1   **A framework for prioritising conservation translocations to mimic natural ecological**

2   **processes under climate change: a case study with African antelopes**

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ABSTRACT: Ongoing climate change is leading to significant range shifts in many taxa. Although climate-induced spatiotemporal dynamics have subtle implications for prioritization of translocation release areas, the terminology underlying current guidelines for conservation translocation remains focused on a dichotomy between 'reintroductions' within the indigenous range and 'assisted colonisations' anywhere else. We here propose a dispersal barrier-based framework for categorizing release areas according to their compatibility with natural ecological processes under climate change. Setting as a criterion that consistently suitable conditions are forecast over the timeframe considered, we define six translocation types corresponding to six translocation release zones: 'reinforcement' within the 'stable current range'; 'assisted dispersal *sensu stricto*' within the 'expected novel range'; 'compensatory dispersal' within the 'idealized novel range' (ie. projected only if simulating absence of anthropogenic dispersal barriers); 'accelerated dispersal' within the 'expected connected envelope' (ie. the spatiotemporally connected bioclimatic envelope beyond dispersal range); 'accelerated compensatory dispersal' within the 'idealized connected envelope' (ie. unreachable connected envelope only if simulating absence of anthropogenic dispersal barriers); and 'artificial dispersal' within the 'unconnected envelope' (ie. separated by natural physical barriers). Analysing projected range change in African antelopes by 2080, translocation across natural dispersal barriers was associated with elevated potential for interspecific competition with allopatric species and hence possible interference with ecosystem function. We argue that where translocation within the indigenous range is not an option, priority ranking of release sites would benefit from explicit consideration of dispersal barriers, favouring projected novel ranges above areas separated by distance and, especially, natural physical obstacles.

37 **KEYWORDS: Assisted migration; Habitat fragmentation; Invasive species;**

38 **Reintroduction; Species distribution modelling; Mammals.**

1. INTRODUCTION

Translocation has been used as a conservation tool for more than a century in order to reverse species declines caused by human activities (Griffith et al., 1989; Seddon et al., 2007; Ewen et al., 2012). Although translocation is often a compelling solution for species facing a high risk of extinction in the wild, its implementation is far from straightforward: it is an intervention that by definition interferes with natural ecological and evolutionary processes, the maintenance of which is the very goal of conservation. Over the past decade, translocation has received broad interest as a means of adapting to human-induced climate change for species that are unable to track habitat changes in fragmented landscapes (Harris et al., 2006; Hunter, 2007; Seddon, 2010; Sansilvestri et al., 2015). Still, the need remains for a systematic framework that prioritizes options for translocation according to their compatibility with natural eco-evolutionary processes in a world where climate change itself is changing what may be considered a natural process (Parmesan, 2006).

As a starting point, the International Union for Conservation of Nature (IUCN) Reintroduction Specialist Group (RSG), which was established in 1988 to promote best practice in conservation translocations, argues that translocation into indigenous areas, i.e. 'reintroduction', is generally preferable to translocation into non-indigenous areas, i.e. 'assisted colonisation' (IUCN/SSC, 2013). The justification is convincing: reintroductions can be expected to entail relatively low risks because population restoration in this case is supported by historical data on the performance of the species as a natural part of the ecosystem. However, the IUCN RSG guidelines also point out that under some conditions the non-indigenous area may in fact be more suitable for translocation than the indigenous range. Hence a wide range of potential threats faces species in the wild - including overexploitation, land use changes, civil conflict, disease transmission, invasive aliens, pollution, as well as climate change (IUCN, 2015) - and if the critical cause of a species' decline within its

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64   indigenous range has not been identified and dealt with, reintroduction is unlikely to result in

65   a stable, self-sustaining population. Even in cases where the threat that caused local

66   extinction is no longer present, a concern may be the subsequent emergence of new threats

67   within the indigenous range. Moreover, future threats, such as climate change, may

68   sometimes be more likely to affect the indigenous range than climatically suitable parts of the

69   non-indigenous area. The IUCN RSG guidelines thus refer to assisted colonisation as the

70   solution of choice "where protection from current or likely future threats in current range is

71   deemed less feasible than at alternative sites" (IUCN/SSC, 2013). However, the guidelines

72   point out that a "wide spectrum of operations" is currently covered by the term 'assisted

73   colonisation' (IUCN/SSC, 2013). In this study, we view the highly heterogeneous area

74   potentially suitable for translocation release as a continuum in terms of the degree to which

75   translocation would mimic a likely natural change in space use under climate change.

76   How then can the likelihood of future distributional changes be estimated? When the climate

77   induces habitat changes, the probability of a species colonising a given area will depend on

78   its species-specific dispersal ability and whether barriers to dispersal are present. Dispersal

79   barriers can be physical features of the natural world which make colonisation impossible,

80   e.g. rivers, mountains, or intercepting hostile habitats and/or climate (Foden et al., 2008).

81   Alternatively, the barrier can be distance in which case colonisation may be expected

82   eventually, time being the crucial limiting factor. Also, barriers can be anthropogenic, e.g.

83   due to wildlife incompatible human land-use or infrastructural developments, such as roads,

84   fences or pipelines. From a conservation perspective, translocations across natural physical

85   barriers may be considered the most artificial and therefore least desirable. More compatible

86   with natural eco-evolutionary processes are translocations that speed up dispersal events

87   likely to occur naturally by traversing unoccupied expanses of suitable habitat at an

88 accelerated pace. Finally, translocations across anthropogenic barriers effectively restore

89 natural eco-evolutionary processes by overcoming artificial obstacles to dispersal.

90 Following this logic, we here propose a dispersal barrier-based framework for prioritizing

91 translocation release areas to protect natural eco-evolutionary processes under climate

92 change. Taking as a prerequisite that conditions must remain bioclimatically suitable over the

93 relevant timeframe (Chauvenet et al., 2013), we define six translocation types corresponding

94 to six distinct translocation release zones that differ in the degree to which translocation

95 would approximate a natural event (Fig. 1): (i) 'Reinforcement' within the 'stable current

96 range'; (ii) 'Assisted dispersal *sensu stricto*' within the 'expected novel range'; (iii)

97 'Compensatory dispersal' within the 'idealized novel range' (ie. the range projected only if

98 simulating the absence of anthropogenic dispersal barriers); (iv) 'Accelerated dispersal'

99 within the 'expected connected envelope' (ie. the part of the bioclimatic envelope beyond

100 dispersal range); (v) 'Accelerated compensatory dispersal' within the 'idealized connected

101 envelope' (ie. the unreachable, connected envelope projected only if simulating the absence

102 of anthropogenic dispersal barriers); and (vi) 'Artificial dispersal' within the 'unconnected

103 envelope' (ie. the part of the bioclimatic envelope that is spatiotemporally separated from the

104 current range by natural physical barriers).

105 As our empirical model, we focus on African antelopes, a group expected to be significantly

106 affected by future climate change (Payne and Bro-Jørgensen, 2016), and of which 23% of the

107 species are already listed as threatened on the IUCN Red List (IUCN 2015). Translocation

108 has a particularly strong history as a conservation tool in ungulates, from the first

109 conservation translocation ever which targeted the American bison (*Bison bison*) in 1907

110 (Kleiman 1989), through several subsequent successful reintroductions, for example of the

111 Arabian oryx (*Oryx leucoryx*) in the 1980s (resulting in down-listing from 'extinct in the

112 wild' to 'vulnerable'; Stanley Price, 2016), to today's efforts to restore populations of the

wild-extinct scimitar-horned oryx (*Oryx dammah*) within its former range (Woodfine and Gilbert, 2016). Our study is thus intended also to address a more specific urgent challenge to conservation. To delimit translocation release zones for our empirical study system, we project spatial responses of species and their habitats to climate change using species distribution models (SDMs) with the critical timeframe set to 2080, the time horizon of the climate forecasts (IPCC, 2015).

Though we advocate for the ecological changes expected under climate change to be incorporated more firmly into translocation guidelines, we also agree that translocation initiatives should aim to retain current ecosystem structure as far as possible to avoid functional perturbation (IUCN/SSC, 2013), especially considering the uncertainty inherent in forecasting future species distributions (Synes and Osborne, 2011). A particular concern is the introduction of previously allopatric species, which can trigger unprecedented ecological processes with potentially devastating consequences; in particular, competitive exclusion can lead to both extinction of indigenous species where introduced species behave invasively (e.g. the extinction of the thylacine *Thylacinus cynocephalus* following introduction of domestic dogs *Canis lupus familiaris*; IUCN, 2015) and establishment failure of introduced populations where the indigenous species are the stronger competitors (e.g. the failure of introduced roan antelope *Hippotragus equinus* to become established in the ungulate community in Shimba Hills National Park, Kenya; Schiøtz, 1987). The risk of ecological interference in this case increases with the dietary overlap between species, which can promote unnatural interspecific competition. By contrast, interspecific competition between naturally sympatric species is an integral component of natural ecosystem function, where stable coexistence is evidenced by historical data. To assess the extent to which our classification system captures differences between translocation release zones in the similarity of community structure to current ranges, we compare zones within our empirical

138 model system in terms of the projected occurrence of currently allopatric antelope species as
139 well as the degree of dietary niche overlap with these.

140

2. MATERIALS AND METHODS

2.1. Species distribution modelling

143 The study used the 73 extant African antelope species as an empirical model. Current species
144 distributions, represented by Esri shape files rasterised to 10' grid scale, were modelled as
145 quadratic generalised linear models (GLM) in the R package BIOMOD (Thuiller et al.,
146 2009). Distributions were derived from Extent Of Occurrence (EOO) ranges reported by
147 IUCN (IUCN 2015), approximating the 'Area Of Occupancy' (AOO) by removing areas
148 from which species were assumed *a priori* to be absent due to human land-use (coded in both
149 a 'human footprint'-filter; Sanderson et al., 2002; Thuiller et al., 2006; and a habitat-filter;
150 USGS, 1999) and, for open- and closed-habitat specialists only, incompatible natural habitat
151 (coded in the habitat-filter; USGS, 1999). The habitat-filter categorized land cover as either
152 open (i.e. grassland, savannah, open woodland), closed (i.e. forests), or human-dominated
153 (i.e. built up areas, cropland) (USGS, 1999). The 'human footprint'-filter reduced the
154 predicted probability of species occurring in areas under human impact by incorporating data
155 on population density, land transformation, accessibility, and electrical power infrastructure
156 (Sanderson et al., 2002); specifically, the initial probability (*IP*) of occurrence from the SDM
157 was weighted by the 'human footprint' (*HFP*) to provide a final probability (*FP*) for each
158 grid cell: $FP_i = IP_i \times HFP_i$, where *i* is a 10' grid cell (Thuiller et al., 2006).

159 Predictive variables were selected from 34 environmental variables relating to climate,
160 topography, land cover, and soil (see online supplementary material). Climate data were
161 obtained from WorldClim (Hijmans et al., 2005), and the distributional information was

162 related to climatic conditions between 1950 and 2000. Since covariation precluded their

163 simultaneous inclusion in the models, variables were ranked by variable importance

164 assessment following Thuiller et al. (2010), and principal component analysis was performed

165 to detect collinearity; on this basis, we selected the set of mutually independent variables with

166 the highest explanatory power. In parallel with Pigot et al. (2010), this approach resulted in

167 the inclusion of annual precipitation (log), and hottest and coldest monthly temperature as

168 explanatory factors. SDMs informed by a random data sample (70%) were selected according

169 to their Akaike Information Criterion scores (using the stepwise search function *stepAIC*,

170 direction: "both"; Thuiller et al., 2003) and subsequently evaluated against the remaining

171 30% of the data. For assessment, we calculated both True Skills Statistics (TSS) (Landis and

172 Koch, 1977; Allouche et al., 2006; Eskildsen et al., 2013) and Area Under the Curve (AUC)

173 values, sensitivity, and specificity (Swets, 1988). Using TSS, model accuracy was classified

174 as 'excellent' for 65 species (TSS>0.75) and 'good' (0.75>TSS>0.4) for the remaining eight

175 (Fig. S1), and using AUC, as 'high' (AUC>0.9) for 70 species and 'useful' (0.9>AUC>0.7)

176 for the remaining three (Fig. S1; Fig. S2).

177 Next, SDMs were used to predict future ranges based on climate projections for three

178 different Atmosphere-Ocean Global Circulation Models (AOGCMs), i.e. UKMO HADCM3,

179 NCAR CCSM3 and BCCR BCM2, and the moderate A1B greenhouse gas emission storyline

180 (IPCC, 2015). Multi-climate-model ensemble forecasts defined areas with concordant

181 predictions under at least two of the three AOGCMs climate models (Payne and Bro-

182 Jørgensen, 2016). Future bioclimatic envelopes were delimited as the area predicted to have

183 suitable climatic conditions according to the SDMs. The bioclimatic envelopes were

184 subdivided according to whether or not an area was spatiotemporally connected to the current

185 range by suitable habitat; intermediate time steps for assessing connectivity were 2030 and

186 2050.

187 Based on the bioclimatic envelopes, we projected species distributions in 2080 by assuming

188 that species will disappear from climatically unsuitable habitat and expand into climatically

189 suitable habitat connected to their current range. Species-specific dispersal velocities were

190 calculated as the yearly dispersal distance (km) for an herbivore, D_{Herb}, according to Schloss

191 et al. (2012):

$$D_{Herb} = 1.45 * M^{0.54}$$

192 where M is body mass (kg) which we obtained from Jarman (1974), Gagnon and Chew

193 (2000) and Bro-Jørgensen (2007; 2008). The dynamics leading to future species ranges were

194 modelled in two ways. A 'realistic' approach was used to project the 'expected' ranges by

195 applying the 'human footprint'- and habitat-filters to the forecasts to reduce the likelihood of

196 species dispersing into areas dominated by human land-use (USGS, 1999; Sanderson et al.,

197 2002; Thuiller et al., 2006) and, for habitat specialists, incompatible natural habitat (USGS,

198 1999). A 'hypothetical' approach was used to simulate natural dynamics in an 'idealized'

199 world without impact from modern man. Here the 'human footprint'-filter (Sanderson et al.,

200 2002) was removed and the habitat-filter (USGS, 1999) was applied only to habitat

201 specialists to remove areas with incompatible natural habitat; due to uncertainty regarding the

202 natural habitat of human-dominated landscapes, we took a liberal approach assuming that

203 both open and closed habitat specialists might have been able to disperse through these areas

204 in the absence of man (for example, on the dynamic state between savannahs and forests, see

205 Parr et al., 2014). Note, that the human land-use filters were still applied as a final step to the

206 'idealized' projections in order to remove areas with inappropriate land cover from

207 consideration as release areas. Areas in grid cells were converted to km^2 by applying an

208 algorithm accounting for latitudinal variation in the extent of grid cells (Burrows et al., 2011).

Based on the SDMs, we defined species as particularly threatened by climate change if they satisfied any of the following criteria: (i) an elevated threat status was predicted for 2080 due to (a) projected population decline rate (estimated from range size, following IUCN criteria A3c; IUCN, 2015) and/or (b) reduction in the absolute range size (IUCN criteria B2; IUCN, 2015), and/or (ii) the range in 2080 was projected to fall entirely outside the protected area network as reported by the IUCN/United Nations Environment Programme (UNEP) World Database on Protected Areas (including only protected areas assigned an IUCN category I-VI; UNEP-WCMC, 2012).

The models were generated and analysed in R (R Development Core Team, 2014).

2.2. Ecological assessment of translocation release zones

For each species, we determined for every cell within its total potential translocation release area: (i) the number of currently allopatric antelope species projected to be present by 2080, and (ii) its mean dietary niche overlap with these. For each species, we then calculated the mean of these two indices for each of the six translocation release zones. The dietary niche overlap was calculated as the Pianka index O_{jk} for a focal species (j) against all allopatric antelope species (k) within a given cell (Pianka, 1973):

$$O_{jk} = \frac{\sum_{i=1}^{n} p_{ki} p_{ji}}{\sqrt{\sum_{i=1}^{n} (p_{ki}^2)(p_{ji}^2)}}$$

where p refers to the proportion of each resource type i in the diet, with resource types categorized into fruit, browse, and grass based on Gagnon and Chew (2000) and Cerling et al. (2003). The Pianka index ranges from 0 (no overlap with any species) and 1 (complete overlap with all species). For both indices, we compared differences between translocation

230 release zones in Kruskal-Wallis tests with Bonferroni-corrected post-hoc tests using SPSS

231 version 22 (IBM, Armonk, NY, U.S.A.).

232

3. RESULTS

234 *3.1.Distribution of translocation release zones*

235 Table 1 shows the division of the area projected as suitable for translocation release of

236 African antelopes (i.e. with stable, suitable environmental conditions until 2080) into the six

237 translocation release zones based on the separation from current species ranges by

238 anthropogenic and natural dispersal barriers. Examples of the spatial distribution of these

239 zones for individual species are shown in Fig. 2. On average, a 43.8% decline in the current

240 ranges of African antelopes was predicted by 2080. However, for most species, a

241 considerable area suitable for conservation translocation was found elsewhere, on average

242 equivalent to 162.6% of the current species range. On average, around half of this area was

243 cut off from the current range by natural barriers ('unconnected envelope'), but more than a

244 third was within the 'expected novel ranges' due to natural dispersal; the extent of the

245 connected bioclimatic envelope beyond reach by dispersal ('expected connected envelope')

246 and areas separated by anthropogenic barriers ('idealized novel ranges' and 'idealized

247 connected envelope') were relatively modest (Table 1). Large standard errors indicate that

248 individual species differed drastically in the potential importance of the different zones for

249 their conservation; for details pertaining to the species most threatened by climate change, see

250 sec. 3.3.

251

252 *3.2. Ecological assessment of translocation release zones*

253 The projected occurrence of allopatric antelope species by 2080 differed between

254 translocation release zones (Kruskal-Wallis: df 5, H=44.03, P<0.001; Fig. 3a). Post-hoc tests

255 showed that significantly more allopatric antelope species were projected to be present in the

256 unconnected envelope than in the stable current range (P<0.001) and the expected and

257 idealized novel ranges (both P=0.001); also the expected and idealized connected envelopes

258 were projected to have more allopatric species than the stable current range (P=0.002 and

259 P=0.015 respectively). Moreover, average dietary niche overlap with allopatric species

260 differed between translocation release zones (Kruskal-Wallis: df 5, H=15.25, P=0.009; Fig.

261 3b). Post-hoc tests showed that the overlap within the unconnected envelope was

262 significantly higher than within the stable current range (P=0.021).

263

264 *3.3.Translocation options for species most threatened by climate change*

265 Fourteen African antelope species were identified as particularly threatened by climate

266 change based on the models (Table 1 and 2). Nine qualified due to projected population

267 decline (IUCN criteria A3c), nine due to small range (IUCN criteria B2) and five because

268 their projected ranges showed no overlap with the protected area network (Table 2). The

269 species showed contrasting patterns in the relative importance of the various translocation

270 release zones; percentages in brackets in the remainder of this section refer to the area of a

271 zone relative the species' current range.

272 For the hirola (*Beatragus hunteri*) (critically endangered, CR) and the Nile lechwe (*Kobus*

273 *megaceros*) (endangered, EN), the areas with suitable conditions at present and by 2080

274 showed no overlap and hence no suitable release areas were identified. For the Aders' duiker

275 (*Cephalophus adersi*) (CR), only a small area within the unconnected envelope, of similar

276 size to the current range, was identified as suitable for release by the forecasts. The addax

277 (*Addax nasomaculatus*) (CR) was predicted to depend on accelerated dispersal to its expected

278 connected envelope (131%), and potentially on accelerated compensatory dispersal to a

279 similar-sized area within the idealized connected envelope (113%). The dibatag

280 (*Ammodorcas clarkei*) (vulnerable, VU) was predicted to decline drastically, by 98%, within

281 its current range and depend heavily on natural dispersal into the expected novel range

282 (52%), pointing to assisted dispersal *sensu stricto* as a conservation option. Peters' duiker

283 (*Cephalophus callipygus*) (least concern, LC) and the white-bellied duiker (*Cephalophus*

284 *leucogaster*) (LC) were both predicted to undergo 86% decline within their current ranges. Of

285 their potential translocation release areas, 7.1% resp. 11% were situated within their expected

286 novel ranges, and only 1.1% resp. 2.7% within their idealized novel ranges, suggesting

287 limited options for assisted and compensatory dispersal. Expected connected envelopes were

288 projected to cover 24% resp. 11% of the potential translocation release area, which points to

289 the feasibility of accelerated dispersal. Jentink's duiker (*Cephalophus jentinki*) (EN) and

290 Abbott's duiker (*Cephalophus spadix*) (EN) were forecast to decline by 48% resp. 50%

291 within their already restricted ranges; with only modest natural dispersal into expected novel

292 ranges (14% resp. 19%), artificial dispersal into the relatively extensive unconnected

293 envelopes projected could become necessary (624% resp. 1,555%), although for the Abbott's

294 duiker also the preferred option of compensatory dispersal would be realistic with a

295 considerable idealized novel range (19%). The beira (*Dorcatragus megalotis*) (VU) and

296 Speke's gazelle (*Gazella spekei*) (EN), which were predicted to undergo more modest

297 declines of 33% resp. 18% within their current ranges, were expected to increase their ranges

298 significantly by natural dispersal (expected novel range: 815% resp. 69%); assisted dispersal

299 *sensu stricto* would therefore be preferable to artificial dispersal if translocation were to

300 become necessary. Piacentini's dikdik (*Madoqua piacentinii*) (data deficient, DD) was

301 expected to show a drastic range decline of 87%, and the only significant translocation option

302 suggested by the projections was assisted dispersal *sensu stricto* which could bolster the

303 natural dispersal into expected novel range (17%). A similar situation was predicted for the

304 dama gazelle (*Nanger dama*) (CR) for which a 96% decline in the current range was

305 accompanied by a significant gain of expected novel range (50%); in this case the expected

306 connected envelope (26%) also suggests scope for accelerated dispersal. Finally, the current

307 range of the mountain nyala (*Tragelaphus buxtoni*) (EN) was projected to decline by 40%,

308 but gain of expected novel range (67%) was considerable and artificial dispersal into the

309 unconnected envelope (277%) may thus not be desirable.

310

4. DISCUSSION

312 Where assisted colonisation is contemplated as a conservation solution, the systematic

313 dispersal barrier-based approach presented here offers both a conceptual and a practical

314 framework for prioritizing potential release areas according to their compatibility with natural

315 ecological processes in a changing world (Mouquet et al., 2015). A major strength of the

316 framework is that it assumes a dynamic worldview, explicitly acknowledging change as a

317 fundamental part of ecosystems (Choi, 2007). Thereby it adds precision to the current

318 translocation terminology which is centred on a dichotomy between 'reintroductions' within

319 the indigenous area and 'assisted colonisations' anywhere else (Hallfors et al., 2014). Whilst

320 this dichotomy is important, it is essentially based on a static worldview, and we believe that

321 our reference system can promote more effective communication regarding the management

322 of dynamic landscapes.

323 Our approach is intended to complement, rather than replace, a historical management

324 approach based on the concept of 'indigenous range'. We thus recommend that potential

325 release areas are assessed by evaluating the distribution of the translocation release zones

326 together with any information available on the extent of historical ranges. Sites within the

327 indigenous range should be preferred wherever possible, and especially the 'expected novel

328 range' will often include both indigenous and non-indigenous areas. Our framework

329 specifically offers a way around the notorious challenge of defining the critical time period

330 since local extinction beyond which the historical range should no longer considered

331 indigenous: a key factor in this regard is the speed of environmental change, and our model

332 incorporates this by removing the part of the historical range that is no longer climatically

333 suitable.

334 Our modelling framework provides scope for further sophistication in support of

335 conservation planning. The current models approximate the fundamental Grinellian niche of

336 species and may be less accurate in reflecting the realized Eltonian niche which also includes

337 interspecific interactions (Soberon, 2007; Devictor et al., 2010). In our empirical model, the

338 higher occurrence of allopatric species, and the higher dietary overlap with these, in the

339 unconnected envelope compared to the stable current range suggests that the potential for

340 competition with allopatric competitors to affect the realized niche is of particular concern if

341 release areas are separated from current ranges by natural physical dispersal barriers. The

342 higher dietary niche overlap in this case is interesting in that it suggests that communities in

343 the unconnected envelope are more likely to have evolved to include allopatric species that

344 occupy similar ecological niches to the focal species. The results moreover suggest that

345 compared to the stable current range, the occurrence of allopatric species is significantly

346 higher also in the connected envelope, but not in the projected novel range; the ecological

347 similarity suggested by the lack of significant difference between the expected and idealized

348 novel range in particular may be due to the fact that anthropogenic barriers are too recent to

349 have had detectable consequences for community structure. Overall, these findings indicate

350 that our classification framework at least to some extent captures the ecological impact of

351 dispersal barriers on the degree of similarity in community structure and possibly also

352 function. A valuable next step, however, would be to express the impact of interspecific

353 interactions explicitly in the species distribution models; in particular, it may allow

354 identification of species likely to behave invasively (Blackburn et al., 2011), which is a main

355 concern in relation to translocation release in non-indigenous areas (Chauvenet et al., 2013).

356 Other priorities for model improvement include the development of more realistic land-cover

357 filters that are dynamic rather than static. Especially, incorporation of pressures from non-

358 climatic threats such as overexploitation would enhance the accuracy of projections for the

359 species whose current ranges have been severely affected by these threats: at present, their

360 bioclimatic envelopes are likely to be underestimated and should be interpreted cautiously.

361 As more data on local species densities become available, it will also increasingly become an

362 option to model species abundance rather than distribution and generate projections at finer

363 spatial and temporal resolution.

364 For antelope biodiversity, the present study suggests that considerable distributional changes

365 may be expected over the decades to come. For many species, conditions in significant parts

366 of their current range are projected to deteriorate while new habitat is expected to become

367 available in adjacent areas. As they stand, our results indicate that dispersal ability may not

368 be a major limiting factor for antelopes in general within the timeframe considered: overall,

369 species were projected to spread naturally into most of the suitable areas opening up (i.e. the

370 expected connected envelope was markedly smaller than the expected novel range). Our

371 results also suggest that although human land-use significantly reduces the areas available for

372 translocation release, it may have a limited effect on the ability of species to disperse into the

373 areas remaining (cfr. idealized versus expected projections in Table 1). However, the impact

374 of man-made obstructions may have been underestimated due to lack of continent-wide

375 information on the distribution of fences within wilderness areas. Although most fences

376 erected to reduce human-wildlife conflicts separate areas with human land-use from

377 wilderness areas (Durant et al., 2015), their effect thus approximated by our human land-use

378 filters, fences are also sometimes erected *within* wilderness areas, notably bordering protected

379 areas, private land, countries and roads, and/or for veterinary reasons (Durant et al., 2015).

380 Such fences can have profound ecological consequences which are not accounted for in this

381 study, and we stress the need for large-scale databases on the distribution of fences within

382 wilderness areas to inform ecological modelling for conservation management.

383 For practical conservation, averages across species are of course frequently less relevant than

384 the often drastic differences in projections between species. While it is also here important to

385 recognize that species distribution modelling can be associated with a considerable degree of

386 uncertainty (Synes and Osborne, 2011), the specific results pertaining to individual species in

387 this study still provide a useful initial assessment pointing to cases of concern for further

388 evaluation.

389 What will be the role of assisted colonisations in the future? Given the present combination

390 of drastic climate change and progressive habitat fragmentation, a logical expectation is not

391 only that translocation will become more important as a conservation intervention, but also

392 that the non-indigenous area will become increasingly relevant in this regard. However, the

393 warning of Ricciardi and Simberloff (2009), that our knowledge of ecosystem function is

394 generally too limited to advocate translocation outside indigenous ranges, remains sobering.

395 Since the effect on both the genetic and ecological balance is difficult to predict, it may be

396 argued that, according to the precautionary principle, assisted colonisations should only ever

397 be considered as a very last resort to restore natural populations. Regardless of the viewpoint

398 taken on assisted colonisations, when they do take place, it is crucial that the selection of

399 translocation release sites is based on rigorous evaluation of the likely future changes in

400 species distributions. To this end, we strongly recommend increased integration of projective

species distribution modelling into translocation planning and propose our dispersal barrier-based framework as a tool in the assessment.

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529 Table 1 Relative extent of translocation release zones for African antelope species.

Translocation release zone	Dispersal barrier	Translocation type	Area relative to current range (mean±SEM)		Area in proportion of total area suitable for translocation (mean±SEM)	
			All	CC-threatened[1]	All	CC-threatened[1]
			(N=73 spp)	(N=14 spp)	(N=71 spp)[2]	(N=12 spp)[2]
Stable current range	None	Reinforcement	56.2±3.2%	25.6±7.9%	49.3±3.4%	20.9±7.7%
Expected novel range	None	Assisted dispersal *sensu stricto*	58.9±14.5%	79.1±57.0	25.7±2.4%	25.5±8.6%
Idealized novel range	Man-made	Compensatory dispersal	5.0±1.5%	2.1±1.4%	2.1±0.4%	0.7±0.3%
Expected connected envelope	Distance	Accelerated dispersal	9.9±3.4%	14.0±9.4%	4.8±1.2%	10.4±5.0%
Idealized connected envelope	Man-made & distance	Accelerated compensatory dispersal	5.7±2.3%	8.1±8.1%	3.0±1.1%	3.8±3.8%
Unconnected envelope	Natural physical	Artificial dispersal	83.1±32.4%	295.9±145.8%	15.1±2.8%	38.4±12.1%

530 [1]'Climate change-threatened', see sec. 2.1.

531   [2]Reduced sample size due to lack of potential release areas projected for the hirola *Beatragus hunteri* and Nile lechwe *Kobus megaceros*.

532   Table 2 Absolute extent of translocation release zones for individual species particularly threatened by climate change.

Species	Current range (km²)	Translocation release zone (km²)					
		Stable current range	Expected novel range	Idealized novel range	Expected connected envelope	Idealized connected envelope	Unconnected envelope
Addax (*Addax nasomaculatus*)[1,2]	32,272	0	324	323	42,430	36,449	322
Dibatag (*Ammodorcas clarkei*)[1,2,3]	83,250	1,695	43,344	0	0	0	1,643
Hirola (*Beatragus hunteri*)[1,2]	11,280	0	0	0	0	0	0
Aders' duiker (*Cephalophus adersi*)[1,2]	342	0	0	0	0	0	341
Peters' duiker (*Cephalophus callipygus*)[1]	703,408	100,105	10,569	1,700	35,860	0	681

27

Species							
Jentink's duiker (*Cephalophus jentinki*)[3]	95,171	49,297	13,217	1,346	0	0	593,435
White-bellied duiker (*Cephalophus leucogaster*)[3]	1,185,476	161,618	22,528	5,786	22,788	0	1,363
Abbott's duiker (*Cephalophus spadix*)[2]	5,437	2,725	1,023	1,024	1,689	0	84,552
Beira (*Dorcatragus megalotis*)[3]	38,332	25,553	312,425	2,385	0	0	567,203
Speke's gazelle (*Gazella spekei*)[3]	154,508	127,413	107,044	0	0	0	160,834
Nile lechwe (*Kobus megaceros*)[1,2]	108,911	0	0	0	0	0	0
Piacentini's dikdik (*Madoqua piacentinii*)[1,2,3]	34,082	4,425	5,767	342	342	0	341
Dama gazelle (*Nanger dama*)[1,2]	273,206	11,695	136,738	0	69,950	0	0

| Mountain nyala (*Tragelaphus buxtoni*)[2] | 5,087 | 3,055 | 3,393 | 0 | 0 | 0 | 14,073 |

[1]Threatened due to population decline. [2]Threatened due to small range. [3]Threatened due to lack of protection.
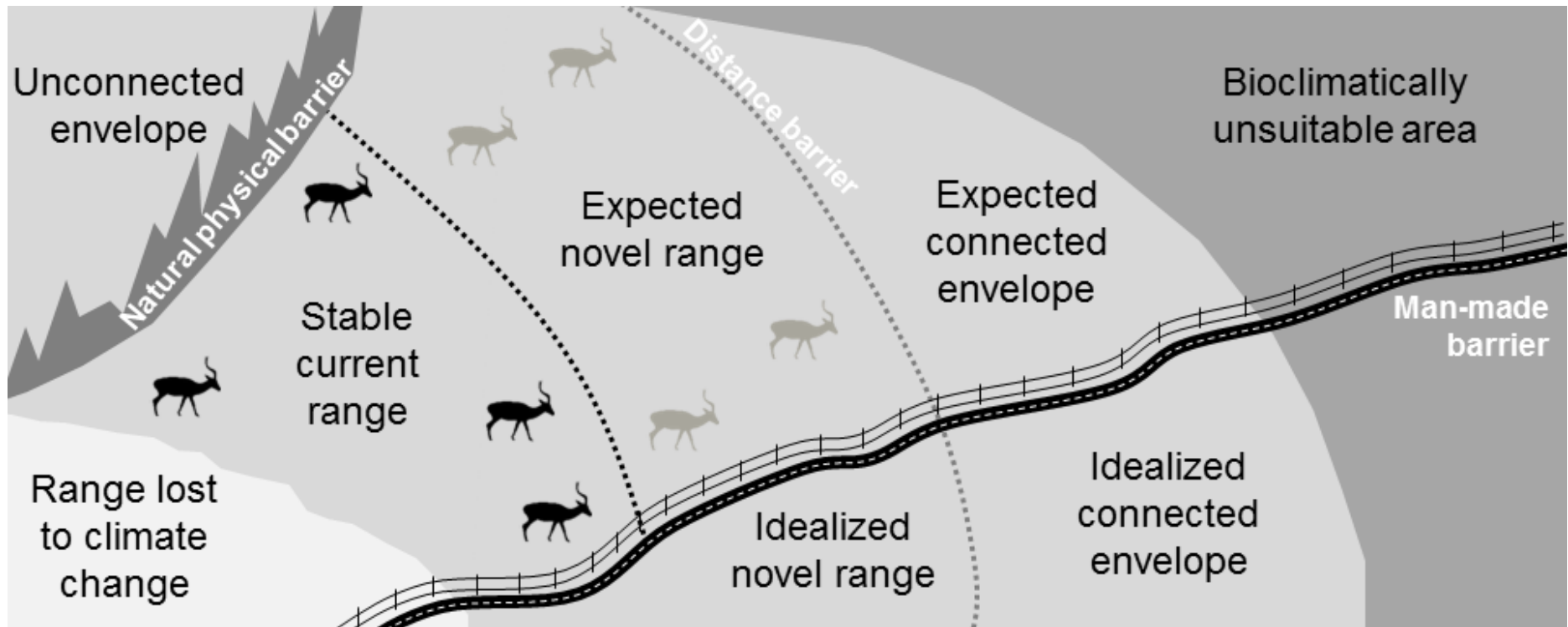
534   FIGURE LEGENDS

535   **Figure 1.** Schematic representation of the translocation release zones in relation to dispersal

536   barriers.

537   **Figure 2.** Translocation release zones for six selected antelopes assessed against a 2080-time

538   horizon. The solid outline indicates the extent of occurrence reported by the IUCN; note the

539   current range is smaller due to application of land-cover filters. (Addax: *Addax*

540   *nasomacultus*; Salt's dikdik: *Madoqua saltiana*; dibatag: *Ammodorcas clarkei*; bay duiker:

541   *Cephalophus dorsalis*; suni: *Nesotragus moschatus*; Cape grysbok: *Raphicerus melanotis*).
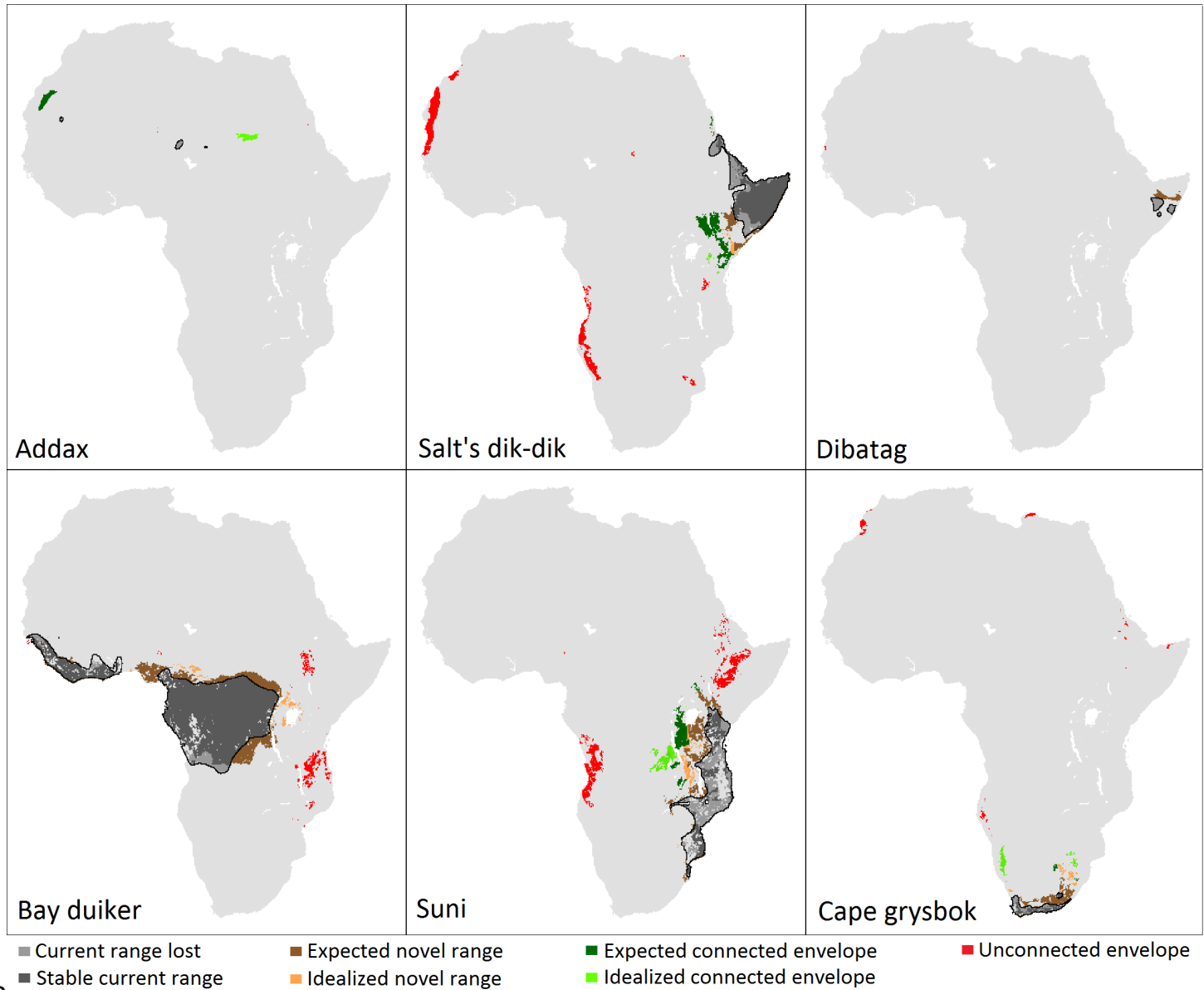
542

543   **Figure 3.** (a) Occurrence of allopatric antelope species according to translocation release

544   zone (mean number per cell). (b) Dietary niche overlap with allopatric antelope species

545   according to translocation release zone (mean of the mean Pianka index per cell). Boxes

546   delimit the interquartile ranges (IQR, i.e. the 2nd and 3rd quartiles), with horizontal lines

547   indicating the median, whiskers delimit values within 1.5 IQR from the 1st and 3rd quartiles,

548   and circles indicate outliers. Numbers above the graphics refer to sample sizes; these are <73

549   because all translocation release zones were not represented in all species and, if present, did

550   not always contain allopatric species. Significant differences between translocation release

551   zones in post-hoc tests are shown (***P<0.001; **P<0.01; *P<0.05).
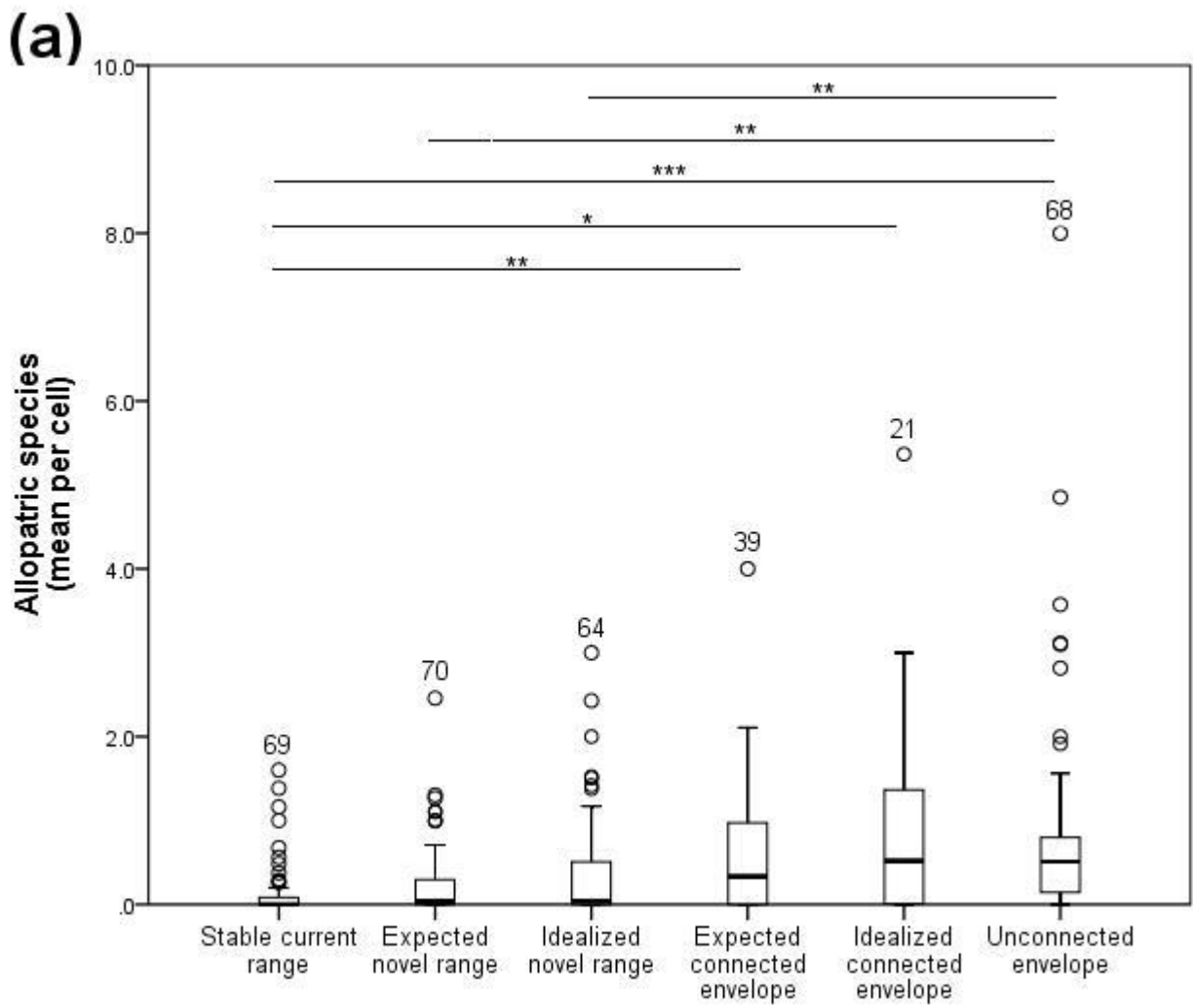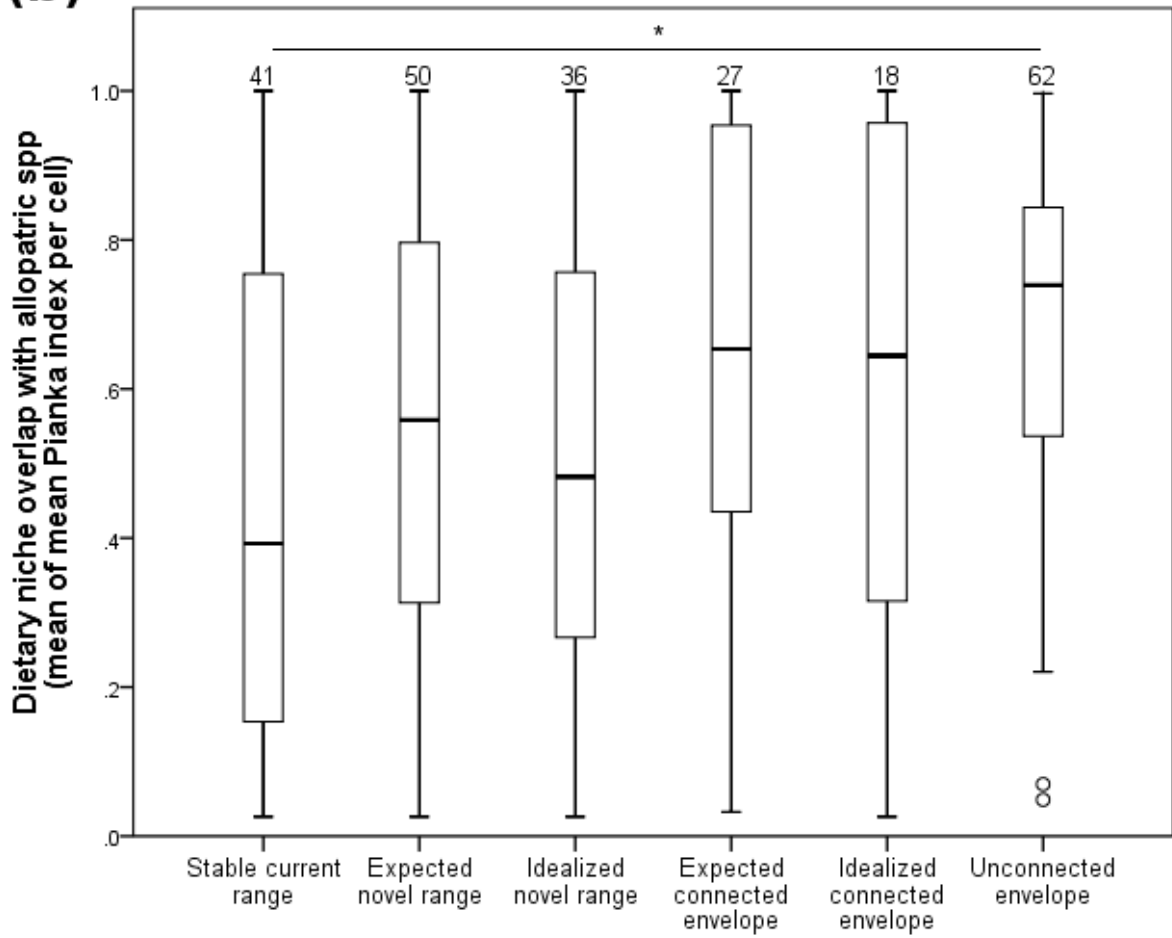
552
553   Figure 1

Addax

Salt's dik-dik

Dibatag

Bay duiker

Suni

Cape grysbok

■ Current range lost	■ Expected novel range	■ Expected connected envelope	■ Unconnected envelope
■ Stable current range	■ Idealized novel range	■ Idealized connected envelope	

554   Figure 2

Figure 3a

(b)

559
560   Figure 3b