

1 Title: Risks to pollinators from different land-use transitions: bee species' responses to
2 agricultural expansion show strong phylogenetic signal

3 Running title: Phylogenetic signal in bee sensitivity

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15

16 **Abstract**

17 Bee species worldwide are facing a future of further land-use change and
18 intensification. Populations of closely-related species with similar ecological
19 characteristics are likely to respond similarly to such pressures. Such phylogenetic
20 signal in species' responses could undermine the stability of pollination services in
21 agricultural and natural systems. We use abundance data from a global compilation of
22 bee assemblages in different land uses to assess the sensitivity of 573 bee species to
23 agricultural expansion, intensification and urbanization; and combine the results with the
24 Bee Tree of Life to assess phylogenetic signal. In addition, we assess whether variation
25 in species' sensitivity to land-use change is better explained by phylogenetic or
26 available functional trait differences. Bee species show strong phylogenetic signal in
27 sensitivity to agricultural land expansion but only a weak signal in sensitivity to
28 agricultural intensification and urbanisation. Sensitivities were usually best explained
29 by a combination of functional and phylogenetic distances. This finding suggests that
30 the commonly-recorded traits, despite being meaningful as functional response traits,
31 do not capture all important determinants of bee species' vulnerability or resistance.
32 However, it also suggests that model-based predictions of the sensitivity of poorly
33 known species may be sufficient to help guide conservation efforts.

34 **Keywords**

35 Land-use change, pollination services, correlates of risk, species decline,
36 conservation

37

38 **Introduction**

39 Land-use change is the most important driver of present-day terrestrial biodiversity
40 loss [1,2] and is predicted to cause continued damage in the future [3,4]. Most
41 scenarios incorporate further loss of natural and semi-natural land, driven by
42 agricultural expansion and urbanisation, as well as increased degradation due to
43 agricultural intensification [5]. The effect such global change will have on bee
44 populations could have serious consequences for crop pollination worldwide [6] and—
45 as bee species are the most important pollinators of flowering plants globally [7]—for
46 wild plant populations too [8].

47 Predicting likely effects of land-use change on ecosystem functions such as

48 pollination requires an understanding of whether and how species' sensitivities to land-
49 use change are shaped by their functional traits and evolutionary history [9,10]. Traits
50 are known to predict responses of European bee populations to land use and related
51 pressures, but associations are inconsistent [11–13]. In bumblebees, long-term
52 population declines in North America show phylogenetic signal (i.e., closer relatives
53 tend to show more similar trends) [14], as does their global conservation status as
54 assessed by the IUCN Red List [15], but information on other bees is limited. The
55 relative usefulness of phylogeny and available functional trait data in predicting
56 species' responses is an open question. Although phylogenetic relatedness is in this
57 context only a proxy for similarity of species' functional responses [16], it may
58 outperform functional trait data if responses are driven by a broader set of
59 (phylogenetically patterned) ecological differences than are captured by available trait
60 data.

61 A strong phylogenetic signal in species' responses to a particular pressure
62 increases the risk that the pressure could impact ecosystem functioning [16], as the
63 order of species losses can strongly influence pollination networks [17]. Phylogenetic
64 diversity and redundancy of bee communities may also decline; although debate is
65 ongoing [18,19], phylogenetic diversity can be important for ecosystem functioning and
66 stability [20]. The protection of phylogenetic diversity (by conserving those clades that
67 are most vulnerable) may also be important for maintaining robust pollination networks:
68 high phylogenetic diversity can correlate with interaction diversity [21], as closely-
69 related species also tend to share resources [22,23]. The strength of phylogenetic
70 signal can vary among pressures [e.g. 24], meaning that different land-use transitions
71 could carry different risks of pollination impairment that might not be apparent from the
72 effects on species diversity or overall abundance. Nonetheless, so far there has been
73 no exploration of the phylogenetic pattern of bee sensitivities to particular threats such
74 as agricultural expansion, agricultural intensification and urbanization.

75 Understanding which disturbances prompt the most phylogenetically patterned response
76 may therefore indicate where ecosystem services might be at greatest risk and so where
77 conservation action will be most important. However, it is unclear whether responses to
78 different pressures will all show phylogenetic signal [16] as the links between ecological
79 traits and the response to human impacts are not always straightforward [11,16]. We
80 use data from 86 studies and 2,599 sites to assess the sensitivity of 573 bee species
81 (from 96 genera) to human-dominated land uses, including agriculture and urban areas,
82 and to increasing agricultural intensity. We quantify the strength of phylogenetic signal

83 in these sensitivity estimates, accounting for uncertainty in sensitivities. Using trait data
84 for a subset of 143 bee species, we assess whether phylogenetic differences are better
85 able than functional traits to explain variation in species' sensitivities.

86 **Materials and methods**

87 Site-level data on bee abundance and occurrence were extracted from the PREDICTS
88 database [25] and De Palma et al. [26]. We refer to each survey of multiple sites that
89 used the same sampling method within the same season and the same country as a
90 'study'. Differences in sampling effort among sites within a study were corrected for
91 where necessary, assuming that recorded abundance increases linearly with sampling
92 effort [26]. Within each study, we recorded any blocked or split-plot design. See
93 Appendix Table S1.1 for a list of data sources (some containing multiple studies).

94 The major land use and land-use intensity at each site was recorded based on
95 information in the associated paper, supplementary files or other information provided
96 by the original authors, as described in [27]. Land use was classified as primary
97 vegetation, secondary vegetation, cropland, plantation forest, pasture or urban. The
98 use-intensity scale assesses human disturbance on a three-level qualitative scale within
99 each land use (minimal, light and intense) [28]. For instance, intensively-used cropland
100 includes monocultures with characteristic features of intensification (e.g., large fields,
101 high levels of external inputs, irrigation and mechanization); lightly-used cropland would
102 show some, but not all, or the same features; whereas minimally-used cropland would
103 include small mixed-cropping fields with little or no external input, irrigation or
104 mechanization.

105 *Species sensitivity*

106 We focus on four land-use transitions (Table 1). The first, with the largest sample size,
107 compares species abundances in natural/semi-natural land (i.e., primary or secondary
108 vegetation) with all human-dominated land uses combined (i.e., all other land-use
109 classes) as a recent synthesis showed that, in terms of species composition,
110 assemblages in human-dominated land uses are more similar to each other than to
111 those in natural or semi-natural land [3]. However, within this broad categorisation,
112 particular transitions may influence species in different ways, so we also explore
113 separately the impact of conversion to agricultural land, conversion to urban land, and
114 increases in agricultural intensity. The land-use classes within the dataset were

115 coarsened depending upon the land-use comparison of interest, allowing species
116 abundances to be compared between intact (natural and semi-natural) land uses and
117 converted (human-dominated, agricultural or urban, respectively) land uses, or with
118 increasing agricultural intensity (Table 1).

119 We define the Species Sensitivity Index (SSI) as the log-response ratio:

$$SSI = \ln\left(\frac{n_c}{n_i}\right)$$

120

121 where n_c is the mean abundance of the species in converted land uses, and n_i is the
122 mean abundance in intact land-uses. SSI was estimated as follows. For each species,
123 abundance was modelled statistically as a function of the land-use category (intact vs
124 converted) or agricultural intensity. Study identity was included as a factor to account
125 for among-study differences in methodology, sampling effort and biogeography. Study
126 identity would ideally be treated as a random variable, but many species were in too
127 few studies to accurately estimate random-effect variances [29] (~80% of species in
128 our dataset were represented in six or fewer studies). Bayesian generalized linear
129 models were used [with weakly informative default priors, as described in 30,
130 implemented in the arm package using the bayesglm function] with a Poisson error
131 structure unless overdispersion required use of a quasi-Poisson structure [31]. This
132 approach provides more realistic coefficient estimates and more conservative
133 standard errors than frequentist generalized linear models given that there can be
134 complete separation of the data (for example, when a species is always absent from
135 converted sites but always present in intact sites). The land-use coefficient (the log
136 response ratio) from the model was used as the estimate of SSI and the standard
137 error as its associated uncertainty.

138 In all further analyses, we use data for species that have abundance values in at
139 least six sites (three intact and three converted), aiming for a balance between
140 maximizing numbers of species and having sufficient data for each one. Repeating the
141 analyses with a more stringent threshold (at least 12 sites: six intact and six converted
142 site) produced qualitatively similar results, so we show results with the more lenient
143 threshold, which include more species.

144 *Phylogenetic tree*

145 We used the Bee Tree of Life [32], a recent phylogeny of over 1,300 bee species from

146 around the world, after rate-smoothing using PATHd8 [a computationally efficient method
147 for large phylogenetic trees 33] with the root age constrained to one. Of the species
148 present in our dataset, 141 were also in the phylogeny. Although there was no difference
149 in mean SSI between these and the species absent from the phylogeny (two-tailed t-test:
150 $t_{1,245.0} = -0.33$, n.s.), the latter tended to have higher uncertainty in SSI (two tailed t-test:
151 $t_{1,230.1} = -4.29$, $p < 0.001$). Because of this non-randomness, we used the *pastis* package
152 in R [a birth-death polytomy resolver, 34] to estimate—1000 times—possible placements
153 for missing species, given their taxonomic affinities [35], to produce 1000 complete trees.
154 See Appendix S2 for full details. Birth-death polytomy resolvers can bias trait-based
155 analyses [36], so we perform all analyses on the rate-smoothed incomplete tree of 141
156 species as well as the 1000 complete trees.

157 *Phylogenetic analyses*

158 Phylogenetic signal was quantified using Pagel's [37] λ , which produces reliable
159 estimates when sample sizes are large [38], as here. We used the implementation in
160 the R package *phytools* [39,40], which accommodates uncertainty in the SSI estimates,
161 though we also estimated λ without accounting for uncertainty in species sensitivity, for
162 comparison. As bumblebees (*Bombus*) may respond differently from other species to
163 human impacts [14,41,42], which could drive phylogenetic signal in the overall dataset,
164 we also estimated λ for both bumblebees alone and all other species.

165 We used 'traitgrams' [43] to assess the relative power of phylogenetic and functional
166 distances to explain variation in SSI. Phylogenetic and functional distances were
167 combined into a single set of Euclidean distances [43] according to:

168

$$FPDist = \sqrt{(aPDist^2 + (1 - a)FDist^2)}$$

169 where *PDist* is the phylogenetic (cophenetic) species distance [*pez* package: 47], *FDist*
170 is the trait pairwise distance [Gower's dissimilarity with transformation to provide
171 Euclidean properties: 48,49], and *a* governs the relative weighting of *FDist* and *PDist* in
172 *FPDist*. Setting $a = 0$ computes functional diversity and $a = 1$ computes phylogenetic
173 diversity. We calculated 11 distance matrices using *a* values spaced evenly from 0 to 1,
174 and compared their explanatory power to find which best explained our data in
175 distance-based generalised linear models [*dbstats* package, 47,48] weighted by the
176 inverse squared standard errors of the SSI. We also modelled SSI as a function of a
177 randomly-generated distance matrix (with original values drawn from a normal distribution)

178 as a null model. Models were compared using an adapted version of Akaike's Information
179 Criterion (AIC) [47,48]. We calculated models' pseudo R^2 as: $1 - \left(\frac{\text{Residual deviance}}{\text{Null deviance}}\right)$.

180 Ecological trait data were collated for 556 of the species in our dataset by SPMR,
181 MK and EF by assessing peer-reviewed and grey literature and by measuring available
182 museum specimens. Traits included inter-tegular distance (ITD) [a proxy for foraging
183 range, 52], flight season duration, dietary breadth, nesting strategy, and reproductive
184 phenology and strategy [11], and are generally phylogenetically conserved (see
185 Appendix Table S3.2). However, because data for the complete set of seven traits were
186 available for only 75 species in both our data set and the original phylogeny, we re-ran
187 this analysis using a reduced set of traits (ITD, nesting strategy and reproductive
188 strategy), enabling inclusion of 143 species. We also repeated the analysis using the
189 completed trees (259 species with data for all traits; 537 species with the minimal set).

190 **Results**

191 *SSI values*

192 Species' sensitivities to different land-use transitions were relatively normally
193 distributed (see Fig 1), with wide variation in species responses. For the comparison
194 between natural and human-dominated land-uses, for instance, 40 species had $SSI < -$
195 2 and 28 species had $SSI > 2$; 82 species had SSI estimates that were significantly
196 non-zero (44 negative, 38 positive; coloured lines on Fig 1).

197

198 *Phylogenetic signal*

199 The strength of phylogenetic signal in SSI differed among land-use comparisons (Fig.
200 2a). The strongest signal was in comparisons between (semi-)natural and human-
201 dominated land uses, with high and significantly non-zero λ values for all but one of the
202 completed phylogenetic trees ($p < 0.05$; Fig. 2a and Fig. 3). SSIs comparing semi-
203 natural and natural land to agriculture showed λ values nearly as high: λ was
204 significantly non-zero for the rate-smoothed tree ($\lambda = 0.59$, $p < 0.05$), and for >99% of
205 the completed trees. The signal in sensitivity to urbanization and to increasing
206 agricultural intensity depended on which phylogeny was used, being very low except
207 with the completed trees (Fig. 2a). Weighting the analyses by the standard error of
208 species sensitivity was extremely important: λ values were always low when standard

209 errors were not accounted for (Fig. 2b).

210 There was no significant phylogenetic signal within the bumblebees. Phylogenetic
211 signal was also lower among non-bumblebees, particularly when assessing species'
212 sensitivity to all human-dominated land-uses, and particularly when analyzing only the
213 species in the rate-smoothed tree (Table 2); analyses using the complete phylogenies
214 often found significant, albeit reduced, phylogenetic signal in non-bumblebees for both
215 agricultural expansion and loss of natural vegetation (Table 2).

216

217 *Relative importance of traits and phylogeny*

218 Species' sensitivities to human-dominated land uses were best explained by a
219 combination of both phylogeny and functional distances: this was true when using the
220 rate-smoothed tree and across the completed trees (with $\alpha \geq 0.7$ producing the highest
221 AIC weights and high R^2 values; Figure 4 and Appendix Figure S5.1). However,
222 phylogenetic distance was more important than functional distances for transitions
223 whose SSIs showed higher phylogenetic signal (i.e., sensitivity to human dominated
224 land and agricultural land), whereas sensitivity to agricultural intensification seemed to
225 be more strongly influenced by functional distances ($\alpha < 0.4$ had the highest AIC
226 weights and R^2 values; Figure 4 and Appendix Figure S5.1).

227

228 **Discussion**

229

230 Bee species show strong heterogeneity in their responses to land-use practices with, in
231 our data set, roughly as many 'winners' (positive SSI) as 'losers' (negative SSI) (Fig 1).
232 This is in line with the wide range of responses reported in the literature (e.g.,
233 urbanization has been reported as having positive [50,51], neutral [52] and negative
234 [50,51,53] effects on bee populations). Clearly many bee species are able to benefit
235 from the environmental changes (potentially including removal of competitors: [54]),
236 while others struggle to persist.

237 The strong phylogenetic signal ($\lambda \sim 0.7$) seen in species' responses to human-
238 dominated land uses is not surprising: SSI estimates a species' susceptibility to one
239 particular driver (land-use change), which will be mediated by functional response traits
240 [11,12,55,56] that are often phylogenetically conserved [57] (though estimated
241 responses will also be influenced by the contexts of individual studies, probably
242 reducing the phylogenetic signal).

243 The different focused land-use comparisons find different degrees of phylogenetic
244 signal in species' responses (Fig 2), with conversion to agriculture and urbanization
245 producing moderately strong signal ($\lambda \sim 0.6$, except for the analysis of urbanization
246 using the rate-smoothed tree, where sample size is small) while agricultural
247 intensification elicits negligible signal ($\lambda \sim 0$). Accounting for measurement error was
248 crucial for estimating phylogenetic signal strength; omitting it led to much lower estimates
249 of λ (Fig 2), as expected [39], though results were consistent. Results were also not
250 strongly driven by bumblebees; clustering of sensitivity was seen throughout the tree.

251 Why does agricultural intensification not produce a stronger phylogenetic signal? We
252 consider three possible biological explanations. First, species' responses to agricultural
253 intensity may be mediated by features of landscapes—not considered in our models—
254 more than by features of sites. Field diversity and landscape composition, for example,
255 have been shown to shape the biotic effects of agricultural intensity [58]; because such
256 attributes are not recorded in the PREDICTS database, we were not able to consider
257 them, perhaps causing responses to appear idiosyncratic. Second, the low-intensity
258 agricultural habitats to which higher-intensity agriculture is compared may have already
259 filtered out the most vulnerable native bee species (i.e., those with the most negative
260 SSI values), and perhaps had synanthropic (i.e., SSI > 0) non-natives added, by the
261 original conversion from natural to agricultural land. Such SSI-biased turnover of
262 species would tend to erode SSI's phylogenetic signal. This explanation—that the initial
263 conversion of a landscape to an 'anthrome' [59] leaves a strong phylogenetic signal
264 whereas subsequent intensification of use does not—requires that much the same
265 traits mediate responses to agricultural expansion and agricultural intensification. Such
266 trait-based extinction filters are likely why mammalian extinction risk shows no
267 phylogenetic signal in regions with a long history of intense human activity [60]. If this
268 explanation is correct, then even though low-intensity agricultural practices score better
269 than more intensive systems for community-level measures of bee biodiversity [35,58],
270 they may have already altered community composition irreversibly [42]. The third
271 possibility is that the ability of species to persist in the face of agricultural
272 intensification depends most strongly on traits that are not phylogenetically conserved.
273 For instance, we found no strong phylogenetic signal in diet breadth (Appendix Table
274 3.2). Diet breadth can be flexible for some species (e.g. *Bombus terrestris* can increase
275 diet breadth when faced with increased resource competition [61]), but on the other
276 hand, even generalist species can have rigid host-plant preferences [62]. A fourth, non-

277 biological, explanation for the lack of phylogenetic signal in responses to agricultural
278 intensification is that our use-intensity criteria mix multiple pressures (e.g. pesticide
279 and fertilizer use); each component might on its own elicit phylogenetically patterned
280 responses, but the signal may be lost by mixing them.

281 Although SSI values usually showed phylogenetic signal, in the subset of bee species
282 with available trait information, SSIs were generally better explained by a combination of
283 both phylogenetic and trait distances [43], highlighting the added value of ecological
284 trait data for species. These results are in line with previous analyses revealing that
285 functional traits can significantly influence species sensitivities to a number of land
286 uses and land-use practices in a variety of systems [11,12,55]. However, such trait-
287 environment relationships can have low explanatory power and results across studies
288 can be contradictory [13]. Taken with our results, this suggests that species'
289 sensitivities may be influenced by ecological differences that are not fully captured by
290 the commonly measured traits, while phylogeny may provide a closer approximation to
291 these unmeasured characteristics [63]. For instance, the phylogenetic relatedness of
292 bee species can inform the structure of plant-pollinator networks [23,64]; as ecological
293 interactions are lost more quickly than species from a system [65], a given species'
294 network could have a strong influence on its resilience to disturbances. Responses to
295 agricultural intensification do not fit this model: trait differences explained some
296 variation in SSI but phylogenetic distance did not. This combination of results is
297 consistent with the suggestion that trait-mediated competition may underlie the
298 responses [66].

299 Although the importance of traits in mediating species' sensitivities to land-use
300 changes is congruent with previous work [12], our dataset may not be representative; it
301 is therefore possible that a more complete set of species with trait data would change the
302 relative importance of traits and phylogeny. The species in our dataset capture
303 significantly less phylogenetic diversity than expected from a random selection of
304 species from the Bee Tree of Life (see Appendix 6). Local assemblages are often a non-
305 random subset of the global phylogeny [67,68]; our analyses focus on such assemblages
306 and so this is, in part, an inescapable consequence of our study's objectives.

307 The strong phylogenetic signal in bee species' sensitivities to human-dominated land
308 uses like agriculture means that losses of diversity are likely to be concentrated within a
309 subset of clades, where they will be correspondingly more severe; likewise, any gains in
310 diversity will be restricted to groups of related species. Clustering of losses can greatly

311 reduce the phylogenetic and functional diversity of a system [16], potentially
312 jeopardizing its ability to function under environmental change [20]. Crop pollination may
313 be more robust than other ecosystem functions to species losses as a few dominant
314 species are the main contributors at local scales [69]. However, higher species diversity
315 may be necessary at larger spatial scales [70]. Furthermore, some wild plant species
316 require specialist pollinators, potentially meaning that they face a double threat from
317 conversion of land to agriculture: directly, through loss of habitat, and indirectly, through
318 the decline in their pollinators.

319 Our results suggest that the phylogenetic risk assessment framework set out by
320 Díaz et al. [16] could inform management practices and highlight gaps in knowledge.
321 Even though bees are well studied relative to many other invertebrate groups, there are
322 still uncertainties about their current status and vulnerability to human impacts [71] as
323 well as gaps in trait data. The strong phylogenetic patterning in species' sensitivities to
324 agricultural expansion could help to predict the sensitivity of understudied species,
325 identifying those that are most vulnerable or resistant to guide conservation planning
326 [72,73]. For instance, many species of bumblebees showed positive or neutral
327 responses to agricultural land, but negative responses to increased agricultural
328 intensity (Appendix Figure S4.2 and S4.4); this combination of results suggests that
329 agricultural production can support many species of bumblebees, but only if intensity is
330 low. However, our estimate of sensitivity to particular pressures—SSI—does not
331 necessarily indicate the conservation status of a species, which is a product of both
332 sensitivity to combined pressures and exposure to those pressures. This may explain
333 why we found no phylogenetic signal in bumblebee SSIs, even though extinction risk in
334 these species is significantly non-random [15]. Phylogenetically patterned responses
335 may also open opportunities to monitor bee communities at higher taxonomic levels
336 [74–76]: this would reduce the need for species identification by expert taxonomists
337 and the need for destructive sampling of bees [77,78], save time and money, and
338 facilitate citizen science.

339 Our results provide a basis from which to make, test, and inform predictions about
340 bee species' sensitivities to land-use change, with potentially important benefits for
341 monitoring and conservation prioritization, as well as identifying land-use pressures that
342 may most affect pollination services to crops and wild species. Analyses of how these
343 results scale up to changes in abundance-weighted phylogenetic diversity of
344 communities are necessary to identify spatial patterns in diversity and potential areas of

345 pollination deficit [35,79].

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357 **Author Contributions**

358 ADP and AP conceived the study. ADP carried out statistical analyses and wrote the first
359 draft of the manuscript. MK assessed species taxonomy. EF, MK, SPMR and SP collated
360 trait data. WP provided guidance on phylogenetic analyses. All authors contributed
361 significantly to revisions of the manuscript. All authors gave final approval for publication.

362 **References**

- 363 1. Maxwell SL, Fuller RA, Brooks TM, Watson JEM. 2016 Biodiversity: The ravages of
364 guns, nets and bulldozers. *Nature* **536**, 143–145. (doi:10.1038/536143a)
- 365 2. WWF. 2016 Living Planet Report 2016 Risk and resilience in a new era.
- 366 3. Newbold T *et al.* 2015 Global effects of land use on local terrestrial biodiversity.
367 *Nature* **520**, 45–50. (doi:10.1038/nature14324)
- 368 4. Pereira HM *et al.* 2010 Scenarios for global biodiversity in the 21st century. *Science*
369 **330**, 1496–501. (doi:10.1126/science.1196624)
- 370 5. Hurtt GC *et al.* 2011 Harmonization of land-use scenarios for the period 1500-2100:
371 600 years of global gridded annual land-use transitions, wood harvest, and resulting
372 secondary lands. *Clim. Change* **109**, 117–161. (doi:10.1007/s10584-011-0153-2)
- 373 6. Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham S a, Kremen C,
374 Tschamntke T. 2007 Importance of pollinators in changing landscapes for world crops.
375 *Proc. Biol. Sci.* **274**, 303–13. (doi:10.1098/rspb.2006.3721)
- 376 7. Danforth BN, Sipes S, Fang J, Brady SG. 2006 The history of early bee diversification
377 based on five genes plus morphology. *Proc. Natl. Acad. Sci. U. S. A.* **103**, 15118–
378 15123. (doi:10.1073/pnas.0604033103)
- 379 8. Ollerton J, Winfree R, Tarrant S. 2011 How many flowering plants are pollinated by
380 animals? *Oikos* **120**, 321–326. (doi:10.1111/j.1600-0706.2010.18644.x)
- 381 9. Suding KN *et al.* 2008 Scaling environmental change through the community-level: a
382 trait-based response-and-effect framework for plants. *Glob. Chang. Biol.* **14**, 1125–

- 383 1140. (doi:10.1111/j.1365-2486.2008.01557.x)
- 384 10. D\`iaz S *et al.* 2013 Functional traits, the phylogeny of function, and ecosystem
385 service vulnerability. *Ecol. Evol.* **3**, 2958–2975. (doi:10.1002/ece3.601)
- 386 11. De Palma A, Kuhlmann M, Roberts SPM, Potts SG, Börger L, Hudson LN, Lysenko I,
387 Newbold T, Purvis A. 2015 Ecological traits affect the sensitivity of bees to land-use
388 pressures in European agricultural landscapes. *J. Appl. Ecol.* **52**, 1567–1577.
389 (doi:10.1111/1365-2664.12524)
- 390 12. Rader R, Bartomeus I, Tylianakis JM, Laliberté E. 2014 The winners and losers of
391 land use intensification: pollinator community disassembly is non-random and alters
392 functional diversity. *Divers. Distrib.* **20**, 908–917. (doi:10.1111/ddi.12221)
- 393 13. Bartomeus I, Cariveau DP, Harrison T, Winfree R. 2017 On the inconsistency of
394 pollinator species traits for predicting either response to land-use change or functional
395 contribution. *Oikos*, doi: 10.1111/oik.04507. (doi:10.1111/oik.04507)
- 396 14. Bartomeus I, Ascher JS, Gibbs J, Danforth BN, Wagner DL, Hedtke SM, Winfree R.
397 2013 Historical changes in northeastern US bee pollinators related to shared
398 ecological traits. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 4656–60.
399 (doi:10.1073/pnas.1218503110)
- 400 15. Arbetman MP, Gleiser G, Morales CL, Williams P, Aizen MA. 2017 Global decline of
401 bumblebees is phylogenetically structured and inversely related to species range size
402 and pathogen incidence. *Proceedings. Biol. Sci.* **284**, 20170204.
403 (doi:10.1098/rspb.2017.0204)
- 404 16. D\`iaz S *et al.* 2013 Functional traits, the phylogeny of function, and ecosystem
405 service vulnerability. *Ecol. Evol.* **3**, 2958–2975. (doi:10.1002/ece3.601)
- 406 17. Kaiser-Bunbury CN, Muff S, Memmott J, Müller CB, Caflisch A. 2010 The robustness
407 of pollination networks to the loss of species and interactions: a quantitative approach
408 incorporating pollinator behaviour. *Ecol. Lett.* **13**, 442–452. (doi:10.1111/j.1461-
409 0248.2009.01437.x)
- 410 18. Cardinale BJ *et al.* 2015 Further re-analyses looking for effects of phylogenetic
411 diversity on community biomass and stability. *Funct. Ecol.* (doi:10.1111/1365-
412 2435.12540)
- 413 19. Cadotte MW, Livingstone SW, Yasui S-LE, Dinnage RD, Li J-T, Marushia R,
414 Santangelo J, Shu W. 2017 Explaining ecosystem multifunction with evolutionary
415 models. *Ecology* **98**, 3175–3187. (doi:10.1002/ecy.2045)
- 416 20. Cadotte MW, Dinnage R, Tilman D. 2012 Phylogenetic diversity promotes ecosystem
417 stability. *Ecology* **93**, S223–S233. (doi:10.1890/11-0426.1)
- 418 21. Miranda M, Parrini F. 2015 Congruence between species phylogenetic and trophic
419 distinctiveness. *Biodivers. Conserv. Conserv.* **24**, 355–369. (doi:10.1007/s10531-014-
420 0813-4)
- 421 22. Naisbit RE, Rohr RP, Rossberg a. G, Kehrl P, Bersier L-F. 2012 Phylogeny versus
422 body size as determinants of food web structure. *Proc. R. Soc. B Biol. Sci.* **279**, 3291–
423 3297. (doi:10.1098/rspb.2012.0327)
- 424 23. Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J. 2007 Non-
425 random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**,
426 925–928. (doi:10.1038/nature05956)
- 427 24. Fritz SA, Purvis A. 2010 Selectivity in mammalian extinction risk and threat types: a
428 new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* **24**, 1042–
429 1051. (doi:10.1111/j.1523-1739.2010.01455.x)
- 430 25. Hudson LN *et al.* 2017 The database of the PREDICTS (Projecting Responses of
431 Ecological Diversity In Changing Terrestrial Systems) project. *Ecol. Evol.* **7**, 145–188.
432 (doi:10.1002/ece3.2579)
- 433 26. De Palma A *et al.* 2016 Predicting bee community responses to land-use changes:
434 Effects of geographic and taxonomic biases. *Sci. Rep.* **6**, 31153.
435 (doi:10.1038/srep31153)
- 436 27. Hudson LN *et al.* 2014 The PREDICTS database: a global database of how local
437 terrestrial biodiversity responds to human impacts. *Ecol. Evol.* **4**, 4701–4735.

- 438 (doi:10.1002/ece3.1303)
- 439 28. Hudson LN *et al.* 2014 The PREDICTS database: a global database of how local
440 terrestrial biodiversity responds to human impacts. *Ecol. Evol.* **4**, 4701–4735.
441 (doi:10.1002/ece3.1303)
- 442 29. Fox GA, Negrete-Yankelevich S, Sosa VS. 2015 *Ecological Statistics: Contemporary*
443 *Theory and Application*. Oxford: Oxford University Press.
- 444 30. Gelman A, Jakulin A, Pittau MG, Su Y-S. 2008 A weakly informative default prior
445 distribution for logistic and other regression models. *Ann. Appl. Stat.* **2**, 1360–1383.
446 (doi:10.1214/08-AOAS191)
- 447 31. Crawley MJJ. 2007 *The R book*. Chichester: John Wiley & Sons Ltd. See
448 [http://books.google.com/books?hl=en&lr=&id=XYDI0mlH-](http://books.google.com/books?hl=en&lr=&id=XYDI0mlH-moC&oi=fnd&pg=PA2008&dq=The+R+Book&ots=HYTI-mHeHF&sig=ut_4HwPVkTuZ-bg-gk7N2Zwrn1s)
449 [moC&oi=fnd&pg=PA2008&dq=The+R+Book&ots=HYTI-](http://books.google.com/books?hl=en&lr=&id=XYDI0mlH-moC&oi=fnd&pg=PA2008&dq=The+R+Book&ots=HYTI-mHeHF&sig=ut_4HwPVkTuZ-bg-gk7N2Zwrn1s)
450 [mHeHF&sig=ut_4HwPVkTuZ-bg-gk7N2Zwrn1s](http://books.google.com/books?hl=en&lr=&id=XYDI0mlH-moC&oi=fnd&pg=PA2008&dq=The+R+Book&ots=HYTI-mHeHF&sig=ut_4HwPVkTuZ-bg-gk7N2Zwrn1s).
- 451 32. Hedtke SM, Patiny S, Danforth BN. 2013 The bee tree of life: a supermatrix approach
452 to apoid phylogeny and biogeography. *BMC Evol. Biol.* **13**, 138. (doi:10.1186/1471-
453 2148-13-138)
- 454 33. Britton T, Anderson CL, Jacquet D, Lundqvist S, Bremer K. 2007 Estimating
455 divergence times in large phylogenetic trees. *Syst. Biol.* **56**, 741–752.
456 (doi:10.1080/10635150701613783)
- 457 34. Thomas GH, Hartmann K, Jetz W, Joy JB, Mimoto A, Mooers AO. 2013 PASTIS: an
458 R package to facilitate phylogenetic assembly with soft taxonomic inferences.
459 *Methods Ecol. Evol.* **4**, 1011–1017. (doi:10.1111/2041-210X.12117)
- 460 35. De Palma A, Kuhlmann M, Bugter R, Ferrier S, Hoskins AJ, Potts SG, Roberts SPM,
461 Schweiger O, Purvis A. 2017 Dimensions of biodiversity loss: Spatial mismatch in
462 land-use impacts on species, functional and phylogenetic diversity of European bees.
463 *Divers. Distrib.* **23**, 1435–1446. (doi:10.1111/ddi.12638)
- 464 36. Rabosky DL. 2015 No substitute for real data: phylogenies from birth-death polytomy
465 resolvers should not be used for many downstream comparative analyses. , 1–23.
466 (doi:arXiv:1503.04978)
- 467 37. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**,
468 877–884. (doi:10.1038/44766)
- 469 38. Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schifffers K, Thuiller W.
470 2012 How to measure and test phylogenetic signal. *Methods Ecol. Evol.* **3**, 743–756.
471 (doi:10.1111/j.2041-210X.2012.00196.x)
- 472 39. Ives AR, Midford PE, Garland T. 2007 Within-species variation and measurement
473 error in phylogenetic comparative methods. *Syst. Biol.* **56**, 252–270.
474 (doi:10.1080/10635150701313830)
- 475 40. Revell LJ. 2012 phytools: An R package for phylogenetic comparative biology (and
476 other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-
477 210X.2011.00169.x)
- 478 41. De Palma A *et al.* 2016 Predicting bee community responses to land-use changes:
479 Effects of geographic and taxonomic biases. *Sci. Rep.* **6**. (doi:10.1038/srep31153)
- 480 42. Carvalheiro LG *et al.* 2013 Species richness declines and biotic homogenisation have
481 slowed down for NW-European pollinators and plants. *Ecol. Lett.* **16**, 870–878.
482 (doi:10.1111/ele.12121)
- 483 43. Cadotte M, Albert CH, Walker SC. 2013 The ecology of differences: Assessing
484 community assembly with trait and evolutionary distances. *Ecol. Lett.* **16**, 1234–1244.
485 (doi:10.1111/ele.12161)
- 486 44. Pearse WD, Cadotte MW, Cavender-Bares J, Ives AR, Tucker C, Walker SC, Helmus
487 MR. 2015 pez: Phylogenetics for the Environmental Sciences.
- 488 45. Gower JC. 1971 A General Coefficient of Similarity and Some of Its Properties.
489 *Biometrics* **27**, 857. (doi:10.2307/2528823)
- 490 46. Debastiani VJ, Pillar VD. 2012 SYNCSEA--R tool for analysis of metacommunities
491 based on functional traits and phylogeny of the community components.
492 *Bioinformatics* **28**, 2067–8. (doi:10.1093/bioinformatics/bts325)

- 493 47. Boj E, Caballe A, Delicado P, Fortiana J. 2014 dbstats: Distance-Based Statistics.
494 48. Boj E, Caballé A, Delicado P, Esteve A, Fortiana J. 2015 Global and local distance-
495 based generalized linear models. *TEST* (doi:10.1007/s11749-015-0447-1)
496 49. Greenleaf SS, Williams NM, Winfree R, Kremen C. 2007 Bee foraging ranges and
497 their relationship to body size. *Oecologia* **153**, 589–596. (doi:10.1007/s00442-007-
498 0752-9)
499 50. Hernandez JL, Frankie GW, Thorp RW. 2009 Ecology of Urban Bees: A Review of
500 Current Knowledge and Directions for Future Study. *Cities Environ.* **2**, 1–15.
501 51. Fortel L, Henry M, Guilbaud L, Guirao AL, Kuhlmann M, Mouret H, Rollin O, Vaissière
502 BE. 2014 Decreasing Abundance, Increasing Diversity and Changing Structure of the
503 Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient.
504 *PLoS One* **9**, e104679. (doi:10.1371/journal.pone.0104679)
505 52. Baldock KCR *et al.* 2015 Where is the UK's pollinator biodiversity? The importance of
506 urban areas for flower-visiting insects. *Proc. R. Soc. B Biol. Sci.* **282**.
507 (doi:10.1098/rspb.2014.2849)
508 53. Bates AJ, Sadler JP, Fairbrass AJ, Falk SJ, Hale JD, Matthews TJ. 2011 Changing
509 bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS One* **6**,
510 e23459. (doi:10.1371/journal.pone.0023459)
511 54. Tuck SL, Porter J, Rees M, Turnbull LA. 2018 Strong responses from weakly
512 interacting species. *Ecol. Lett.* (doi:10.1111/ele.13163)
513 55. Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG. 2010
514 Ecological and life-history traits predict bee species responses to environmental
515 disturbances. *Biol. Conserv.* **143**, 2280–2291. (doi:10.1016/j.biocon.2010.03.024)
516 56. Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007 Let
517 the concept of trait be functional! *Oikos* **116**, 882–892. (doi:10.1111/j.2007.0030-
518 1299.15559.x)
519 57. Srivastava DS, Cadotte MW, Macdonald a. AM, Marushia RG, Mirotnick N. 2012
520 Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* **15**, 637–648.
521 (doi:10.1111/j.1461-0248.2012.01795.x)
522 58. Kennedy CM *et al.* 2013 A global quantitative synthesis of local and landscape effects
523 on wild bee pollinators in agroecosystems. *Ecol. Lett.* **16**, 584–599.
524 (doi:10.1111/ele.12082)
525 59. Ellis EC, Ramankutty N. 2008 Putting people in the map: anthropogenic biomes of the
526 world. *Front. Ecol. Environ.* **6**, 439–447. (doi:10.1890/070062)
527 60. Fritz S a, Bininda-Emonds ORP, Purvis A. 2009 Geographical variation in predictors
528 of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**, 538–
529 549. (doi:10.1111/j.1461-0248.2009.01307.x)
530 61. Fontaine C, Collin CL, Dajoz I. 2008 Generalist foraging of pollinators: diet expansion
531 at high density. *J. Ecol.* **96**, 1002–1010. (doi:10.1111/j.1365-2745.2008.01405.x)
532 62. Kleijn D, Raemakers I. 2008 A retrospective analysis of pollen host plant use by
533 stable and declining bumble bee species. *Ecology* **89**, 1811–1823. (doi:10.1890/07-
534 1275.1)
535 63. Faith DP. 2013 Biodiversity and evolutionary history: useful extensions of the PD
536 phylogenetic diversity assessment framework. *Ann. N. Y. Acad. Sci.* **1289**, 69–89.
537 (doi:10.1111/nyas.12186)
538 64. Chamberlain S a, Cartar R V, Worley AC, Semmler SJ, Gielens G, Elwell S, Evans
539 ME, Vamosi JC, Elle E. 2014 Traits and phylogenetic history contribute to network
540 structure across Canadian plant – pollinator communities. , 545–556.
541 (doi:10.1007/s00442-014-3035-2)
542 65. Valiente-Banuet A *et al.* 2015 Beyond species loss: the extinction of ecological
543 interactions in a changing world. *Funct. Ecol.* **29**, 299–307. (doi:10.1111/1365-
544 2435.12356)
545 66. Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM. 2015 Community
546 assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* **29**,
547 592–599. (doi:10.1111/1365-2435.12345)

- 548 67. Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009 The merging of
549 community ecology and phylogenetic biology. *Ecol. Lett.* **12**, 693–715.
550 (doi:10.1111/j.1461-0248.2009.01314.x)
- 551 68. Vamosi SM, Heard SB, Vamosi C, Webb CO. 2009 Emerging patterns in the
552 comparative analysis of phylogenetic community structure. *Mol. Ecol.* **18**, 572–592.
553 (doi:10.1111/j.1365-294X.2008.04001.x)
- 554 69. Kleijn D *et al.* 2015 Delivery of crop pollination services is an insufficient argument for
555 wild pollinator conservation. *Nat. Commun.* **6**, 7414. (doi:10.1038/ncomms8414)
- 556 70. Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM, Gibbs J. 2018 Species
557 turnover promotes the importance of bee diversity for crop pollination at regional
558 scales. *Science (80-.)*. **359**, 791–793. (doi:10.1126/SCIENCE.AAO2117)
- 559 71. Nieto A *et al.* 2015 *European Red List of Bees*. Luxembourg: Publication Office of the
560 European Union. (doi:10.2779/77003)
- 561 72. Mace GM, Gittleman JL, Purvis A. 2003 Preserving the tree of life. *Science (80-.)*.
562 **300**, 1707–1709. (doi:10.1126/science.1085510)
- 563 73. Bland LM, Collen B, Orme CDL, Bielby J. 2015 Predicting the conservation status of
564 data-deficient species. *Conserv. Biol.* **29**, 250–259. (doi:10.1111/cobi.12372)
- 565 74. Bevilacqua S, Terlizzi A, Claudet J, Frascchetti S, Boero F. 2012 Taxonomic
566 relatedness does not matter for species surrogacy in the assessment of community
567 responses to environmental drivers. *J. Appl. Ecol.* **49**, 357–366. (doi:10.1111/j.1365-
568 2664.2011.02096.x)
- 569 75. Guénard G, Von Der Ohe PC, De Zwart D, Legendre P, Lek S. 2011 Using
570 phylogenetic information to predict species tolerances to toxic chemicals. *Ecol. Appl.*
571 **21**, 3178–3190. (doi:10.1890/10-2242.1)
- 572 76. Kallimanis AS, Mazaris AD, Tsakanikas D, Dimopoulos P, Pantis JD, Sgardelis SP.
573 2012 Efficient biodiversity monitoring: Which taxonomic level to study? *Ecol. Indic.* **15**,
574 100–104. (doi:10.1016/j.ecolind.2011.09.024)
- 575 77. Lebuhn G *et al.* 2013 Detecting Insect Pollinator Declines on Regional and Global
576 Scales. *Conserv. Biol.* **27**, 113–120. (doi:10.1111/j.1523-1739.2012.01962.x)
- 577 78. Tepedino VJ, Durham S, Cameron SA, Goodell K. 2015 Documenting bee decline or
578 squandering scarce resources. **29**, 280–282. (doi:10.1111/cobi.12439)
- 579 79. Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araujo MB. 2011
580 Consequences of climate change on the tree of life in Europe. *Nature* **470**, 531–4.
581 (doi:10.1038/nature09705)
582

583 **Figure Legends**

584 Figure 1: Spread of SSI values (points) and their standard error (lines) for each land-use
585 transition, for all species in the dataset. Coloured points indicate that SSI values were
586 significantly different from 0. Particularly vulnerable species (i.e., those with an SSI
587 significantly below 0) are coloured in yellow to red, while species that strongly benefit
588 from land-use change (i.e., those with SSI values significantly above 0) are coloured light
589 to dark blue.

590

591 Figure 2: Phylogenetic signal in species' sensitivity to various land use pressures, when
592 (a) standard errors are accounted for and (b) when they are ignored. Red triangles
593 indicate the values for the rate-smoothed tree, where some species are missing from the
594 tree. Numbers in red show the number of species included in these tests. Boxplots show
595 the distribution of values across the 1,000 completed trees, with numbers in black
596 showing the number of species included in these tests.

597

598 Figure 3: Phylogenetic signal in species' sensitivity to all human-dominated land uses
599 using the rate-smoothed (incomplete) tree. Tips of the phylogeny are coloured according
600 to the species' sensitivity: from blue to red indicate less to more sensitive. The right
601 panel shows species sensitivity \pm the standard error. See Appendix Figures S4.2 to S4.4
602 for similar figures for other land-use transitions.

603

604 Figure 4: Akaike's Weights of models assessing species sensitivities as a function of
605 *alpha* value, where *alpha* = 0 uses only functional traits to calculate the distance, *alpha*
606 = 1 uses only phylogeny to calculate the distance, and *alpha* = 0.5 considers both traits
607 and phylogeny equally. Model performance was also calculated where distances were
608 randomly computed. Red triangles indicate the values for the rate-smoothed tree, where
609 some species are missing from the tree. Numbers in red show the number of species
610 included in these tests. Boxplots show the distribution of values across the 1,000
611 completed trees, with numbers in black showing the number of species included in these
612 tests. For a similar figure assessing explanatory power of models, see Appendix Figure
613 S5.5.

614 Tables

615

616 Table 1: Land-use transitions of interest and the component land-use classes. Dataset
617 sample sizes are also given: number of studies, species and species that match with the
618 recently-published Bee Tree of Life [32].

Land use comparison	Intact	Converted	Number of studies	Number of species	Number of species in the phylogeny
Loss of natural and semi-natural habitat	Primary & Secondary vegetation	Cropland, Pasture, Plantation forest & Urban	86	488	141
Agricultural expansion	Primary & Secondary vegetation	Cropland, Pasture & Plantation forest	84	437	121
Urbanisation	Primary & Secondary vegetation	Urban	54	146	56
Agricultural intensification	Agricultural sites (as defined above) with a continuous use-intensity scale from 1 (minimal use) to 3 (intense use)		53	268	87

619

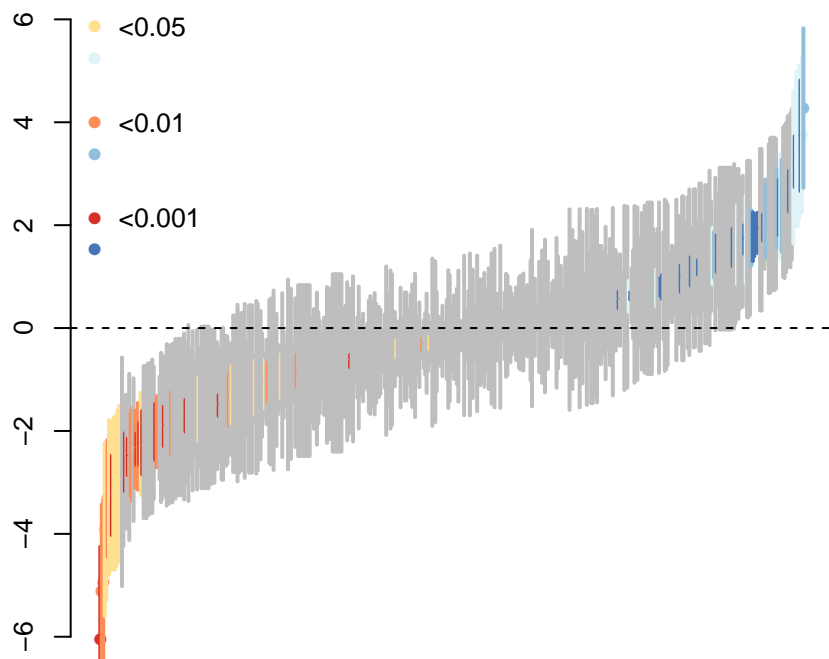
620

621 Table 2: λ values of the sensitivity of all bee species, bumblebees only and other
 622 species (bumblebees excluded from the phylogenetic tree) to land-use change. For the
 623 completed trees, this is the mean $\lambda \pm$ standard deviation across the 1000 phylogenies.
 624

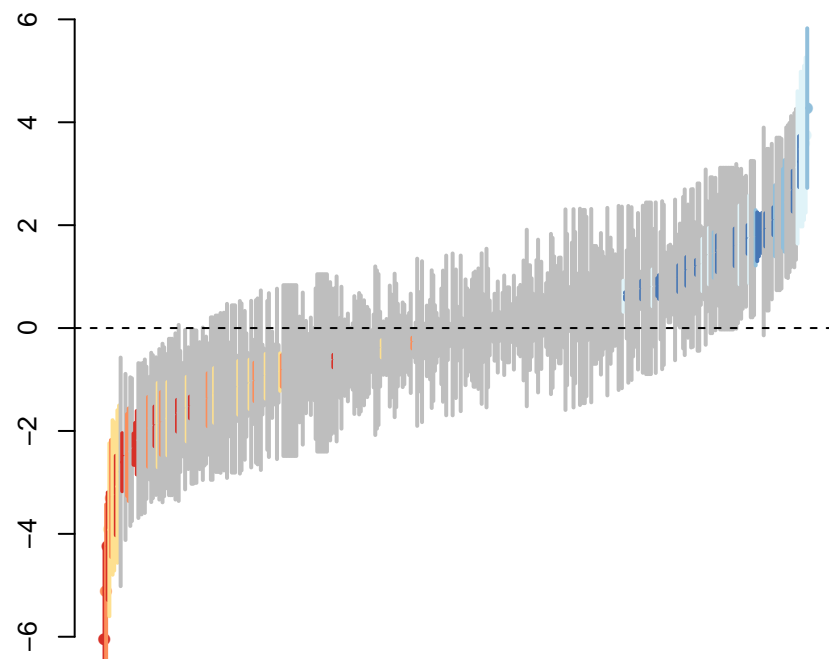
Sensitivity to:	Tree	λ		
		All species	Bumblebees	Other species
Human-dominated land	Rate-smoothed	0.741	0	0
	Completed	0.672 \pm 0.09	0 \pm 0	0.626 \pm 0.14
Agricultural land	Rate-smoothed	0.594	0	0
	Completed	0.64 \pm 0.1	0 \pm 0	0.586 \pm 0.16
Urban land	Rate-smoothed	0	0	0.143
	Completed	0.633 \pm 0.15	0.256 \pm 0.44	0.2 \pm 0.12
Higher-intensity agriculture	Rate-smoothed	0.046	0	0.041
	Completed	0.116 \pm 0.03	0 \pm 0	0.121 \pm 0.04

625

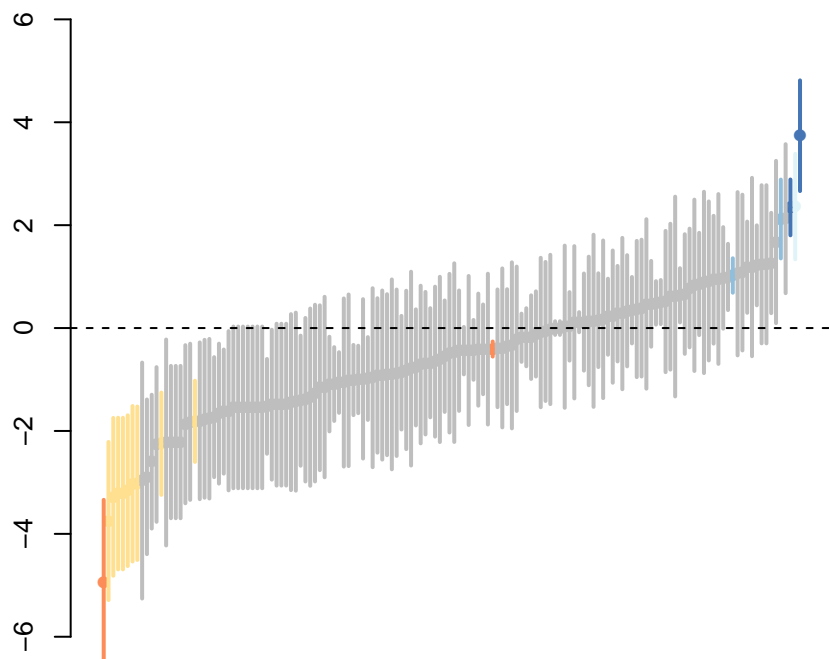
Sensitivity to human-dominated land use



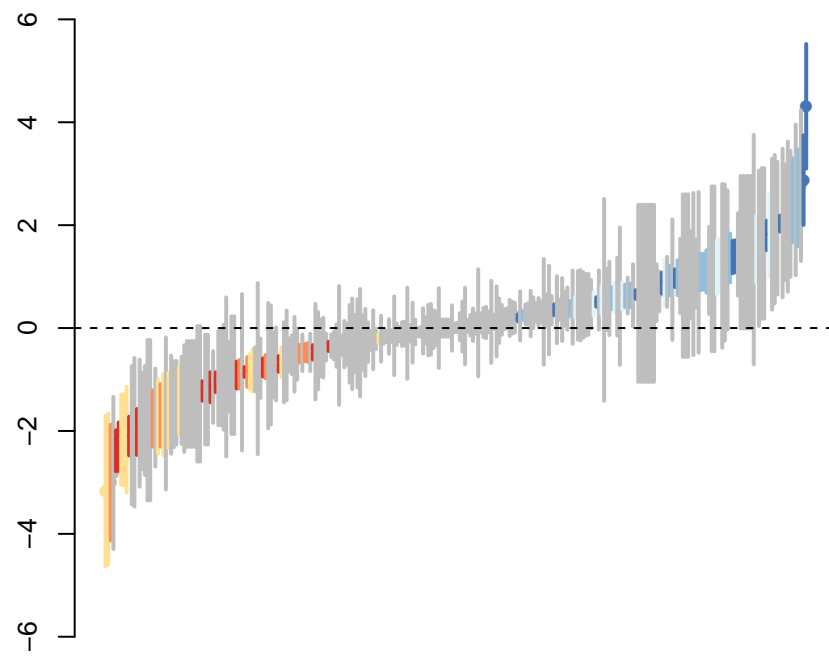
Sensitivity to agricultural land



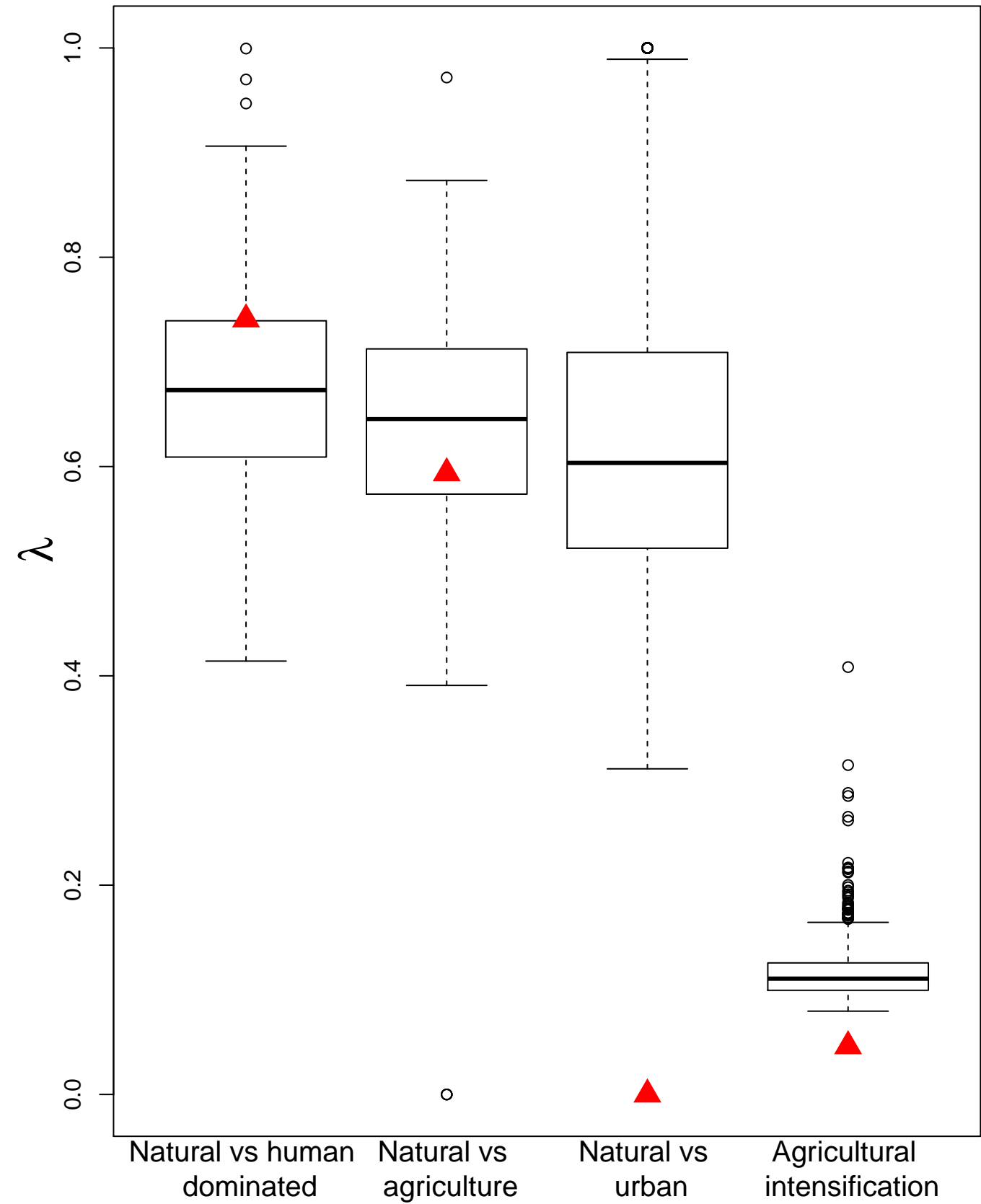
Sensitivity to urban land



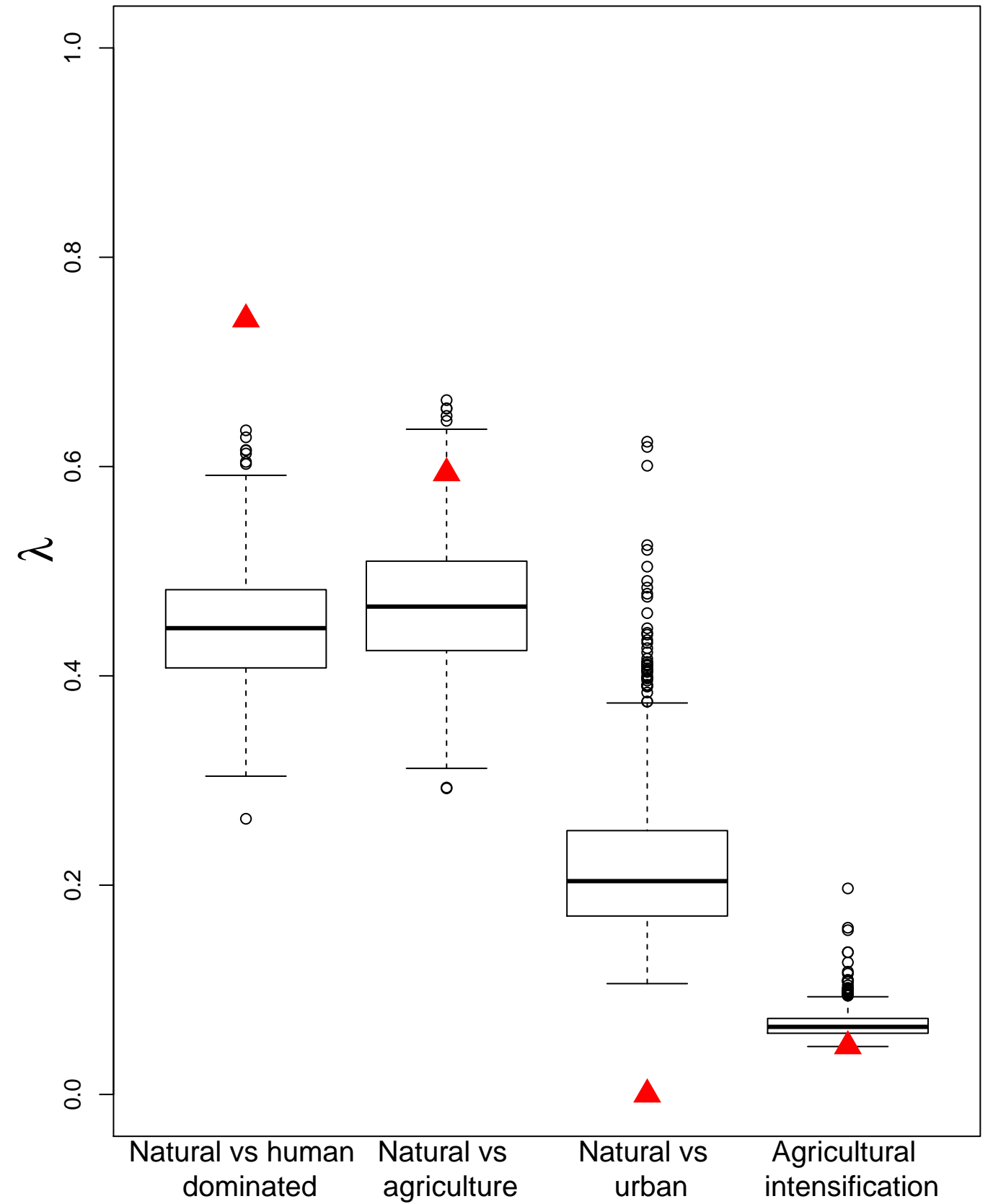
Sensitivity to agricultural intensification

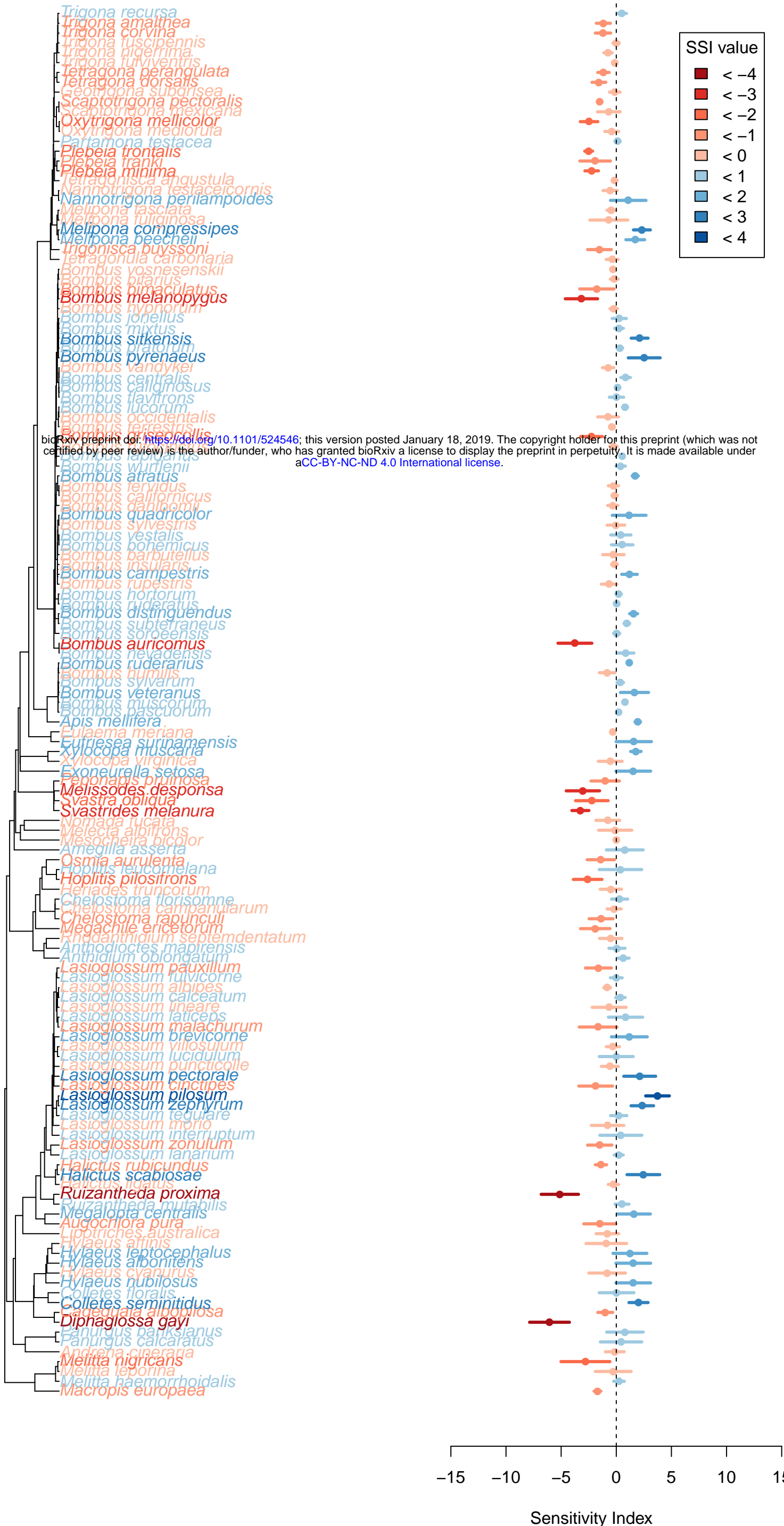


a) 429 species
130 species 378 species
110 species 140 species
52 species 268 species
87 species



b) 429 species
130 species 378 species
110 species 140 species
52 species 268 species
87 species

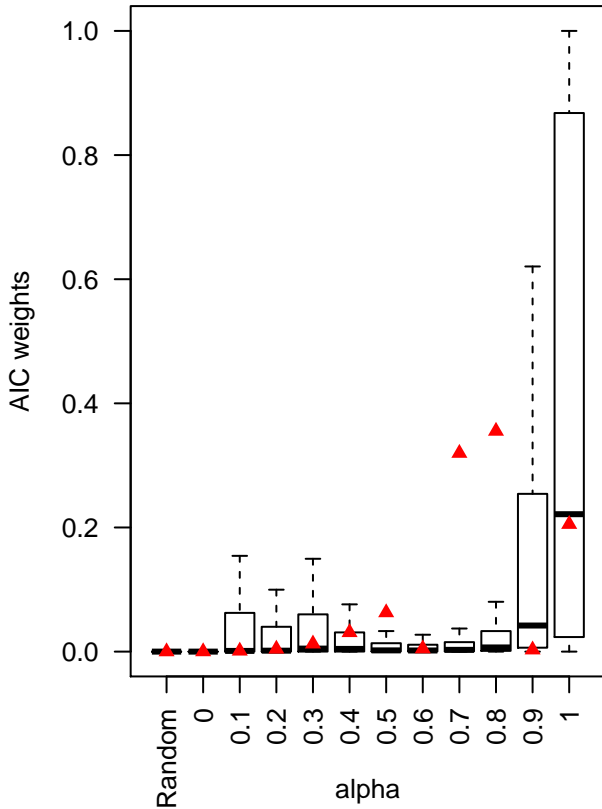




Sensitivity to Human dominated land

138 Species

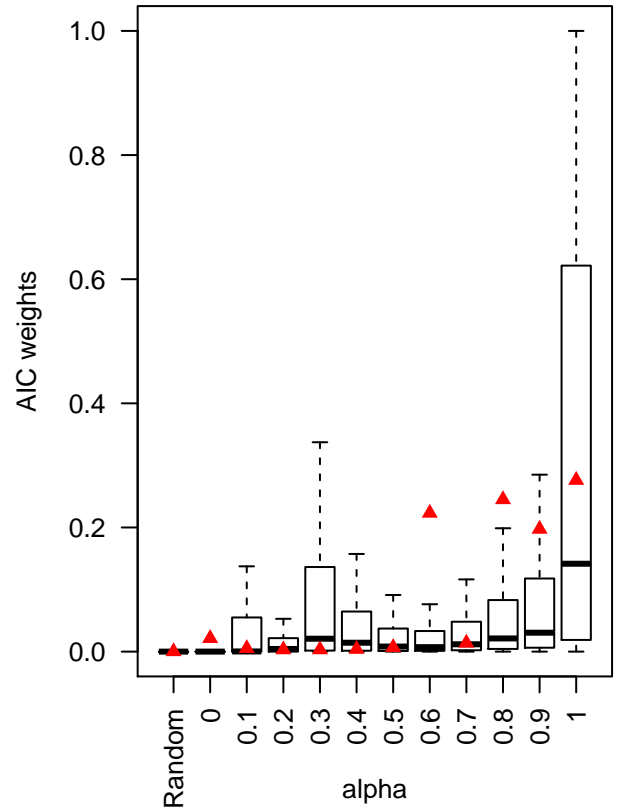
55 Species



Sensitivity to Agricultural land

134 Species

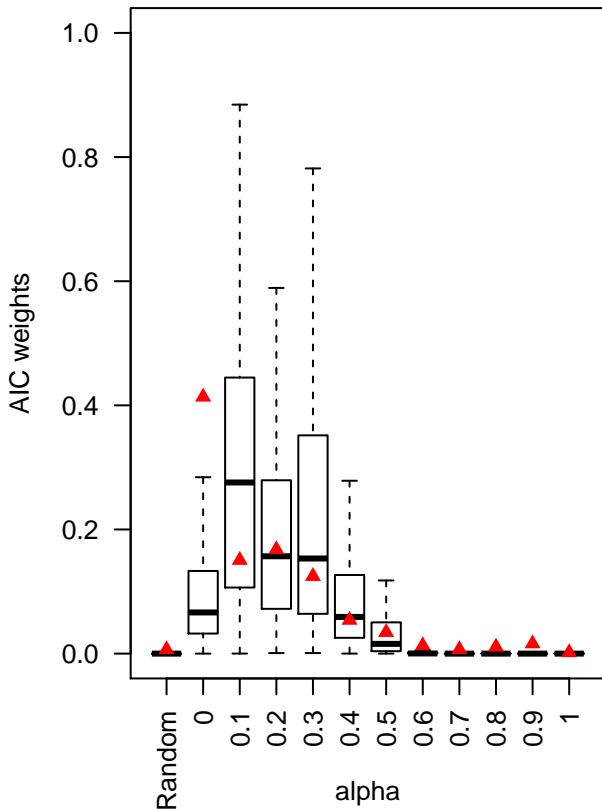
52 Species



Sensitivity to Agricultural intensification

148 Species

50 Species



Sensitivity to Urban land

64 Species

29 Species

