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Land-use strategies to balance livestock production, biodiversity conservation and carbon storage in Yucatán, Mexico

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Abstract

Balancing the production of food, particularly meat, with preserving biodiversity and maintaining ecosystem services is a major societal challenge. Research into the contrasting strategies of land sparing and land sharing has suggested that land sparing—combining high-yield agriculture with the protection or restoration of natural habitats on nonfarmed land—will have lower environmental impacts than other strategies. Ecosystems with long histories of habitat disturbance, however, could be resilient to low-yield agriculture and thus fare better under land sharing. Using a wider suite of species (birds, dung beetles and trees) and a wider range of livestock-production systems than previous studies, we investigated the probable impacts of different land-use strategies on biodiversity and aboveground carbon stocks in the Yucatán Peninsula, Mexico—a region with a long history of habitat disturbance. By modelling the production of multiple products from interdependent land uses, we found that land sparing would allow larger estimated populations of most species and larger carbon stocks to persist than would land sharing or any intermediate strategy. This result held across all agricultural production targets despite the history of disturbance and despite species richness in low- and medium-yielding agriculture being not much lower than that in natural habitats. This highlights the importance, in evaluating the biodiversity impacts of land use, of measuring population densities of individual species, rather than simple species richness. The benefits of land sparing for both biodiversity and carbon storage suggest that safeguarding natural habitats for biodiversity protection and carbon storage alongside promoting areas of high-yield cattle production would be desirable. However, delivering such landscapes will probably require the explicit linkage of livestock yield increases with habitat protection or restoration, as well as a deeper understanding of the long-term sustainability of yields, and research into how other societal outcomes vary across land-use strategies.

KEYWORDS
agroecosystems, beef production, birds, carbon stocks, cattle production, dung beetles, land sharing, land sparing, trees, tropical dry forest

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1 | INTRODUCTION

How to best balance food production with biodiversity conservation and carbon storage is a major research topic and of vital importance for preserving biodiversity and limiting anthropogenic climate change (Steffan-Dewenter, Kessler, & Barkmann, 2007; Perfecto & Vandermeer, 2008; Godfray et al., 2010; Phalan, Balmford, Green, Scharlemann, 2011; Balmford, Green, & Phalan, 2012; Ekroos, Ödman, & Andersson, 2016). Much of the recent literature concerns the merits of two contrasting strategies (Phalan, Onial, Balmford, Green, 2011; Hulme, Vickery, & Green, 2013; Gilroy, Edwards, Medina Uribe, Haugaasen, Edwards, 2014; Gilroy et al., 2014; Dotta, Phalan, Silva, Green, & Balmford, 2015; Edwards, Gilroy, Thomas, Uribe, & Haugaasen, 2015; Kamp et al., 2015): land sharing, which prioritizes on-farm biodiversity, but at the potential cost of lowering farm yields; and land sparing, whereby high-yield agriculture is encouraged, in order to limit the area needed for farming and thereby spare (or restore) nonfarmed habitats elsewhere. Several studies and reviews conclude that land sharing, wildlife-friendly farming or low-yielding agriculture would be preferable (Steffan-Dewenter et al., 2007; Bhagwat, Willis, Birks, & Whittaker, 2008; Clough, Barkmann, & Juhrbandt, 2011; Mastrangelo & Gavin, 2012), but have been criticized for not considering intact natural habitats or high-yielding farm systems, for using uncalibrated proxy (rather than direct) measures of yield, or for measuring biodiversity simply in terms of species richness (rather than using measures of individual species' abundance, which better reflect their likely persistence; Phalan, Balmford, et al., 2011; Balmford et al., 2012; Balmford, Green, & Phalan, 2015). In contrast, studies assessing abundance-based responses to variation in yield across the full range of potential land uses have consistently concluded that land sparing would be less harmful than sharing, or any intermediate approach, for both biodiversity conservation (Phalan, Onial, et al., 2011; Hulme et al., 2013; Gilroy et al., 2014; Dotta et al., 2015; Kamp et al., 2015) and maintaining carbon stocks (Gilroy et al., 2014).

However, despite the range of systems investigated, it is possible that these results may not be general, and could instead vary with a region's evolutionary and ecological history and, in particular, its exposure to disturbance. The consistently high sensitivity of biodiversity to farming observed in studies to date makes biological sense if most species are disturbance-sensitive habitat specialists (Balmford et al., 2015). However, persistent high levels of disturbance may act as an extinction filter: removing disturbance-sensitive species, and selecting, among remaining species, for traits such as wide habitat tolerance or high dispersal rates (Balmford, 1996). Both processes would leave behind a biota which is more resilient to agriculture, and which may therefore be favoured by land sharing. Understanding how disturbance history interacts with land-use strategies is important because much of the world has experienced large natural or anthropogenic disturbance, over time scales from decades to millennia (Willis, Gillson, & Brncic, 2004).

Another major knowledge gap surrounds the relative impacts of different livestock-production systems. This is important because livestock production is the most widespread land use on earth, occupying over 20% of its land surface (Ramankutty, Evan, Monfreda, & Foley, 2008), and ruminant meat in particular has a far higher greenhouse gas, land use, water and nitrogen footprint than do other foods (Eshel, Shepon, Makov, & Milo, 2014; Tilman & Clark, 2014). Moreover, meat consumption is expected to increase substantially over the coming decades (Tilman & Clark, 2014). However, examining how best to limit its negative impacts raises particular challenges because livestock production is increasingly characterized by complex, nonclosed systems. In many regions, these are characterized by three interlinked land uses: breeding ranches produce young animals and sell them to finishing ranches, which then fatten them to slaughter weight, while specialized ranches produce fodder to support livestock production. The area required for livestock production is thus far greater than that used to produce animals for slaughter. Not accounting for the area occupied by breeding and fodder ranches will underestimate the impact of livestock production, and the size of this area depends on the yields of all three ranch types. High-yield finishing ranches will require more young animals as inputs, and use greater amounts of fodder, therefore requiring larger areas of breeding and fodder ranches to supply them. Evaluating different systems therefore requires data on all three ranch types, as well as an understanding of the relationships between them.

The Yucatán Peninsula (henceforth 'the Yucatán') in Mexico offers an excellent opportunity to investigate the effects of different livestock-production strategies on biodiversity and carbon storage in a previously disturbed system. The region's natural vegetation is predominantly comprised of tropical dry, semi-deciduous and evergreen forests—some of the most threatened ecosystems in the world (Hoekstra & Wiedmann, 2014)—which have expanded and contracted with climatic fluctuations (Vázquez-Domínguez & Arita, 2010). The region is also hit by an average of one hurricane or tropical storm every year (Wilson, 1980). In addition, there is a long history of anthropogenic disturbance, with waves of deforestation occurring from the Pre-Classic Mayan civilization (1,000 BCE–250 CE, Gómez-Pompa & Kaus, 1999) through to 19th century sisal *Agave sisalana* and henequen *Agave fourcroydes* cultivation (Gonzalez-Iturbe, Olmsted, & Tun-Dzul, 2002), and finally 20th century cattle ranching, which is now the dominant land use across much of Yucatán (Busch & Vance, 2011). Despite these major disturbances, there is no evidence of major floristic change over the past six thousand years (Gómez-Pompa & Kaus, 1999), supporting the idea of a relatively resilient biota. Here, we assess how different land-use strategies would affect bird, dung beetle and tree species and carbon storage in the Yucatán using a novel method that accounts for the nonclosed nature of different ranch types. We estimate the species abundance, carbon storage, food production and input requirements of study sites spanning a wide range of agricultural yields. We then use an iterative site-selection method to build land-use scenarios that differ in agricultural yields, but which are matched for production levels, and which not only produce finished cows for slaughter and calves for export but also the calf and fodder production needed to support this. Finally, we use our biodiversity and carbon data to estimate region-wide population sizes and aboveground carbon stocks for each of these land-use scenarios.

2 | MATERIALS AND METHODS

2.1 | Study region and site selection

We selected twenty-five 1 km^2 study sites in Tizimín District, Yucatán State, Mexico—the centre of cattle production in the Yucatán (SAGARPA, 2015). We restricted our sites to a region of uniform climate and topography and ensured even representation of different land uses across the range of available soil types (Fig. S1). We selected five sites in zero-yielding forests and 20 agricultural sites. Agricultural sites contained multiple ranches with a range of management types: traditional ranches with pastures, as well as grazed primary and secondary vegetation; intensive silvopastoral systems (ISPs); intensive ranches with improved or irrigated pastures and intensive cattle management; and intensive fodder-producing ranches. We classified each ranch within a site as either "breeding" or "finishing". Breeding ranches produce calves and raise them to approximately 200 kg, while finishing ranches buy calves and fatten them to a slaughter weight of approximately 500 kg. A few ranches both bred animals and raised them to slaughter weight, but these were too rare to analyse separately and so were modelled as combinations of breeding and finishing ranches (see below). Since most sites contained multiple ranches with different management types, each site produced a mix of calves, finished cows, and maize or fodder grass. Where possible, we selected sites surrounded by a 500 m buffer of similar land uses to reduce edge effects, and sought sites at least 5 km from sites of the same type and 1 km from all other sites (Table S1).

We mapped each site using a combination of Google Earth imagery and site visits. We classified land as grazed land; maize and grass for fodder; ungrazed natural vegetation and regrowth; and artificial habitats such as roads and buildings. We further divided grazed land into pasture, grazed forest, grazed secondary vegetation, improved pasture or irrigated pasture (including ISPs, which were too rare in our sites to analyse separately).

2.2 | Yield data collection

To quantify the yields of study sites, we needed estimates of production per unit area of maize and fodder grass, the animal protein produced per hectare of different grazed lands, and the feed efficiency (FE; kilograms of animal protein produced per tonne of fodder used). We also needed to estimate the mass of calf protein required by finishing ranches for every kilogram of finished cow protein they produced. However, ranch managers keep production and input data for entire ranches, rather than for individual land uses (with the exception of maize and fodder grass yields). We therefore needed to collect data at the ranch level and used this to model the animal protein produced per hectare of different grazed lands, and the feed efficiency.

We used structured questionnaire surveys to collect agricultural data from owners and managers of 77 ranches across Tizimín District (including ranches both within and outside our study sites to ensure a large enough sample size). We obtained data from 49 breeding and 28 finishing ranches. For each ranch, we obtained data on: the area of different types of grazed land and maize/fodder grass fields in the ranch; the number and mass of animals bought each year; the number and mass of animals sold each year; the mass of different fodders used by the ranch each year; and the volume of milk sold annually (for the few ranches that did this). We standardized fodder inputs to "maize equivalents" using relative metabolizable energy contents (Table S2). We used energy content, rather than protein or another measure, as this is the factor that most commonly limits cattle production in Yucatecan ranches. We converted production of animal products into kilograms of edible protein using a dressing percentage of 50% (FAO, 1972) and a protein content of ruminant meat of 17.4% (USFDA, 2015). When ranches produced milk, we converted volumes to masses at 1.03 kg L^{-1} and assumed a protein content of 3.15% (USFDA, 2015).

2.3 | Calculating yields in nonclosed systems

The three classes of ranch in the Yucatán are mutually dependent: breeding ranches need finishing ranches to raise their calves to slaughter weight and fodder ranches to provide fodder; finishing ranches need to be supplied with both calves and fodder; and fodder ranches need breeding and finishing ranches to convert fodder into meat (Figure 1). For future land-use scenarios to be viable, they therefore had to not only meet a production target (a realistic level of production) for animal protein but also provide the necessary supporting production of fodder and calves. We, therefore, evaluated the production and requirements of all three products for each of the 20 agricultural study sites using a five-step process (refer to Figure 1):

1. Fodder production: We used published values for mean maize and fodder grass yields in Tizimín District (SAGARPA, 2015), adjusting the latter to the equivalent maize yields using digestible energy content (Table S2; Animal Feed Resources Information System, 2014). We then multiplied the area of maize and fodder grass in each study site by these yields to get estimated fodder production.
2. Fodder requirements: We modelled fodder use in each of the 77 ranches as a function of the grazed land uses in the ranch by fitting positively constrained linear regressions of fodder use against the area of each land use. We constrained regressions to prevent the implausible situation of fodder use decreasing as the area of grazed land increased. We used the port algorithm of the nls function in R (R Core Team, 2015) and used *F* tests to assess whether the inclusion of ranch type (breeding or finishing) or splitting land-use classifications significantly improved model fit (see SI). This "Fodder Use Model" provided us with estimates of the tonnes of fodder used annually per hectare of each land use,

which we then multiplied by the areas of each land use in each site to get a site's estimated fodder requirements. We estimated the per-hectare fodder requirements of the few ranches that both bred animals and raised them for slaughter as the mean of breeding and finishing ranches.

3. Animal protein production: We modelled animal protein production in a similar way, as a function of the grazed land uses in a ranch and the fodder used. We fitted positively constrained linear regressions of protein production against the area of each land use and the mass of fodder used, and used *F* tests to assess whether the inclusion of ranch type (breeding or finishing) or splitting land-use classifications significantly improved model fit (see SI). This 'Protein Production Model' provided estimates of the yield of each grazed land use—the kilograms of animal protein produced per hectare—and the FE—the kilograms of animal protein produced for each tonne of fodder used. To calculate the overall protein production of a site we summed the production from grazed land—the yields of each grazed land use multiplied by its area in a site—and the additional production from fodder use—the site's fodder requirements multiplied by the FE. We did this separately for calf and finished cow protein, using the areas of each grazed land use in breeding and finishing ranches, respectively (steps 3a and 3b in Figure 1). Again, we estimated the protein production of land in the few ranches that both bred animals and raised them for slaughter as the mean of breeding and finishing ranches.
4. Calf requirements: Every finished cow produced by a finishing ranch has to be imported into the ranch as a calf. The mass of calves required by a finishing ranch can therefore be estimated using the mass of finished cows the ranch produces. To estimate calf requirements, we therefore calculated the calf conversion ratio (CCR): the ratio of the modal masses of calves to finished cows across the surveyed ranches. We then multiplied the total production of finished cow protein in a site (from step 3) by the CCR to estimate the mass of calf protein required.
5. Net production: These steps provided, for each agricultural site, the total fodder produced; the total fodder required; the total mass of calf protein produced; the total mass of calf protein required and the total mass of finished cow protein produced. We then calculated the net production of fodder and calves for each site as the production minus the requirements. Finally, we converted all production into the equivalent value in finished cow protein: multiplying fodder production by the FE for cows and calf production by the CCR.

2.4 | Land-use scenarios

To investigate the impacts of land-use strategies on biodiversity and carbon storage, we needed to construct plausible land-use scenarios to meet future production targets. Tizimín District produces both finished cows for slaughter and calves for export (Fig. S2), and so our scenarios used production targets for both. In turn, meeting these targets requires inputs of both fodder and calves, implying that we could not model biodiversity as a function of a single-yield metric as previous studies have done (Phalan, Onial, et al., 2011; Dotta et al., 2015; Hulme et al., 2013; Kamp et al., 2015). Instead, we constructed land-use scenarios using our sites as building blocks which could be combined (with replacement) in different ways to meet both production targets for finished cows and calves for export, while also producing the required calves and fodder.

To construct the scenarios, we first classified agricultural sites as fodder, breeding or finishing sites based on which product (fodder, calf protein and finished cow protein) they produced the most of, although most produced a combination of the three. We then iteratively built land-use scenarios by picking agricultural sites at random and with replacement, until the production target was met and the fodder and calf requirements were also satisfied (Figure 2). To investigate different land-use strategies, we used different weighting schemes to determine the probability of picking a site at each step, based on the sites' yields. First, we adjusted the total production of

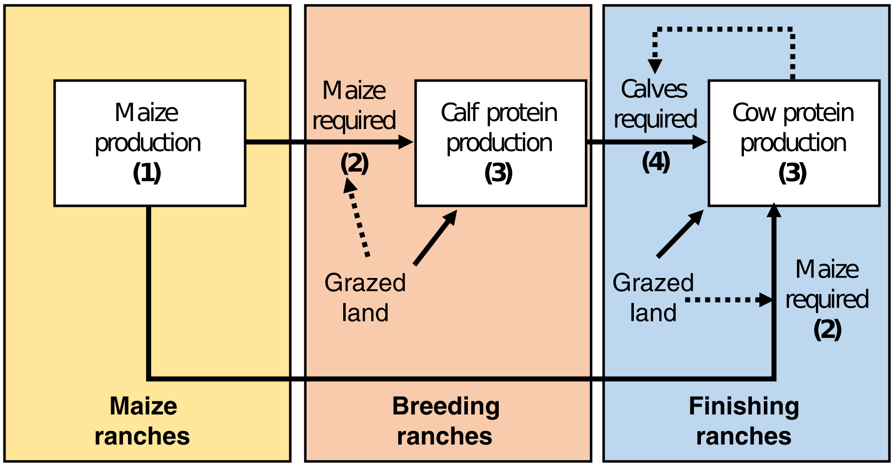

FIGURE 1 Schematic of the ranching system in Tizimín District. Solid lines represent energy or biomass flows; dashed lines show that information on the grazed land in a ranch is needed to estimated fodder use and that calf requirements depend on cow protein production. Numbers refer to the calculation steps in main text [Color figure can be viewed at wileyonlinelibrary.com]

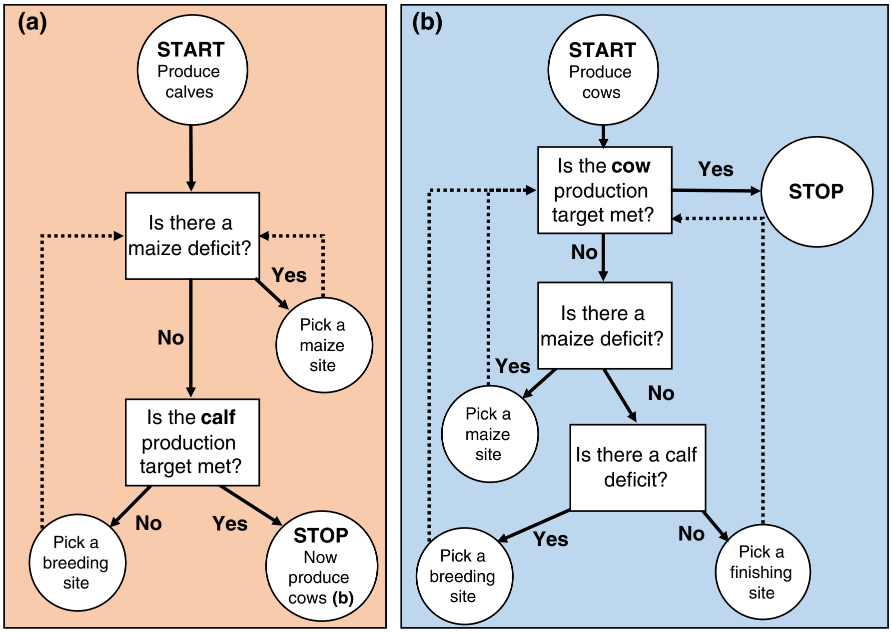

FIGURE 2 Schematic of scenario-building process, starting by (a) meeting the calf protein production target and then (b) the finished cow production target [Color figure can be viewed at wileyonlinelibrary.com]

each site (the sum of fodder, calf and finished cow protein) by dividing by the area needed to support it (i.e. the area of the site—1 km^2—plus any additional area needed to produce its fodder requirements). We then used a logit function to generate a probability density distribution that weighted the probability of picking a site according to this adjusted production value, and varied the shape of this function to simulate nine different land-use strategies (Fig. S3). We repeated the scenario-building process 50 times for each scenario and calculated the mean number of times each site was selected across these repetitions. To confirm that 50 repetitions were sufficient to obtain consistent land-use patterns we used nonparametric bootstrapping: we sampled with replacement from the different scenarios and observed how the mean and standard deviation of the number of times a site was selected varied with sample size (see Fig. S4 for a detailed explanation).

To investigate how our results varied with the production target, we estimated future changes in production based on recent trends (Fig. S2) and set production targets ranging from near-zero to higher than probable 2025 levels. This allowed us to investigate the effects of the nine land-use strategies under both increased and decreased production.

Different land-use strategies had different land-use requirements. For each land-use scenario we subtracted the total area of all agricultural sites selected during the scenario-building process from the total area of available land in Tizimín District (excluding water and urban areas) and assigned any unused land to zero-yielding forest. We discarded scenarios that required more land for agriculture than was available in Tizimín District. For each production target, we then defined the remaining land-use strategies as land sharing (the strategy with the lowest yields that was able to meet the production target), land sparing (the strategy with the highest yields) or as intermediate strategies. As production targets increased, fewer low-yielding scenarios met the production target in the available land and so the strategy defined as land sharing became progressively higher yielding (Fig. S5).

2.5 | Species population densities

To quantify the consequences for conservation of alternative food production strategies, we estimated bird, dung beetle and tree population densities in each of our study sites. We sampled birds via point counts, at 24 points per site, stratified across land uses. Points were at least 142 m apart, with six points counted on each of four visits to each site (three visits at one site), spread across 3 years and spanning both early- and late-breeding seasons (April–May and May–July respectively). This resulted in 594 point counts in total. We counted birds for 10 min at each point, using distance sampling techniques (Buckland, 2001; Buckland, Anderson, Burnham, & Laake, 2005), with no settling-in period. We included birds flushed as the point was approached, but not individuals that entered the point after the count began. We recorded flying individuals during a single "snapshot" at the end of the point count. We visited each point between half an hour before dawn and 3 hr after (following Blake, 1992). All point counts were performed by DRW and were recorded using a Sony PCM-M10 digital recorder and a Seinnheiser ME 66 microphone, with uncertain identifications checked later using online reference material (www.xeno-canto.org). We discarded all observations more than 70 m from the point and all records of nonbreeding migrants and species that point counts are unlikely to survey effectively: largely aerial species such as swifts, swallows and raptors (see SI). We used the package mrds in R version 3.2 (Laake, Borchers, Thomas, Miller, & Bishop, 2015; R Core Team, 2015) to estimate effective detection radii for each species at each point (see SI), calculated the area effectively surveyed for each species in each site, and then used these areas, the mean group size for each species and the number of observations to estimate population densities of each species in each site. To test the sensitivity of our analysis to this method of density estimation, we also performed all analyses on raw count data, as well as detection-adjusted densities.

We sampled dung beetles using 25 regularly spaced, baited pitfall traps in 24 of the study sites following da Silva and Hernández (2015); we were refused permission to collect beetles at the remaining site. Each trap consisted of a 1 L container with an 11.5 cm diameter opening buried to be flush with the ground and baited with approximately 20 g of a 1:1 mix of human and pig dung suspended over the trap. Traps were left for 48 hr and beetles placed in 70% alcohol solution before being identified to species level by FA and Fernando Escobar at the Institute of Ecology A. C. (INECOL), Xalapa, Mexico. Voucher specimens were deposited at Entomological Collection of INECOL; the Oxford Entomological Collection, Oxford University Museum of Natural History, UK; and the Entomological Collection of the National Museum, Prague, Czech Republic. We estimated beetle abundance in each site as the total number of captures of a species divided by the number of intact traps in each site (after accounting for those destroyed by animals).

To sample trees we used a modified Gentry plot (based on Baraloto et al. 2012) at 20 points in each site (10 in zero-yielding forest sites and at one agricultural site that was entirely grazed forest), stratified across land uses. Plots consisted of six parallel 50 × 2 m transects (Fig. S5), and we identified all individuals with a diameter at breast height (dbh) ≥10 cm. In addition, we used one central transect as a subplot and identified all individuals with a dbh ≥5 cm. Trees were identified to Spanish or Mayan names by local experts (Don Miguel Poot and Edilberto Poot) and then matched to scientific names using a range of resources (CICY Herbarium, 2014; UCR Herbarium, 2014) and a standardized taxonomy (Boyle, Hopkins, & Lu, 2013). In addition, we measured each tree's dbh and estimated the height of most individuals for carbon stock calculations—see below. For biodiversity analyses we discarded records of non-native and cultivated species and estimated site population densities as the total number of individuals of each species recorded in each site, divided by the total area surveyed.

2.6 | Aboveground carbon stocks

For all species except palms we estimated individual aboveground biomass (AGB) using Model (4) or Model (7) from Chave, Réjou-Méchain, and Búrquez (2014); SI. We used species-, genus- or family-level estimates of wood specific gravity from Zanne, Lopez-Gonzalez, and Coomes (2009), where possible, and the mean of all values for unidentified trees. For palm biomass we used equations (1) or (2) from Goodman, Phillips, and del Castillo (2013); SI. We did not record dead trees but scaled AGB estimates for partially dead trees by the proportion that was estimated to be alive. We assumed that 50% of AGB was carbon (Brown & Lugo, 1982) and estimated carbon stock densities in each site by dividing the total estimated stock by the total area surveyed, adjusting for the different areas surveyed for large and small trees.

2.7 | Biodiversity and carbon stocks under different scenarios

To explore the impacts of different land-use scenarios on biodiversity and carbon stocks we estimated the total population of each species, and total carbon stock, that would be supported by the combination of sites associated with that scenario. We estimated each species' population size and total carbon stocks in agricultural land from the number of times each agricultural site was used in the scenario-building process multiplied by the species' population density or carbon stock density in the site, summed across sites. We then added this to its estimated population size, or carbon stock, in natural habitats—its mean population density or carbon stock in the five zero-yielding forest sites multiplied by the area of land not required to meet the production target. We compared total population sizes and carbon stocks between scenarios and, in the case of species populations, to a prehuman baseline. To estimate pre-human population sizes we assumed the entirety of Tizimín District was forested and multiplied mean population densities in the five zero-yielding forest sites by the total area of the region.

2.8 | Classifying species' responses

We defined the optimal land-use strategy for each species at each production target as the strategy (land sharing, land sparing or an intermediate strategy) that allowed the largest population to persist. For each production target, we also defined each species at each production target as either a "winner" from agriculture (for those species with larger population sizes than that estimated in a zero-agriculture baseline) or a "loser" (those with smaller than baseline population sizes).

3 | RESULTS

We investigated nine land-use strategies for each of 16 production targets, ranging from 10% to 170% of current production. For each land-use scenario we estimated the land-use patterns that would result; the responses of birds, dung beetles, trees and carbon stocks to these patterns; regional populations of each species and regional carbon stocks.

3.1 | Land-use patterns under different strategies

As the yields of land-use strategies increased, the area required to meet the production target decreased (Figure 3), for example, for 2010 production levels, an extreme land-sharing strategy would require 94% of the area of Tizimín District to meet the production target, while an extreme land-sparing strategy would need only 55%.

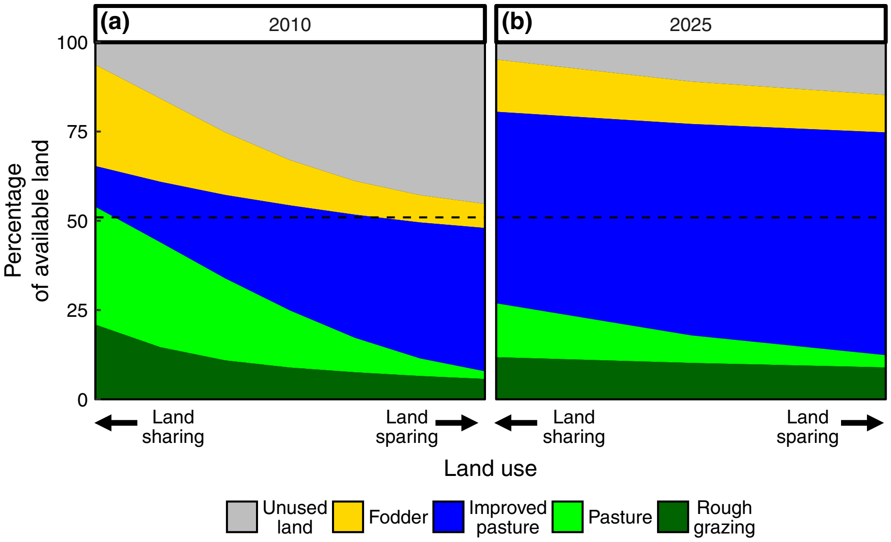

FIGURE 3 Area of different land uses under different land-use strategies for two of the production targets investigated: (a) 2010 production levels, (b) projected 2025 levels. Values are percentages of the total area of Tizimín District. Unused land could in theory be spared for nature conservation. For comparison, the black dashed line shows the total area currently under pasture, improved pasture and maize (from SAGARPA, 2015). In reality the area currently used for agriculture is larger because some of the forest and secondary regrowth in the region is grazed [Color figure can be viewed at wileyonlinelibrary.com]

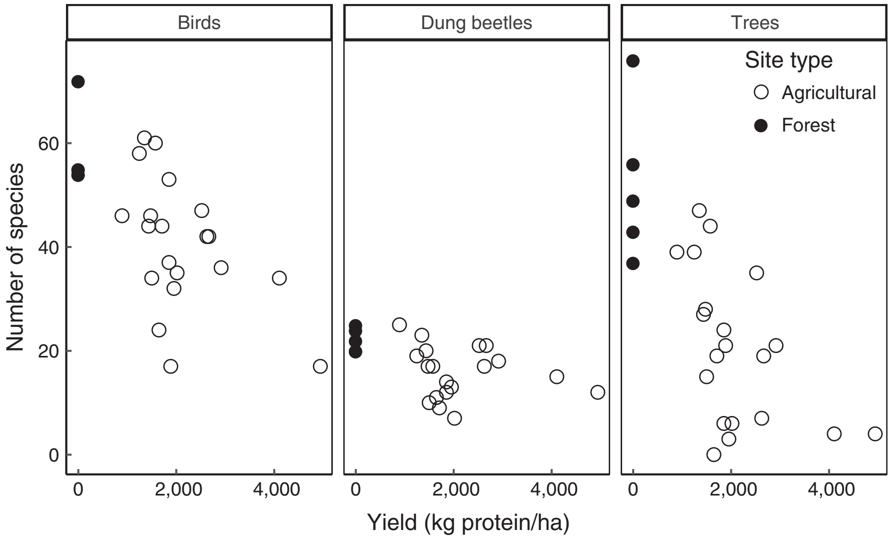

FIGURE 4 Observed species richness of birds, dung beetles and trees in forest and agricultural sites of different yields. Yields are summed across fodder, calves and finished cow production and converted to the equivalent in finished cow protein. Results for estimated effective species number are similar (Fig. S8)

Higher yielding strategies were predicted to use a larger area of improved pasture, both in total and as a proportion of all farmland, than did low-yielding strategies, and used correspondingly less pasture. As production targets increased, all strategies used larger total areas (Figures 3, S7), meaning that the lowest-yielding strategies were increasingly unable to meet the target within the available land, and land-sharing strategies relied more on improved pasture. Because the scenario-building process used real, rather than modelled, landscapes, the transition between different land-sharing strategies was not smooth and sudden transitions to using higher yielding sites to meet demand meant that the area required to meet a production target using land sharing sometimes decreased as the target increased (Figs. S5, S7).

3.2 | Responses of species and carbon stocks to agriculture

In total, we recorded 6,626 birds of 112 species; 210,522 dung beetles of 32 species; and 5,350 trees of 159 species, of which 59 could not be assigned to a binomial name (see SI). For each taxon, species richness decreased as site yields increased (Figure 4), but moderate- and low-yielding sites held only slightly fewer species than zero-

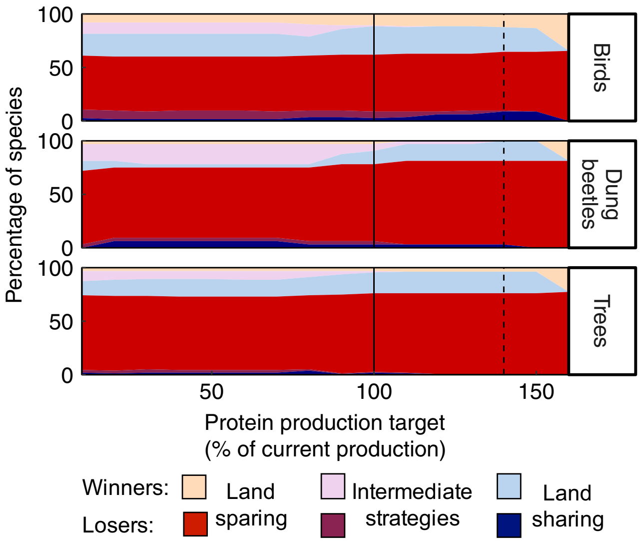

FIGURE 5 The proportion of species showing different responses to agriculture across all taxa and production targets. The solid vertical line shows current production levels, the dashed line the projected 2025 production target [Color figure can be viewed at wileyonlinelibrary.com]

yielding forest sites. The same pattern was seen for effective species number, calculated as the exponential of the Shannon–Weaver entropy of a site (Fig. S8). However, across all production targets, most species were "losers" that had lower population sizes in agriculture than in natural vegetation (Figure 5), and of these losers, the majority would maintain their largest population sizes with land sparing: highest-yield agriculture combined with habitat protection. More than 65% of tree and dung beetle species were "losers" that would do least badly with land sparing at all production targets. In contrast, a higher proportion of birds (approaching 40% at the lowest production target) were "winners". These results were consistent whether analyses were performed on all data, or on a subset of common species with ≥10 records (which also excluded all but two of the 59 tree species that could not be assigned a binomial name; Fig. S9), and on the detection-adjusted density estimates for birds, or on the raw count data (Fig. S10). Carbon stocks also declined rapidly with increasing agricultural yields (Figure 6).

3.3 | Population sizes and carbon stocks under different scenarios

Relative population sizes of most species were considerably lower under land sharing than land sparing (Figure 7), as were carbon stocks (Figure 8). These differences were largest at intermediate production targets, when differences in the area under agriculture of the different strategies was greatest (Fig. S7). Again, these results were consistent whether analyses were performed on all data, on a subset of common species with ≥10 records (Fig. S11) and on the detection-adjusted density estimates for birds, or on the raw count data (Fig. S12).

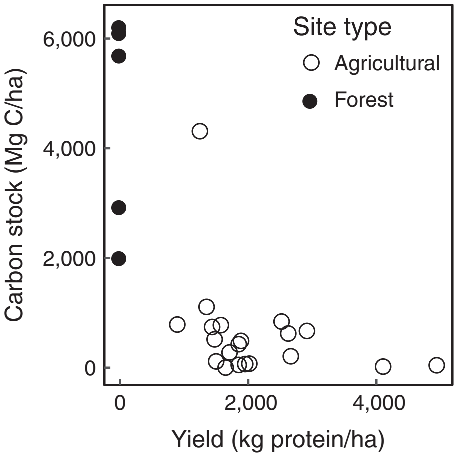

FIGURE 6 Estimated aboveground carbon stocks in forest and agricultural sites of different yields. Yields are summed across fodder, calves and finished cows and converted to the equivalent in finished cow protein

4 | DISCUSSION

We found that a land-sparing strategy, combining high-yield agriculture and habitat conservation, consistently allowed larger populations of more species to survive across all taxonomic groups and all production targets. Our study is the first to investigate how individual species and carbon stocks respond to different cattle production strategies in tropical semi-deciduous forests, and its findings are similar to those of previous work highlighting the importance of natural habitat conservation for safeguarding both biodiversity (Phalan, Onial, et al., 2011; Hulme et al., 2013; Gilroy et al., 2014; Dotta et al., 2015; Kamp et al., 2015) and carbon stocks (Gilroy et al., 2014).

Importantly, we found that low- and intermediate-yielding sites held nearly as many species as forest sites, but that this did not translate into land sharing, or intermediate, strategies being less damaging for biodiversity. Previous work in the Dry Chaco, Argentina (Mastrangelo & Gavin, 2012), also found similar levels of bird species richness in low- and intermediate-yielding cattle ranching systems and concluded that intermediate-yielding systems may be optimal for bird conservation. However, we found that such sites held considerably lower population densities of most species, and particularly of species that were losers with agriculture. This means that the biodiversity benefits of these sites were greatly outweighed by their cost, in terms of reduced areas of natural habitats, compared with high-yield agricultural systems. This conclusion confirms the importance of investigating how populations of individual species, rather than metrics such as species richness or effective species number, are affected by different agricultural strategies.

The clear benefits of land sparing in Yucatán are somewhat surprising because the region has a long history of both natural and anthropogenic disturbance. Forests in the Yucatán have expanded and contracted with climatic changes (del Socorro Lozano-García, 2007), the region is regularly subject to hurricanes and tropical

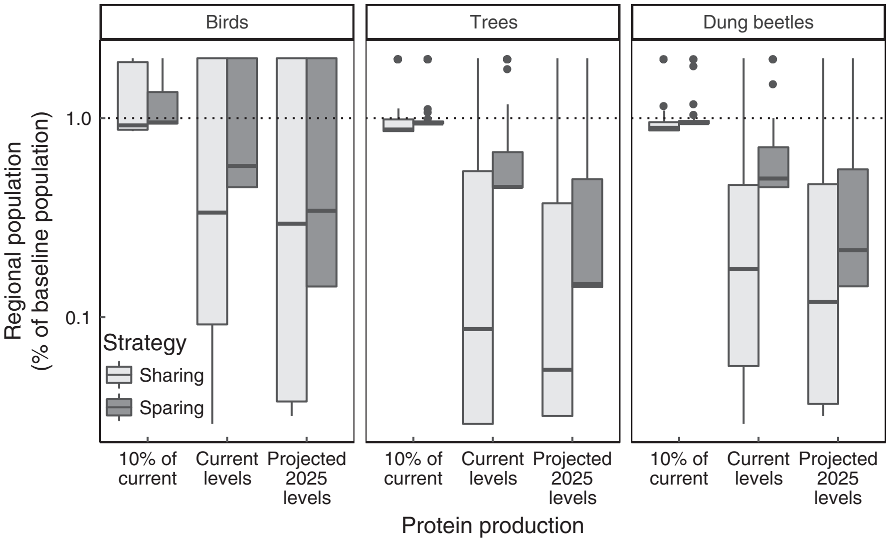

FIGURE 7 Estimated regional population sizes of birds, dung beetles and trees under different land-use strategies and production targets relative to estimated pre-human baseline populations. The *y*-axis uses a $\log_{10}$ scale and relative population sizes are truncated at 2.0, equivalent to a 100% increase in population size

storms (Boose, Foster, Barker Plotkin, & Hall, 2003; Whigham, Olmsted, Cano, & Curtis, 2003) and there have been repeated waves of anthropogenic deforestation (Gómez-Pompa & Kaus, 1999; Gonzalez-Iturbe et al., 2002; Busch & Vance, 2011). However, these strong evolutionary and ecological pressures do not appear to have resulted in a biota resilient to agriculture. In fact, the relative benefits of land sparing seen here are similar to those recorded in previous studies, with the proportion of winners slightly higher than in some systems (e.g. birds in South American pampas or Kazakh steppe, Dotta et al., 2015; Kamp et al., 2015) and lower than in others (e.g. birds in Uttarakhand, India, Phalan, Onial, et al., 2011).

The importance of natural habitats for carbon stocks is well known and the basis for international policy frameworks such as the UN Reducing Emissions from Deforestation and Forest Degradation in Developing Countries (REDD+) programme (e.g. Gibbs, Brown, Niles, & Foley, 2007). Agroforestry and silvopastoral systems are frequently promoted as methods for increasing carbon storage in agricultural land (e.g. Broom, Galindo, & Murgueitio, 2013), but our results show that, in the Yucatán, aboveground carbon stocks decreased extremely rapidly with conversion to agriculture, with the one agricultural site that maintained high carbon stocks consisting entirely of grazed forest. This rapid decline meant that there would be no benefit for carbon stocks of maintaining low agricultural yields, and that regional carbon stocks would instead be maximized under a land-sparing strategy.

These patterns are robust to changes in production target, meaning that land sparing would continue to be the least damaging strategy for both biodiversity and regional carbon stocks irrespective of increases or decreases in food demand. However, the relative benefits of land sparing, compared to land sharing, do vary across production targets: at very low targets, very little of the available land is cultivated under either strategy, and so relative population sizes or carbon stocks are not greatly dependent on the approach adopted. Conversely, at very high production targets, almost all available land is cultivated, and because low-yielding strategies cannot meet the production target, the land uses employed by both strategies are similar—with large areas of irrigated pasture, and smaller amounts of pasture, fodder and rough grazing. This highlights the fact that low-yielding agriculture simply cannot meet probable future production targets, and so pursuing strategies that support it will likely result in

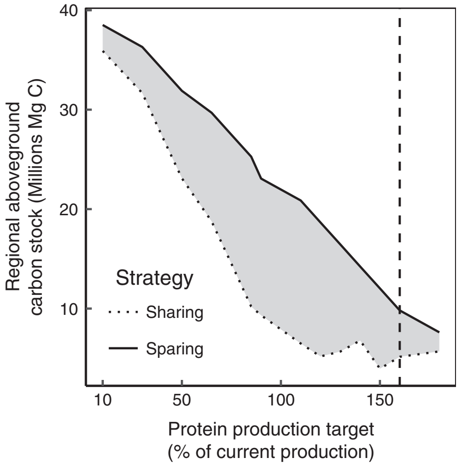

FIGURE 8 Estimated regional aboveground carbon stock under different land-use strategies and production targets. As production targets increase, the lowest-yielding land-use strategies can no longer meet the production target, and so the land-uses in the land-sharing strategy change. Because the scenarios are built using real, not modelled, landscapes, these transitions are not perfectly smooth. Because of the far higher carbon stocks in natural habitats than agricultural sites, this results in some increases in carbon stocks under land sharing as the production target increases. See text and Figs. S6, S7 for details

increased land-use change outside the region. It is also important to note that the population sizes of most species, and regional carbon stocks, are much lower at high production targets for all land use strategies. Reducing demand for animal protein therefore has the potential to greatly reduce pressure on wild populations and on regional carbon stocks (Erb et al., 2016). These benefits are likely to be greatest if they are combined with a land-sparing strategy.

In theory, a reduction in demand for animal protein, coupled with land sparing could make land available for habitat restoration. Initially, restored habitats are unlikely to hold the biodiversity or carbon stocks of older forests, but the forest sites we surveyed were young (approximately 15–50 years old) and had far higher biodiversity and carbon storage values than agricultural sites. Restoration would therefore likely bring significant benefits over relatively short, and politically and socially relevant, timescales.

4.1 | Land sparing in Yucatán

The land-sparing strategies that maintained the largest populations of most species and the largest regional carbon stocks were dominated by improved pastures: areas of introduced grasses such as *Panicum maximum* and *Brachiaria brizantha* where the bedrock has been broken up and the thin Yucatecan soils improved with manure and soil. These are often irrigated and can incorporate banks of densely planted legumes such as *Leucaena leucocephala* as part of an ISP. While we were not able to separate the effects of ISPs from other improved pastures, due to their rarity in the region, they have been promoted as offering additional benefits to animal welfare, on-farm biodiversity and ecosystem services, and reductions to ruminant methane production (Broom et al., 2013; Cuartas-Cardona, Naranjo-Ramírez, & Tarazona-Morales, 2014 but see Beauchemin, Kreuzer, O'mara, & Mcallister, 2008), potentially further increasing the relative benefits of a high-yielding approach. More extreme land sparing in the region could involve raising cattle in intensive feedlots which will have very low land demands, although there are concerns over the impacts of feedlots on water quality (Tamminga, 2003), animal welfare (Blackshaw & Blackshaw, 1994) and zoonotic diseases (Jones, Grace, & Kock, 2013). These externalities would have to be quantified per unit of production before such an approach could be recommended.

Although we modelled Tizimín District as a closed system, our results are robust to modifying this assumption. Adjusting the scenario-building process so that the region only produces cows for export and imports the required calves and fodder gave qualitatively similar results (Figs. S11–S13). This suggests that the overarching result—that land sparing would be the least damaging land-use strategy—is unlikely to change, even as increasing globalization further alters Yucatán production systems.

Both agricultural and environmental organizations have been promoting the use of ISPs and other yield-increasing measures in the Yucatán, suggesting that land sparing may be politically acceptable. However, land sparing is unlikely to occur passively: while increased yields can reduce land clearance to some extent through market effects alone (Ewers, Scharlemann, Balmford, & Green, 2009), for goods with highly elastic demand, such as meat, increased yields can increase the profitability of farming and so the opportunity cost of conserving natural habitats (Angelsen, 2010). Linking yield increases with habitat protection is therefore likely to be very important in delivering land sparing in the real world (Phalan et al., 2016). In the Yucatán, two of the mechanisms identified by Phalan et al. (2016) for coupling yield growth and habitat conservation are already in place: current laws largely prohibit habitat clearance ("land-use zoning") and existing subsidy schemes, such as The Programme for the Sustainable Production and Management of Livestock and Beekeeping, include environmental conditions ("economic instruments"). However, the continued loss of forest cover in the region (CONABIO, 2015) highlights the need for more effective systems of monitoring and enforcement.

4.2 | Expanding the assessment of land-use strategies

Our analyses are not spatially explicit, implicitly assume that populations within each site are "closed" and self-sustaining, and do not include edge effects or population dynamics, which have important effects on population persistence (Fischer & Lindenmayer, 2007). Previous studies have been criticized for failing to address metapopulation dynamics and the effects of matrix permeability on the probability of population persistence in natural habitat patches (e.g. Perfecto & Vandermeer, 2008). However, the negative relationship between matrix suitability (which is likely to decline with increasing yields) and patch size (which can increase with increasing yields) means that the direction of the effects of incorporating spatial structure and metapopulation dynamics into our analyses are hard to predict. Investigating this issue through spatially explicit population modelling would, however, allow increased confidence in these results. Such an approach has been adopted for investigating the impact of edge effects on optimal land-use strategies, where land sparing remains the least damaging strategy unless very large edge effects are combined with a very high degree of habitat fragmentation (Lamb, Balmford, Green, & Phalan, 2016). Including demographic information such as reproduction and mortality rates is similarly unlikely to qualitatively alter our conclusions unless natural habitats act as a sink habitat and low-yield farmland as a source (Gilroy & Edwards, 2017)—a situation not supported by the relative population densities of most species we observed.

We defined strategies as "land sharing" based on their relative yields, not their use of "wildlife-friendly" management practices. Actively managing for biodiversity could, therefore, increase their biodiversity value, but our data strongly suggest this approach would not alter our conclusions. Land-sharing landscapes contained low densities of forest species that are losers with agriculture and restricted to remnant vegetation, and higher densities of open, or mixed habitat species (normally winners). Our analyses, and theoretical work (Ekroos et al., 2016), predict the former group will do least badly with land sparing at a regional scale, and that maintaining viable populations within productive landscapes would require conserving impractically large areas of natural habitats. The latter group contains relatively few species, and many of them are abundant generalists with higher populations in agricultural than natural habitats (e.g. blue-black grassquit *Volatinia jacarina*; *Canthon indigaceus*; *Leucaena leucocephala*). They appear to be favoured by large areas of unimproved grasslands with scattered trees and low management intensity (e.g. very limited use of macrocyclic anthelmintics, which have severe impacts on dung beetle communities; Basto-Estrella, Rodríguez-Vivas, Delfin-González, & Reyes Novelo, 2013). Land-use strategies that favour these species would be detrimental for the greater number of species from all three taxa that require large areas of natural habitats. It may, however, be possible to reduce the impact of high-yield agriculture on these species with little or no yield penalty, through the adoption of ISPs and more targeted used of antihelminthics. Another possibility, given the low yields of land-sharing landscapes, would to maintain them as an explicit conservation strategy for these species, managed for biodiversity, rather than food production, although the land needed for this would come at the expense of greater forest conservation and so be detrimental for both the majority of species and regional carbon stocks.

Taxonomic groups respond differently to land-use strategies (Gardner et al., 2008) and investigating less well-known taxa would increase our understanding of these responses. However, the wide range ecological requirements of our study taxa and their worth as ecological indicators (Gardner et al., 2008), combined with the strength of our results, suggest our conclusions are unlikely to change with the addition of new taxonomic groups.

Our study is one of the few analyses of land-use strategies to incorporate food production, biodiversity and carbon storage. However, additional research is needed into the wider environmental impacts and long-term sustainability of different strategies: soil protection, nutrient cycling, water quality regulation and zoonotic disease dynamics are all important considerations and could be adversely affected by high-yield agriculture (Tilman, Cassman, Matson, & Polasky, 2002). All cattle ranches we surveyed corralled animals, leading to the build-up of effluent, potentially posing serious water quality problems (Tamminga, 2003). Such problems are likely to be greater with higher stocking densities (Tamminga, 2003), while many improved pastures use irrigation, potentially reducing water availability. However, our land-sparing scenarios had smaller areas of fodder production than other strategies (see Figure 3), reducing the risk of soil erosion and agrochemical pollution. Converting unimproved pastures to ISPs, could also reduce externalities: compared with unimproved pastures ISPs have reduced incidences of disease and disease vectors, and increased soil turnover (Giraldo, Escobar, Chará, & Calle, 2010; Broom et al., 2013). Finding further ways to minimize the externalities of high-yield livestock systems is a major challenge for sustainability research (Tilman et al., 2002).

Food systems are also fundamentally social and economic systems (Ericksen, 2008), and the effects of land-use strategies on food security and sovereignty; social welfare and equity; and human well-being are poorly understood (Ericksen, 2008; Ericksen, Ingram, & Liverman, 2009). More explicit consideration of these aspects of food systems could help not only to uncover optimal land-use strategies but also the means of implementing them.

Our analyses demonstrate that land sparing would do less damage to biodiversity and carbon stocks than other land-use strategies in Tizimín District. This is the first test of how individual species respond to different livestock yields in tropical dry forests and our results hold for all plausible production targets and despite the long history of disturbance in the region. In addition, our analyses are the first of their kind to assess yields in nonclosed production systems, with multiple interdependent Land uses and with scenarios designed to meet demand for multiple products. This marks an important advance in modelling land-uses in the real world, where food systems are almost always interconnected and operate in networks, rather than in isolation. In practice, land sparing would involve increasing the yields of pastures by improving them or via the use of ISPs, and combining these changes with strict habitat protection or restoration—changes that are largely aligned with the interests of most stakeholders in the region. However, to safeguard the region's biodiversity and reduce its contribution to climate change, active land-sparing mechanisms must be linked to these agricultural shifts, and efforts made to limit the growing demand for beef.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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