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1 **Creation of forest edges has a global impact on forest vertebrates**

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60

61

62 **Summary**

63 Forest edges influence more than half the world's forests and contribute to worldwide declines
64 in biodiversity and ecosystem functions. However, predicting these declines is challenging in
65 heterogeneous fragmented landscapes. We assembled an unmatched global dataset on species
66 responses to fragmentation and developed a new statistical approach for quantifying edge
67 impacts in heterogeneous landscapes to quantify edge-determined changes in abundance of
68 1673 vertebrate species. We show that 85% of species' abundances are affected, either
69 positively or negatively, by forest edges. Forest core species, which were more likely to be
70 listed as threatened by the IUCN, only reached peak abundances at sites farther than 200-400
71 m from sharp high-contrast forest edges. Smaller-bodied amphibians, larger reptiles and
72 medium-sized non-volant mammals experienced a larger reduction in suitable habitat than
73 other forest core species. Our results highlight the pervasive ability of forest edges to
74 restructure ecological communities on a global scale.

75

76 **Introduction**

77 Fragmentation of forest ecosystems has critical and on-going impacts that erode biodiversity
78 and ecological processes¹⁻⁶. Fragmentation is a ubiquitous phenomenon, with nearly 20% of
79 the world's remaining forest now found within 100 m of an edge, 50% within 500 m and 70%
80 within 1 km¹. Efforts to understand and manage the impacts of fragmentation have thus become
81 critical for effective conservation action⁷. Ecological effects emanating from edges between
82 forest and non-forest habitat change biophysical environments for species⁸ and can drive
83 species that otherwise inhabit core forest to extinction over spatial scales of more than 1 km⁹.
84 Moreover, edge effects alter the amount of 'effective' habitat area in a landscape^{4,10}, suggesting
85 they are at least as important as habitat amount¹¹ in driving biodiversity responses to land use
86 change. However, our capacity to predict which species and ecosystem functions are likely to
87 disappear first from edge-dominated landscapes is still limited. In particular, we lack consistent
88 approaches to quantify the impacts of edge effects in a rigorous manner¹² across species¹³ and
89 key functional groups¹⁴, leading to potentially distorted projections of overall changes in
90 biodiversity in fragmented landscapes.

91

92 Species' traits frameworks^{15,16} should form a reliable, heuristic tool to predict species'
93 sensitivities to edge effects in the way that they do for predicting species' extinction risks^{17,18}.
94 A paucity of meta-analyses in the fragmentation literature¹² has prevented such frameworks
95 from being tested robustly, despite an abundance of hypotheses and data. We expect, for
96 example, that species body size — a commonly measured vertebrate trait that correlates with
97 many extinction-promoting traits¹⁸ — will be significantly associated with how species
98 respond to habitat edge effects. Forest ectotherms (i.e. amphibians, reptiles) should have
99 desiccation-driven relationships responding to decreased humidity and increased temperature
100 at forest edges and in the matrix⁸. Edge sensitivity should decrease with body size for
101 amphibians as their desiccation tolerance increases due to reduced surface-to-volume ratio in
102 larger species¹⁹. The opposite should be true for reptiles (and in particular snakes) whose often
103 elongated body shape does not lend themselves to a similar decrease in surface to volume ratio.
104 By contrast, we expect mobility and metabolism to drive relationships between body size of
105 forest endotherms (i.e. mammals, birds) and their sensitivity to edges. Larger or more vagile
106 forest species should have lower edge sensitivities compared to smaller-bodied species,
107 because the former are better equipped to traverse and forage in the matrix as well as to detect
108 suitable habitat and resources in a fragmented landscape^{20,21}.

109

110 Simplistic approaches to quantifying edge effects treat landscapes as binary entities (e.g. forest
111 versus non-forest) and quantify biodiversity responses to the nearest forest edge¹⁰. These ignore
112 the role of the habitat that surrounds forests²² in human-modified landscapes (referred to as the
113 “matrix”³), overlooks the additive effects of multiple edges that arise in fragments with
114 irregular shapes²³, and makes no predictions about the identity of species that might go
115 extinct²⁴. These unsophisticated approaches stand in contrast to widespread recognition that
116 habitat quality varies continuously in space and shapes the contrast between forest and
117 matrix^{25,26}, thus modulating edge impacts in the landscape. Matrix habitat can in some cases
118 provide resources for some species²⁷, and in combination with species-specific requirements
119 may determine whether forest edges act as ‘hard’ or ‘soft’ boundaries to species populations²⁸.
120 How species respond to edges affects abundance and persistence in a landscape⁹, with declines
121 in abundance reliably indicating that a species is at increased risk of local extinctions²⁹.

122

123 We use a novel approach to quantify the impacts of habitat edges on biodiversity. We map and
124 quantify changes in the landscape-scale abundances³⁰ of 1673 vertebrate species (103
125 amphibians, 146 reptiles, 1158 birds and 266 mammals) that can be attributed to edge effects
126 in fragmented forest landscapes, using data collected in 22 landscapes distributed across seven
127 major biogeographic realms (Fig. 1 and Extended Data Tables 1 and 2). Our approach defines
128 two novel spatially explicit metrics, which together address two challenges that have so far
129 prevented the detection of generalities in the edge responses of species. (1) Edge Influence (EI)
130 assesses the configuration of landscapes and is calculated as a continuous, bounded spatial
131 metric that quantifies local variations in percentage tree cover (Methods). We developed this
132 metric to account specifically for the cumulative effects of multiple edges (including edge
133 shape and patch size) that exacerbate the realised impact of habitat edges on species^{4,12,23}
134 (Methods). Additionally, by computing EI from continuous gradients in percentage tree cover
135 (measured at the levels of pixels and ranging from 0 to 100 %), as opposed to computing it
136 from a binary classification of forest/non-forest habitat, we also account for variation in edge
137 contrast and breadth (Methods) and thereby quantify the controlling influence of matrix habitat
138 on the fragmented forest³. Absolute values of EI range from 0 (when there are no edges within
139 a 1 km radius) to 100 (when a pixel is surrounded by different habitat for 1 km in all directions).
140 EI does not correlate closely with any single traditional landscape fragmentation metric such
141 as distance to the nearest edge, edge structure, fragment shape or fragment size, but rather aims
142 to represent them all in one metric. (2) We measured the Edge Sensitivity (ES) of species as a

143 biologically meaningful metric of changes in abundance¹². ES is the proportion of the EI range
144 that is avoided by the species (Methods), and is a bounded metric that ranges from
145 0.0 (inclusive) to 1.0 (exclusive). Species whose ES is equal to 0 have no change in local
146 abundance due to edge effects, whereas species whose ES is close to 1 are restricted to
147 a specific habitat because of edge effects (e.g. abundant in core habitat only or at edges only).
148 Because ES is defined on a bounded landscape metric, it facilitates rigorous quantification and
149 comparison of species' edge responses between landscapes.

150

151 **Pervasive impact of forest edges**

152 For each species, we classified their observed abundance variations in the fragmented
153 landscape with respect to EI and percentage tree cover as one of seven categorical edge
154 response types⁹: forest core and matrix core (both edge-avoiding), forest edge and matrix edge
155 (both edge-seeking), forest and matrix species with no preference regarding the edge, and
156 generalist species (with no preference for either forest or matrix habitat). Edge responses of
157 species that could not be classified into one of these types are referred to as unknown. We used
158 a Naïve Bayes classifier to estimate the most likely edge response type for each species from a
159 training set comprising simulated abundance patterns defining each edge response type
160 (Methods).

161

162 We found that the abundance of 85% of all vertebrate species were affected by forest edges
163 (46% positively and 39% negatively), excluding 369 species of unknown edge responses. The
164 most common edge response type was forest core with 519 species, followed by forest edge
165 (338 species), matrix edge (165 species), forest and matrix with no preference regarding the
166 edge (112 and 34 species), matrix core (80 species), and generalist (56 species). The apparent
167 'good news' that marginally more species were positively rather than negatively impacted by
168 edges should be interpreted with caution. Simple vote-counting the number of positive vs
169 negative impacts, and assuming that one cancels out the other, ignores the more important fact
170 that 85% of species are impacted and that the resultant community that now persists near edges
171 bears little resemblance to that of forest interiors. Such large turnover in vertebrate community
172 composition at edges likely reflects dramatic changes to the ecological functioning of these
173 modified forest habitats³¹. Species negatively affected by edges include threatened forest core
174 species of immediate conservation concern, such as the Sunda pangolin (*Manis javanica*, ES =
175 0.72), the Bahia Tapaculo (*Eleoscytalopus psychopompus*, ES = 0.88), the Long-billed Black

176 Cockatoo (*Zanda baudinii*, ES = 0.77) and Baird's tapir (*Tapirus bairdii*, ES = 0.73). Species
177 positively affected by edges include invasives such as (*Canis lupus*, forest edge, ES = 0.6), the
178 green iguana (*Iguana iguana*, matrix edge, ES = 0.56) and the common boa (*Boa constrictor*,
179 forest edge, ES = 0.61).

180

181 Taking into account sampling bias by computing species density (Methods) and excluding
182 species whose edge response was unknown, we found that most species found in the forest and
183 classified as species that preferred forest (i.e. forest core, forest edge, forest no preference)
184 were sensitive to habitat edges, displaying either edge-seeking or edge-avoiding abundance
185 distributions in the landscape (Fig. 2a). The abundances of 11%, 30%, 41% and 57% of bird,
186 reptile, amphibian and mammal species, respectively, showed strong declines towards forest
187 edges. We observed an analogous pattern for matrix-preferring species measured in the matrix
188 (Extended Data Fig. 1a).

189

190 **Edge sensitivities across species**

191 As expected, species that were classified as having no preference for either edge or core habitat
192 displayed the lowest edge sensitivities and were significantly less sensitive than species that
193 were classified as preferring core habitats in either forest or matrix (Extended Data Fig. 2). The
194 more edge sensitive a species is the less area it can use across fragmented landscapes. Although
195 this is true for all edge response types, quantifying sensitivity is particularly critical for forest
196 core species who are more likely to be threatened due to forest loss³² and whose suitable habitat
197 area is decreasing due to fragmentation in addition to habitat loss resulting from deforestation⁵
198 (Methods). Thus, we particularly focus our analyses on the 519 forest core species (51
199 amphibians, 296 birds, 123 mammals, 49 reptiles; Extended Data Table 1).

200

201 Our data show that core forest habitat supported a larger number of amphibian, reptile and
202 mammal species compared with forest edge, matrix core or matrix edge habitats (Extended
203 Data Fig. 1b). Furthermore, forest core species were 3.7 times more likely to be listed as
204 threatened on the IUCN Red List compared with species exhibiting other edge response types
205 (two-sided 2-sample test for equality of proportions with continuity correction, $P < 0.001$) (see
206 also Extended Data Table 3).

207

208 Edge sensitivities of forest core species varied more within than among all four vertebrate
209 groups (Fig. 2b). However, on average, forest core species displayed edge sensitivities of ~ 0.7
210 across endotherms and ectotherms (Fig. 2b), which corresponds with a peak (or plateau) in
211 species abundance from a minimum of 200-400 m away from sharp and high-contrast forest
212 edges (Methods). This highlights how the amount of optimal forest habitat within fragmented
213 forest patches can be much smaller than the total land area encompassed by the patch.

214

215 Of 277 high edge sensitivity species ($ES \geq 0.8$) overall that have been assessed for the IUCN
216 Red List (excluding 'data deficient' species), 8.6% were listed as threatened compared with
217 just 3.3% of the 988 remaining species, demonstrating the conservation relevance of our edge
218 sensitivity metric. Forest core species were more likely to have very high edge sensitivities
219 (25.4% of forest core species) compared with forest species with other edge responses (20.6%)
220 (two-sided 2-sample test for equality of proportions with continuity correction, $P < 0.05$). Very
221 high edge sensitivities were particularly prevalent among forest core mammals (30.1% of
222 species) and birds (24.0%), compared with forest core amphibian and reptile species (9.8%
223 combined).

224

225 **Size and edge sensitivity of ectotherms**

226 Edge sensitivity decreased with body size for forest core amphibians (generalized additive
227 models, deviance explained = 39.6%, $n = 32$, $P < 0.05$) (Fig. 3a), but increased with body size
228 for forest core reptile species (generalized additive models, deviance explained = 35.9%, $n =$
229 45 , $P < 0.01$) (Fig. 3b). Avoiding overheating and severe water loss is likely to be an important
230 driver of edge responses in forest core amphibians and reptiles, as most of the data were
231 collected in tropical landscapes (Extended Data Tables 1 and 2), where year-round ambient
232 temperatures are high but humidity can fluctuate considerably depending on microhabitat
233 conditions³³. Amphibians require moisture to maintain gas exchange, cultivate bacterial
234 symbionts with immune-function and protect their eggs³⁴. These physiological constraints
235 make forest core amphibians, adapted to the high humidity interior of forests, prone to
236 desiccation in dry environments such as habitats with lower tree cover, e.g. at the forest edge
237 and in the matrix³⁵. Small-bodied forest core amphibian species are particularly sensitive to
238 forest edges (Fig. 3a) because their high surface area to volume ratios¹⁹ (except perhaps for
239 salamander and newts) make them more susceptible to desiccation. By contrast, the body shape
240 of forest core reptiles does not show a similar decrease in surface-to-volume ratio with

241 increasing body size (Fig. 3b). Larger forest core reptiles are thus left more vulnerable to
242 overheating in sun-exposed environments such as forest edges, particularly if they are too large
243 to successfully exploit microhabitats such as shaded leaf litter (Fig. 3b).

244

245 **Size and edge sensitivity of endotherms**

246 Edge sensitivity of forest core mammals displayed a significant hump-shaped relationship with
247 body mass (generalized additive models, deviance explained = 23.3%, $n = 116$, $P < 0.001$), a
248 pattern driven mainly by non-volant species (Fig. 3c). We attribute this relationship to the
249 compound effects of species-specific means of locomotion (aerial or terrestrial) and energetic
250 and other resource requirements. On average, forest core bats displayed significantly lower
251 edge sensitivities (Mean ES \pm SE = 0.59 ± 0.03 , $n = 53$) compared with non-volant forest core
252 mammals (0.77 ± 0.02 , $n = 63$) (ANOVA with post-hoc Tukey HSD, $P < 0.001$). This suggests
253 that the ability to fly may render mammals that prefer the forest interior less sensitive to
254 changes in habitat. But forest core bats were also significantly smaller ($P < 0.001$) with only
255 two species being slightly larger than the median body size of all studied forest core mammals
256 (Fig. 3c).

257

258 Energy demands and home range size increase with body size in non-volant mammals³⁶. Larger
259 forest core mammals are less likely than smaller ones to meet their resource needs in highly
260 fragmented landscapes comprising small forest patches with many edges but little core habitat
261 to provide those resources³⁷. Increasing energetic constraints are therefore hypothesized to
262 account for the positive body size-edge sensitivity relationship for small to medium-sized forest
263 core species (Fig. 3c). Yet, larger species are also predicted to roam more widely in search of
264 resources in fragmented landscapes if habitat loss results in a loss of resource density³⁸,
265 decreasing their edge sensitivity in the landscape. This, together with other general features of
266 large mammals, such as their lower vulnerability to predation³⁹, may explain why the largest
267 forest core mammals have lower edge sensitivities than do medium-sized species (which are
268 also susceptible to hunting¹⁷).

269

270 The combination of energetic constraints that are partly mitigated by dispersal capacity may
271 also explain the similarly hump-shaped relationship of edge sensitivity with body mass in forest
272 mammals that showed no edge preference (Extended Data Fig. 3). Conversely, dispersal
273 capacity is likely to be the main driver explaining the decline in edge sensitivity with increasing

274 body size in matrix edge mammals (Extended Data Fig. 3), with the exception of *Bos javanicus*,
275 a large but threatened wild cattle species that displayed high edge sensitivity.

276

277 Edge sensitivity of forest core birds showed a weak increase with body size (generalized
278 additive models, deviance explained = 1.5%, $n = 289$, $P < 0.05$). There was a tendency for
279 small birds ($< 31\text{g}$, the median size of core forest birds analysed in this study) to have more
280 variable responses (Fig. 3d), as also seen in bats (Fig. 3c). Some forest core bird species
281 certainly are sensitive to forest edges (Fig. 2b), especially in tropical landscapes and during the
282 non-breeding period⁴⁰, yet there is little evidence in our data to support a body size link of edge
283 sensitivity, probably because other traits such as trophic guild are more important⁴¹.

284

285 **Other species traits & edge sensitivity**

286 The ability of some endotherms to adapt to a diverse array of environments²⁰ may enable them
287 to respond better to habitat changes in a landscape²⁰. By contrast, many amphibian species are
288 habitat specialists with small home ranges⁴² and should be susceptible to changes in their
289 environment. However, for both forest core endotherms and forest core ectotherms, our data
290 do not support a habitat specialisation effect. Single predictor models of habitat trait-edge
291 sensitivity models were not significant, and the direction of the coefficient for habitat traits
292 retained in multiple predictor models could not be estimated with confidence except for forest
293 core reptiles (Extended Data Tables 4 a-d). For forest core endotherms, our data instead
294 emphasize the importance of species locomotion, which correlates with a species' vulnerability
295 to hunting or predation when traversing non-forest habitats: edge sensitivity was consistently
296 higher in non-volant mammals compared to volant species with similar habitat breadths
297 (Extended Data Table 4c).

298

299 Birds in particular may additionally be more susceptible to biophysical drivers such as
300 disturbance history⁵ confounding the detection of patterns between life history traits and
301 species responses to edges separating forest from non-forest habitat. This may explain why we
302 found no evidence for direct effects of diet, range size, migratory status or clutch size on edge
303 sensitivities of core forest birds in single predictor-models (Methods). Multiple-predictor
304 models for edge sensitivities of core forest birds retained range size, body mass, migratory
305 status, forest dependency and number of habitats (Extended Data Table 4d). Yet, none of the

306 predictor coefficients were significant and the overall deviance explained by the model was
307 negligible.

308

309 **A ubiquitous phenomenon**

310 Tracking changes in species' abundances in response to edge effects allows us to predict
311 biodiversity responses to forest loss and fragmentation at scales useful for land management.
312 This is an important difference compared with previous global analyses and projections of
313 biodiversity responses to global land use changes⁴³, which do not account for the continuous
314 variation in habitat quality of either matrix or forest habitat²⁴ that are known to affect species
315 and the ecosystem processes that they control⁴⁴.

316

317 Considering edge effects (and hence landscape configuration and forest-matrix contrast) is at
318 least as important as habitat amount when predicting species richness from habitat distribution
319 in a landscape. Although forest core endotherms and ectotherms vary greatly in how their
320 abundance changes in response to edge effects, on average they reach peak abundances in forest
321 habitats farther than 200-400 m from sharp high-contrast forest edges. This seems to
322 corroborate the traditional perception that edge effects operate within a relatively small spatial
323 window of just a few hundred metres⁴⁵⁻⁴⁷. We cannot, however, exclude the possibility that the
324 effect of edges on core species extend further within the forest, but rigorously testing this would
325 require data from many more studies examining edge effects over scales of one kilometre or
326 more⁹, which are currently rare. Regardless of whether larger-scale edge effects are as
327 ubiquitous as small-scale effects, our data strongly indicate that small forest fragments with no
328 forest located farther than 200-400 m from sharp high contrast edges (or alternatively, with no
329 forest located farther than 100 m from low contrast edges) should probably be seen as extended
330 forest edge habitat⁴⁸. Such habitats may support lower abundances of forest core species and
331 may act as a stepping stone or corridor for improving patch interconnectedness⁴⁹, but maximum
332 abundances for many species will only be achieved within much larger core forest fragments.
333 Distances to edges given here are, however, only indicative. In practice, to account for multiple
334 edges and forest-matrix contrast, it will be necessary to compute the EI map, using for example
335 our software²⁹, and delineate forest areas of EI < 30 as suitable for most forest core species.

336

337 Anthropogenic disturbances to tropical forests were recently shown to double biodiversity
338 losses incurred directly from deforestation⁵. Our data demonstrate this pattern, observed in the

339 Amazon, holds globally. Approximately half of the global forest area lies within 500 m of a
340 forest edge¹, likely of high contrast, the range over which the abundances of many core forest
341 species can be diminished. The direct implication is that less than 50% of Earth's remaining
342 forests can be considered free from edge effects, yet even that proportion is under threat from
343 the chaotic expansion of road networks, selective logging, wildfires, widespread hunting and
344 other human encroachment into the last intact forest frontiers⁵⁰.

345

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353

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356 all other authors contributed data. All authors commented on manuscript drafts.

357

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359 www.nature.com/reprints. The authors declare no competing financial interests.

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480

481 **Figure Legends**

482 **Fig. 1 Global distribution of the 22 study landscapes.** Some of these were sampled for more
483 than one vertebrate group. We sampled abundance data from a total of 1673 vertebrate species
484 (103 amphibians, 146 reptiles, 1158 birds and 266 mammals). Landscape centroids are shown
485 on the background of vertebrate species richness maps showing the total number of bird,
486 mammal, and amphibian species³¹ combined using data from Clinton Jenkins, BirdLife, and
487 IUCN (Credits: Clinton Jenkins, Instituto de Pesquisas Ecológicas / SavingSpecies).

488

489 **Fig. 2 Forest occupancy (a) and edge sensitivities for forest core species (b).** (a) Species
490 density accounting for sampling bias in the datasets is shown for forest species, a subset of the
491 seven edge response types (see Methods for details). (b) Edge sensitivity for forest core
492 amphibian (n = 51) and reptile species (n = 49) (ectotherms) and forest core bird (n = 296) and
493 mammals (n = 123) species (endotherms). Notched boxes show the median, 25th and 75th
494 percentiles, error bars show 10th and 90th percentiles, and points show outliers. Notches
495 display the 95% confidence interval around the median.

496

497 **Fig. 3 Edge sensitivity and body size in forest core vertebrates.** Relationships are shown for
498 forest core amphibians, n = 32 (a), birds, n = 289 (b), mammals, n = 116 (c) and reptiles, n =
499 45 (d). Vertical lines in each panel indicate median body size of forest core species
500 (amphibians, 40.5 mm; birds, 31.0 g; mammals, 61 g; reptiles, 75 mm). We excluded two
501 amphibian species of the order Gymnophiona, who have an elongated body shape. Smoothed
502 curves and 95% confidence bands were obtained from general additive models weighted by
503 dataset reliability (Methods), which better explained the data than a null model for all taxa.

504

505 **Methods**

506 **Species abundance data and species traits data**

507 We compiled primary biodiversity datasets containing abundance measurements at plot level
508 acquired in 22 anthropogenically fragmented forest landscapes around the world (BIOFRAG
509 database²). All landscapes encompassed anthropogenic forest edges and - except for one
510 landscape which is dominated by forests with only a small amount of habitat conversion in the
511 north-west corner - a mosaic of natural forests and other land uses (Extended Data Table 2). In
512 seven of the landscapes, the natural forests were bordered at least in part by managed,
513 plantation forest. Eighteen of the 22 landscapes were from continents with the remaining four
514 from islands, and six of the 22 landscapes could reasonably be described as coastal (Extended
515 Data Table 2). For our analysis, we only used datasets that measured abundance of vertebrates
516 in at least nine plots per landscape. We only used datasets for which geographic coordinates of
517 plots were provided at high spatial accuracy by the dataset authors, as the location of each plot
518 in relation to forest edges was important. Datasets represented full gradients of distance to edge
519 and edge influence. All datasets in our analysis were from community-level surveys of a focal
520 taxonomic group (rather than sampling for a target list of species). The final datasets used in
521 this analysis came from 22 landscapes, with some landscapes sampled for more than one
522 taxonomic group in separate or combined studies (Fig. 1)⁵¹⁻⁷¹.

523

524 The majority of taxa represented in the datasets were true species (i.e. not morpho-species)
525 (Extended Data Table 1). We matched taxonomic names given by the dataset author using steps
526 outlined in Pfeifer et al.² to obtain the full taxonomic classification for each species. We used
527 *lets.iucn* and *let.iucn.ha* functions in the *letsR*⁷² package to extract, for each true species from
528 the IUCN online database, the Red List conservation status (IUCN status), and habitat
529 information (IUCN Tree: species present in forests + savannah or shrub habitats only, IUCN
530 Forest: species present in forests only, IUCN Habitat: number of main IUCN habitat categories
531 listed).

532

533 For each species, we extracted life history trait data from literature and database sources. For
534 amphibians and reptiles, we extracted trait data (body size: maximum snout-vent length in mm
535 and maximum total length in mm for snakes; mean clutch size; thermal niche: average
536 temperature and temperature range; adult and larvae habitats; vertical stratification (i.e.

537 arboreal, semi-arboreal, terrestrial) from academic literature^{73–113}, region - specific guide
538 books^{114–116}, text books^{117–119}, and websites (all last accessed 24/06/2016) including
539 <http://amphibiaweb.org/>, <http://frogs.org.au/>, <http://www.anolislizards.myspecies.info/>,
540 <http://www.reptile-database.org/db-info/news.html>, <http://www.iucnredlist.org/>,
541 <http://research.amnh.org/vz/herpetology/amphibia/index.php>, <http://eol.org/>, and
542 <http://tolweb.org/tree/>. For birds, we extracted information on body size (mean body mass in
543 g), range size, migratory status (Not Migrating, Altitudinal Migrant, Full Migrant, Nomadic),
544 generation length in years and mean clutch size from the trait database compiled by Bird
545 International. We extracted information on bird diet from the Willman et al.¹²⁰ global dataset,
546 focussing on the Diet-5Cat attribute (i.e. assignment to the dominant category among five
547 categories based on the summed scores of constituent individual diets: plant and seed-eating
548 species; fruit and nectar-eating species; invertebrate eating species; vertebrate, fish-eating, and
549 scavenging species; omnivores). For mammals, we extracted body size (mean body mass in g),
550 trophic status, litter size and litter numbers per year, maximum longevity in months, migratory
551 behaviour, range extent in km and age at first birth from the PanTHERIA database¹²¹
552 complemented by information from <http://animaldiversity.org/accounts/Mammalia/> (last
553 accessed 11/05/2016). We also recorded whether or not species can fly (volant: all from the
554 order Chiroptera, non-volant)

555

556 **Quantifying abundance responses to variations in tree cover**

557 We analysed a species' abundance distribution in the landscape with respect to two spatial
558 variables, percentage of Tree Cover (TC) and Edge Influence (EI), to characterise both the
559 species' edge response and the species' habitat preference. For each landscape we obtained
560 30m pixel resolution percentage TC maps¹²², which were generated from Landsat imagery
561 using percent tree cover training data and decision trees classification algorithm implemented
562 in the Google Earth Engine. These maps define tree cover in the year 2000 as canopy closure
563 for all vegetation taller than 5m, encoded as a percentage per output grid cell and ranging
564 between 0 and 100%.

565

566 *Quantifying Edge Influence (EI) within and among landscapes*

567 We computed the EI metric from the regional standard deviation of TC (a measure of regional
568 heterogeneity), and the regional average TC subtracted to point TC (a measure of point
569 heterogeneity and direction)³⁰. EI is the maximum of regional and point heterogeneity for each
570 pixel and has the sign of the point heterogeneity (Eq. 1).

571

$$EI = \max(\text{regional standard deviation of } TC, |\text{regional average of } TC - \text{point } TC|) \\ \times \text{sign}(\text{regional average of } TC - \text{point } TC) \quad \text{Eq.1}$$

574

575 Regional average and standard deviation of TC were computed using a Gaussian filter of 1 km
576 radius, the distance previously shown to impact animal abundance⁹, to ensure that all TC
577 variations (i.e. edges) contained within a window of 1 km radius contribute to the value of EI.
578 Absolute values of EI range from 0 (no edges within a 1 km radius) to 100 (one pixel
579 surrounded by different habitat for 1 km in all directions). The sign of EI is determined by the
580 point heterogeneity (regional average TC minus point TC): forest habitat near the matrix has a
581 negative EI and matrix habitat near the forest has a positive EI (Extended Data Fig. 4).

582

583 The amplitude of EI depends on the landscape configuration (Extended Data Fig. 5a) and forest
584 - matrix contrast (Extended Data Fig. 5b). EI measured at a focal point increases as the point
585 approaches all nearby edges, and hence varies with the shape and with the size of the forest
586 patch (Extended Data Fig. 5a). EI also varies with the contrast between forest and matrix
587 habitats, i.e. the contrast in TC (Extended Data Fig. 5b). Hence, there is no general relationship
588 between EI and the distance to a defined edge, and no direct relationship between the % forest
589 cover in a buffer as EI is sensitive to contrast in TC whereas % forest cover is computed from
590 a binary forest-non-forest map.

591

592 *Categorising species into edge response types*

593 Species abundance within each landscape was plotted in 2D space based on TC and EI values
594 (TC - EI graph in Universal Transverse Mercator WGS 84 projection; Extended Data Fig. 6c).
595 We defined seven edge response types⁹: “forest core”, “forest edge”, “forest no preference”,
596 “matrix core”, “matrix edge”, “matrix no preference”, and “generalist” species.

597

598 We used a Naïve Bayes classifier to estimate the most likely edge response type for each
599 species from a training set of simulated abundance patterns on the TC - EI graph (see Extended
600 Data Fig. 4 for the TC - EI graph, Extended Data Fig. 6d for an illustration of a training set and
601 Lefebvre et al.³⁰, particularly pages 23 & 24 in the user manual for an illustration of
602 classification). The training set contained, on average, 15 different abundance patterns for each
603 edge response type to fully describe each type (span all possible patterns that may be classified
604 as a specific type when measured on the TC - EI graph). We created the training sets using

605 sigmoidal surfaces of varying means (location of maximum abundance) and standard
606 deviations (spread) along the TC and EI axis, thereby defining areas of high and low abundance
607 on the TC - EI graph. For “forest” and “matrix” types, the location of maximum abundance
608 along the TC axis ranged from 60% to 100% and from 0% to 20%, respectively. We defined
609 the training set by assuming that a species that is most abundant for $TC > 60$ has a high
610 probability to be a forest species, whereas a species most abundant for TC around 50 is likely
611 to be a forest species but retains a significant probability to be a matrix species (sigmoidal
612 threshold). The classification of the preferred habitat depends on the full shape of the species
613 abundance curve along the TC axis and how it compares to the training set patterns we defined.
614 Similarly, we defined “core” and “edge” types in the training set with the location of maximum
615 abundance ranging from $|EI| = 0$ to 10, and from $|EI| = 30$ to 100, respectively. By definition
616 types of “no preference” have flat abundance along the EI axis, whereas “generalist” types have
617 flat abundance along the TC axis. Location and spread parameters of sigmoid curves along the
618 TC and EI axis were combined to create an ensemble of abundance surfaces describing each
619 categorical edge response type in the TC - EI graph (see examples provided in Extended Data
620 Fig. 6d). The collection of these simulated abundance patterns on the TC - EI graph forms the
621 training set. The classifier compares the measured abundance distribution of each species to
622 the ensemble of abundance patterns for each type in the training set and estimates the most
623 likely match, depending on the area (or areas) in which the species was most abundant on the
624 TC - EI graph and the shape of the abundance surface. For example, species whose abundance
625 increases with TC are very likely to be classified as forest even if they are mostly abundant for
626 TC below 60%.

627

628 Species that did not match any defined type were classified as “unknown” (e.g. species
629 abundant in both the matrix core and forest edge but not on the matrix edge). Our approach of
630 defining a training set to use a classifier is effective to categorize species with similar edge
631 response pertaining to known types and is more flexible than fitting a parametric model to each
632 species’ abundance distribution or using thresholds.

633

634 *Quantifying edge sensitivity (ES) for each species*

635 We developed the edge sensitivity (ES) metric to quantify and compare the edge responses of
636 species that were measured in different landscapes but on the same scale, and to do so
637 independently of landscape configuration¹²³. ES is derived from comparing the species’
638 abundance surface on the TC - EI graph with the abundance surface it would have if it was

639 insensitive to edge effects. A species' ES hence corresponds to the proportion of the EI
640 spectrum that is not occupied by this species.

641

642 We obtained each species' abundance surface by linearly interpolating its abundance to the full
643 graph (for $TC \in [0,100] \in \mathbb{N}$, and $EI \in [0 - TC, 100 - TC] \forall TC$), assuming zero
644 abundance for locations with no measurements. We estimated the abundance surface for each
645 species assuming it was insensitive to edge effects by obtaining the maximum abundance at
646 each TC value, and replicating maximum abundance along the EI axis of the graph, so that the
647 abundance surface varies with TC only, and not with EI. We then computed ES from the ratio
648 of the sum of the species abundance surface on the TC-EI graph and the sum of the abundance
649 surface the species would have if it was insensitive to edge effects ("EI insensitive abundance
650 surface"):

$$651 \quad ES = 1 - \frac{\text{sum species abundance surface}}{\text{sum species "EI insensitive abundance"}} \text{ Eq. 2}$$

652 Because the "EI insensitive abundance surface" is computed from the maximum for each TC
653 of the species abundance surface, its sum is larger or equal to that of the species abundance
654 surface, therefore ES is bounded between zero and one. Species with ES values equal to zero
655 are species whose abundance is not influenced by the presence of habitat edges. Species with
656 ES values larger than zero are species that either increase or decrease in abundance in response
657 to edge effects. Species with values close to one are species that are only abundant for a specific
658 edge influence value.

659

660 ES does not quantify the abundance variation of a species directly, as this depends on the
661 configuration of the landscape. Also, ES does not quantify whether species abundance
662 increases or decreases with the presence of edges as this depends on the EI values preferred by
663 the species (i.e. low values for core species, high values for edge species). ES quantifies the
664 length of the range of EI values for which a species is abundant: if the range is as wide as the
665 EI spectrum (i.e. the species is abundant for large portions of the EI domain) then the species
666 is not sensitive to edge effects and ES is low (and the species has a high tolerance to habitat
667 change). If the range is small compared to the EI spectrum (i.e. the species is abundant at a
668 small portion of the EI domain only) then the species is sensitive to EI, and ES is high (and the
669 species has low tolerance to habitat change). Species whose ES value is close to 1 can only be
670 abundant in narrow ranges of EI, .e.g. $|EI| < 10$ (core species) or $45 < |EI| < 55$ (edge species).

671

672 The ES metric is useful to compare species sensitivity for edges, and its computation is
673 independent from the species categorisation described in the previous section. Two species
674 with the same ES may have different predictions about the spatial distribution of their preferred
675 habitat if they belong to different edge response types. Core forest species with $ES > 0.7$ will
676 only be found within the forest interior far away from edges, whereas core forest species with
677 ES of ~ 0.6 will be found near edges of large forest patches but not in peninsulas or small forest
678 patches. Core forest species with $ES < 0.6$ will be found throughout the forest and in large
679 forest patches but not in the smallest forest patches (size depending on the window size used
680 to compute EI, which was 1 km in this study). We compared the distribution of ES for forest
681 core species within taxonomic groups using notched boxplots (Fig. 2b), thereby notches display
682 the 95% confidence interval around the median. If box notches do not overlap there is strong
683 evidence that medians differ.

684

685 ES cannot generally be converted to a “distance to nearest edge” equivalent as it is based on
686 Edge Influence (EI), which varies depending on landscape configuration (Extended Data Fig.
687 5a) and patch contrast (Extended Data Fig. 5b). However, in the special case that a species’
688 abundance was measured across a straight edge of constant and maximum contrast, core forest
689 species with $ES = 0.5$ will be abundant up to this edge, and core forest species with $ES = 0.7$
690 will be abundant up to 400 m from this edge (for an EI computed with a 1 km window). A core
691 forest species of low sensitivity would also be found near edges and even in small forest
692 patches, albeit at lower abundance.

693

694 We provide these distance estimates as indication only, as there is no direct relationship
695 between distance to the nearest edge and EI. In practice, instead of computing the distance to
696 nearest edges using binary forest - non-forest maps, we urge decision-makers to utilise EI maps
697 computed from bounded landscape measurements (e.g. percentage tree cover) using the
698 provided software³⁰. This would allow them to identify areas where EI is below 30 as suitable
699 for most forest core species (whose ES is around 0.7) thereby taking into account edges varying
700 in contrast, breadth and shape.

701

702 **Rating datasets based on their capacity to assess species’ responses to edges**

703 Each dataset was rated based on the accuracy of its TC map and the distribution of sampling
704 points within the TC and EI spectra. To evaluate TC map accuracy we computed the proportion
705 of sampling points whose TC value matches the description given by the dataset authors (e.g.

706 the TC value of points identified as “forest” should be over 50%). We also rated the sampling
 707 design based on the distribution of plots on the TC - EI graph, because accurate classification
 708 of species responses requires data to be collected from each habitat type (forest core, forest
 709 edge, matrix edge and matrix core). We downgraded the dataset rating for each missing
 710 category. Datasets ratings were then used as weights when comparing ES of species across
 711 datasets.

712

713 **Estimating the relative number of species belonging to edge response types**

714 Due to sampling bias present in most datasets (for example, many datasets include more sample
 715 sites in core forest compared to forest edges), simple counts of the number of species belonging
 716 to each edge response type partly reflects the relative abundance of measurement locations
 717 within different habitat categories (Extended Data Table 1). For example, out of 103 amphibian
 718 species, 49 were categorised as core forest species. This could arise either because $49/103 =$
 719 48% of amphibian species show a preference for core forest habitats, or alternatively because
 720 48% of sampling locations were in core forest habitats, or a mixture of both. Therefore, the
 721 number of sampling sites within different habitat categories must be considered when
 722 estimating the number of species belonging to each edge response type.

723

724 We addressed the ambiguity resulting from sampling bias across different habitat categories by
 725 computing the average number of species per site (termed “species density” or SD). Species
 726 density was computed separately for sites located within each of the four habitat categories (H:
 727 forest core, forest edge, matrix edge and matrix core) and for species classified in each of the
 728 seven edge response types. Thus, for each H and each species edge response type (T) we
 729 computed the average number of species of T recorded in sites located in H, formally termed
 730 “species density of species of type T in habitat H” and denoted SD_H^T :

731

$$732 \quad SD_H^T = \frac{\sum_{i=1}^{nb \text{ sites in } H} \text{number of } T \text{ species in } H \text{ site } i}{nb \text{ of sites in } H} \quad \text{Eq.3}$$

733 For example, the average number of core forest species (FC) recorded in sites located in forest
 734 core habitat was calculated as:

$$735 \quad SD_{H=FC}^{T=FC} = \frac{\sum_{i=1}^{nb \text{ sites in } FC} \text{number of } FC \text{ species in } FC \text{ site } i}{nb \text{ of sites in } FC \text{ habitat}} \quad \text{Eq.4}$$

736 the average number of core forest species recorded in sites located in the forest edge (FE) as:

737
$$SD_{H=FE}^{T=FC} = \frac{\sum_{i=1}^{nb \text{ sites in } FE} \text{number of FC species in FE site } i}{nb \text{ of sites in FE habitat}} \quad \text{Eq.5}$$

738 the average number of forest edge species recorded in sites located in the forest core as:

739
$$SD_{H=FC}^{T=FES} = \frac{\sum_{i=1}^{nb \text{ sites in } FC} \text{number of FES species in FC site } i}{nb \text{ of sites in FC habitat}} \quad \text{Eq.6}$$

740 and so on for each combination of T and H.

741

742 Species densities within the forest habitat, including the density of forest core species in the
 743 forest (F), were determined as the average of species densities for the forest core and forest
 744 edge habitats:

745
$$SD_{H=F}^{T=FC} = \frac{SD_{H=FC}^{T=FC} + SD_{H=FE}^{T=FC}}{2} \quad \text{Eq.7}$$

746 Similarly, the average number of forest edge species in the forest was given by

747
$$SD_{H=F}^{T=FE} = \frac{SD_{H=FC}^{T=FE} + SD_{H=FE}^{T=FE}}{2} \quad \text{Eq.8}$$

748 and the average number of forest no preference (NEP) species in the forest was given by

749
$$SD_{H=F}^{T=NEP} = \frac{SD_{H=FC}^{T=NEP} + SD_{H=FE}^{T=NEP}}{2} \quad \text{Eq.9}$$

750 This corresponds to the average number of species of edge response type T per forest site
 751 weighted by the number of sites in the forest core and the forest edge (Fig. 2a: forest occupancy
 752 per edge response type). If there were the same number of sites in the forest core and the forest
 753 edge then $SD_{H=F}^T$ would simplify to the average number of species of type T per site in the
 754 forest. However, we weighted the average number of species per forest site (number of forest
 755 sites $n = 4359$: 203 for both amphibians and reptiles, 1805 for birds, 2148 for mammals) so
 756 that the contributions of core and edge habitats are equivalent. The weighted average allows us
 757 to compare for example the number of FC and FE species in the forest as if the same areas of
 758 edge and core forest habitats had been sampled (Fig. 2a).

759

760 We also quantified the average number of species (regardless of edge response type) per dataset
 761 in each habitat category to identify the habitat that can support the largest number of species.

762
$$SD_H = \frac{\sum_{i=1}^{nb \text{ sites in } H} \text{number of species in H site } i}{nb \text{ of sites in H}} \quad \text{Eq.10}$$

763 SD_H was computed for all four habitat categories (Extended Data Fig 1b). To compute SD,
 764 sampling sites and species were pooled from all landscapes used in this study, i.e. SD was
 765 computed across rather than within landscapes.

766

767 **Modelling edge sensitivity as a function of species life history traits**

768 To test whether body size predicts species responses to edges, we used general additive models
769 implemented in the *mgcv* package¹²³ (using log10-transformed body size as predictor), with
770 smoothers fitted separately for each taxonomic group. We used dataset ratings (see above) as
771 a weighting factor for the smoothing. Data were visualized using the R package *ggplot2*¹²⁴.

772

773 We also wanted to know whether we can use additional species' traits, in particular their habitat
774 specialisation, as a proxy for abundance when predicting sensitivities to habitat edge. Within
775 each taxonomic group, we first tested for single-predictor relationships between edge
776 sensitivity of core forest species and their life history traits (see above). We then fitted multiple
777 predictor general linear models using automated model selection via information theoretic
778 approaches and multi-model averaging using Maximum Likelihood. First, we constructed a
779 global model for each taxonomic group, modelling edge sensitivity as a function of predictors.
780 We excluded highly inter-correlated predictors ($V > 0.5$, $R^2 > 0.5$, $P > 0.6$) from these models
781 using Pearson's Chi-squared test with Yates' continuity correction and Cramer's V measure of
782 association to test for correlations among categorical predictors (*lsr* package), Pearson's
783 product-moment correlation P for associations between numeric predictors and the coefficient
784 of determination R^2 of linear models for relationships between numeric and categorical
785 predictors. For each global model, we used the dredge function in the R MuMIn package
786 v1.10.5 (Barton 2014), which constructs models using all possible combinations of the
787 explanatory variables supplied in each global model. These models were ranked, relative to the
788 best model, based on the change in the Akaike Information Criterion (delta AIC). A multi-
789 model average (final model) was calculated across all models with delta AIC < 2.

790

791 Global models were restricted to a subset of life history traits in mammals, amphibians and
792 reptiles due to a large number of missing values. Predictors in the global models for ectotherms
793 include IUCN Habitats, IUCN Forest, IUCN Tree (this variable correlated strongly with IUCN
794 Forest and was excluded together with its two-way interaction from the mammal and the
795 amphibian models), body size (decadic logarithmic; in mm), and two-way interactions of body
796 size with each habitat trait. Predictors in the global models for endotherms include IUCN
797 Habitats, IUCN Forest (this variable correlated strongly with IUCN Habitats and was excluded
798 together with its two-way interaction from the reptile model), IUCN Tree, body mass (decadic
799 logarithmic; in g), and two-way interactions of body mass with each habitat trait. For mammals,

800 we also included body mass squared (given the hump-shaped relationship with edge sensitivity,
801 Fig. 3c), flying status, and two – way interactions of flying status with body mass, and habitat
802 traits. For birds, we also included: range size, mean clutch size, migratory status, diet and two-
803 way interactions of migratory status with body mass and habitat traits, and of body mass with
804 diet and extent of occurrence.

805

806 **Code availability**

807 We used R 3.2.1 statistical software for all statistical analyses. We used in house generated
808 software for analyses central to the manuscript: computing edge influence, categorising species
809 into edge response types, quantifying edge sensitivity, rating datasets and estimating the
810 relative number of species belonging to edge response types. Details on these analyses are
811 described in the Methods section of the manuscript. The software itself is accessible at
812 <https://github.com/VeroL/BioFrag> (see reference 30 in the manuscript).

813

814 **Data availability**

815 The *.xls and *.kml data that support the findings of this study are available in figshare with the
816 identifier doi: 10.6084/m9.figshare.4573504. Original BIOFRAG data are available on request
817 from the corresponding author but restrictions apply to the availability of these data, which are
818 not publicly available. Data are however available from the authors upon reasonable request
819 and with permission of dataset authors as specified in the BIOFRAG database²
820 (<https://biofrag.wordpress.com/>).

821

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1005 **Extended Data Legends**

1006 **Extended Data, Table 1 Summary statistics of species and landscapes assessed in our**
1007 **study.** We include information of the number of species measured across datasets (**n**), the
1008 number of those species that were not morpho-species (**n, true**) and that were assessed by
1009 IUCN (**n, IUCN**), and the number of landscapes (**LS**) sampled overall and in the tropics only
1010 (in parentheses). The number of forest core (**n, fc**) species (all and true species only) after
1011 grouping species into edge response types based on their abundance distribution in the
1012 fragmented landscapes is also shown. Note that 299 birds (25.8%), 35 mammals (13.2%), 21
1013 reptiles (14.4%) and 14 amphibians (13.6%) could not be categorised, as their abundance in
1014 the landscape was either too low or too variable to reliably classify them into any of the edge
1015 response types.

1016

1017 **Extended Data, Table 2 Attributes describing the geographic context for each landscape.**

1018 PA - Protected Area, within - w, outside - o, within & outside - wo, primarily within - pw.
1019 Islands shown in bold in the column 'Geographic context'. Landscape minimum convex
1020 polygons created to encompass the plots sampled in each landscape are available for display as
1021 *kml. All landscapes have anthropogenic forest edges present in them. The majority encompass
1022 a mosaic of natural forests and other land uses. Only one landscape (LS_30, Madagascar) is
1023 forest-dominated with few anthropogenic edges present at the northern edge.

1024

1025 **Extended Data, Table 3 Number of threatened and not threatened species for forest core**
1026 **and all other species in each taxonomic group.** We excluded species that were not assessed

1027 or that were listed as 'data deficient' by the IUCN Red Lists (IUCN status data were not
1028 accessible for the majority of reptile species). We used a two-sided 2-sample test for equality
1029 of proportions with continuity correction and confidence level = 0.95. *P* value is significant if
1030 forest core species were more threatened than species of other edge response types.

1031

1032 **Extended Data, Table 4 Importance of predictor variables in explaining Edge Sensitivities**
1033 **of forest core ectotherms and forest core endotherms.** I, Importance; Coeff, Coefficient; P,
1034 significance of coefficient estimate; 2.5% and 97.5%, lower and upper limits for coefficient
1035 estimates; outputs as conditional average. L - only one species identified as IUCN forest

1036 dependent. We fitted two-sided general linear models and selected models from a global model
1037 for edge sensitivity via information theoretic approaches and multi-model averaging.
1038 Predictors in global models are detailed in Methods. This yielded 1 model for reptiles (n = 9
1039 species), 5 models for amphibians (n = 34 species), 7 models for mammals (n = 111 species)
1040 and 20 models for birds (n = 190). The deviance explained by the final model was 98%
1041 (reptiles), 31% (amphibians), 24% (mammals) and 3% (birds).

1042

1043 **Extended Data, Fig. 1 Matrix occupancy by matrix species per edge response type and**
1044 **average number of species per habitat category. (a)** Average number of species per matrix
1045 site (number of matrix sites = 727, 7 for amphibians, 659 for birds, 51 for mammals and 10 for
1046 reptiles), weighted so that the contributions of core and edge habitats are equivalent (Methods,
1047 Eq. 7-9). Only species classified as preferring the matrix are shown (i.e. matrix core, matrix
1048 edge, matrix with no edge response). **(b)** Average number of species (regardless of edge
1049 response type) in each habitat category showing which habitat can support the largest number
1050 of species after addressing the ambiguity resulting from sampling bias across different
1051 landscape configurations (Methods, Eq.10). Plots were categorised by their locations into:
1052 forest core (n=2955), forest edge (n=1404), matrix core (n=388), and matrix edge plots
1053 (n=339). For each configuration we computed the average number of species present per
1054 habitat category plot, which identifies the habitat that can support larger numbers of species.
1055 For amphibians, reptiles and mammals, core forest habitat supported more species than did
1056 forest edge, core matrix or matrix edge habitats. In contrast, bird species were found in larger
1057 numbers in edge habitats (in forest and matrix) than in core habitats.

1058

1059 **Extended Data, Fig. 2 Distribution of edge sensitivities for seven recognised edge response**
1060 **types.** Forest core species (n = 519) and matrix core species (n = 80) displayed significantly
1061 higher edge sensitivities compared to generalists (n = 56) and to forest (n = 112) and matrix
1062 species (n = 34) with no preference for either edge or core habitats (two-sided Pairwise
1063 Wilcoxon Signed-Rank Test with Bonferroni correction: $P < 0.001$). We excluded species that
1064 could not be classified (n = 113). Forest edge species (n = 338) had significantly higher edge
1065 sensitivities compared to forest no preference, matrix no preference, generalist and matrix edge
1066 species ($P < 0.001$). Matrix edge species (n = 165) also displayed significantly lower edge
1067 sensitivities compared to matrix core species and higher edge sensitivities compared to
1068 generalists ($P < 0.001$). Notched boxes show the median, 25th and 75th percentiles, error bars

1069 show 10th and 90th percentiles, and points show outliers. Notches display the 95% confidence
1070 interval around the median.

1071

1072 **Extended Data, Fig. 3 Significant relationship between edge sensitivity and body size**
1073 **across edge response types** (except forest core species that are shown in Figure 3 in main
1074 manuscript). Vertical lines in each panel indicate median body size of the species per
1075 taxonomic group and edge response type (mammals forest no preference, 43.8 g; mammals
1076 matrix edge, 47.0 g; reptiles, unknown 97.5 mm). Smoothed curves and 95% confidence bands
1077 were obtained from general additive models (GAMs), with the model weighted by a variable
1078 that reflects dataset reliability (Methods). GAMs better explained the data than a null model
1079 for taxa and edge response types shown. Edge sensitivity ranges from 0.0 (no declines in local
1080 abundance due to edge effects) to 1.0 (local extinction due to edge effects).

1081

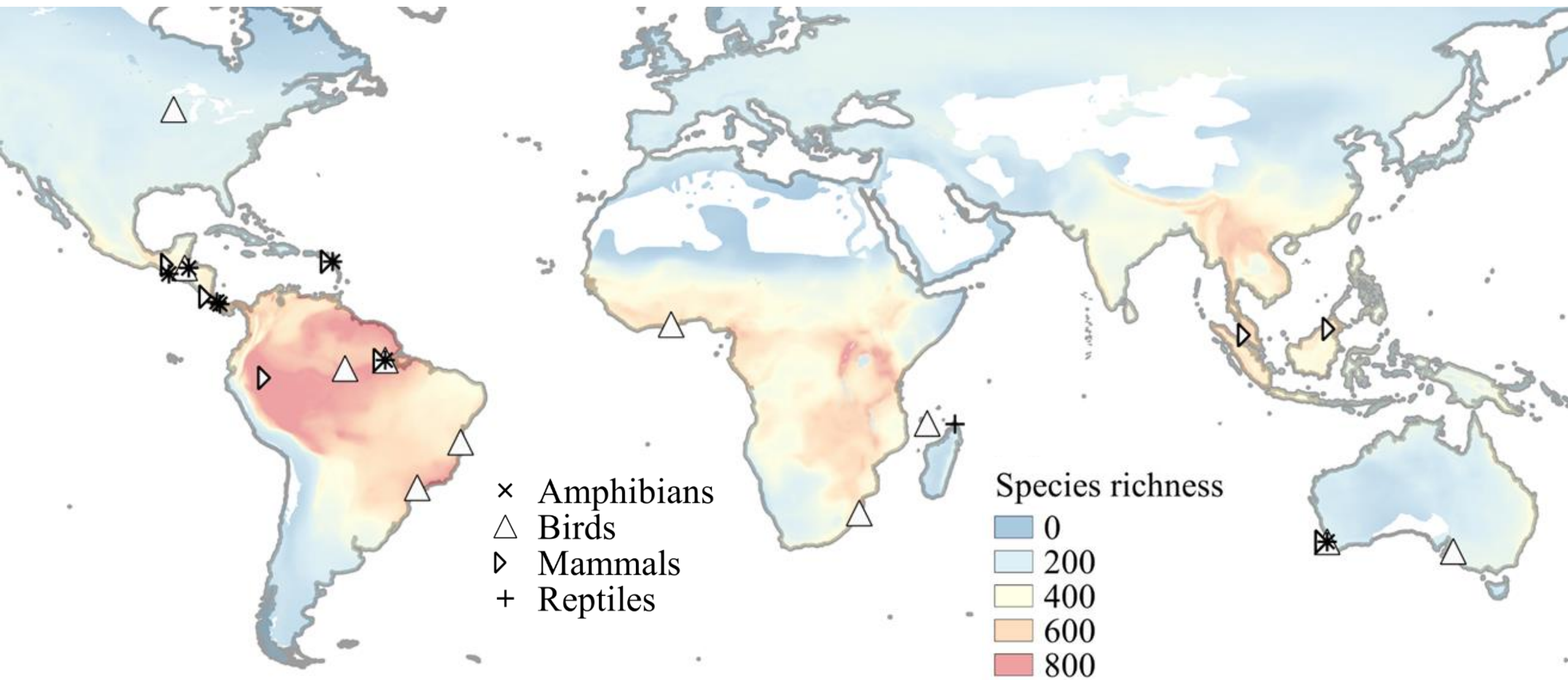
1082 **Extended Data, Fig. 4 Illustration of the TC – EI graph.** Combinations of point TC and EI
1083 characterize different landscape configurations, and some combinations are impossible by
1084 design (grey areas). The x - axis represents the percentage of tree cover at the scale of a pixel.
1085 The y - axis represents the EI metric, computed from the regional standard deviation of TC (a
1086 measure of regional heterogeneity), and the regional average TC subtracted to point TC (a
1087 measure of point heterogeneity and direction).

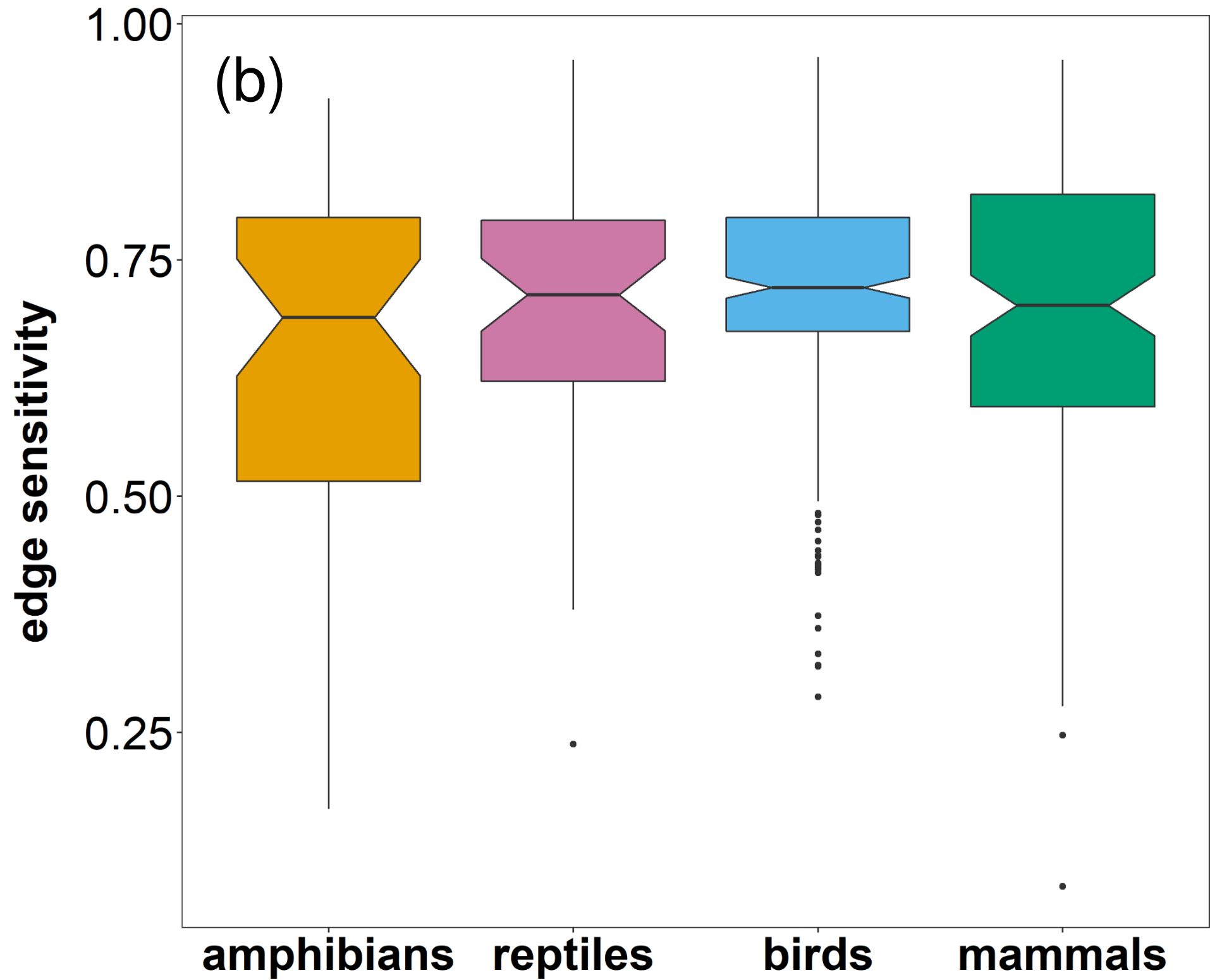
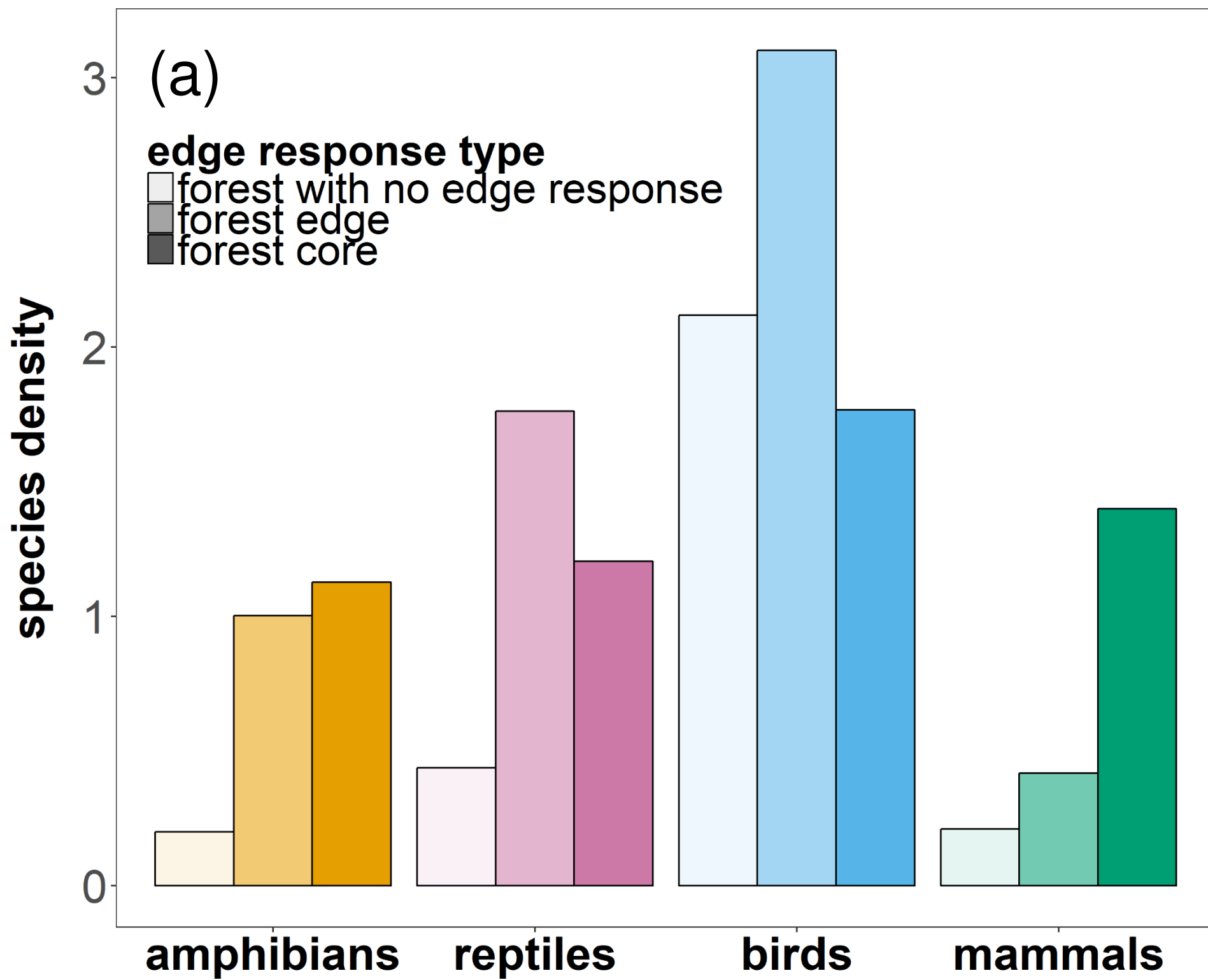
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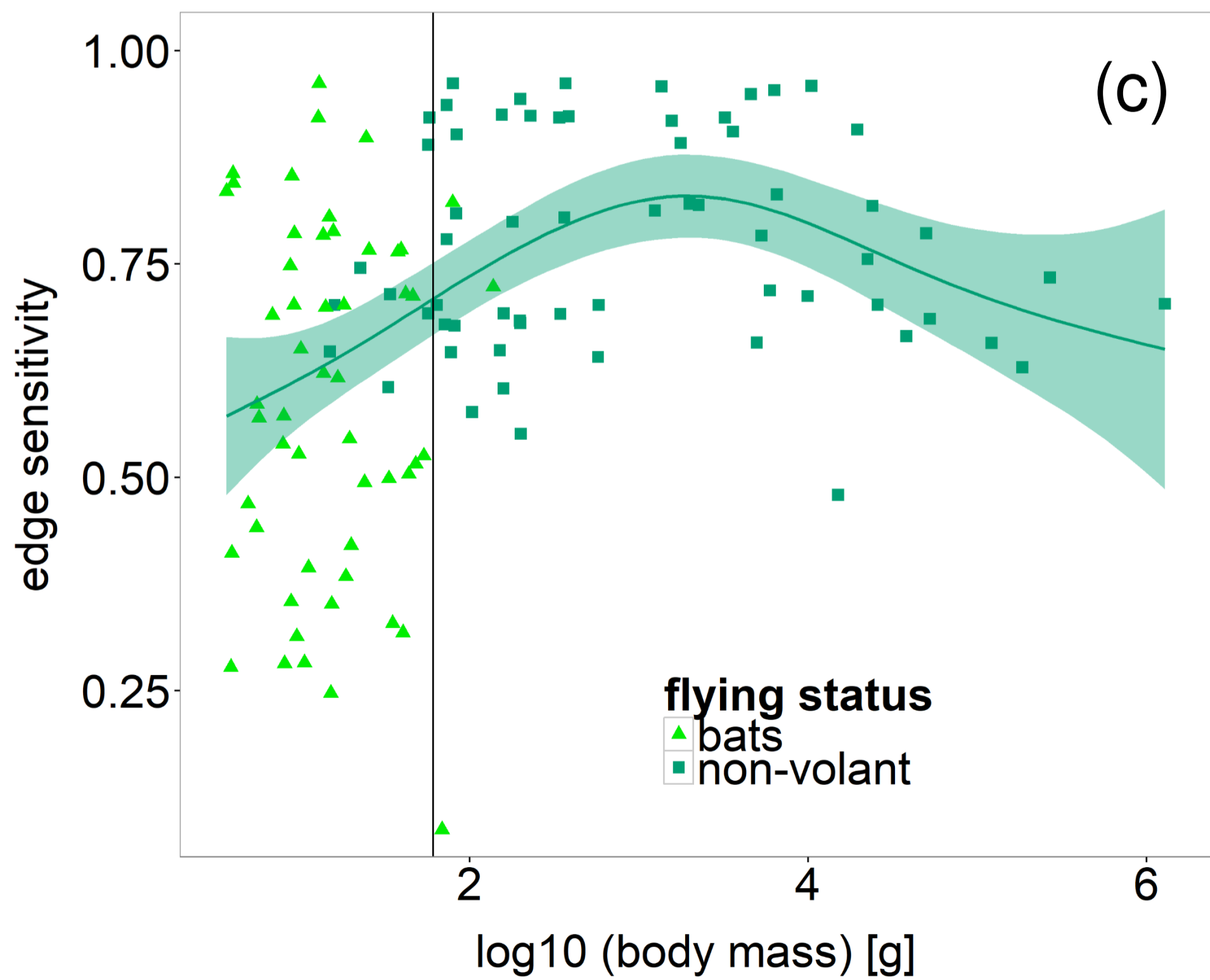
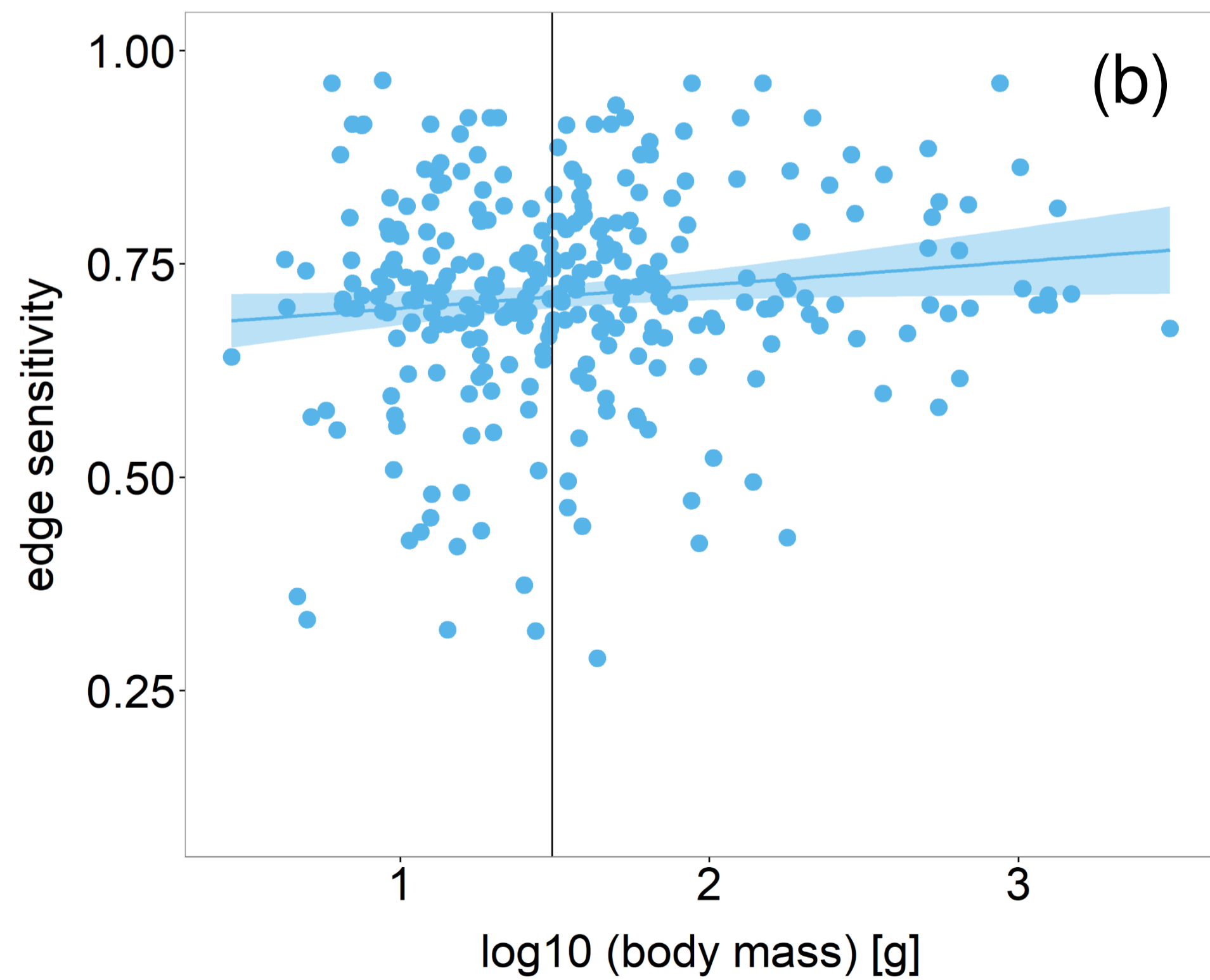
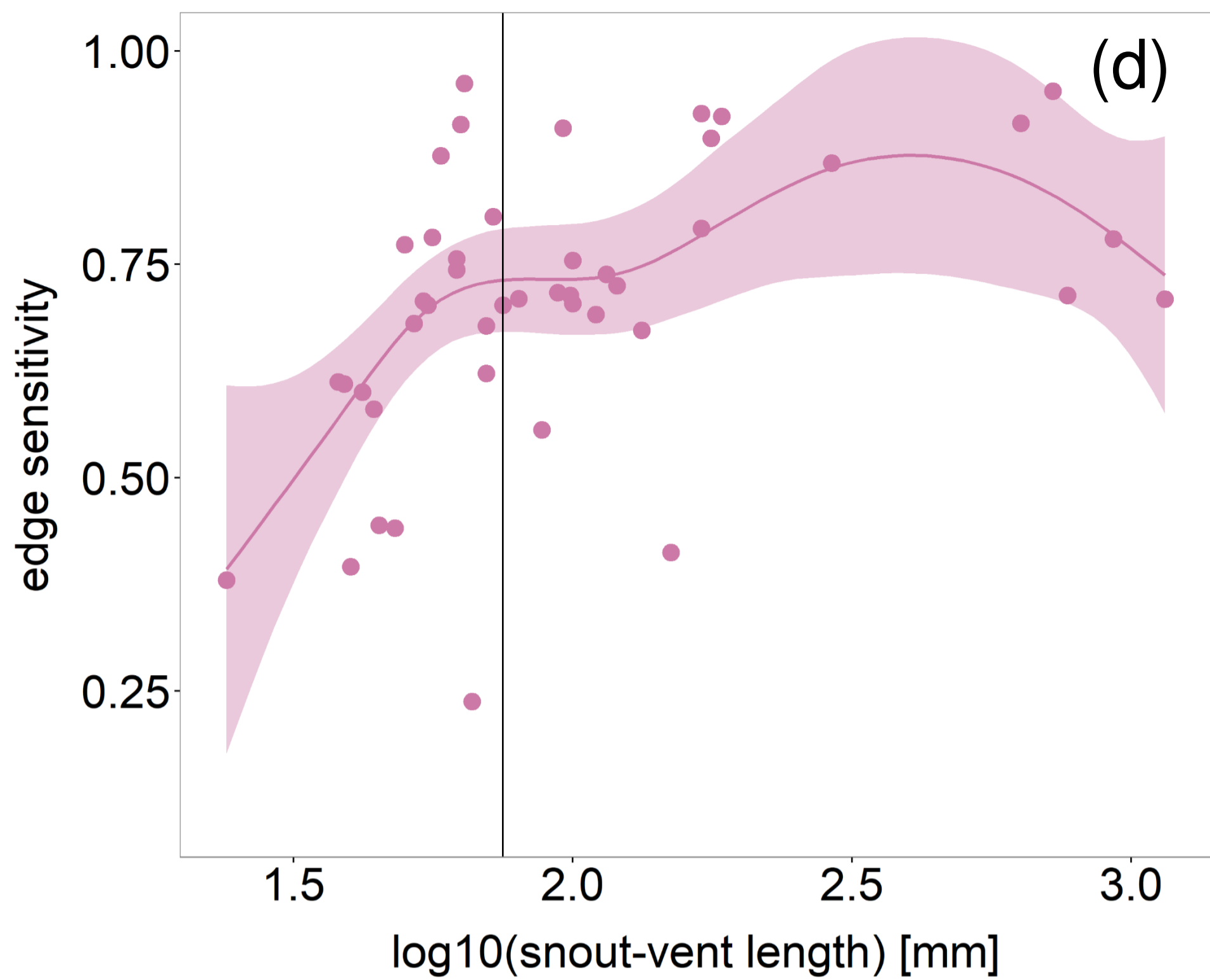
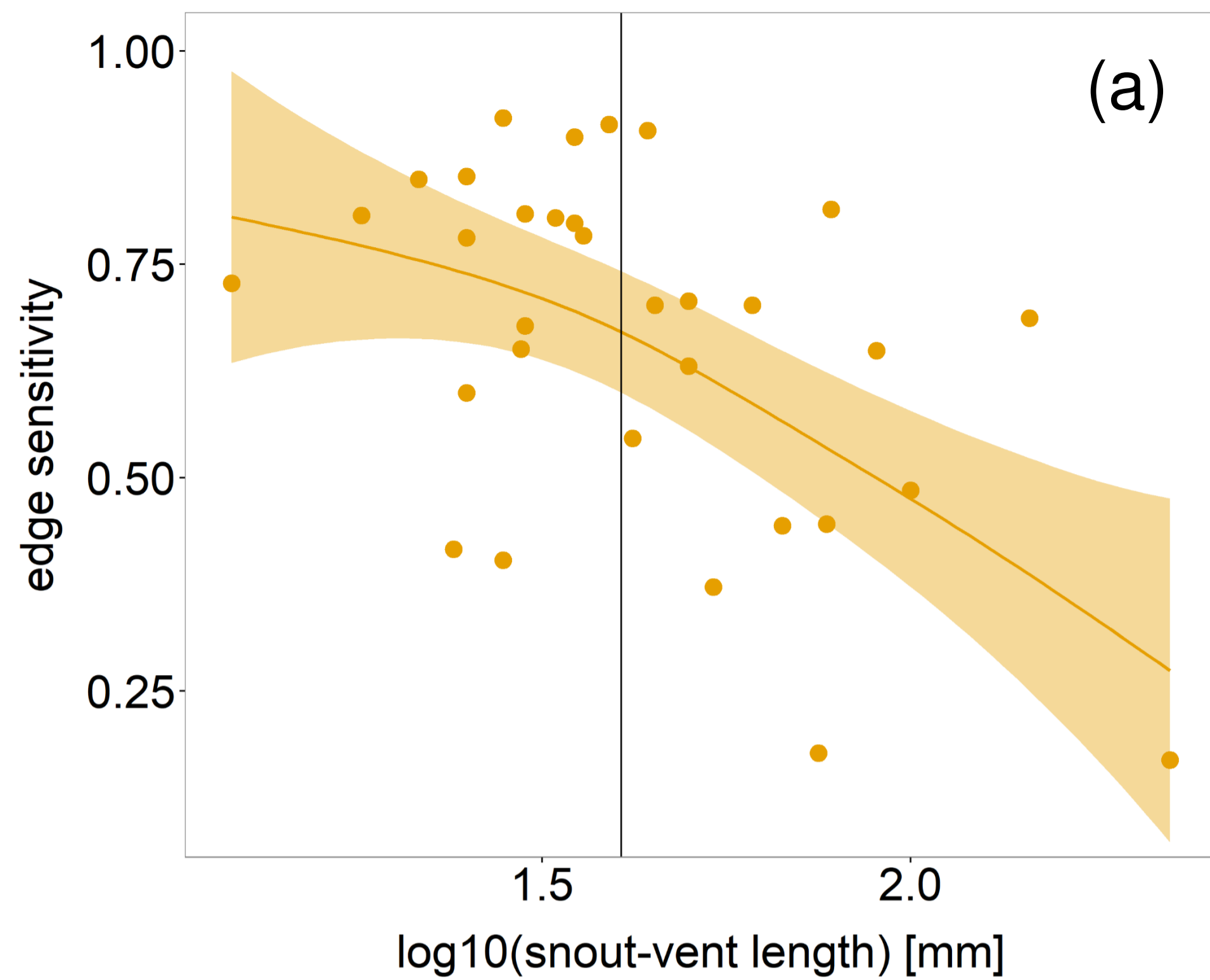
1089 **Extended Data, Fig. 5 Variations of Edge Influence (EI) with Tree Cover (TC)**
1090 **configuration (a) and contrast (b).** **(a, top row)** Four examples of landscape configurations
1091 comprising dense tree cover habitats (green) and matrix (cream). From left to right: creek edge,
1092 straight edge, peninsula edge and small forest patch. **(a, bottom row)** EI maps that correspond
1093 to above landscape configurations. The EI value at the central point (cross) is given for each
1094 configuration. The central point is always located on an edge and its distance to nearest edge
1095 is always zero. Nonetheless, EI increases in absolute value as the central point is increasingly
1096 surrounded by a different type of habitat. **(b, top row)** Four examples of peninsula edges
1097 between matrix (cream, TC=0%) and habitats of varying tree density (shades of green). From
1098 left to right: 25%, 50%, 75% and 100%. **(b, bottom row)** EI maps that correspond to above
1099 landscape contrasts. The EI value at the central point (cross) is given for each configuration.
1100 The central point is always located on an edge and its distance to nearest edge is always zero.
1101 EI increases as the edge contrast increases.

1102

1103 **Extended Data, Fig. 6 Computing species abundance surfaces on the TC - EI graph and**
1104 **simulated edge response types on the TC – EI graph. (a)** Plots superimposed on an
1105 hypothetical TC map. Marker colours correspond to the abundance of a hypothetical species
1106 and follow the colour bar shown in (c). **(b)** EI map corresponding to (a). **(c)** TC - EI graph:
1107 species abundance (warm colour = higher abundance) is plotted as a function of TC and EI
1108 measured at the species' plots. In this example, the species is predominantly found in sites
1109 characterised by high TC and low |EI|, and would be classified as a core forest species. **(d)**
1110 Illustration of the training set of edge response types used for classification. Each of the 7
1111 response type has around 15 patterns associated with it in the training set; here we show 2
1112 examples for the forest core type and forest edge type and one example for the forest no-
1113 preference type. Each graph is a TC – EI graph with TC on the x-axis and EI on the y-axis.
1114 Warmer colours means high abundance, dark blue is 0.







Taxon	n	n, true	n, IUCN	LS (tropical)	n, fc (tropical)	n, fc + true (tropical)
Amphibians	103	72	72	7 (6)	51 (48)	35 (32)
Birds	1158	1139	1139	11 (7)	296 (275)	293 (273)
Mammals	266	260	258	8 (7)	123 (121)	118 (117)
Reptiles	146	124	49	8 (7)	49 (41)	45 (37)

Landscape	Ocean present in landscape	Geographic context	Forest within & outside PAs	Plots within & outside PAs	Land use in the matrix
LS_01	yes	Africa	pw	wo	Crops, Plantation forest
LS_02	no	S America	wo	wo	Clear cuts
LS_03	yes	Island^a	o ^e	o	Clear cuts, Crops, Cattle pasture, Settlements
LS_06	no	S America	o	o	Clear cuts, Crops
LS_10	yes	Australia	pw	wo	Clear cuts, Crops, Settlements
LS_15	no	Island^b	o ^e	o	Clear cuts, Grassland, Settlements
LS_16	no	SE Asia	wo	wo	Plantation forest (oil palm rubber)
LS_18	no	S America	o	o	Clear cuts, Crops, Plantation forest (Eucalyptus)
LS_25	no	N America	o	o	Savannah, Grassland
LS_30	no	Island^c	o ^{e,f}	o	Clear cuts, Orchards
LS_37	no	C America	wo	wo	Grassland
LS_38	no	C America	wo	wo	Crops, Plantation forest, Settlements
LS_39	no	C America	wo	wo	Clear cut, Settlements
LS_40	yes	C America	wo	wo	Clear cut, Crops, Settlements
LS_42	yes	C America	pw	wo	Cattle pasture, Crops, Plantation forest
LS_44	no	Australia	wo	wo	Plantation forest
LS_46	no	C America	wo	wo	Crops, Grassland, Settlements
LS_47	no	S America	wo	wo	Clear cuts, Settlements
LS_57	no	C America	wo	wo	Crops, Pasture, Settlements
LS_59	no	Island^d	wo	wo	Clear cuts, Plantation forest (oil palm)
LS_60	no	S America	w	w	Pasture, Plantation forest (rubber, eucalyptus, cocoa)
LS_62	yes	Africa	wo	wo	Crops, Plantation forest

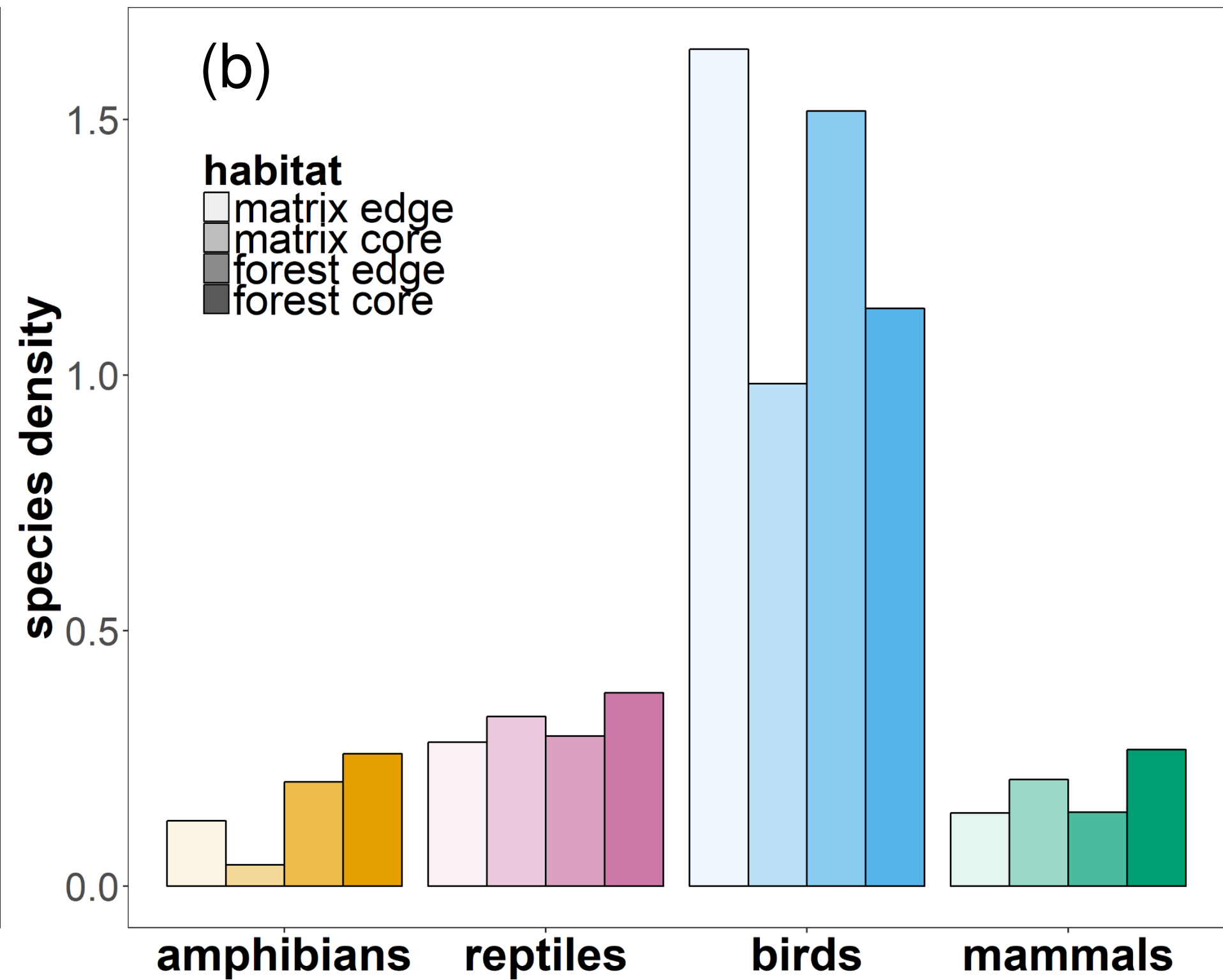
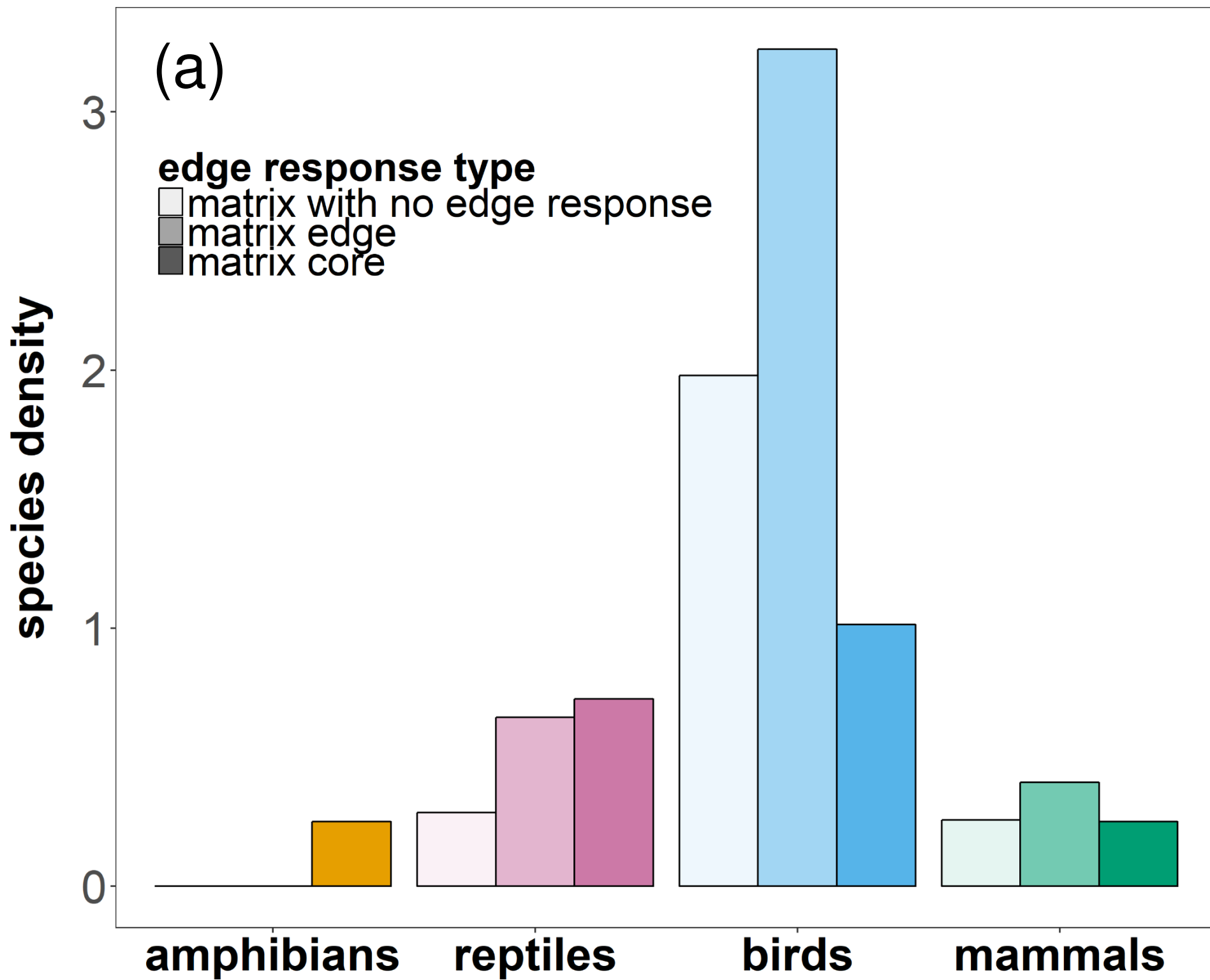
Taxon	<i>P</i>	Forest core species		Not forest core species	
		Not threatened	Threatened	Not threatened	Threatened
Amphibians	1.0	32	3	32	3
Birds	< 0.01	280	13	835	10
Mammals	< 0.05	92	21	120	11
Reptiles	1.0	9	0	37	1

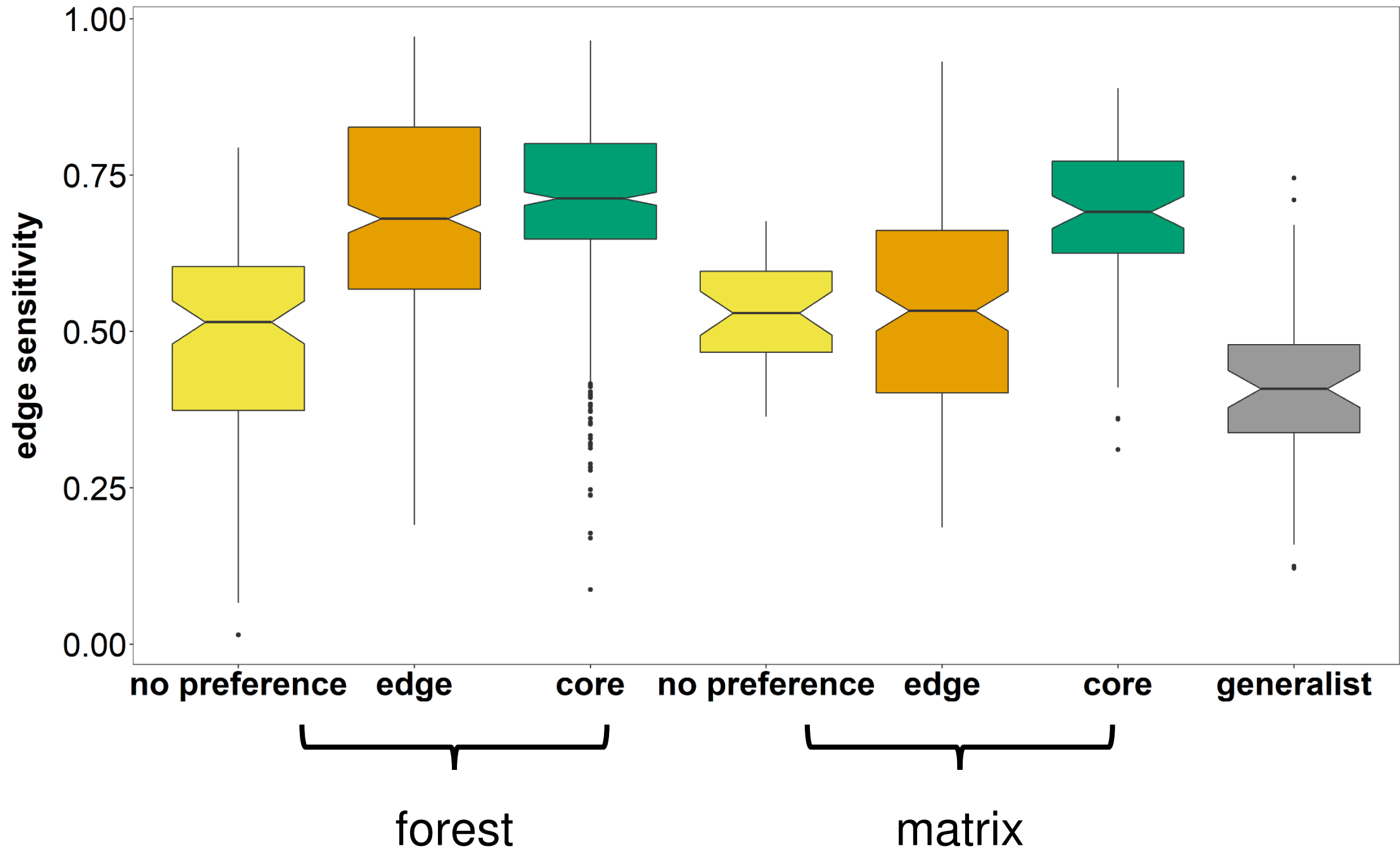
4a Predictors retained, Reptiles	I	Coeff	P	2.5%	97.5%
Body size	-	3.11	< 0.01	2.33	3.89
IUCN Tree	-	2.94	< 0.01	2.02	3.86
IUCN Habitats	-	2.53	< 0.01	1.88	3.17
Body size : IUCN Tree	-	-1.54	< 0.01	-2.04	-1.04
IUCN Habitats : Body size	-	-1.34	< 0.01	-1.69	-1.00

4b Predictors retained, Amphibians	I	Coeff	P	2.5%	97.5%
IUCN Habitats	1.00	0.03	0.73	-0.16	0.23
Body size	1.00	-0.02	0.77	-0.17	0.13
IUCN Forest	0.89	-0.36	0.07	-0.75	0.02
Body size: IUCN Habitats	0.56	-0.03	0.18	-0.07	0.01
Body size: IUCN Forest	0.45	-	L	-	-

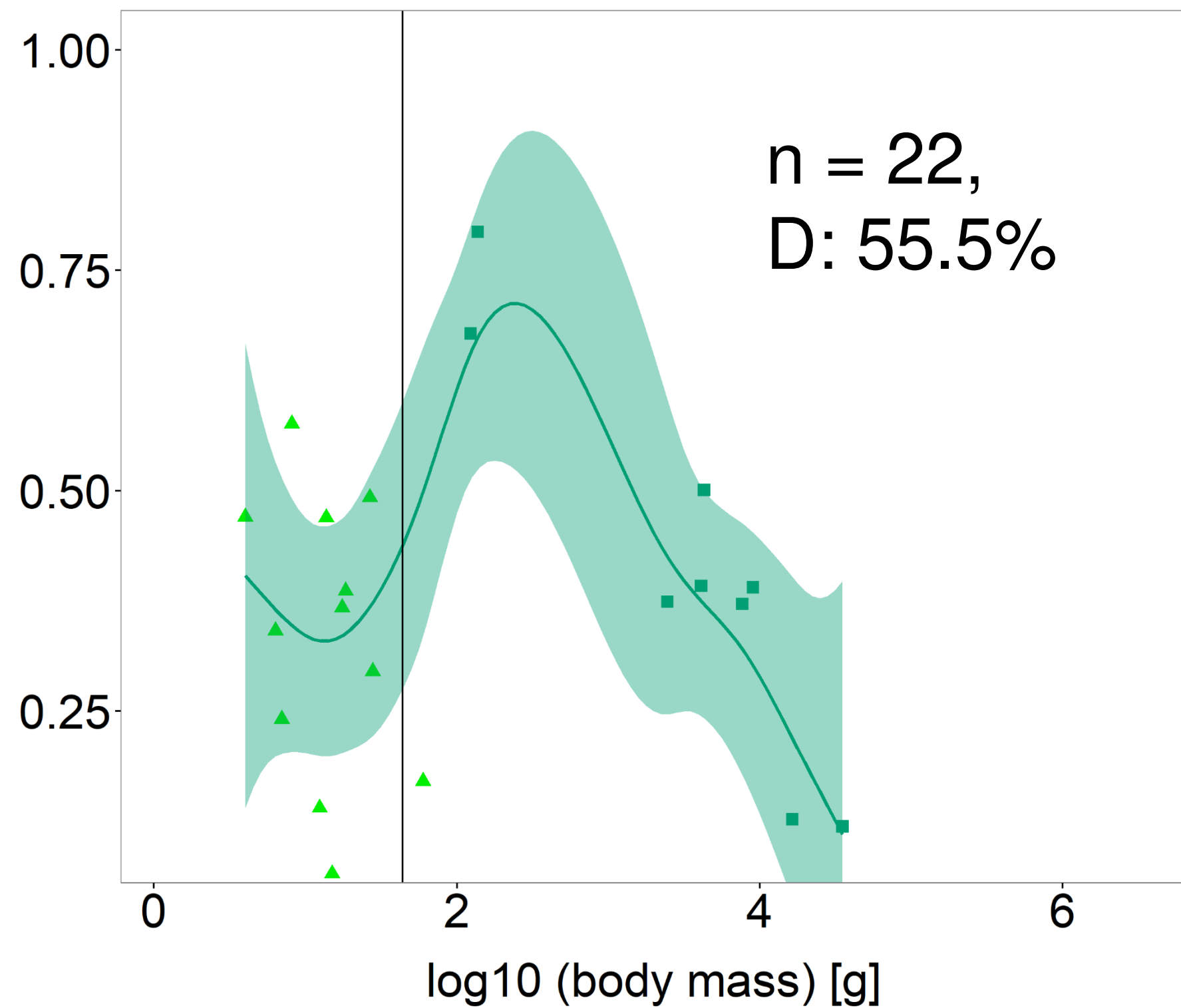
4c Predictors retained, Mammals	I	Coeff	P	2.5%	97.5%
Non-volant	1.00	0.20	< 0.001	0.10	0.30
IUCN Habitats	0.24	0.02	0.40	-0.03	0.07
IUCN Forest	0.23	-0.04	0.39	-0.14	0.06
(Body size) ²	0.13	-0.00	0.55	-0.01	0.00
IUCN Habitats : Non-volant	0.12	-0.04	0.16	-0.10	0.01
IUCN Forest : Non-volant	0.11	0.09	0.21	-0.05	0.23
Body size	0.11	-0.01	0.78	-0.04	0.03

4d Predictors retained, Birds	I	Coeff	P	2.5%	97.5%
IUCN Forest	0.51	-0.04	0.27	-0.10	0.03
IUCN Tree	0.29	0.00	0.97	-0.16	0.17
Body size	0.26	0.01	0.36	-0.02	0.04
Migrant = Full Migrant	0.16	0.13	0.10	-0.03	0.29
Migrant = Nomadic	-	0.06	0.70	-0.24	0.35
Migrant = Not migrating	-	0.13	0.08	-0.02	0.28
Range size	0.09	0.00	0.50	-0.00	0.00
IUCN Habitats	0.08	0.00	0.93	-0.02	0.02
Mean clutch	0.08	-0.01	0.55	-0.02	0.01
IUCN Forest : Full Migrant	0.07	0.05	0.45	-0.08	0.19
IUCN Forest : Full Nomadic	-	0.30	0.04	0.02	0.58
IUCN Forest : Body size	0.05	0.04	0.23	-0.02	0.10
IUCN Tree : Full Migrant	0.05	-0.12	0.45	-0.42	0.18
IUCN Tree : Nomadic	-	0.12	0.56	-0.27	0.51
IUCN Tree : Not migrating	-	-0.18	0.21	-0.46	0.10

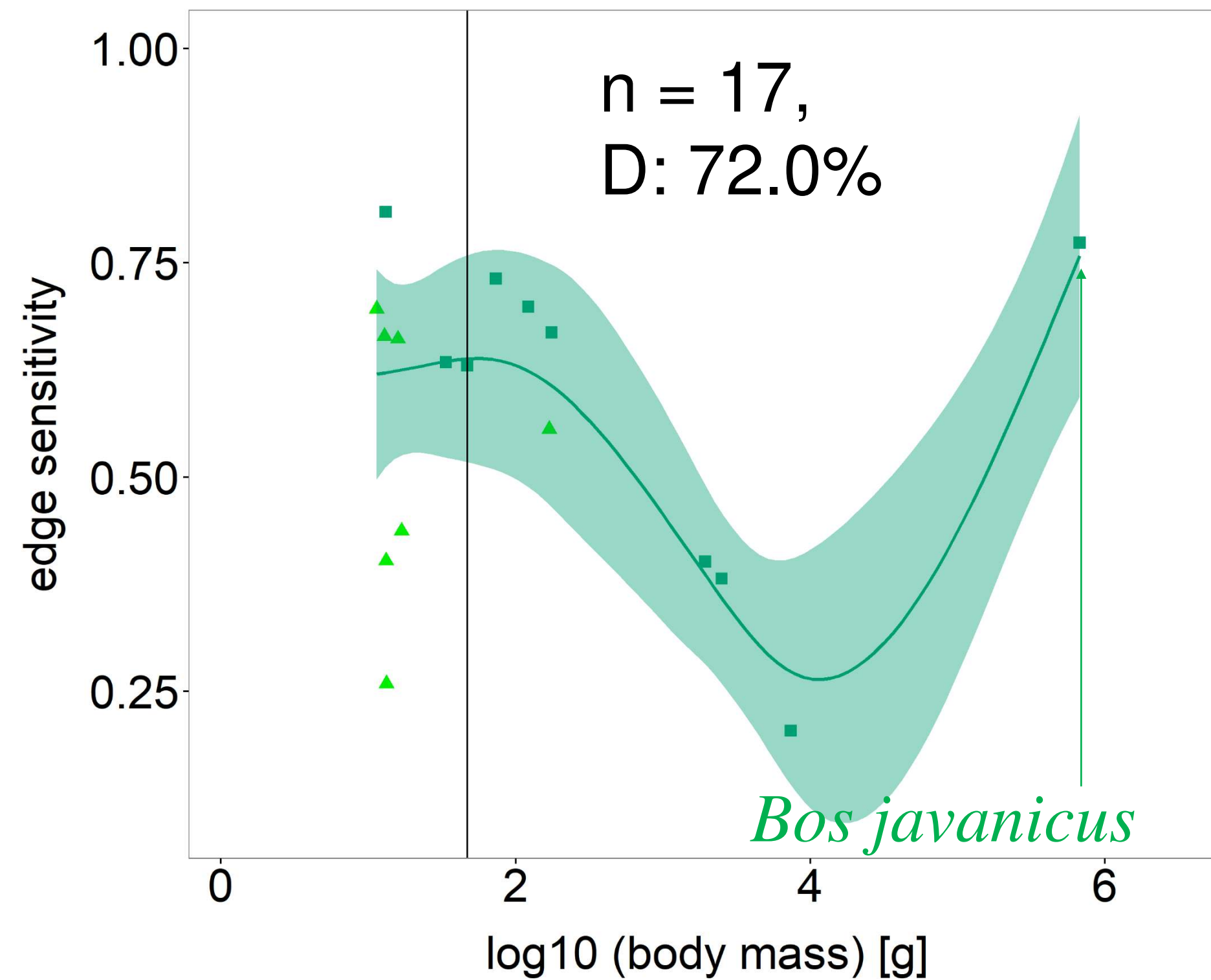




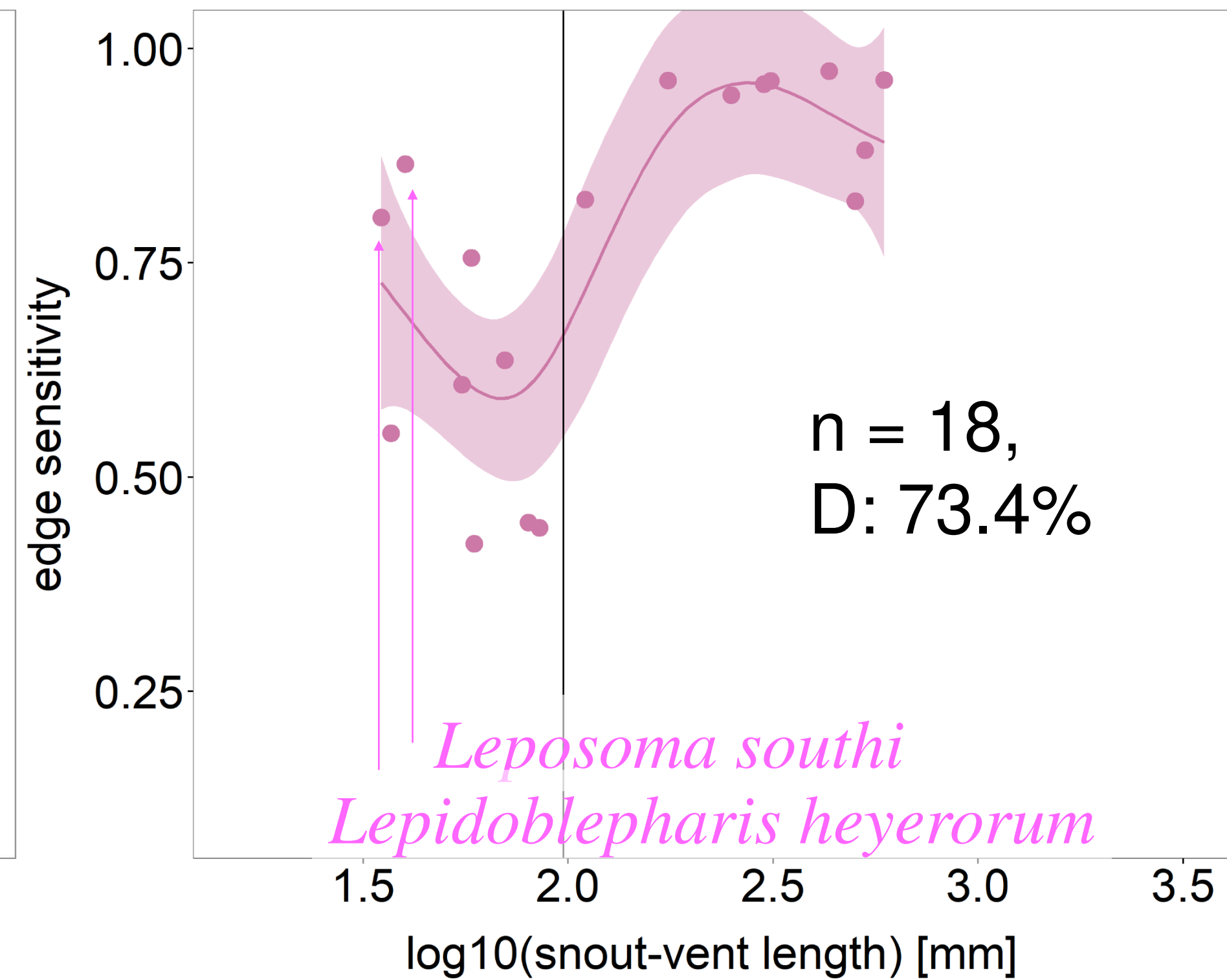
mammal, forest no preference



mammal, matrix edge



reptile, unknown



forest perforations



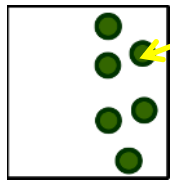
matrix edge



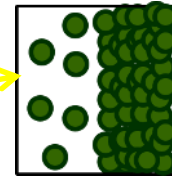
matrix



woodland/matrix edge



woodland/forest edge



forest core



forest edge



forest patches

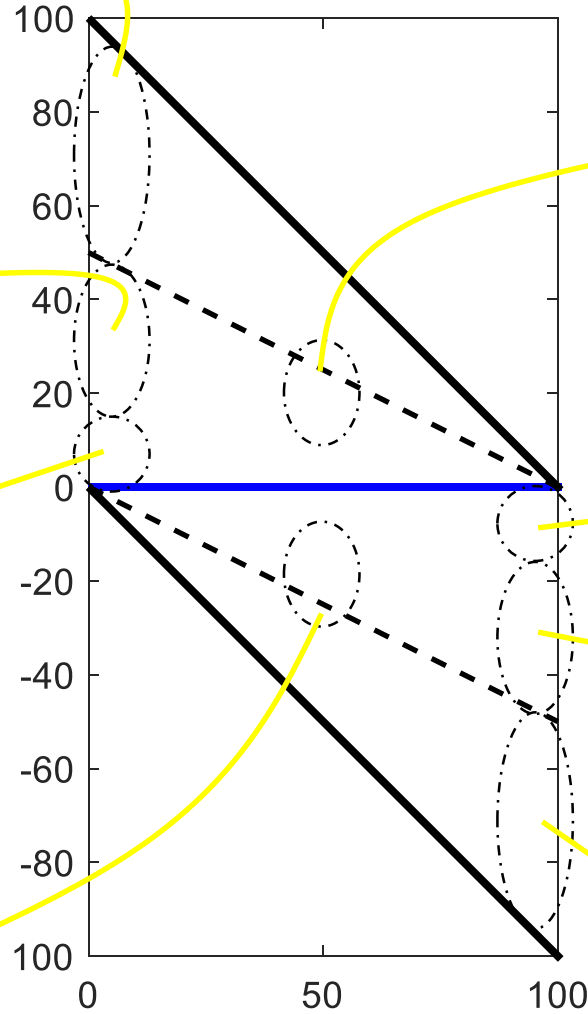


more trees around



Edge Influence

fewer trees around

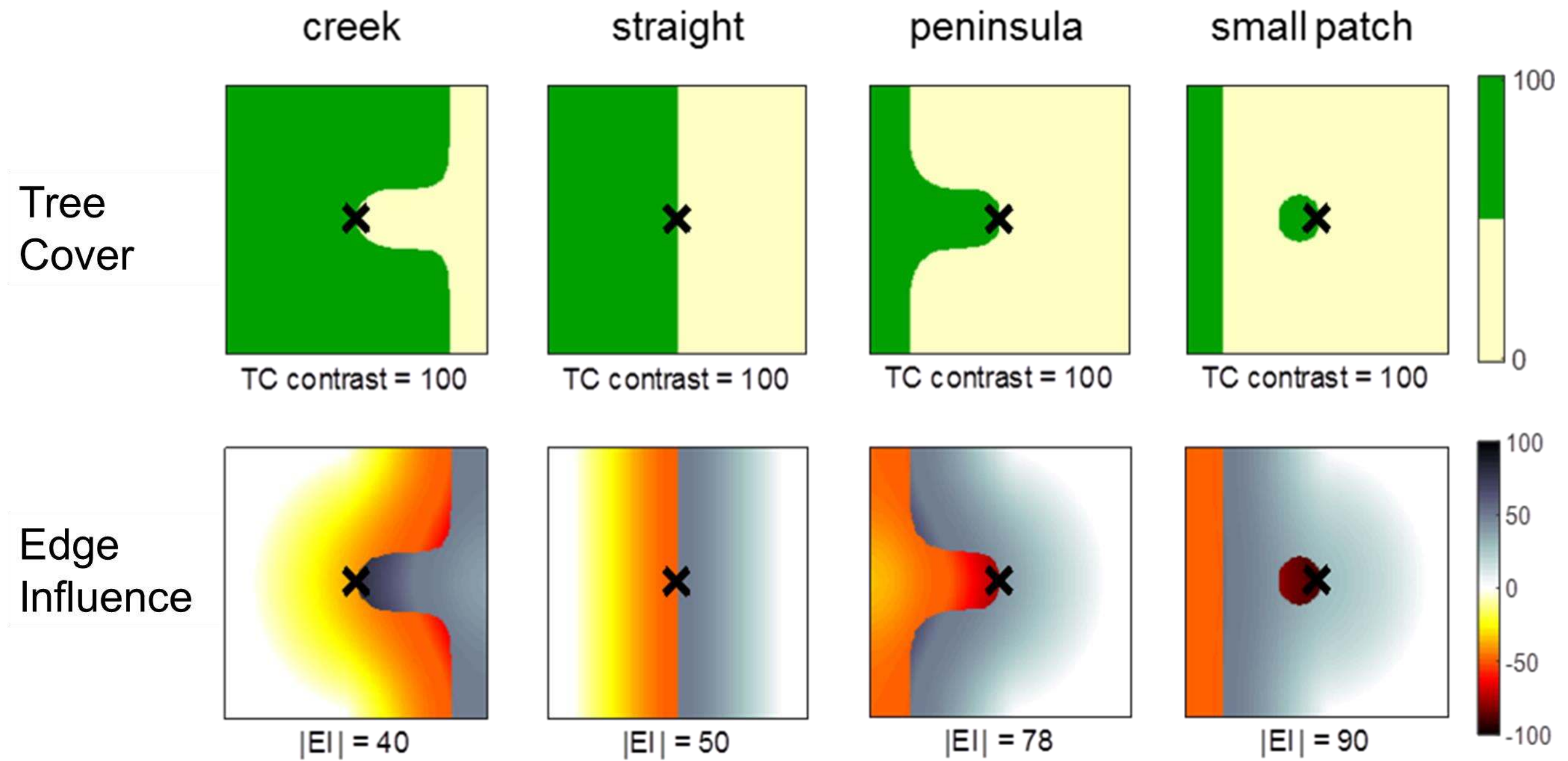


Point Tree Cover

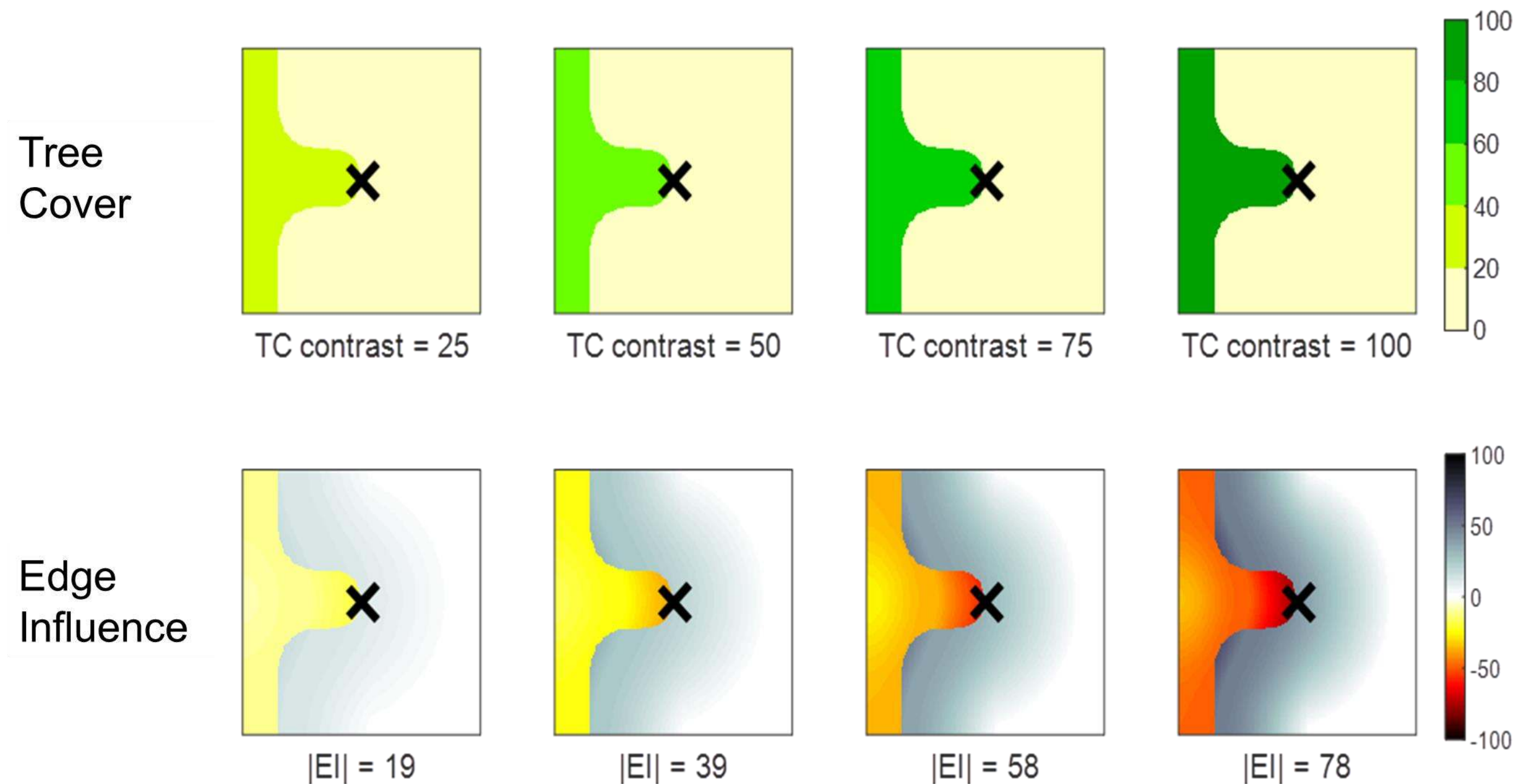


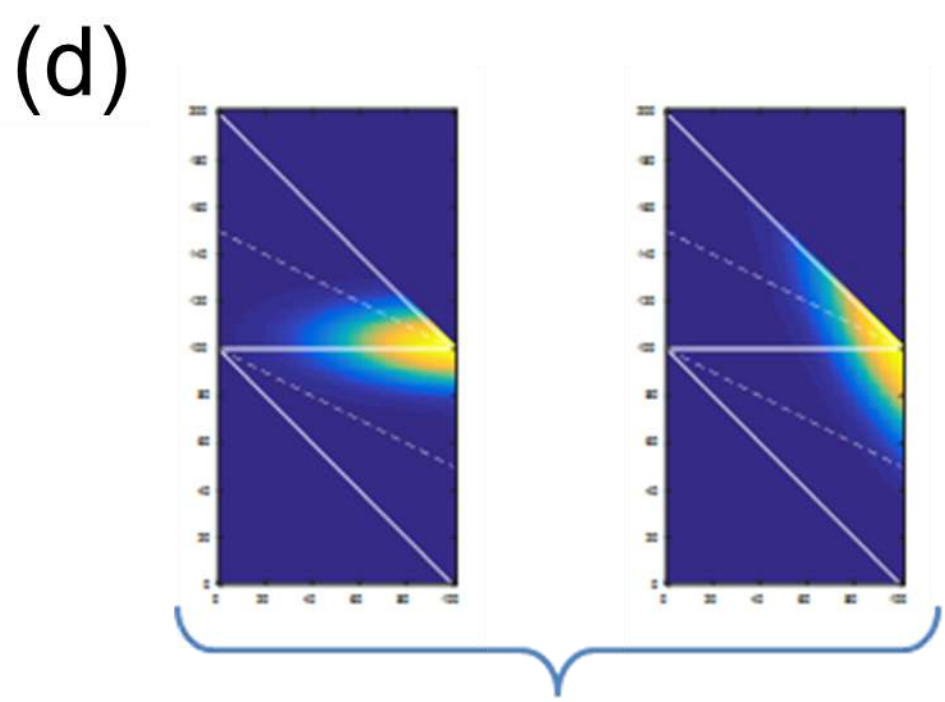
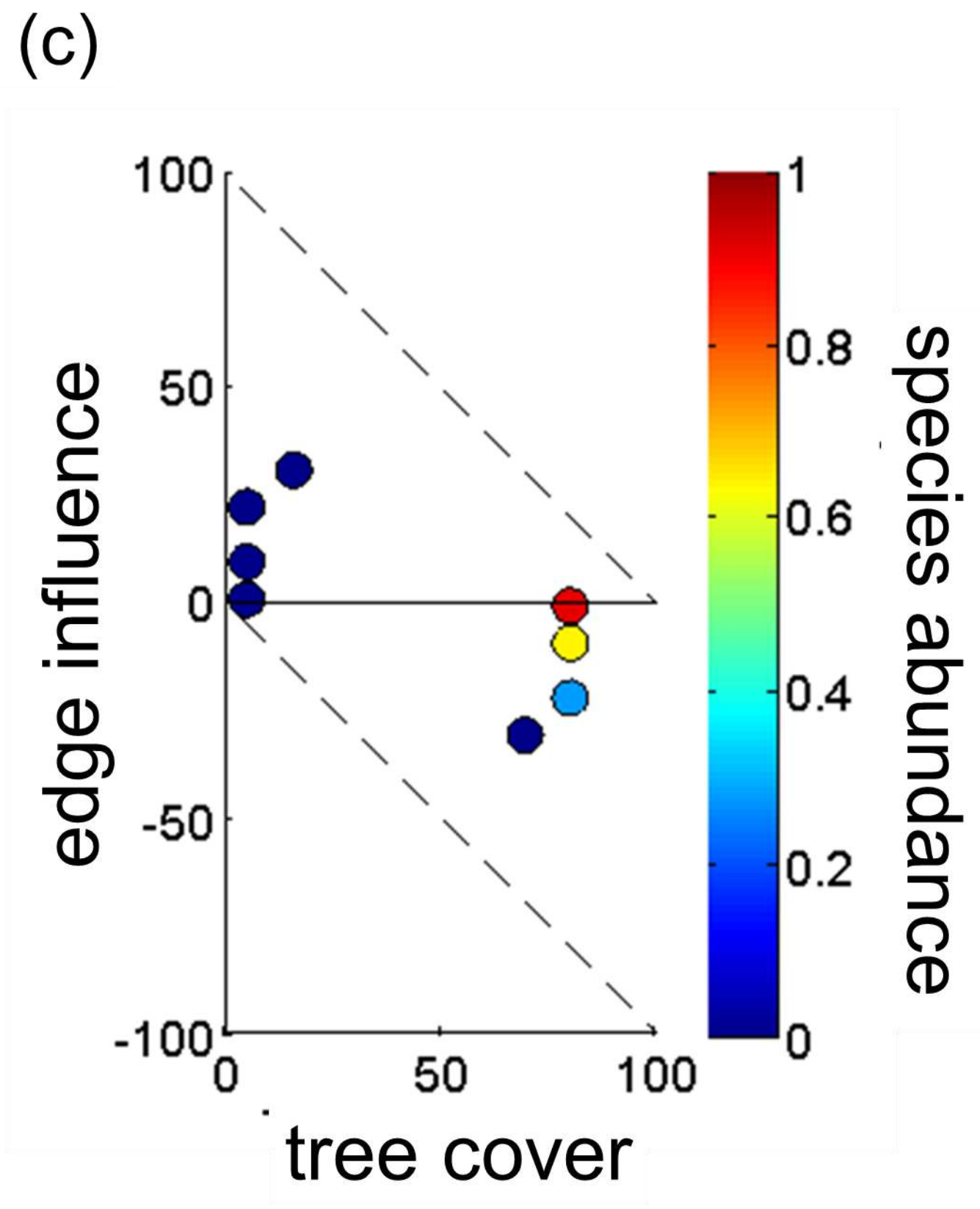
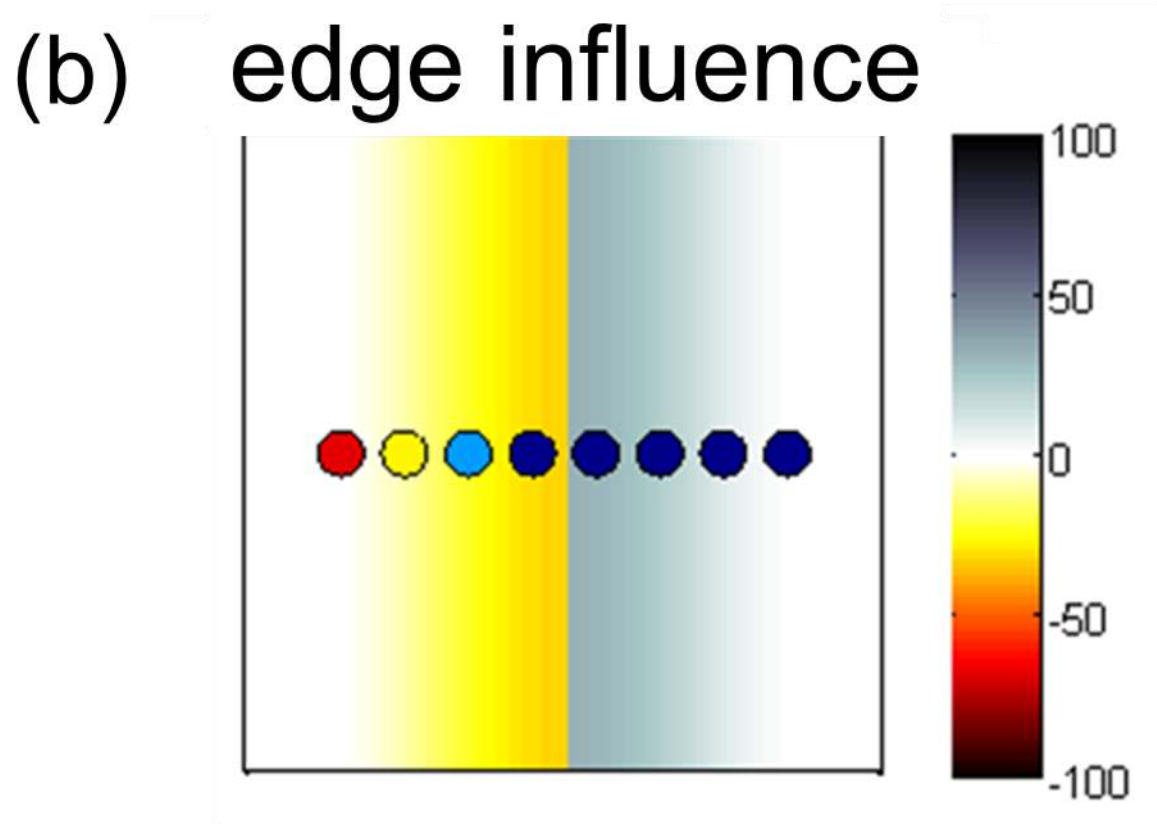
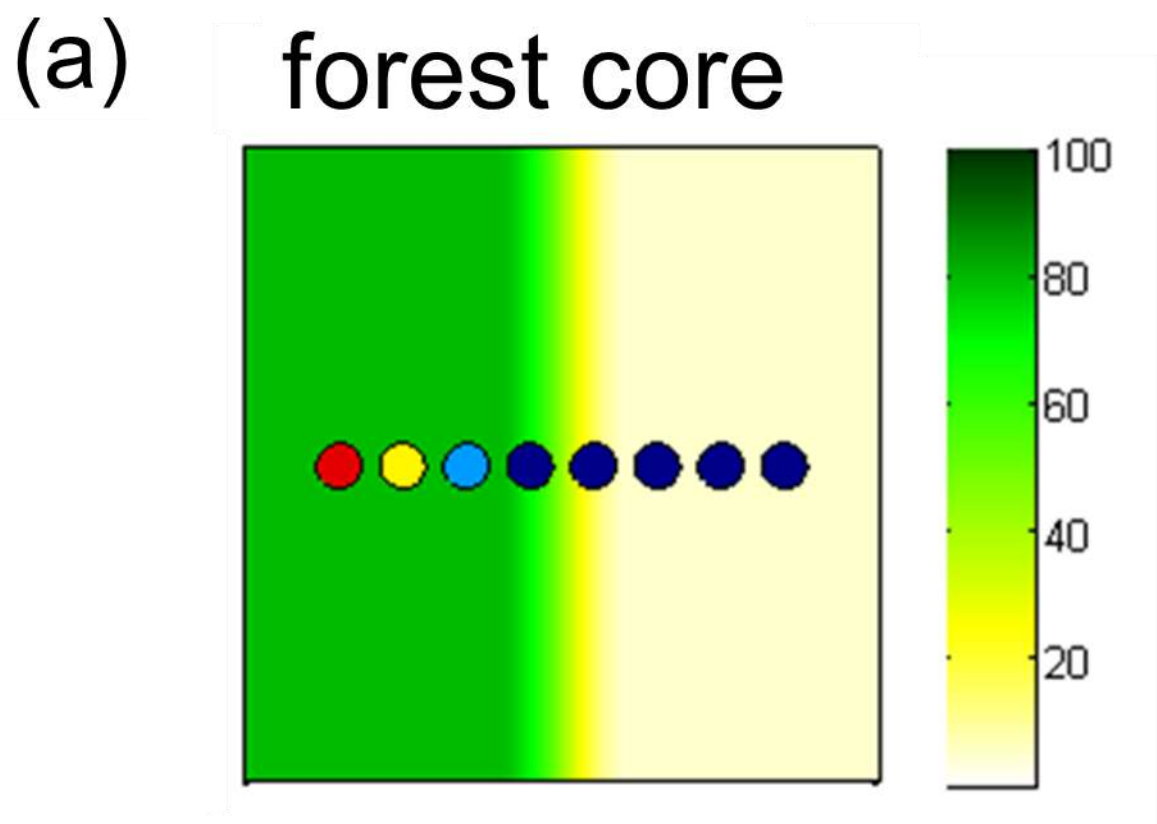
more trees (point)

(a) Landscape configuration & the amplitude of the Edge Influence

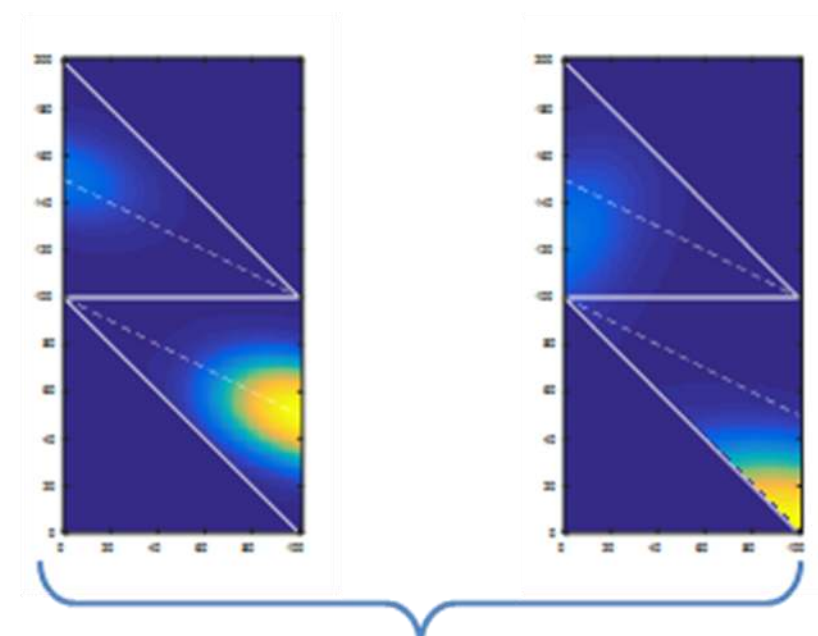


(b) Forest - matrix contrast & the amplitude of the Edge Influence

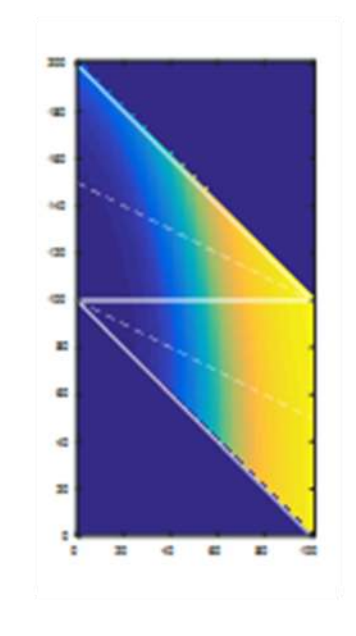




forest core



forest edge



forest no preference