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

Anthony Lamb[a*], Andrew Balmford[a], Rhys E. Green[a,b] and Ben Phalan[a]

[a]Conservation Science Group, Department of Zoology, University of Cambridge, Downing St, Cambridge CB2 3EJ, UK

[b]RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy SG19 2DL, UK

[*]Corresponding author: email: ajl85@cam.ac.uk; ph. +44(0)1223 762936;
fax: +44 (0) 1223 336676

Abstract

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

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

1 Introduction

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

Empirical studies to date have assessed the potential effects of land sparing and sharing on region-wide total population size of species of birds and trees in Ghana and India (Phalan et al., 2011b), birds in Uganda (Hulme et al., 2013), birds in the Eurasian steppes (Kamp et al., 2015) and birds, dung beetles and grasses in the Brazilian and Uruguayan pampas (Dotta, 2013). These studies concluded that in every region and for each taxon studied, land sparing would benefit more of the species assessed than land sharing, by allowing larger total populations in farmed and unfarmed landscapes combined (Chandler et al., 2013; Hulme et al., 2013; Phalan et al., 2011b). An analysis of 'small-scale land sparing' similarly concluded that it had greater biodiversity value than a land-sharing alternative (Chandler et al., 2013). However, none of these studies took into account the possible influence of edge effects – changes in physical and ecological parameters (population densities, species richness, community composition, vegetation structure, microclimate, light intensity, nutrient concentrations etc.) that occur near patch boundaries (Ries et al., 2004). It has been demonstrated that edge effects spilling onto farmland can alter conclusions about whether land sparing or land sharing is optimal (Gilroy et al., 2014a), but no study has quantified whether edge effects in natural habitats on spared land itself might similarly affect the optimal strategy.

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

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

2 Materials and methods

2.1 Study region and test landscapes

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

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

To develop land-sharing landscapes we assumed that the farmed areas within the test landscape were entirely covered by farm mosaic. We therefore applied the following sequential procedure, starting with 2007 observed land cover and modifying it until the production target was met: (i) areas of high-yield plantation were converted to farm mosaic; (ii) low-yielding farm mosaic was converted to mid-yielding farm mosaic; and finally (iii) forest was cleared to make way for additional mid-yielding farm mosaic (assuming that forest adjoining farmland was cleared first). The resulting land-sharing landscapes were dominated by farm mosaic with scattered remnant forest blocks (Shr1 and Shr2, Figure 1).

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

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

2.2 Modelling hypothetical edge effects

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

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

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

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

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

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

where d is the distance to the nearest fragment edge; ρ_{fo} and ρ_{fa} are the population densities beyond the influence of edges in forest and farmland (high-yield plantation or farm mosaic) respectively, obtained from density-yield functions in Phalan et al., (2011b); following the notation of Ewers and Didham (2008), β_2 dictates the distance from the fragment edge to the inflection point of the sigmoid curve (hereafter the "edge penetration distance"); and β_3 dictates the steepness of the sigmoid curve. Together, β_2 and β_3 dictate the distance to which hypothetical edge effects penetrate into forest.

We varied these parameters to reflect different degrees of sensitivity in the focal species and to specify edge effects that extended further into forest when farming was at high yields (as assumed under land sparing). The latter was achieved by setting the edge penetration distance to zero in land-sharing landscapes and varying it between zero and 800 m in land-sparing landscapes (Table A3; Figure 2). Our assumptions for β_2 and β_3 in land-sparing landscapes were such that, at the upper-end of the range, 90% of the change in population density between farmland and forest was realised 1600 m in from the fragment edge, greatly exceeding the normal edge penetration distance typically observed in birds (Fletcher, 2005; Laurance et al., 2002; Ries et al., 2004; Sisk et al., 1997). Equation (1) predicts a positive 'spill-over' effect on farmland near to forest: we retained this spill-over in land-sharing landscapes (Figure 2a), but conservatively assumed no spill-over in land-sparing landscapes (Figure 2b). In aggregate, these assumptions resulted in significantly lower population densities in natural habitat patches near patch edges in land-sparing compared with land-sharing landscapes.

2.3 Computing population sizes

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

We next compared the population impacts of different scenarios. To do this we needed a baseline population against which to measure change and we elected to calculate this baseline assuming the entire region was forested. For each scenario we then grouped species by predicted population change relative to this baseline. To derive an aggregate measure of population change across all species, following Gregory et al., (2005) we calculated the geometric mean population change, $[\Pi_i (P_i / P_{i,fo})]^{1/120}$, where P_i is the predicted population of the i^{th} species and $P_{i,fo}$ is its all-forest baseline population. Finally, we examined results separately for groups of species classified by global range size. After Phalan et al., (2011b), we classified species with a global extent of occurrence of less than 3 million km^2, as defined by the World Bird Database (BirdLife International, 2010), as having a small global range; remaining species were classified as having a large global range. We made this distinction to investigate whether species with a small global range – those potentially at a greater risk of global extinction – are more or less susceptible to edge effects and habitat fragmentation.

3 Results

3.1 Species-level responses

Population size simulations indicated that hypothetical edge effects reduced region-wide population sizes under land sparing, with total population size decreasing as fragmentation and edge penetration distance increased. In contrast, modelled population sizes were insensitive to hypothetical edge effects in land-sharing landscapes (Figure 3) because of the assumption that the negative edge effect within forest was balanced by a positive spill-over effect in farmland. The consequences for the relative benefits of land sparing and land sharing varied among species. Species favoured by land sparing in the absence of hypothetical edge effects (89 of the 120 focal species at the 2050 production target) exhibited a variety of responses. In some cases, land sparing remained the most favourable strategy regardless of edge effects and habitat fragmentation (e.g. Figure 3a), while for other species the optimal strategy switched to land sharing (e.g. Figure 3b). However, species favoured by land sharing in the absence of hypothetical edge effects (23 species at the 2050 production target) all continued to be favoured by land sharing in the presence of edge effects (e.g. Figure 3c), again reflecting the assumed difference in edge response for land-sparing and land-sharing landscapes. Random variation in the Modified Random Cluster algorithm had negligible impact. The standard error in predicted population sizes was in general less than 0.5% of the mean, and in no case exceeded 2% of the mean predicted population size.

3.2 Comparing land sparing and land sharing across all species

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

3.3 Population declines relative to the all-forest baseline

The vast majority of species were predicted to have smaller total populations in the presence of agriculture than would be the case with an all-forest baseline (Figure 5), as expected given the set of species analysed. The potential conservation benefits of land sparing depended strongly on the degree of habitat fragmentation and the scale of land sparing. If land was spared in small fragments, hypothetical edge effects eroded the benefits of land sparing and population sizes declined. However, sparing large blocks of land (e.g. 785 ha or more assuming a 200 m edge penetration distance; Table A1; Figure 5c) resulted in a better outcome, with the populations of all species remaining above 50% of the all-forest baseline population at the 2007 production target. Under the equivalent land-sharing scenario, around half of species were predicted to decline in number by more than 50% relative to the baseline. At the 2050 production target population effects were more severe, with well over half of all species predicted to decline to less than 50% of the all-forest baseline in all scenarios tested. But a land-sparing strategy based on large blocks of spared land (e.g. 1,425 ha or more assuming a 200 m edge penetration distance; Table A1; Figure 5d) minimised population declines, maintaining the populations of all species above 25% of the all-forest baseline. Under the equivalent land-sharing scenario, 77 of the 120 focal species were predicted to suffer severe declines to below 25% of the baseline. The geometric mean population change for all species reinforced these findings (Figure 3d). Irrespective of edge effects, mean population size was maximised under a land-sparing strategy based on large-scale spared land. Importantly, this gain in population size in non-fragmented landscapes was greatest when edge penetration distances were largest, suggesting that the most sensitive species have the most to gain from a large-scale land-sparing approach.

4 Discussion

For the Ghanaian bird species we assessed, our results suggest that a land-sparing strategy in which high-yield farming is linked to retention or restoration of large blocks of natural habitat would offer substantial conservation benefits over land sharing, over sparing smaller fragments, and over intermediate-yield approaches to meeting production targets. The species with the most to lose from the loss and fragmentation of forest habitat were the most edge-sensitive species. Population sizes were maximised with contiguous patches 1,000 or even 10,000 ha in size. Although we assessed only a limited number of species of a single taxonomic group and in one tropical region, these findings are in accord with previous investigations of edge effects across a range of taxa and global regions: it has been argued that species of greatest conservation concern, which tend to be the most sensitive to edges and the most reliant on core areas, require large, intact blocks of habitat to ensure long-term persistence (Banks-Leite et al., 2010; Connor et al., 2000; Ewers and Didham, 2008; Ferraz et al., 2003; Laurance et al., 2011; Woodroffe and Ginsberg, 1998; Zakaria et al., 2013). The framework we present here formalises this in a land-sparing – land-sharing context for the first time.

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

Some observers argue in favour of land sharing because of concerns about the impact of high yield farming on farmland biodiversity, pollinator services, soil structure, animal welfare, local air and water quality and ecosystem services provided by farmland (Fischer et al., 2014; Tscharntke et al., 2012; Vandermeer and Perfecto, 2007). Land sparing could also have profound consequences for rural communities, the cultural value of landscapes and the livelihoods of those that live in and depend on the agricultural matrix (Perfecto and Vandermeer, 2010). Other observers argue that the land sparing - land sharing framework introduces an unhelpful dichotomy and that real-world solutions should draw on both approaches (Kremen, 2015). We did not address these topics directly in this study (but see Phalan et al. 2011a and Balmford et al., (2015)). We acknowledge that they are of critical importance and encourage quantitative comparison of a broader range of land-use outcomes across sparing, sharing and intermediate approaches.

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

Our projections assume that population densities (in the absence of edge effects) on spared land equal those in the existing forest blocks surveyed by Phalan et al., (2011b). Timescales for forest regeneration can be substantial, but because the forest surveyed by Phalan et al., (2011b) was already degraded to varying degrees by logging, hunting and trapping, mining and small-scale farming (Annorbah et al., in press; Arcilla et al., 2015), two to three decades may be sufficient for well-managed secondary forest on spared land to support similar population densities for many species (Gilroy et al., 2014b). In addition, we assumed that population densities derived from Phalan et al., (2011b) were free from any distorting influence of edge effects. In practice, edge effects within forest and spill-over effects on farmland near to forest may distort those density estimates. However, we expect any distortion to be small because the Phalan et al., (2011b) data were collected more than 800 m away from edges.

We made three key assumptions in modelling the response of species to fragment edges. First, we assumed that the focal species were ‘edge avoiding’, with population densities that increased with distance from the fragment edge. This assumption reflects both the nature of the focal species, which are known to decline in the presence of agriculture (Phalan et al., 2011b), and the empirical observation that sensitive species tend to avoid habitat edges (Banks-Leite et al., 2010; Zakaria et al., 2013). It is possible that some of the focal species are in fact ‘edge preferring’, exhibiting a peak in population densities near edges. These species would do better in fragmented landscapes, but such species tend to be habitat generalists of limited conservation concern (Laurance et al., 2002; Zakaria et al., 2013) so were not a focus of this study, though our method could be adapted to incorporate such species. Under land sharing, we conservatively assumed an edge penetration distance of zero and negative edge effects in forest that were offset by positive spill-over on farmland. This is likely to overestimate populations under land sharing for many of the focal species, which are known to avoid farmland altogether (Phalan et al., 2011b). On the other hand, under land sparing we modelled edge penetration distances of up to 800 m (corresponding to 90% of the population density change occurring 1600 m inside forest). Edge effects reported in birds typically extend to no more than a few hundred metres (Brand and George, 2001; Fletcher, 2005; Laurance et al., 2002; Ries et al., 2004; Sisk et al., 1997) but we included higher values to allow for the fact that field studies may be biased towards underestimating the true extent of edge effects (Ewers and Didham, 2008), to allow for edge effects potentially being more pervasive in higher-yielding landscapes (Barnes et al., 2014; Didham et al., 2015), and because greater edge extents are observed in other taxa (Brodie et al., 2015; Ewers and Didham, 2008; Lenz et al., 2014; Woodroffe and Ginsberg, 1998).

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

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

Acknowledgements A.L. was funded by a Gates Cambridge Scholarship.

References

Annorbah, N.N.D., Collar, N.J., Marsden, S.J., in press. Trade and habitat change virtually eliminate the Grey Parrot Psittacus erithacus from Ghana. Ibis. doi:10.1111/ibi.12332

Arcilla, N., Holbech, L.H., O'Donnell, S., 2015. Severe declines of understory birds follow illegal logging in Upper Guinea forests of Ghana, West Africa. Biol. Conserv. 188, 41–49. doi:10.1016/j.biocon.2015.02.010

Balmford, A., Green, R.E., Phalan, B., 2015. Land for food and land for nature? Daedalus 144, 57–75. doi:10.1162/DAED_a_00354

Banks-Leite, C., Ewers, R.M., Metzger, J.-P., 2010. Edge effects as the principal cause of area effects on birds in fragmented secondary forest. Oikos 119, 918–926. doi:10.1111/j.1600-0706.2009.18061.x

Barnes, A.D., Emberson, R.M., Chapman, H.M., Krell, F.-T., Didham, R.K., 2014. Matrix habitat restoration alters dung beetle species responses across tropical forest edges. Biol. Conserv. 170, 28–37. doi:10.1016/j.biocon.2013.12.006

BirdLife International, 2010. World Bird Database.

Brand, L.A., George, T.L., 2001. Response of passerine birds to forest edge in coast redwood forest fragments. The Auk 118, 678–686. doi:10.2307/4089929

Brodie, J.F., Giordano, A.J., Ambu, L., 2015. Differential responses of large mammals to logging and edge effects. Mamm. Biol. - Z. Für Säugetierkd. 80, 7–13. doi:10.1016/j.mambio.2014.06.001

Chandler, R.B., King, D.I., Raudales, R., Trubey, R., Chandler, C., Arce CháVez, V.J., 2013. A small-scale land-sparing approach to conserving biological diversity in tropical agricultural landscapes. Conserv. Biol. 27, 785–795. doi:10.1111/cobi.12046

Connor, E.F., Courtney, A.C., Yoder, J.M., 2000. Individuals–area relationships: the relationship between animal population density and area. Ecology 81, 734–748. doi:10.1890/0012-9658(2000)081[0734:IARTRB]2.0.CO;2

Crockatt, M.E., Bebber, D.P., 2015. Edge effects on moisture reduce wood decomposition rate in a temperate forest. Glob. Change Biol. 21, 698–707. doi:10.1111/gcb.12676

Daily, G.C., Ceballos, G., Pacheco, J., Suzán, G., Sánchez-Azofeifa, A., 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conserv. Biol. 17, 1814–1826. doi:10.1111/j.1523-1739.2003.00298.x

Didham, R.K., Barker, G.M., Bartlam, S., Deakin, E.L., Denmead, L.H., Fisk, L.M., Peters, J.M.R., Tylianakis, J.M., Wright, H.R., Schipper, L.A., 2015. Agricultural intensification exacerbates spillover effects on soil biogeochemistry in adjacent forest remnants. PLoS ONE 10, e0116474. doi:10.1371/journal.pone.0116474

Dotta, G., 2013. Agricultural production and biodiversity conservation in the grasslands of Brazil and Uruguay. University of Cambridge, Cambridge, U.K.

Efford, M.G., 2014. secr: Spatially explicit capture-recapture models. R package version 2.8.2. URL http://CRAN.R-project.org/package=secr.

Ewers, R.M., Didham, R.K., 2008. Pervasive impact of large-scale edge effects on a beetle community. Proc. Natl. Acad. Sci. 105, 5426–5429. doi:10.1073/pnas.0800460105

Ewers, R.M., Didham, R.K., 2007. The effect of fragment shape and species' sensitivity to habitat edges on animal population size. Conserv. Biol. 21, 926–936. doi:10.1111/j.1523-1739.2007.00720.x

Ewers, R.M., Didham, R.K., 2006. Continuous response functions for quantifying the strength of edge effects. J. Appl. Ecol. 43, 527–536. doi:10.1111/j.1365-2664.2006.01151.x

Falcy, M.R., Estades, C.F., 2007. Effectiveness of corridors relative to enlargement of habitat patches. Conserv. Biol. 21, 1341–1346. doi:10.1111/j.1523-1739.2007.00766.x

FAO, 2010. Global Forest Resources Assessment: 2010 Main Report, FAO Forestry Paper. Food and Agriculture Organization of the United Nations, Rome.

Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O., Pimm, S.L., Lovejoy, T.E., 2003. Rates of species loss from Amazonian forest fragments. Proc. Natl. Acad. Sci. 100, 14069–14073. doi:10.1073/pnas.2336195100

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., von Wehrden, H., 2014. Land sparing versus land sharing: moving forward. Conserv. Lett. 149–157. doi:10.1111/conl.12084

Fletcher, R.J., 2005. Multiple edge effects and their implications in fragmented landscapes. J. Anim. Ecol. 74, 342–352. doi:10.1111/j.1365-2656.2005.00930.x

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks, D.P.M., 2011. Solutions for a cultivated planet. Nature 478, 337–342. doi:10.1038/nature10452

Frost, C.M., Didham, R.K., Rand, T.A., Peralta, G., Tylianakis, J.M., 2014. Community-level net spillover of natural enemies from managed to natural forest. Ecology 96, 193–202. doi:10.1890/14-0696.1

Geist, H.J., Lambin, E.F., 2002. Proximate causes and underlying driving forces of tropical deforestation. BioScience 52, 143–150. doi:10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2

Gilroy, J.J., Edwards, F.A., Medina Uribe, C.A., Haugaasen, T., Edwards, D.P., 2014a. Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. J. Appl. Ecol. 51, 1337–1346. doi:10.1111/1365-2664.12284

Gilroy, J.J., Woodcock, P., Edwards, F.A., Wheeler, C., Baptiste, B.L.G., Medina Uribe, C.A., Haugaasen, T., Edwards, D.P., 2014b. Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. Nat. Clim. Change 4, 503–507. doi:10.1038/nclimate2200

Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. Science 307, 550–555. doi:10.1126/science.1106049

Gregory, R.D., Strien, A. van, Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B., Gibbons, D.W., 2005. Developing indicators for European birds. Philos. Trans. R. Soc. B Biol. Sci. 360, 269–288. doi:10.1098/rstb.2004.1602

Guimarães, C.D.D.C., Viana, J.P.R., Cornelissen, T., 2014. A meta-analysis of the effects of fragmentation on herbivorous insects. Environ. Entomol. 43, 537–545. doi:10.1603/EN13190

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011. Habitat area, quality and connectivity: Striking the balance for efficient conservation. J. Appl. Ecol. 48, 148–152.

Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. J. Appl. Ecol. 46, 964–969. doi:10.1111/j.1365-2664.2009.01695.x

Holbech, L.H., 2005. The implications of selective logging and forest fragmentation for the conservation of avian diversity in evergreen forests of south-west Ghana. Bird Conserv. Int. 15, 27–52. doi:10.1017/S0959270905000031

Hulme, M.F., Vickery, J.A., Green, R.E., Phalan, B., Chamberlain, D.E., Pomeroy, D.E., Nalwanga, D., Mushabe, D., Katebaka, R., Bolwig, S., Atkinson, P.W., 2013.

Conserving the birds of Uganda's banana-coffee arc: Land sparing and land sharing compared. PLoS ONE 8, e54597. doi:10.1371/journal.pone.0054597

IUCN, 2015. The IUCN Red List of Threatened Species (No. Version 2015.2). at <www.iucnredlist.org>.

Kamp, J., Urazaliev, R., Balmford, A., Donald, P.F., Green, R.E., Lamb, A.J., Phalan, B., 2015. Agricultural development and biodiversity conservation on the Eurasian steppes: a comparison of land-sparing and land-sharing approaches. J. Appl. Ecol. 52, 1578–1587. doi:10.1111/1365-2664.12527

Knight, E.C., Mahony, N.A., Green, D.J., 2014. Crop type influences edge effects on the reproduction of songbirds in sagebrush habitat near agriculture. Avian Conserv. Ecol. 9. doi:10.5751/ACE-00662-090108

Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. Ann. N. Y. Acad. Sci. 1355, 52–76. doi:10.1111/nyas.12845

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Bruce Williamson, G., Benítez-Malvido, J., Vasconcelos, H.L., Van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biol. Conserv. 144, 56–67. doi:10.1016/j.biocon.2010.09.021

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16, 605–618. doi:10.1046/j.1523-1739.2002.01025.x

Lenz, B.B., Jack, K.M., Spironello, W.R., 2014. Edge effects in the primate community of the biological dynamics of forest fragments project, Amazonas, Brazil. Am. J. Phys. Anthropol. 155, 436–446. doi:10.1002/ajpa.22590

McKenzie, A.J., Emery, S.B., Franks, J.R., Whittingham, M.J., 2013. Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? J. Appl. Ecol. 50, 1274–1280. doi:10.1111/1365-2664.12122

Núñez-Ávila, M.C., Uriarte, M., Marquet, P.A., Armesto, J.J., 2013. Decomposing recruitment limitation for an avian-dispersed rain forest tree in an anciently fragmented landscape. J. Ecol. 101, 1439–1448. doi:10.1111/1365-2745.12148

Perfecto, I., Vandermeer, J., 2010. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. Proc. Natl. Acad. Sci. 107, 5786–5791. doi:10.1073/pnas.0905455107

Perkins, D.G., Perlut, N.G., Strong, A.M., 2013. Minor fitness benefits for edge avoidance in nesting grassland birds in the northeastern United States. The Auk 130, 512–519. doi:10.1525/auk.2013.12163

Phalan, B., Balmford, A., Green, R.E., Scharlemann, J.P.W., 2011a. Minimising the harm to biodiversity of producing more food globally. Food Policy, The challenge of global food sustainability 36, Supplement 1, S62–S71. doi:10.1016/j.foodpol.2010.11.008

Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011b. Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. Science 333, 1289–1291. doi:10.1126/science.1208742

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ries, L., Jr., R.J.F., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu. Rev. Ecol. Evol. Syst. 35, 491–522.

Saura, S., Martínez-Millán, J., 2000. Landscape patterns simulation with a modified random clusters method. Landsc. Ecol. 15, 661–678. doi:10.1023/A:1008107902848

Sisk, T.D., Haddad, N.M., Ehrlich, P.R., 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecol. Appl. 7, 1170–1180. doi:10.1890/1051-0761(1997)007[1170:BAIPWM]2.0.CO;2

Soga, M., Kanno, N., Yamaura, Y., Koike, S., 2012. Patch size determines the strength of edge effects on carabid beetle assemblages in urban remnant forests. J. Insect Conserv. 17, 421–428. doi:10.1007/s10841-012-9524-x

Suvorov, P., Svobodová, J., Albrecht, T., 2014. Habitat edges affect patterns of artificial nest predation along a wetland-meadow boundary. Acta Oecologica 59, 91–96. doi:10.1016/j.actao.2014.06.003

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. 151, 53–59. doi:10.1016/j.biocon.2012.01.068

Vandermeer, J., Perfecto, I., 2007. The agricultural matrix and a future paradigm for conservation. Conserv. Biol. 21, 274–277. doi:10.1111/j.1523-1739.2006.00582.x

Wilson, J.D., Anderson, R., Bailey, S., Chetcuti, J., Cowie, N.R., Hancock, M.H., Quine, C.P., Russell, N., Stephen, L., Thompson, D.B.A., 2014. Modelling edge effects of mature forest plantations on peatland waders informs landscape-scale conservation. J. Appl. Ecol. 51, 204–213. doi:10.1111/1365-2664.12173

Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. Science 280, 2126–2128. doi:10.1126/science.280.5372.2126

Zakaria, M., Rajpar, M.N., Moradi, H.V., Rosli, Z., 2013. Comparison of understorey bird species in relation to edge–interior gradient in an isolated tropical rainforest of Malaysia. Environ. Dev. Sustain. 16, 375–392. doi:10.1007/s10668-013-9482-9

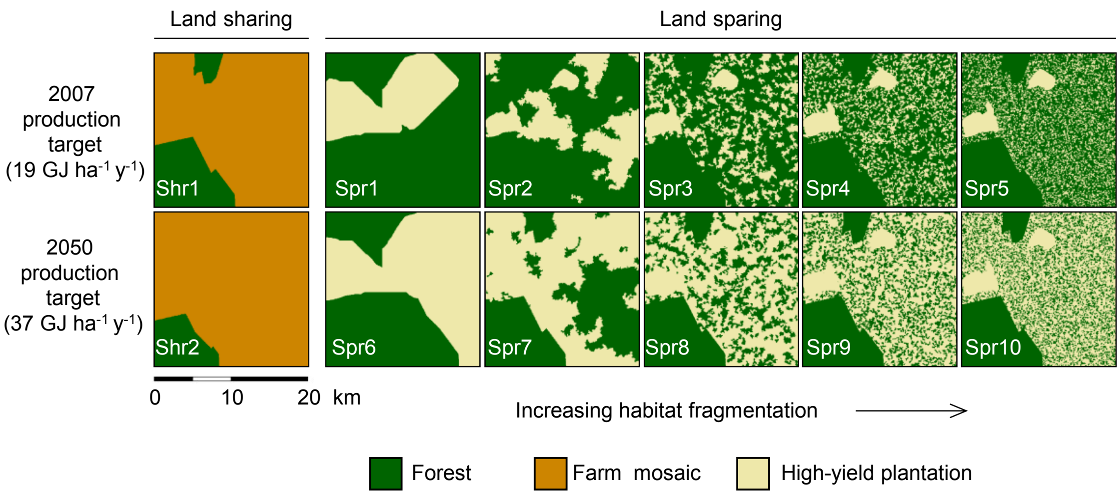

Figure 1: The land-sparing and land-sharing test landscapes. Shown for both the 2007 and 2050 production targets. Ten replicates of each random landscape (Spr2 through Spr5 and Spr7 through Spr10) were generated; representative examples are shown here.

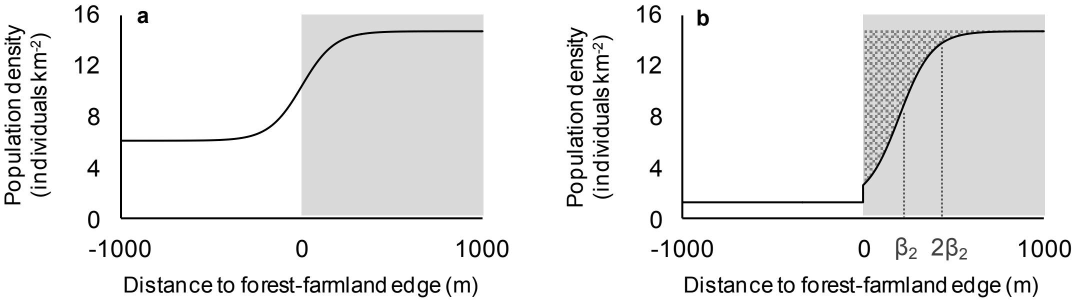

Figure 2: Assumed edge responses. Figures indicate the change in population density where forest (indicated by light-grey shading) meets farm mosaic under land sharing **a**, or meets high-yield plantation under land sparing **b**. Shown for the example species African green pigeon (*Treron calvus*). Parameter β_2 dictates the position of the inflection point of the sigmoid. Our assumptions for β_2 and for the slope parameter β_3 under land sparing (Table A3) were such that 90% of the change in population density was realised at a distance of $2\beta_2$ into the forest. In **a**, the negative edge effect within forest is balanced by a positive spill-over effect in farmland. In **b**, hatching indicates the net reduction in population density near edges caused by the assumed edge response in land-sparing landscapes.

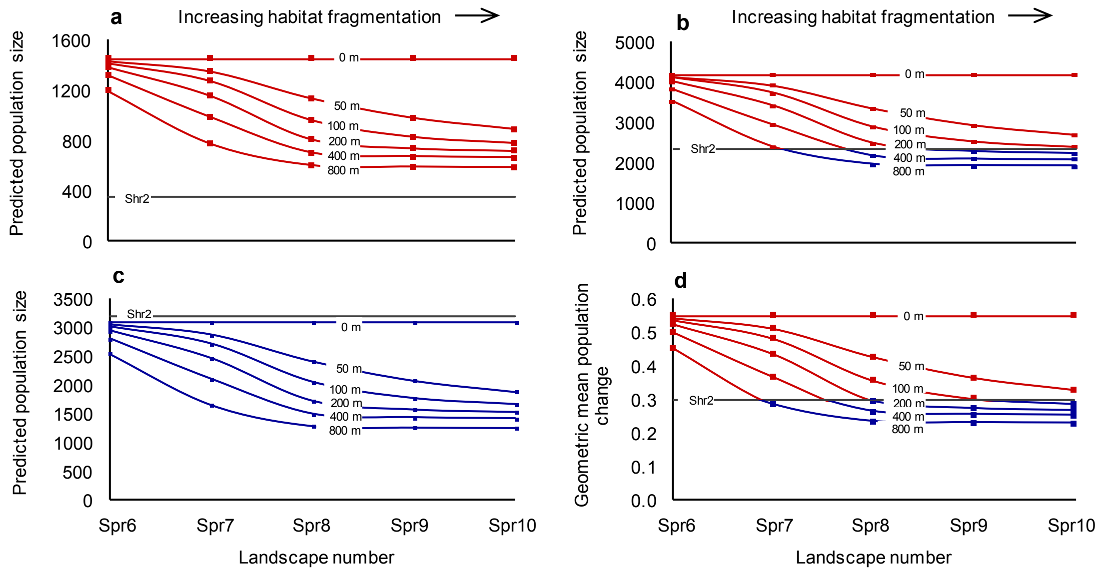

Figure 3: The influence of habitat fragmentation and edge penetration distance on predicted population size. Red and blue lines represent the predicted population size under land-sparing landscapes at the 2050 production target (Spr6 through Spr10). Each line is labelled with the applicable edge penetration distance. Grey lines indicate the predicted population size under the equivalent land-sharing landscape (Shr2) and are shown for reference – the symmetrical edge response (Figure 2a) means that the variation in population size at different edge penetration distances in land-sharing landscapes is negligible on the scale of the plot. Colouring indicates whether land sparing (red) or land sharing (blue) maximised the population size. Results are shown for three representative species: **a** Large-billed puffback (*Dryoscopus sabini*), favoured by land sparing irrespective of hypothetical edge effects and habitat fragmentation; **b** Chestnut wattle-eye (*Platysteira castanea*), a species favoured by land sparing in the absence of hypothetical edge effects for which the best strategy can switch to land sharing in fragmented landscapes; and **c** Buff-throated sunbird (*Nectarinia adelberti*), favoured by land sharing in all cases. Panel **d** shows the geometric mean population change over all 120 focal species relative to an all-forest baseline.

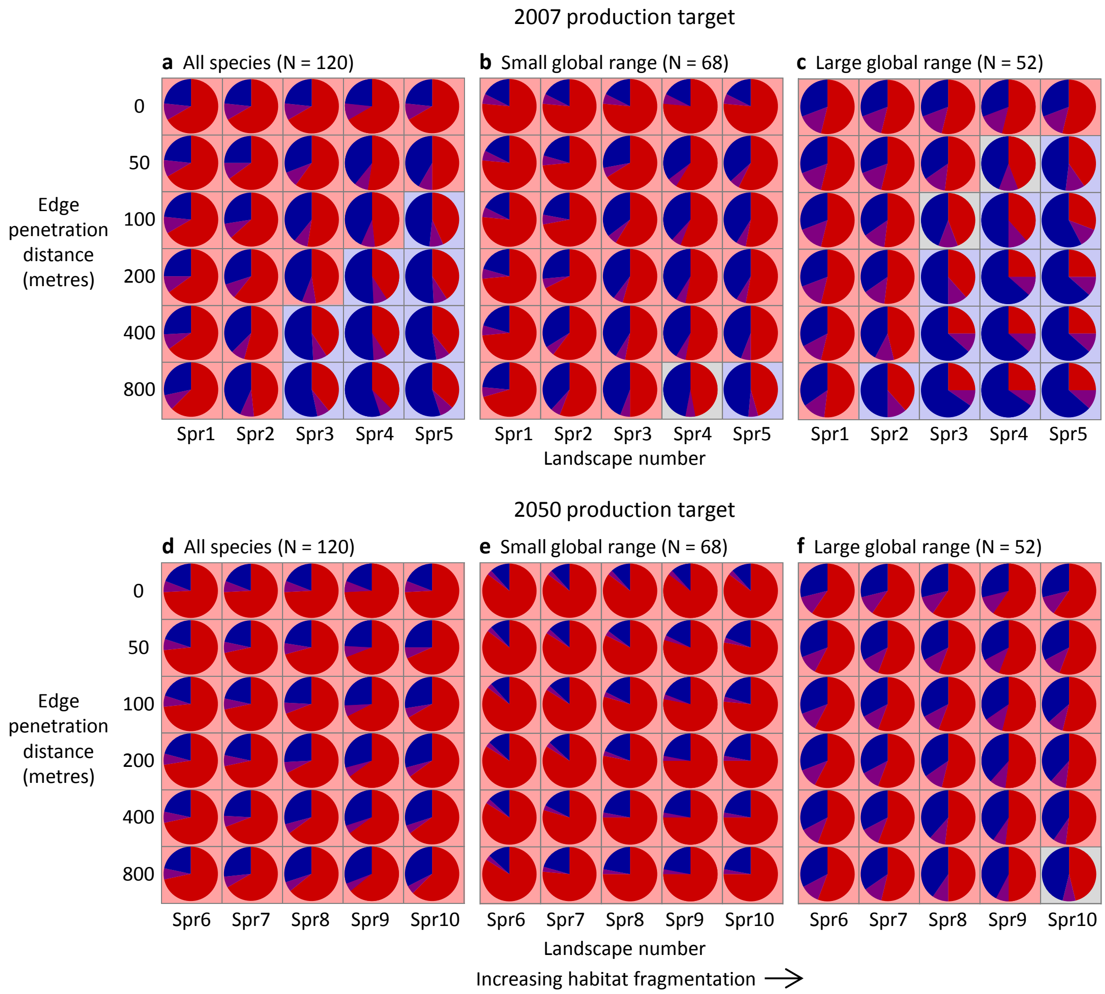

Figure 4: Comparing land sparing and land sharing across all species. Proportions of species for which land sparing (pie chart segments coloured dark red), land sharing (dark blue) or some intermediate strategy (purple) gave the highest population size for each combination of production target, edge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

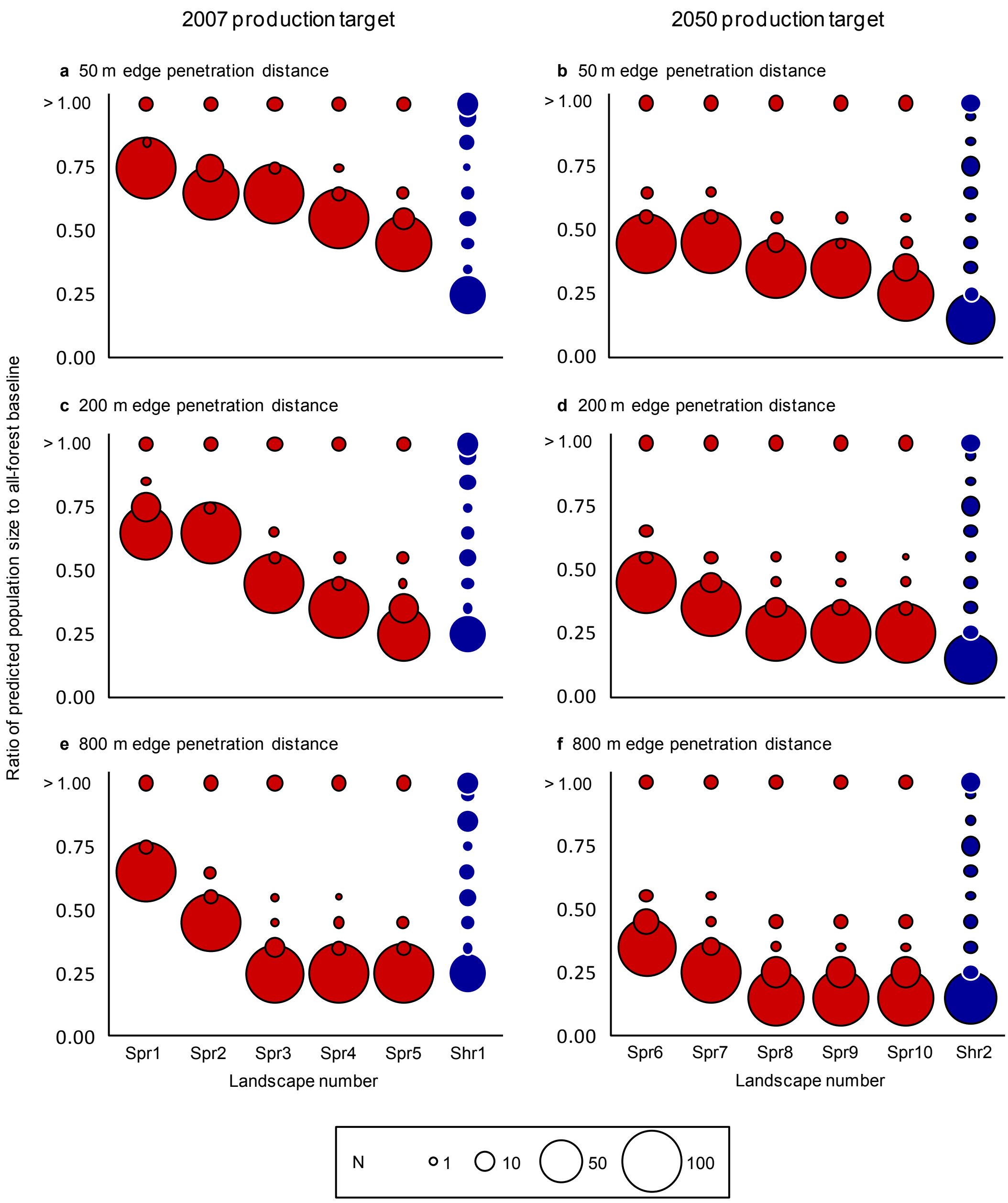

Figure 5: Predicted population size relative to the all-forest baseline. Relative population size shown in relation to edge penetration distance, fragmentation and production target. Species grouped by predicted relative population in 2007 and 2050. Number of species (N) in each group is indicated by the size of circles. Results compare land sharing (coloured blue; landscapes Shr1 and Shr2) with land sparing (coloured red; landscapes 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.

Appendix A. Supplementary material

Figure A1. Study region and test landscape.

Table A1. Characteristics of the land sparing landscapes.

Table A2. List of study species.

Table A3. Edge effect parameters.

Supplementary Methods 1. Intermediate species.

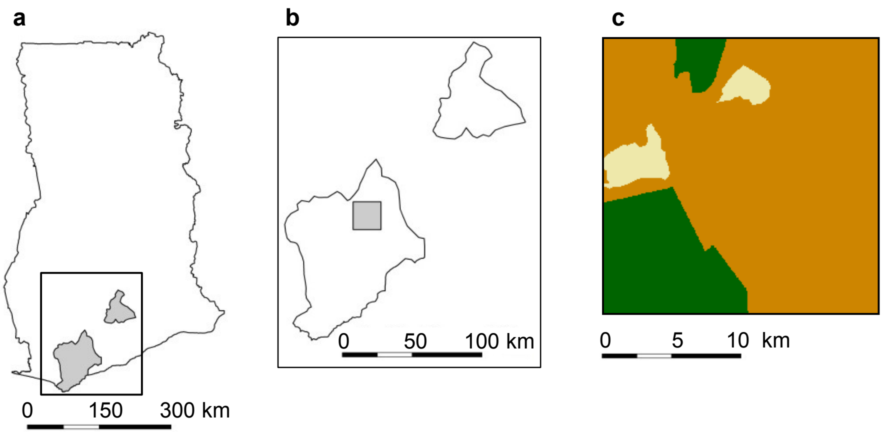

Figure A1: Study region and test landscape. **a** Map of Ghana with study region shaded. **b** Enlargement of the study region showing the test landscape shaded. **c** Land cover in 2007 in the test landscape comprising forest (dark green), farm mosaic (brown-orange), and high-yield plantation (pale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

Table A1: Characteristics of the land sparing landscapes

		Specified parameters			
Landscape number	Production target (GJ ha^{-1} y^{-1})	Proportion of landscape forested	Fragmentation parameter (p)	Minimum patch size (ha)	Mean patch size (± std. error) (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)

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

Table A2: List of study species

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

Table A3: Edge effect parameters

Land sparing landscapes (forest - high-yield plantation edges)		Land sharing landscapes (forest - farm mosaic edges)	
Edge penetration distance (β_2) (m)	Steepness (β_3) (m)	Edge penetration distance (β_2) (m)	Steepness (β_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

Parameters used in equation (1) for land-sparing and land-sharing landscapes. Following Ewers & Didham (2008), we maintained constant proportionality between β_2 and β_3 in land-sparing landscapes, reflecting an assumption that edge responses that penetrate deeper into forest should exhibit a shallower slope.

Supplementary Methods 1: Intermediate species

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

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

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

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

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

where ρ_i^j is the population density in farmland in grid cell j in the presence of edge effects, and the summation is taken over all grid cells within farmland; A_{fa} is the area of farmland; ρ_{fo}^k is the population density in forest in grid cell k in the presence of edge effects, and the summation is taken over all grid cells within forest; and A_{fo} is the area of forest. Thus ρ_i and ρ_{fo} in equation (A2) are replaced with the area-weighted mean population densities in the presence of hypothetical edge effects in farmland ($\rho_i{}^*$) and forest ($\rho_{fo}{}^*$), respectively. To compute $\rho_i{}^*$ and $\rho_{fo}{}^*$ for the intermediate species we used the test landscapes generated for the main analysis. We first calculated the peak yield Y_i for each species and found that for all intermediate species Y_i occurs in farm mosaic. Intermediate landscapes for these species would therefore contain areas of forest and farm mosaic. We next computed ρ_i* and ρ_{fo}* for each of the intermediate species and for each combination of production target, habitat fragmentation and edge penetration distance by applying equation (1) in the main text to each of the test landscapes in Figure 1. We used the values of β_2 and β_3 applicable to forest-farm mosaic edges in Table A3, we set ρ_{fa} in equation (1) equal to ρ_i, and we measured the area-weighted mean population densities in farmland and forest across the test landscape. Substituting the known values of P and Y_i along with the computed values of ρ_i* and ρ_{fo}* into equation (A2) allowed us to solve for the population of species under intermediate strategies. We found that three of the 12 intermediate species (*Lophoceros semifasciatus*, *Sylvietta virens* and *Nectarinia chloropygia*) switched to being favoured by land sharing in certain scenarios (see purple pie chart segments in Figure 4).