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# **High variability in patterns of population decline: the importance of local processes in species extinctions**

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**short title:** local processes in species declines

**key words:** extinction, population decline, conservation, biodiversity, primates

23 **ABSTRACT**

24 A fundamental goal of conservation science is to improve conservation practice.  
25 Understanding species extinction patterns has been a central approach towards this objective.  
26 However, uncertainty remains about the extent to which species-level patterns reliably indicate  
27 population phenomena at the scale of local sites, where conservation ultimately takes place.  
28 Here we explore the importance of both species- and site-specific components of variation in  
29 local population declines following habitat disturbance, and test a suite of hypotheses about  
30 their intrinsic and extrinsic drivers. To achieve these goals, we analyse an unusually detailed  
31 global dataset for species responses to habitat disturbance (primates in timber-extraction  
32 systems) using cross-classified generalised linear mixed models. We show that while there are  
33 consistent differences in the severity of local population decline between species, an equal  
34 amount of variation also occurs between sites. The tests of our hypotheses further indicate that  
35 a combination of biological traits at the species level, and environmental factors at the site  
36 level, can help to explain these patterns. Specifically, primate populations show a more marked  
37 decline when the species is characterised by slow reproduction, high ecological requirements,  
38 low ecological flexibility and small body size; and when the local environment has had less  
39 time for recovery following disturbance. Our results demonstrate that individual species show  
40 a highly heterogeneous, yet explicable, pattern of decline. The increased recognition and  
41 elucidation of local-scale processes in species declines will improve our ability to conserve  
42 biodiversity in the future.

43

44 **1. INTRODUCTION**

45 Comparative studies have made an invaluable contribution to our knowledge of extinction risk  
46 in a wide range of taxa. These studies have demonstrated that some species are at greater risk  
47 than others because they possess biological traits that predispose them towards extinction (e.g.  
48 large body size) and/or they occur in areas of intense anthropogenic disturbance (e.g. high  
49 human population density) (e.g. Cardillo et al. 2005; Fisher et al. 2003; Jones et al. 2003;  
50 Owens & Bennett 2000; Purvis et al. 2000; Reynolds et al. 2005). By enhancing our  
51 understanding of these patterns, and the mechanisms that underpin them, this research allows  
52 us to predict the future vulnerability of species and to improve the efficacy of conservation  
53 planning. However, the translation of science into action on the ground requires that the  
54 knowledge gained from these emergent species-level analyses can be reliably applied to local  
55 sites, where conservation management is implemented. Unfortunately, there are challenges to  
56 this process, not least because the local mechanisms responsible for driving population declines  
57 may be both variable across a species range and difficult to detect or identify when analyses are  
58 conducted at the species level. As a result, the extent to which this application can be made is  
59 poorly known (Fisher & Owens 2004; Purvis et al. 2005). This is an important gap in our  
60 knowledge for two reasons. First, there has been a proliferation of species-level studies over  
61 the last decade, yet there remains uncertainty about how we can most effectively apply their  
62 findings. Second, without this information it is difficult to know how we might best improve  
63 the quality of our science to make it more useful to conservation practitioners in the future.

64 In order to address this problem, we investigate how the risk of population extinction  
65 across species varies across a range of sites subject to a range of human pressure. Such  
66 analyses require a taxonomic group that is sufficiently well-studied to provide reliable data on  
67 local-scale population change across a variety of different species and sites in response to a  
68 specific threat process (a single threat focus is necessary, since different threats can lead to

69 different patterns of species response, confounding the interpretation of emergent patterns:  
70 Isaac & Cowlshaw 2004). We therefore looked at the responses of primate populations to  
71 timber extraction (selective logging). Primates are among the most threatened of all mammals  
72 (Cowlshaw & Dunbar 2000), which in turn are one of the most important “flagship” groups for  
73 conservation (Ceballos et al. 2005), while timber extraction is one of the most important threats  
74 to tropical forest biodiversity (Asner et al. 2005; Curran et al. 2004).

75 In the first part of our analysis, we ask what is the magnitude of the variation in  
76 population decline between species and sites. In the second part of our analysis, we investigate  
77 what factors might explain this variation. At the site level, we test four hypotheses about  
78 extrinsic (environmental) factors: that species declines will be more severe where there has  
79 been less time for forest recovery and where logging was more damaging (Dunn 2004), where  
80 there is more seasonal environmental stress (Wright 1992), and where there is more ecological  
81 competition (Peres & Dolman 2000). At the species level, we test five hypotheses about  
82 intrinsic (biological) factors: that species will be more vulnerable if they have slow  
83 reproductive rates (reproductive rate is related to recovery rate at small population sizes)  
84 (Johnson 2002; Reynolds 2003), high ecological requirements (Jones et al. 2001; Woodroffe &  
85 Ginsberg 1998), low ecological flexibility (Vazquez & Simberloff 2002), a high dependence on  
86 conspecifics (Courchamp et al. 1999), and a high dependence on the forest canopy (Harcourt  
87 1998). These hypotheses are in line with those tested in previous comparative studies of  
88 extinction risk (e.g. Cardillo et al. 2005; Fisher et al. 2003; Owens & Bennett 2000; Reynolds  
89 et al. 2005), including studies of primates (Harcourt 1998; Isaac & Cowlshaw 2004; Johns &  
90 Skorupa 1987). We also investigate whether the relationship between each explanatory  
91 variable and species vulnerability is a function of body size (following Cardillo et al. 2005).

92

93

## 94 2. MATERIALS AND METHODS

95 Changes in population abundance were collated from published studies and quantified as a  
96 *response ratio* ( $r$ ), i.e. the abundance of a population in an area of logged forest divided by its  
97 abundance in a matching area of unlogged forest. Hence, a value of  $r=1.0$  indicates no change  
98 in abundance, but values above and below one indicate an increase and decrease respectively,  
99 while a value of zero indicates extinction. Response ratios provide a useful metric for the  
100 measurement of effect size in ecological research (Hedges et al. 1999), and in this case allowed  
101 us to compare across studies that used different units of abundance, such as individual density,  
102 group density, and group encounter rates along transect. We used the natural logarithm of the  
103 response ratio (response ratio + 1.0) to linearize the metric and normalize the data (following  
104 Hedges et al. 1999), and ran our statistical models with Normally distributed errors. The  
105 assumptions of Normality and homoscedasticity were tested post-modelling by examining the  
106 standardised residuals versus both the normalised scores and the fixed part predictions (the  
107 former gave a straight-line plot, whilst the latter was a cloud of points, supporting our model  
108 assumptions).

109 The full dataset contained 293 response ratios across 66 primate species at 34 sites, and  
110 is provided in the electronic supplementary material accompanying this paper (see also Isaac &  
111 Cowlshaw 2004). Sites were defined as distinct geographic areas, e.g. national parks, although  
112 these areas were variable in size. At these sites, logged forest areas and matching unlogged  
113 (control) forest areas were defined following the authors of the original studies, on the basis of  
114 the presence/absence of selective logging, habitat similarity, and spatial proximity. At eleven  
115 sites, data were collected from several ( $n=2-6$ ) areas (“plots”) that experienced logging at  
116 different times and to different levels of timber extraction. In total, 38 species and 26 sites  
117 occur more than once. Data were discarded where additional disturbances, such as hunting or  
118 habitat fragmentation, had a significant presence.

119           The hypotheses under test, and their associated explanatory variables, encompassed  
120 both extrinsic (site) and intrinsic (species) factors. The four hypotheses about extrinsic factors  
121 required data collected at the site level (or plot level within site, where appropriate) and were  
122 taken from the source papers for the response ratios. The four key variables comprised: (1)  
123 recovery time (years since logging); (2) damage at logging, given by the % loss of trees (where  
124 damage was reported by extraction rate it was converted into % tree loss using relationships  
125 derived from those studies that used multiple damage measures: Chapman et al. 2000; Johns &  
126 Skorupa 1987); (3) seasonal environmental stress (climatic seasonality, indexed by site  
127 latitude); and (4) ecological competition, using two different indices: the number of congeneric  
128 species, and the number of primate species occupying a similar niche (i.e. same diet [frugivore,  
129 folivore, insectivore] and habit [arboreal, terrestrial]: Rowe 1996), at that site.

130           The five hypotheses about intrinsic factors required species-level data that were taken  
131 from the wider literature. The full dataset is given in the electronic supplementary material (see  
132 also Isaac & Cowlshaw 2004). Although patterns in species traits at the site level would also  
133 be of interest, these are unavailable in almost all cases, and are only likely to show minimal  
134 variation relative to interspecific patterns. The five hypotheses under test involved eight  
135 species traits: (1) species reproductive rate/recovery potential was indexed by gestation period  
136 (days) and population density (individuals km<sup>-2</sup>); (2) species ecological requirements was  
137 indexed by body mass (female, kg), home range size (ha), and frugivory (% feeding time eating  
138 fruit and seeds); (3) species ecological flexibility was measured indirectly as the range of  
139 environmental variation to which the species is naturally exposed (i.e. the annual temperature  
140 range and rainfall seasonality at the centre of the species' geographic range: Cowlshaw &  
141 Hacker 1997; Isaac & Cowlshaw 2004); (4) species dependency on conspecifics was indexed  
142 by group size (individuals); and (5) species dependency on the forest canopy was indexed by

143 degree of terrestriality (% time spent at or below  $5\text{m} \pm 2\text{m}$  in the canopy). All data were log<sub>e</sub>  
144 transformed prior to inclusion in the models.

145 We used Generalised Linear Mixed Models (GLMMs) (Goldstein 2003) to model our  
146 data and to establish statistical significance. This approach is necessary to partition the variance  
147 in response into between- and within-species components, as well as allowing for differences  
148 within and between sites. Our data were structured such that each observation referred to a  
149 particular species at a given site at a specific point in time: most sites contain several species,  
150 and most species occur at several sites. In other words, we have multiple observations of  
151 individual species across a varying number of sites, such that individual data points are not  
152 mutually independent. We therefore used cross-classified GLMMs, implemented in MLwiN  
153 (Rasbash et al. 2000), to partition the variance appropriately and to test the significance of these  
154 random effects (i.e. observation, species, and site). These were then mapped onto a unique  
155 classification set (Browne et al. 2001) that provided a means for controlling for repeated  
156 observations within sites and species. Our model thus took the form:

$$157 \quad y_i = \beta X + u_{species(k)} + u_{site(j)} + e_i$$

158 where the value  $y$  of the  $i^{\text{th}}$  observation was modelled by the overall mean  $\beta$  together with  
159 random departures  $u_{species}$  due to the species ( $k$ ) in question, random departures  $u_{site}$  referencing  
160 the site ( $j$ ) in which the observation was made, and individual-level random departures  $e_i$  for  
161 each specific observation (Rasbash et al. 2000; Rasbash & Goldstein 1994). Fixed effects,  $X$ ,  
162 were explanatory variables that were added in the normal manner. The final model was a  
163 minimum adequate model obtained through backwards deletion that included all extrinsic and  
164 intrinsic variables. We ran our models for  $5 \times 10^5$  iterations using a Markov-chain Monte Carlo  
165 algorithm (Goldstein 2003).

166 We also modelled other forms of potential non-independence in our data by fitting  
167 additional random effects that represent spatial scale (continent, and plot within site) and other



168 levels of taxonomy (suborder, infraorder, genus, and family). Taxonomy above the species  
169 level followed Groves (2001), with the exception of the Platyrrhini & Catarrhini which we  
170 treated as infraorders.

171

### 172 **3. RESULTS**

173 An initial summary of these data for each site and species (Figure 1) indicates that both show  
174 considerable variation around the median response ratio ( $r$ ). The site-level variation (Figure  
175 1a) may simply reflect differences in the species composition of the different sites.

176 Alternatively, this variation may reflect genuine differences between sites, such that the same  
177 species has responded in dissimilar ways at different sites. Such differences could be the result  
178 of natural environmental variation (e.g. some sites might be ecologically more vulnerable, or  
179 contain more competitors) or anthropogenic variation (although we have controlled for threat  
180 type, there may still be differences in threat intensity). The presence of genuine differences  
181 between sites is supported by the pattern of species-level variation (Figure 1b). This figure  
182 reveals a remarkable degree of intraspecific variability, such that while on average most species  
183 populations decline following logging ( $r_{\text{median}} < 1.0$  for 20/35 species), most of these declining  
184 species also show an increase in abundance following logging in some instances (maximum  
185  $r > 1.0$  for 13/20 species).

186 To explore this pattern in more detail, we investigated how variation in the response  
187 ratio is partitioned across the hierarchical levels of both taxonomic classification (suborder,  
188 infraorder, family, genus, and species) and spatial scale (continent, site, and plot within site).  
189 We found no significant variance between suborders, infraorders, families or genera (all  
190  $P > 0.1$ ), reflecting the fact that species median response ratios to logging show no phylogenetic  
191 signal (Isaac & Cowlshaw 2004). We also found no significant variance due to intercontinent  
192 or interplot differences. However, there was significant variation elsewhere. Specifically, we

193 found that differences between species account for 18.4% of the total variance, and differences  
194 between sites account for a further 20.2% of the total variance. (The remaining 61.4% is  
195 residual error that incorporates other unexplained sources of variance, including measurement  
196 error). This result indicates that, although species show consistent differences in their patterns  
197 of population decline, there is also comparable variability within species that is related to local  
198 site differences.

199 We then explored what factors might explain these patterns of variation. We began by  
200 exploring extrinsic site-level factors. In the four hypotheses under test, we found no support  
201 for an influence of logging damage (% tree loss), seasonal environmental stress (latitude), or  
202 ecological competition (number of competitor species at site). However, there was a strong  
203 effect of recovery time (time since logging):  $X^2_1=9.69$ ,  $P<0.002$ . Thus, population declines are  
204 recorded as less severe at those sites where there has been more time for recovery since timber  
205 extraction. We then tested our five hypotheses about species vulnerability by adding the eight  
206 intrinsic species characteristics to our recovery-time effect model. Our results indicate that  
207 slow reproductive rate (long gestation period), high ecological requirements (large home  
208 range), and low ecological flexibility (small annual temperature range at the centre of the  
209 species geographic range) are all associated with a population decline following timber  
210 extraction, as predicted (table 1). In addition, an unexpected positive body-mass effect was  
211 also obtained. No other variables were statistically significant in the model. We also found no  
212 significant interactions between any intrinsic or extrinsic fixed effect and body size (all  $P>0.1$ ).

213 The predictions of our model are illustrated in Figure 2. In the case of recovery time  
214 (time since logging), the response ratios are at their lowest immediately following logging and  
215 gradually ascend towards a value of one (the baseline population abundance in undisturbed  
216 forest) over the following 50 years. In contrast, the four species traits vary across the baseline.  
217 Thus, some species characteristics are associated with a population decline following logging

218 (e.g. small body size, long gestation period) while others are associated with an increase (e.g.  
219 large body size, short gestation period) when all other effects are held constant.

220

#### 221 **4. DISCUSSION**

222 The main purpose of our study has been to enhance our understanding of how patterns of  
223 extinction risk at the species level might translate to the local scale where conservation action is  
224 usually implemented. We have sought to do this through an exploration of how patterns of  
225 variation in local population decline can be influenced by both species biology and site  
226 characteristics. Our results indicate that, at the local level, the nature of the site can explain as  
227 much variation in patterns of population decline as the biology of the species. This finding  
228 builds on two previous strands of work. The first investigated how well species-level traits can  
229 predict population-level time to extinction (O'Grady et al. 2004; Saether et al. 2005) and  
230 minimum viable population size (Brook et al. 2006; Traill et al. 2007) across a variety of  
231 species. The second investigated biological correlates of local population decline in exploited  
232 marine fish, in comparisons between areas of high and low exploitation (Jennings et al. 1998;  
233 Jennings et al. 1999), inside and outside marine reserves (Mosquera et al. 2000), and over time  
234 (Dulvy et al. 2000) (see also Reynolds et al. 2005). Both areas of research have provided  
235 pioneering insights into the links between species- and population-level vulnerability to  
236 extinction. But to date only the latter work in marine fisheries has incorporated site-specific  
237 information in their analysis, specifically the level of threat (harvesting pressure). To our  
238 knowledge, ours is the first study to incorporate information on threat intensity together with  
239 the wider environmental characteristics of the site, and – most importantly – to assess the  
240 relative importance of species-level and site-level characteristics in determining the emergent  
241 patterns of population decline.

242           Recent studies at the species level have established that a full explanation of variation in  
243 species global declines requires an understanding of both the species biological traits and the  
244 threat processes that drive these declines (Cardillo et al. 2005; Fisher et al. 2003; Owens &  
245 Bennett 2000; Reynolds et al. 2005). Our analysis at the site level demonstrates that the same  
246 holds true for the understanding of local declines. This is an important result, because it is at  
247 this spatial scale where the mechanisms of population regulation and extinction operate, and  
248 where conservation ultimately takes place. In addition, the present study adds another layer of  
249 complexity to our knowledge of extinction processes. Previously, we have shown that  
250 individual species exhibit different patterns of decline in response to different threat types (e.g.  
251 hunting and habitat disturbance), and to the different anthropogenic processes that comprise  
252 these threats (e.g. selective logging and shifting cultivation, within habitat disturbance) (Isaac  
253 & Cowlshaw 2004). Here we show that different responses can also emerge within these  
254 specific anthropogenic processes (in this case, selective logging), and that these responses are  
255 influenced by local processes (i.e. recovery time). This intraspecific variation indicates that the  
256 mechanisms involved in most species declines are likely to be heterogeneous and complex.  
257 One implication of this heterogeneity for analytical study is that we should therefore approach  
258 “typical” values for species susceptibility to decline with caution (especially when such values  
259 are based on data drawn from only a handful of sites).

260           In light of these results, it is also apparent that patterns of intraspecific variation contain  
261 useful information, and that we should make full use of this information wherever possible.  
262 This is well illustrated by an earlier analysis of the same dataset used here, based solely on  
263 median response-ratio values, that only managed to detect one of the four species traits  
264 associated with population decline following logging, namely ecological flexibility (i.e. annual  
265 temperature range at the centre of the species geographic range) (Isaac & Cowlshaw 2004).

266 The difference between these two studies also highlights the strengths of GLMMs over more  
267 conventional statistical approaches in such analyses.

268 Moreover, our study has allowed us to obtain a more textured understanding of how  
269 certain biological traits can influence extinction risk. Most notable among our species-level  
270 results is the relationship between population response ratio and body mass. While larger  
271 species are usually identified as more vulnerable due to their slower reproductive rates and  
272 higher ecological demands (Purvis et al. 2000), our results show that once these effects are  
273 controlled body mass can have a positive influence. Several previous studies have reported  
274 comparable findings across island communities of both shrews (Peltonen & Hanski 1991) and  
275 birds (Cook & Hanski 1995) once the effects of population size were controlled. Similarly,  
276 Owens & Bennett (2000) reported that larger birds are less susceptible to habitat disturbance.  
277 These patterns have been attributed to the fact that bigger species have larger energy reserves  
278 (Lindstedt & Boyce 1985), making them better able to survive periods of food scarcity. The  
279 relationship between body mass and extinction risk is thus more complex than often assumed.  
280 More recent modelling work suggests that the best body size to minimise extinction risk is  
281 contingent upon the type of environment: larger species are at lower risk of extinction than  
282 smaller species in fluctuating environments, but at greater risk of extinction when catastrophes  
283 occur (Johst & Brandl 1997).

284 In addition to the body mass effect, gestation period, ecological flexibility (indexed by  
285 annual temperature range at the centre of species geographic range), and home range size also  
286 influenced the pattern of population response, in each case in the predicted direction. When  
287 these patterns are assessed in relation to the baseline of 'no change' ( $r=0$ ) (Figure 2), it is also  
288 clear that certain species characterised by particular biological traits may benefit from logging.  
289 This is most clear for the fast reproducers (short gestation periods) and more adaptable species  
290 (those naturally occurring in more variable environments). This pattern is consistent with the

291 fact that these traits tend to characterise those primate species that colonise more variable  
292 habitats such as secondary forest (Ross 1992), a habitat associated with logged forest areas (e.g.  
293 Cowlshaw & Dunbar 2000). Nevertheless, while these relationships provide useful insights  
294 into the mechanisms that might underpin primate responses to logging, and the associated traits  
295 that might act as indicators of vulnerability, it should also be remembered that a considerable  
296 proportion of the variance in our analysis still remains unexplained. No doubt some of this  
297 partially reflects methodological differences between studies, including measurement error, but  
298 other factors are also likely to be involved that it has not been possible to include here, e.g.  
299 forest regenerates more quickly following logging at some sites than at others (Lawes &  
300 Chapman 2006).

301         The most important message of our study is that more attention needs to be paid to  
302 understanding the local patterns of population decline across sites, and to integrating this  
303 information into analyses at the species level. This follows from our finding that species  
304 extinction is not a unitary or homogeneous phenomenon, even within a specific anthropogenic  
305 process. Such an approach will substantially enhance the applied value of comparative studies  
306 of extinction risk in at least two ways. In the short term, it will help us to identify more  
307 accurately both priority species (in this case, those primate taxa that are slow-reproducers, with  
308 high ecological requirements, low ecological flexibility, and small body size) and priority sites  
309 (in this case, the most valuable sites will be those where long recovery periods have elapsed  
310 since the last logging disturbance). In the long term, by bridging the gap between local site-  
311 level processes and global species-level patterns, we will be able to develop a more powerful  
312 science to guide and underpin effective conservation action.

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321

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437 **Figure legends**

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439 Figure 1. Variation in response ratios ( $r$ ) across sites and species. The response ratio is the  
440 population change in response to logging (calculated as the abundance in logged forest divided  
441 by the abundance in matching unlogged forest), where  $r=1.0$  is no change,  $r>1$  and  $r <1$  is an  
442 increase and decrease respectively, and  $r=0$  is extinction. Median  $r$  values are shown by the  
443 black horizontal bars, interquartile ranges are shown by the grey vertical bars, and minimum  
444 and maximum values are indicated by the vertical lines. The y-axis is square-root transformed  
445 (for ease of presentation). (a) Response ratios across sites. (b) Response ratios across species.  
446 All sites and species where sample size  $n>2$  are plotted. Sites are grouped by country and then  
447 by continent, from the Americas eastward to Africa and Asia: BR=Brazil, CR=Costa Rica;  
448 GB=Gabon, GH=Ghana, MA=Madagascar, UG=Uganda; ID=Indonesia, MY=Malaysia.  
449 Species are listed alphabetically.

450

451 Figure 2. The effects of selective logging on primate populations. The response ratio is the  
452 population change in response to logging (calculated as the abundance in logged forest divided  
453 by the abundance in matching unlogged forest), where  $r=1.0$  is no change,  $r>1$  and  $r <1$  is an  
454 increase and decrease respectively, and  $r=0$  is extinction. Panels show how the response to  
455 logging is a function of both extrinsic and intrinsic variables. The extrinsic variable is recovery  
456 time (years since logging). The four intrinsic variables are body size, gestation period, home  
457 range size and ecological flexibility (indexed by the annual temperature range at the centre of  
458 the species geographic range). Data are predicted values obtained from the overall best-fitting  
459 model, back-transformed from the  $\log_e$ -transformed data, holding other variables constant at  
460 their median value.

461

462 Table 1. Intrinsic and extrinsic factors in local primate population declines following timber  
463 extraction. Recovery time (years since logging) is a site characteristic, while body mass,  
464 gestation period, ecological flexibility (indexed by the annual temperature range at the centre of  
465 the species geographic range) and home range size are species characteristics. Parameter  
466 estimates, standard errors, and associated Wald Chi-square values for the fixed effects of the  
467 minimum adequate model of primate population response ratios are given.

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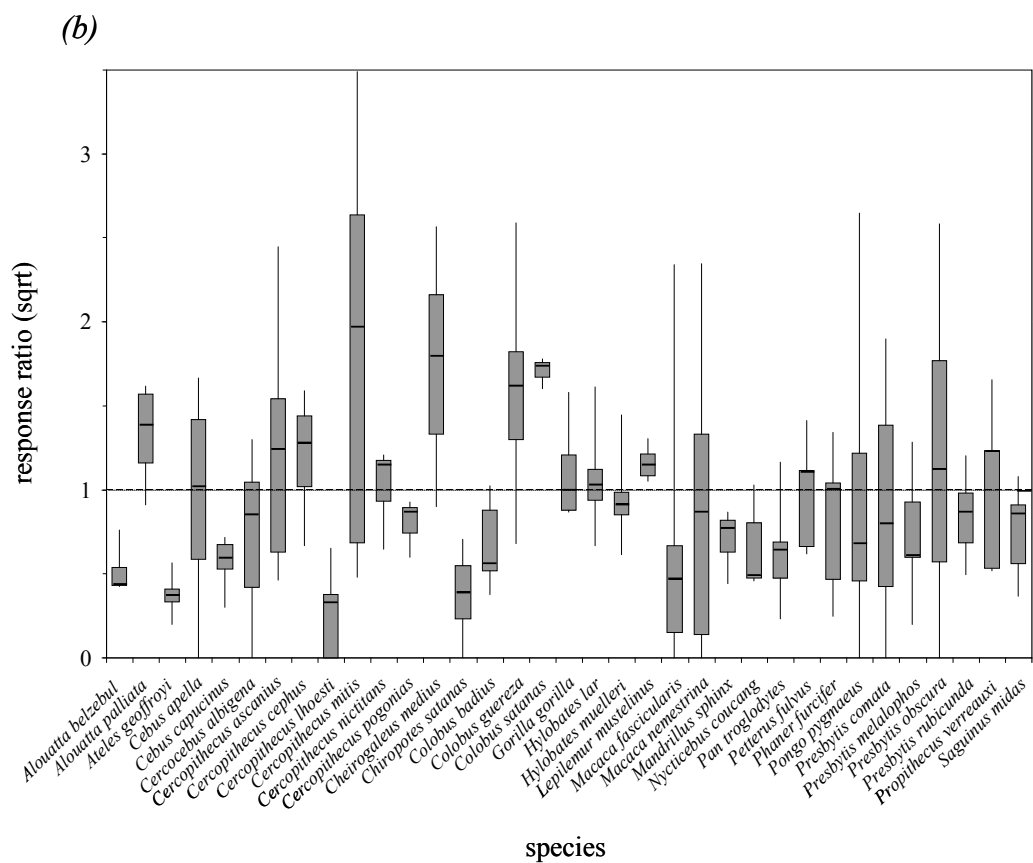
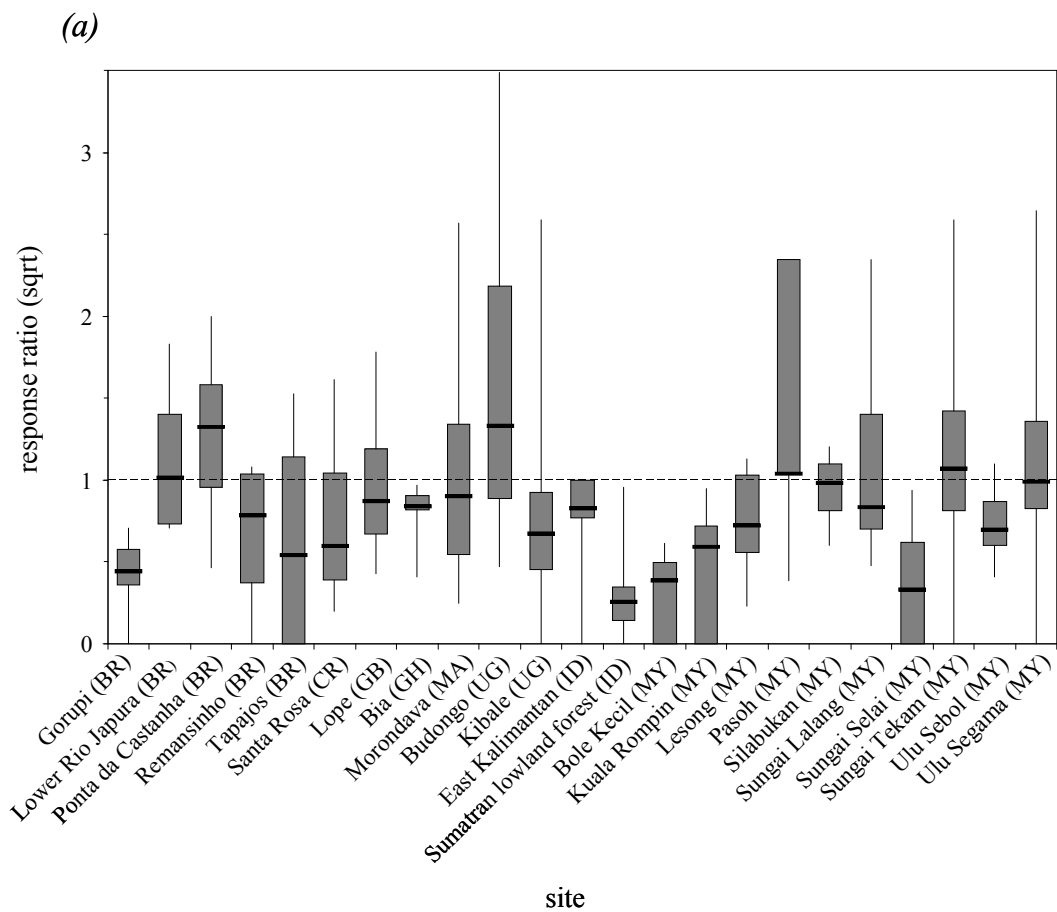
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471	Parameter	estimate	se	$\chi^2$	df	P
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474	Intercept	2.58	1.13	5.24	1	<0.05
475	Recovery time	0.09	0.03	7.74	1	<0.01
476	Body mass	0.16	0.06	6.47	1	<0.02
477	Gestation period	-0.50	0.22	5.34	1	<0.05
478	Ecological flexibility	0.07	0.03	6.52	1	<0.02
479	Home range	-0.08	0.04	4.70	1	<0.05

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484 Figure 2.

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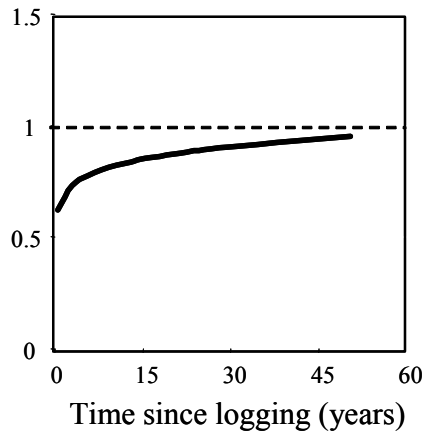
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Extrinsic  
factors



Intrinsic  
factors

