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► **To cite this version:**

Ugo Arbieu, Claudia Grünewald, Berta Martín-López, Matthias Schleuning, Katrin Böhning-Gaese. Large mammal diversity matters for wildlife tourism in Southern African Protected Areas: Insights for management. *Ecosystem Services*, 2018, 31, pp.481-490. 10.1016/j.ecoser.2017.11.006 . hal-04087842

HAL Id: hal-04087842

<https://hal.science/hal-04087842>

Submitted on 3 May 2023

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2 Southern African protected areas: insights for management.

3
4 **JOURNAL**

5 Ecosystem Services

6 <https://doi.org/10.1016/j.ecoser.2017.11.006>

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23
24 **CITATION**

25 Arbieu, U., Grünewald, C., Martín-López, B., Schleuning, M., & Böhning-Gaese, K. (2018).
26 Large mammal diversity matters for wildlife tourism in Southern African Protected Areas:
27 Insights for management. *Ecosystem Services*, **31**, 481-490. [10.1016/j.ecoser.2017.11.006](https://doi.org/10.1016/j.ecoser.2017.11.006)

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30

31 **Highlights**

32 Relationships between supply and demand can reveal the use of recreational services

33 We assess supply and demand for the recreational service of wildlife tourism

34 We test the influence of 13 mammal diversity measures on tourists' distributions

35 Diversity and subsets of large mammal diversity affected tourists' distributions

36 Effects of biodiversity measures on visitors were mostly context-specific

37 We give management implications for reducing potential negative impacts on wildlife

38

39 **Abstract**

40 Relationships between biodiversity and cultural ecosystem services have been little studied

41 compared to other ecosystem services, although fundamental for environmental

42 management. Recreational ecosystem services like wildlife tourism are specific cultural

43 ecosystem services that often involve relationships between the supply of opportunities to

44 interact with biodiversity and the demand of wildlife tourists. Here, we first investigated

45 whether different biodiversity measures based on three metrics applied to four components

46 of large mammal diversity influenced the distribution of visitors within four Protected Areas

47 (PAs) in Southern Africa. Second, we explored whether these effects were context-specific

48 across the four PAs. We counted large mammals and visitor numbers along 196 road

49 transects to test these relationships. All species-mammal diversity metrics related positively

50 to visitor numbers. Subsets of mammal diversity were also positively associated with the

51 distribution of visitors in all PAs. Relationships between supply and demand for the

52 recreational service of wildlife tourism were mainly context-specific: the relationships

53 between biodiversity measures and visitor numbers differed among PAs. Our results could

54 help managers to optimize the use of recreational services within PAs, by diversifying

55 viewing opportunities while reducing disturbance to wildlife. The supply-demand approach
56 presented here offers promising avenues for further assessments of recreational ecosystem
57 services.

58

59 **Keywords:** Africa; Mammals; Nature-based tourism; Predators; Protected areas; Ungulates.

60 **1. Introduction**

61
62 Biodiversity is assumed to provide multiple benefits to human societies through ecosystem
63 services; yet little is known on the actual relationships between biodiversity and ecosystem
64 services (Balvanera et al. 2013; Mace et al. 2012). In particular, there is a lack of studies
65 investigating the inter-linkages between cultural ecosystem services (CES) and biodiversity
66 (Cardinale et al. 2012). Cultural ecosystem services are the “non-material benefits people
67 obtain from ecosystems through spiritual enrichment, cognitive development, reflection,
68 recreation and aesthetic experience” (Millennium Ecosystem Assessment 2005). These non-
69 material benefits provided by biodiversity contribute to shaping people’s relation to nature
70 (Chan et al. 2016; Cooper et al. 2016, Hausmann et al. 2016) and can improve human well-
71 being (Hausmann et al. 2016; Milner-Gulland et al. 2014; Naeem et al. 2016). Investigating
72 the relationships between biodiversity and CES is, however, problematic because these
73 relationships are often indirect, difficult to measure and to manipulate experimentally
74 (Balvanera et al. 2015; Cardinale et al. 2012). Further, because CES are inherently co-
75 produced by bio-cultural and social-ecological processes (Díaz et al. 2015; Palomo et al.
76 2016), it is also difficult to ascertain to what extent biodiversity is contributing to CES
77 (Dallimer et al. 2012). Consequently, little is known on the quantitative relationships
78 between biodiversity and CES (Cardinale et al. 2012; Hevia et al. 2017; Mace et al. 2012),
79 even though they are recognized as important in environmental management and
80 conservation policies (Laurila-Pant et al. 2015).

81 Recreational ecosystem services have been the most studied form of CES (Milcu et
82 al. 2013). Recreational services represent the potential contribution of landscapes and
83 biodiversity to specific recreation opportunities, involving people’s physical, intellectual and
84 representational interaction with ecosystems and biodiversity, as defined in the Common

85 International Classification of Ecosystem Services (CICES, Haynes-Young & Potschin 2013).
86 Novel approaches have emerged to estimate the recreation potential associated with
87 biodiversity, involving the collection of local field data (Arbieu et al. 2017; Grunewald et al.
88 2016; Winterbach et al. 2015), social-media data (Hausmann et al. 2017a,b; Martínez-Pastur
89 et al. 2016; Willemen et al. 2015), or economic methods such as choice experiments
90 (Verissimo et al. 2009) or social-ecological approaches to assess wildlife tourists'
91 preferences (Maciejewski & Kerley 2014). These novel approaches offer promising evidence
92 that biodiversity can support recreational services in different places, particularly in
93 Protected Areas (e.g. Hausmann et al. 2017a; Martínez-Pastur et al. 2016).

94 Protected Areas (PAs) are prime conservation units expected to achieve several
95 objectives such as the conservation of biodiversity and ecosystem services (Watson et al.
96 2014). PAs play a prominent role in providing recreational services, particularly for nature-
97 based tourism, as they receive worldwide approximately 8 billion visitors per year (Balmford
98 et al. 2015). Nature-based tourism, and in particular wildlife tourism (defined here as a form
99 of nature-based tourism involving encounters with non-domesticated animals), represents a
100 unique opportunity to study the capacity of biodiversity to provide recreational services
101 (Daniel et al. 2012; Wood et al. 2013). Despite this, only few recent studies have
102 demonstrated positive relationships between biodiversity and wildlife tourism in PAs. For
103 example, Siikamäki et al. (2015) showed that PAs with high biodiversity were most attractive
104 for visitors in Finland. Similarly, Booth *et al.* (2011) highlighted the importance of rare bird
105 species in attracting visitors to PAs in the United Kingdom. Therefore, a comprehensive
106 assessment of how various components of biodiversity actually affect the recreational
107 service of wildlife tourism is currently lacking.

108 This study seeks to contribute to this assessment of the recreational service of
109 wildlife-tourism by exploring the role of different components of biodiversity in the actual
110 use of this service. Biodiversity metrics, such as species richness, phylogenetic diversity and
111 abundance, can be relevant measures of biodiversity that are essential for the recreational
112 service of wildlife tourism. People may be interested in interacting with many species (high
113 species richness), with dissimilar species (high phylogenetic diversity) or with many
114 individuals (high abundance) (Winterbach et al. 2015). However, these metrics can also be
115 applied to specific subsets of biodiversity in the assessment of the service of wildlife
116 tourism, since people may also be attracted to specific groups of species. In particular, they
117 may prefer charismatic (Arbieu et al. 2017; Di Minin et al. 2013; Di Minin & Moilanen 2014),
118 rare (Angulo & Courchamp 2009; Booth et al. 2011) or threatened species (Siikamäki et al.
119 2015). Assessments of the recreational service of wildlife tourism should therefore cover
120 different components of biodiversity that reflect different recreational opportunities (see
121 Fig. 1), not only considering all species present in an area, but also subsets of charismatic,
122 rare and threatened species (see Dallimer et al. 2012; Siikamäki et al. 2015).

123 The recreational service of wildlife tourism can be assessed from the perspective of
124 the relationship between supply and demand (Fig. 1). The supply-side refers to the
125 biophysical components and properties, often in combination with human capitals (e.g.
126 infrastructure, machines or knowledge), that are required to provide an ecosystem service
127 in a particular area over a period of time (Burkhard et al. 2012; Geijzendorffer et al., 2015;
128 Palomo et al. 2016; Wei et al. 2017). The demand-side refers to the consumption, use or
129 desire to enjoy a particular ecosystem service by stakeholders to fulfil their needs in a
130 particular area over a period of time (Geijzendorffer et al., 2015; Wei et al. 2017; Wolff et al.
131 2015). In the context of the recreational service of wildlife tourism, the supply-side refers to

132 the different biodiversity components (i.e. all species, subsets of charismatic, rare and
133 threatened species) and metrics (i.e. richness, phylogenetic diversity, abundance) that offer
134 opportunities of recreational experiences (Fig. 1). The demand of wildlife tourism can be
135 expressed by the number of visitors (Balmford et al. 2015; Schägner et al. 2016), their
136 preferences and desires to encounter or see particular species (Ament et al. 2016; Arbieu et
137 al. 2017) or their actual costs and willingness to pay for seeing particular species (Di Minin et
138 al. 2013; Naidoo et al. 2016). This demand can be also influenced by human infrastructure,
139 such as tourism facilities, development of roads or available tourist information (Fig. 1).

140 The supply- and demand-sides of wildlife tourism can vary across space because of
141 variation in ecosystem capacity, such as habitat structure, and variation in infrastructures,
142 such as tourism facilities (de Vos et al. 2016; Lacitignola et al. 2007; Martínez-Pastur et al.
143 2016; Torres-Sovero et al. 2012). The spatial heterogeneity of the supply- and demand-sides
144 of recreational services is difficult to jointly assess, and few studies have shed light on this
145 (see Crouzat et al. 2015). However, understanding the spatial variation in supply and
146 demand can inform management decisions in PAs (Palomo et al. 2014). For example, the
147 distribution of wildlife tourists can reveal spatial patterns of potential disturbances to
148 wildlife (Lunde et al. 2016, Mulero-Pázmány et al. 2016). Therefore, analysing the spatial
149 variation of the supply and demand of the recreational service of wildlife tourism might
150 provide useful guidance for management within and across PAs.

151 The main objective of this research was to test the spatial relationship between
152 different biodiversity measures and wildlife tourism in order to understand the supply and
153 demand dimensions of this recreational service within and across four PAs in in three
154 countries (Namibia, Botswana, South Africa). We specifically aimed to: (1) test the influence
155 of biodiversity metrics (species richness, phylogenetic diversity, abundance) applied to four

156 components of biodiversity (all species, and subsets of charismatic, rare and threatened
157 species) on visitor numbers along road transects within the four PAs, while testing whether
158 factors related to infrastructure affected the spatial distribution of visitors in the PAs; and
159 (2) to test whether the effects of biodiversity measures on visitor numbers were consistent
160 across the four PAs. In doing so, we conducted transect counts of mammal diversity and
161 abundance (i.e. supply) as well as visitor numbers (i.e. demand) along road transects in the
162 four PAs. This study offers a novel approach to assess the recreational service of wildlife
163 tourism by considering different biodiversity metrics and components relevant for its supply
164 and by taking into account the spatial variation of its supply and demand.

165

166 **2. Methods**

167 **2.1 Study area**

168 We conducted fieldwork in four PAs (Fig. 2), namely Etosha National Park (Namibia), Chobe
169 National Park (Botswana), Kruger National Park and Hluhluwe-Imfolozi Park (South Africa).
170 The four PAs were selected because they cover a wide gradient in environmental conditions,
171 in particular in rainfall (mean annual rainfall was obtained from the WorldClim database
172 (<http://www.worldclim.org>)), and represent a variety of savannah landscapes (Methods S1
173 in Supporting Information, see also Table 1 in Arbieu et al. 2017). Savannah ecosystems
174 harbour a unique diversity of large mammals, such as large ungulates and predators, and
175 are prime destinations for wildlife tourists (Akama & Kieti 2003; Boshoff et al. 2007; Di
176 Minin et al. 2013; Okello et al. 2008). The four PAs were also selected because they contain
177 predator and especially lion populations (the most abundant species of predators and the
178 most sought after by tourists, see Arbieu et al. 2017), and offer the possibility for visitors to

179 use own vehicles or tour-operators (*i.e.* guided drives). All data were collected during the
180 dry season, which is the recommended period for visiting these PAs. The study was
181 conducted in Etosha in October 2014, in Chobe in June/July 2014, in Kruger from June to
182 August 2012, and in Hluhluwe in May 2014. Description and maps of the four PAs can be
183 found in the Supporting Information (Methods S1, Fig. S1).

184

185 **2.2 Transect counts**

186 We distributed 50, 40, 78 and 28 road transects along the public road and track network of
187 Etosha, Chobe, Kruger and Hluhluwe, respectively (see Fig. S1 in Supporting Information),
188 covering the vegetation gradient in each PA. Transects were 5 km long with a minimum
189 distance of 1 km between transects and to the next main camp or gate. Our approach using
190 road transects consequently allows us to directly link the distribution of large mammals (*i.e.*
191 supply-side) with the one of wildlife tourists (*i.e.* demand-side) within PAs (Fig. 1). Along
192 each road transect, we simultaneously counted large mammals and visitors and replicated
193 transect counts three times (at different times of day, *i.e.* morning, mid-day and afternoon),
194 with at least three days between temporal replicates.

195 We conducted animal and visitor counts by driving along each transect at a constant
196 speed (ca. 15 km/h) in a four-wheel drive truck with two observers, each scanning one side
197 of the road. We counted all large ungulates and predators (see Table S1 for species list in
198 Supporting Information). When an animal or a group of animals was spotted, each species
199 was identified and individuals were counted. Among the predators, we only considered lion
200 (*Panthera leo*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), cheetah
201 (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*) because they are the largest and most
202 regularly observed predators in the region. Because of the elusive nature of predators, we

203 estimated predator occurrences using two methods: own predator sightings and data from
204 a social survey based on visitor questionnaires (Section III of the questionnaire in Methods
205 S2 in Supporting Information). For own predator sightings, we noted species and number of
206 individuals and recorded the sighting location using a GPS-device, whenever we sighted one
207 of the five predator species either when conducting the regular transect counts or while
208 commuting. The questionnaires were conducted at lunch time and in the evenings, resulting
209 in 153, 158, 204 and 136 questionnaires in Etosha, Chobe, Kruger and Hluhluwe,
210 respectively. We asked the visitors about sightings of any of the five predator species on the
211 respective day and noted species and number of individuals. We further asked the visitors
212 to mark the sighting location on the map provided at the entrance of the PA. If respondents
213 were unsure about the sighting location, we excluded these sightings from the analysis.
214 Own and visitors' predator sightings were pooled, digitized (using ARCGIS v. 10.1) and only
215 those located within our road transects were retained for the analyses. To correct predator
216 sightings for sampling effort, we recorded the total number of times we drove each transect
217 during the study period. We also asked visitors to mark the routes they had driven on the
218 interview day to assess which transects they had passed. We combined these data to
219 determine the total number of times each transect was driven by us and the visitors.

220 As a proxy for the demand of the recreational service of wildlife tourism, we
221 estimated the number of visitor vehicles (professional guided tours and private vehicles)
222 passing us in opposite direction during each mammal transect count along the road
223 transects. Therefore, we did not count vehicles twice. When a vehicle was parked on the
224 side of the road with no specific travelling direction, we did not count it. The demand of
225 wildlife tourism can be influenced by factors related to infrastructure and habitat structure
226 within PAs (de Vos et al. 2016). Thus, we accounted for PA infrastructure, road conditions

227 and visibility as factors potentially affecting spatial distribution of visitors in the PAs. To
228 assess effects of PA infrastructure, we measured the minimum distance from the centre of
229 each transect to the nearest PA entry gate, camp or lodge, and stretch-point (defined here
230 as places where visitors are allowed to get off their vehicles) using ARCGIS (v. 10.1). We
231 classified roads into three categories (*i.e.*, main tar road, main secondary road, and sandy
232 tracks or small loops) to account for accessibility of different areas within each PA. To
233 account for varying habitat attributes, we quantified visibility at the start of each transect,
234 after every kilometre and at the end of it (*i.e.* kilometre 0, 1, 2, 3, 4 and 5). We recorded
235 visibility only once, as little changes were observed over the time spent in the four PAs. To
236 assess visibility, we estimated the perpendicular distance at which we would be able to
237 identify an adult warthog (*Phacochoerus africanus*; see Caro 1999), to the left and to the
238 right side of the road, using a laser range finder. We calculated the average of the resulting
239 12 values for each transect (*i.e.* kilometre 0, 1, 2, 3, 4 and 5 at the right and left sides).
240 Finally, we recorded the time spent passing each transect, since the number of vehicles is
241 directly related to the sampling time.

242 Our final dataset included 196 replicated transects and 33 mammal species over the
243 four PAs, which enabled us to link mammal diversity and visitor distributions at the fine
244 scale of 5 km transects within the PAs, while considering tourism infrastructure.

245

246 **2.3 Biodiversity measures definition and calculations**

247 To test the influence of mammal diversity on vehicle distribution and numbers, we assessed
248 four components of large mammal diversity (all large mammals, subsets of charismatic, rare
249 and threatened species) and used three biodiversity metrics (species richness, phylogenetic
250 diversity, abundance) (Fig. 1), all reflecting different potential supply of the recreational

251 service of wildlife tourism. The diversity of large mammals was assessed by recording all
252 ungulate species encountered along the road transects, the five species of large predators
253 described above, and excluded other species (like small predators and primates), thus
254 reflecting the species for which tourists' stated demand is highest (see Arbieu et al. 2017).
255 We also classified species according to their charisma, rarity and threat. We defined
256 charisma in two ways. First, the large *predator species* were considered to be charismatic
257 species (Ripple et al. 2014; Willemen et al. 2015). Second, the *Big Five* – lion, leopard,
258 African elephant (*Loxodonta africana*), black (*Diceros bicornis*) and white rhinoceros
259 (*Ceratotherium simum*), and African buffalo (*Syncerus caffer*) – were considered charismatic
260 (Arbieu et al. 2017, Okello et al. 2008). We defined the rarity of ungulate species in two
261 ways, avoiding redundancy to predator species, which are also rare (Table S2 in Supporting
262 Information). First, we defined *regionally rare species* based on range sizes of ungulate
263 species within Africa (IUCN database; <http://www.iucnredlist.org/technical->
264 [documents/spatial-data](http://www.iucnredlist.org/technical-documents/spatial-data)). A species was categorized as regionally rare if it belonged to the
265 50% of the species with the smallest range sizes in Africa. Second, we defined *locally rare*
266 *species* based on our own counts within each PA. Here, a species was categorized as locally
267 rare if it belonged to the 50% of the species with the lowest probabilities to be encountered
268 within each PA. Finally, all species classified as near threatened, vulnerable, endangered or
269 critically endangered (following IUCN's Red List of Threatened Species) were categorized as
270 threatened species.

271 Three biodiversity metrics were applied to the four components of large mammal
272 diversity. These biodiversity metrics defined hereafter reflect the *perceived* species richness
273 and abundance observed by us and by the wildlife tourists, but do not quantify *true* species
274 richness and abundance. While such measures could be criticised in studies on mammal

275 populations and communities, they are suitable in CES studies because they quantify the
276 actual visitors' experience of mammal communities while driving within PAs (Arbieu et al.
277 2017). Species richness reflected the sum of sighting probabilities of individual mammal
278 species in each transect. Phylogenetic diversity reflecting the dissimilarity of mammal
279 species in the road transects was calculated using an abundance-weighted phylogenetic
280 diversity index. Abundance was the average total number of animals recorded in the road
281 transects, regardless of species identity. Calculation details of these metrics can be found in
282 the Supporting Information (Methods S3).

283 We calculated richness and abundance for all biodiversity components (*i.e.* all
284 species, charismatic, rare and threatened species) (see Supporting Information Methods S3).
285 We calculated the phylogenetic diversity only for the biodiversity component including all
286 species because the metric is not meaningful for the subset components. Consequently, we
287 tested effects of 13 measures of biodiversity on vehicle numbers along transects: richness,
288 phylogenetic diversity and abundance of all species, and richness and abundance of
289 predators, Big Five, regionally and locally rare ungulates and threatened species.

290

291 **2.4 Statistical analysis**

292 All statistical analyses were done with R 3.1.1 software (R Core Team 2014) and dedicated
293 packages. We used Generalized Linear Mixed Models to model the influence of biodiversity
294 measures on vehicle numbers along each transect across the four PAs, accounting for the
295 other factors that might determine visitor distributions within PAs. We are aware that
296 vehicle numbers could also affect wildlife distribution, but assume that tourist vehicles
297 would only influence wildlife behaviour and do not lead to numerical responses of wildlife

298 along the studied road transects (Mulero-Pázmány et al. 2016). Moreover, we expect a
299 positive relationship between biodiversity and vehicle numbers, whereas an effect of vehicle
300 numbers on biodiversity variables should rather lead to a negative relationship between the
301 two variables. We used Poisson regressions to model the count data of vehicle numbers in
302 response to biodiversity measures (Zuur et al. 2009). We log-transformed all biodiversity
303 measures, scaled and centred them to zero mean and unit variance to obtain model
304 estimates that are comparable in their effect sizes. Because biodiversity measures were
305 correlated (Table S3 in Supporting Information), we fitted separate models for each
306 biodiversity measure. We adopted a model averaging procedure to test the effect of
307 biodiversity on vehicle numbers (Bolker et al. 2009). Thus, each full model contained as
308 fixed effect one of the 13 biodiversity measures, and further included as fixed effects
309 distances to closest park entry gate, camp or lodge and stretch-point, visibility and time
310 spent driving along each transect. The full models contained as random effects the road
311 categories (*i.e.* main tar road - main secondary road - sandy tracks or small loops), the date
312 of sampling, and the transects nested within PA. By including PA also as a random factor, we
313 correct for the variation of absolute visitor numbers observed in the road transects across
314 PAs. In total, we fitted three models for richness, phylogenetic diversity and abundance of
315 all large mammal species, and five richness-based and five abundance-based models for
316 charisma, rarity and threat, resulting in 13 full models in total.

317 For each full model, we identified the best subset of models based on the Akaike
318 Information Criterion (AIC) by testing all possible combinations of fixed effects specified in
319 the full model (MuMIn package). We kept the respective biodiversity measure in all subset
320 models. We obtained model estimates for each fixed effect by averaging model estimates
321 across all subset models with $\Delta AIC < 2$. We additionally quantified the amount of variation in

322 vehicle numbers that was explained by the fixed and random effects in each of the 13
323 models which yields an estimate of model performance (`rsquare.glm` function, MuMIn
324 package, Nakagawa & Schielzeth 2013). For this calculation, we included all fixed effects
325 that were present at least once in the respective subset of best models. Finally, we visually
326 checked for signals of spatial autocorrelation in the residuals of these 13 models, using
327 spatial correlograms (`correlog` function, `ncf` package).

328 In a second analysis, we tested whether biodiversity effects on vehicle numbers were
329 consistent across PAs. To this end, we built additional models with PA identity as fixed
330 effect, in addition to the fixed effects that were present at least once in the subset of best
331 models. We compared models including an interaction term between the respective
332 biodiversity measure and PA identity to models without this interaction term using analyses
333 of deviance. A significant interaction term identifies PA-specific effects of the respective
334 biodiversity measure on vehicle numbers.

335

336 **3. Results**

337 Visitors vehicle numbers along 588 transect counts in Etosha, Chobe, Kruger and Hluhluwe
338 PAs ranged from 0 to 67 vehicles per replicate (mean = 4.67, standard deviation = 7.72, n =
339 588). Vehicle numbers were highest in Kruger (mean = 9.29, sd = 10.30, n = 234), followed
340 by Etosha (mean = 1.90, sd = 2.36, n = 150), Hluhluwe (mean = 1.80, sd = 1.92, n = 84) and
341 Chobe (mean = 1.11, sd = 2.59, n = 120). Species richness of large mammals ranged from 0
342 to 7.04 species (mean = 2.68, sd = 1.42) per transect, and abundance varied between 0 and
343 730 animals per transect (mean = 65, sd = 104.95).

344 The model-averaging procedure resulted in almost identical statistical models of the
345 effects of large mammal diversity on vehicle numbers along transects in the four PAs (Table

346 1). All models retained by the model selection included as fixed effects the respective
347 biodiversity measure, the distance to the closest camp or lodge, the distance to the nearest
348 stretch-point, visibility, and the time spent driving the transect. The distance to the closest
349 PA gate was excluded in 5 of the 13 models by the model selection procedure. Each of the
350 13 models explained more than 70% of the variation of vehicle numbers along the road
351 transects, demonstrating good model specifications. Random effects' standard deviations
352 were quite high (Table 1), and the random model component related to variation among
353 road transects, categories and counting days generally explained more variation than the
354 fixed effects. We did not detect signals of spatial autocorrelation in model residuals.

355

356 **3.1 Biodiversity and infrastructure effects on vehicle numbers in Protected Areas**

357 The three biodiversity metrics involving all species (i.e. species richness, phylogenetic
358 diversity, abundance) had a positive influence on visitor vehicle numbers across the four PAs
359 (Fig. 3A, Table 1). In the richness-based analysis of diversity subsets (circle symbols in Fig.
360 3B), we found significant effects of predator species richness and of locally rare ungulate
361 species richness on vehicle numbers (Table 1). The richness of the Big Five, regionally rare
362 ungulates and threatened species were not significantly related to vehicle numbers. For the
363 abundance-based models of diversity subsets (square symbols in Fig. 3B), we found that all
364 metrics had a significant positive influence on the number of vehicles except the abundance
365 of the Big Five species. The abundance of regionally rare species of ungulates had the largest
366 effect on vehicle numbers among all subset metrics (Fig. 3B; Table 1).

367 Distance to closest gate, camps or stretch points, visibility and time spent sampling
368 were differently affecting vehicle numbers along the transects (Table 1). Distance to closest
369 camp was significantly negatively related to vehicle numbers in all 13 models. Visibility had a

370 significant negative effect in only three models (abundance and richness of all species, and
371 abundance of regionally rare species of ungulates). Finally, distance to nearest PA gates and
372 stretch-points never had significant effects on vehicle numbers.

373

374 **3.2 Park-specific assessment of biodiversity effects on vehicle numbers**

375 Only the richness and abundance of predators, and the abundance of threatened species
376 had a consistent effect on vehicle numbers across the four PAs. The interaction terms
377 between PA and predator richness, predator abundance and abundance of threatened
378 species were not significant (Table S4 in Supporting Information). All other models
379 contained a significant interaction term between the respective biodiversity measure and
380 PA identity, demonstrating context-specific effects of biodiversity measures on vehicle
381 numbers. In Etosha, species richness and abundance of all species as well as the richness of
382 predators and locally rare ungulates had significant positive effects on vehicle numbers
383 along transects (Fig. 4). Abundance-based models of diversity subsets revealed a positive
384 relationship between visitor numbers in Etosha and the two rarity metrics (Fig. S3 in
385 Supporting Information). In Chobe, we found a strong positive relationship between all
386 biodiversity measures and vehicle numbers, both for richness- and abundance-based
387 models (Fig. 4, Fig. S3 in Supporting Information). In Kruger and Hluhluwe, only one
388 biodiversity measure was significant (total abundance of mammals in Kruger, Fig. 4A;
389 abundance of predators in Hluhluwe, Fig. S3 in Supporting Information).

390

391 **4. Discussion**

392 Our study showed that the supply of recreational opportunities to observe large mammals
393 had a direct influence on the demand of wildlife tourists within PAs in Southern Africa. All

394 diversity measures reflecting all large mammals and subsets of large mammal diversity, such
395 as richness of predators and rare ungulates (Fig. 3), positively related to vehicle numbers
396 along road transects. Interestingly, all biodiversity measures, except richness and
397 abundance of predators and abundance of threatened species, had PA-specific effects,
398 confirming that the realization of the recreational service of wildlife tourism is contingent on
399 the local context shaped by ecosystem capacity, tourism infrastructure and societal
400 demands (Cong et al. 2014, Torres-Sovero et al. 2014). The diversity of large mammals has
401 been a central (although not exclusive) element of recreational activities in Southern African
402 PAs (Winterbach et al. 2015), but this study is the first one testing the role of different
403 metrics and components of biodiversity on the visitors' demand of the recreational service
404 of wildlife tourism.

405 **4.1 Biodiversity measures' effects on vehicle numbers within PAs**

406 The majority of biodiversity measures used in this study (9 out of 13) were positively
407 associated with visitor vehicle numbers along the road transects accounting for a multitude
408 of other factors. This suggests that the demand for wildlife tourism in a PA is positively
409 related to high mammal diversity. Nevertheless, tourists may not only be interested in large
410 mammals, but could also be interested in the diversity of other taxonomic groups (e.g. birds,
411 reptiles), primarily enjoy the scenery (e.g. the salt pan in Etosha or the riverfront in Chobe)
412 or may simply transit through the PA. Although other species than large mammals can affect
413 the decision of visitors to choose specific routes in these PAs (Buckley 2013; Hausmann et al.
414 2017c), observing large mammals was the priority of wildlife tourists surveyed in each of the
415 PAs of this study (see answers in Section II-II of the questionnaire, see Methods S2 in
416 Supporting Information; see also Grünewald et al. 2016). Furthermore, it is possible that
417 scenery plays a role in attracting visitors to specific areas (or could have an indirect role via

418 mammal distributions, see Grünewald et al. 2016). Here we only tested for visibility (a
419 habitat attribute) and therefore cannot quantify potential other scenery effects.
420 Nevertheless, we expect that also scenery influenced visitor distributions (Grünewald et al.
421 2016). In addition, visitors transiting through PAs might have weakened the relationship
422 between biodiversity measures and wildlife tourists. We indeed found significant effects of
423 distance to camps and stretch-points in the models. However, in spite of accounting for
424 these effects, we detected significant relationships between different diversity measures of
425 large mammals and visitor vehicle numbers (Fig. 3A). Thus, the distribution of wildlife
426 tourists within PAs was not random and was partly explained by the diversity of large
427 mammals.

428 Because the three biodiversity metrics were positively correlated across all mammal
429 species (Table S3 in Supporting Information), their respective effects on wildlife tourists are
430 difficult to disentangle. It is possible that wildlife tourists actively search for sites with a high
431 number of species (*i.e.* species richness; see Siikamäki et al. 2015) and a high number of
432 dissimilar species (*i.e.* phylogenetic diversity). However, these relationships between visitor
433 numbers and species richness and phylogenetic diversity may also be related to the effect of
434 large mammal abundance, since visitors tracking locations with high animal abundance are
435 likely to see many species (species richness) and dissimilar species (phylogenetic diversity).
436 Indeed, mammal abundance had consistently the strongest effect among all tested
437 biodiversity measures and all abundance-based metrics of diversity subsets (except
438 abundance of Big Five species) were significant. These findings suggest that mammal
439 abundance is a particularly important component influencing the distribution of tourists
440 within PAs.

441 Our results also highlight that subsets of mammal diversity and in particular the
442 charisma and rarity of species showed a positive relationship with visitor distributions in
443 PAs. Our results on the importance of richness and abundance of predator species are in
444 accordance with an earlier study on tourists' behaviour in Amboseli National Park in Kenya
445 (Okello et al. 2008), where tourists always stopped their drive when they encountered a lion
446 or a cheetah. However, the charisma measures based on the Big Five species did not have
447 any influence on number of visitors as neither richness nor abundance of Big Five species
448 had a significant effect on vehicle numbers along transects. This result contradicts the
449 traditional assumption that Big Five species are the main attraction for wildlife tourists
450 (Lindsey et al. 2007, Maciejewski & Kerley 2014) and is rather in line with recent
451 publications arguing that other species than the renown Big Five are crucial for providing
452 the recreational service of wildlife tourism (Buckley 2013; Di Minin et al. 2013; Hausmann et
453 al. 2017a,c).

454 Another measure of large mammal diversity, namely the abundance of regionally
455 rare species of ungulates, was also closely associated with visitor numbers along transects
456 (Fig. 3B). Regionally rare species of ungulates include the blue wildebeest, the
457 hippopotamus, or the plains zebra that usually occur in large herds. This suggests that
458 visitors might particularly appreciate and look for these large herds of regionally rare
459 ungulates (Di Minin et al. 2013). Furthermore, according to our findings, visitors
460 preferentially drove along roads with high probabilities of encounters with locally rare
461 ungulates, such as those occurring only in a specific PA (*e.g.* the red lechwe in Chobe) or
462 rarely seen in others (*e.g.* rhinoceros in Etosha). Finally, although previous studies detected
463 significant relationships between threatened species (based on the IUCN Red List) and
464 number of visitors in PAs (see Siikamäki et al. 2015), we found that only the abundance of

465 threatened species (and not richness) affected visitor distributions in Southern African PAs.
466 This result suggests that metrics based on the IUCN Red List might have inconsistent effects
467 on wildlife tourists depending on the study design and context.

468

469 **4.2 Context-dependency of biodiversity metrics**

470 Species richness, phylogenetic diversity, and overall abundance of large mammals had PA-
471 specific effects on the spatial distribution of visitors in the PA. Furthermore, the majority of
472 the effects of biodiversity subsets on visitors were context-dependent. This high level of
473 context-dependency (10 out of 13 biodiversity measures showed PA-specific effects)
474 illustrates the spatial heterogeneity of the relationship between the supply- and demand-
475 sides of the recreational service of wildlife tourism within specific PAs. The context-
476 dependency of these relationships can be explained by ecological or social factors or both,
477 as detailed below. Understanding the interplay between these different factors is of prime
478 importance for biodiversity conservation and PA management (Laurila-Pant et al. 2015).

479 The PAs used for our assessment are located across an ecological gradient
480 comprising a wide range of habitat types and different mammal communities (Methods S2
481 in Supporting Information). Consequently, the different PAs of our study provide different
482 aesthetic backgrounds (partly accounted for by visibility and road condition in our analysis)
483 that can influence the demand for recreation potential. Thus, differences in ecological
484 factors among the four PAs might explain why biodiversity metrics did not have the same
485 effects across PAs. In Etosha, for instance, the overall abundance of ungulates and predators
486 was the measure with the greatest effect on visitor vehicle numbers. Etosha is the driest PA
487 with comparatively open vegetation and harbours large animal herds that tend to
488 concentrate in specific areas of the PA. Consequently, areas with better opportunities to

489 observe such large herds are potentially most attractive to visitors. In Chobe, most of the
490 biodiversity measures had large effects on visitor numbers per transect. This result could be
491 related to the absence of artificial waterholes in Chobe, which creates steep gradients in
492 biodiversity and visitor numbers between transects located close to permanent water
493 bodies (riverfront and Savuti marsh) and those located further away from water. Because
494 the distance to water was not available for all PAs, we could not formally test for its effect
495 on visitor distributions and cannot rule out its importance in affecting visitors' distributions.
496 A previous study in Kruger showed that artificial waterholes did not have any effect on
497 vehicle numbers, whereas natural riverbeds did (Grünewald et al. 2016), which calls for
498 more research on this topic.

499 In addition to ecological factors, social factors may also explain the differences in
500 mammal diversity-wildlife tourism relationships observed among the PAs. For instance,
501 origin and experience of wildlife tourists have been shown to influence visitors' expectations
502 and behaviour (Di Minin et al. 2013; Lindsey et al. 2007). Moreover, PA characteristics, such
503 as their size and infrastructure (Neuvonen et al. 2010), are expected to influence the
504 demand for the recreational ecosystem service of wildlife tourism. Our analysis
505 demonstrates that distances to the closest campsites or lodges was an important factor
506 predicting spatial distributions of vehicles in the different PAs. Thus, the tourism
507 infrastructure and its distribution within the PAs are also important factors explaining the
508 relationship between the supply and demand of the service of wildlife tourism. The small
509 number of significant relationships in Hluhluwe might be due to its small size in comparison
510 to the other PAs. Consequently, visitors might drive along all available roads in Hluhluwe,
511 regardless of the diversity and number of animals they may encounter. The recreational

512 service based on wildlife-watching is consequently more easily exploited by tourists in this
513 PA.

514 Finally, despite the context-dependency of most other relationships between
515 biodiversity and wildlife tourists, predator richness and abundance had consistent effects on
516 vehicle numbers per transect across the four PAs (Table 1). This is consistent with the notion
517 that carnivores are key species in African PAs (Arbieu et al. 2017; Ferreira & Hofmeyr 2014),
518 are generally the most attractive species group for wildlife tourists and satisfy a specific
519 demand for observing these species (Maciejewski & Kerley 2014; Willemen et al. 2015).

520

521 **5. Management implications**

522 The relationships between the supply and demand of the recreational service of wildlife
523 tourism revealed by large mammal diversity and tourists' distributions in Southern African
524 PAs can contribute to PA management. Through increased tourist satisfaction, the actual
525 use of the recreational service of wildlife tourism can enhance the popularity of a PA among
526 visitors, with consequences for the PA management. This cascade would lead, in the long
527 run, to generate sustainable PA revenues which ideally transfer into benefits for tourism
528 development and biodiversity conservation. The use of road networks in PAs revealed by
529 relationships between supply and demand for wildlife tourism reflects the knowledge built
530 up by tourists about the areas with high mammal diversity in each PA. Although we did not
531 investigate how tourists obtained the knowledge on large mammal occurrence in PAs, the
532 direct exchange of information between tourists and the existence of information boards at
533 PA gates and camps constitute important sources of information. In addition, the increasing
534 use of social media within PAs (see Hausmann et al. 2017a,b; Wood et al. 2013) can increase
535 real time information on hotspots of wildlife viewing within PAs. This development should

536 be considered by managers in the different PAs, as this phenomenon could have direct
537 consequences for wildlife. The real-time information provided through means of radio or
538 mobile applications can cause fast driving and overcrowding, potentially causing disturbance
539 to wildlife behaviour (Hausmann et al. 2017b; Lunde et al. 2016; Mulero-Pázmány et al.
540 2016) and jeopardize responsible tourism practices. Therefore, enforcement of PA
541 regulations (e.g. driving speed limitations, getting off vehicles at stretch-points only, etc.),
542 monitoring of social media use and a better control of information flow within PAs would
543 help controlling traffic and related negative impacts on wildlife along the road network.

544 Our study could incite PA managers to play an active role in this information flow at
545 the local scale. The context-dependency of our results suggests that information exchange
546 about areas with good supply of opportunities to observe locally and regionally rare species
547 of ungulates is important for wildlife tourists. An increased attention of managers on locally
548 and regionally rare ungulates would diversify the supply-side of the relationship by not only
549 focussing on the charismatic predator species. This is especially helpful for managing the
550 spatial distribution of tourists in the PA because the spatial distributions of abundance of
551 predators and rare ungulates were not correlated (Table S3). Such communication efforts
552 from PA managers are expected to reduce speeding and overcrowding, thereby alleviating
553 tourism pressure on wildlife populations. Hence, by maintaining the provision of
554 appropriate tourism infrastructure, by quantifying visitor distributions over the road
555 networks within PAs and by monitoring changes in habitat attributes and animal
556 distributions, PA managers can obtain fundamental information about the recreational
557 service of wildlife tourism in the specific context of each PA.

558 We only addressed wildlife tourism in the form of large mammal viewing within PAs
559 in this study, while the long-term sustainability of PA management is contingent on

560 complementary evaluations of other potential CES (Ament et al. 2016). Nevertheless, our
561 paper highlights the importance of several measures of large mammal diversity in the CES
562 framework, by attracting visitors, in concert with other factors, to specific areas in the PA.
563 Hence, the supply-demand approach in the context of recreational services can contribute
564 to the development of tailor-made management programs for PAs benefitting biodiversity
565 conservation and the satisfaction of PA visitors.

566

567 **Acknowledgements**

568 The authors would like to thank the Ministry of Environment and Tourism of Namibia, the
569 Ministry of Environment, Wildlife and Tourism of Botswana, SANParks and Ezemvelo KZN
570 Wildlife for supporting the project and granting research permits in Etosha, Chobe, Kruger
571 National Parks and Hluhluwe-Imfolozi Park respectively. We thank M. Templin and T.
572 Caprano for their assistance, S. Higgins for project facilitation in Kruger and S. Fritz for
573 comments on phylogenetic diversity. We thank field assistants and L. Birkmann and O.
574 Lepeigneul for helping on data processing. We thank two anonymous reviewers for helpful
575 comments and suggestions on the Manuscript. This work was supported by the Deutsche
576 Forschungsgemeinschaft (DFG, grant number BO 1221/19-1) and the Landes-Offensive zur
577 Entwicklung Wissenschaftlich-ökonomischer Exzellenz (LOEWE excellence initiative) of
578 Hesse's Ministry of Higher Education, Research, and the Arts.

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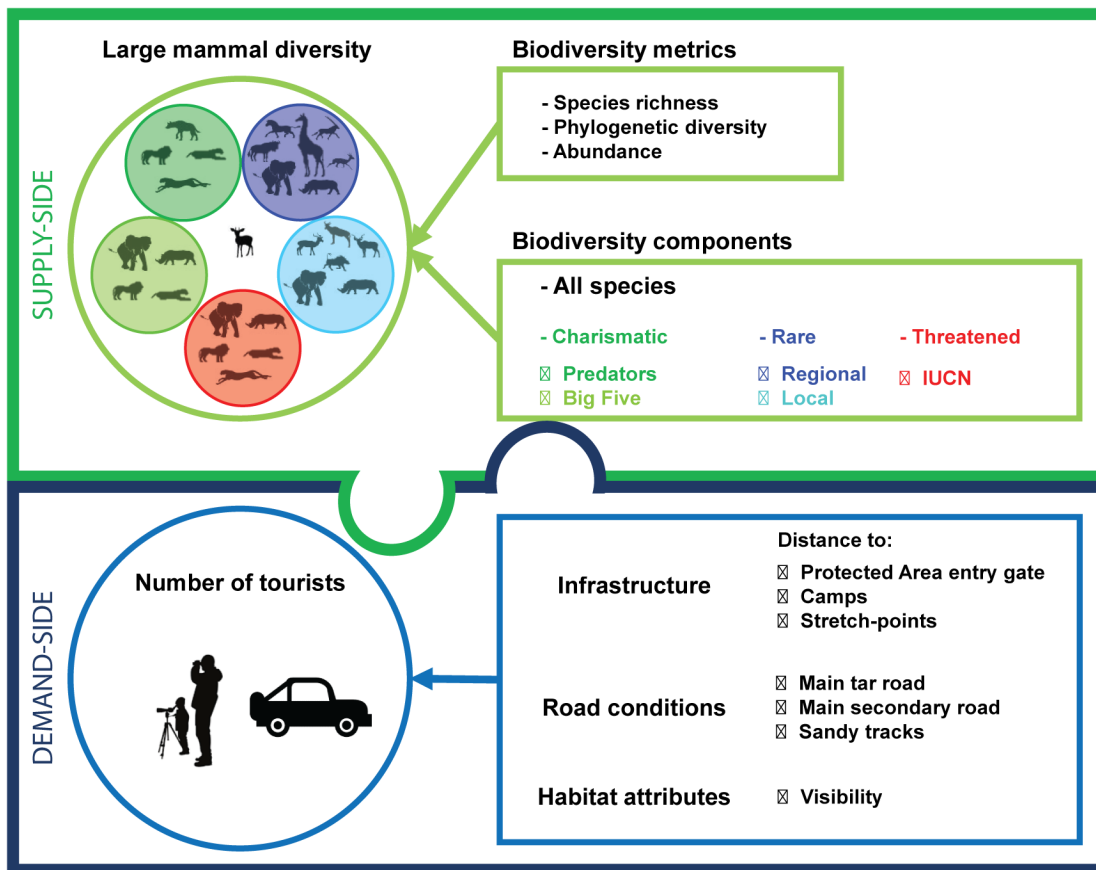
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Table 1. Relationships between vehicle numbers and biodiversity measures, infrastructure (Dist_gate, Dist_camp, Dist_stretch), habitat attribute (Visibility) and sampling-related factors (see Methods). Fixed effects' estimates on the log-scale are averaged across all models which $\Delta AIC < 2$ with standard errors in brackets. Significant effects are marked with a (*). Random effects' standard deviations are also shown.

	Fixed effects						Random effects			
	Biodiversity measure	Dist_gate	Dist_camp	Dist_stretch	Visibility	Time	Park	Park/Transects	Road	Date
Models including all large mammals										
Abundance	0.46 (0.07)*	0.01 (0.04)	-0.24 (0.07)*	-0.03 (0.07)	-0.25 (0.09)*	0.17 (0.04)*	0.76	0.59	0.89	0.45
Phylogenetic diversity	0.23 (0.08)*	0.01 (0.04)	-0.25 (0.07)*	-0.07 (0.09)	-0.09 (0.10)	0.22 (0.04)*	0.80	0.64	0.87	0.45
Richness	0.34 (0.07)*	0.01 (0.04)	-0.24 (0.07)*	-0.09 (0.10)	-0.20 (0.09)*	0.19 (0.04)*	0.81	0.62	0.86	0.45
Richness-based models for large mammal diversity subsets										
Predator	0.20 (0.06)*	X	-0.22 (0.07)*	-0.02 (0.05)	-0.03 (0.07)	0.22 (0.04)*	0.74	0.64	0.85	0.45
Big five	0.12 (0.07)	0.00 (0.03)	-0.22 (0.07)*	-0.05 (0.08)	-0.02 (0.06)	0.23 (0.04)*	0.76	0.64	0.83	0.46
Regional rarity	0.11 (0.07)	0.00 (0.03)	-0.26 (0.07)*	-0.06 (0.09)	-0.08 (0.10)	0.23 (0.04)*	0.80	0.65	0.87	0.45
Local rarity	0.21 (0.06)*	X	-0.19 (0.07)*	-0.03 (0.07)	-0.01 (0.04)	0.22 (0.04)*	0.76	0.63	0.84	0.46
IUCN threat	0.11 (0.06)	0.00 (0.03)	-0.23 (0.07)*	-0.05 (0.08)	-0.02 (0.06)	0.23 (0.04)*	0.76	0.63	0.84	0.46
Abundance-based models for large mammal diversity subsets										
Predator	0.20 (0.06)*	X	-0.23 (0.07)*	-0.03 (0.07)	-0.04 (0.08)	0.22 (0.04)*	0.78	0.64	0.86	0.45
Big five	0.12 (0.07)	X	-0.22 (0.07)*	-0.05 (0.08)	-0.02 (0.06)	0.23 (0.04)*	0.79	0.64	0.85	0.45
Regional rarity	0.34 (0.08)*	0.01 (0.05)	-0.25 (0.07)*	-0.06 (0.08)	-0.27 (0.10)*	0.21 (0.04)*	0.83	0.63	0.89	0.46
Local rarity	0.18 (0.06)*	X	-0.22 (0.07)*	-0.02 (0.06)	-0.01 (0.04)	0.22 (0.04)*	0.75	0.64	0.86	0.46
IUCN threat	0.15 (0.06)*	-0.04 (0.07)	X	-0.22 (0.07)*	-0.06 (0.08)	0.23 (0.04)*	0.81	0.63	0.85	0.46



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Figure 1. Relationship between the supply- and demand-sides in the context of the

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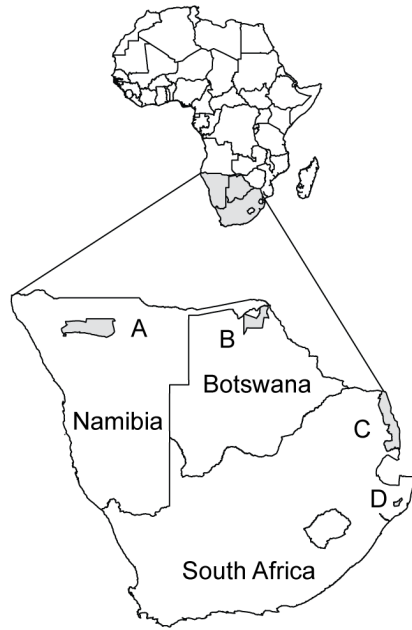
recreational service of wildlife tourism. Three biodiversity metrics were applied to four

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components of biodiversity to explain the distribution of wildlife tourists' vehicles,

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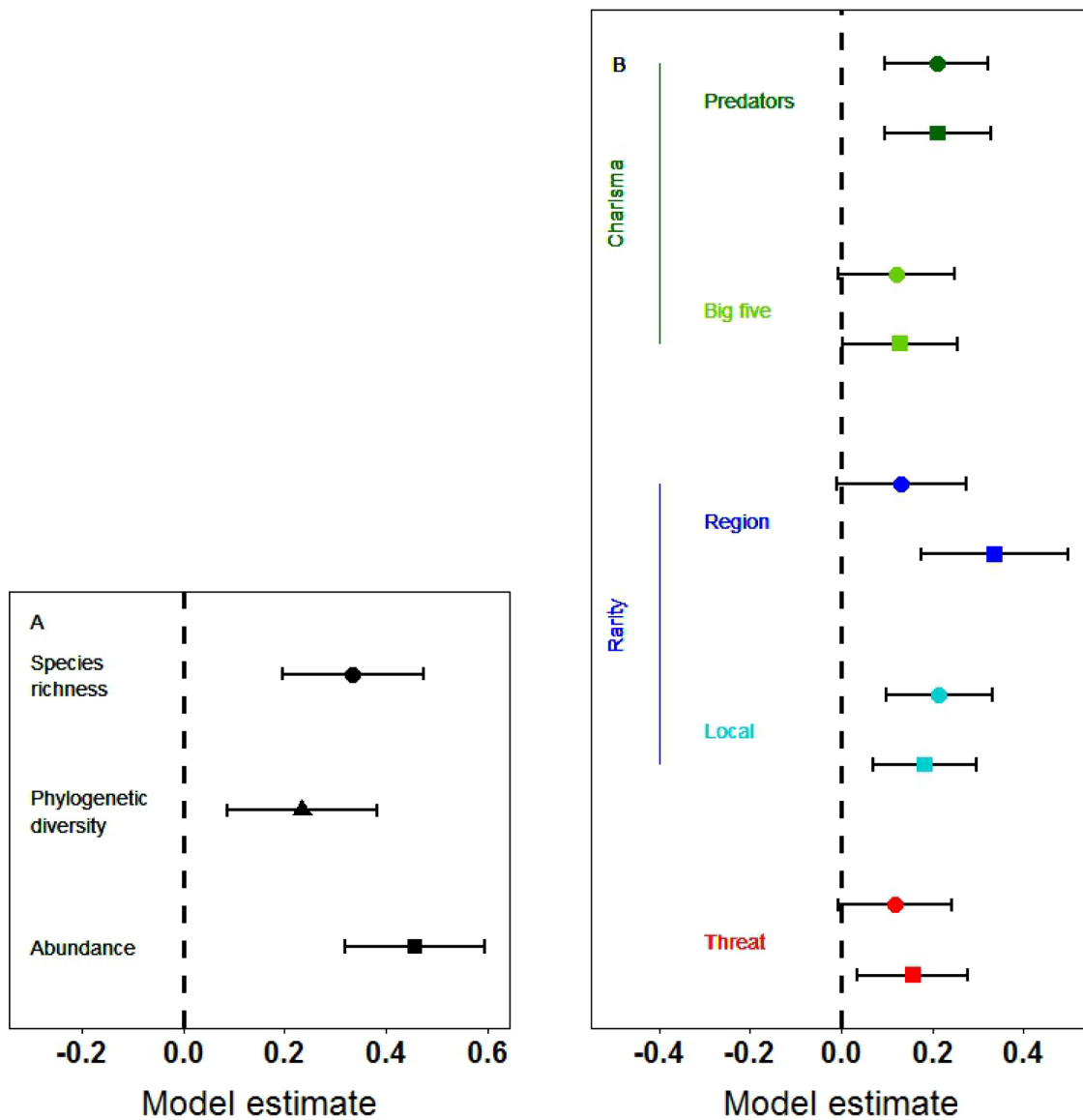
accounting for Protected Areas' infrastructure and habitat attributes.



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795 **Figure 2.** Location of the four Protected Areas studied in Southern Africa; A, Etosha National

796 Park; B, Chobe National Park; C, Kruger National Park; D, Hluhluwe-Imfolozi Park.



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798 **Figure 3.** Effects of (A) biodiversity measures including all large mammal species and (B)

799 biodiversity subsets on vehicle numbers along 196 transects (5 km) across the four

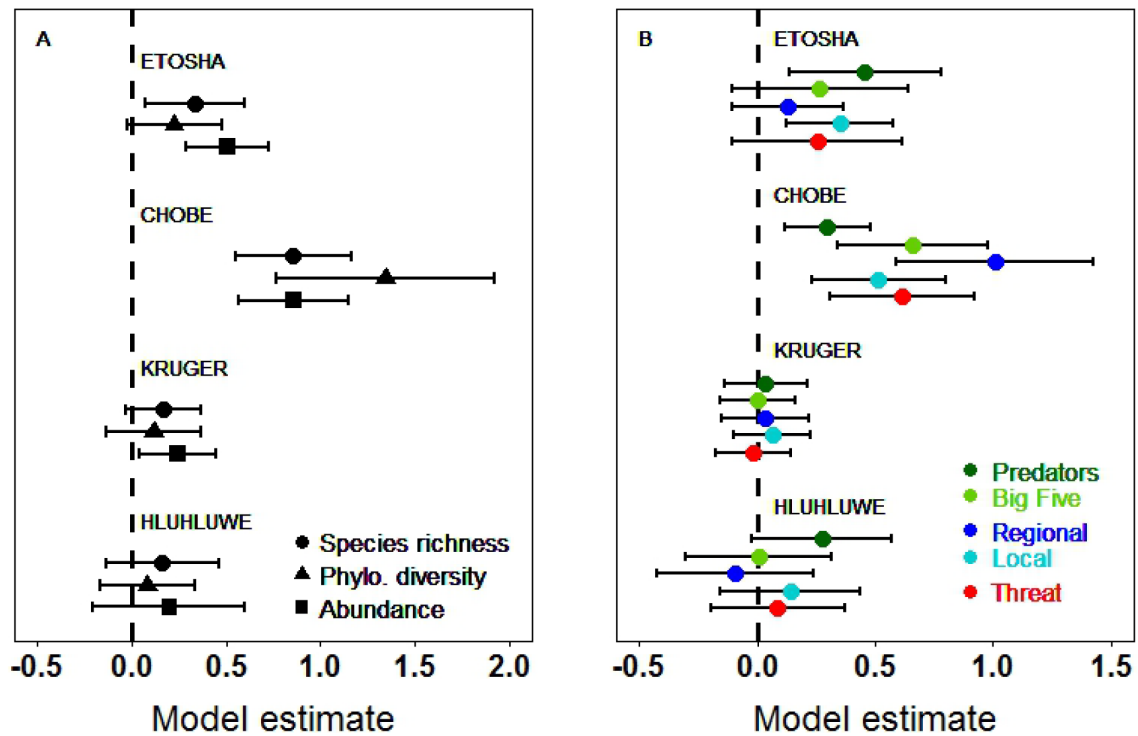
800 Protected Areas. Panel B displays estimates for richness-based metrics (circle symbols) and

801 abundance-based metrics of biodiversity subsets of charismatic, rare and threatened

802 species (square symbols). Horizontal bars (95% confidence intervals) that do not cross the

803 vertical dashed lines (significance thresholds) have significant effects on vehicle numbers.

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Figure 4. PA-specific effects of (A) biodiversity measures including all large mammal species and (B) biodiversity subsets on vehicle numbers along 196 transects (5 km) across the four Protected Areas. Panel B only displays estimates for richness-based metrics of biodiversity subsets of charismatic, rare and threatened species (for abundance-based metrics see Fig. S3 in Supporting Information). Horizontal bars (95% confidence intervals) that do not cross the vertical dashed lines (significance thresholds) have significant effects on vehicle numbers. ‘Regional’ and ‘local’ refer to regionally and locally rare species of ungulates, respectively.

815

Supporting Information

816

817 **Methods S1.** Description of the four individual Protected Areas

818 **Methods S2.** Questionnaire for the social survey.

819 **Methods S3.** Definition and calculation of the 13 biodiversity measures.

820

821 **Figure S1.** Maps of the four individual Protected Areas, showing transect location and tourist
822 infrastructure (gates, roads, camps)

823 **Figure S2.** Classification tree used in the phylogenetic diversity calculations

824 **Figure S3.** Park-specific effects of the five abundance-based subcomponents of biodiversity

825

826 **Table S1.** List of large mammal species (ungulates and predators) recorded in each Protected
827 Area and their respective IUCN threat level

828 **Table S2.** List of ungulate species categorized as regionally and locally rare

829 **Table S3.** Multiple correlation tests between biodiversity metrics (richness and abundance-
830 based metrics)

831 **Table S4.** Analyses of deviance assessing the interaction between Park ID and each

832 biodiversity metric

833 **Methods S1. Study areas description**

834 *Etosha National Park*: Etosha is located in northern Namibia (18°30' to 19°30' S and 14°15'
835 to 17°10' E, elevation 1100-1200 m) and occupies an area of 22,270 km². We conducted
836 fieldwork east of the Ozonjuitji m'Bari artificial waterhole (see Fig. S1 for study area maps).
837 In the study area, mean annual rainfall ranges from 320 to 450 mm and mean annual
838 temperature is 22°C. Etosha vegetation is a typical arid savannah, with grassy plains around
839 the Etosha pan, and Mopane savannah woodland. Etosha is the main tourism venue in
840 Namibia and 100,000 visitors entered through the main gate (Anderson gate) in 2014, with
841 probably about 200,000 visitors in total per year (Etosha Ecological Institute staff,
842 unpublished statistics).

843 *Chobe National Park*: Chobe is located in northern Botswana (17°49' S to 19°11' and 23°53'
844 to 25°22' E, elevation 950-1000 m), and covers an area of 10,700 km². We conducted
845 fieldwork in two distinct areas, the Chobe riverfront in the north and the Savuti marsh in the
846 south. Climate in Chobe is semi-arid to sub-humid, with average rainfall of 550 mm in the
847 south and almost 700 mm in the north. Mean annual temperature is about 22°C. Vegetation
848 consists mainly of dry woodland and scattered grasslands. The riverfront is characterized by
849 riparian woodland, shrubland and alluvial terraces, and the Savuti marsh is sandveld
850 savannah, dominated by mopane trees. Chobe is the largest park in Botswana and ca. 240,000
851 people visited the park in 2013 (Ministry of environment, wildlife and tourism, unpublished
852 statistics).

853 *Kruger National Park*: Kruger is located in the north-eastern South Africa (22°25' to 25°32'
854 S and 30°50' to 32°2' E, elevation 100-850 m) and covers an area of 18,992 km². Mean
855 annual temperature in Kruger is 22°C. We conducted fieldwork in the southern part of the
856 park, which is more humid than the northern part (500-700 mm per year). Vegetation in
857 southern Kruger is mainly characterized as lowveld bushveld zone, *i.e.* plain grasslands

858 interspersed with woody vegetation. Kruger is the largest wildlife park in South Africa,
859 visited by ca. 1,400,000 visitors in 2010.

860 *Hluhluwe-Imfolozi Game Reserve*: Hluhluwe is located in south-eastern South Africa (28°00'
861 to 28°26' S and 31°43' to 32°09' E, elevation 60-450 m) and covers an area of a 900 km².

862 Hluhluwe presents contrasting characteristics between north and south: mean annual rainfall
863 is higher in Hluhluwe in the north (990 mm) than in Imfolozi in the south (635mm). Mean
864 annual temperature is 18.5°C. The north is covered by semi-deciduous woodland whereas the
865 south is a more open savannah woodland. Hluhluwe is the third largest game reserve in South
866 Africa and ca. 140,000 people visited the reserve in 2014 (Hluhluwe staff, unpublished data).

867

868 **Methods S2. Questionnaire of the social survey**

869 Date _____ Time _____ Interview/Map ID _____

870 Location:
871 _____

872 Interviewer: _____
873 _____

874 Interview
875 language: _____

876

877 **SECTION I: Visit details**

878 a. Where are you from? _____

879

880 b. For how long are you staying in the park? _____

881

882 c. Is it your first stay in the Park? _____

883

884 d. If not, how many times have you been here before? _____

885

886 e. At which Camp are you staying? _____

887

888 f. Have you been staying in this Camp all the time or have you been staying elsewhere in the
889 park on this trip?

890 _____

891

892 g. Accommodation type (camping, hut, lodge etc.)?
893 _____

894

895 h. Are you travelling on your own or in a group? _____

896

897 i. Is your trip self-organized or by a tour operator? _____

898

899 j. What is the main reason(s) behind your visit to this Park (not more than 3)?
900 1. _____

901

902 2. _____

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3. _____

SECTION II: DRIVING ROUTE AND PERSONAL PREFERENCES

I. Did you do a (game) drive today in the park?

a. If no: What else did you do? Was there any reason for doing so?

b. If yes: Did you go by yourself or did you join a guided tour? (maybe time/ start of tour/name of guide)

c. For how long have you been on the (game) drive? _____

II. Where in the park did you go to?

a. Can you please show on this map (**provided by interviewer**) where you went? Please mark/indicate approximately the route (if possible).

b. Was there any particular reason for going to this area in the park or for booking this game drive?

c. Which were your topmost expectations (not more than 3) for that day?

1. _____

2. _____

3. _____

d. Have your expectations been met? (On a scale from 1 to 10, 1 being not met at all, 10 being absolutely met)

e. Can you rank the following park features by order of importance (from 1-5)?

Landscape uniqueness _____

937 Wildlife viewing _____

938 Calm and quietness _____

939 Luxury of some accommodations _____

940 Botany _____

941

942 f. Are there any park features missing that you think are of high interest?
943 Which ones?

944 _____

945 _____

946 g. Could you rank the following animal groups by order of spotting
947 preference (from 1 to 6)?

948 - Birds _____

949 - Reptiles _____

950 - Insects _____

951 - Small mammals (meerkat, mongoose, ground squirrel...) ____

952 - Ungulates (gemsbok, springbok, eland...) _____

953 - Big cats _____

954 h. Are there any animal groups missing that you think are of high interest?
955 Which ones?

956 _____

957 _____

958 i. For your route in the park today have you had any expectations which
959 animals you would see in that area of the park?

960 _____

961 _____

962 j. Which animals did you hope to see/did you want to see?

963 _____

964

965 **SECTION III: PREDATOR SIGHTINGS**

966 a. Did you see one of the following predators (give number, and locate on the map)?

967

	Lion	Cheetah	Leopard	Spotted Hyena	Wild dog
Number					
Distance					

Number					
Distance					

968

969

b. At what distance from the car/road (suggest categories)?

970

a) directly next to car b) less than 200 m c) 500 m d) more than 500 m

971

972 **Methods S3. Biodiversity measures definition and calculations**

973 To test the influence of biodiversity on vehicle numbers, we used three diversity metrics (species
974 richness, phylogenetic diversity, abundance) applied to four components of large mammal diversity
975 subcomponents of biodiversity (all species, charismatic, rare, threatened species, Fig. 1 We calculated
976 richness and abundance for all biodiversity components (*i.e.* all species, charismatic, rare and
977 threatened species). We calculated the phylogenetic diversity only for the biodiversity component
978 including all species because the metric is not meaningful for the subset components.

979 To calculate species richness, we used a probabilistic approach, reflecting ungulate and
980 predator sighting probabilities along each transect. In a given transect, the probability of occurrence
981 (P_{occ}) of a single species s is equal to:

982 $P_{occ, s} = \sum r_i / D$; where i enumerates each drive along a given transect, $r_i = 1$ if the species is
983 seen during the i^{th} drive through the transect (0 if not), and D is the number of times the
984 transect was driven ($D=3$ for ungulate species). Following Calabrese *et al.* (2014), the species
985 richness along a transect is the sum of P_{occ} over the total number of species occurring along
986 this transect (ungulates and predators). This calculation is referred to as ‘richness-based’
987 calculation in the main text.

988 Phylogenetic diversity along each transect was calculated using an abundance-
989 weighted phylogenetic diversity index as suggested by Vellend *et al.* (2011). We used the
990 species-level phylogeny of mammals from Fritz *et al.*(2009), pruned it to the 33 species
991 recorded during fieldwork (Fig. S2 in Supporting Information) and calculated the
992 phylogenetic diversity along each transect using the same phylogenetic tree. Simplifying
993 from Vellend *et al.* (2011), we defined the phylogenetic diversity value of a given transect
994 (PD) as:

995 $PD = \sum L_j \cdot Av(P_{occ})_j$; where the full phylogeny of all 33 species has j branches, L_j is the
996 length of the j^{th} branch in the tree and $Av(P_{occ})_j$ is the average occurrence probability of
997 species sharing the j^{th} branch in the tree. The reason for simplifying the equation is that our

998 weighting parameter, $Av(P_{occ})_j$, is already a relative measure of abundance and does not need
999 to be weighted further (see Vellend *et al.* 2011 for the full equation).

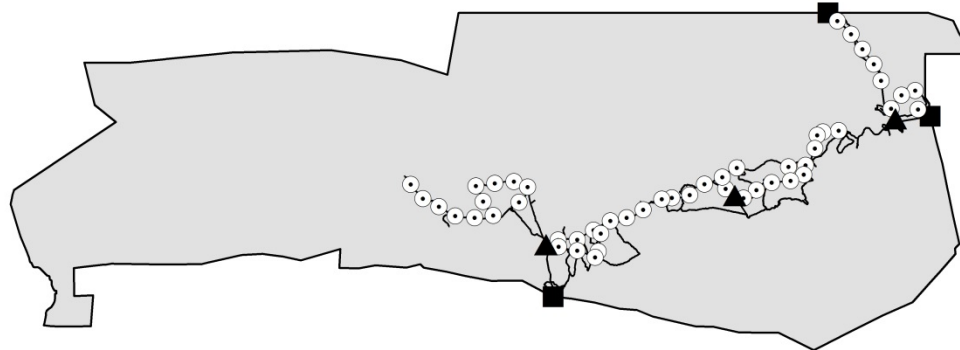
1000 We calculated abundance as the average total number of animals recorded in the three
1001 replicates of each transect (for ungulates) or across all drives along each transect (for
1002 predators), regardless of species identity. The calculation of abundance A is similar to the one
1003 of species richness, replacing r_i by the number of individuals of a given species s observed
1004 along the transect, thus:

1005 $A_s = \sum n_i / D$; where i enumerates each drive along a given transect and n is the number of
1006 individuals of the species counted during the i^{th} drive. The average total abundance along a
1007 transect is then the sum of A_s over the total number of species detected along this transect
1008 (ungulates and predators). This calculation is referred to as ‘abundance-based’ calculation in
1009 the main text.






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1022








Study area - Etosha National Park (Namibia)

-  Park boundaries
-  Roads
-  Transect midpoints
-  Park gates
-  Camps or lodges

0 10 20 40 60 80 Kilometers



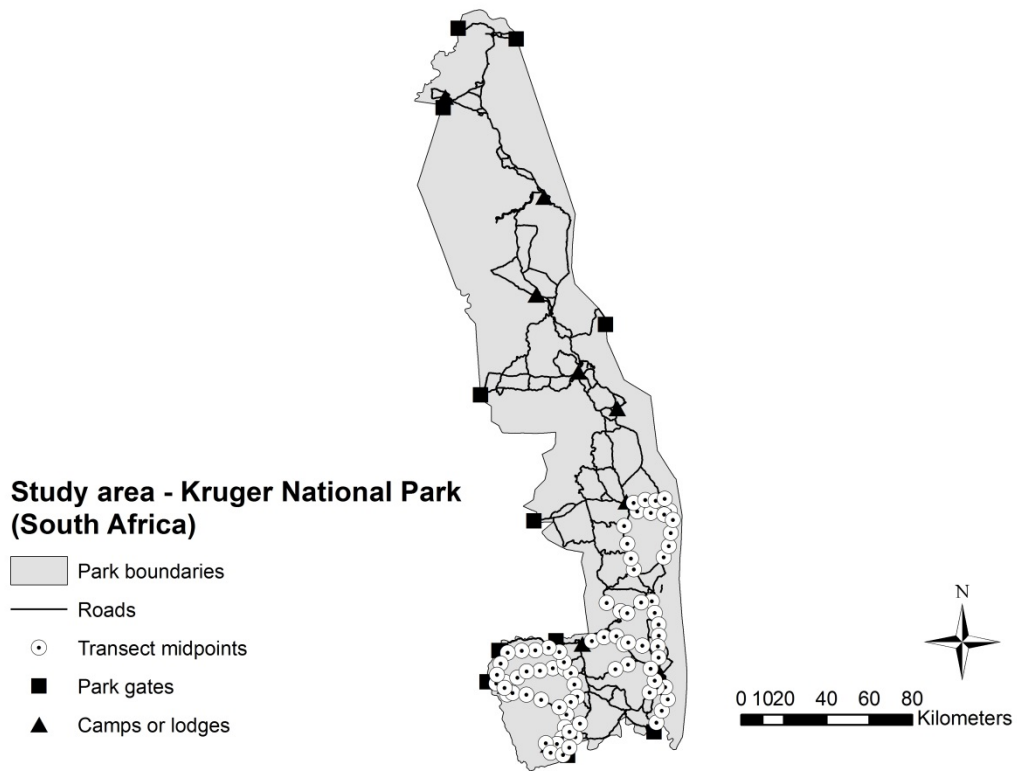
Study area - Chobe National Park (Botswana)

-  Park boundaries
-  Roads
-  Transect midpoints
-  Park gates
-  Camps or lodges

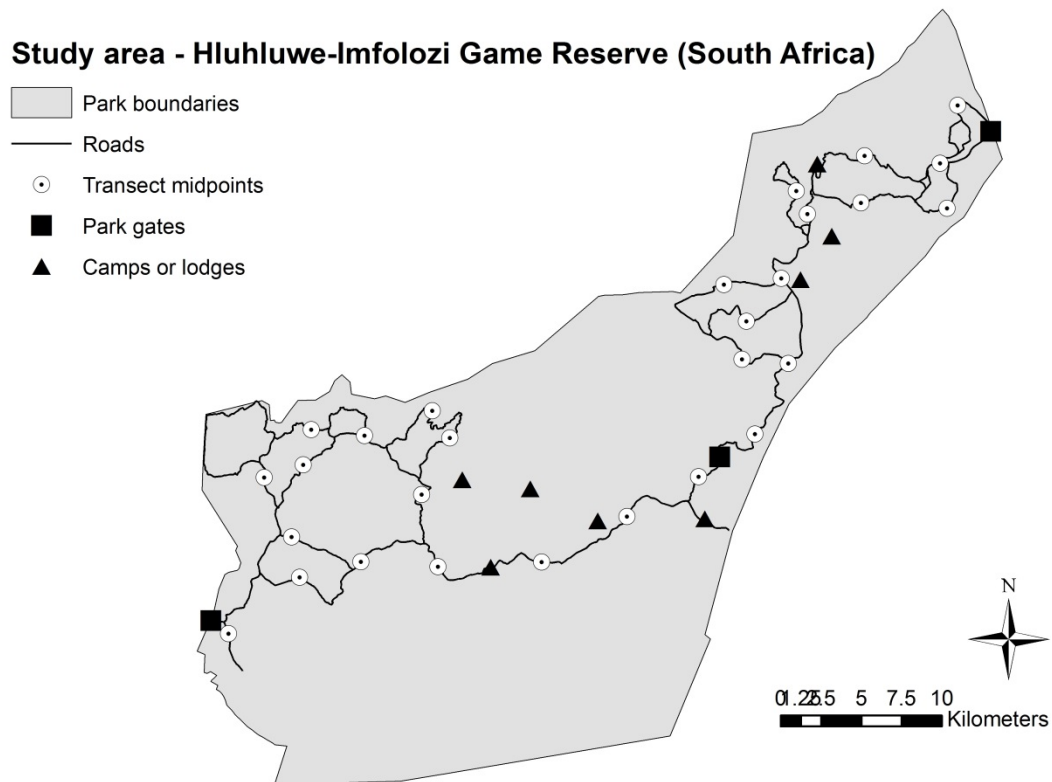
0 5 10 20 30 40 Kilometers



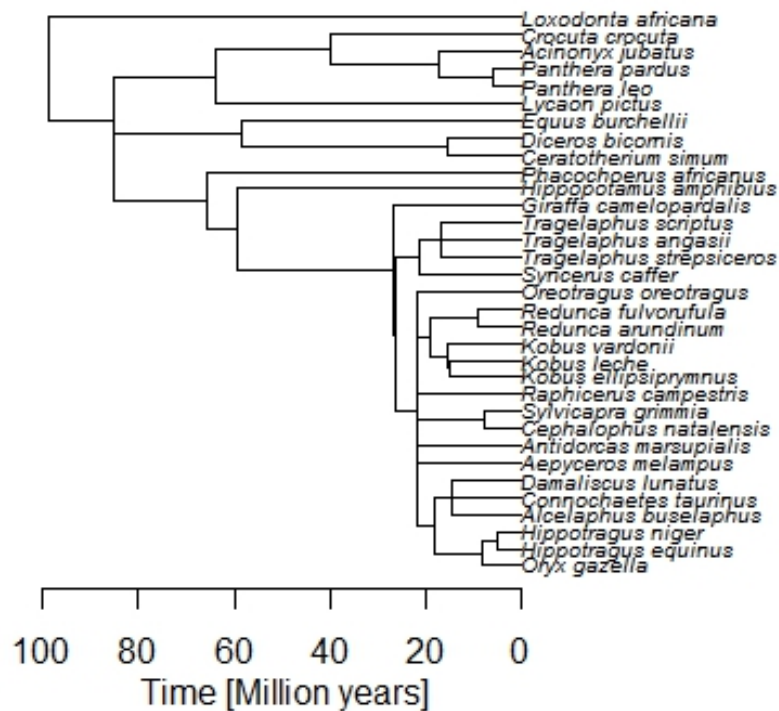
1023 **Figure S1.** Maps of the the four individual parks, showing transect location and tourist
 1024 infrastructure.



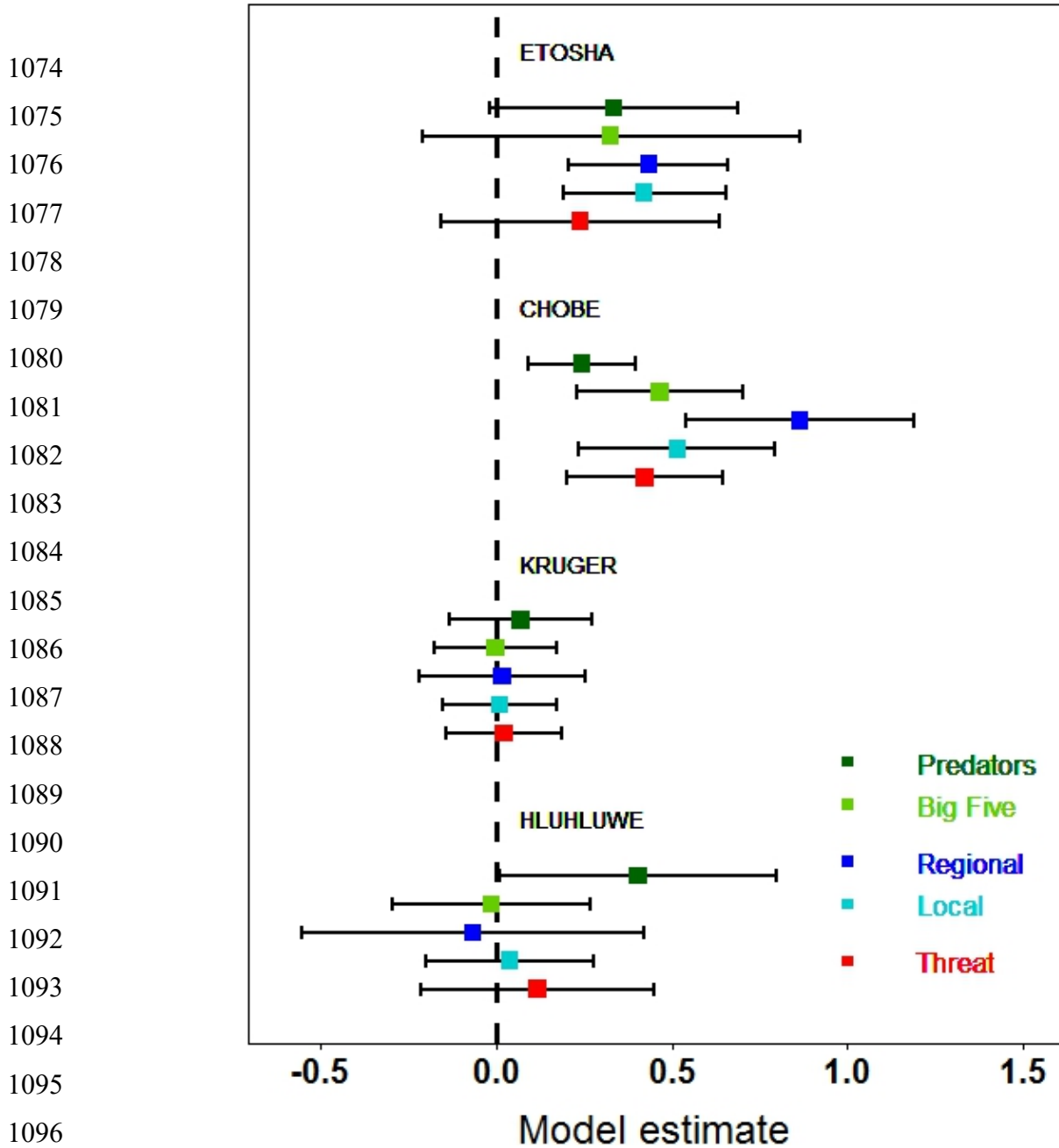
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1047 **Figure S1 (continued).** Maps of the four individual parks, showing transect location and
 1048 tourist infrastructure.



1069 **Figure S2.** Phylogenetic tree used in phylogenetic diversity calculations in each transect,
 1070 containing the 33 large mammal species counted during field work in four wildlife parks in
 1071 Southern Africa (Etosha, Chobe, Kruger National Parks and Hluhluwe-Imfolozi Game
 1072 Reserve). The x-axis represents the phylogenetic distance along branches, in million years.
 1073



1098 **Figure S3.** PA-specific effects of abundance-based metrics of biodiversity subsets on vehicle
 1099 numbers along 196 transects (5 km) across the four Protected Areas. Horizontal bars (95%
 1100 confidence intervals) that do not cross the vertical dashed lines (significance thresholds) have
 1101 significant effects on vehicle numbers. ‘Regional’ and ‘local’ refer to regionally and locally
 1102 rare species of ungulates, respectively.

1103 **Table S1.** List of all larger mammal species of predators and ungulates recorded in Etosha,
 1104 Chobe, Kruger National Parks and Hluhluwe-Imfolozi Game Reserve. Common and
 1105 scientific names are based on the Atlas of Mammals of Africa (volumes V & VI, Kinton &
 1106 Hoffmann 2013). The threat level for each species is indicated and was assessed with the
 1107 IUCN's Red List of Threatened Species

English name	Scientific name	IUCN Threat level	Etosh a	Chobe	Kruger	Hluhluw e
African lion	<i>Panthera leo</i>	Vulnerable A2abcd	X	X	X	X
African leopard	<i>Panthera pardus</i>	Near Threatened	X	X	X	X
Cheetah	<i>Acinonyx jubatus</i>	Vulnerable A2acd	X	X	X	X
Spotted hyena	<i>Crocuta crocuta</i>	Least Concern	X	X	X	X
Wild dog	<i>Lycaon pictus</i>	Endangered C2a(i)	-	X	X	X
African elephant	<i>Loxodonta africana</i>	Vulnerable A2a	X	X	X	X
African buffalo	<i>Syncerus caffer</i>	Least Concern	-	X	X	X
Black rhinoceros	<i>Diceros bicornis</i>	Critically Endangered A2abcd	X	-	-	-
Blue wildebeest	<i>Connochaetes taurinus</i>	Least Concern	X	X	X	X
Bushbuck	<i>Tragelaphus scriptus</i>	Least Concern	-	-	X	X
Common hippopotamus	<i>Hippopotamus amphibius</i>	Vulnerable A4cd	-	X	*	-

Common duiker	<i>Sylvicapra grimmia</i>	Least Concern	-	-	X	X
Common warthog	<i>Phacochoerus africanus</i>	Least Concern	X	X	X	X
Gemsbok	<i>Oryx gazella</i>	Least Concern	X	-	-	-
Giraffe	<i>Giraffa camelopardalis</i>	Least Concern	X	X	X	X
Greater kudu	<i>Tragelaphus strepsiceros</i>	Least Concern	X	X	X	X
Impala	<i>Aepyceros melampus</i>	Least Concern	X	X	X	X
Klipspringer	<i>Oreotragus oreotragus</i>	Least Concern	-	-	X	-
Mountain reedbuck	<i>Redunca fulvorufula</i>	Least Concern	-	-	X	-
Nyala	<i>Tragelaphus angasii</i>	Least Concern	-	-	-	X
Plains zebra	<i>Equus quagga</i>	Least Concern	X	X	X	X
Puku	<i>Kobus vardonii</i>	Near Threatened	-	X	-	-
Red duiker	<i>Cephalophus natalensis</i>	Least Concern	-	-	-	X
Red hartebeest	<i>Alcelaphus buselaphus</i>	Least Concern	X	-	-	-
Red lechwe	<i>Kobus leche</i>	Least Concern	-	X	-	-
Roan antelope	<i>Hippotragus equinus</i>	Least Concern	-	X	-	-
Sable antelope	<i>Hippotragus niger</i>	Least Concern	-	X	X	-

Southern reedbuck	<i>Redunca arundinum</i>	Least Concern	-	-	X	-
Springbok	<i>Antidorcas marsupialis</i>	Least Concern	X	-	-	-
Steenbok	<i>Raphicerus campestris</i>	Least Concern	X	X	X	-
Tsessebe	<i>Damaliscus lunatus</i>	Least Concern	X	-	-	-
Waterbuck	<i>Kobus ellipsiprymnus</i>	Least Concern	-	X	X	-
White rhinoceros	<i>Ceratotherium simum</i>	Near Threatened	-	-	X	X

1108 *Hippos were excluded in Kruger for methodological reasons.

1109

1110 **Table S2.** List of all ungulate species recorded during fieldwork in the four PAs (Etosha,
 1111 Chobe, Kruger National Parks and Hluhluwe-Imfolozi Game Reserve; for scientific names
 1112 see Table S1). Species were categorized as regionally rare if they belonged to the 50% of the
 1113 species with the smallest range sizes in Africa (based on IUCN database;
 1114 <http://www.iucnredlist.org/technical-documents/spatial-data>). Species were categorized as
 1115 locally rare if they belonged to the 50% of the species with the lowest probabilities of
 1116 occurrence within the respective park (based on our own animal counts)

English name	Regionally rare	Locally rare in			
		Etosha	Chobe	Kruger	Hluhluwe
African elephant	X	X	-	-	X
African buffalo	-	-	-	X	X
Black rhinoceros	-	X	-	-	-
Blue wildebeest	X	-	-	-	X
Bushbuck	-	-	-	X	X
Common hippopotamus	X	-	X	-	-
Common duiker	-	-	-	X	X
Common warthog	-	X	-	-	-
Gemsbok	X	-	-	-	-
Giraffe	X	-	-	-	-
Greater kudu	-	X	-	-	X
Impala	-	X	-	-	-
Klipspringer	-	-	-	X	-
Mountain reedbuck	X	-	-	X	-
Nyala	X	-	-	-	-
Plains zebra	X	-	-	-	-
Puku	X	-	X	-	-
Red duiker	X	-	-	-	X
Red hartebeest	-	X	-	-	-

Red lechwe	X	-	X	-	-
Roan antelope	-	-	X	-	-
Sable antelope	X	-	X	X	-
Southern reedbuck	-	-	-	X	-
Springbok	X	-	-	-	-
Steenbok	-	-	X	-	-
Tsessebe	X	-	X	-	-
Waterbuck	-	-	X	X	-
White rhinoceros	-	-	-	X	-

1117

1118

1119

1120 **Table S3.** Multiple correlation test (Pearson coefficients, n=588) between all biodiversity
 1121 measures used in the Generalized Linear Mixed Models of this study. The lower left panel
 1122 refers to correlations between measures used in richness-based models; the upper right panel
 1123 refers to correlations between measures used in abundance-based models. Bonferroni
 1124 correction was implemented for adjusting p-values (due to multiple testing). Only one
 1125 correlation estimate was not significant and is highlighted in bold font

Species richness	-	-	-	-	-	-	-
0.88	Phylogenetic diversity	-	-	-	-	-	-
0.79	0.66	Abundance	-	-	-	-	-
0.32	0.23	0.34	Predators	0.26	0.14	0.11	0.25
0.41	0.50	0.25	0.27	Big Five	0.17	0.53	0.79
0.73	0.64	0.60	0.08	0.24	Regionally rare	0.18	0.25
0.42	0.37	0.24	0.17	0.48	0.19	Locally rare	0.28
0.43	0.53	0.21	0.23	0.89	0.34	0.46	Threat

1126

1127 **Table S4.** Analyses of deviance to investigate the PA-specific effects of all biodiversity
 1128 measures (see Methods). The tests compared two models, one including an interaction term
 1129 between the biodiversity measure and PA identity, and one without the interaction term. The
 1130 majority of models (10 out of 13 models) indicated PA-specific effects of biodiversity
 1131 measures on vehicle numbers along road transects within PAs
 1132

Biodiversity*PA	Chi-square	Df	p-value	1133 1134
All mammal species				1135
- richness	14.03	3	< 0.01	1136
- phylo. diversity	17.53	3	< 0.01	1137
- abundance	12.20	3	< 0.01	1138
Predator species				1139
- richness	7.23	3	0.07	1140
- abundance	3.44	3	0.33	1141
Big Five species				1142
- richness	12.51	3	< 0.01	1143
- abundance	9.86	3	0.02	1144
Regionally rare species				1145
- richness	19.71	3	< 0.01	1146
- abundance	20.54	3	< 0.01	1147
Locally rare species				1148
- richness	8.45	3	0.04	1149 1150
- abundance	14.62	3	< 0.01	1151
Threatened species				1152 1153
- richness	11.77	3	< 0.01	1154 1155
- abundance	7.06	3	0.07	1156