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3 **Categorizing species by niche characteristics can clarify conservation**  
4 **planning in rapidly-developing landscapes**

5

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12 analysis, flagship species, multiple-use landscape, surrogate species, umbrella species.

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15

16 Abstract

17 In biodiversity-rich landscapes that are developing rapidly, it is generally impossible to delineate  
18 land-use and prioritize conservation actions in relation to the full variability of species and their  
19 responses to anthropogenic activity. Consequently, conservation policy often focuses on  
20 protecting habitat used by a few flagship, indicator, or umbrella species like tigers (*Panthera*  
21 *tigris*) and Asian elephants (*Elephas maximus*), which potentially leaves out species that do not  
22 share these habitat preferences. We demonstrate an empirical approach that clustered 14  
23 mammals into surrogate groups that reflect their unique conservation needs. We surveyed a 787  
24 km<sup>2</sup> multiple-use area in the Shencottah Gap of the Western Ghats, India, using foot surveys and  
25 camera-trap surveys. Using Ecological Niche Factor Analysis, we generated indices of species  
26 prevalence (marginality and tolerance) and habitat preferences (factor correlations to marginality  
27 axis). We then clustered species by both of the above index types, to reveal four clusters based  
28 on prevalence and four clusters based on habitat preference. Most clusters contained at least one  
29 threatened species. Low-prevalence lion-tailed macaques (*Macaca silenus*) and tigers were  
30 strongly associated with closed forests and low human disturbance. But elephants, sloth bears  
31 (*Melursus ursinus*) and gaur (*Bos gaurus*) were more tolerant of anthropogenic impact, and sloth  
32 bears and gaur preferred open forests and grasslands. Dhole (*Cuon alpinus*) and sambar (*Rusa*  
33 *unicolor*) were associated with completely anthropogenic habitat (farmland, cash-crop and  
34 forestry plantations) with high human use. Thus, reliance on flagship species for conservation  
35 planning can both underestimate and overestimate the ability of other species to persist in  
36 multiple-use landscapes; protecting flagship species would only protect species with similar  
37 habitat preferences. For species that avoid human impacts more than the flagship species, core

38 habitat must be protected from human disturbance. For more tolerant species, conservation in  
39 anthropogenic habitat may hinge on policies that bolster coexistence with humans.

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42 Introduction

43 Species-rich regions of the world are often especially threatened by human activity (e.g.,  
44 the biodiversity hotspots; Myers *et al.*, 2000). As human pressure grows (Cincotta, Wisnewski &  
45 Engelman, 2000), and political support for reserves decreases (Schwartz, 1999; Singh & Bagchi,  
46 2013), biodiversity must increasingly be conserved in anthropogenic landscapes (Daily, Ehrlich  
47 & Sanchez-Azofeifa, 2001; DeFries *et al.*, 2005). Yet, there is scanty enough time to identify,  
48 let alone characterize the habitat preferences all species in such landscapes (Ehrlich, 1992; Wiens  
49 *et al.*, 2008). To address the intersecting challenges of securing societal support and simplifying  
50 management practices, conservation initiatives often focus on the needs of surrogate species  
51 (flagship, indicator or umbrella species; reviewed by Caro, 2010). Unfortunately, this approach  
52 necessarily ignores the well-known variation in niche characteristics among species (*sensu*  
53 Hutchinson, 1957), whose tolerance for human activity also varies substantially (Mace *et al.*,  
54 2008) and often independently of habitat associations (Karanth *et al.*, 2009).

55 Discordance between species-specific conservation requirements and the need for  
56 generalizable management policies can limit both the identification of conservation problems  
57 and solutions (Van Jaarsveld *et al.*, 1998). A potential solution to this conundrum is to cluster  
58 species into ‘surrogate groups’ (*sensu* Wiens *et al.*, 2008) defined by their common habitat  
59 associations and response to anthropogenic activity (Lambeck, 1997). Surrogate groups have  
60 been used in several ways to aid management; for example, coarse-filter approaches (Noss,  
61 1990) prioritize habitat elements for conservation by identifying groups of species with similar  
62 habitat requirements. McKinney (2002) helped identify management priorities in the face of  
63 urban expansion, by classifying mammals into ‘avoiders’, ‘adapters’ and ‘exploiters’ of urban  
64 sprawl. Connectivity conservation may also be improved by identifying corridors used by

65 different groups of species (Beier et al. 2008). Thus, the use of surrogate groups can  
66 simultaneously avoid over-reliance on single surrogate species while not getting bogged down by  
67 the immensity of biodiversity.

68 Despite the utility of surrogate groups, they are rarely straightforward to define, due to  
69 variability in habitat preference within and among species, and the limited availability of data to  
70 quantify this variation. Many species may select different types of habitat under different  
71 ecological and anthropogenic contexts (Chetkiewicz & Boyce, 2009). Hence, surrogate groups  
72 for conservation planning in a given region may be better defined by empirical data from that  
73 region, rather than meta-analysis, literature review or expert knowledge (e.g., Lambeck, 1997;  
74 McKinney, 2002; Manne & Williams, 2003). Empirical data may be particularly important for  
75 multiple-use landscapes, because studies based on reserves may either over estimate or  
76 underestimate animal responses to anthropogenic change (Knopff *et al.*, 2014). However, the  
77 data that do exist in multiple-use landscapes may consist of only presence-background records,  
78 which may have been aggregated using multiple survey methods over several years (e.g. Sattler  
79 *et al.*, 2007).

80 These challenges of human pressure, variability in species responses and uneven data  
81 availability commonly intersect in rapidly-developing tropical landscapes (Laurance *et al.*, 2012)  
82 such as the Western Ghats biodiversity hotspot of India. Large mammals in this region exhibit a  
83 range of prevalence characteristics and habitat preferences (Table 1). This variation suggests that  
84 habitat protection based only on the presence of charismatic flagship species (principally, tiger  
85 [*Panthera tigris*] and Asian elephant [*Elephas maximus*; hereafter, elephant]; e.g., Lewis, 2005)  
86 may not adequately fulfil the requirement of other species. Instead, we hypothesized that  
87 classifying species into surrogate groups, defined by their characteristics of prevalence and by

88 their habitat associations, would help identify priority locations and management needs. Our  
89 main goal was to identify surrogate groups from empirical data collected in the multiple-use  
90 Shencottah Gap region of the Western Ghats, and hence (a) compare them to *a priori* surrogate  
91 groups defined from the literature, (b) evaluate how well the two flagship species above  
92 represent the needs of other species, particularly threatened species, and hence (c) identify  
93 priorities for management.

94         Prevalence characteristics indicate how much of the landscape a species can use (Lele,  
95 2009). We quantified prevalence using two parameters: marginality (which summarizes how  
96 much the most frequently-used habitat differs from what is available), and tolerance (which  
97 summarizes how narrow is the range of habitat types used by the species relative to what is  
98 available; Hirzel *et al.*, 2002). For example, we predicted that threatened species (Endangered or  
99 Vulnerable; IUCN, 2010), such as lion-tailed macaques (*Macaca silenus*), would occur in fewer,  
100 more specific habitat types (high marginality) and tend not to occur in the more degraded habitat  
101 that is common in the Shencottah Gap (low tolerance; Figure 1a). By contrast, habitat  
102 associations identify the characteristics of the areas that species preferentially use, separate from  
103 their overall prevalence. For example, we predicted that species with similar prevalence (e.g.,  
104 gaur [*Bos gaurus*] and Nilgiri langur [*Trachypithecus johnii*] would nevertheless vary in the  
105 habitat they prefer (Fig. 1b).

## 106 Methods

### 107 Study area

108         We surveyed the 787 km<sup>2</sup> Shencottah Gap between the Periyar and Kalakkad-  
109 Mundanthurai Tiger Reserves in Kerala and Tamil Nadu states (Fig. 2a). The northern limit of

110 our study area did not extend up to Periyar due to inaccessibility. Our study area is  
111 approximately 3.2 times larger than the average protected area in India (230 km<sup>2</sup>; ENVIS, 2014).  
112 Approximately 25% of the region consists of anthropogenic habitat types, including government-  
113 owned monoculture timber plantations (14%), private cash crop plantations (6%) and settlements  
114 consisting of buildings interspersed with gardens (5%; Fig. 2b). The remaining area is owned by  
115 the government and consists of evergreen and semi-evergreen forest (Ramesh, Menon & Bawa,  
116 1997) in varying states of degradation.

#### 117 Field methods

118 The study area was divided into 1.5-km cells to allocate effort and surveyed using five  
119 different methods between 2008 and 2013 to maximize detections of multiple cryptic mammals.  
120 We conducted (a) surveys of sign (scat, markings, tracks, sightings and calls) that were carried  
121 out away from trails; (b) comparable sign surveys carried out on trails; (c) camera-trap surveys;  
122 (d) surveys focussed on carnivore sign; and (e) opportunistic detections. The area sampled by  
123 each survey type is depicted on a map (Fig. 2c) and summarized by total effort (Table 2). Across  
124 all methods, survey effort was concentrated in the most fragmented subset of the study area  
125 where the need for conservation planning is most urgent.

126 Off-trail and on-trail surveys covered all land-use types, and were conducted in the dry  
127 season (December 2008 to May 2009 and December 2009 to June 2010). Off-trail surveys  
128 followed a systematic sampling protocol (Gopaldaswamy *et al.*, 2012) targeting terrestrial  
129 herbivores and arboreal species, while also recording carnivores opportunistically. On-trail  
130 surveys were conducted along existing human and animal trails, and unpaved roads (hereafter  
131 trails). These targeted terrestrial herbivores, arboreal mammals and especially carnivores (which  
132 are more detectable on trails; Sunquist, 1981, Karanth *et al.*, 2011). For both off-trail and on-trail

133 surveys, we recorded detections of a given species at a resolution of 100 m. We conducted 840  
134 km of off-trail surveys over 536 km<sup>2</sup>, and 334 km of on-trail surveys over 430 km<sup>2</sup>.

135 Camera trap surveys for terrestrial and semi-terrestrial species were conducted in all  
136 seasons between September 2011 and April 2013. Single cameras (Scoutguard SG 565V and  
137 Scoutguard SG 560V, HCO Outdoor Products, GA, USA) were placed on the trail nearest to  
138 randomly-generated sampling locations. We placed more cameras in areas where previous work  
139 suggested greater importance for corridor use by large mammals (Gangadharan, 2015). We  
140 intended cameras to sample each location for three months, but logistical constraints (access,  
141 theft and elephant damage) sometimes caused them to be operational for more or less time.  
142 Ninety-six percent of camera traps were located in government-owned areas. We expended  
143 37,476 trap-days of effort at 523 camera locations over 302 km<sup>2</sup>.

144 Additionally, on-trail surveys specifically targeted at large carnivores were conducted in  
145 government-owned areas between September 2012 and January 2013. This effort targeted signs  
146 left by tiger, leopard (*Panthera pardus*) and dhole (*Cuon alpinus*), and were also recorded at a  
147 resolution of 100 m. On-trail carnivore surveys totalled 301 km of effort over 141 km<sup>2</sup>.

148 Finally, we also used two types of opportunistic data. One consisted of detections made  
149 while field teams were travelling anywhere in the study area, but were not engaged in a specified  
150 survey activity. The second type consisted of detections of a given species that were made using  
151 methods that were not targeted at it (Table 2). For example, all carnivore detections made in off-  
152 trail surveys were considered to be opportunistic. Detections of arboreal lion-tailed macaques,  
153 Nilgiri langur and Indian giant squirrel (*Ratufa indica*; hereafter, giant squirrel) on camera traps  
154 were also classified as opportunistic, but those of the semi-terrestrial bonnet macaque (*Macaca*

155 *radiata*) were not. The percentage of opportunistic detections was highest for tiger and lion-  
156 tailed macaque (18% each).

#### 157 Habitat variables

158 We modelled animal presence with respect to 10 habitat variables of three broad types:  
159 land use and vegetation characteristics, human impact characteristics and physical habitat  
160 attributes. Similar variables have previously been found to influence habitat use by our study  
161 species (references in Table 1). Vegetation type was quantified using the eco-climatic distance,  
162 an index of ‘evergreenness’ measuring the deviation from a reference category of wet evergreen  
163 forest (Krishnaswamy *et al.*, 2009; see Appendix 1 for details on computation). Land use  
164 consisted of five categories (closed forest, open forest and grassland, forestry plantation,  
165 commercial plantation and settlement), which were sampled at a 100-m resolution in the field  
166 and mapped out using governmental data (Appendix 1). We summarized vegetation and land-use  
167 variables at progressively larger neighbourhood sizes (300 m, 600 m, 1200 m and 2400 m)  
168 around each cell centroid, because the finest resolution of a variable is not necessarily the  
169 resolution at which a species responds to it (Meyer & Thuiller, 2006).

170 To quantify human impact characteristics, we measured the distance to the nearest human  
171 settlement, commercial plantation and major road. We also calculated the density of buildings  
172 within circular neighbourhoods of 300 m, 600 m and 1200 m (Appendix 1; maximum  
173 neighbourhood sizes were based on data availability). To describe the physical habitat of each  
174 survey location, we measured slope as well as local curvature at the centroid of each 100-m cell.  
175 As we expected steeper slopes to enable animals to come closer to anthropogenic habitat, we also  
176 measured mean slope to nearest settlement and mean slope to nearest commercial plantation. For  
177 all variables that were measured at multiple neighbourhood resolutions, we used the scale that

178 maximized discrimination between locations where species were detected and where they were  
179 not (measured using Pearson's  $r$ ).

180 Ecological niche factor analysis

181 Ecological Niche Factor Analysis (ENFA) is a multivariate method that compares habitat  
182 characteristics at cells where a given species was present with the habitat characteristics in all  
183 background cells available in the study area, hence extracting successive orthogonal axes (Hirzel  
184 *et al.*, 2002; Basille *et al.*, 2008). The first axis, termed marginality, maximizes the difference  
185 between the mean habitat characteristics of locations where a species is present, and the mean  
186 habitat characteristics of the study area. The subsequent axes, termed specialization axes,  
187 maximize the ratio between the variance of habitat characteristics of locations where a species is  
188 present, to the variance in habitat characteristics of the study area. The specialization axes are  
189 often combined and expressed as their inverse, termed tolerance, which describes niche breadth  
190 (Basille *et al.*, 2008). For all species, we compared locations where they were present to  
191 locations that we surveyed but we did not detect them (i.e., surveyed locations without detections  
192 formed the background data).

193 We applied the square-root transformation to increase normality of eco-climatic distance,  
194 nearest distance to commercial plantation, nearest distance to settlement and distance to major  
195 road (Basille *et al.*, 2008). To evaluate the effect size of each covariate, we computed its  
196 correlation with the marginality axis and the first specialization axis (similar to factor loadings  
197 for a Principal Components Analysis). For the marginality axis, a negative correlation with a  
198 covariate indicates preference for lower values than the mean value prevalent in the study area  
199 (Hirzel *et al.*, 2002). For the specialization axes, which are ratios of used locations to available  
200 locations, only the absolute value of the correlation coefficient can be interpreted; a higher

201 absolute value indicates a higher contribution towards restricting the variance of species presence  
202 (Hirzel *et al.*, 2002). For all analyses, we evaluated the statistical significance of the marginality  
203 axis and the first specialization axis by comparing the distribution of presence locations to  
204 randomly-distributed locations using a Monte-Carlo procedure with 1000 permutations (Basille  
205 *et al.*, 2008). We conducted these analyses in R 3.0.3 statistical software (R Foundation for  
206 Statistical Computing, Vienna, Austria), using the adehabitatHS package (Calenge, 2006).

207 Inferences from presence-background data collected from multiple sources are  
208 problematic if sampling is not randomized (Royle *et al.*, 2012), which is the case in our study. To  
209 make these potential biases transparent, we compared the cells that were sampled for each  
210 species with the cells in the study area that were not sampled at all (following Botts, Erasmus &  
211 Alexander, 2013). These analyses (Appendix 2) indicated that we invested greater sampling  
212 effort in areas that were flatter, closer to human settlements and containing less closed forest but  
213 more forestry plantations – i.e., areas with a higher human footprint (*sensu* Sanderson *et al.*,  
214 2002), with the most urgent need for conservation planning. Hence, we believe our data are  
215 conservative and realistically reflect habitat preferences in human-dominated areas.

#### 216 Surrogate group classification

217 Using the parameters produced from the above analyses, we clustered species into  
218 surrogate groups in two different ways. Firstly, we clustered species by their marginality and  
219 tolerance scores, which may be considered as the equivalents of central tendencies. Then, we  
220 also clustered species using the correlation coefficients (Pearson's  $r$ ) between each explanatory  
221 variables and the marginality axis for that species (i.e., the habitat associations of that species).  
222 For each of these two sets of indices, we classified species using a distance-based clustering  
223 algorithm that minimizes the dissimilarities within each group (partitioning around medoids;

224 Kaufman & Rousseeau, 1990, Anderlucci & Hennig, 2014). To identify the optimal number of  
225 groups, we selected the classification that maximized the silhouette width ( $s$ ) when averaged  
226 over all species (Rousseeuw, 1987; Anderlucci & Hennig, 2014). The silhouette width is a  
227 measure of how well a species fits into its assigned group. For species  $i$ ,

$$228 \quad s(i) = \frac{b(i) - a(i)}{\max\{a(i), b(i)\}}$$

229 where  $a(i)$  is the average dissimilarity of species  $i$  to all other species in its group, and  $b(i)$  is the  
230 minimum average dissimilarity of species  $i$  with the species in each of the other groups  
231 (Rousseeuw, 1987). The average silhouette width for a surrogate group is scaled between -1 and  
232 1, with higher values indicating better fit.

233 We log-transformed, centred, and scaled the raw marginality and tolerance values before  
234 analysis. We did not perform a clustering analysis based on the specialization axes, because only  
235 the absolute values of these correlations are interpretable (Hirzel *et al.*, 2002). This would make  
236 it difficult to evaluate, for example, whether a high correlation with settlements indicates  
237 preference or avoidance of settlements. We performed the above cluster analysis using R  
238 package `fpc` (Hennig, 2014).

## 239 Results

240 The number of detections varied from 39 for lion-tailed macaque to 4774 for sambar  
241 (*Rusa unicolor*; Table 2). None of the 14 species used habitat in proportion to availability, and  
242 both the marginality axis and first specialization axis were statistically significant ( $P < 0.001$  in  
243 all cases). Prevalence-based classification resulted in four surrogate groups, with varying levels  
244 of fit (from top-left to bottom-right of Fig. 3a: average silhouette widths of 0, 0.16, 0.53 and  
245 0.45), and a more continuous distribution over the marginality-tolerance space than expected ( $r_s$

246 = -0.81,  $P < 0.001$  between marginality and tolerance values). When species were plotted based  
247 on their habitat associations, however, they revealed more clumped surrogate groups (Fig. 3b)  
248 but with similarly variable goodness of fit among groups (average silhouette width values, top-  
249 left to bottom-right of 0.50, 0.36, 0.16 and 0.45).

250         Although the distribution of prevalence characteristics among species was relatively  
251 continuous (Fig. 3a), three species stood out due to their area-restricted nature: tigers (with  
252 relatively high marginality and very low tolerance), Nilgiri langur (very high marginality and  
253 relatively low tolerance) and lion-tailed macaque (highest marginality and lowest tolerance). At  
254 the other extreme, sambar and wild pig (*Sus scrofa*), which exhibited the lowest marginality and  
255 the highest tolerance, were clustered with leopard, dhole and gaur as the most widely-distributed  
256 surrogate group.

257         Surrogate groups based on habitat associations were more clumped (Table 3 and  
258 Appendix 3). Elephant, tiger, lion-tailed macaque, Nilgiri langur and giant squirrel were  
259 positively correlated to closed forest and negatively to anthropogenic habitat or features. Gaur  
260 and bear were positively correlated to open forest and grassland, and negatively to anthropogenic  
261 habitat or features. Leopard, Northern red muntjac *Muntiacus vaginalis* [hereafter, muntjac],  
262 Indian chevrotain (*Moschiola indica*) and bonnet macaque were positively correlated to closed  
263 forest and to anthropogenic features. Dhole, sambar and pig were positively associated with  
264 anthropogenic habitat types. For illustration only, we depict these habitat-based groupings on  
265 two principal component axes that explained 73% of the variance (Fig. 3b; see Appendix 4 for  
266 complete factor loadings). Covariate correlations with the first specialization axis are given in  
267 Appendix 5.

268 Discussion

269 Our goal was to identify empirical surrogate groups, and hence (a) compare them to *a*  
270 *priori* surrogate groups, (b) evaluate how well the two flagship species (elephant and tiger)  
271 represent the needs of other species, and hence (c) identify management priorities. Empirical  
272 classification based on prevalence was broadly consistent with predictions, although threatened  
273 species were more widely distributed across the two dimensions of marginality and tolerance  
274 than expected. This distribution was also more continuous than expected, hence reducing the  
275 distinctiveness of some surrogate group classifications. Empirical classification based on habitat  
276 associations were broadly supported, but some threatened species (dhole and sambar) were more  
277 associated with anthropogenic habitat than expected. Both elephants and tigers were associated  
278 with closed forest and low human disturbance, but other threatened species preferred other kinds  
279 of habitat (e.g., open forests and grasslands or even anthropogenic habitat). These results suggest  
280 that (a) empirically-derived surrogate groups have a different species composition and habitat  
281 associations than literature-based *a priori* groups, (b) threatened species may be more tolerant, or  
282 less tolerant, of anthropogenic activity than flagship species, and (c) conservation of such  
283 widely-varying species in a multiple-use landscape may require both traditional ‘protectionist’  
284 policies towards core habitat, and ‘coexistence’ based policies in anthropogenic areas.

285 Marginality and tolerance scores provided useful starting points to classify species by  
286 how much of the landscape they currently use; tiger, Nilgiri langur and lion-tailed macaque were  
287 the most area-restricted species. However, Nilgiri langurs were relatively more tolerant of  
288 degraded habitat than tigers, despite having more marginal habitat preferences; this quality may  
289 enable them to remain relatively widespread in the Western Ghats (Pillay et al., 2011). The  
290 marginality score of tigers was close to that of the widely-distributed giant squirrel, Indian

291 chevrotain, muntjac and sloth bear, suggesting that the Shencottah Gap has the potential to  
292 support a moderate level of tiger use. However, the low tolerance of tigers to departures from  
293 these optimal conditions suggests that their persistence may be tied to protection of their core  
294 habitat (Karanth *et al.*, 2011). For other threatened species (particularly dhole and sambar), lower  
295 marginality and higher tolerance suggest a much greater ability to retain their spatial distribution  
296 under anthropogenic change than the area-restricted species above.

297 Surrogate groups derived from habitat associations added a further layer of insight, by  
298 identifying convergences and divergences in habitat preferences. Closed forest is important  
299 habitat for species that are as area-restricted as lion-tailed macaques (e.g., Singh *et al.* 2002) and  
300 as widely-distributed as giant squirrels (Sushma & Singh, 2006; Pillay *et al.*, 2011). Protecting  
301 such areas would also benefit elephants, but not sloth bear and gaur (which used open forests and  
302 grassland more; Choudhury, 2002; Yoganand *et al.*, 2006). Finally, two threatened species –  
303 dhole and sambar – used areas that were much more open, degraded and closer to anthropogenic  
304 habitat. Sambar may benefit from human-mediated opportunities for forage or refuge in such  
305 areas (Meijaard & Sheill, 2008) like other generalist ungulates such as elk (*Cervus elaphus*;  
306 Hebblewhite *et al.*, 2005). Dhole use of anthropogenic habitat may potentially result from  
307 displacement by tigers (Steinmetz *et al.*, 2013), similar to avoidance of lions (*Panthera leo*) by  
308 African painted dogs (*Lycaon pictus*; Creel & Creel, 1996) and cheetahs (*Acinonyx jubatus*;  
309 Durant, 1998). However, dholes are also cursorial hunters that select for smaller prey than tigers  
310 (Karanth & Sunquist, 2000), and their use of open anthropogenic habitat may simply reflect the  
311 habitat preferences of sambar and wild pigs.

312 The integration of the above results suggests three broad types of management actions  
313 that are required in this multiple-use landscape. A traditional preservationist approach, focused

314 on the protection of core habitat from human disturbance, is important for the conservation of  
315 area-restricted or human-avoiding species such as lion-tailed macaques (Karanth, Nichols &  
316 Hines, 2010) and tigers (Walston *et al.*, 2010) in the face of large-scale conversion of land to  
317 anthropogenic uses. More generalist herbivores and omnivores (e.g., sloth bears and gaur) may  
318 persist with a small amount of human use, because they may benefit from forage opportunities  
319 provided by human activities that open up tropical evergreen forests (Choudhury, 2002;  
320 Yoganand *et al.*, 2006; Meijaard & Sheill, 2008). The decisive factor enabling their persistence  
321 in such areas may be the control of poaching (Brodie, Giodano & Ambu, 2015), which should  
322 therefore be management priority. Finally, the conservation of some threatened species (e.g.,  
323 dhole and sambar) may depend on anthropogenic habitat – such as privately-owned tea gardens,  
324 rubber plantations and farmland – which are rarely included in management planning for large  
325 mammals (Bhagwat *et al.*, 2008; Athreya *et al.*, 2013). Conservation initiatives in such areas will  
326 require considerable investment in participatory conservation initiatives, especially to control  
327 crop damage or other depredation (e.g., Fernando *et al.*, 2005; Karanth & Gopal, 2005).

328         Our study is subject to two sources of uncertainty. Each survey method covered a  
329 different subset of the study area at a different time – i.e., the data was sampled non-randomly in  
330 both space and time. Hence, if animal habitat selection varied between different regions or time  
331 periods, our inferences may be biased towards the region and time period contributing the largest  
332 proportion of detections. Further, opportunistic data comprised nearly a fifth of tiger and lion-  
333 tailed macaque detections, which may also bias inferences (Durant *et al.*, 2010). A second source  
334 of uncertainty derives from the fact that the detectability of animal signs may vary over space  
335 (e.g. as a function of habitat type), thus biasing estimates of habitat association. In either case,  
336 these biases can be tested by building a habitat use model with camera trap data, and validating

337 this model with the independent sign data. In a separate study, we have found that for elephant,  
338 gaur and tiger, regression models from camera trap data predicted the frequency of signs ( $0.9 < r_s$   
339  $< 0.98$ ) binned into deciles (elephant, gaur) or quintiles (for tigers, due to small sample sizes;  
340 Gangadharan, 2015). We also note that large sample size and site/habitat fidelity may influence  
341 the predictive power of species distribution models more than survey design (Tessarolo *et al.*,  
342 2014), and therefore we combined all our methods to maximize the amount of data.

343 We conclude with three main recommendations: conservation priorities in multiple-use  
344 habitats may be better identified by using surrogate groups rather than single flagship species;  
345 surrogate group identification may be more accurate if based on local empirical data than  
346 literature from other areas; and, the divergences in conservation needs among surrogate groups  
347 may require simultaneous implementation of both preservationist and coexistence-based policies  
348 in multiple-use landscapes. While the charisma of flagship species will remain critical to  
349 leverage public support for conservation, actual conservation planning should be based on  
350 habitat assessments for multiple species (Di Minin & Moilanen, 2014).

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### 359 Supplementary Material

360 Appendix 1. Details on the measurement and computation of covariates used for statistical  
361 analysis

362 Appendix 2. Comparison of covariate values at cells that were sampled versus those that were  
363 not, to identify potential biases in the areas that were surveyed for each species.

364 Appendix 3. Correlation of all covariates with the marginality axis for all species.

365 Appendix 4. Factor loading of principal component axes of Fig. 3b.

366 Appendix 5. Correlation of all covariates with the first specialization axis for all species.

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610 Tables

611 Table 1. Literature sources used in predicted classification of 14 mammalian species in the  
612 Shencottah Gap, India into the functional groups depicted in Figure 1.

Species	Representative sources
Tiger <i>Panthera tigris</i>	Jhala <i>et al.</i> 2011; Karanth <i>et al.</i> 2011
Lion-tailed macaque <i>Macaca silenus</i>	Singh <i>et al.</i> 2002; Singh <i>et al.</i> 2006; Karanth, Nichols & Hines 2010
Asian elephant <i>Elephas maximus</i>	Fernando <i>et al.</i> 2005; Gaucherel <i>et al.</i> 2010
Dhole <i>Cuon alpinus</i>	Karanth & Sunquist 2000; Pillay <i>et al.</i> 2011; Steinmetz, Seuaturien & Chutipong 2013
Sloth bear <i>Melursus ursinus</i>	Yoganand <i>et al.</i> 2006; Karanth <i>et al.</i> 2009
Gaur <i>Bos gaurus</i>	Choudhury 2002; Steinmetz <i>et al.</i> 2010
Nilgiri langur <i>Trachypithecus johnii</i>	Karanth, Nichols & Hines 2010; Pillay <i>et al.</i> 2011
Sambar <i>Rusa unicolor</i>	Meijaard & Sheill 2008; Karanth <i>et al.</i> 2009
Leopard <i>Panthera pardus</i>	Karanth <i>et al.</i> 2009; Athreya <i>et al.</i> 2013
Indian chevrotain <i>Moschiola indica</i>	Pillay <i>et al.</i> 2011; Ramesh, Kalle & Shankar 2013
Indian giant squirrel <i>Ratufa indica</i>	Sushma & Singh 2006; Baskaran <i>et al.</i> 2011

Wild pig *Sus scrofa* Karanth *et al.* 2009; Pillay *et al.* 2011

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Northern red muntjac *Muntiacus vaginalis* Meijaard & Sheill 2008; Pillay *et al.* 2011

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Bonnet macaque *Macaca radiata* Bali, Kumar & Krishnaswamy 2007; Karanth, Nichols & Hines 2010

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620 Table 2. Total effort (number of 100-m cells sampled) using off-trail surveys (OFT), on-trail surveys (ONT), camera trap surveys (CT)  
 621 and on-trail carnivore surveys (ONTC) in the Shencottah Gap, India from 2008 to 2013, which resulted in both targeted and  
 622 opportunistic detections of 14 mammal species.

Species	Targeted sampling methods	Cells sampled	Number of detections			Detection rate (cell <sup>-1</sup> )
			Targeted	Opportunistic	Total	
Tiger	ONT, CT, ONTC	5474	62	14	76	0.01
Leopard	ONT, CT, ONTC	5474	489	22	511	0.09
Dhole	ONT, CT, ONTC	5474	268	10	278	0.05
Bear	OFT, ONT, CT	11984	311	17	328	0.03
Elephant	OFT, ONT, CT	11984	2526	138	2664	0.22
Gaur	OFT, ONT, CT	11984	1317	53	1370	0.11
Sambar	OFT, ONT, CT	11984	4507	207	4714	0.39
Pig	OFT, ONT, CT	11984	1389	39	1428	0.12
Muntjac	OFT, ONT, CT	11984	994	26	1020	0.09
Chevrotain	OFT, ONT, CT	11984	350	3	353	0.03
Lion-tailed macaque	OFT, ONT	11642	32	7	39	0.00
Nilgiri langur	OFT, ONT	11642	293	13	306	0.03
Bonnet macaque	OFT, ONT, CT	11984	231	9	240	0.02
Giant squirrel	OFT, ONT	11642	258	12	270	0.02

623 Table 3. Correlation coefficients (Pearson's  $r$ ;  $|r| > 0.3$  depicted in bold lettering) of selected  
624 covariates with marginality axis of an Ecological Niche Factor Analysis comparing cells where  
625 each of the eight threatened species (out of 14 species in total) was detected or not detected in the  
626 Shencottah Gap, India from 2008 to 2013. Footnotes indicate scale of covariate measurement.  
627 See Appendix 3 for all covariates for the eight threatened and six non-threatened species.

Covariate	Elephant	Tiger	Lion-tailed macaque	Nilgiri langur	Gaur	Bear	Sambar	Dhole
Closed forest	<b>0.44</b> <sup>4</sup>	<b>0.46</b> <sup>3</sup>	<b>0.49</b> <sup>1</sup>	<b>0.39</b> <sup>4</sup>	0.05 <sup>2</sup>	-0.26 <sup>4</sup>	<b>-0.49</b> <sup>4</sup>	-0.13 <sup>4</sup>
Open forest/grassland	-0.05 <sup>4</sup>	-0.20 <sup>4</sup>	-0.22 <sup>1</sup>	-0.08 <sup>1</sup>	<b>0.36</b> <sup>4</sup>	<b>0.49</b> <sup>4</sup>	<b>0.30</b> <sup>1</sup>	0.30 <sup>2</sup>
Forestry plantation	-0.08 <sup>2</sup>	<b>-0.31</b> <sup>2</sup>	-0.28 <sup>3</sup>	-0.21 <sup>4</sup>	-0.05 <sup>1</sup>	-0.04 <sup>1</sup>	0.21 <sup>3</sup>	-0.16 <sup>4</sup>
Commercial plantation	<b>-0.30</b> <sup>3</sup>	-0.14 <sup>1</sup>	-0.11 <sup>1</sup>	-0.20 <sup>4</sup>	<b>-0.36</b> <sup>3</sup>	<b>-0.32</b> <sup>4</sup>	-0.20 <sup>1</sup>	-0.10 <sup>1</sup>
Settlement	<b>-0.33</b> <sup>3</sup>	-0.28 <sup>3</sup>	-0.19 <sup>4</sup>	-0.21 <sup>3</sup>	<b>-0.37</b> <sup>2</sup>	-0.18 <sup>2</sup>	<b>0.34</b> <sup>4</sup>	-0.21 <sup>1</sup>
Eco-climatic distance	<b>-0.40</b> <sup>4</sup>	-0.22 <sup>4</sup>	<b>-0.50</b> <sup>1</sup>	<b>-0.36</b> <sup>3</sup>	-0.10 <sup>1</sup>	0.24 <sup>4</sup>	<b>0.48</b> <sup>4</sup>	0.24 <sup>1</sup>
House density	<b>-0.32</b> <sup>3</sup>	-0.22 <sup>2</sup>	-0.13 <sup>2</sup>	-0.20 <sup>3</sup>	<b>-0.39</b> <sup>3</sup>	-0.23 <sup>2</sup>	-0.12 <sup>1</sup>	-0.13 <sup>1</sup>
Distance to settlement	<b>0.43</b>	0.19	0.06	<b>0.45</b>	<b>0.37</b>	0.18	<b>-0.39</b>	<b>-0.55</b>
Distance to commercial plantation	0.21	<b>-0.43</b>	-0.20	0.11	<b>0.36</b>	<b>0.50</b>	-0.04	<b>-0.32</b>
Distance to major road	0.17	-0.05	0.11	0.27	0.18	<b>0.31</b>	-0.19	<b>-0.34</b>

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629 <sup>1</sup>300 m; <sup>2</sup>600 m; <sup>3</sup>1200 m; <sup>4</sup> 2400 m.

630 Figure captions

631 Figure 1. *A priori* predicted classification of 14 mammalian species in the Shencottah Gap, India  
632 into surrogate groups using two methods (a) marginality and tolerance scores, and (b) relative  
633 sensitivity to anthropogenic impacts and land-use preference. Our predictions were derived from  
634 literature sources given in Table 1.

635 Figure 2. (a) Location of the Shencottah Gap in India (inset) between Periyar Tiger Reserve  
636 (PTR), Kalakkad-Mundanthurai Tiger Reserve (KMTR) and Shendurney Wildlife Sanctuary  
637 (SWLS), (b) land use types within the study area, and (c) distribution of sampling effort through  
638 four methods: off-trail, on-trail, camera trap and on-trail carnivore surveys.

639 Figure 3. Empirical classification of 14 mammalian species occurring in the Shencottah Gap,  
640 India into surrogate groups using two methods (a) marginality and tolerance scores, and (b)  
641 correlation coefficients of habitat variables with marginality axes. For (b), the three strongest  
642 correlations with component 1 were: slope to nearest commercial plantation (-0.90), slope to  
643 nearest settlement (-0.81) and eco-climatic distance (0.84). The three strongest correlations with  
644 component 2 were: distance to nearest commercial plantation (-0.95), proportion of open forest (-  
645 0.84) and proportion of commercial plantation (0.82). See Appendix 4 for complete factor  
646 loadings.

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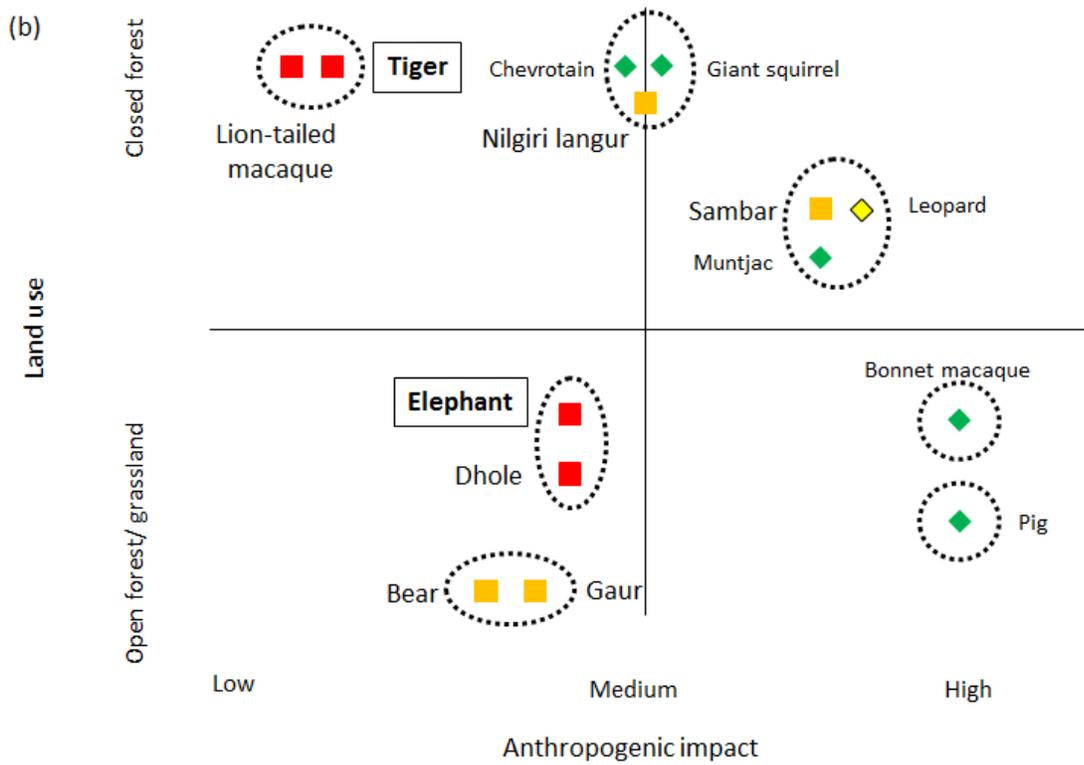
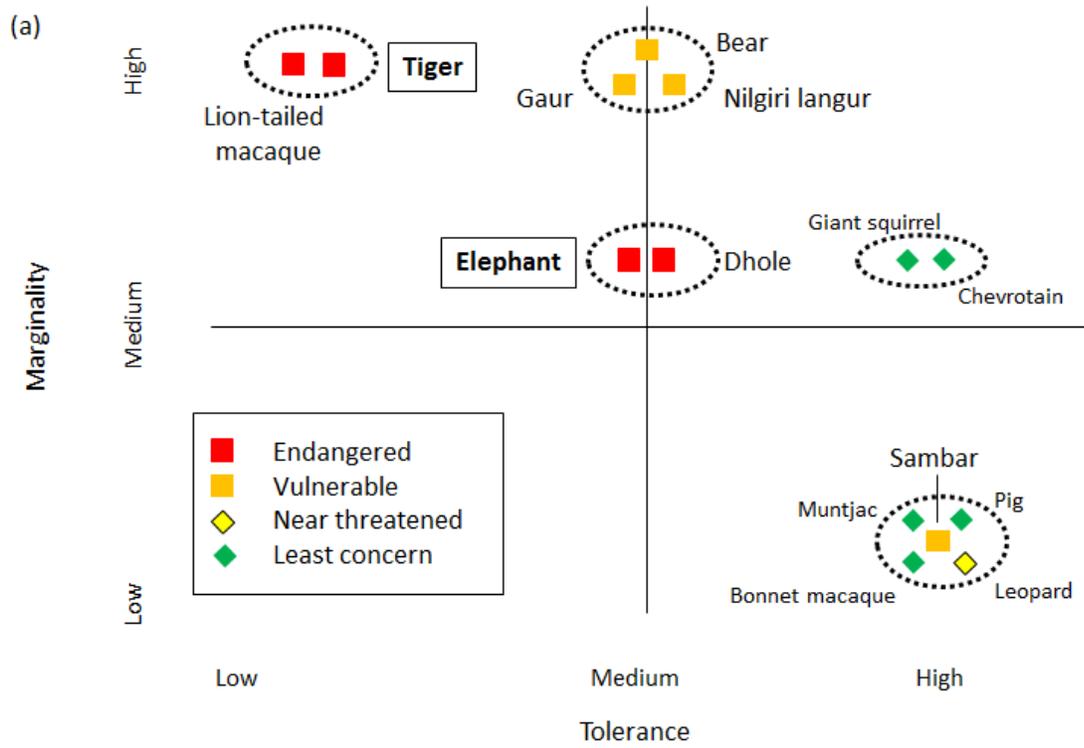
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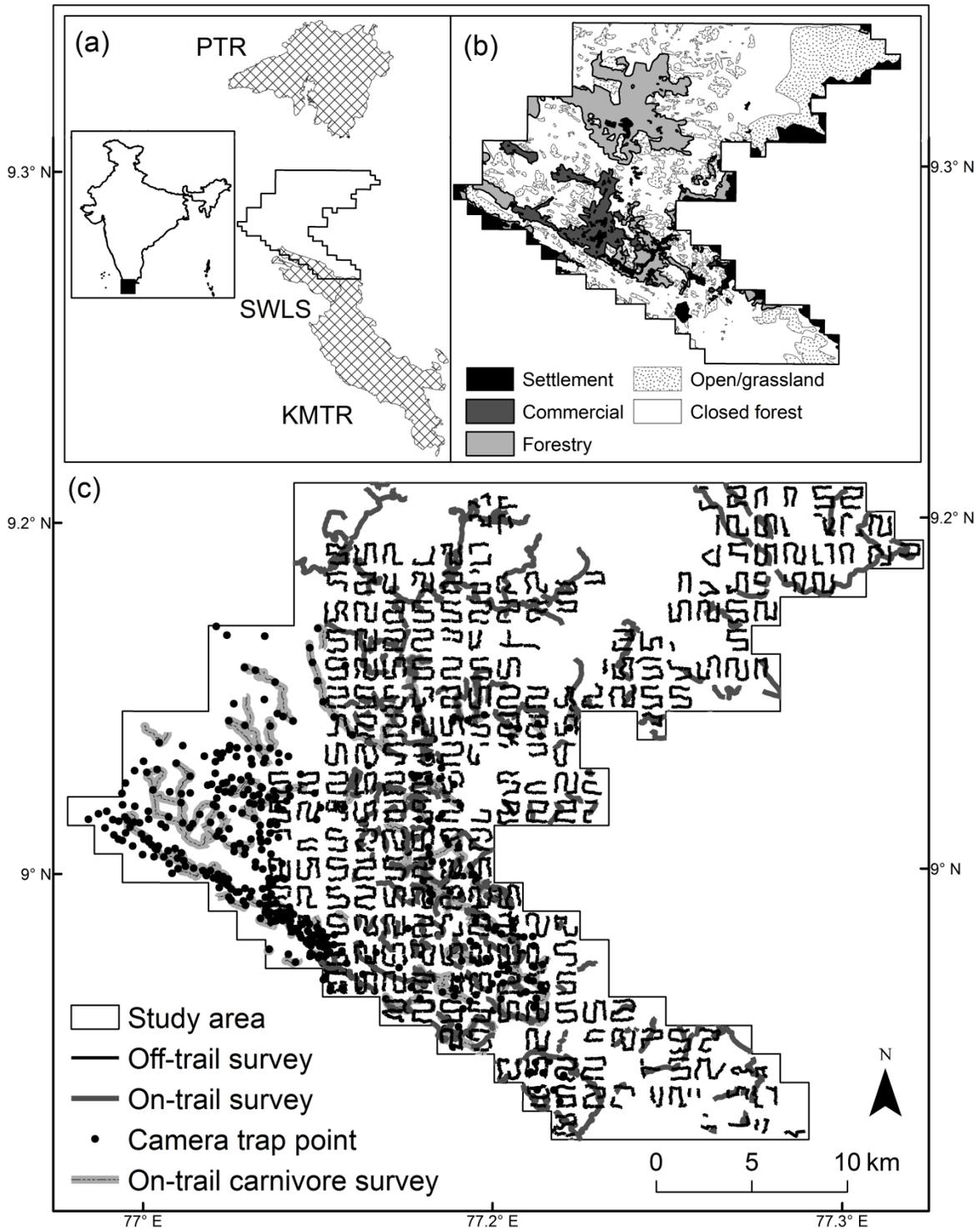
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652 Figure 1



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654 Figure 2.

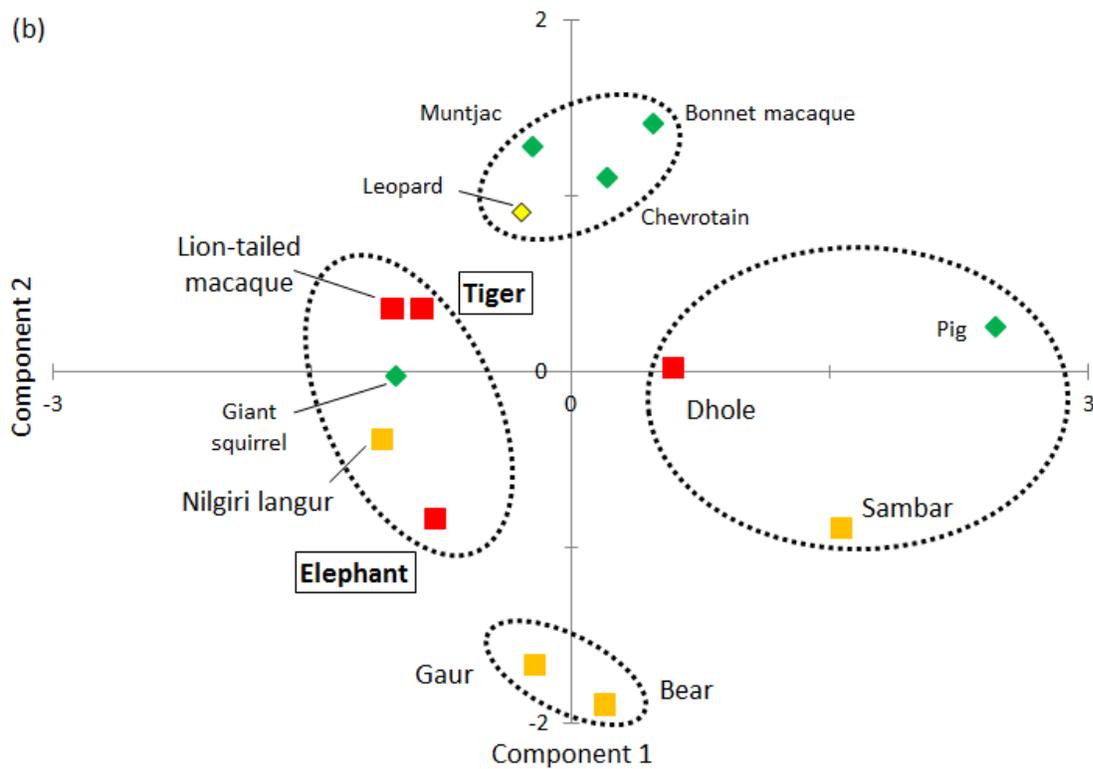
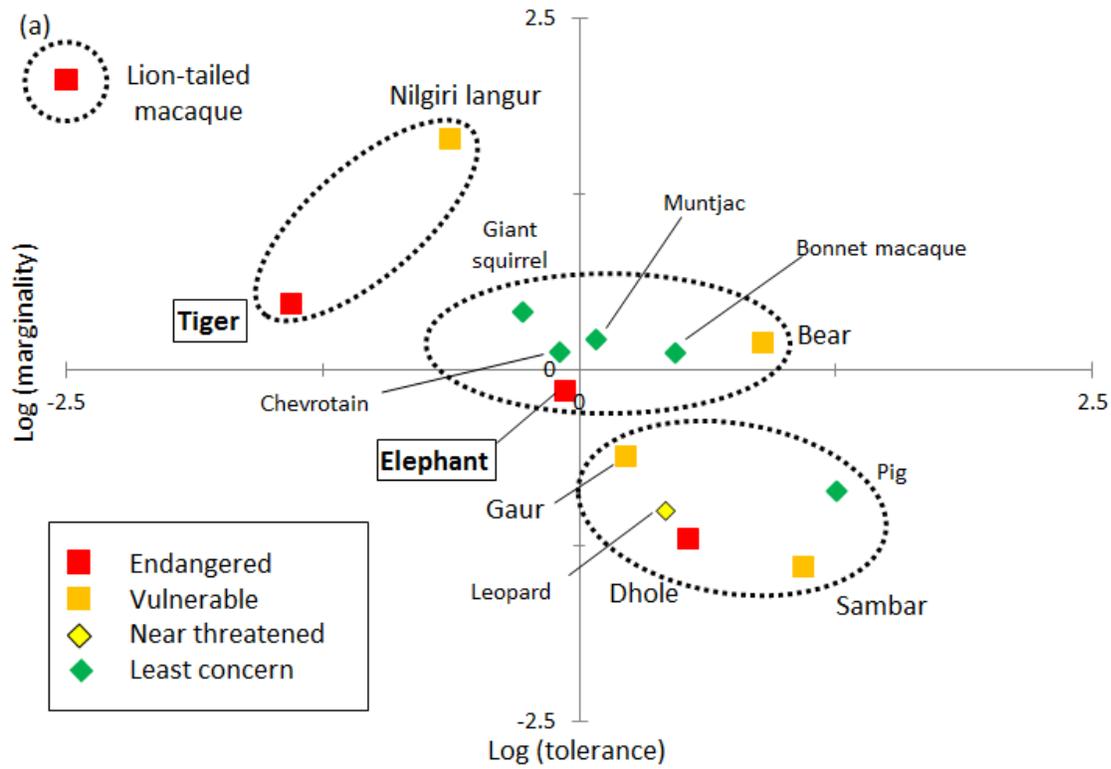


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658 Figure 3.



660 Supporting Information

661 Appendix 1. Details on the measurement and computation of covariates used for statistical  
662 analysis of the presence of 14 large mammal species in the Shencottah Gap, India between 2008  
663 and 2013.

664 Because of the non-availability of an accurate land use map of this area, we generated a field-  
665 verified alternative. Every 0.1 km along sampling routes, we classified habitat into five  
666 categories relevant to the focal species of this study - closed forest, grassland dominated, forestry  
667 plantation (teak, acacia, eucalyptus, bamboo), commercial plantation (rubber, tea, cardamom),  
668 and settlement/ farmland. We then used a combination of physical mapping in the field, data  
669 from the management plans of Thenmala and Achenkovil Divisions (KFD, 2010, MOEF, 2006),  
670 Google Earth and large scale vegetation maps (Ramesh et al. 1997) to trace out polygons  
671 representing closed forest, grassland, forestry plantations, commercial plantations and  
672 settlements/farmland. We verified and modified these polygons using habitat categorizations  
673 measured at 12082 locations in the field (above), and rasterized the resulting polygons to a  
674 resolution of 100 m.

675 Because our land use categorization is approximate, we also used the eco-climatic distance  
676 (Krishnaswamy et al. 2009) as an index to deciduousness. This index represents the Mahalanobis  
677 distance of the vegetation in a particular cell from a reference category of wet evergreen forest,  
678 and has been shown to correlate well with forest types in south India (Krishnaswamy et al.  
679 2009). We derived this index using Enhanced Vegetation Index data from MODIS (Oak Ridge  
680 National Laboratory Distributed Active Archive Center 2011) at a 250-m resolution.

681 We also mapped the point locations of all houses within the study area using Google Earth. We  
682 measured the Euclidean distance from the centroid of each cell to the nearest settlement,

683 commercial plantation and major road (NH 208 and Shencottah-Achenkovil-Punalur road). We  
684 corrected all these distance measurements for terrain, using a linear interpolation based on a  
685 digital elevation model (DEM) derived from 90-m LANDSAT data (USGS 2008). We conducted  
686 all the above spatial analysis in ArcGIS 10.1 (ESRI, Redlands, USA) and Geospatial Modeling  
687 Environment 0.7.2.1 (Beyer 2012).

688

689

690 Appendix 2. Correlation (Pearson's  $r$ ;  $|r| > 0.3$  depicted in bold) of all environmental covariates to the marginality axis of an  
691 Ecological Niche Factor Analysis comparing cells that were surveyed for each of 14 species in the Shencottah Gap, India from 2008 to  
692 2013, to cells within the study area that were not surveyed, to quantify potential biases in sampling intensity across habitat types.  
693 Footnotes indicate scale of covariate measurement.

Covariate	Threatened species							Non-threatened species						
	ELP	GAR	SBR	TGR	DHL	BER	LTM	NLG	LPD	PIG	MJK	CHV	GSQ	BNT
Closed forest	<b>-0.41<sup>4</sup></b>	<b>-0.44<sup>2</sup></b>	<b>-0.43<sup>4</sup></b>	0.05 <sup>3</sup>	0.07 <sup>4</sup>	<b>-0.41<sup>4</sup></b>	-0.26 <sup>1</sup>	<b>-0.45<sup>4</sup></b>	0.10 <sup>1</sup>	<b>-0.42<sup>4</sup></b>	<b>-0.43<sup>1</sup></b>	<b>0.43<sup>1</sup></b>	<b>-0.46<sup>1</sup></b>	<b>-0.45<sup>1</sup></b>
Open forest/grassland	0.00 <sup>4</sup>	0.00 <sup>4</sup>	-0.02 <sup>1</sup>	-0.25 <sup>4</sup>	-0.28 <sup>2</sup>	0.00 <sup>4</sup>	-0.11 <sup>1</sup>	-0.01 <sup>1</sup>	-0.25 <sup>4</sup>	-0.03 <sup>1</sup>	0.00 <sup>4</sup>	0.00 <sup>4</sup>	-0.01 <sup>1</sup>	0.00 <sup>4</sup>
Forestry plantation	<b>0.49<sup>2</sup></b>	<b>0.54<sup>1</sup></b>	<b>0.43<sup>3</sup></b>	0.20 <sup>2</sup>	0.10 <sup>4</sup>	<b>0.52<sup>1</sup></b>	<b>0.37<sup>3</sup></b>	<b>0.40<sup>4</sup></b>	0.18 <sup>3</sup>	<b>0.49<sup>2</sup></b>	<b>0.54<sup>1</sup></b>	<b>0.54<sup>1</sup></b>	<b>0.55<sup>1</sup></b>	<b>0.39<sup>4</sup></b>
Commercial plantation	0.01 <sup>3</sup>	0.02 <sup>3</sup>	0.04 <sup>1</sup>	-0.09 <sup>1</sup>	-0.09 <sup>1</sup>	-0.01 <sup>4</sup>	0.03 <sup>1</sup>	-0.06 <sup>4</sup>	-0.03 <sup>4</sup>	-0.01 <sup>4</sup>	-0.01 <sup>4</sup>	0.04 <sup>1</sup>	0.04 <sup>1</sup>	-0.01 <sup>4</sup>
Settlement	0.21 <sup>3</sup>	0.11 <sup>2</sup>	0.24 <sup>4</sup>	0.17 <sup>3</sup>	0.08 <sup>1</sup>	0.11 <sup>2</sup>	0.19 <sup>4</sup>	0.23 <sup>3</sup>	0.07 <sup>1</sup>	0.22 <sup>3</sup>	0.05 <sup>1</sup>	0.05 <sup>1</sup>	0.12 <sup>2</sup>	0.05 <sup>1</sup>
Eco-climatic distance	0.24 <sup>4</sup>	0.06 <sup>1</sup>	0.27 <sup>4</sup>	-0.04 <sup>4</sup>	-0.04 <sup>1</sup>	0.26 <sup>4</sup>	0.04 <sup>1</sup>	0.29 <sup>3</sup>	-0.01 <sup>2</sup>	0.22 <sup>3</sup>	0.11 <sup>1</sup>	0.06 <sup>1</sup>	0.05 <sup>1</sup>	0.28 <sup>4</sup>
House density	0.02 <sup>3</sup>	0.03 <sup>3</sup>	-0.11 <sup>1</sup>	0.03 <sup>2</sup>	-0.05 <sup>1</sup>	-0.07 <sup>2</sup>	-0.04 <sup>2</sup>	0.00 <sup>3</sup>	-0.05 <sup>1</sup>	0.03 <sup>3</sup>	0.03 <sup>3</sup>	0.03 <sup>3</sup>	0.00 <sup>3</sup>	-0.08 <sup>2</sup>
Distance to	<b>-0.30</b>	<b>-0.31</b>	<b>-0.33</b>	-0.16	-0.17	<b>-0.31</b>	<b>-0.36</b>	-0.29	-0.17	<b>-0.31</b>	<b>-0.32</b>	<b>-0.32</b>	-0.28	<b>-0.34</b>

settlement

Distance to  
commercial  
plantation

0.08 0.07 0.06 -0.11 -0.11 0.07 -0.09 0.14 -0.11 0.07 0.07 0.07 0.14 0.07

Distance to  
major road

-0.14 -0.15 -0.15 -0.21 -0.22 -0.14 -0.24 -0.10 -0.22 -0.15 -0.15 -0.15 -0.10 -0.16

Slope to  
settlement

-0.21 -0.21 -0.20 -0.29 -0.29 -0.21 -0.26 -0.23 -0.29 -0.21 -0.21 -0.21 -0.22 -0.22

Slope to  
commercial  
plantation

-0.15 -0.16 -0.15 -0.20 -0.21 -0.16 -0.19 -0.16 -0.21 -0.16 -0.16 -0.16 -0.16 -0.17

Slope

**-0.52 -0.52 -0.50 -0.77 -0.78 -0.51 -0.64 -0.51 -0.78 -0.51 -0.52 -0.52 -0.50 -0.55**

Curvature

-0.19 -0.18 -0.18 -0.23 -0.24 -0.18 -0.18 -0.20 -0.24 -0.18 -0.18 -0.18 -0.19 -0.19

694

695 <sup>1</sup>300 m; <sup>2</sup>600 m; <sup>3</sup>1200 m; <sup>4</sup> 2400 m.

696 ELP Elephant; GAR Gaur; SBR Sambar; TGR Tiger; DHL Dhole; BER Sloth Bear; LTM Lion-tailed Macaque; NLG Nilgiri Langur;

697 LPD Leopard; PIG Wild Pig; MJK Northern Red Muntjac; CHV Indian Chevrotain; GSQ Indian Giant Squirrel; BNT Bonnet

698 Macaque.

699

700 Appendix 3. Correlation (Pearson's  $r$ ;  $|r| > 0.3$  depicted in bold lettering) of all covariates to the marginality axis of an Ecological  
 701 Niche Factor Analysis comparing sampled cells where each of 14 species was detected or not detected in the Shencottah Gap, India  
 702 from 2008 to 2013. See Appendix 2 for scales of covariate measurement.

Covariate	Threatened species							Non-threatened species						
	ELP	GAR	SBR	TGR	DHL	BER	LTM	NLG	LPD	PIG	MJK	CHV	GSQ	BNT
Closed forest	<b>0.44</b>	0.05	<b>-0.49</b>	<b>0.46</b>	-0.13	-0.26	<b>0.49</b>	<b>0.39</b>	0.30	-0.25	<b>0.44</b>	<b>0.36</b>	<b>0.51</b>	<b>0.36</b>
Open forest/grassland	-0.05	<b>0.36</b>	<b>0.30</b>	-0.20	0.30	<b>0.49</b>	-0.22	-0.08	-0.11	-0.21	-0.30	-0.28	-0.21	-0.28
Forestry plantation	-0.08	-0.05	0.21	<b>-0.31</b>	-0.16	-0.04	-0.28	-0.21	-0.19	0.29	-0.17	-0.13	-0.19	-0.26
Commercial plantation	<b>-0.30</b>	<b>-0.36</b>	-0.20	-0.14	-0.10	<b>-0.32</b>	-0.11	-0.20	0.27	0.15	0.24	-0.13	-0.22	0.28
Settlement	<b>-0.33</b>	<b>-0.37</b>	<b>0.34</b>	-0.28	-0.21	-0.18	-0.19	-0.21	<b>-0.37</b>	0.18	-0.19	-0.14	-0.26	-0.05
Eco-climatic distance	<b>-0.40</b>	-0.10	<b>0.48</b>	-0.22	0.24	0.24	<b>-0.50</b>	<b>-0.36</b>	-0.20	0.20	-0.26	-0.20	<b>-0.39</b>	-0.08
House density	<b>-0.32</b>	<b>-0.39</b>	-0.12	-0.22	-0.13	-0.23	-0.13	-0.20	-0.22	0.29	0.10	0.25	-0.21	0.21
Distance to settlement	<b>0.43</b>	<b>0.37</b>	<b>-0.39</b>	0.19	<b>-0.55</b>	0.18	0.06	<b>0.45</b>	-0.23	<b>-0.33</b>	-0.15	-0.23	<b>0.37</b>	<b>-0.35</b>

Distance to commercial plantation	0.21	<b>0.36</b>	-0.04	<b>-0.43</b>	<b>-0.32</b>	<b>0.50</b>	-0.20	0.11	<b>-0.48</b>	-0.27	<b>-0.47</b>	<b>-0.45</b>	-0.01	<b>-0.53</b>
Distance to major road	0.17	0.18	-0.19	-0.05	<b>-0.34</b>	<b>0.31</b>	0.11	0.27	<b>-0.37</b>	<b>-0.45</b>	<b>-0.32</b>	<b>-0.52</b>	-0.08	<b>-0.39</b>
Slope to settlement	0.18	0.03	-0.01	<b>0.33</b>	0.15	0.00	0.26	0.26	0.26	-0.25	<b>0.31</b>	0.28	0.29	0.19
Slope to commercial plantation	0.21	0.17	0.10	0.28	0.11	0.24	0.30	0.24	0.18	-0.25	0.19	0.09	0.29	0.04
Slope	-0.07	-0.28	0.10	-0.06	-0.12	-0.03	0.21	<b>0.32</b>	0.11	<b>-0.34</b>	0.15	0.01	0.18	0.03
Curvature	0.01	0.16	0.09	0.21	<b>0.41</b>	0.07	0.24	0.12	0.21	-0.02	0.13	0.15	0.03	0.04

703

704 ELP Elephant; GAR Gaur; SBR Sambar; TGR Tiger; DHL Dhole; BER Sloth Bear; LTM Lion-tailed Macaque; NLG Nilgiri Langur;  
705 LPD Leopard; PIG Wild Pig; MJK Northern Red Muntjac; CHV Indian Chevrotain; GSQ Indian Giant Squirrel; BNT Bonnet  
706 Macaque.

707 Appendix 4. Loadings on two principal component axes that together explained 73% of the  
 708 variance of covariate correlations with the marginality axis for 14 mammals in the Shencottah  
 709 Gap, India from 2008 to 2013. These components are reflected in Figure 3b. See Appendix 2 for  
 710 scales of covariate measurement.

Covariate	Principal component 1	Principal component 2
Closed forest	-0.80	0.51
Open forest/ grassland	0.21	-0.84
Forestry plantation	0.83	-0.39
Commercial plantation	0.30	0.82
Settlement	0.81	0.04
Eco-climatic distance	0.84	-0.33
House density	0.57	0.68
Distance to settlement	-0.72	-0.49
Distance to commercial plantation	-0.15	-0.95
Distance to major road	-0.54	-0.76
Slope	-0.56	0.27
Curvature	-0.23	0.13
Slope to commercial plantation	-0.90	-0.20
Slope to settlement	-0.81	0.48

711

712 Appendix 5. Correlation (Pearson's  $r$ ;  $|r| > 0.3$  depicted in bold lettering) of all covariates with  
 713 the first specialization axis of an Ecological Niche Factor Analysis comparing sampled cells  
 714 where each of 14 species was detected or not detected in the Shencottah Gap, India from 2008 to  
 715 2013. Only the absolute value of the correlation coefficient is meaningful. See Appendix 3 for  
 716 scales of covariate measurement.

Covariate	Threatened						Not threatened					
	ELP	GAR	SBR	TGR	DHL	BER	LTM	NLG	LPD	PIG	MJK	CHV
Closed forest	-0.14	0.06	0.12	-0.06	-0.14	-0.03	-0.20	0.02	0.02	0.17	0.03	0.11
Open forest/grassland	-0.15	0.02	-0.06	-0.07	-0.01	-0.05	-0.16	0.01	0.05	0.27	<b>-0.43</b>	-0.07
Forestry plantation	-0.05	0.10	0.02	-0.04	-0.20	-0.02	0.12	0.04	0.06	0.10	0.01	-0.04
Commercial plantation	<b>-0.81</b>	<b>-0.84</b>	<b>-0.82</b>	-0.06	0.00	<b>-0.56</b>	0.13	<b>-0.54</b>	-0.04	0.09	-0.07	-0.11
Settlement	0.28	<b>0.40</b>	0.16	<b>-0.50</b>	<b>0.58</b>	-0.06	-0.19	-0.25	<b>-0.38</b>	-0.26	<b>0.86</b>	<b>0.92</b>
Eco-climatic distance	0.17	0.04	-0.26	-0.04	-0.02	0.05	0.01	-0.01	-0.05	<b>0.75</b>	0.04	0.12
House density	0.23	0.26	<b>-0.43</b>	<b>0.85</b>	<b>-0.75</b>	<b>0.82</b>	<b>-0.90</b>	<b>0.80</b>	<b>0.90</b>	0.00	-0.14	-0.14
Distance to settlement	0.22	0.07	0.12	-0.04	0.10	0.07	-0.18	-0.03	0.01	<b>-0.37</b>	0.16	0.09
Distance to commercial plantation	-0.27	-0.19	0.06	-0.06	0.00	-0.05	0.16	0.04	-0.15	0.14	-0.14	-0.17

Distance to													
major road	0.10	0.06	0.14	-0.05	-0.14	0.00	0.04	-0.03	0.00	0.16	-0.08	-0.16	0.00
Slope to													
settlement	-0.10	-0.06	0.00	0.03	-0.03	-0.01	-0.04	0.01	-0.04	0.17	-0.01	-0.12	0.00
Slope to													
commercial													
plantation	0.03	0.01	-0.06	0.04	-0.03	0.09	0.02	0.03	0.08	-0.10	0.03	0.04	0.00
Slope	0.01	0.06	0.04	-0.04	0.00	-0.02	0.00	0.01	-0.02	0.13	-0.03	-0.05	0.00
Curvature	0.01	-0.01	0.03	-0.04	0.00	-0.01	0.02	0.01	0.01	0.14	-0.02	0.00	0.00

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