

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

37 **KEYWORDS:** Assisted migration; Habitat fragmentation; Invasive species;
38 Reintroduction; Species distribution modelling; Mammals.

39 1. INTRODUCTION

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

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

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

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

119 Though we advocate for the ecological changes expected under climate change to be
120 incorporated more firmly into translocation guidelines, we also agree that translocation
121 initiatives should aim to retain current ecosystem structure as far as possible to avoid
122 functional perturbation (IUCN/SSC, 2013), especially considering the uncertainty inherent in
123 forecasting future species distributions (Synes and Osborne, 2011). A particular concern is
124 the introduction of previously allopatric species, which can trigger unprecedented ecological
125 processes with potentially devastating consequences; in particular, competitive exclusion can
126 lead to both extinction of indigenous species where introduced species behave invasively
127 (e.g. the extinction of the thylacine *Thylacinus cynocephalus* following introduction of
128 domestic dogs *Canis lupus familiaris*; IUCN, 2015) and establishment failure of introduced
129 populations where the indigenous species are the stronger competitors (e.g. the failure of
130 introduced roan antelope *Hippotragus equinus* to become established in the ungulate
131 community in Shimba Hills National Park, Kenya; Schiøtz, 1987). The risk of ecological
132 interference in this case increases with the dietary overlap between species, which can
133 promote unnatural interspecific competition. By contrast, interspecific competition between
134 naturally sympatric species is an integral component of natural ecosystem function, where
135 stable coexistence is evidenced by historical data. To assess the extent to which our
136 classification system captures differences between translocation release zones in the
137 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

141 **2. MATERIALS AND METHODS**

142 *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).

209 Based on the SDMs, we defined species as particularly threatened by climate change if they
210 satisfied any of the following criteria: (i) an elevated threat status was predicted for 2080 due
211 to (a) projected population decline rate (estimated from range size, following IUCN criteria
212 A3c; IUCN, 2015) and/or (b) reduction in the absolute range size (IUCN criteria B2; IUCN,
213 2015), and/or (ii) the range in 2080 was projected to fall entirely outside the protected area
214 network as reported by the IUCN/United Nations Environment Programme (UNEP) World
215 Database on Protected Areas (including only protected areas assigned an IUCN category I-
216 VI; UNEP-WCMC, 2012).

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

218

219 2.2. *Ecological assessment of translocation release zones*

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

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

226 where p refers to the proportion of each resource type i in the diet, with resource types
227 categorized into fruit, browse, and grass based on Gagnon and Chew (2000) and Cerling et al.
228 (2003). The Pianka index ranges from 0 (no overlap with any species) and 1 (complete
229 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

233 **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

311 **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 Grinnellian 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

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

403

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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 <i>sensu stricto</i>	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 ²Reduced 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 (km ²)	Translocation release zone (km ²)					
		Stable current range	Expected novel range	Idealized novel range	Expected connected envelope	Idealized connected envelope	Unconnected envelope
Addax <i>(Addax nasomaculatus)</i> ^{1,2}	32,272	0	324	323	42,430	36,449	322
Dibatag <i>(Ammodorcas clarkei)</i> ^{1,2,3}	83,250	1,695	43,344	0	0	0	1,643
Hirola <i>(Beatragus hunteri)</i> ^{1,2}	11,280	0	0	0	0	0	0
Aders' duiker <i>(Cephalophus adersi)</i> ^{1,2}	342	0	0	0	0	0	341
Peters' duiker <i>(Cephalophus callipygus)</i> ¹	703,408	100,105	10,569	1,700	35,860	0	681

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

Mountain nyala (<i>Tragelaphus buxtoni</i>) ²	5,087	3,055	3,393	0	0	0	14,073
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533 ¹Threatened due to population decline. ²Threatened due to small range. ³Threatened due to lack of protection.

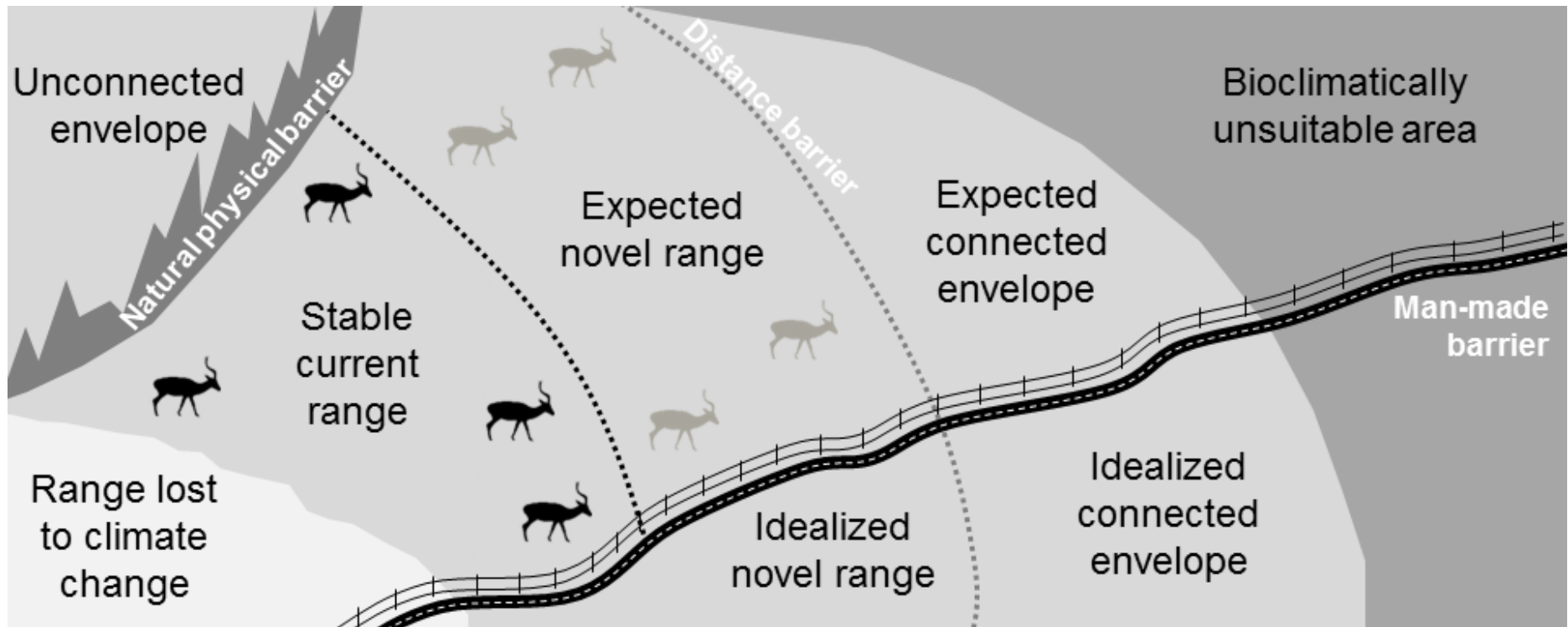
534 FIGURE LEGENDS

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*).

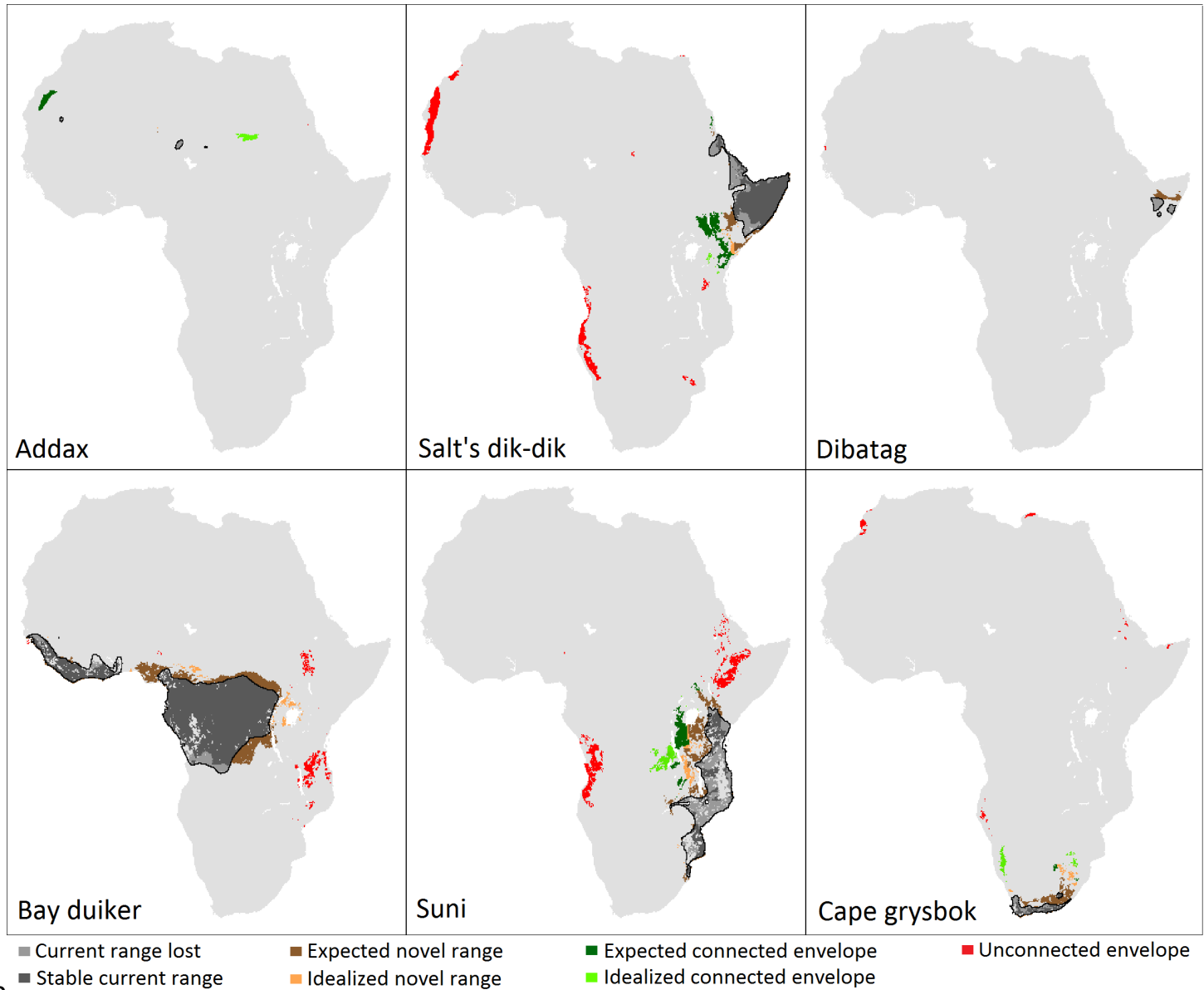
542

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).

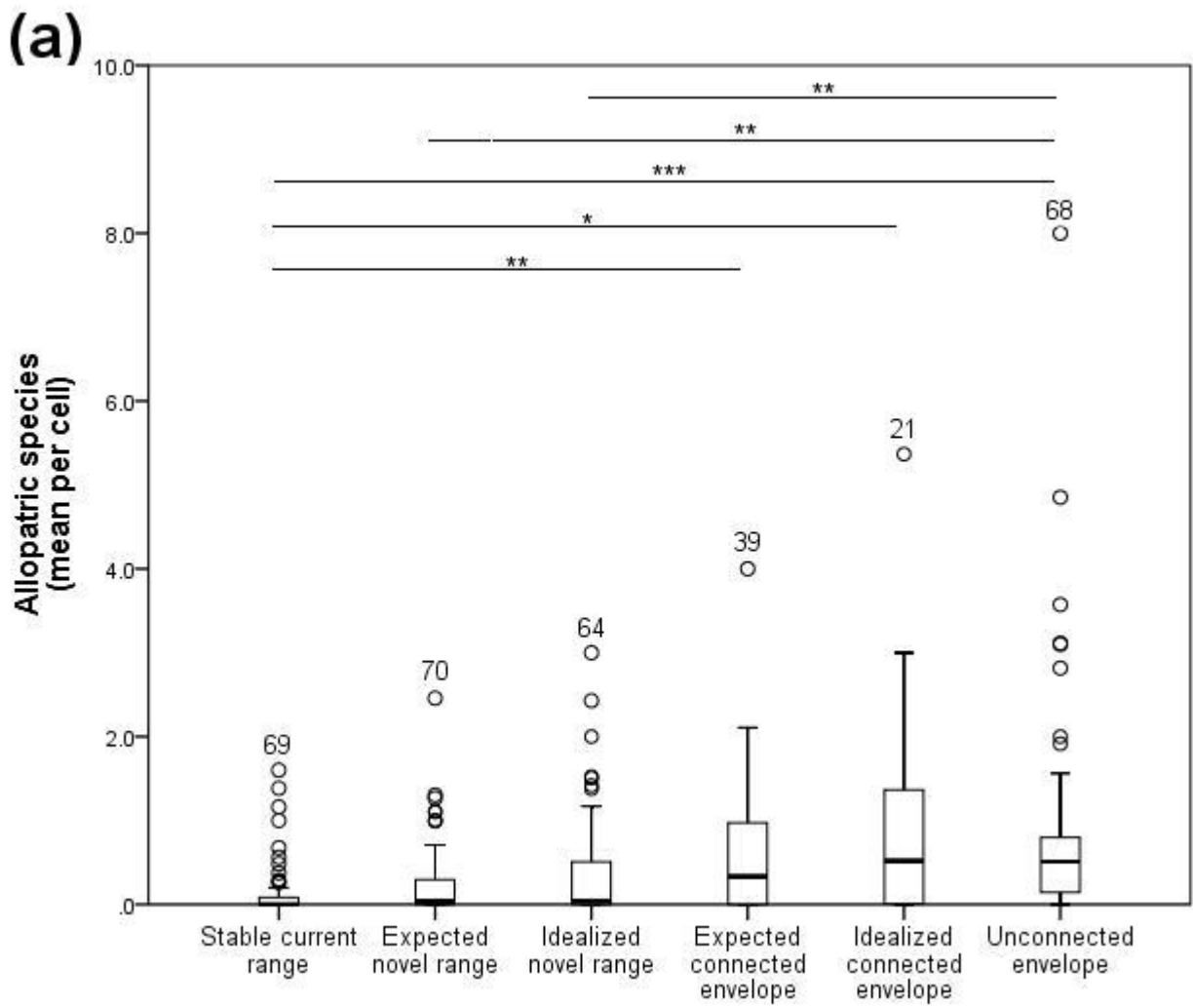


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Figure 1

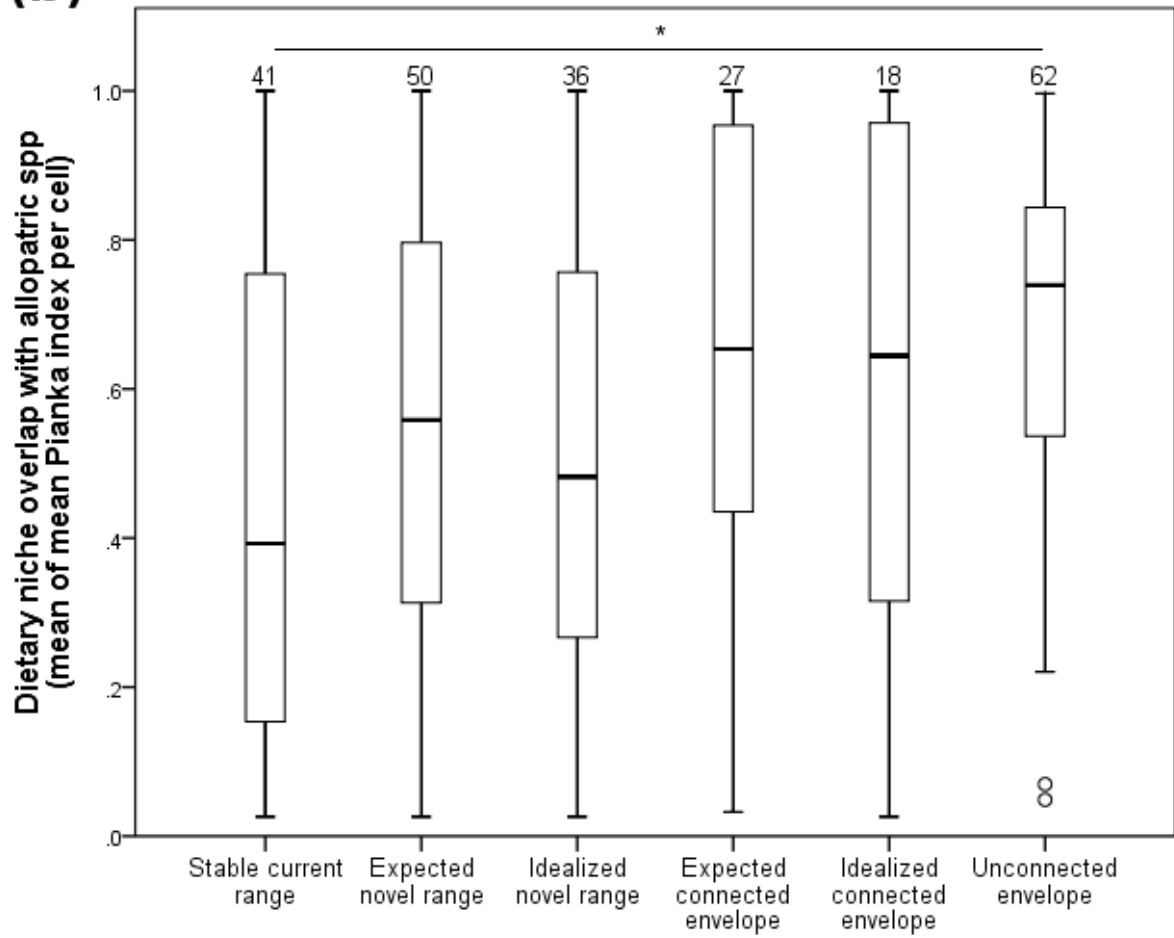


554 Figure 2



555
 556
 557 Figure 3a

(b)



559
560 Figure 3b