$$V_z = \frac{1}{n-3} \quad [2]$$

181 where  $r$  is the correlation coefficient and  $n$  is the sample size. To estimate the overall trend  
182 and agreement across species, we performed a meta-analysis on the  $z$  scores and their  
183 variance (Borenstein et al. 2009). Correlations with  $n < 5$  were excluded from the analysis as  
184 they do not allow the estimation of variance. We ran a mixed-effect meta-analysis on the  
185 transformed effect size values and the associated variance to calculate a summary effect size,  
186 where species were treated as random effects. We tested the residual heterogeneity using the  
187 Q-statistic, where a significant Q test indicates that a significant amount of variability exists  
188 between the effect sizes. Then, to estimate the summary effect size per genus, we repeated the  
189 same meta-analysis including genera as fixed effects and removing the model's intercept  
190 (Schwarzer et al. 2015). We tested the difference between genera with the Tukey test. Finally,  
191 to test whether species body mass, the elevational range, and the median elevation affected  
192 the relationship between abundance and elevation, we used these three variables as  
193 moderators (covariates) in three meta-regressions. Body masses for all species in our dataset  
194 were collected from MADA (the Malagasy animal trait data archive) and were log10-  
195 transformed for the meta-regression (Razafindratsima et al. 2018). We tested the overall  
196 effect of fixed effects and moderators using the omnibus test. A significant omnibus test  
197 indicated that fixed effects and moderators contributed to explaining a significant part of the  
198 residual variance in the effect sizes. We used an alpha level of 0.05 to test significance. We



199 also tested for phylogenetic signal in the residuals of the meta-analysis using Pagel's Lambda  
200 test (Freckleton et al. 2002) and the phylogeny from Herrera and Davalos (2016), and we did  
201 not find an effect ( $\text{Lambda}=6.611e^{-05}$ ;  $p=1.000$ ). The analysis was done using the 'metafor'  
202 package (Viechtbauer 2010) in R v. 3. 3.2 (R Core Team 2016).

203 To test whether lemur abundance and elevation had a quadratic relationship, we ran a  
204 Generalised Linear Mixed Model with a Poisson family. Firstly, we multiplied each  
205 encounter rate with the transect length to obtain the observation counts as response variable,  
206 and then we used transect length ( $\log_{10}$ ) as an offset in the analysis (Benítez-López et al.  
207 2017). We included body mass ( $\log_{10}$ ), elevation ( $\log_{10}$ ), and NDVI,  $\text{NDVI}_{\text{sd}}$ , and HII ( $\log_{10}$ )  
208 as fixed effects in the model, using both linear and quadratic effects. We used nested random  
209 effects with Family, Genus and Species levels to allow for different intercepts due to  
210 taxonomic-specific encounter rates. We then ran a full model selection and selected the best  
211 model based on the Akaike information criterion (Appendix S1). We tested for phylogenetic  
212 signal in the residuals of the model using Pagel's Lambda and found no significant effect  
213 ( $\text{Lambda}=0.280$ ;  $p=0.214$ ). Since the model including HII detected an effect that seemed  
214 likely to be spurious, we ran a second model without HII and considered this model for  
215 spatial predictions. As in the first model, we did not find a phylogenetic signal in this second  
216 model ( $\text{Lambda}=0.295$ ;  $p=0.131$ ). We predicted from the model only within a buffer of 0.5  
217 degrees from our observations and using the digital elevation model in Robinson et al.  
218 (2014).

219

## 220 **RESULTS**

221 In total, we included 492 abundance data-points from 26 lemur species (10 genera)  
222 distributed throughout the extent of Madagascar's eastern rainforest in the meta-analysis  
223 (Appendix S2, Figure 1, Table 1). Overall, the abundance of lemur species in rainforests was

224 negatively correlated with elevation, but a significant amount of residual heterogeneity  
225 existed between effect sizes, indicating a substantial variability between species (Figure 2,  
226 Table 2). Only a limited number of species showed significant correlation coefficients  
227 (Figure 2) and peaks of abundance at low elevations (Appendix S3). For the species *Avahi*  
228 *meridionalis*, *Avahi laniger*, *Eulemur albifrons*, *Eulemur collaris*, *Lepilemur fleuretae*, and  
229 *Microcebus tanosi* a significant negative correlation existed between abundance and  
230 elevation, while for *Lepilemur microdon* and *Propithecus candidus* there was a significant  
231 positive correlation (Figure 2). The meta-analysis using genera as fixed effects did not detect  
232 any significant correlation coefficients between abundance and elevation (Figure 3, Table 2).  
233 Similarly, the Tukey post-hoc test did not detect any significant difference between  
234 correlation coefficients per genus (Appendix S4). We found that species' body sizes were not  
235 significantly related to the correlation coefficients obtained via the meta-analysis (Appendix  
236 S5, Table 2). The correlation coefficients between lemur abundance and elevation were  
237 negatively related to the species' elevational range (Appendix S5, Table 2) and positively  
238 related to the species' median elevation (Appendix S5, Table 2).

239         The selected mixed effect model estimating the trend across species also showed a  
240 negative relationship between lemur encounter rates and elevation (Appendix S6, Figure 4).  
241 Furthermore, encounter rates were negatively related to species' body mass, positively related  
242 to NDVI and negatively related to NDVI<sub>sd</sub> (Appendix S7). When HII was included in the  
243 model, the relationship between lemur abundance and the other variables in the model  
244 remained the same, and HII was positively related to lemur abundance (Figure 4). We only  
245 report the spatial predictions for the model without HII, since the predictions based on the  
246 model with HII are likely to reflect a spurious effect (Appendix S8). The model predicted the  
247 highest lemur abundances to occur in the lowland rainforests of Makira-Masoala,  
248 Tsitongambarika, and in forest fragments at intermediate latitudes (Figure 5). We also tested

249 the relationship between elevation and NDVI; it is described by a loess curve that peaks at  
250 low elevation (Appendix S9).

251

## 252 **DISCUSSION**

253 Elevation was significantly related to the abundance of lemurs. Within species, encounter  
254 rates were negatively correlated with elevation, and the average encounter rate for all species  
255 also decreased with increasing elevation. While we expected lemurs to reach their maxima of  
256 abundance at intermediate elevations, lowland rainforests appear to host higher lemur  
257 abundance than habitats at intermediate elevations. Our prediction was based on the  
258 observation that plant production should reach its maximum at intermediate elevation, where  
259 optimal values of mean temperature, around 20°C, and annual global radiation, around 6800  
260 MJ/m<sup>2</sup>, are expected in rainforests (White et al. 2000, Propastin 2011). Given the latitudinal  
261 extent of the eastern rainforest of Madagascar (from 14°10' to 24°57' S), the elevations at  
262 which conditions are optimal for plant productivity are likely to show large variation. An  
263 average temperature of 20°C can be found, for example, at an elevation of around 600 m a.s.l.  
264 in the Andohahela National Park (24°-25° S), and at around 950 m a.s.l. in the Marojejy  
265 National Park (14°-15° S; Karger et al. 2017a, b). In fact, plant productivity in our dataset is  
266 higher at low elevations (Appendix S9) and this figure is in accordance with the finding that  
267 the highest lemur abundance is found in lowland rainforests.

268 Our results indicate that the remnant lowland rainforests that have a low habitat  
269 disturbance host lemur species at higher abundances than other sites. For example, most of  
270 the lemur species (*Avahi meridionalis*, *Eulemur collaris*, *Lepilemur fleuretae*, and  
271 *Microcebus tanosi*) inhabiting one of the largest areas of lowland rainforest, the  
272 Tsitongambarika Protected Area in south-eastern Madagascar, showed higher abundances at  
273 low elevations. The other species that showed higher abundance at low elevations, *Eulemur*

274 *albifrons*, also inhabits a large area of undisturbed lowland rainforests in north-eastern  
275 Madagascar, the Makira Protected Area. This species of *Eulemur* is also present at high  
276 densities in the other large area of lowland rainforest in Madagascar, the Masoala National  
277 Park (148 individuals/km<sup>2</sup>; Sterling & Rakotoarison 1998). Among nocturnal species, *Avahi*  
278 *laniger* reached peak abundance in the lowland rainforest fragments of Antsahanadraitry,  
279 located at intermediate latitudes, and at Manompana, located in the north-east (Appendix S2).

280 Small fragments of lowland rainforests are of great value for conservation (Turner &  
281 Corlett 1996). Our results support this, and indicate that remnant lowland rainforests with low  
282 habitat disturbance may contain abundant lemurs. Nevertheless, lemur species that have their  
283 maxima of abundance in lowland rainforests may be particularly vulnerable to habitat  
284 degradation, since they are adapted to more stable ecological conditions (Green & Sussman  
285 1990, Turner 1996, Myers et al. 2000, Gibson et al. 2011). For example, Sharma et al. (2014)  
286 found that primate specialists of lowland rainforests are reduced in abundance or extirpated in  
287 small fragments, while generalist species are more abundant there as a consequence of their  
288 ability to adapt to different environments. However, the tolerance of species to human  
289 disturbance may, in fact, vary considerably (Ewers & Didham 2006). Several lemur species  
290 are known to tolerate some levels of habitat degradation via shifts in activity patterns and  
291 dietary choices (Irwin et al. 2010, Donati et al. 2016, Sato et al. 2016). This tolerance may  
292 explain why we found a positive relationship between abundance and HII. Also, low levels of  
293 habitat disturbance may provide benefits, such as high food availability and higher food  
294 nutritional content (Ganzhorn 1995). Some species actually benefit from modified habitats, as  
295 previously reported in lemurs (e.g. Herrera et al. 2011, Eppley et al. 2017), in other primates  
296 (e.g. Zarate et al. 2014, Nekaris et al. 2017), and in animal species in general (Bhagwat et al.  
297 2008).

298 Most lemur species are able to occupy the entire elevation gradient that, at least in the  
299 tropics, is strictly associated with a temperature gradient (Malhi et al. 2010) and with other  
300 environmental variables such as plant productivity. This tolerance to variation in elevation  
301 can be explained by the fact that lemurs exhibit several behavioural and physiological  
302 adaptations to cope with low temperatures and lean periods. For example, some cheirogaleids  
303 of the genera *Cheirogaleus* and *Microcebus* enter prolonged periods of torpor or hibernation  
304 during the cold, dry season when resource availability is low (Dausmann et al. 2009). These  
305 physiological responses to cold and harsh environments are exceptional in the tropics and are  
306 rarely shown in other tropical taxa (McKechnie & Mzilikazi 2011, Ruf & Geiser 2015).  
307 Larger lemur species cope with low temperatures by sun-basking (e.g. *Varecia*; Vasey 2002)  
308 or huddling in groups (*Eulemur*; Donati et al. 2011; *Hapalemur* Eppley et al. 2017). Huddling  
309 is a common strategy used by social mammals and birds to reduce energy expenditure  
310 (Gilbert et al. 2010). Other proposed adaptations to the harsh Malagasy environment include  
311 low basal metabolic rate (Wright 1999) and other flexible behaviours related to the energy  
312 minimiser strategy (Donati & Borgognini-Tarli 2006, Norscia et al. 2012, Campera et al.  
313 2014). These adaptations allow lemurs to be more taxonomically diverse throughout a wider  
314 range of elevations than primates on other continents (Goodman & Ganzhorn 2004).

315 The only lemur species that was most abundant at high elevations was *Propithecus*  
316 *candidus*. This finding is in line with previous studies indicating that this species can inhabit  
317 several types of high-elevation habitats, including sclerophyllous forests and low ericoid  
318 bushes (Patel 2014). *Propithecus candidus* is also known for its thick pelage that may  
319 represent an adaptation for cold climates at high elevations (Lehman et al. 2005). This species  
320 can also be found at low elevations (235 m a.s.l.) in the Makira National Park at very low  
321 densities, although abundance has not been estimated (Patel & Andrianandrasana 2008). The  
322 highest abundance of *Propithecus candidus* was recorded in the Marojejy National Park,

323 which represents a priority conservation site for this Critically Endangered lemur (Patel  
324 2014).

325         We predicted a negative relationship between body mass and tolerance of high  
326 elevations, reflecting the ability of large animals to cope with cold environments (Blackburn  
327 et al. 1999). Yet, we found no significant relationship, suggesting that body mass was not an  
328 important factor explaining the elevation gradients of lemur abundance in the eastern  
329 rainforest. For example, the genus *Microcebus*, which includes the smallest lemurs in  
330 Madagascar ranging from 30 to 70 g in weight (Mittermeier et al. 2010), did not show higher  
331 abundances at low elevations. Only the abundance of *Microcebus tanosi* was significantly  
332 negatively related to elevation. The negative correlation coefficient between elevation and  
333 abundance was stronger for species present over a large elevation range, including lowland  
334 rainforests (Appendix S5). This finding contradicts our hypotheses, since the best conditions  
335 were expected at intermediate elevations (around 900 m a.s.l.) for most species. These results  
336 may be due to the fact that encounter rates were only available in two large portions of  
337 lowland rainforest, the Tsitongambarika Forest in the south-east and the Makira Forest in the  
338 north-east of Madagascar. Most of the lowland rainforests at intermediate latitudes have been  
339 cleared or reduced to small fragments where lemurs have been largely extirpated (Green &  
340 Sussman 1990, Vieilledent et al. 2018). Few remaining lowland forest fragments in central  
341 Madagascar can support populations of large lemurs (Ganzhorn et al. 2001), and even in  
342 larger fragments there has been an increase in human impacts. As a result, most of the  
343 encounter rates are from sites above 450 m a.s.l. We cannot exclude the possibility that some  
344 species have a larger elevational range not reflected by data on abundance in the literature.  
345 Nevertheless, the data considered for this analysis encompass all the elevation strata and we  
346 consider them representative for the eastern rainforest.

347           It is likely that the current distribution of many extant lemurs does not reflect their  
348 niche tolerance, but it is rather limited to areas of low anthropogenic impact where they were  
349 able to persist. A reduction of the elevational range of occurrence may have reduced the  
350 strength of the abundance – elevation relationship, thus masking a stronger dependence of  
351 species on low-elevation habitats. Indeed, the distortion of natural macroecological pattern is  
352 a common phenomenon that can limit our understanding of causal relationships in nature  
353 (Varela et al. 2009, Di Marco & Santini 2015, Santini et al. 2017). Other factors (e.g. plant  
354 productivity, competition; Herrera et al. 2018, Santini et al. 2018) may have contributed to  
355 lemur abundance patterns, although understanding the complexity of these interactions was  
356 beyond the scope of this study.

357           Although lemur species are well-known for their ecological, physiological, and  
358 behavioural flexibility, we found that their abundance was generally higher at lower  
359 elevations. Given the limited extent of undisturbed lowland rainforests in Madagascar, it is  
360 pivotal to promote conservation measures to maintain this habitat that hosts high abundances  
361 of several lemur species (Kremen et al. 1999, Campera et al. 2017). Rapid habitat degradation  
362 is occurring elsewhere in lowland rainforests (Myers et al. 2000, Gibson et al. 2011), so a  
363 similar analysis could be extended to other regions of the world where endemic taxa occur at  
364 different elevations, to determine their ability to occupy elevation gradients. Our results  
365 suggest that the lowland rainforest at intermediate latitudes in Madagascar may have  
366 contained large populations of lemurs, and that some of the most suitable areas for  
367 conservation may have already disappeared. Although there are no lemur species that are  
368 exclusively found in lowland forests and thus, strictly speaking, lemurs may be less  
369 vulnerable than other taxa to the disappearance of this habitat, losing this environment is not  
370 only important for conservation reasons. The eastern rainforest of Madagascar represents a  
371 continuum from low to high elevations, and the ability of the lemurs to use this elevational

372 range has been hypothesised to explain the macroevolution of this group (Goodman &  
373 Ganzhorn 2004, Wilmé et al. 2006). The vanishing of the lowland habitats will thus hamper  
374 forever our ability to understand fully the adaptations and flexibility of this extraordinary  
375 group of primates.

376

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382

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605

606 **Table 1:** Number of study locations (N; 492 in total), body mass (g), and expected and  
607 observed elevation range (m a.s.l.) for each of the 26 lemur species included in the meta-  
608 analysis. The data are derived from 26 publications. The expected elevation range includes all  
609 the locations in which the species is expected to be found based on species accounts,  
610 including sites where it was not encountered during transects, while the observed elevation  
611 range includes only the locations where the species was encountered. Body mass was  
612 retrieved from Razafindratsima et al. (2018), apart from *Microcebus tanosi* which was  
613 retrieved from Rasoloarison et al. (2013).

614

Species	N	Body mass (g)	Elevation range (expected; m a.s.l.)	Elevation range (observed; m a.s.l.)
<i>Avahi laniger</i>	15	1180	210–1550	210–1260
<i>Avahi meridionalis</i>	10	1213	178–1875	178–1500
<i>Avahi peyrierasi</i>	34	1034	180–1625	180–1625
<i>Cheirogaleus crossleyi</i>	19	292	638–1262	638–1262
<i>Cheirogaleus major</i>	24	468	178–1625	178–1625
<i>Eulemur albifrons</i>	11	1896	275–1875	275–1260
<i>Eulemur albocollaris</i>	6	2250	67–1625	67–1210
<i>Eulemur collaris</i>	13	2180	125–1875	125–1875
<i>Eulemur fulvus</i>	6	1633	905–1224	905–1224
<i>Eulemur rubriventer</i>	57	1978	180–1875	180–1625
<i>Eulemur rufifrons</i>	40	2151	180–1625	180–1625
<i>Hapalemur aureus</i>	6	1580	720–1625	810–1625
<i>Hapalemur griseus</i>	37	813	638–1283	638–1283
<i>Hapalemur meridionalis</i>	16	855	178–1875	178–1625
<i>Hapalemur occidentalis</i>	11	847	450–1875	450–1625
<i>Indri indri</i>	12	6593	500–1550	500–1224
<i>Lepilemur fleuretae</i>	9	890	178–1875	178–440
<i>Lepilemur microdon</i>	31	1105	638–1625	720–1625
<i>Lepilemur seali</i>	10	952	450–1625	520–1625
<i>Microcebus mittermeieri</i>	7	45	450–1625	450–1625
<i>Microcebus rufus</i>	33	44	638–1625	638–1625
<i>Microcebus tanosi</i>	11	52	178–1875	178–1875
<i>Prolemur simus</i>	8	2395	180–1625	180–1224
<i>Propithecus candidus</i>	10	5270	450–1875	520–1875
<i>Propithecus edwardsi</i>	37	5686	638–1625	638–1262
<i>Varecia variegata</i>	19	3524	180–1224	180–1224

615 **Table 2.** Results of the intercept-only meta-analysis, the meta-analysis using genera as fixed  
616 effects and the three metaregressions with body mass, median elevation and elevational  
617 range. SE = standard error; QE = statistic for the test of residual heterogeneity; QM= test  
618 statistic for the omnibus test of coefficients; P-values: \* = p <0.05.

Model	Term	Estimate (SE)	QE	QM
Intercept-only	Intercept	-0.238 (0.010) *	76.426 *	
Genus as Fixed effects	<i>Avahi</i>	-0.423 (0.339)	64.945 *	7.215
	<i>Cheirogaleus</i>	-0.217 (0.399)		
	<i>Eulemur</i>	-0.460 (0.253)		
	<i>Hapalemur</i>	0.013 (0.307)		
	<i>Indri</i>	-0.389 (0.612)		
	<i>Lepilemur</i>	-0.135 (0.351)		
	<i>Microcebus</i>	-0.365 (0.356)		
	<i>Prolemur</i>	-0.384 (0.681)		
	<i>Propithecus</i>	0.143 (0.413)		
	<i>Varecia</i>	-0.066 (0.571)		
Body mass metaregression	Intercept	-0.308 (0.236)	76.669 *	0.138
	Body mass	0.002 (0.006)		
Median elevation metaregression	Intercept	-1.765 (0.488) ***	59.087	10.215 **
	Median elevation	0.150 e <sup>-2</sup> (0.047 e <sup>-2</sup> ) **		
Elevational range metaregression	Intercept	0.455 (0.341)	70.192 *	4.447 *
	Elevational range	-0.053 e <sup>-2</sup> (0.025 e <sup>-2</sup> ) *		

619

620 **Figure 1:** Map of Madagascar, showing the ?? sites included in the meta-analysis of the  
621 relationship between lemur encounter rate and elevation in the eastern rainforest of  
622 Madagascar.

623

624 **Figure 2:** Forest plot of effect sizes (Fisher's  $Z$ ) for abundance in relation to elevation for  
625 each of the 26 lemur species and in summary (bottom bar), with 95% confidence intervals  
626 (horizontal bars). Overall, lemur abundance is negatively related to elevation. The size of the  
627 square for each species is proportional to the sample size (ranging from 6 to 57 samples for  
628 each species). The dashed line indicates zero (no relationship between abundance and  
629 elevation).

630

631 **Figure 3:** Forest plot of the effect sizes (Fisher's  $Z$ ) for abundance in relation to elevation for  
632 each lemur genus estimated as fixed effects in the meta-analysis, with 95% confidence  
633 intervals (horizontal bars). The dashed line indicates zero (no relationship between abundance  
634 and elevation).

635

636 **Figure 4:** Results of the Generalised Linear Mixed Model with encounter rates ( $\sim$ abundance;  
637  $\Delta ER$ ) of lemurs in Madagascar's eastern rainforest as the dependent variable. BM: Body  
638 Mass; El: Elevation; NDVI: Normalised Difference Vegetation Index (proxy of plant  
639 productivity); NDVI<sub>sd</sub>: proxy of seasonality in plant productivity; HII: Human Influence  
640 Index (proxy of anthropogenic disturbance).

641

642 **Figure 5:** Model predictions for encounter rates (?????) of lemurs in Madagascar's eastern  
643 rainforest from the Generalised Linear Mixed Model.

644 .

## **SUPPORTING INFORMATION.**

Additional supporting information may be found in the online version of this article at the publisher's website.

**Appendix S1.** Model selection for the Generalised Linear Mixed Models with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable.

**Appendix S2.** List of data on the abundance of lemur species in the eastern rainforest in Madagascar included in the meta-analysis.

**Appendix S3.** Mean lemur abundance (encounter rates or densities) in elevation categories (every 400 m a.s.l.).

**Appendix S4.** Results of the Tukey post-hoc tests between lemur genera included in the meta-analysis.

**Appendix S5:** Metaregression between the correlation coefficient of the relationship between encounter rate and elevation and species body mass, elevational range, and median elevation.

**Appendix S6:** Model output of the Generalised Linear Mixed Models with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable.

**Appendix S7:** Results of the Generalised Linear Mixed Model with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable (excluding the Human Influence Index; HII).

**Appendix S8:** Model prediction for the Generalised Linear Mixed Model with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable (including the Human Influence Index; HII).

**Appendix S9:** Relationship between elevation (in m a.s.l.) and the Normalised Difference Vegetation Index (NDVI) in Madagascar's eastern rainforest.