

1 **To what extent could edge effects and habitat fragmentation diminish the potential**  
2 **benefits of land sparing?**

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10 **Abstract**

11 Land sharing and land sparing are contrasting proposals for minimising the impacts of  
12 agriculture on wild species. Edge effects (biophysical gradients near habitat boundaries)  
13 might reduce population sizes on spared land, particularly in highly-fragmented landscapes,  
14 so might change conclusions about whether land sparing or land sharing is better for species'  
15 persistence. We assessed this possibility by modelling the population sizes of 120 Ghanaian  
16 bird species in the presence of a range of hypothetical edge effects under land-sparing and  
17 land-sharing strategies, and at different levels of habitat fragmentation and agricultural  
18 production. We found that edge effects can reduce population densities on spared land, and in  
19 highly-fragmented landscapes can - at modest levels of agricultural production combined  
20 with high edge penetration distances - cause the optimal strategy to switch from land sparing  
21 to land sharing. Nevertheless, land sparing maximised population sizes for more species in  
22 most cases tested. This conclusion was best supported for sensitive species with small global  
23 geographical ranges, which are likely to include those of greatest future conservation  
24 concern. The size of patches of spared land affected conservation outcomes: population sizes  
25 were maximised under a land-sparing strategy that spared large blocks of natural habitat of  
26 ~1,000 or, better, ~10,000 ha. To effect land sparing in practice would require policies that  
27 promoted both increases in agricultural yield and the establishment or protection of natural  
28 habitats on spared land. Because the optimum scale of patches of spared land for edge-  
29 sensitive species is generally larger than the size of individual farms, policies that facilitate  
30 coordinated action by farmers or other land managers might be required.

31

32 **Keywords:** agriculture; agri-environment; biodiversity conservation; habitat fragmentation;  
33 habitat loss; land sharing.

34 **1 Introduction**

35 Agriculture represents one of the greatest threats to the future persistence of wild species.  
36 Cropland and pasture occupy around 40% of ice-free land (Foley et al., 2011), and growing  
37 demand for agricultural products drives ongoing deforestation (Geist and Lambin, 2002),  
38 threatening more terrestrial species with extinction than any other sector (IUCN, 2015). Two  
39 divergent, although not mutually exclusive, strategies have been proposed in response to this  
40 threat: land sparing and land sharing. Land sparing involves increasing agricultural yields  
41 (production per unit area) so that the area required for farmland can be reduced, compared  
42 with what would otherwise be required to produce the same quantity of products, allowing  
43 natural habitats to be retained or restored in other places (Green et al., 2005). Land sharing  
44 integrates conservation and farming in the same landscape through wildlife-friendly farming  
45 practices such as the retention of small woodlots, hedges and ponds or the adoption of  
46 agricultural practices that allow wild species to persist within the cropland or pasture itself  
47 (Fischer et al., 2014; Tschardt et al., 2012). However, land sharing can reduce yields if it  
48 requires the presence of small unfarmed areas within the farmed landscape or reduction of  
49 inputs to crop or pasture management. It can therefore require more farmland for a given  
50 level of agricultural production, increasing pressure to convert natural habitats (Green et al.,  
51 2005).

52 Empirical studies to date have assessed the potential effects of land sparing and  
53 sharing on region-wide total population size of species of birds and trees in Ghana and India  
54 (Phalan et al., 2011b), birds in Uganda (Hulme et al., 2013), birds in the Eurasian steppes  
55 (Kamp et al., 2015) and birds, dung beetles and grasses in the Brazilian and Uruguayan  
56 pampas (Dotta, 2013). These studies concluded that in every region and for each taxon  
57 studied, land sparing would benefit more of the species assessed than land sharing, by  
58 allowing larger total populations in farmed and unfarmed landscapes combined (Chandler et

59 al., 2013; Hulme et al., 2013; Phalan et al., 2011b). An analysis of ‘small-scale land sparing’  
60 similarly concluded that it had greater biodiversity value than a land-sharing alternative  
61 (Chandler et al., 2013). However, none of these studies took into account the possible  
62 influence of edge effects – changes in physical and ecological parameters (population  
63 densities, species richness, community composition, vegetation structure, microclimate, light  
64 intensity, nutrient concentrations etc.) that occur near patch boundaries (Ries et al., 2004). It  
65 has been demonstrated that edge effects spilling onto farmland can alter conclusions about  
66 whether land sparing or land sharing is optimal (Gilroy et al., 2014a), but no study has  
67 quantified whether edge effects in natural habitats on spared land itself might similarly affect  
68 the optimal strategy.

69           This is an important gap for at least three reasons. First, species classified as  
70 'losers' from agriculture that are favoured by land sparing (sensu Phalan et al. (2011b) have  
71 higher population densities in spared natural habitats than on farmland, but edge effects might  
72 reduce this difference (Laurance et al., 2011). This is especially true of many species of  
73 conservation concern, which tend to be sensitive to patch edges and reliant on intact core  
74 areas within large patches of natural habitat for long-term persistence (Banks-Leite et al.,  
75 2010; Laurance et al., 2002; Zakaria et al., 2013). Second, edge effects become increasingly  
76 important in highly-fragmented landscapes (Ewers and Didham, 2007; Laurance et al., 2002),  
77 so the effectiveness of land sparing might depend upon the scale of spared habitat patches  
78 (Phalan et al., 2011a). Finally, if the higher yields required for land sparing are accompanied  
79 by greater agro-chemical use or result in greater structural contrast with natural habitats, this  
80 could result in high-yield farming causing larger edge effects within adjacent natural habitat  
81 than low-yield farming (Barnes et al., 2014; Didham et al., 2015; Frost et al., 2014), which  
82 might compromise the conservation benefits of the land-sparing strategy.

83                   Hence, there is a need to better understand the consequences of edge effects for  
84 land-sparing and land-sharing strategies. To address this we developed simulation models for  
85 120 Ghanaian bird species previously assessed in a sparing–sharing context and known to be  
86 negatively affected by agriculture (Phalan et al., 2011b). We defined a range of plausible  
87 land-use and ecological scenarios that varied in the degree of habitat fragmentation, the  
88 magnitude of hypothetical edge effects and the level of agricultural production, and  
89 quantified species’ region-wide population sizes under both land-sparing and land-sharing  
90 strategies. We used these models to re-assess, for this set of study species, the relative  
91 benefits of land sparing and land sharing in the presence of edge effects, and to shed light on  
92 the importance of the spatial scale of spared land.

93 **2 Materials and methods**

94 **2.1 Study region and test landscapes**

95 The study region comprised 9,117 km<sup>2</sup> of cultivable land in the Western, Central and Eastern  
96 Regions of Ghana (Figure A1) and has three main land uses: tropical forest (“forest”),  
97 extensive low- and mid-yielding mixtures of cropland, small plantations and fallow bushland  
98 (“farm mosaic”), and high-yielding plantations of oil palm and other crops (“high-yield  
99 plantation”). This region was selected because it contains a wide range of farming systems  
100 from low-yielding wildlife-friendly smallholder systems through to large-scale industrial  
101 plantations of oil palm, a globally important and rapidly expanding crop (Phalan et al.,  
102 2011b). It contains forests of global conservation importance subject to ongoing deforestation  
103 (FAO, 2010) and fragmentation (Holbech, 2005), as is also the case in much of the humid  
104 tropics.

105 We selected a 20 x 20 kilometre test landscape within the study region to conduct  
106 our analysis of hypothetical edge effects (Figure A1). Its size was chosen to be as large as  
107 possible whilst keeping the computational demands of the spatial modelling tractable. The  
108 test landscape had similar proportions of different land-covers to those of the wider study  
109 region. Using recorded land-cover in this landscape in 2007 as a starting point, we generated  
110 a series of alternative landscapes to reflect land-sparing and land-sharing strategies, varying  
111 the degree of future total agricultural production and habitat fragmentation. The mean  
112 agricultural production per unit area per year averaged over the whole area covered by the  
113 test landscape (the “production target”) was varied between actual annual production per unit  
114 area in the study region in 2007 (19 GJ ha<sup>-1</sup> y<sup>-1</sup>; food energy basis) and estimated production  
115 in 2050 (37 GJ ha<sup>-1</sup> y<sup>-1</sup>) (Phalan et al., 2011b).

116 To develop land-sharing landscapes we assumed that the farmed areas within the  
117 test landscape were entirely covered by farm mosaic. We therefore applied the following

118 sequential procedure, starting with 2007 observed land cover and modifying it until the  
119 production target was met: (i) areas of high-yield plantation were converted to farm mosaic;  
120 (ii) low-yielding farm mosaic was converted to mid-yielding farm mosaic; and finally (iii)  
121 forest was cleared to make way for additional mid-yielding farm mosaic (assuming that forest  
122 adjoining farmland was cleared first). The resulting land-sharing landscapes were dominated  
123 by farm mosaic with scattered remnant forest blocks (Shr1 and Shr2, Figure 1).

124 Under a land-sparing approach, the objective is to minimise farmland area, so we  
125 assumed that the entire production target was met through high-yield plantation, with the  
126 remainder of the test landscape being converted to forest. We created five types of land-  
127 sparing landscapes with varying degrees of fragmentation in the restored forest. The  
128 alternatives encompassed a range in habitat fragmentation that might plausibly develop under  
129 different policy and planning regimes. At one extreme, land-use planning driven by the state  
130 or co-operative action by groups of landholders might produce non-fragmented landscapes  
131 dominated by large blocks of unfarmed land and farmland. We generated two landscapes of  
132 this type (panels Spr1 and Spr6, Figure 1) by enlarging pre-existing areas of forest and high-  
133 yield plantation within the test landscape, resulting in forest blocks in the order of 10,000 ha  
134 in area (Table A1). At the other extreme, land-use planning at the scale of the individual land-  
135 holder might produce a highly-fragmented landscape with farm-scale spared fragments.  
136 Whether or not a strategy that resulted in such fine-scaled patches should be termed land-  
137 sparing is debatable (Fischer et al., 2014; Phalan et al., 2011a; Balmford, Green & Phalan,  
138 2015). Nonetheless, we included these landscapes to make our assessment as broad as  
139 possible. We generated two such landscapes (Spr5 and Spr10), with patches as small as 1 ha  
140 (Table A1), and a series of landscapes of intermediate degrees of fragmentation (Spr2 to Spr4  
141 and Spr7 to Spr9). We generated these landscapes by allocating 50 m x 50 m grid squares (a  
142 0.25 ha planning unit chosen to represent a small field) to different land uses using the

143 Modified Random Cluster algorithm (Saura and Martínez-Millán, 2000) implemented in the  
144 “secr” package (Efford, 2014) of the R programming language (R Core Team, 2014). We  
145 specified the degree of habitat fragmentation (via a fragmentation parameter  $p$ ), the minimum  
146 area of individual patches (between 1 and 40 ha) and the proportion of forest in the landscape  
147 such that the production target was met (Table A1). We generated ten replicates of each  
148 randomly generated landscape and report all results as a mean over those ten replicates.

## 149 **2.2 Modelling hypothetical edge effects**

150 We developed population models for 120 bird species present in the study region and known  
151 to be negatively affected by agriculture (all those species classified as ‘losers’ by Phalan et  
152 al., 2011b; Table A2). We selected these species because their populations can be reduced by  
153 agricultural expansion (Phalan et al., 2011b) and because we could make reasonable  
154 assumptions about the form of edge response for such species (see below). We did not assess  
155 the 47 species recorded in the study region that benefit from agriculture (species classified as  
156 ‘winners’ by Phalan et al., 2011b) because farming has positive or neutral effects on their  
157 populations regardless of land sparing or land sharing (Phalan et al., 2011b), and because we  
158 had insufficient information to make reasonable assumptions about edge responses for such  
159 species. However, in principle our approach could be extended to these species also.

160 Population densities in forest, farm mosaic and high-yield plantation at least 800  
161 m from fragment edges were obtained using existing regression models (“density-yield  
162 functions”) that relate local (1 km square) population density of each species to agricultural  
163 production per unit area of the whole farmed landscape (yield) reported by Phalan et al.,  
164 (2011b). We combined these functions with assumptions about hypothetical edge effects to  
165 predict the change in population densities near forest-farmland edges.

166 Our assumptions about hypothetical edge effects were derived from the literature  
167 on edge responses and attempted to capture three important patterns observed empirically.



168 Firstly, it is widely-observed that many species associated with natural habitats tend to avoid  
169 habitat edges, with population densities that increase with distance from the edge to a  
170 maximum in core areas (Banks-Leite et al., 2010; Ewers and Didham, 2007, 2006; Laurance  
171 et al., 2002; Zakaria et al., 2013). Secondly, there is increasing evidence that edge effects can  
172 extend further into patches of natural habitat where the farming system is higher-yielding  
173 (Barnes et al., 2014; Didham et al., 2015; Frost et al., 2014). Finally, it is observed in practice  
174 that edge effects do not only apply within patches of natural habitat; in addition, a ‘spill-over’  
175 effect can boost population densities on farmland near to forest edges (Ewers and Didham,  
176 2008; Gilroy et al., 2014a).

177 To model these dynamics, we adapted the approach of Ewers and Didham (2008)  
178 and defined population density  $\rho(d)$  as a sigmoidal function:

$$179 \quad \rho(d) = \rho_{fa} + (\rho_{fo} - \rho_{fa}) / (1 + \exp((\beta_2 - d)/\beta_3)), \quad (1)$$

180 where  $d$  is the distance to the nearest fragment edge;  $\rho_{fo}$  and  $\rho_{fa}$  are the population densities  
181 beyond the influence of edges in forest and farmland (high-yield plantation or farm mosaic)  
182 respectively, obtained from density-yield functions in Phalan et al., (2011b); following the  
183 notation of Ewers and Didham (2008),  $\beta_2$  dictates the distance from the fragment edge to the  
184 inflection point of the sigmoid curve (hereafter the “edge penetration distance”); and  $\beta_3$   
185 dictates the steepness of the sigmoid curve. Together,  $\beta_2$  and  $\beta_3$  dictate the distance to which  
186 hypothetical edge effects penetrate into forest.

187 We varied these parameters to reflect different degrees of sensitivity in the focal  
188 species and to specify edge effects that extended further into forest when farming was at high  
189 yields (as assumed under land sparing). The latter was achieved by setting the edge  
190 penetration distance to zero in land-sharing landscapes and varying it between zero and 800  
191 m in land-sparing landscapes (Table A3; Figure 2). Our assumptions for  $\beta_2$  and  $\beta_3$  in land-  
192 sparing landscapes were such that, at the upper-end of the range, 90% of the change in

193 population density between farmland and forest was realised 1600 m in from the fragment  
194 edge, greatly exceeding the normal edge penetration distance typically observed in birds  
195 (Fletcher, 2005; Laurance et al., 2002; Ries et al., 2004; Sisk et al., 1997). Equation (1)  
196 predicts a positive ‘spill-over’ effect on farmland near to forest: we retained this spill-over in  
197 land-sharing landscapes (Figure 2a), but conservatively assumed no spill-over in land-sparing  
198 landscapes (Figure 2b). In aggregate, these assumptions resulted in significantly lower  
199 population densities in natural habitat patches near patch edges in land-sparing compared  
200 with land-sharing landscapes.

### 201 **2.3 Computing population sizes**

202 Each test landscape was converted to a 25 m x 25 m grid (after Fletcher 2005) and for each  
203 combination of production target, habitat fragmentation and edge penetration distance, the  
204 population density of each species was computed in each grid cell using equation (1). Each  
205 species’ total population size under land sparing (landscapes Spr1 to Spr10) was compared  
206 with that under the land-sharing landscape with the equivalent production target (Shr1 and  
207 Shr2). Of the 120 focal species, 12 exhibit a peak in population density at an intermediate  
208 level of yield so can be favoured instead by some intermediate strategy (Phalan et al., 2011b).  
209 We therefore also computed the population sizes of these species in landscapes with  
210 intermediate yield, applying the same edge effect assumptions, and classifying species as  
211 ‘intermediate’ if this was the best strategy (see Supplementary Methods 1). To check whether  
212 our findings were sensitive to random variation in the Modified Random Cluster algorithm,  
213 we computed the standard error in predicted population size for each species across the 10  
214 replicates of each type of random landscape.

215 We next compared the population impacts of different scenarios. To do this we  
216 needed a baseline population against which to measure change and we elected to calculate  
217 this baseline assuming the entire region was forested. For each scenario we then grouped

218 species by predicted population change relative to this baseline. To derive an aggregate  
219 measure of population change across all species, following Gregory et al., (2005) we  
220 calculated the geometric mean population change,  $[\prod_i (P_i / P_{i,fo})]^{1/120}$ , where  $P_i$  is the  
221 predicted population of the  $i^{\text{th}}$  species and  $P_{i,fo}$  is its all-forest baseline population. Finally, we  
222 examined results separately for groups of species classified by global range size. After Phalan  
223 et al., (2011b), we classified species with a global extent of occurrence of less than 3 million  
224  $\text{km}^2$ , as defined by the World Bird Database (BirdLife International, 2010), as having a small  
225 global range; remaining species were classified as having a large global range. We made this  
226 distinction to investigate whether species with a small global range – those potentially at a  
227 greater risk of global extinction – are more or less susceptible to edge effects and habitat  
228 fragmentation.

## 229 **3 Results**

### 230 **3.1 Species-level responses**

231 Population size simulations indicated that hypothetical edge effects reduced region-wide  
232 population sizes under land sparing, with total population size decreasing as fragmentation  
233 and edge penetration distance increased. In contrast, modelled population sizes were  
234 insensitive to hypothetical edge effects in land-sharing landscapes (Figure 3) because of the  
235 assumption that the negative edge effect within forest was balanced by a positive spill-over  
236 effect in farmland. The consequences for the relative benefits of land sparing and land  
237 sharing varied among species. Species favoured by land sparing in the absence of  
238 hypothetical edge effects (89 of the 120 focal species at the 2050 production target) exhibited  
239 a variety of responses. In some cases, land sparing remained the most favourable strategy  
240 regardless of edge effects and habitat fragmentation (e.g. Figure 3a), while for other species  
241 the optimal strategy switched to land sharing (e.g. Figure 3b). However, species favoured by  
242 land sharing in the absence of hypothetical edge effects (23 species at the 2050 production

243 target) all continued to be favoured by land sharing in the presence of edge effects (e.g.  
244 Figure 3c), again reflecting the assumed difference in edge response for land-sparing and  
245 land-sharing landscapes. Random variation in the Modified Random Cluster algorithm had  
246 negligible impact. The standard error in predicted population sizes was in general less than  
247 0.5% of the mean, and in no case exceeded 2% of the mean predicted population size.

### 248 **3.2 Comparing land sparing and land sharing across all species**

249 The relative numbers of species favoured by land sparing, land sharing or an intermediate  
250 strategy depended upon the production target, the edge penetration distance and the degree of  
251 habitat fragmentation (Figure 4). At the 2007 production target, the best overall strategy was  
252 land sparing except in highly-fragmented landscapes combined with high edge penetration  
253 distances (Figure 4a). This finding was more pronounced for species with a small global  
254 range (68 of the 120 focal species). More of these species were favoured by land sparing than  
255 by land sharing except under the most extreme fragmentation tested (Figure 4b). For species  
256 with a large global range (52 species), results were mixed (Figure 4c). Land sharing was  
257 favoured over a highly-fragmented land-sparing strategy, but land sparing based on large  
258 (approaching 1,000 ha or more) blocks of spared land favoured more species than land  
259 sharing. At the 2050 production target these trends were amplified. Land sparing and land  
260 sharing were equivalent in the most extreme case tested, but otherwise land sparing  
261 consistently benefited more species irrespective of edge effects, habitat fragmentation and  
262 species' range size (Figure 4d-f).

### 263 **3.3 Population declines relative to the all-forest baseline**

264 The vast majority of species were predicted to have smaller total populations in the presence  
265 of agriculture than would be the case with an all-forest baseline (Figure 5), as expected given  
266 the set of species analysed. The potential conservation benefits of land sparing depended

267 strongly on the degree of habitat fragmentation and the scale of land sparing. If land was  
268 spared in small fragments, hypothetical edge effects eroded the benefits of land sparing and  
269 population sizes declined. However, sparing large blocks of land (e.g. 785 ha or more  
270 assuming a 200 m edge penetration distance; Table A1; Figure 5c) resulted in a better  
271 outcome, with the populations of all species remaining above 50% of the all-forest baseline  
272 population at the 2007 production target. Under the equivalent land-sharing scenario, around  
273 half of species were predicted to decline in number by more than 50% relative to the baseline.  
274 At the 2050 production target population effects were more severe, with well over half of all  
275 species predicted to decline to less than 50% of the all-forest baseline in all scenarios tested.  
276 But a land-sparing strategy based on large blocks of spared land (e.g. 1,425 ha or more  
277 assuming a 200 m edge penetration distance; Table A1; Figure 5d) minimised population  
278 declines, maintaining the populations of all species above 25% of the all-forest baseline.  
279 Under the equivalent land-sharing scenario, 77 of the 120 focal species were predicted to  
280 suffer severe declines to below 25% of the baseline. The geometric mean population change  
281 for all species reinforced these findings (Figure 3d). Irrespective of edge effects, mean  
282 population size was maximised under a land-sparing strategy based on large-scale spared  
283 land. Importantly, this gain in population size in non-fragmented landscapes was greatest  
284 when edge penetration distances were largest, suggesting that the most sensitive species have  
285 the most to gain from a large-scale land-sparing approach.

#### 286 **4 Discussion**

287 For the Ghanaian bird species we assessed, our results suggest that a land-sparing strategy in  
288 which high-yield farming is linked to retention or restoration of large blocks of natural habitat  
289 would offer substantial conservation benefits over land sharing, over sparing smaller  
290 fragments, and over intermediate-yield approaches to meeting production targets. The species  
291 with the most to lose from the loss and fragmentation of forest habitat were the most edge-

292 sensitive species. Population sizes were maximised with contiguous patches 1,000 or even  
293 10,000 ha in size. Although we assessed only a limited number of species of a single  
294 taxonomic group and in one tropical region, these findings are in accord with previous  
295 investigations of edge effects across a range of taxa and global regions: it has been argued  
296 that species of greatest conservation concern, which tend to be the most sensitive to edges  
297 and the most reliant on core areas, require large, intact blocks of habitat to ensure long-term  
298 persistence (Banks-Leite et al., 2010; Connor et al., 2000; Ewers and Didham, 2008; Ferraz et  
299 al., 2003; Laurance et al., 2011; Woodroffe and Ginsberg, 1998; Zakaria et al., 2013). The  
300 framework we present here formalises this in a land-sparing – land-sharing context for the  
301 first time.

302           For species with a large global range and at the 2007 production target, land  
303 sharing was favoured over a highly-fragmented land-sparing strategy (Figure 4c). However,  
304 if agricultural production increases as expected in Ghana (Phalan et al., 2011b), pursuing a  
305 land-sharing strategy would commit the majority of the focal species to severe population  
306 declines (Figure 5). These declines reflect the fate of forest-dependent species as forest is  
307 cleared to meet rising agricultural demand under land-sharing scenarios (compare Shr2 with  
308 Shr1 in Figure 1). These findings complement previous work demonstrating that land sharing  
309 benefits from the presence of large proximate areas of intact natural habitats (Gilroy et al.,  
310 2014a), but our results go further by highlighting that such a strategy will become  
311 increasingly untenable for the species we assessed as agricultural demand rises.

312           Some observers argue in favour of land sharing because of concerns about the  
313 impact of high yield farming on farmland biodiversity, pollinator services, soil structure,  
314 animal welfare, local air and water quality and ecosystem services provided by farmland  
315 (Fischer et al., 2014; Tscharntke et al., 2012; Vandermeer and Perfecto, 2007). Land sparing  
316 could also have profound consequences for rural communities, the cultural value of

317 landscapes and the livelihoods of those that live in and depend on the agricultural matrix  
318 (Perfecto and Vandermeer, 2010). Other observers argue that the land sparing - land sharing  
319 framework introduces an unhelpful dichotomy and that real-world solutions should draw on  
320 both approaches (Kremen, 2015). We did not address these topics directly in this study (but  
321 see Phalan et al. 2011a and Balmford et al., (2015)). We acknowledge that they are of critical  
322 importance and encourage quantitative comparison of a broader range of land-use outcomes  
323 across sparing, sharing and intermediate approaches.

324           Our analyses could be improved by modelling explicitly species' dispersal and  
325 metapopulation dynamics. Landscapes arising from a land-sharing strategy might be more  
326 permeable for the dispersal of some species (Daily et al., 2003; Tschardt et al., 2012), but  
327 these benefits may not be realised if remaining forest refuges are converted to agriculture in  
328 response to growing demand. Land sharing may not enhance connectivity for the species that  
329 need it most: many forest species in the present study region were never recorded in even the  
330 lowest-yielding farm mosaic (Phalan et al., 2011b), echoing findings elsewhere (Laurance et  
331 al., 2002). Under a land-sparing strategy, higher-yielding farmland might be less hospitable  
332 for species dispersal, but total forested area would be larger, with increased mean patch size  
333 and reduced inter-patch distance both likely to benefit metapopulation dynamics (Falcu and  
334 Estades, 2007; Hodgson et al., 2011, 2009).

335           Our projections assume that population densities (in the absence of edge effects)  
336 on spared land equal those in the existing forest blocks surveyed by Phalan et al., (2011b).  
337 Timescales for forest regeneration can be substantial, but because the forest surveyed by  
338 Phalan et al., (2011b) was already degraded to varying degrees by logging, hunting and  
339 trapping, mining and small-scale farming (Annorabah et al., in press; Arcilla et al., 2015), two  
340 to three decades may be sufficient for well-managed secondary forest on spared land to  
341 support similar population densities for many species (Gilroy et al., 2014b). In addition, we

342 assumed that population densities derived from Phalan et al., (2011b) were free from any  
343 distorting influence of edge effects. In practice, edge effects within forest and spill-over  
344 effects on farmland near to forest may distort those density estimates. However, we expect  
345 any distortion to be small because the Phalan et al., (2011b) data were collected more than  
346 800 m away from edges.

347           We made three key assumptions in modelling the response of species to fragment  
348 edges. First, we assumed that the focal species were ‘edge avoiding’, with population  
349 densities that increased with distance from the fragment edge. This assumption reflects both  
350 the nature of the focal species, which are known to decline in the presence of agriculture  
351 (Phalan et al., 2011b), and the empirical observation that sensitive species tend to avoid  
352 habitat edges (Banks-Leite et al., 2010; Zakaria et al., 2013). It is possible that some of the  
353 focal species are in fact ‘edge preferring’, exhibiting a peak in population densities near  
354 edges. These species would do better in fragmented landscapes, but such species tend to be  
355 habitat generalists of limited conservation concern (Laurance et al., 2002; Zakaria et al.,  
356 2013) so were not a focus of this study, though our method could be adapted to incorporate  
357 such species. Under land sharing, we conservatively assumed an edge penetration distance of  
358 zero and negative edge effects in forest that were offset by positive spill-over on farmland.  
359 This is likely to overestimate populations under land sharing for many of the focal species,  
360 which are known to avoid farmland altogether (Phalan et al., 2011b). On the other hand,  
361 under land sparing we modelled edge penetration distances of up to 800 m (corresponding to  
362 90% of the population density change occurring 1600 m inside forest). Edge effects reported  
363 in birds typically extend to no more than a few hundred metres (Brand and George, 2001;  
364 Fletcher, 2005; Laurance et al., 2002; Ries et al., 2004; Sisk et al., 1997) but we included  
365 higher values to allow for the fact that field studies may be biased towards underestimating  
366 the true extent of edge effects (Ewers and Didham, 2008), to allow for edge effects



367 potentially being more pervasive in higher-yielding landscapes (Barnes et al., 2014; Didham  
368 et al., 2015), and because greater edge extents are observed in other taxa (Brodie et al., 2015;  
369 Ewers and Didham, 2008; Lenz et al., 2014; Woodroffe and Ginsberg, 1998).

370           The approach we present here could easily be adapted to accommodate different  
371 focal taxa and regions with different natural biomes and agriculture. Although we assessed  
372 only a limited number of species of a single taxon and in one tropical region, it is possible  
373 that our broad conclusions might hold for some other regions and taxa too, because key  
374 features of this study system appear to be ubiquitous. Edge-sensitive species reliant on core  
375 area are found almost universally across taxa, including in trees (Núñez-Ávila et al., 2013),  
376 primates (Lenz et al., 2014) and other mammals (Brodie et al., 2015; Woodroffe and  
377 Ginsberg, 1998), invertebrates (Ewers and Didham, 2008, 2006; Soga et al., 2012) and  
378 herbivorous insects (Guimarães et al., 2014). Likewise, while we investigated a tropical forest  
379 biome, edge effects are pervasive in other natural biomes, including temperate forests  
380 (Crockatt and Bebb, 2015), peatlands (Wilson et al., 2014), grasslands (Perkins et al.,  
381 2013), wetlands (Suvorov et al., 2014) and steppe (Knight et al., 2014).

382           Implementing land sparing in practice requires linked policies that promoted both  
383 increases in agricultural yield and the retention or restoration of natural habitats on spared  
384 land. Our results suggest that, for edge-sensitive species, the conservation potential of a land-  
385 sparing strategy would be greatest if large blocks of natural habitat could be restored in the  
386 farmed landscape. Because the optimum scale of spared land for some species is likely to be  
387 larger than the scale of most individual farms, policies that facilitate coordinated action by  
388 farmers or other land managers might be most effective (McKenzie et al., 2013).

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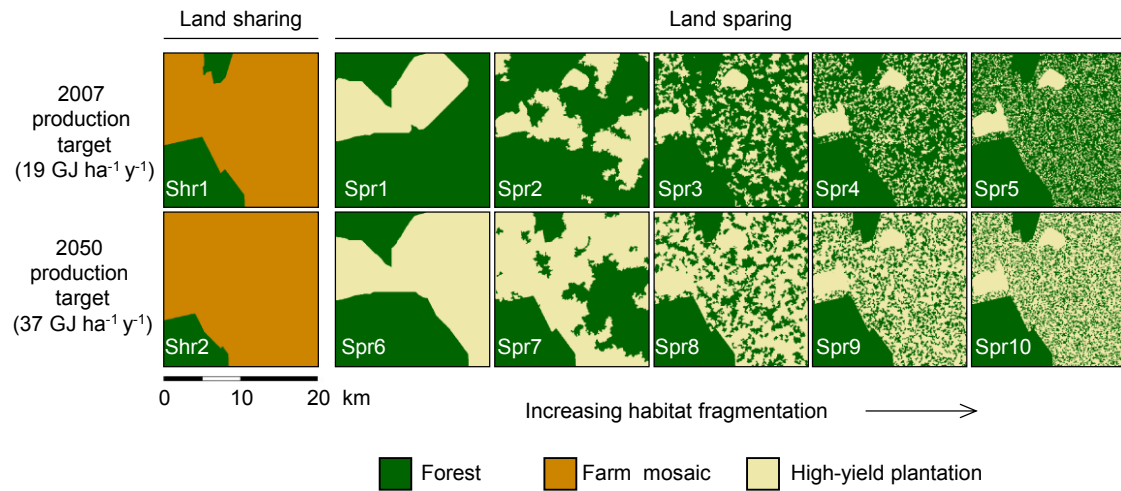
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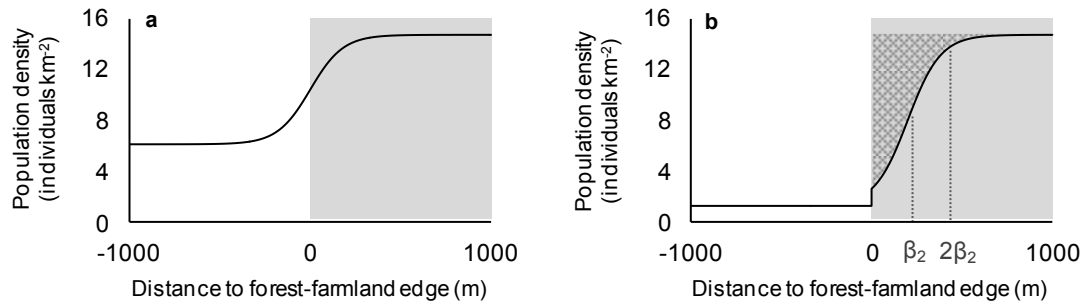
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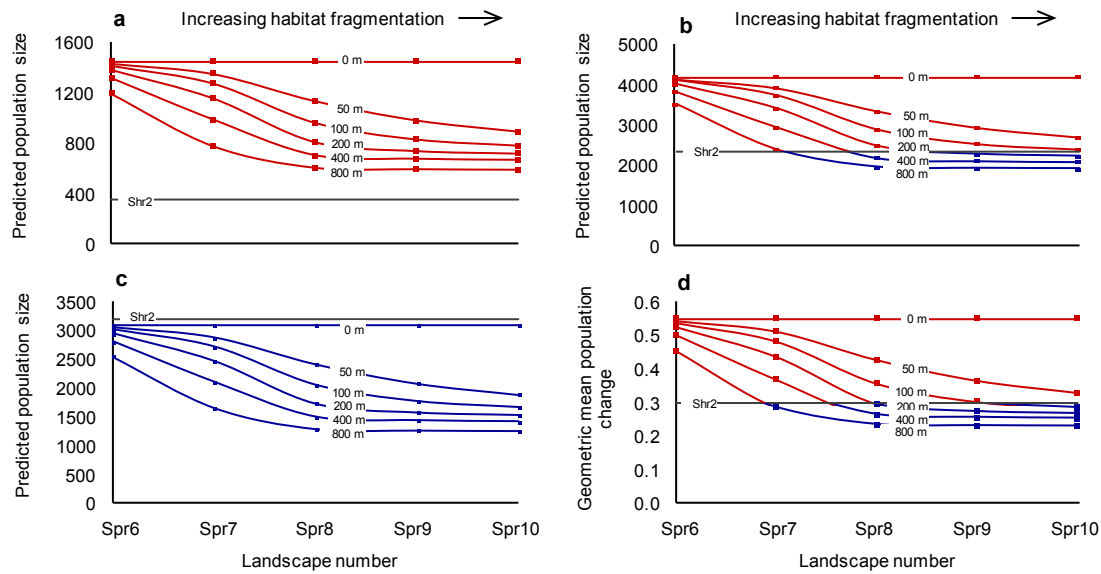
564

565 **Figure 1: The land-sparing and land-sharing test landscapes.** Shown for both the 2007 and 2050 production  
 566 targets. Ten replicates of each random landscape (Spr2 through Spr5 and Spr7 through Spr10) were generated;  
 567 representative examples are shown here.



568

569 **Figure 2: Assumed edge responses.** Figures indicate the change in population density where forest (indicated  
 570 by light-grey shading) meets farm mosaic under land sharing **a**, or meets high-yield plantation under land  
 571 sparing **b**. Shown for the example species African green pigeon (*Treron calvus*). Parameter  $\beta_2$  dictates the  
 572 position of the inflection point of the sigmoid. Our assumptions for  $\beta_2$  and for the slope parameter  $\beta_3$  under land  
 573 sparing (Table A3) were such that 90% of the change in population density was realised at a distance of  $2\beta_2$  into  
 574 the forest. In **a**, the negative edge effect within forest is balanced by a positive spill-over effect in farmland. In  
 575 **b**, hatching indicates the net reduction in population density near edges caused by the assumed edge response in  
 576 land-sparing landscapes.



577

578 **Figure 3: The influence of habitat fragmentation and edge penetration distance on predicted population**

579 **size.** Red and blue lines represent the predicted population size under land-sparing landscapes at the 2050

580 production target (Spr6 through Spr10). Each line is labelled with the applicable edge penetration distance. Grey

581 lines indicate the predicted population size under the equivalent land-sharing landscape (Shr2) and are shown

582 for reference – the symmetrical edge response (Figure 2a) means that the variation in population size at different

583 edge penetration distances in land-sharing landscapes is negligible on the scale of the plot. Colouring indicates

584 whether land sparing (red) or land sharing (blue) maximised the population size. Results are shown for three

585 representative species: **a** Large-billed puffback (*Dryoscopus sabini*), favoured by land sparing irrespective of

586 hypothetical edge effects and habitat fragmentation; **b** Chestnut wattle-eye (*Platysteira castanea*), a species

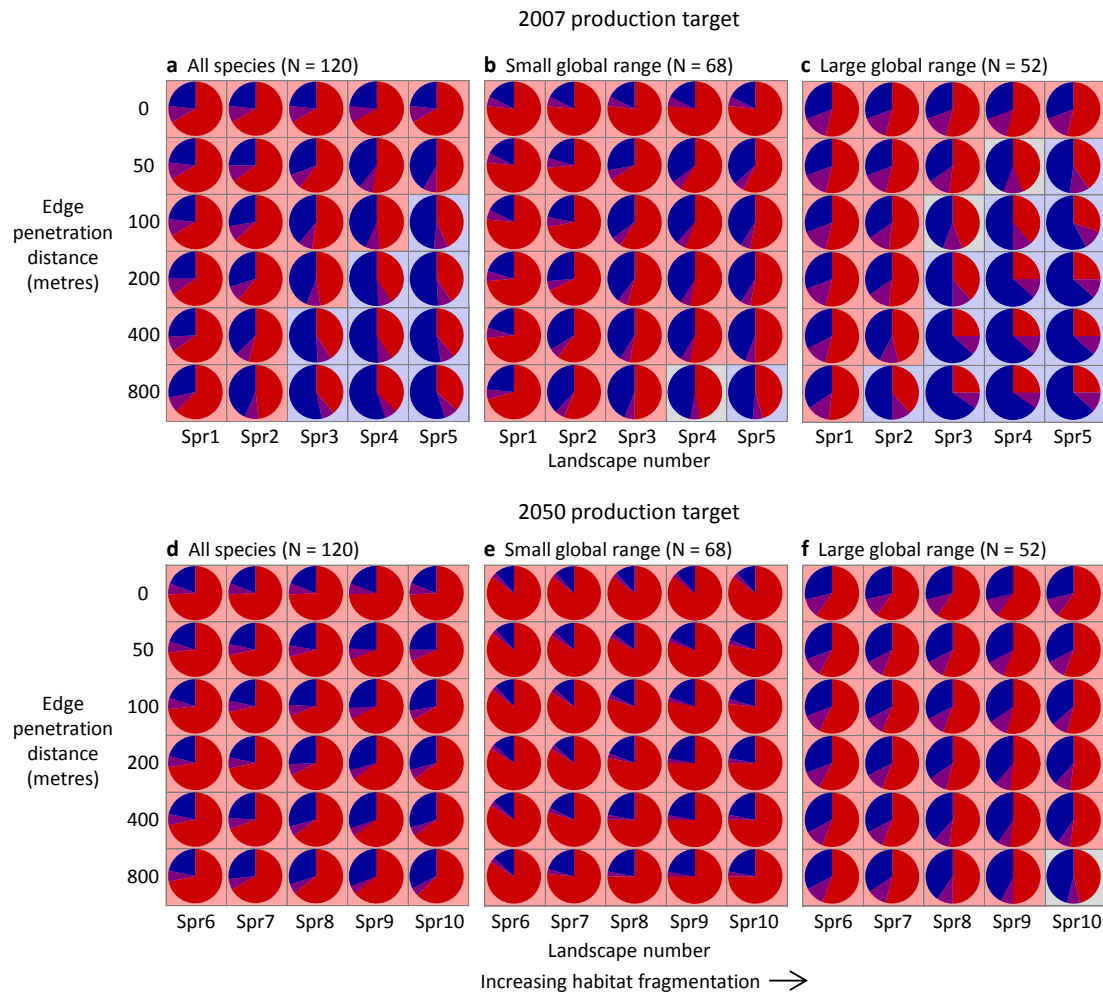
587 favoured by land sparing in the absence of hypothetical edge effects for which the best strategy can switch to

588 land sharing in fragmented landscapes; and **c** Buff-throated sunbird (*Nectarinia adelberti*), favoured by land

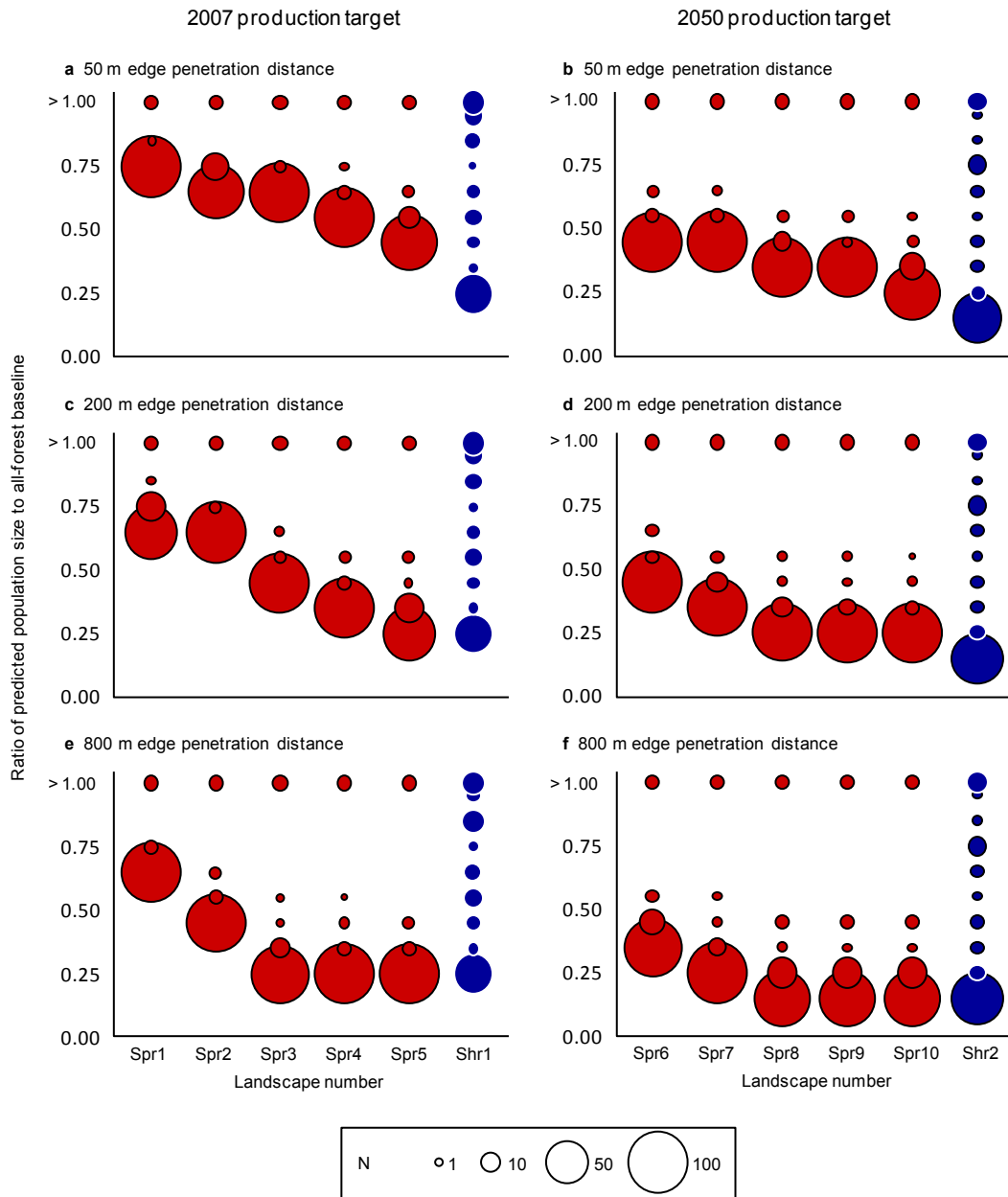
589 sharing in all cases. Panel **d** shows the geometric mean population change over all 120 focal species relative to

590 an all-forest baseline.





591  
 592 **Figure 4: Comparing land sparing and land sharing across all species.** Proportions of species for which land  
 593 sparing (pie chart segments coloured dark red), land sharing (dark blue) or some intermediate strategy (purple)  
 594 gave the highest population size for each combination of production target, edge penetration distance and habitat  
 595 fragmentation. In each case, the population size under land-sparing landscapes (Spr1 through Spr10) was  
 596 compared with the equivalent land-sharing landscape (Shr1 and Shr2) to assess the better strategy. Background  
 597 shading indicates whether land sparing (light red) or land sharing (light blue) favoured a greater number of  
 598 species, or whether the strategies were equivalent (light grey). N indicates the number of species assessed in  
 599 each panel.



600

601 **Figure 5: Predicted population size relative to the all-forest baseline.** Relative population size shown in  
 602 relation to edge penetration distance, fragmentation and production target. Species grouped by predicted relative  
 603 population in 2007 and 2050. Number of species (N) in each group is indicated by the size of circles. Results  
 604 compare land sharing (coloured blue; landscapes Shr1 and Shr2) with land sparing (coloured red; landscapes  
 605 Spr1 through Spr10) for a subset of the edge penetration distances tested: **a-b** 50 m; **c-d** 200 m; and **e-f** 800 m.

606 **Appendix A. Supplementary material**

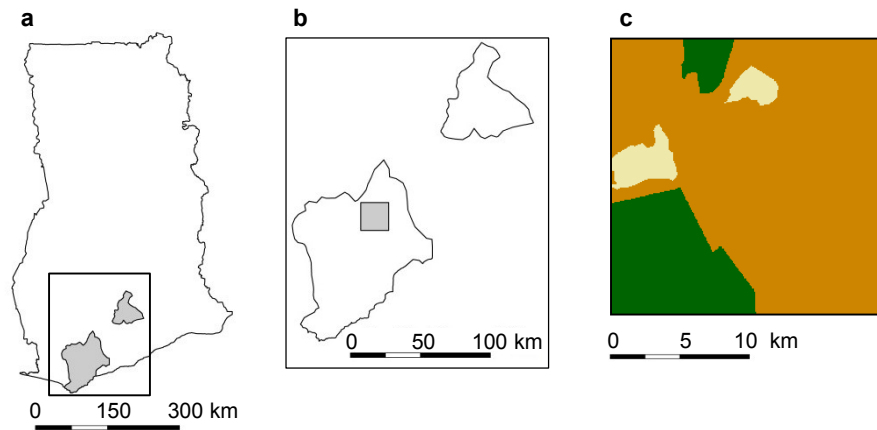
607 **Figure A1.** Study region and test landscape.

608 **Table A1.** Characteristics of the land sparing landscapes.

609 **Table A2.** List of study species.

610 **Table A3.** Edge effect parameters.

611 **Supplementary Methods 1.** Intermediate species.



612

613

614

615

**Figure A1: Study region and test landscape.** **a** Map of Ghana with study region shaded. **b** Enlargement of the study region showing the test landscape shaded. **c** Land cover in 2007 in the test landscape comprising forest (dark green), farm mosaic (brown-orange), and high-yield plantation (pale yellow).

**Table A1: Characteristics of the land sparing landscapes**

Landscape number	Production target (GJ ha <sup>-1</sup> y <sup>-1</sup> )	Specified parameters			Mean patch size (± std. error) (ha)
		Proportion of landscape forested	Fragmentation parameter ( <i>p</i> )	Minimum patch size (ha)	
Spr1	19	0.72	NA	NA	11,337
Spr2	19	0.72	0.59	40	785 (± 86)
Spr3	19	0.72	0.50	10	95 (± 3)
Spr4	19	0.72	0.30	5	31 (± 0.4)
Spr5	19	0.72	0.10	1	10 (± 0.1)
Spr6	37	0.45	NA	NA	9,003
Spr7	37	0.45	0.59	40	1,425 (± 93)
Spr8	37	0.45	0.50	10	157 (± 5)
Spr9	37	0.45	0.30	5	50 (± 0.6)
Spr10	37	0.45	0.10	1	17 (± 0.1)

617 Landscape number corresponds to Figure 1. Specified parameters were used in generating random landscapes  
618 using the Modified Random Cluster algorithm. Landscapes Spr1 and Spr6 were not generated at random and  
619 parameters not needed in such cases are marked NA. Mean patch sizes for randomly generated landscapes are  
620 reported as the mean (± standard error) over the ten replicates. The fragmentation parameter *p* has a threshold  
621 value at 0.593 (Saura and Martínez-Millán, 2000), which is reflected in the chosen *p* values.

**Table A2: List of study species**

<i>Columba iriditorques</i>	<i>Platysteira castanea</i>	<i>Illadopsis cleaveri</i>
<i>Streptopelia semitorquata</i>	<i>Prionops caniceps</i>	<i>Illadopsis rufipennis</i>
<i>Turtur tympanistria</i>	<i>Dryoscopus gambensis</i>	<i>Illadopsis fulvescens</i>
<i>Turtur brehmeri</i>	<i>Dryoscopus sabini</i>	<i>Zosterops senegalensis</i>
<i>Treron calvus</i>	<i>Laniarius leucorhynchus</i>	<i>Lamprotornis cupreocauda</i>
<i>Centropus leucogaster</i>	<i>Coracina azurea</i>	<i>Lamprotornis splendidus</i>
<i>Ceuthmochares aereus</i>	<i>Oriolus brachyrhynchus/nigripennis</i>	<i>Onychognathus fulgidus</i>
<i>Chrysococcyx klaas</i>	<i>Dicrurus atripennis</i>	<i>Neocossyphus poensis</i>
<i>Chrysococcyx cupreus</i>	<i>Dicrurus adsimilis</i>	<i>Stizorhina fraseri</i>
<i>Chrysococcyx caprius</i>	<i>Trochocercus nitens</i>	<i>Alethe diademata</i>
<i>Cercococcyx olivinus</i>	<i>Terpsiphone rufiventer</i>	<i>Stiphornis erythrothorax</i>
<i>Cuculus solitarius</i>	<i>Erythrocerus mcallii</i>	<i>Fraseria ocreata</i>
<i>Cuculus clamosus</i>	<i>Pholidornis rushiae</i>	<i>Fraseria cinerascens</i>
<i>Sarothrura pulchra</i>	<i>Apalis nigriceps</i>	<i>Muscicapa tessmanni</i>
<i>Tauraco macrorhynchus</i>	<i>Apalis sharpii</i>	<i>Myioparus griseigularis</i>
<i>Polyboroides typus</i>	<i>Camaroptera superciliaris</i>	<i>Anthreptes fraseri</i>
<i>Urotiorchis macrourus</i>	<i>Andropadus gracilis</i>	<i>Anthreptes rectirostris</i>
<i>Buteo auguralis</i>	<i>Andropadus ansorgei</i>	<i>Anthreptes collaris</i>
<i>Apaloderma narina</i>	<i>Andropadus curvirostris</i>	<i>Nectarinia seimundi</i>
<i>Lophoceros semifasciatus</i>	<i>Andropadus gracilirostris</i>	<i>Nectarinia olivacea</i>
<i>Horizocerus albocristatus</i>	<i>Andropadus latirostris</i>	<i>Nectarinia cyanolaema</i>
<i>Bycanistes fistulator</i>	<i>Calyptocichla serina</i>	<i>Nectarinia adalberti</i>
<i>Halcyon badia</i>	<i>Baeopogon indicator</i>	<i>Nectarinia chloropygia</i>
<i>Halcyon malimbica</i>	<i>Ixonotus guttatus</i>	<i>Nectarinia minulla</i>
<i>Halcyon senegalensis</i>	<i>Thescelocichla leucopleura</i>	<i>Nectarinia cuprea</i>
<i>Buccanodon duchaillui</i>	<i>Phyllastrephus albigularis</i>	<i>Nectarinia coccinigaster</i>
<i>Gymnobucco peli/calvus</i>	<i>Phyllastrephus icterinus</i>	<i>Nectarinia superba</i>
<i>Pogoniulus scolopaceus</i>	<i>Bleda syndactylus</i>	<i>Passer griseus</i>
<i>Pogoniulus atroflavus</i>	<i>Bleda eximius</i>	<i>Ploceus aurantius</i>
<i>Pogoniulus subsulphureus</i>	<i>Bleda canicapillus</i>	<i>Ploceus tricolor</i>
<i>Pogoniulus bilineatus</i>	<i>Criniger barbatus</i>	<i>Ploceus albinucha</i>
<i>Tricholaema hirsuta</i>	<i>Criniger calurus</i>	<i>Malimbus scutatus</i>
<i>Lybius vieilloti</i>	<i>Criniger olivaceus</i>	<i>Malimbus nitens</i>
<i>Trachylaemus goffinii</i>	<i>Nicator chloris</i>	<i>Malimbus malimbicus</i>
<i>Prodotiscus insignis</i>	<i>Hippolais polyglotta</i>	<i>Malimbus rubricollis</i>
<i>Verreauxia africana</i>	<i>Macrosphenus kemp</i>	<i>Euplectes macroura</i>
<i>Dendropicops pyrrhogaster</i>	<i>Macrosphenus concolor</i>	<i>Nigrita fusconotus</i>
<i>Poicephalus gulielmi</i>	<i>Hylia prasina</i>	<i>Nigrita canicapillus</i>
<i>Smithornis rufolateralis</i>	<i>Eremomela badiceps</i>	<i>Pyrenestes ostrinus</i>
<i>Platysteira cyanea</i>	<i>Sylvietta virens</i>	<i>Motacilla flava</i>

**Table A3: Edge effect parameters**

Land sparing landscapes (forest - high-yield plantation edges)		Land sharing landscapes (forest - farm mosaic edges)	
Edge penetration distance ( $\beta_2$ ) (m)	Steepness ( $\beta_3$ ) (m)	Edge penetration distance ( $\beta_2$ ) (m)	Steepness ( $\beta_3$ ) (m)
0	0	0	0
50	23	0	23
100	46	0	46
200	91	0	91
400	182	0	182
800	364	0	364

625 Parameters used in equation (1) for land-sparing and land-sharing landscapes. Following Ewers & Didham  
626 (2008), we maintained constant proportionality between  $\beta_2$  and  $\beta_3$  in land-sparing landscapes, reflecting an  
627 assumption that edge responses that penetrate deeper into forest should exhibit a shallower slope.

## 628 **Supplementary Methods 1: Intermediate species**

629 12 of the 120 focal species exhibit a peak in population density at an intermediate level of  
630 yield, so can be favoured by some intermediate strategy (Phalan et al., 2011b). It is possible  
631 that in the presence of hypothetical edge effects these species may switch to being favoured  
632 by land sharing. Because generating 12 additional sets of test landscapes for these species  
633 (requiring approximately 1,000 additional landscapes in total, including random replicates)  
634 would be computationally impractical, we instead developed an approach allowing us to use  
635 the test landscapes generated for the main analysis. We estimated the populations  $Pop_i$  of  
636 these species in landscapes of intermediate yield using the model outlined in Green *et al.*  
637 (2005), which can be expressed in the absence of hypothetical edge effects as follows:

$$638 \quad Pop_i = (P/Y_i) \rho_i + (1 - P/Y_i) \rho_{fo}, \quad (A1)$$

639 where  $P$  is the production target,  $\rho_i$  is the peak population density exhibited at yield  $Y_i$  and  $\rho_{fo}$   
640 is the population density in forest. In the absence of edge effects,  $Pop_i$  can be calculated for a  
641 given production target by obtaining  $Y_i$ ,  $\rho_i$  and  $\rho_{fo}$  from the parameters for the density-yield  
642 curve for a given species (Phalan et al., 2011b).

643 In the presence of hypothetical edge effects, equation (A1) is modified as follows:

$$644 \quad Pop_i^* = (P/Y_i) \frac{\sum_j \rho_i^j}{A_{fa}} + (1 - P/Y_i) \frac{\sum_k \rho_{fo}^k}{A_{fo}} = (P/Y_i) \rho_i^* + (1 - P/Y_i) \rho_{fo}^*, \quad (A2)$$

645 where  $\rho_i^j$  is the population density in farmland in grid cell  $j$  in the presence of edge effects,  
646 and the summation is taken over all grid cells within farmland;  $A_{fa}$  is the area of farmland;  
647  $\rho_{fo}^k$  is the population density in forest in grid cell  $k$  in the presence of edge effects, and the  
648 summation is taken over all grid cells within forest; and  $A_{fo}$  is the area of forest. Thus  $\rho_i$  and  
649  $\rho_{fo}$  in equation (A2) are replaced with the area-weighted mean population densities in the  
650 presence of hypothetical edge effects in farmland ( $\rho_i^*$ ) and forest ( $\rho_{fo}^*$ ), respectively. To  
651 compute  $\rho_i^*$  and  $\rho_{fo}^*$  for the intermediate species we used the test landscapes generated for



652 the main analysis. We first calculated the peak yield  $Y_i$  for each species and found that for all  
653 intermediate species  $Y_i$  occurs in farm mosaic. Intermediate landscapes for these species  
654 would therefore contain areas of forest and farm mosaic. We next computed  $\rho_i^*$  and  $\rho_{fo}^*$  for  
655 each of the intermediate species and for each combination of production target, habitat  
656 fragmentation and edge penetration distance by applying equation (1) in the main text to each  
657 of the test landscapes in Figure 1. We used the values of  $\beta_2$  and  $\beta_3$  applicable to forest-farm  
658 mosaic edges in Table A3, we set  $\rho_{fa}$  in equation (1) equal to  $\rho_i$ , and we measured the area-  
659 weighted mean population densities in farmland and forest across the test landscape.  
660 Substituting the known values of  $P$  and  $Y_i$  along with the computed values of  $\rho_i^*$  and  $\rho_{fo}^*$  into  
661 equation (A2) allowed us to solve for the population of species under intermediate strategies.  
662 We found that three of the 12 intermediate species (*Lophoceros semifasciatus*, *Sylvietta*  
663 *virens* and *Nectarinia chloropygia*) switched to being favoured by land sharing in certain  
664 scenarios (see purple pie chart segments in Figure 4).