

Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism

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Climate change and biodiversity loss can be addressed simultaneously by well-planned conservation policies, but this requires information on the alignment of co-benefits under different management actions^{1–3}. One option is to allow forests to naturally regenerate on marginal agricultural land: a key question is whether this approach will deliver environmental co-benefits in an economically viable manner^{4–7}. Here we report on a survey of carbon stocks, biodiversity and economic values from one of the world's most endemic-rich and threatened ecosystems: the western Andes of Colombia. We show that naturally regenerating secondary forests accumulate significant carbon stocks within 30 years, and support biodiverse communities including many species at risk of extinction. Cattle farming, the principal land use in the region, provides minimal economic returns to local communities, making forest regeneration a viable option despite weak global carbon markets. Efforts to promote natural forest regeneration in the tropical Andes could therefore provide globally significant carbon and biodiversity co-benefits at minimal cost.

As the financial resources available to tackle climate change and biodiversity loss are limited, there is an urgent need to identify actions that simultaneously address both issues^{1,2}. Carbon-based payments for ecosystem services (PES) can fund such actions, although current economic pressures are tending to shift priority towards maximizing carbon gains at the lowest cost^{2,3}. With weak carbon markets, there is a danger that biodiversity will be left behind in the drive to make schemes economically viable^{4–7}. A critical challenge at the interface of climate change and ecosystems science is to identify points of convergence between carbon storage, biodiversity protection and the economic viability of conservation actions, allowing PES co-benefits to be maximized^{1,7–9}. One possibility is to allow forests to naturally regenerate on marginal agricultural lands, although this option has been overshadowed by a focus on avoiding further deforestation, for example in the literature discussing the United Nations' programme for reducing emissions from deforestation and forest degradation (REDD+; refs 2,5–7). An important question is whether natural forest regeneration represents a cost-effective tool to combat climate change and biodiversity loss, particularly in the hyperdiverse tropics^{5–7}.

Here we examine the alignment of carbon and biodiversity co-benefits from natural forest regeneration in one of the world's most threatened ecosystems: the tropical Andes. Global assessments highlight this region as an unparalleled centre of biological endemism^{10,11}, housing one of the highest concentrations of

threatened species worldwide^{12,13}. Andean landscapes have a long history of deforestation for agriculture (Supplementary Fig. 1), suffering the highest predicted extinction rate of all biodiversity hotspots^{13,14}. Recently, however, there are signs of land abandonment and rural depopulation associated with low economic returns from agriculture, followed by a wave of natural forest regeneration¹⁵. We conducted field studies across three regions in Western Colombia, a zone where prior research has been scant owing to political and social unrest¹⁴, despite exceedingly high conservation priority^{12,13}. We performed *in situ* carbon assessments in primary forest, naturally regenerating secondary forest and cattle pastures (Supplementary Fig. 2 and Table 1), combining these with biodiversity surveys (birds and dung beetles) and economic analyses to examine whether carbon-based PES can provide cost-effective conservation benefits.

Carbon assessments indicated that non-soil carbon stocks accumulated at a rate of $4.29 \text{ t C ha}^{-1} \text{ yr}^{-1}$ ($\pm 0.56 \text{ s.d.}$) in naturally regenerating secondary forests, with stocks reaching approximately half the levels found in primary forests within 15–30 years (Fig. 1a and Supplementary Table 2). We calculated the cost of payment initiatives to encourage forest regeneration (for example, REDD+ for carbon enhancement) by estimating the opportunity cost of taking agricultural lands out of production, as well as managing and implementing a PES project (Fig. 1b). We focus on cattle farming, which accounts for 75% of agricultural land and 49% of total land in the Colombian Andes (Supplementary Table 3). We estimated the median net present value (NPV) of cattle pasture in the region to be $\text{US}\$149.83 \text{ ha}^{-1}$ (Fig. 1d), with a 95% credible interval (CI) ranging from $-\text{US}\$51.81 \text{ ha}^{-1}$ to $\text{US}\$383.81 \text{ ha}^{-1}$, accounting for uncertainty in economic parameters (Methods).

Over a 30-year time horizon, the median market price for viable forest regeneration under a long-term certified emissions reduction scheme (ICER; ref. 16) was $\text{US}\$1.99 \text{ t}^{-1} \text{ CO}_2$ (CI $\text{US}\$0.59\text{--}\3.66 , Fig. 1c). Under a temporary credit accounting system, where each credit is re-issued at five-year intervals (tCER; ref. 16), the median price was $\text{US}\$0.80$ (CI $\text{US}\$0.25\text{--}\1.67 , Supplementary Fig. 3). As forest regeneration is a riskier investment than avoided deforestation, willingness to pay for temporary credits may be lower than for permanent credit schemes that apply to standing forests¹⁶. Consequently, the market value of tCERs may be several times lower than that of permanent credits, whereas ICERs are more directly comparable¹⁶. Globally, permanent credits traded at a mean of $\text{US}\$7.80 \text{ t}^{-1} \text{ CO}_2$ in 2013¹⁷, suggesting that both ICERs and tCERs for natural forest regeneration should be economically

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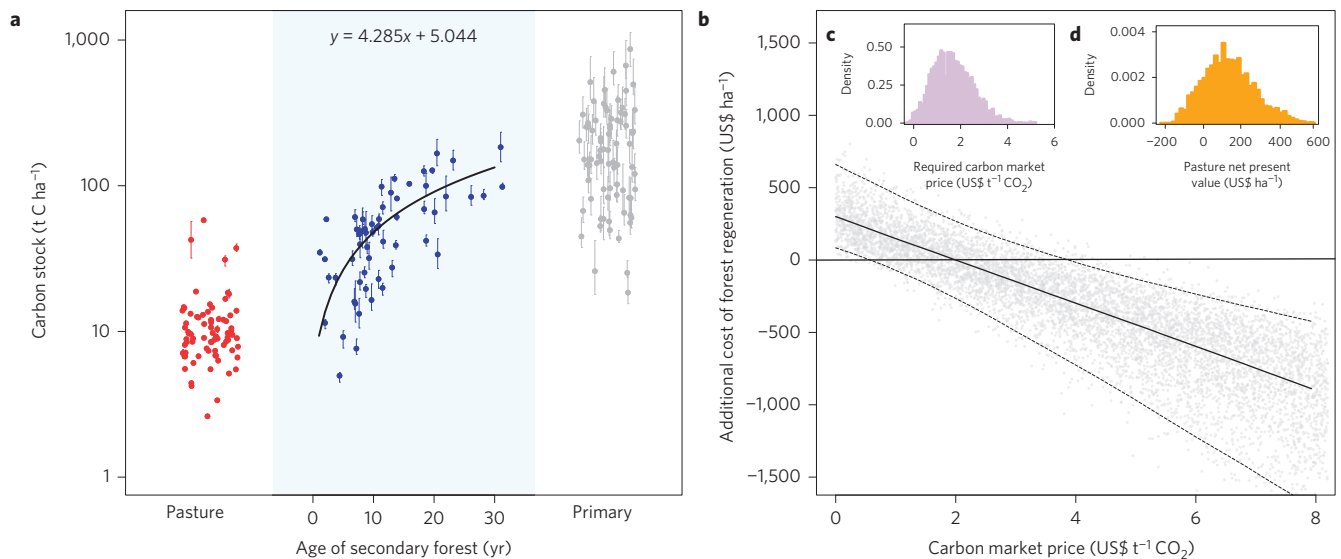


Figure 1 | Carbon accumulation and the cost of forest regeneration on cattle pasture in the Colombian Andes. a, Carbon stocks increase linearly with secondary forest age (blue data points), exceeding levels in pasture (red data points) and approaching those of primary forest (grey data points) after 30 years (error bars show maxima and minima across a range of tree carbon estimation methods; black line shows fitted linear mixed model). **b**, The cost of secondary forest regeneration is the additional payment required to offset the net present value of cattle pasture, accounting for uncertainty in economic values, project implementation costs and carbon accumulation rates, across a range of possible carbon market prices (points show 3,000 model runs for ICER prices; lines show mean and 95% CI). **c,d**, Probability distributions of ICER market prices required to make natural forest regeneration cost-effective (**c**), given the uncertainty in NPV values for pasture (**d**).

viable in the tropical Andes. Indeed, our break-even price estimates fall at the cheap end of the spectrum reflected in other tropical studies worldwide (Supplementary Table 4). A precautionary re-analysis relaxing the assumption that secondary forest ages were known precisely (Supplementary Methods) gave median ICER and tCER prices of US\$2.56 t⁻¹ CO₂ and US\$1.04 t⁻¹ CO₂ respectively (Supplementary Fig. 4).

To assess the potential for biodiversity co-benefits from natural forest regeneration, we modelled the occupancy dynamics of 323 bird and 28 dung beetle species across sampling points arrayed within each major habitat type in our study region. Communities of both taxa were impoverished in cattle pastures relative to forests (Fig. 2a,b), with pastures being markedly species-poor for both birds (Fig. 2c) and dung beetles (Fig. 2g). Species occurrence probabilities showed almost no correlation between primary forest and pasture sites (birds $R^2 = 0.01$; dung beetles $R^2 = 0.18$), confirming that forest taxa were generally unlikely to persist in pastures, and vice versa (Fig. 2e,i).

In contrast, bird and dung beetle communities in secondary forests closely resembled those of primary forests after 15–30 years of regeneration (Fig. 2). Point-level community resemblance to primary forests increased steadily with secondary forest maturity, mirroring changes in carbon stocks (Fig. 2a,b). Constrained community ordinations failed to resolve a clear difference between advanced secondary and primary forests for either taxonomic group, and advanced secondary forest communities were compositionally nested within the ordination cloud of primary forest points (Supplementary Fig. 5). Species accumulation curves indicated that advanced secondary forests held similar species richness to primary forests for both taxonomic groups (Fig. 2d,h), and habitat-specific point occurrence probabilities were strongly correlated between primary and advanced secondary forests ($R^2 = 0.97$ for birds, $R^2 = 0.99$ for dung beetles), indicating that these habitats were occupied at similar levels for the majority of species (Fig. 2f,j).

To examine how secondary forest regeneration might benefit the subset of species most threatened with extinction, we modelled the

occupancy dynamics of 40 IUCN red-listed and range-restricted bird species detected within our study areas, including seven vulnerable, four endangered and one critically endangered species (Supplementary Table 5). Of these, only 11 (27.5%) were detected in cattle pastures, and their mean occurrence probabilities were 70.5% lower in pastures than in primary forest. In contrast, 33 of the 40 threatened species were detected in secondary forest (28 in advanced secondary forest and a further five in young secondary), where their mean occurrence probabilities were only 20.8% lower relative to primary forest. We detected a further seven threatened bird species as incidental observations outside standardized point counts, meaning that we were unable to model their occupancy dynamics; six of these species were detected in secondary forests and only one in pastures (Supplementary Table 5). Collectively, these observations suggest that secondary forests provide suitable habitat for many of the threatened bird taxa in the region.

In the absence of data on habitat-specific demographic rates, we cannot assess whether secondary forest populations are buffered by immigration from nearby primary forest¹⁸. We are therefore unable to predict whether biodiversity will benefit significantly from secondary forest regrowth in areas where undisturbed forests have been completely removed. Similarly, our carbon accumulation estimates refer to naturally regenerating forests with some degree of connectivity to primary forest; secondary forests without this connectivity may not achieve such high rates of carbon accumulation without costly active management measures such as planting¹⁹. Nevertheless, our results show that natural forest regeneration in cattle pastures surrounding extant primary forests could significantly enhance both carbon stocks and Andean biodiversity. Forest regeneration will directly boost population sizes of many species, whilst primary forest specialists should benefit from enhanced dispersal potential between remaining primary forests²⁰. Zones with highest potential for biodiversity and carbon recovery (that is, agricultural areas close to existing forest tracts) are perhaps also likely to be most economically favourable for PES, as the profitability of agriculture tends to decrease with distance from population centres²¹.

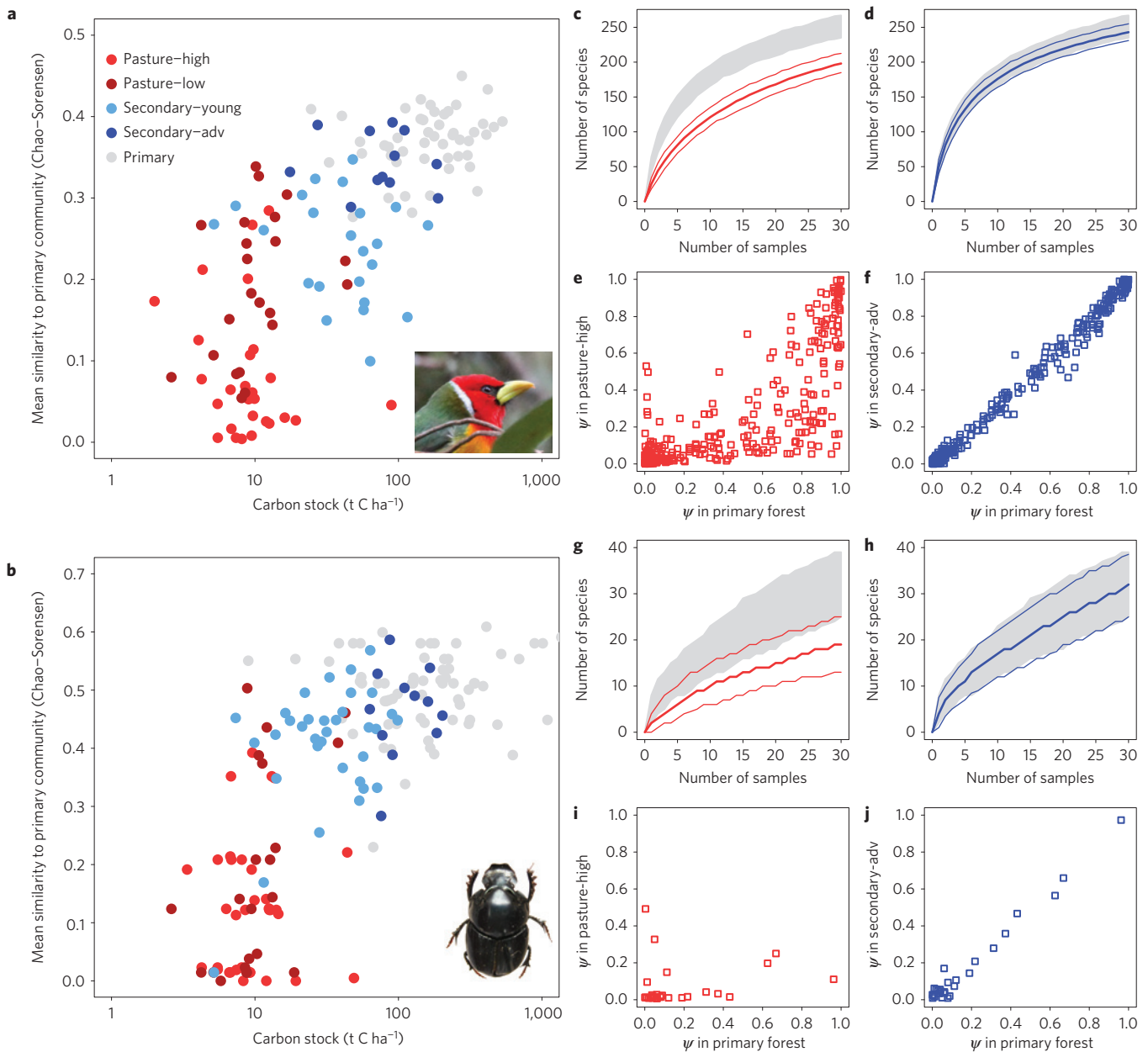


Figure 2 | Biodiversity in cattle pastures and secondary forests of the Colombian Andes relative to primary forest. Bird (a) and dung beetle (b) community similarity to primary forest increases across a continuum from cattle pasture (higher and lower intensity) through younger secondary forests (<15 yr, ‘secondary young’) to advanced secondary forests (15–30 yr, ‘secondary adv’), correlating closely with carbon stocks. c–i, Species accumulation curves show considerably lower richness in higher-intensity cattle pasture (birds (c); dung beetles (g); red lines show median and 95% confidence intervals) relative to primary forest (grey shaded area shows 95% confidence interval), but similar species richness in advanced secondary and primary forests (birds (d); dung beetles (h); blue lines show median and 95% confidence intervals for advanced secondary forest). Occurrence probabilities for each species (ψ) are poorly correlated between higher-intensity pasture and primary forest (birds (e); dung beetles (i)), but are strongly correlated between advanced secondary and primary forest (birds (f); dung beetles (j)), indicating that the latter two habitats are similar for most taxa.

An important problem associated with carbon-based PES schemes is the potential for ‘leakage’, whereby conservation actions indirectly lead to environmental degradation elsewhere^{22,23}. For example, the widespread establishment of forest regeneration projects on cattle pastures might lead to a regional fall in beef production, and in turn a rise in market price. This could incentivize the conversion of natural habitats to pasture in areas outside PES agreements²³. Most studies overlook the costs associated with leakage when calculating break-even carbon prices (Supplementary Table 4), although evidence suggests that they can be as high as agricultural opportunity costs²².

Leakage could theoretically be minimized by coupling forest regeneration PES with policies to promote yield improvement, for example by education programs (farmer field schools), improved husbandry, forage or stocking techniques²⁴. To examine how the inclusion of such measures might influence PES break-even carbon prices, we extended our economic analyses to incorporate a mitigation cost equivalent to twice the opportunity cost of pasture. This elevated the median carbon price to US\$4.74 t⁻¹ CO₂ under an ICER scheme (CI \$0.96–\$8.76), or US\$1.78 t⁻¹ CO₂ for tCERs (CI \$0.37–\$4.03). This suggests that there is significant scope to incorporate leakage mitigation measures into

forest regeneration PES in the tropical Andes without limiting economic viability.

To predict the long-term feasibility of forest regeneration, it is necessary to consider how market changes could influence the profitability of agriculture in the future. A sensitivity analysis suggested that pasture NPV (and hence break-even carbon price) depends strongly on cattle yields per hectare and beef market prices (Supplementary Fig. 6). To forecast how future changes might influence PES viability, we examined a hypothetical scenario in which both parameters were doubled in unison (Supplementary Fig. 7), giving median break-even ICER prices of US\$13.78 t⁻¹ CO₂ (CI \$9.13–\$19.05), or US\$39.90 t⁻¹ CO₂ (CI \$26.17–\$55.01) when incorporating leakage mitigation costs at double the agricultural opportunity cost (see Supplementary Fig. 8 for a graphical summary of all scenarios). Although cattle production and beef market prices have shown gradual increases across the tropical Andes over the past decade (Supplementary Fig. 7), we believe that market changes are unlikely to be of sufficient magnitude to render carbon-based PES economically uncompetitive, at least in the near future.

Our results empirically demonstrate the potential for carbon enhancement initiatives under REDD+ to deliver cost-effective carbon and biodiversity co-benefits. The socioeconomic and environmental conditions within our study areas are typical of those found in pasture-dominated landscapes throughout the Colombian Andes (Supplementary Fig. 9), suggesting that PES schemes could be viable across a wide geographical area. The implementation of such schemes may prove challenging²², requiring a strong system of governance to ensure the enforcement of property rights and that carbon payments reach farmers^{25,26}. Nevertheless, our work suggests that cloud forest zones in the tropical Andes could offer golden opportunities for REDD+ carbon-recuperation schemes, delivering multiple environmental benefits at minimal economic cost.

Methods

We selected three study areas straddling the agricultural frontier in the western Andes of Colombia (Supplementary Fig. 1 and Table 1). Cattle farming is the primary land-use regionally (Supplementary Table 3), and the only major agriculture within the study areas. We sampled 400 m × 400 m squares located randomly across primary forest, advanced secondary forest (>15 yr), young secondary forest (<15 yr), and pasture (incorporating some primary and secondary forest fragments). Squares were spaced ≥300 m apart between habitats and ≥400 m within habitats. Sample effort was proportional to habitat cover: primary = 23 squares (368 ha); advanced secondary = 6 squares (96 ha); young secondary forest = 9 squares (144 ha); and pasture = 20 squares (336 ha). All younger secondary forests (<15 yr) were owned by conservation NGOs (Supplementary Table 1), who provided detailed records of stand ages. Ages of older secondary forests (15–30 yr) were estimated through informal interviews with locals and reserve managers, taking the mean when reported ages differed. Beyond excluding cattle, all secondary forests were unmanaged, and all had some degree of connectivity to primary forest.

We sampled non-soil carbon in 43 squares, establishing 15 m × 5 m plots at five evenly spaced points along a triangular 400 m transect (all overlapping with biodiversity sampling locations). We measured aboveground living tree biomass, tree root biomass, dead wood, leaf litter and living vines, estimating tree biomass using a range of allometric equations derived from harvested tree studies in both primary and secondary forests (Supplementary Methods). We used a large number of relatively small plots (215 in total) to best capture the small-scale habitat heterogeneity typical of the tropical Andes²⁷.

We sampled birds at three points within each square (174 in total with minimum 200 m spacing; Supplementary Table 1), conducting 100 m radius point counts of 10 min duration on four mornings (06:00–12:00), avoiding conditions of rain or high winds (>10 mph). We excluded records of transient species (non-breeding migrants, soaring raptors and swifts). Unknown vocalizations were recorded and subsequently identified using reference material (www.xeno-canto.org). We sampled dung beetles using five pitfall traps baited with human dung within each of 36 squares (180 in total with minimum 100 m spacing; Supplementary Table 1). We collected samples at 24 h intervals across four days and re-baited after two days. Species determinations were made using reference materials from Instituto Alexander von Humboldt, Colombia.

We used government datasets to estimate cattle stock density, meat per head, market price and the costs of raising cattle to market—including labour,

medicine, dietary supplements and transport costs (Supplementary Table 6). All price and cost values were inflation-adjusted to 2013 US\$ rates. We used these values to estimate the NPV of a hectare of cattle pasture, accounting for uncertainty by resampling uniform distributions for each parameter, bounded by the highest and lowest values derived across all data sources (Supplementary Methods and Supplementary Table 6). To calculate the break-even CO₂ market price needed to make PES cost-effective, we assumed that carbon payments must offset agricultural opportunity costs (measured as NPV), as well as the costs of project implementation and management—again using uniform distributions bounded by values derived from the literature. We used two accounting methods to calculate break-even prices: long-term credit schemes (ICERs) and temporary schemes (tCERs; ref. 16), both of which issue certified carbon credits for fixed time periods (Supplementary Methods). To incorporate estimates of carbon sequestration, we used a linear mixed model linking carbon stocks to forest stand age, accounting for potential spatial autocorrelation by including sampling square as a random effect. We allowed discount rate to vary across a plausible range (4–12%), and estimated NPV and the break-even carbon price for 10,000 random samples, assuming a 30 yr time horizon. We also conducted a precautionary re-analysis relaxing our assumptions about forest age, along with a sensitivity analysis examining potential future variation in yield, market price and production costs. To examine the effects of incorporating leakage mitigation measures, we further extended the analysis to incorporate an additional cost equating to double the NPV of pasture (see Supplementary Methods for full details).

We evaluated the similarity of bird and dung beetle communities across habitats using the Chao–Sørensen abundance-based similarity index, which is robust to incomplete detection of species-rich communities²⁸. We also used canonical discriminant analyses (CDA) to evaluate the significance of differences between habitats, performing permutation tests in Program CAP (ref. 29). To examine variation in species richness and occupancy probability across habitats, we modelled the occupancy dynamics of each species using a Bayesian hierarchical community-level framework³⁰. For each habitat type, we estimated occurrence probabilities (ψ) for each species by modelling heterogeneity in detections over repeated visits to each sampling location (Supplementary Methods). Occurrence probabilities therefore reflect the likelihood that a species occurs in a given habitat type, controlling for the confounding effects of detection heterogeneity³⁰. To estimate total species richness, we generated spatially independent predictions of species accumulation curves using a data augmentation approach³⁰, allowing for full integration across uncertainty in habitat-specific species occurrences.

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Author contributions

D.P.E., T.H. and J.J.G. conceived the study. D.P.E., J.J.G., F.A.E., P.W., C.W. and C.A.M.U. collected data. J.J.G. analysed the data and wrote the first draft. All authors contributed substantially to revisions.

Additional information

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Competing financial interests

The authors declare no competing financial interests.