

1 **How imperfect can land sparing be before land sharing is more favourable for wild**  
2 **species?**

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16

17 **Abstract**

18 1. Two solutions, at opposite ends of a continuum, have been proposed to limit negative  
19 impacts of human agricultural demand on biodiversity. Under land sharing, farmed  
20 landscapes are made as beneficial to wild species as possible, usually at the cost of lower  
21 yields. Under land sparing, yields are maximized and land not needed for farming is spared  
22 for nature. Multiple empirical studies have concluded land-sparing strategies would be the  
23 least detrimental to wild species, provided land not needed for agriculture is actually spared  
24 for nature. However, the possibility of imperfections in the delivery of land sparing has not  
25 been comprehensively considered.

26 2. Land sparing can be imperfect in two main ways: land not required for food  
27 production may not be used for conservation (incomplete area sparing), and habitat spared  
28 may be of lower quality than that assessed in surveys (lower habitat quality sparing). Here we  
29 use published data relating population density to landscape-level yield for birds and trees in  
30 Ghana (167 and 220 species, respectively) and India (174 birds, 40 trees) to assess effects of  
31 imperfect land sparing on region-wide population sizes and hence population viabilities.

32 3. We find that incomplete area and lower habitat quality imperfections both reduce the  
33 benefits of a land-sparing strategy. However, sparing still outperforms sharing whenever  
34  $\geq 28\%$  of land that could be spared is devoted to conservation, or the quality of land spared is  
35  $\geq 29\%$  of the value of that surveyed. Thresholds are even lower under alternative assumptions  
36 of how population viability relates to population size and for species with small global  
37 ranges, and remain low even when both imperfections co-occur.

38 4. Comparison of these thresholds with empirical data on the likely real-world  
39 performance of land sparing suggests that reducing imperfections in its delivery would be  
40 highly beneficial. Nevertheless, given plausible relationships between population size and  
41 population viability, land sparing outperforms land sharing despite its imperfections.

42 5. *Policy implications.* Our results confirm that real-world difficulties in implementing  
43 land sparing will have significant impacts on biodiversity. They also underscore the need for  
44 strategies which explicitly link yield increases to setting land aside for conservation, and for  
45 adoption of best practices when spared land requires restoration. However, land-sparing  
46 approaches to meeting human agricultural demand remain the least detrimental to  
47 biodiversity, even with current imperfections in implementation.

48

49 **Keywords:** Density-yield curve; Habitat restoration; Imperfect land sparing; Land sharing;  
50 Land sparing; Wildlife-friendly farming; Agricultural demand; Biodiversity

51

52 **Introduction**

53 Agriculture currently covers 40% of the world's ice-free land (Foley et al., 2011), and poses  
54 the single greatest threat to biodiversity of any sector (IUCN, 2016). Moreover, with an  
55 increasingly large and wealthy human population, agricultural demand is rising quickly  
56 (Godfray et al., 2010). Indeed, it is expected that as much food will be produced this half-  
57 century as since the beginning of agriculture (DEFRA, 2009). More equitable distribution of  
58 food, reduction in post-harvest waste, and switching to more plant-based diets would help  
59 limit the footprint of agriculture (Godfray et al., 2010). However, food production is still  
60 predicted to increase, so managing land-use to minimise the negative impacts on wild nature  
61 is crucial (Foley et al., 2011).

62

63 This concern has prompted two contrasting solutions, at the extremes of a continuum. Land  
64 sharing describes the adoption of wildlife-friendly practices (see Tschamtker et al., 2012) such  
65 as retaining small patches of unfarmed natural or semi-natural vegetation within farms or  
66 adopting production methods that reduce negative effects on wild species living on farms.  
67 However, such practices usually lower overall yield – production per unit area of the entire  
68 farmed landscape (Green et al., 2005) – such that more land needs to be farmed to produce a  
69 given amount of food. In contrast, under land sparing, different landscapes have discrete  
70 primary objectives – food production or biodiversity conservation – with high yields on  
71 farmland permitting the retention or restoration of native vegetation elsewhere (Green et al.,  
72 2005), albeit often at a cost to on-farm biodiversity (Phalan et al., 2011).

73

74 Tests of which approach would be better for biodiversity involve quantifying how the  
75 population densities of wild species respond to agricultural yield (Green et al., 2005). So-  
76 called density-yield curves, describing the relationship between individual species'



77 population density and agricultural yield, are derived from field surveys of large (typically  
78 1km<sup>2</sup>) sample areas with comparable soils, climate and topography, but different land-uses  
79 (including some sample areas supporting native vegetation). For any specified level of  
80 region-wide production, fitted density-yield functions are used to estimate each species' total  
81 population size, given a particular yield on farmed land and assuming that land not required  
82 to meet this level of production supports vegetation similar to that of the non-farmed land  
83 surveyed. For a given total production level, species' regional population sizes are predicted  
84 for all yields between the lowest permissible (which requires the entire region to be farmed to  
85 deliver the specified production level: land sharing) and the highest possible (where all land  
86 not needed is assigned to native vegetation: land sparing). It is then possible to tally the  
87 numbers of species that would have their highest regional population with farming at the  
88 lowest permissible yield, the highest possible yield or at some intermediate yield.

89

90 Studies of birds and trees in Ghana and India (Phalan et al., 2011); birds in Uganda (Hulme et  
91 al., 2013); birds in Kazakhstan (Kamp et al., 2015); birds, dung beetles, Asteraceae and  
92 grasses in the pampas (Dotta, 2013); and birds, trees and dung beetles in Mexico (Williams et  
93 al., 2017) have all reached the same conclusion. Extreme land sparing is associated with  
94 larger total population sizes for more species than extreme land sharing or any intermediate-  
95 yield approach. This conclusion applies for current production levels; and as total production  
96 (as is likely) the advantage of sparing over sharing increases. Hence if it could be delivered in  
97 practice, land sparing would be the least bad option for wild nature in all these regions.

98 Indeed we are unaware of any study which quantifies yields, examines both native vegetation  
99 and high-yield landscapes, and uses population-based metrics of biodiversity outcomes, in  
100 which sharing out-performs sparing.

101

102 However, the scenarios explored in these studies assume that land sparing is perfect, in two  
103 different ways. First, they assume that all land not needed for crop production is maintained  
104 under or restored to native vegetation. Second, the native vegetation assessed in field surveys  
105 is assumed to be representative, in terms of species' population densities, of land that would  
106 be protected or restored through land sparing. In the real world neither of these assumptions  
107 holds completely (Ewers et al., 2009; Rey Benayas et al., 2009).

108

109 Yield increases in the real world do not always result in proportionate increases in land  
110 spared for native vegetation (Tscharntke et al., 2012; see left of Fig. 1a), for several reasons.  
111 Increased farm efficiency may reduce costs of production and hence increase farm profits.  
112 Reduced commodity prices could also increase demand, leading to a rebound effect  
113 sometimes labelled Jevons paradox (Ewers et al., 2009; Villoria et al 2013; Byerlee et al.,  
114 2014). Land potentially spared by yield increases of staple crops might be used to produce  
115 luxury or cash crops, or for other land uses (Ewers et al. 2009). Government subsidies may  
116 incentivise farmers to produce more than would otherwise be the case (Ewers et al., 2009).  
117 Last, land speculation in agricultural frontiers could mean that land is occupied and cleared  
118 irrespective of demand for farm products (Baumann et al., 2017; le Polain de Waroux et al.,  
119 2018). Any of these mechanisms would encourage farming on land that could otherwise have  
120 been spared. In the absence of explicit land-sparing policies, such effects have been observed  
121 to reduce the area of land spared to little over 5% of its potential level (Ewers et al., 2009).

122

123 In addition, native vegetation on spared land might be of lower average quality for wild  
124 species than that of reference areas surveyed during fieldwork (see right of Fig. 1a), again for  
125 several reasons. If the land that is spared was previously farmed, sparing would require its  
126 restoration, but restored vegetation is often lower quality than existing vegetation (Rey

127 Benayas et al., 2009; Law and Wilson, 2015; Bull et al., 2017); at least in the short term,  
128 pioneer species may dominate, with negative consequences for other species (MacDonald et  
129 al., 2000). Second, edge effects, which can reduce population densities close to farmland,  
130 might be greater near high-yield farming, leading to densities in spared native vegetation  
131 being lower than those observed in field surveys (Didham et al., 2015; Lamb et al., 2016a).  
132 Finally, spared land may be poorly protected, as suggested for Tanzania, where agricultural  
133 intensification might mean demand for woody products is redirected towards forests rather  
134 woodlands on farms (Quandt, 2016). Alternatively, land spared for conservation purposes  
135 might be of higher value for wild species than non-farmed areas covered by the field surveys,  
136 if land sparing enabled the creation (or protection) of larger habitat tracts. However, such an  
137 outcome would only underline the case for land sparing and so is not considered further.

138

139 To our knowledge, no study has yet examined how the relative merits of sparing and sharing  
140 change under incomplete area sparing. One element of lower habitat quality sparing was  
141 explored in Lamb et al.'s (2016a) study of edge effects, and the potential effects of spared  
142 land being of lower quality for wild species than pristine habitat were modelled by Law and  
143 Wilson (2015). Here we assess for the first time the effects of both types of imperfection,  
144 operating in isolation, and co-occurring, using fieldwork-derived, species-specific density-  
145 yield functions to calculate region-wide populations and estimate population viabilities for  
146 large numbers of species.

147

## 148 **Materials and methods**

### 149 *Landscapes and population sizes*

150 We followed the framework of Green et al. (2005) and Phalan et al. (2011) to compare the  
151 effects of meeting region-wide food production targets in contrasting ways. Our perfect two-

152 compartment model of extreme land sparing (shown by regions on the right of Fig. 1b)  
153 comprised high-yield agriculture over an area  $A_{HY}$  (in year  $i$  for region  $j$ ) just sufficient to  
154 meet the production target ( $PT$ ) when it is farmed at maximum yield ( $MY$ ):

155

$$156 \text{ (Eq. 1)} \quad A_{HY\ ij} = \frac{PT_{ij}}{MY_{ij}}$$

157

158 with the rest of the region  $A_{NV\ ij}$  under native vegetation:

159

$$160 \text{ (Eq. 2)} \quad A_{NV\ ij} = TA_j - A_{HY\ ij}$$

161

162 where  $TA$  is the total area of the region. Our model of extreme land sharing involves the  
163 whole region being farmed at  $ShY_{ij}$ , the lowest yield sufficient to just meet the production  
164 target:

165

$$166 \text{ (Eq. 3)} \quad ShY_{ij} = \frac{PT_{ij}}{TA_j}$$

167

168 We then assessed the region-wide population sizes of wild species under our scenarios using  
169 density-yield curves. Under land sharing the population size ( $P_{Sh}$ ) of species ( $k$ ) is given by:

170

$$171 \text{ (Eq. 4)} \quad P_{Sh\ k} = TA_j \times PD_{ShY_{ij}\ k}$$

172

173 where the species' population density ( $PD$ ) is that under the lowest-yielding agriculture just  
174 sufficient to meet the production target (from Equation 3).

175 Under land sparing region-wide population sizes are calculated incorporating each of the two  
 176 types of imperfections of land sparing, which we introduce through a perfection score ( $\psi$ )  
 177 which ranges from 0 to 1. Under incomplete area sparing the amount of land set aside for  
 178 nature, as a proportion of that which theoretically could be, is gradually reduced to zero (Fig.  
 179 1b, upper panel), and the reduction in area spared is translated into a reduction in each  
 180 species' population size  $P_{IAk}$ :

$$181 \text{ (Eq. 5)} \quad P_{IAk} = PD_{NVk} \times A_{NV} \times \psi_A + PD_{HYk} \times (TA_j - A_{NV} \times \psi)$$

182

183 calculated as the product of its population density in native vegetation, the area under native  
 184 vegetation, and the area perfection score ( $\psi_A$ ), plus the product of its population density under  
 185 high yield farming and the area perfection-adjusted area under farming.

186

187 Imperfection due to lower habitat quality on spared land results in reduced population density  
 188 in spared land (Fig. 1b, lower panel), which decreases each species' population size to  $P_{LHQk}$ :

189

$$190 \text{ (Eq. 6)} \quad P_{LHQk} = PD_{NVk} \times \psi_{HQ} \times A_{NV} + PD_{HYk} \times (TA_j - A_{NV})$$

191

192 calculated as the product of its population density in surveyed native vegetation, the habitat  
 193 quality perfection score ( $\psi_{HQ}$ ) and the area under native vegetation, plus the product of  
 194 population density in high-yield agriculture and the area under farming.

195

196 We also considered the effects of the co-occurrence (CO) of incomplete area sparing and  
 197 lower habitat quality sparing. Each species' population size is then given by:

$$198 \text{ (Eq. 7)} \quad P_{COk} = PD_{NVk} \times A_{NV} \times \psi_A \times \psi_{HQ} + PD_{HYk} \times (TA_j - A_{NV} \times \psi_A)$$

199

200 calculated as the product of its population density in native vegetation, the area under native  
201 vegetation, the area perfection score, and the habitat quality perfection score; plus the product  
202 of its population density under high yield farming and the area perfection-adjusted area under  
203 farming.

204

205 To put population sizes under each scenario into context we estimated a baseline pre-  
206 agricultural ( $PA$ ) population size, assuming that the entire region was under native  
207 vegetation:

208

209 (Eq. 8)  $P_{PAk} = TA_j \times PD_{NVk}$

210

211 We then expressed total population sizes under each scenario as a fraction of this pre-  
212 agricultural baseline population. Like previous studies that have adopted the sparing-sharing  
213 framework (Phalan et al. 2011; Dotta, 2013; Hulme et al. 2013; Gilroy et al. 2014a; Kamp et  
214 al. 2015; Williams et al. 2017), we chose a pre-agricultural baseline as our reference because  
215 it is the closest approximation we have to the landscape condition in which a region's species  
216 have persisted for most of their existence.

217

### 218 *Estimating the viability of populations*

219 We next wanted to translate changes in species' relative population sizes under each scenario  
220 into changes in their likely viability. Changes in population viability depend not just on the  
221 number of individuals added or removed, but also on initial population size (losing 1000  
222 individuals will clearly reduce the viability of a starting population of 1010 far more than that  
223 of a population of 10,000, for example). The increasing impact on viability of losing one

224 individual increases as population size decreases, implying that the relationship between  
 225 population size and viability is concave.

226

227 We therefore follow others (Thomas et al., 2004; Phalan, 2009) in converting changes in  
 228 suitable habitat area or population size into changes in population viability using a power-law  
 229 function with an exponent less than one. Adoption of a similar approach in the context of the  
 230 IUCN Red List criteria (Clements et al., 2011) was criticised (e.g. Akçakaya et al., 2011) for  
 231 not using a meaningful baseline to define the point at which a population is certain to persist  
 232 (i.e. for which viability = 1), and above which viability cannot increase with population size.

233 We tackle this here by expressing the population sizes under our agricultural scenarios  
 234 relative to those under our pre-agricultural baseline. We then translate these into viabilities,  
 235 averaged across all  $K$  species of a taxon in a region:

236

237 (Eq. 9) 
$$V_{LU} = \begin{cases} \frac{\sum_{k=1}^K \left(\frac{P_{LUk}}{P_{PAk}}\right)^z}{K} & \text{if } \frac{P_{LUk}}{P_{PAk}} \leq 1 \\ 1 & \text{if } \frac{P_{LUk}}{P_{PAk}} > 1 \end{cases}$$

238

239 where mean species population viability ( $V$ ) under different land-use scenarios ( $LU$ ) is  
 240 calculated by raising each species' population size relative to the pre-agricultural population  
 241 size to the power  $z$ , and taking the mean of this quantity across all species. We use a range of  
 242  $z$ -values (0.12, 0.15, 0.18, 0.25, 0.5, 1) reflecting uncertainty in the nature of the relationship  
 243 between population viability and relative population size. Like others, we consider  $z$ -values  
 244  $< 0.5$  more plausible (Phalan, 2009; Thomas et al., 2004), but include higher values for  
 245 completeness. Note that if a population exceeds baseline then it is assumed to have a viability  
 246 of 1. This means “winner” species (whose population densities are higher under farming than

247 in baseline vegetation – Phalan et al., 2011) do not have higher viabilities under agriculture  
248 than they would without.

249

250 Clearly Equation 9 does not capture all the intricacies of the relationship between population  
251 size and viability, but rather describes a broad pattern. For example, it is possible that Allee  
252 effects may cause a sigmoidal relationship, with an inflection point for low population sizes  
253 (Dennis, 1989). However, populations of most of our species are too large, under most  
254 scenarios, for this simplification to substantially alter our findings.

255

#### 256 *Disaggregating results by global range size*

257 Our analysis enabled us to estimate the effects of imperfect sparing on the average population  
258 viability of large sets of species, and in particular the threshold level of perfection – which we  
259 term the point of indifference – below which mean population viability is greater under land  
260 sharing. However, mean values mask underlying variation across species. We therefore also  
261 used Equations 4-6 and 8-9 to calculate the population viability of each individual species at  
262 the point of indifference. We then examined the distribution of individual species' population  
263 viability estimates, separately for small and large global range species (as defined in Phalan  
264 et al. 2011), under each of sharing, incomplete area sparing, and lower habitat quality  
265 sparing.

266

#### 267 *Study areas*

268 We parameterised our models using the density-yield curves reported by Phalan et al. (2011)  
269 for birds and trees in Ghana and India. The functions were fitted to survey data for 1km<sup>2</sup>  
270 squares (25 across 9117 km<sup>2</sup> in Ghana, 20 across 2039 km<sup>2</sup> in India) chosen to represent the  
271 full variation in yields seen within the study regions and to be similar in terms of climate,



272 topography and soils (so that, all else equal, one would expect similar yields and population  
273 densities). The fitted density-yield curves describe each species' expected mean population  
274 density across a 1km<sup>2</sup> block generating a given yield. For this purpose, it was not necessary to  
275 describe finer-scale variation in species' abundance.

276

277 Phalan et al. (2011) also reported maximum observed and projected yields, and production  
278 targets for each region for 2007 and 2050. Across this interval maximum yields were  
279 projected to increase by 25% (i.e. at 0.5% per year) and production targets by 94.1% and  
280 58.7% for Ghana and India, respectively (based on data from FAO, 2010).

281

### 282 *Expected degree of perfection of land sparing*

283 Finally, to put our results in context we considered the likely degree of perfection that might  
284 be expected under land sparing – assuming that no explicit effort is made to reduce  
285 imperfection. For incomplete area sparing, we sought a benchmark of “passive sparing”  
286 (sensu Phalan et al. 2016, and as described by the Borlaug hypothesis - Stevenson et al.,  
287 2013), whereby increased yields lower the area farmed by reducing prices (Barbier and  
288 Burgess, 1997); this process has been proposed as an explanation of afforestation and  
289 continued protection of native vegetation in India (Ravindranath et al., 2011). The only global  
290 quantification of passive sparing – defined as the change in area farmed, per capita of human  
291 population, with yield change – comes from Ewers et al. (2009). Although their estimates  
292 may incorporate the effects of some broad environmental regulations, they give an indication  
293 of the magnitude of land sparing that might be expected in the absence of explicit land-  
294 sparing policies. Based on data from 124 countries and 23 staple crops over 20 years they  
295 estimate: (1) the average observed proportional decrease in land used for growing 23 staple  
296 crops relative to the proportional increase in their yields (0.143; hereafter our upper-bound

297 estimate); and (2) the proportional decrease in land used for all crops relative to the  
298 proportional increase in the 23-crop yields (0.054; our lower-bound estimate). The former is  
299 more relevant in analyses which involve all crops increasing in yield, while the latter captures  
300 expansion of agricultural land dedicated to cash crops.

301

302 We use two perfection scores to benchmark the quality of native vegetation under lower  
303 habitat quality sparing; both account for time delays in restoration and for species-specific  
304 habitat preferences. The first is the median quality of restored habitat relative to reference  
305 habitat reported in a major meta-analysis (0.86; Rey Benayas et al., 2009). The second  
306 derives from development operations seeking “no net loss” of native vegetation, which use  
307 multipliers to evaluate how much land must be restored in order to compensate for a given  
308 area of habitat conversion. The largest multiplier regarded as operationally feasible is 10  
309 (Gibbons et al., 2016; Bull et al., 2017), and so we use the reciprocal of this (0.1) as a second  
310 illustrative perfection score. It is conceivable that the perfection score for habitat quality for  
311 some biodiversity outcomes could be even lower (i.e. near to zero).

312

## 313 **Results**

### 314 *Imperfection due to incomplete area sparing*

315 For Ghanaian birds at the 2007 production target the solid teal line in Fig. 2a shows mean  
316 species population viability under land sparing given different degrees of perfection and  
317 assuming  $z=1$ . As in all other cases, imperfect sparing reduces mean population viability.  
318 Moving leftwards (away from perfect sparing) this line crosses the dashed teal line – which  
319 describes the same species’ mean population viability under extreme land sharing – at a  
320 perfection score of 0.52. To the right of this point of indifference, incomplete area sparing is  
321 less bad for species’ persistence, and left of it land sharing is less bad. Lines of different

322 colours show results for alternative  $z$ -values (which we consider more plausible than  $z=1$ );  
323 these require greater imperfection (perfection scores of 0.01-0.28 for  $z=0.12-0.5$ ) before land  
324 sharing outperforms incomplete area sparing. Note that all land-sharing lines conservatively  
325 assume that population densities of species recorded in surveys of low-yield farmland apply  
326 across the entire region (which might not be the case – see Discussion).

327

328 For Indian birds the levels of perfection required for sharing to outperform incomplete area  
329 sparing are lower still (perfection scores of 0.01-0.08 for  $z=0.12-0.5$ ; Fig. 2c). This pattern is  
330 even more marked for trees, in both regions (for  $z=0.12-0.5$ , perfection required is 0.01-0.05;  
331 Fig. 2b, d) probably because tree population densities are more sensitive to conversion to  
332 agriculture than are those of birds. Increasing the production target to meet projected demand  
333 for 2050 also results in lower degrees of perfection being required for land sparing to be least  
334 bad (for  $z=0.12-0.5$ , perfection required is 0.01-0.20; Fig. S1 in Supporting Information).

335

336 How do these threshold levels of perfection compare with real-world values? Our upper-  
337 bound estimate of passive sparing (0.143; right-hand vertical lines of Fig. 2) exceeds that  
338 required for incomplete area sparing to outperform land sharing across all plausible  $z$ -values  
339 (0.12-0.5; only for Ghanaian birds with  $z \geq 0.5$  is this not the case). Under the more  
340 conservative assumptions of our lower-bound estimate (i.e. with increased supply cash crops)  
341 the level of perfection recorded under passive sparing alone (0.054; left-hand vertical lines) is  
342 still generally associated with incomplete area sparing outperforming land sharing  
343 (exceptions are for birds with  $z \geq 0.5$  and Ghanaian birds under 2007 production with  $z \geq 0.25$ ).

344

345 *Imperfection due to lower habitat quality of spared land*

346 The results of lowering the quality of native vegetation (Fig. 3) broadly echo those of  
347 incomplete area sparing. As with area imperfection, lower habitat quality sparing reduces  
348 mean species population viabilities. The points of indifference are slightly further right than  
349 for incomplete area sparing (for  $z=0.12-0.5$ , lower habitat quality sparing is better provided  
350 perfection exceeds 0.01-0.29). As before, crossover points shift left (relative to those for  
351 Ghanaian birds at 2007 production levels, Fig. 3a) for trees (Fig. 3b, d), Indian species (Fig.  
352 3c, d), and 2050 production targets (Fig. S2).

353

354 Comparing again with benchmark data, all points of indifference lie to the left of our upper-  
355 bound estimate (0.86; right-hand vertical lines in Fig. 3). Moreover for more plausible  $z$ -  
356 values (0.12-0.5) most points of indifference are left of our lower-bound benchmark (0.1;  
357 left-hand vertical lines) – the only exceptions are for  $z \geq 0.5$ , for Ghanaian birds (at 2007 and  
358 2050 production) and Indian birds (at 2007 production). For most combinations of  $z$ -values,  
359 study regions, taxa and production target, it is only when the quality of spared land is almost  
360 zero that land sharing becomes more favourable.

361

#### 362 *Co-occurrence of incomplete area and lower habitat quality imperfections*

363 Fig. 4 summarises the relative performance of sparing and sharing when both forms of  
364 imperfection operate concurrently. Each curve shows, for a given  $z$ -value, the combinations  
365 of imperfection scores below which sharing performs better than sparing. Hence for any  
366 given taxon, region and  $z$ -value line, the  $y$ -axis value where  $x=1$  (i.e. when habitat quality  
367 perfection=1) is the corresponding point of indifference for imperfect area sparing in Fig. 2;  
368 likewise for the same line the  $x$ -axis value where  $y=1$  is the point of indifference for imperfect  
369 habitat quality sparing in Fig. 3. For combinations of perfection values above the lines which

370 link these points, land sparing outperforms sharing; below these lines, sharing outperforms  
371 sparing.

372

373 Two findings emerge. For most  $z$ -values, both taxa, both regions and both production levels  
374 (Fig. S3), land sparing outperforms sharing except when at least one perfection score is very  
375 low. At our upper-bound benchmarks (grey circles in Fig. 4), land sparing is still favoured  
376 over sharing for  $z \leq 0.5$ . Even when both types of imperfection are operating at our lower-  
377 bound benchmarks (black diamonds in Fig. 4), sparing still outperforms sharing for all cases  
378 where  $z \leq 0.25$ , except for Ghanaian birds. The second observation is that the curves are  
379 convex. This means a moderate increase in whichever perfection score is lower can  
380 compensate for a (sometimes much) greater decrease in the higher perfection score.

381

### 382 *Global range size and population viabilities*

383 The population viabilities of individual small- and large-range species of Ghanaian birds at  
384 the point of indifference between sharing and imperfect sparing (in terms of cross-species  
385 mean viability) are presented in Fig. 5 (for 2007 production). This disaggregation reveals that  
386 sharing and imperfect sparing, even though equivalent in averaged effect, have very different  
387 impacts on small- and large-range species. Sharing is associated with lower viability of small-  
388 range species and greater viability of large-range species than is either form of imperfect  
389 sparing (for Ghanaian trees, Indian birds and trees, and 2050 production, see Table S1 and  
390 Fig. S4). This result means that from the perspective of species with small global ranges,  
391 even lower degrees of perfection are required before imperfect sparing performs as badly as  
392 land sharing.

393

394

395 **Discussion**

396 We set out to assess how imperfections in land sparing affect its performance relative to land  
397 sharing. In the absence of explicit land-sparing policies, rebound effects, land speculation and  
398 expansion of other land uses all mean yield increases spare less land for native vegetation  
399 than is theoretically possible (Ewers et al., 2009; Tschardt et al., 2012; Carrasco et al  
400 2014), while edge effects, inadequate protection, and poor or delayed restoration mean  
401 spared land may be of lower quality for wild species from areas of native vegetation assessed  
402 during field surveys (Rey Benayas et al., 2009; Law and Wilson, 2015; Lamb et al., 2016a).

403

404 Incorporating these imperfections into models does indeed reduce mean species population  
405 viability compared with perfect land sparing. For incomplete area sparing, this underscores  
406 the need (highlighted by Phalan et al. 2016) for effective policy mechanisms linking yield  
407 increases to the protection of unfarmed land for nature. Examples could include subsidy or  
408 loan schemes with coupled incentives for yield improvements and habitat conservation (as in  
409 Gola Forest, Sierra Leone; Stand For Trees, 2015), land-use zoning (used in the National  
410 Afforestation Programme in India; Ministry of Environment and Forest, 2009), and strategic  
411 deployment of yield-enhancing infrastructure away from land conversion frontiers (Laurance  
412 et al. 2014; Phalan et al. 2016). Likewise, for sparing to provide as much conservation benefit  
413 as possible efforts are needed to limit edge effects, protect spared vegetation and deliver  
414 timely, high-quality habitat restoration. But even under pessimistic scenarios for each of these  
415 imperfections, and allowing for them to co-occur, land sparing was almost always the least  
416 bad option for the taxa we examined. Moreover, even lower degrees of perfection would still  
417 outperform sharing for narrowly distributed species, which are typically the main focus of  
418 conservation concern.

419

420 Our conclusions vary somewhat depending upon the relationship between a population's size  
421 and its viability. A better understanding of this relationship is clearly a high priority for  
422 conservation. Our approach builds on the methods of Clements et al. (2011) and addresses the  
423 primary criticism of Akçakaya et al. (2011) by including a baseline population size. It is  
424 possible that Allee effects mean that the true relationship may not be approximated by a  
425 simple power law, but instead be sigmoidal (Dennis, 1989). But Allee effects only occur at  
426 very small population sizes, typically well below those in this study. We thus consider that,  
427 given the range of  $z$ -values we explored, we have identified the likely bounds of the level of  
428 perfection required for land sparing to achieve higher mean population viabilities than land  
429 sharing.

430

431 A key feature of our model is that it compares biodiversity outcomes of land-use strategies  
432 within regions which are homogeneous for climate, soils and topography. This simplification  
433 means our model in its current form is inappropriate for predicting biodiversity outcomes in  
434 heterogeneous regions (Macchi et al. 2016). But such areas are often important for  
435 conservation (e.g. Struebig et al., 2015), and modelling them within a sparing/sharing  
436 framework could be addressed by subdividing them into homogeneous, separately modelled  
437 subareas. An alternative could be to compare spatially-explicit land-use scenarios that use  
438 information linking each species' population density and agricultural yields to those  
439 ecological variables that underpin the region's heterogeneity; in principle this could highlight  
440 areas where either production or conservation could be prioritised at minimal cost (Grau et al.  
441 2013), but would require data on causal relationships between covariates, yields and species'  
442 abundances that are rarely available. One other framework involves building production-  
443 possibility frontiers of land-use for particular regions; results so far have supported land

444 sparing (Law et al., 2015, 2017), but further work is needed using data on a broader suite of  
445 species.

446

447 Our pre-agricultural baselines have limitations. While we believe they are the most  
448 appropriate reference point for comparing the outcomes of different scenarios, there are  
449 uncertainties in estimating pre-agricultural population densities. Remaining areas of native  
450 vegetation have changed since the introduction of farming (Gardner et al., 2009) – in  
451 particular in the absence of pre- and post-colonial human influences (such as the extirpation  
452 of many large mammals), the mixture of successional stages in some landscapes may have  
453 been different. Collecting sufficient information to account for such changes for many  
454 species would be very challenging. However, in the specific landscapes studied here we have  
455 no evidence of gross changes in the composition of native vegetation – we found no  
456 suggestion that moist tropical forests in Ghana were once more open (Phalan 2009), while in  
457 northern India we identified only two grassland-dependent bird species (out of 174 species  
458 studied; Phalan et al., 2011). We therefore suggest that our baselines provide a reasonable  
459 characterization of species' population sizes in each region prior to the advent of farming.

460

461

462 Turning to other concerns about land sparing, there is a perception that land sharing is more  
463 compatible with smallholder farming (e.g. Fischer et al., 2017). However, land sparing could  
464 also be implemented in ways which support and are supported by smallholders (Chandler et  
465 al. 2013). There are concerns that the range and magnitude of ecosystem services could  
466 decrease with a shift from land sharing to sparing (Fischer et al., 2017). However, land  
467 sparing does not mean prioritising high yields at any cost, and will only be viable if it sustains  
468 productive landscapes, including the ecosystem services they provide. We lack data to



469 predict the long-term implications of contrasting approaches to land use for soils (Dupouey et  
470 al., 2002) and ecosystem services (Kremen and Miles 2012), but there is growing evidence  
471 that land sparing would be preferable for carbon storage and sequestration (Gilroy et al.,  
472 2014b; Lamb et al., 2016b; Williams et al., forthcoming). However more evidence is needed  
473 before general conclusions can be drawn.

474

475 One last caveat is that our calculations assume that the low-yielding areas assessed during  
476 field surveys are representative of the agriculture that would be supported under land sharing.  
477 However, this assumption may be false – it is likely that farmers who currently farm at low  
478 yields include those who care most about nature, and/or who farm in more remote areas close  
479 to native vegetation patches which boost on-farm biodiversity via spill-over (as in Gilroy et  
480 al., 2014a). If agri-environment schemes were rolled out more broadly, these would support  
481 less biodiversity if newly-enrolled farmers cared less about nature or newly-enrolled farms  
482 were more distant from native vegetation. This would reduce estimated population sizes and  
483 population viabilities under land sharing below those suggested here.

484

485 Most current policy interventions for reconciling biodiversity conservation with agricultural  
486 production are conceptually aligned with land sharing (e.g. calls by the Ghanaian Ministry of  
487 Food and Agriculture [2002] for greater use of agro-forestry and mixed farming; government  
488 encouragement of agro-forestry in India [Ravindranath et al., 2008]; and Pillar Two funding  
489 under the Common Agricultural Policy [IoG, 2018]). Protected area establishment and  
490 sustainable intensification initiatives are also widespread, but land-sparing policies to link  
491 and coordinate such initiatives are rare (Phalan et al. 2016). If land sharing interventions were  
492 proving sufficient to slow biodiversity loss, there might be little incentive to consider land  
493 sparing. Extinctions and population declines, however, continue. Recently, this dire situation

494 has prompted calls for greatly increased allocation of land for conserving wild nature: the  
495 Half-Earth concept (Wilson 2016) and Nature Needs Half (Nature Needs Half, 2017). To  
496 scale-up conservation to such an extent without compromising agricultural production would  
497 require sustainable high-yield farming in areas that remain cultivated (Balmford and Green  
498 2017).

499

500 We conclude by reiterating that imperfections in the implementation of land sparing  
501 substantially reduce estimated population viabilities and hence the benefits of such an  
502 approach. However, even if such imperfections are not addressed they are unlikely to be of  
503 sufficient magnitude as to make land sharing a more desirable option. For wild species –  
504 especially those with small global ranges – land sparing remains the least bad approach for  
505 reconciling conservation and food production. The challenge remains to develop and test  
506 policy mechanisms that link yield growth directly to reductions in farmland area (or  
507 constraints on its expansion), and to ensure spared native vegetation is of high quality.

508

#### 509 **Authors' contributions**

510 BB, REG and AB conceived the idea, and designed the methods; BP and MO acquired the  
511 data], which BB analysed; BB and AB drafted the paper and REG and BP critically revised it.  
512 All authors approved the final version for publication.

513

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520

521 **Data accessibility**

522 All data used in the article was sourced from the published literature and citations to all  
523 sources are provided in the text.

524

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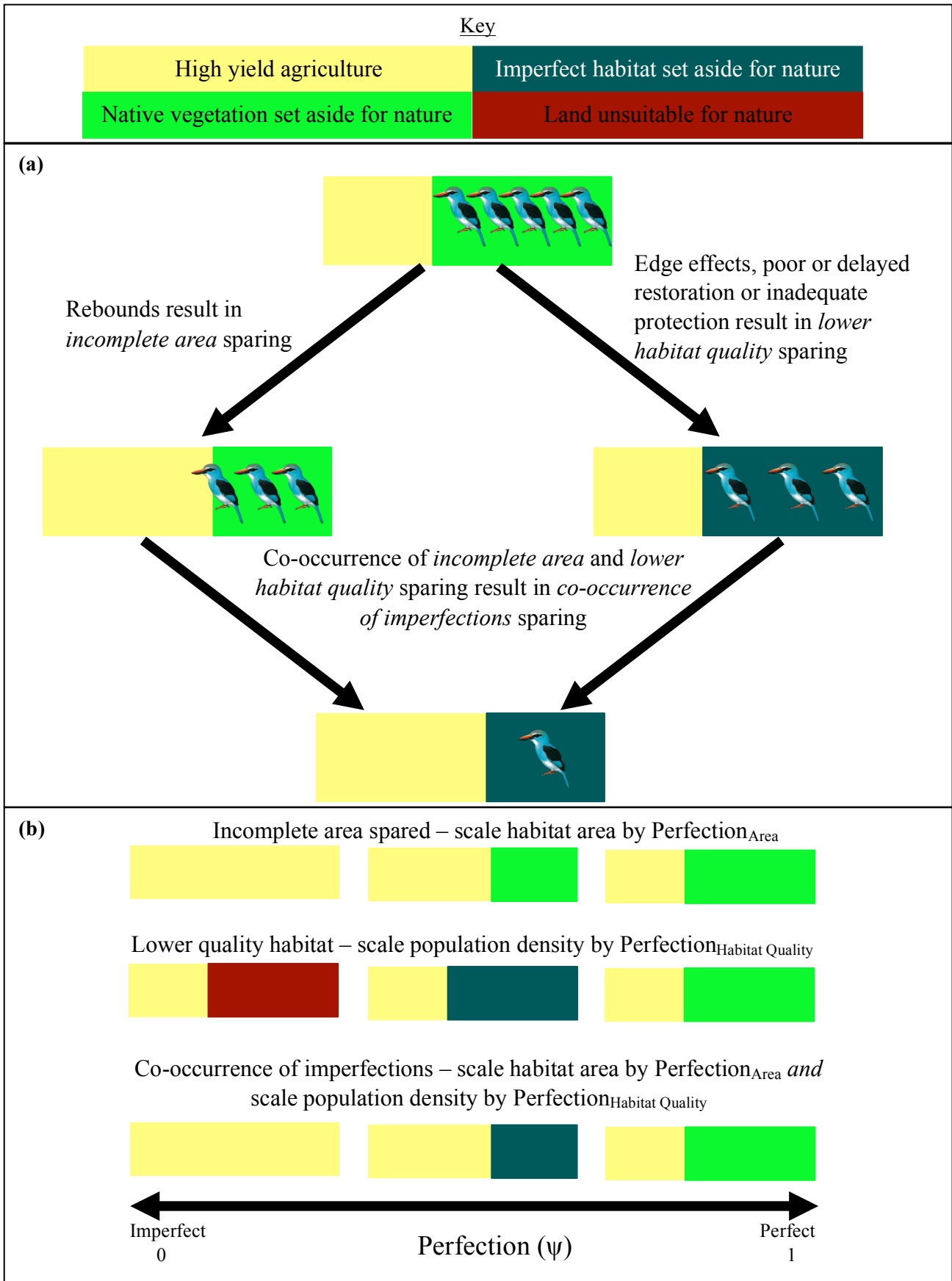
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768 Figure 1 – Potential imperfections in the implementation of land sparing.  
769 Cartoons illustrate (a) how land sparing may be imperfect; and (b) the gradients in  
770 imperfection which we modelled. Bars represent regions composed of native vegetation  
771 (green) and high yield farmland (yellow). Previous analyses, [top of (a)] assume that yield  
772 increases result in proportionate decreases in the area under farming and corresponding  
773 increases in the area of native vegetation, which is the same quality for wild species as that  
774 assessed during surveys. Under incomplete area sparing [middle left of (a)] a portion of the  
775 land that could, in principle, be spared is used for additional high-yield farming. Under lower  
776 habitat quality sparing [middle right of (a)], spared land is of lower quality. These  
777 imperfections can co-occur [bottom of (a)]. We model these imperfections along a gradient  
778 [shown in (b)] from perfect land sparing [extreme right of (b)] to wholly imperfect sparing.  
779 For incomplete area sparing [top of (b)] the area spared land is reduced so that when wholly  
780 imperfect no native vegetation is spared [top left of (b)]. For lower habitat quality sparing  
781 [middle of (b)] the population density of a species in native vegetation is reduced until  
782 eventually the native vegetation supports none of it [middle left of (b)]. For co-occurrence of  
783 imperfection sparing [bottom of (b)], the area of spared land and the population density of a  
784 species in native vegetation are reduced.  $\psi$ =perfection score.

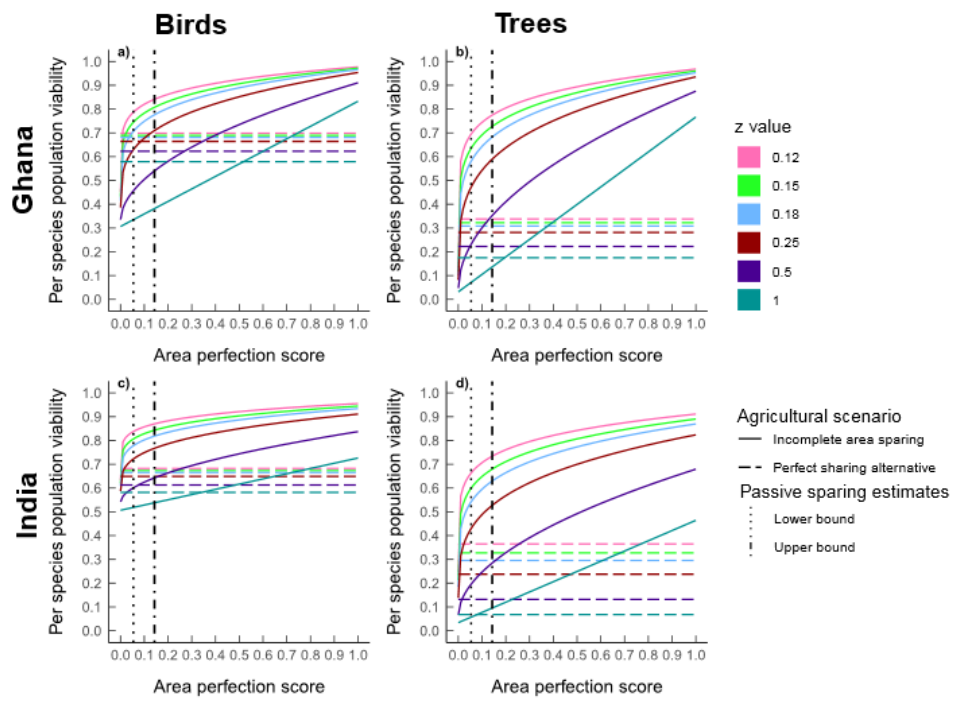
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795 Figure 2 – Population viabilities under incomplete area sparing, for the 2007 production  
796 target.

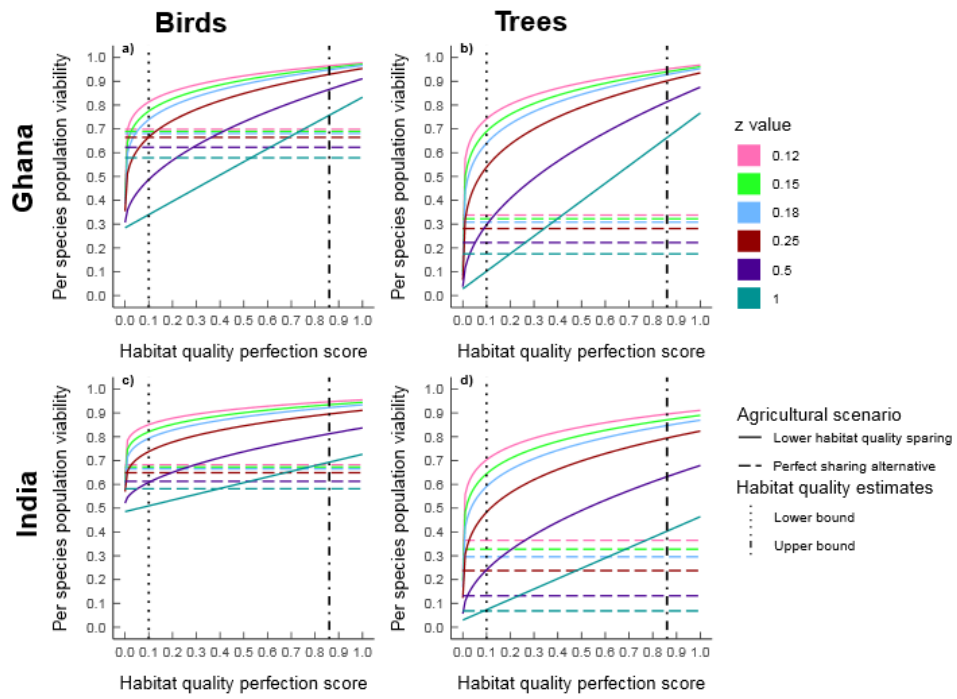
797 Mean population viability in relation to the perfection of land sparing (solid lines), when  
798 rebound effect cause incomplete area sparing. Different  $z$ -values (colours) reflect uncertainty  
799 in the relationship between population size and viability. Curved lines show mean population  
800 viability under land sparing, with dashed horizontal lines showing mean viability (for  
801 corresponding  $z$ -values) under perfect sharing. Lines for imperfect land sparing and perfect  
802 land sharing lines cross at the point of indifference between the two alternatives. To the right  
803 of these points, imperfect land sparing outperforms sharing. Vertical lines represent upper-  
804 and lower-bound empirical estimates of passive sparing (as observed in Ewers et al. 2009).

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817 Figure 3 – Population viabilities under lower habitat quality sparing, for the 2007 production  
818 target.  
819 Mean population viability in relation to the perfection of land sparing (solid lines), when poor  
820 or delayed restoration, inadequate protection, or edge effects results in lower habitat quality  
821 sparing. As in Fig. 2 different  $z$ -values (colours) reflect uncertainty in the relationship  
822 between population size and viability, curved lines show mean population viability under  
823 land sparing, dashed horizontal lines show mean viability (for corresponding  $z$ -values) under  
824 perfect sharing, and vertical lines represent upper- and lower-bound estimates for likely  
825 habitat perfections (see text). To the right of the points where corresponding lines for  
826 imperfect land sparing and perfect land sharing cross, imperfect land sparing outperforms  
827 sharing.

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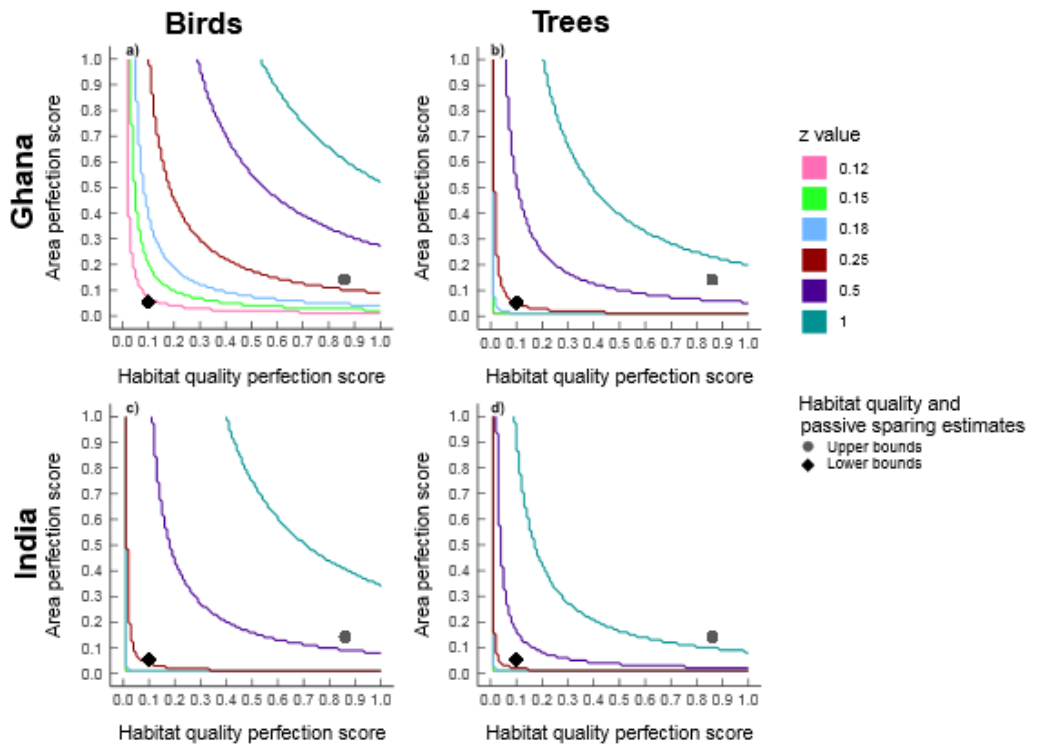
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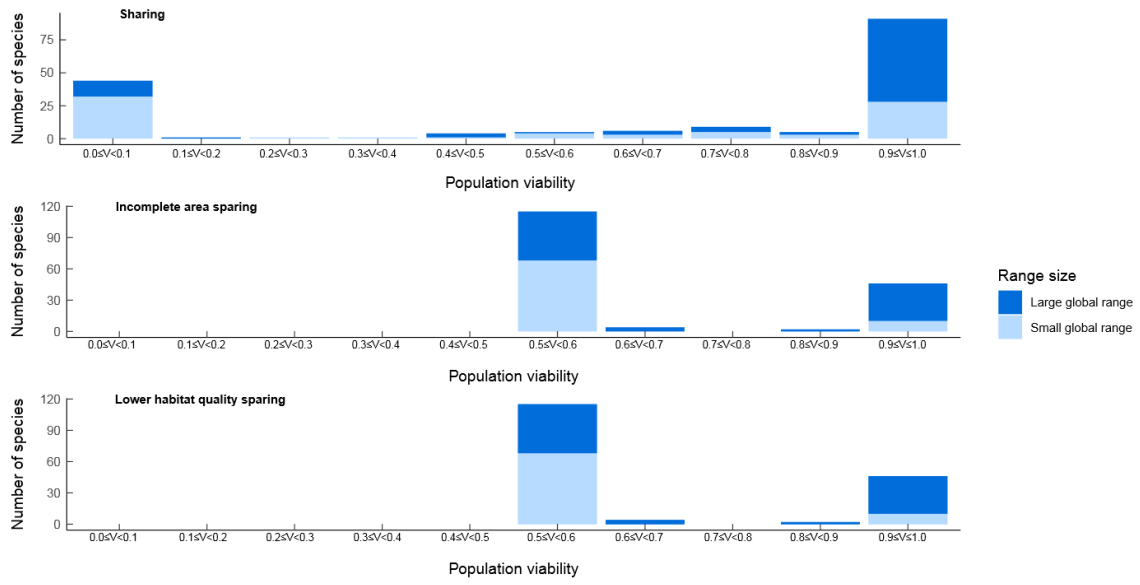
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840 Figure 4 – Combinations of perfection scores resulting in indifference between land sparing  
841 and sharing given co-occurrence of imperfections in land sparing, for the 2007 production  
842 target.

843 As in Figs. 2 and 3, different  $z$ -values (colours) reflect uncertainty in the relationship between  
844 population size and viability. Above lines, land sparing outperforms land sharing. The points  
845 on each plot represent combinations of our benchmark perfection scores (upper bound-upper  
846 bound [grey circle]; and lower bound-lower bound [black diamond]), and reveal that in most  
847 cases even co-occurring incomplete area and lower habitat quality sparing outperforms land  
848 sharing, given plausible values of  $z$  (0.12-0.5).

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853 Figure 5 – frequency distributions of population viabilities of individual species at the point  
854 of indifference between land sharing, incomplete area sparing and lower habitat quality  
855 sparing.  
856 Data are for Ghanaian birds, for the 2007 production target, and for  $z=0.25$  (see also Table  
857 S1; Fig. S4). Species are divided into those with large and small global ranges (as reported in  
858 Phalan et al., 2011). Individual species viabilities ( $V$ ) are calculated at the point of  
859 indifference – in terms of means species population viabilities – between land sparing and  
860 sharing, but when disaggregated to species level both forms of imperfect sparing result in  
861 higher population viabilities (compared to those under land sharing) for species with small  
862 global ranges, and lower ones for large-range species.