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RESEARCH ARTICLE

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Woody vegetation patches in South Indian rice landscapes support tree-affiliated birds but reduce food production, with complex non-linear effects

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Abstract
Context Managing agricultural landscapes for sustainability while maintaining high yields is a pressing challenge. Protecting and restoring native or semi-natural vegetation patches is often a core strategy, but its impacts are seldom measured at scales appropriate to understanding yield-biodiversity relationships.
Objectives In a predominantly rice-growing area of South India, we examined how increasing woody vegetation patch cover impacts (1) harvest- and landscape-level (25 ha) crop yield, (2) densities of birds of different trophic guilds and forest dependencies, and (3) bird community similarity to natural forests.
Methods We sampled landscapes spanning a continuum of embedded vegetation patch cover. We used statistical weighting to account for confounders and fitted generalised linear and hierarchical Bayesian models, using g-computation to assess the effects of these patches on yield and bird biodiversity.
Results Vegetation patches reduced harvest-level yield at low cover levels, with landscape-level yield declining more sharply than expected based on patch-occupied area alone. Above ~ 10% cover, harvest-level yield slightly increased, while landscape-level yield remained constant. Pest control-contributing guild densities rose with vegetation cover, above a ~ 10% area threshold. Forest-dependent species responded positively to increasing vegetation cover, while non-forest species showed mixed responses. Similarity to forest bird communities increased with vegetation cover but remained low.
Conclusions Vegetation patch-free landscapes maximise yield but are of low bird conservation value, and patch covers < 10% entail a yield penalty rather than providing ecosystem-service-related yield benefits, as theory predicts. Increasing vegetation cover from 10 to 20% improves biodiversity with no further yield penalties, suggesting that at least ~ 10% cover

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may be needed for multifunctional management in this South Indian context.

Keywords Agroecology · Ecosystem services · Food production · Vegetation patches · Farmland trees · Birds

Introduction

Identifying and fostering agricultural landscapes that are simultaneously high-yielding, and ecologically and socially sustainable is critical in addressing numerous global challenges, including biodiversity loss, climate change, food security, and social injustices (Leclère et al. 2020; Williams et al. 2021; Balmford et al. 2025). However, trade-offs between land-use objectives, including between biodiversity or ecosystem functioning and agricultural productivity, are the norm rather than the exception (Grau et al. 2013; Balmford 2021; Meyfroidt et al. 2022). Whilst the importance of preventing further agricultural expansion is unequivocal, framing agricultural strategies as land sparing or land sharing alternatives oversimplifies the complexity of land systems (where the former promotes intensification to reduce agricultural land-use and the latter entails lower-yielding biodiversity-friendly farming; Meyfroidt et al. 2018; Baudron et al. 2021; Kuemmerle 2024). Instead, redesigning land systems for multifunctionality and sustainability will necessitate a mixture of different heterogenous land-sharing and land-sparing landscapes (Grass et al. 2019).

Protecting and restoring patches of native- and semi-natural vegetation has been heralded as a promising conservation strategy for some time as they can markedly boost the quality and permeability of agricultural landscapes for biodiversity (Harvey et al. 2006; Kremen and Merenlender 2018; Hendershot et al. 2020; Lecoq et al. 2021; Estrada-Carmona et al. 2022; Riva and Fahrig 2022). However, the relationship between vegetation patches and biodiversity is complex, context dependant, and frequently non-linear (Radford et al. 2005; Banks-Leite et al. 2014). For example, forest-dependent bird species with specialised diets are highly sensitive to forest cover losses in agricultural landscapes, whereas generalist, non-forest species frequently exhibit neutral or even positive responses since they can use resources from a myriad of landscape patches and benefit from increased foraging efficiency (Lindell et al. 2004; Tscharntke et al. 2008; Banks-Leite et al. 2014; Carrara et al. 2015; Morante-Filho et al. 2018, 2021). Thus, bird responses to increasing vegetation patch cover are variable, and likely a product of species' life history traits, the type and strength of biotic interactions, the spatial configuration of different land-use types, land-use history, the scale at which the relationship is examined, and the structure, composition and management of the patches and the land cover within which the patches are embedded (Watson et al. 2005; Tscharntke et al. 2012; Driscoll et al. 2013; Bregman et al. 2014; Lindenmayer et al. 2019; Fletcher et al. 2024; Andreatta et al. 2025). Numerous questions remain on how vegetation patches are best managed and integrated for effective landscape-scale conservation planning that balances the needs of different species in different contexts (Balmford 2021; Fahrig et al. 2022; Valente et al. 2023; Fletcher et al. 2024).

Similarly, the consequences of enriching agricultural landscapes with vegetation patches for food production and other societal needs are surprisingly poorly understood, despite it being widely promoted as an important strategy to transform agricultural land systems for sustainability and multifunctionality (Reed et al. 2017; Albrecht et al. 2020; Olesen et al. 2022). Vegetation patches can deliver crop yield benefits through, for example, pollination (Ricketts et al. 2008; González-Chaves et al. 2022), natural pest suppression (Gurr et al. 2017; Dainese et al. 2019), soil nutrient cycling and erosion mitigation (Crous-Duran et al. 2020), water regulation (Tamburini et al. 2020), and shade-provisioning and temperature regulation (Reed et al. 2017; Blaser et al. 2018). However, in certain systems, they can also have negative impacts on agricultural productivity by competing with food crops for resources such as water, soil nutrients, and pollination services, and by promoting ecosystem disservices such as supporting populations of agricultural pests and diseases (Karp et al. 2018). Overall, the impact of vegetation patches on food production is complex and inconsistent; for example, across the tropics, the effect of individual trees and forest patches on field-level crop yields was positive in around half of the studies examined, whereas the other half suggested negative, neutral, or mixed effects (Reed et al. 2017).

Moreover, almost all existing studies only assessed productivity effects at field- or farm- rather than landscape scale, and do not consider the land taken out of production by these vegetation patches (but see e.g. Pywell et al. 2015; Zemp et al. 2023; d'Albertas et al. 2024) which means forgone food production has not been accounted for (Berger et al. 2023). Biased estimates of the socio-ecological costs and benefits of interweaving vegetation patches in agricultural landscapes could lead to unwanted outcomes, if more widely implemented, such as production losses, failed restoration efforts, and/or leakage as agriculture is displaced into natural ecosystems (Meyfroidt et al. 2018). There is a theoretical expectation that at lower levels of vegetation cover (0–20%), ecosystem service benefits derived from vegetation patches will counter-balance the loss of landscape-level yield that results from taking land out of production, or even increase landscape-level yields, due to effects of natural pest regulation, pollination and prevention of soil erosion (Fig. 1; Garibaldi et al. 2020). The underlying model is described by Eq. 1:

where VPC is Vegetation Patch Cover (a percentage between 0 and 100), B is field-level yield benefit from vegetation patches (a value between 10 and 40, expressed here as a percentage) and e is the base of the natural logarithm. This version of the model assumes, for simplicity, that each 1ha of agricultural land produces 100 kg of product.

To our knowledge, this theory has not been rigorously tested in any specific context. Landscape-level yield-vegetation cover relationships are likely to be highly context-dependent, with their shape moulded by a plethora of factors. These include the maximum attainable yield in a landscape (underpinned by biophysical conditions), the response of yield to field-level management (including external inputs), the dependency of yield on ecosystem functions and the biodiversity underpinning it (for example, a crop's pollinator dependency), and the responses of ecosystem functions and biodiversity to field-level management and vegetation patches (Burian et al. 2024).

$$\textit{Total yield}\ (\text{kg}/100\ \ \text{ha}) = 100\ \text{kg} \times (100 - VPC) + (100\ \text{kg} \times (100 - VPC)) \times \frac{B - Be^{-0.1VPC}}{100} \quad (1)$$

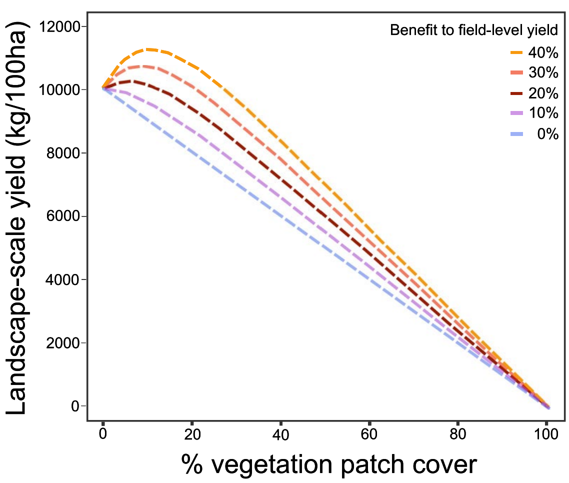

Fig. 1 Theoretical expectation by Garibaldi et al (2020) for the relationship between the relative area occupied by (semi-)native vegetation patches in agricultural landscapes and agricultural productivity, here represented as kg/100 ha (see Eq. 1), with a theoretical production level of 100 kg/ha. Exponential curves assuming increasing benefits (0%, 10%, 20%, 30%, 40%) from vegetation patches to yields of the land under production, suggesting that landscape-level yield could be maximised at low to medium levels of embedded vegetation patches. Adapted from Garibaldi et al (2020) with permission

Currently, we lack a detailed understanding of the relationships between landscape-level food production, biodiversity outcomes, and non-crop vegetation cover in different socio-ecological contexts, hampering our ability to design and govern productive yet sustainable agricultural landscapes. Here, we examine these relationships and test Garibaldi et al (2020)'s theoretical expectation in a tropical smallholder system in South India. The region is characterised by one of the largest transitions to agroecological management globally, namely the Zero Budget Natural Farming (ZBNF) programme, but the focus lies on improving soil health rather than enriching landscapes with non-crop vegetation (see Berger et al. 2024). We specifically assessed how vegetation patches affect (1) harvest- and landscape-level yield; (2) densities of birds of different groups characterised by their trophic guild and dependency on forests for persistence; and (3) bird community integrity in comparison to natural forests.

Methods

Ascertaining the effect of native and semi-natural vegetation patches on agricultural productivity and biodiversity outcomes requires measuring their impact against the counterfactual, i.e., what the outcomes would have been under different amounts of vegetation cover. We aimed to minimise the differences in covariates that co-vary along the continuum of vegetation cover by careful site selection in the field and statistical weighting (Supplementary Figure 1). Weighting entails constructing weights that balance covariate distributions across the treatment (here vegetation patch cover) continuum, and it can thus adjust for possible observation bias and consequently increase the robustness of the treatment effect estimate (Jones and Lewis 2015; Huling et al. 2023; Siegel and Dee 2025).

Sample landscapes ('squares'), point, and field selection

We selected 26 agricultural landscapes and 25 natural forest landscapes in the North of the South Indian state Andhra Pradesh (Supplementary Figure 2; see Supplementary Information 1 for details). All landscapes had similar biophysical characteristics (rainfall, temperature, slope, elevation; Supplementary Figure 3). The farming practice, agrichemical or agroecological (specifically Zero Budget Natural Farming, ZBNF; Berger et al. 2024), varied between agricultural landscapes, but the 13 agroecological and 13 agrichemical landscapes covered a near identical distribution of embedded vegetation patch cover (Supplementary Figure 4). In this study, data from the agricultural landscapes are used to explore effects of embedded vegetation patches on food production and bird biodiversity. Here, the data from forest landscapes are used only to estimate the similarity of agricultural bird communities to local forest communities (Supplementary Figure 1). The contrasting farm management approaches are directly compared in a different study, using some of the same data (Berger et al. 2024).

Each landscape represented a 500 m × 500 m square (25 ha; see Supplementary Information 1 for justifications). Within each square, we positioned four points, each evenly spaced 200 m apart and 150 m from the square edges. We conducted bird counts from these points. At the agricultural sites, we also interviewed the farmers managing the fields where these points were located, as well as up to two additional farmers per square, to gather data on crop yields.

Data collection

Land-use cover

We measured the area under vegetation patch cover, tree crops, and cropland in each landscape by mapping each land cover type with a handheld GPS and visualising them in QGIS. No other land cover types were found within the squares.

Here, we define vegetation patches as small forest fragments (<0.02 km^2), individual native or naturalised trees, riparian buffers, hedges, and herbaceous plants beneath woody canopies (see Supplementary Figure 5 for examples). Farmland trees in Andhra Pradesh consist of remnant forest trees as well as cultivated species (Singh et al. 2024; Andhra Pradesh Forest Department 2024). In our landscapes, we commonly recorded coconut (*Cocos nucifera*), Asian palmyra palm (*Borassus flabellifer*), neem (*Azadirachta indica*), mango (*Mangifera indica*), tamarind (*Tamarindus indica*), gum Arabic tree (*Acacia nilotica*), Malabar plum (*Syzygium cumini*), sacred fig (*Ficus religiosa*), Indian laurel tree (*Terminalia elliptica*), Indian ash tree (*Lannea coromandelica*), madhuka (*Madhuca longifolia*), *Xylia xylocarpa*, black siris (*Albizia odoratissima*), jackfruit (*Artocarpus heterophyllus*), and teak (*Tectona grandis*). All vegetation patches in the study contained at least one tree, woody shrub, or palm.

In our system, tree crops constituted cashew (*Anacardium occidentale*) and coconut. Thus, when they were grown in a plantation as a commodity crop, we counted them under tree crop area and estimated their calorific value. In contrast, we categorised single coconut, palmyra palm, and mango trees (which were grown on field edges and usually accompanied by other farmland trees or herbaceous vegetation) as vegetation patches. Nonetheless, as robustness checks, we repeated harvest-level analyses with all these single trees not included in the total area coverage of vegetation patches, and landscape-level analyses with them classed them under the area of tree crops instead.

Agricultural yield

Assisted by local villagers, we identified the farmers managing the fields at the four designated points in each landscape, along with up to two additional randomly selected fields. We conducted structured interviews which asked for yield and cropping cycle information about the focal field over a 1-year recall period, which therefore included all crops successively grown on the same field per annum (see Supplementary Table 1). Across the 26 agricultural landscapes, we acquired information on 128 fields and obtained yield information on 206 harvests (since most farmers grew multiple crops on the same piece of land over the year). We verified that reported yield values are feasible using district-level government statistics (ICRISAT 2020).

A range of different crops were grown, where, of all harvests we obtained data on, rice constituted 59.2%, black gram 14.1%, maize 6.3%, cashew 4.7%, sesame 3.9%, sugarcane 2.9%, groundnut 1.9%, green gram 1.4%, and ragi, sunflower, tomato, aubergine, beans, bottle gourd, tapioca, and coconut each less than 1%. Most of these crops are largely not dependent on animals for pollination (Supplementary Table 2).

To obtain a total measure of yield per annum per unit area in a common currency, we first subtracted the proportion of the harvested product that is uneaten (such as husks and peels; see Supplementary Table 3) and then converted the estimates of mean net annual yield for each crop into a common unit, namely food energy (gigajoules, GJ). For perennial crops, we developed simple crop lifecycle models and then estimated the energetic value of each harvest and then each field annually (GJ $acre^{-1}$; see Supplementary Information 2 for details).

We calculated the mean of the field-level yield (weighted by field size) for each square for tree and non-tree crops separately and then multiplied these estimates by the area under tree crops and cropland respectively, and then summed the two to obtain estimates of the total annual production (in GJ) per 25 ha square (Supplementary Information 2).

Bird densities

We conducted point counts from the four points in each of the 51 agricultural and forest landscapes during both winter (December–March) and summer (April–June) over 2 years (2021/2022 and 2022/2023). Each point was visited four times (once per season per year) for 10 min each, resulting in 816 point counts and 160 min of observation per square, totalling 8320 min across all sites. We ensured that the order in which landscape types were visited did not systematically vary within or between seasons and that each square was once visited early and once late in each season. To account for varying detectability of different species in different habitats, we used distance-sampling methods (Buckland et al. 2015).

All counts were conducted between 15 min before and 3 h after sunrise. At each point, we counted birds for 10 min without a settling-in period, recording the distance to each bird. Birds flushed while approaching the point were included, but birds seen only in flight or that flew in during the count period were excluded. We identified individuals to species-level based on BirdLife International taxonomy. We measured the direct distance from the point to the location of the centre of each cluster or individual bird when it was first detected using a laser rangefinder, as well as the angle of elevation; from this, we calculated the horizontal distance. For individuals detected aurally but not seen, we measured the distance to the tree (or other feature) from which the bird vocalized. Observations beyond 100 m from the point were truncated, and largely aerial and transient species were excluded (following Gilroy et al. 2014; these included swifts and swallows, large raptors, and oriental pratincoles).

We quantified the proportion of 'closed' habitats (i.e., features that impaired detectability such as trees, hedges, and high crops) around each survey point ($r = 100$ m) using a handheld GPS and QGIS. For forest points, the proportion equalled one. We also verified that the average proportional vegetation patch cover around each of the four points ($r = 100$ m) was not substantially different than that of the square as a whole.

Data analyses

We conducted all statistical analyses using R version 4.3.1. For each analysis, we verified whether the assumptions of normality and homogeneity of variances were satisfied and assessed overdispersion with the *DHARMa* package (Hartig and Lohse 2022). We examined spatial autocorrelation by calculating Moran's I coefficient using the *ape* package (Paradis and Schliep 2019).

Effect of vegetation patches on yield

To examine the effect of vegetation patches on agricultural productivity, we had to ensure balance of potential confounders across the vegetation cover continuum (i.e. that confounders did not co-vary with the amount of vegetation patch cover). To correct for imbalances, we used the R package *WeightIt* (Greifer 2025) to estimate distance covariance optimal weights (Huling et al. 2023). We used the weighting method 'energy balancing' as it has been demonstrated to perform well in a broad range of settings for continuous treatments (Huling et al. 2023), and, for our data, resulted in a better balance and larger effective sample size than propensity score weighting (another commonly used weighting method; see Supplementary Figure 6).

At the harvest-level, we weighted harvests on farming practice (agroecological or agrichemical farming), agroecological suitability (a measure of how suitable the land is for agriculture; obtained from Global Agro-Ecological Zones GAEZ v3.0; FAO and IIASA 2012), crop type, and whether or not a given harvest was irrigated. These variables influence crop yield as well as vegetation patches in the landscape (either directly or via affecting land management decisions made by agrarian communities) and if unaccounted could bias our estimates of the effect of vegetation patches on yield. As robustness checks, we repeated our analysis but (1) with palm and mango trees excluded from the percentage area of vegetation patches (see above); (2) instead of weighting, we included the potentially confounding variables as covariates; (3) instead of weighting on agroecological suitability, we weighted on temperature, rainfall, elevation, and soil type; and (4) only analysing rice harvests from the main growing season (thus not weighting on crop type). We square-root transformed our data to meet model assumptions, and removed four tapioca harvests as they represented outliers (Supplementary Figure 4).

At the landscape-level, we weighted squares on farming practice, agroecological suitability, the average number of harvests grown, the proportion of harvests that were rice, and whether the square was irrigated. As robustness checks, we repeated our analysis but (1) with single palm and mango trees classed as tree crops (see above); (2) instead of weighting, we included the potentially confounding variables as covariates; and (3) instead of weighting on agroecological suitability, we weighted on temperature, rainfall, elevation, and soil type. We removed one landscape (which contained the tapioca harvests) as it represented an outlier.

We fit (generalised) linear models with harvest- or square-level yield respectively as the response variable and the percentage of vegetation cover in the square as the predictor variable on which we used a natural cubic spline with 2, 3 or 4 degrees of freedom (d.f.), in separate analyses. Splines were used as relationships between vegetation patches and biodiversity, ecosystem functions, and agricultural productivity tend to be non-linear (Banks-Leite et al. 2014; Burian et al. 2024). We included the weights obtained from weighting and, for the harvest-level model, we also included square identity as a random term. Predictive techniques are inappropriate for drawing causal conclusions (Arif and MacNeil 2022); thus, we did not use model selection to identify which spline specification resulted in the best-fitting predictions, but we report the results of all three models. For a representative set of 100 percentage vegetation cover values (drawn from the 10th to 90th percentiles of vegetation cover because estimates outside this range of landscapes tend to be imprecise) we used weighted g-computation (a causal inference approach; see Snowden et al. 2011) to estimate the effect on yield. We used the functions *avg_predictions* and *avg_slopes* of the package *marginaleffects* (Arel-Bundock et al. 2024) to compute the expected potential outcomes under a representative set of vegetation cover values and to examine the average marginal effect function.

Effect of vegetation patches on birds

Bird densities To estimate the effect of increased vegetation on bird communities we first estimated detectability. For the 52 species with at least 40 observations, we fitted species-specific detection functions.

Functional trait data were extracted from AVONET (Tobias et al. 2022), and all species were grouped into 18 detectability groups based on taxonomic, dietary, and behavioural characteristics (again with ≥ 40 observations per group). We fitted detection functions using the *mrds* package (Laake et al. 2022). Three models were considered for each species or group: (1) a single detection function with the proportion of closed habitat around each point as a covariate; (2) a single detection function with no covariates; and (3) separate detection functions for forest and/or farmland sites, provided there were at least 40 observations in each. For group-level detection functions, species was included as a covariate in each model. We tested half-normal and hazard-rate key functions with cosine, Hermite polynomial, and simple polynomial adjustment terms in each case. We examined fitted detection models by visually checking quantile–quantile plots and the shape of the detection function, and we conducted Chi-square, Kolmogorov–Smirnov and Cramer-von-Mises tests. We removed models that resulted in a poor fit or failed to converge. A list of feasible detection functions (i.e., those offering a good fit) was obtained. Model (3) was preferred over (1) and (2) if it offered a good fit for a species at each site; otherwise, AICc was used for model selection. These models were used to estimate the effective area surveyed for each species at each point (see Supplementary Table 4 for information on which model was used for which species).

To model the effect of vegetation patches on bird densities, we fitted a Bayesian model to the count data which we adjusted using the estimated detectability parameters (Buckland et al. 2015). We used energy balancing to weight squares on farming practice, rainfall, temperature, and whether or not the square was irrigated (elevation was excluded due to collinearity with rainfall; Supplementary Figure 7). We applied a hierarchical zero-inflated Poisson count model to estimate individual species counts per point, per visit (see Supplementary Information 3). We modelled the zero-inflation using a Bernoulli distribution with the percentage of vegetation patch cover (continuous) as a fixed effect and species as a hierarchical varying intercept. For the Poisson distributed count model, we modelled the number of individuals of a species recorded during a given visit to a point weighted by the above-described weights (applied as frequency weights) as a function of the fixed effect of vegetation patch cover, trophic niche (granivore, frugivore, omnivore, invertivore, and vertivore; obtained from Tobias et al. 2022), and forest dependency (*FD*, obtained from BirdLife International 2022). Only one of the species we recorded (*Oriolus kundoo*) in agricultural landscapes is considered of 'high' *FD* by BirdLife (i.e. requires intact forest in the landscape for breeding and/or foraging). Since the prediction for a group with only one species would be unreliable, we reclassed that species as being of 'medium' *FD* (frequently found in forest but not reliant on intact forest in the landscape). The other categories are 'low' FD and 'non-forest' (low and no reliance on intact forest for breeding and/or foraging respectively; see Supplementary Table 4 for a full species list). Similarly, we re-classed 23 species considered 'aquatic predators' under Tobias et al. (2022) as invertivores or vertivores according to the given species' diet (see Supplementary Table 4). We placed a tensor product smoother on vegetation cover, trophic niche, and FD (using the *t2* function of the *mgcv* package, Wood 2011; following Pedersen et al. 2019) as this allowed us to estimate nonlinear responses to vegetation patch cover for each unique trophic guild-forest dependency group. We further allowed the intercept and slope of vegetation patch effect to vary by species and included a hierarchical structure of points nested within squares to account for our sampling design. The effective area surveyed was included as an offset.

As above, we used weighted g-computation to estimate the effect of vegetation patch cover on the density of each unique guild-FD group, where we held species-level effects constant.

Bird community integrity relative to natural forests We estimated bird community integrity using the abundance-based Bray–Curtis similarity index (calculated using the package *vegan;* Oksanen 2010), where we quantified the difference in species composition between each point in the forest landscapes and each point in the agricultural landscapes (having first summed observations across visits to each point). We then modelled the Bray–Curtis similarity index along the vegetation patch cover continuum using a Bayesian hierarchical model with a zero–one inflated beta distribution to account for the left-skewedness and the bounded nature of the data (in the range of 0–1; see Supplementary Information 3). The zero–one inflated model specifically models the observed Bray–Curtis similarity index as the non-zero-or-one index, the shape parameter of the non-zero-or-one beta distributed index, the zero-and-one probability and the conditional one probability. In this model we included vegetation patch cover as a fixed effect upon which we placed a natural cubic spline with 2, 3, or 4 d.f., and a nested random effect structure indexing each agricultural point nested within a square. We further included the forest point a given agricultural point was compared to as an un-nested random intercept for the non-one-or-zero index values, the one and zero probability and the conditional one probability. We included the same weights as frequency weights as above. As a robustness check, we also repeated the analysis at the square-level (i.e. with observations summed to each square).

Again, we used weighted g-computation to estimate the effect of vegetation patch cover on bird community integrity.

For all Bayesian models, we specified zero-centred diffuse priors for the intercept (normally distributed with a mean of 0 and standard deviation of 10), and ran the models with four chains, each with 1,000 warm up iterations and 2,000 post-warm up sampling iterations: totalling 8,000 posterior sampling iterations. Model convergence was verified by examining trace plots and the *Rhat* statistic, and adequacy evaluated using posterior-predictive plots. We performed all modelling through the *brms* package (Bürkner 2017) as an interface to the Bayesian inference engine Stan.

Results

Effect of vegetation patches on yield

Harvest-level yield was negatively affected by vegetation patches at low levels of cover

Low levels of vegetation cover (up to 5–10%) had a clear negative effect on yield and medium or high levels of cover (> 10%) exerted a subtle positive (under a 2 d.f. spline) or null effect (under a 3 and 4 d.f. spline; Fig. 2). The flexibility of the spline used altered the nuance of the estimated association, however the negative initial association remained across analyses.

The least flexible model (a spline with 2 d.f.), suggested at low levels of vegetation patch cover, up to around 7%, vegetation patches had a negative effect on harvest-level yield (Fig. 2a, b). In contrast, the effect was positive at a cover above 15%. Harvest-level yields did not differ between landscapes with 20% cover and landscapes with no vegetation patch cover (-0.000204 ± 0.000131GJ ha^{-1}, $p = 0.12$) and landscapes with 10% vegetation cover (0.000101 ± 0.000206 GJ ha^{-1}, $p = 0.622$). In contrast, the harvest-level yield of landscapes with a 10% cover was lower than that of landscapes with no vegetation patches (-0.000439 ± 0.000173 GJ ha^{-1}, $p < 0.05$).

With increasing model flexibility (3 d.f.), vegetation patches retained a significant strong negative effect on harvest-level yield below 5% cover, above which the slope was estimated to be positive with a significant effect between 10 and 16% cover (Fig. 2c, d). Landscapes with no vegetation patches had a higher harvest-level yield than landscapes with both a 10% and 20% cover (respectively -0.000976 ± 0.000295 GJ ha^{-1}, $p < 0.01$ and -0.001256 ± 0.000488 GJ ha^{-1}, $p < 0.01$). In contrast, the harvest-level yield did not significantly differ between landscapes of 10% and 20% cover (0.000229 ± 0.000211 GJ ha^{-1}, $p = 0.28$).

These patterns broadly remained under the most flexible model (4 d.f), but higher levels of uncertainty meant that there was only a significant negative effect below around 2% vegetation patch cover (Fig. 2e, f). As before, the harvest-level yield did not differ between landscapes with a 10% and with a 20% cover (0.000187 ± 0.000299 GJ ha^{-1}, $p = 0.53$), but the yield of both was lower than that of landscapes without any vegetation patches (-0.004877 ± 0.001872 GJ ha^{-1}, $p < 0.01$; 0.004335 ± 0.001531 GJ ha^{-1}, $p < 0.01$).

Landscape-level yield was not boosted by vegetation patches

At the landscape (25 ha) level, there was no evidence for ecosystem service benefits derived from vegetation patches counter-balancing the loss of landscape-level yield that results from taking land out of production (Fig. 3). In contrast to this expectation, there was evidence that, at low levels of vegetation cover

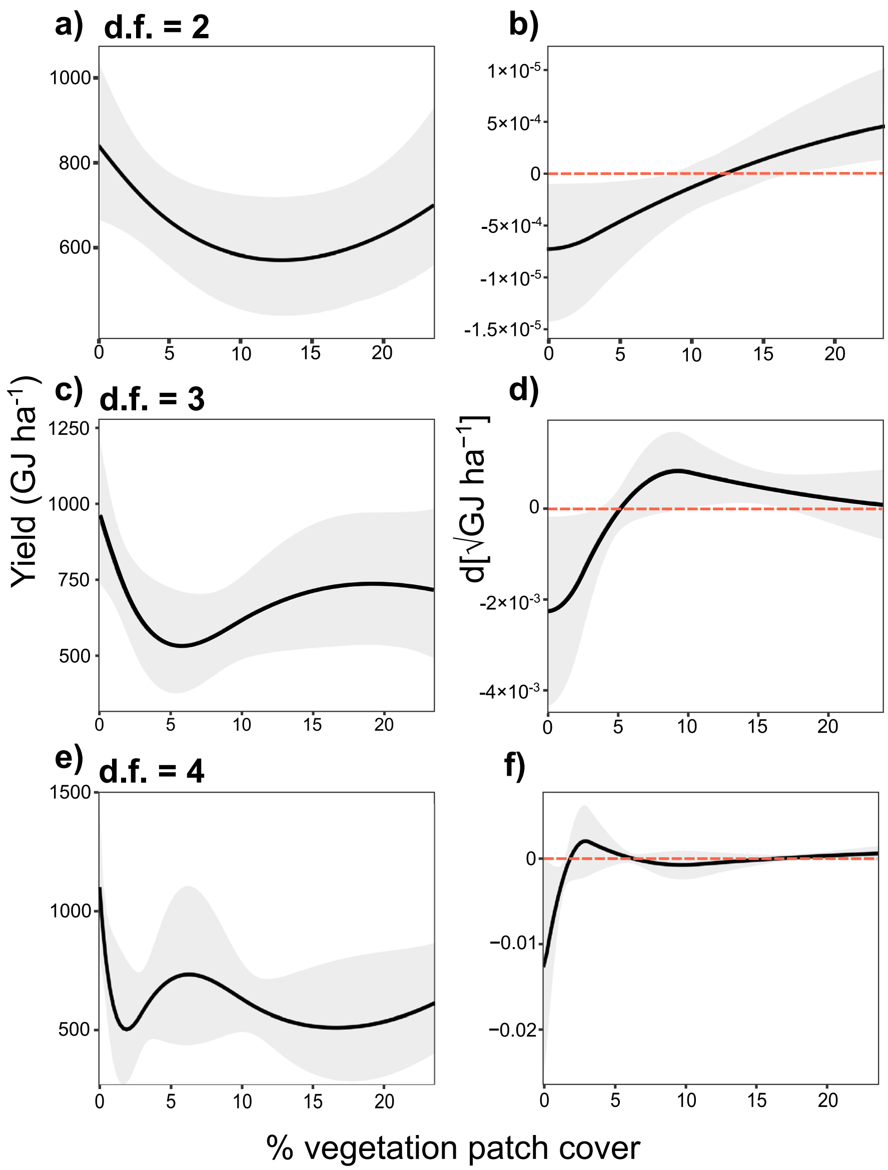

Fig. 2 Effect of vegetation patches on harvest-level agricultural yield. **a**, **c**, **e** Depict the average dose–response function (ADRF), which links the value of vegetation patch cover to the expected potential yield outcome under that vegetation cover value across the full sample, from the model with a natural cubic spline of 2, 3, and 4 degrees of freedom (d.f.) respectively. **b**, **d**, **f** Represent the average marginal effect function (AMEF), which relates the value of vegetation patch cover to the derivative of the ADRF, again under the model with 2, 3, and 4 d.f. respectively. When this derivative is different from zero (i.e. confidence intervals do not cross the red dotted line), there is evidence of a vegetation patch effect at the corresponding yield value

(below ~ 10%), vegetation patches have even greater negative effects on landscape-level yield than would be expected, based on the amount of land taken out of production. At higher levels (~ 10–20%) there was no strong evidence of increasing vegetation patch cover affecting landscape-level yield (Fig. 3). In other words, landscape-level yield declined disproportionally strongly with increasing vegetation cover in landscapes below 10% cover, but this trend levelled off to meet a yield level proportional to the amount of land out of production, in landscapes above 10% cover. The pattern is convex, rather than the concave expectation defined by Eq. 1 and Fig. 1.

Under the model with a spline of 2 d.f. between 0 and around 10% vegetation patches had a significantly negative impact on landscape-level yield. Until around 7% that effect was significantly larger than what would be expected if the decline in yield was in direct proportion to the area under vegetation patches (Fig. 3b). The opposite appeared to be the case above a 15% cover, albeit the slopes did not significantly differ (Fig. 3a, b). More conservatively, above 10% cover, the relationship was neutral, i.e.

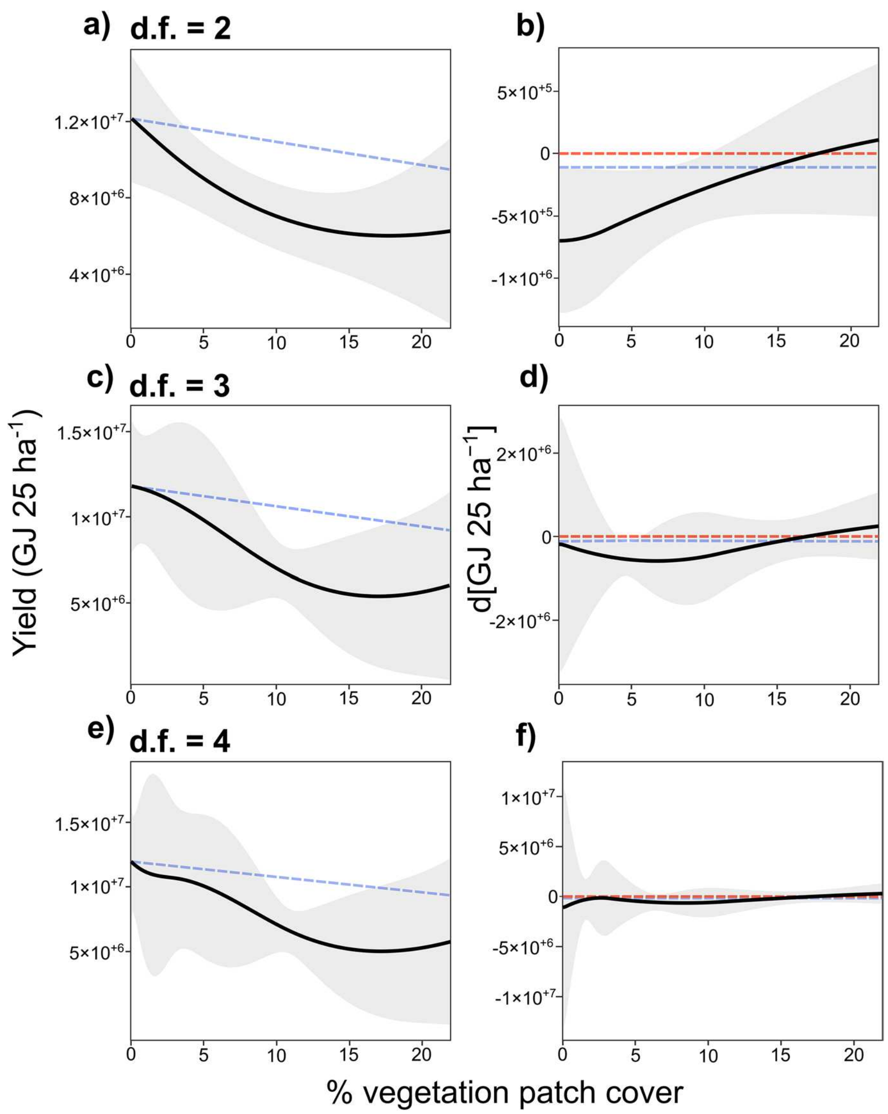

Fig. 3 Effect of vegetation patches on landscape-level agricultural yield. **a**, **c**, **e** Depict the average dose–response function (ADRF), which links the value of vegetation patch cover to the expected potential yield outcome under that vegetation cover value across the full sample, from the model with a natural cubic spline of 2, 3, and 4 degrees of freedom (d.f.) respectively. The blue dotted line represents the relationship expected if landscape-level yield was directly proportional to the area occupied by vegetation patches (i.e. land not under production). **b**, **d**, **f** Represent the average marginal effect function (AMEF), which relates the value of vegetation patch cover to the derivative of the ADRF, again under the model with 2, 3, and 4 d.f. respectively. When this derivative is different from zero (i.e. confidence intervals do not cross the red dotted line), there is evidence of a vegetation patch effect at the corresponding yield value. The blue dotted line represents the slope expected under a directly proportional relationship

landscape-level yield neither significantly decreased nor increased with increasing vegetation patch cover (Fig. 3a, b; average slope between 10 and 20%: $-110{,}000 \pm 192{,}000$ GJ 25ha^{-1}, $p = 0.57$). Hence, a landscape with a 20% cover of vegetation patches did not have a significantly different yield in comparison to a landscape with a 10% cover (- $92{,}700 \pm 216{,}000$ GJ 25ha^{-1}, $p = 0.67$). In contrast, a landscape without any vegetation patches was higher-yielding than a landscape with 10% cover (- $479{,}000 \pm 157{,}000$ GJ 25ha^{-1}, $p < 0.01$) or 20% cover (- $311{,}000 \pm 127{,}000$ GJ 25ha^{-1}, $p < 0.05$).

Increasingly flexible models presented similar average patterns, but higher levels of uncertainty meant less confidence in the responses (Fig. 3c, d). Vegetation patches had a significantly negative effect on landscape-level yield between around 4–6% cover, and at around 4–5% cover the effect was significantly more strongly negative than it would have been under a directly proportional relationship (Fig. 3c, d). The estimated average slope was more negative between 0 and 10% than between 10 and 20% cover, albeit both were non-significant (Fig. 2d; $-336{,}000 \pm 540{,}000$ GJ 25 ha^{-1}, $p = 0.53$; $-164{,}000 \pm 276{,}000$ GJ

25 ha^{-1}, $p = 0.55$). This was mirrored in the most flexible model (4 d.f.) where high-levels of uncertainty meant that there was no robust evidence of vegetation patches affecting landscape-level yield at any amount of cover (Fig. 3e–f).

Our harvest- and landscape-level yield results were robust to how we classified singular coconut, palmyra palm, and mango trees, whether weighting was conducted, which weighting covariates were included, and (for the harvest-level analysis) whether all harvests or only rice harvests of the main growing season were analysed (Supplementary Figures 8–14).

Effect of vegetation patches on birds

Density responses differed by trophic guild and forest dependency level

Overall, the effect of vegetation patches varied markedly by trophic guild and by the level of forest dependency (FD). Consistent positive effects on density were only found amongst birds of medium and low FD, whereas the effect on non-FD birds was variable and frequently negative (Fig. 4). Across all three FD levels, we recorded many invertivore and omnivore species, whereas we recorded far fewer granivore species. Apart from one species, frugivores were of medium FD. Conversely, vertivores tended to be of low or none FD (Fig. 4; see Supplementary Table 4 for a full species list). Overall, 22 bird species in the agricultural landscapes were of conservation importance (Fig. 4; where we regarded a species to be of conservation importance if it was assessed as Near Threatened or Vulnerable under the IUCN Red List and/or if it was considered of 'High' or 'Moderate' conservation priority under the State of India's Birds 2023 report).

Medium FD invertivores were taxonomically diverse, constituting, for example, warblers, babblers, flycatchers, tits, bee-eaters, and drongos. The two granivore species were doves, and the frugivores included taxa such as parrots, hornbills, barbets, and orioles (Supplementary Table 4). On average, all three guilds increased in density with increasing vegetation patch cover, where vegetation patches had a significant positive effect on abundance between ~ 0–8% for invertivores and granivores and between ~ 0–5% for the frugivores (Fig. 4). In other words, the average species in each of these groups was absent or near absent in landscapes with no vegetation patches, but then markedly increased in density (approximately ten-fold) with increasing vegetation cover to reach a relatively stable density at ~ 8% cover (Fig. 4). In contrast, vegetation patches had a negative effect on the density of the average omnivore of medium FD between ~ 0–2.5%, but then this group consistently increased in density with increasing cover, with a significant positive effect between ~ 5–10%. Omnivores included taxa such as parakeets, orioles, sunbirds, crows, white-eyes, and bulbuls.

The average low-FD invertivore (including e.g. bee-eaters and warblers) and the single low-FD frugivore species (white-browed bulbul, *Pycnonotus luteolus*) were not significantly affected by vegetation patches, with their average densities remaining relatively stable through the vegetation cover continuum. Increasing vegetation positively affected the density of the average low-FD omnivore (which encompassed e.g. rollers, bulbuls, mynas, kingfishers, egrets, and larks) between around 2–8% cover, before plateauing at ~ 10% (Fig. 4). Similarly low-FD granivores (constituting Baya weavers and four munia species) increased between ~ 8–17%, and before plateauing at ~ 20%. Vertivores of low FD (which primarily included wading birds such as herons and egrets) significantly declined with increasing vegetation cover between around 19–25% on average; prior to that the relationship was flat (Fig. 4).

The effect of vegetation patches on granivores, omnivores, and non-FD vertivores was mixed (Fig. 4). Non-FD granivores were on average positively affected between around 2–8% cover and negatively between 15–25%, with the density peaking between ~ 8–12%. The average non-FD vertivore (which constituted waders from egrets to storks) was positively affected at medium levels (~ 6–12%), but negatively at high levels of cover (~ 20–25%). Non-FD omnivores (constituting predominantly lark species) followed a somewhat similar trend, where vegetation patches had a significant positive impact on density between around 6–15% vegetation cover and a negative effect at ~ 0–4%. The average non-FD invertivore significantly declined between ~ 0–2%, and this was followed by a non-significant increase between ~ 5–15%, and a significant mild

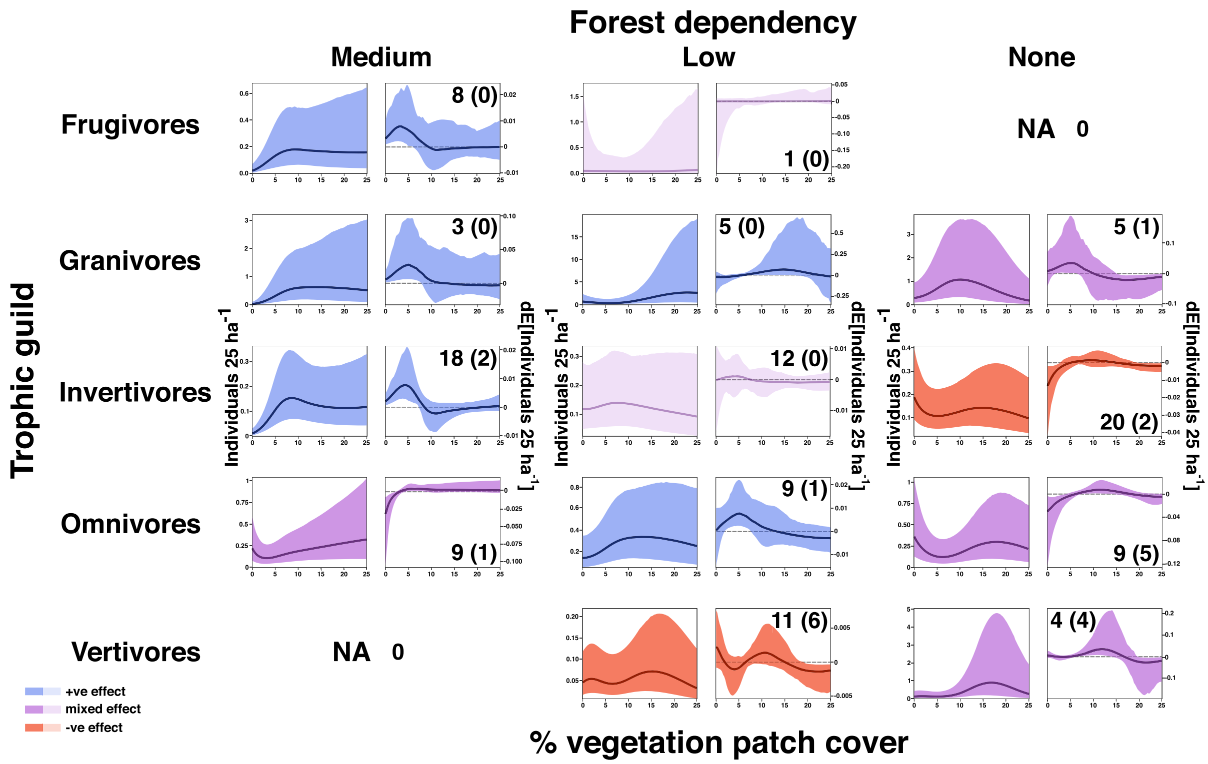

Fig. 4 Effect of vegetation patches on the density of the average species of each trophic guild-forest dependency group. For each group, the figure on the left represents the average dose–response function (ADRF), which links the value of vegetation patches to the expected potential density outcome under that vegetation cover value across the full sample, and the figure on the right depicts the average marginal effect function (AMEF), which relates the value of vegetation patch cover to the derivative of the ADRF. When this derivative is different from zero (dotted line), there is evidence of a vegetation patch effect at the corresponding density value. The number in the right corner represents the number of species that belong to that group, and the number in brackets refers to the number of species of conservation importance. If vegetation patches have a significant positive effect at some point along the vegetation patch continuum, then the relationship and confidence intervals are shaded in blue, if significantly negative then in red, and if both positive and negative then in purple (with 50% opacity when it was not significant)

crease ~ 20–25%. Their average density did not differ between landscapes of no interwoven vegetation patches and landscapes with ~ 12–20% cover (Fig. 4). Non-FD invertivore taxa included, for example, lapwings, pipits, wagtails, and babblers (Supplementary Table 4).

Vegetation patches improved community integrity

With increasing vegetation patch cover, community integrity improved (i.e., the Bray–Curtis dissimilarity index compared to natural forests declined) under all specifications of the spline (Fig. 5). Under the least flexible model (spline with 2 d.f), vegetation patches significantly negatively affected the Bray–Curtis dissimilarity index ~ 0–18% vegetation cover (Fig. 5a, b), meaning that the bird communities in farmland increased in similarity to those in forests the more vegetation patches are interwoven. The trend remained largely the same under the more flexible models (a spline of 3 and 4 d.f., Fig. 5c–f) but entailed higher levels of uncertainty with a neutral relationship at medium levels of cover (~ 7–15%). Our findings remain when reanalysed at the square- rather than point-level (Supplementary Figure 15).

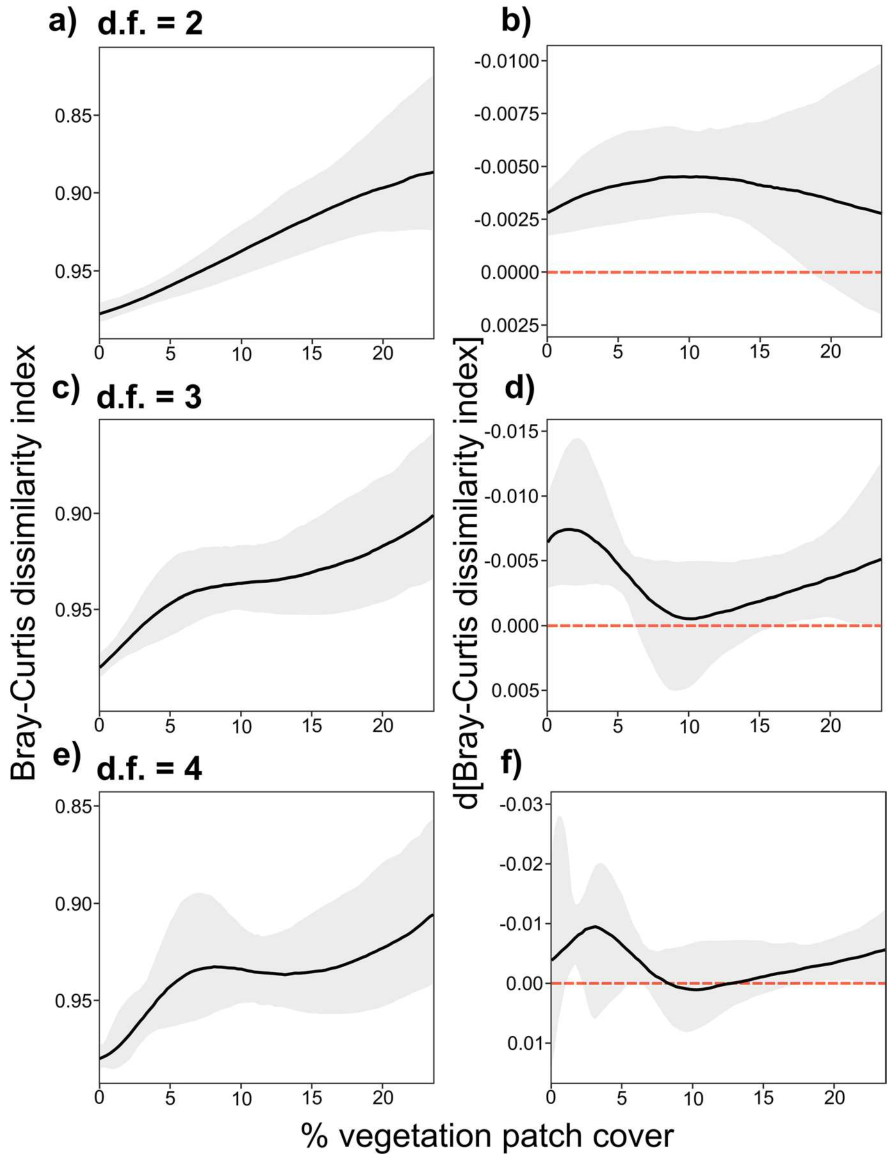

Fig. 5 Effect of vegetation patches on bird community integrity (Bray Curtis dissimilarity to natural forests). **a**, **c**, **e** Depict the average dose–response function (ADRF), which links the value of vegetation patches to the expected potential Bray Curtis dissimilarity index under that vegetation cover value across the full sample, from the model with a natural cubic spline of 2, 3, and 4 degrees of freedom (d.f.) respectively. **b**, **d**, **f** Represent the average marginal effect function (AMEF), which relates the value of vegetation patch cover to the derivative of the ADRF, again under the model with 2, 3, and 4 d.f. respectively. When this derivative is different from zero (i.e. confidence intervals do not cross the red dotted line), there is evidence of a vegetation patch effect at the corresponding Bray Curtis dissimilarity index value. The y-axes were inversed to ease interpretation as 0 indicates the same composition between communities and 1 complete dissimilarity

Discussion

Overall, we have shown that increasing areal cover of native or semi-natural vegetation in smallholder, predominantly rice-producing landscapes in South India has positive benefits for wild bird populations, increasing bird densities in most guilds and enhancing similarity to forest bird communities. Contrary to expectations of ecosystem service provision associated with non-crop vegetation patches (Garibaldi et al. 2020), we found no evidence that these patches enhance agricultural yields in their vicinity, in a way that can account for loss of productive land at low levels of non-crop vegetation cover. In fact, we found the opposite. However, further increasing the areal extent of vegetation cover from 10 to around 20% did not change yields measured at landscape scale. We interpret this as evidence for increasing ecosystem functions such as pest regulation beginning to contribute to agricultural yields at these levels, although still not sufficiently to compensate for the land taken out of production.

Vegetation patch-yield dynamics

Our finding that vegetation patches had a negative effect on harvest-level yield at low levels of vegetation cover, up to ~ 10%, was directly reflected in landscape-level yield disproportionally declining between 0 and 10% vegetation cover. At these levels, landscape-level yield not only declined due to reduced land under agricultural production, but the vegetation patches also exerted a further additional negative effect on farmed land yield. In contrast, at higher levels of vegetation cover, above ~ 10%, vegetation patches had a subtly positive effect on harvest-level yield. This manifested in a largely neutral relationship between vegetation cover and landscape-level yield above ~ 10% cover, suggesting that the food production cost of less land being farmed was partially offset by vegetation patches boosting the yield of the land under production. Nonetheless, landscape-level yield was maximised in landscapes free of vegetation patches. Whilst our predicted relationship between landscape-level yield and vegetation cover entailed considerable uncertainty, our findings clearly disagree with Garibaldi et al.'s (2020) theoretical examination of the relationship. They propose that landscape-level yield at low- to mid-levels of vegetation patch cover (up around 25% or even 40% if spatially targeted) may exceed the yield of landscapes with no embedded vegetation patches. They did not consider that vegetation patches may also have negative impacts on harvest-level yield (rather than merely positive effects) which we found to be the case in our system.

In a systematic review, around half the studies examined across tropical Asia found a negative effect of trees present in farmland and in neighbouring forest habitats on field-level crop yields, a quarter showed a positive effect, and the remainder a mixed or neutral effect (Reed et al. 2017). Across the tropics, around half of the studies demonstrate a yield benefit associated with trees or patches of forest at the field-level (Reed et al. 2017), and numerous other studies since then have found positive or neutral relationships (e.g. Wurz et al. 2022; Zemp et al. 2023). Vegetation patch-yield and vegetation patch-biodiversity relationships are a function of the size and quality of the patches, the crop types examined, field-level management, the biota present, the proximity to other land-use types, and the land-use history (Burian et al. 2024). Thus, they are highly context dependent. For example, in our system, the dominant crops were not or only minimally pollinator-dependent. In contrast, the only previous studies that have quantified landscape-level yield whilst accounting for the land occupied by vegetation patches constituted strongly pollinator-dependent crops (faba beans: Pywell et al. 2015; oil palm: Zemp et al. 2023; coffee: d'Albertas et al. 2024), possibly partially explaining why they did not observe a reduction in yield at the areal cover of vegetation patches they examined (8%, 5%, and 20% respectively). Overall, the relationships we found are unlikely to hold across widely different socio-ecological systems and we stress the need for further landscape-scale studies that similarly account for forgone food production and employ causal inference methods (see Supplementary Information 4).

Naturally, there are also several shortcomings of our investigation: (1) Most of our landscapes had low levels of vegetation patch cover (Supplementary Figure 4) and we thus recommend that future studies should examine a broader continuum. (2) Statistical weighting allowed us to control for variables that we considered to be key confounders, but one of these (agricultural suitability) entailed downscaling a global dataset. Scale mismatches can be problematic for causal inference (Kuemmerle 2024) and we encourage future studies to use the fine-scale data where available. (3) There are most likely other socio-ecological and economic-cultural factors that explain the current vegetation patch cover in a given landscape in our system. Whether these represent confounders (i.e. also directly affect yield or biodiversity outcomes) may not always be readily apparent. Statistical weighting cannot control for unobservable or for time-varying observable confounders (Rasolofoson 2022)—to control for these other causal inference techniques are needed. Approaches that entail leveraging repeat measures across time and those that involve a spatial clustering of landscapes within regions (Supplementary Information 4; Wauchope et al. 2021; Byrnes and Dee 2025; Siegel and Dee 2025) are particularly suitable to address questions like ours. Sensitivity analyses, that give insights into how large an unobservable confounder or set of confounders would have to be in order for them to change research conclusions, can provide further confidence in the findings (see e.g. Cinelli and Hazlett 2020). All these techniques are best complemented with qualitative and process-based analyses (Ordonez et al. 2014). In our study region, a better understanding of the socio-ecological processes that have driven current vegetation patch patterns is needed to identify key levers for land system sustainability. (4) Finally, we did not examine how the plant species composition, structural complexity, and spatial configuration of the vegetation patches affects yield and biodiversity outcomes, but such information is crucial to guide locally appropriate management and policy (see Supplementary Information 5).

Bird-mediated ecosystem (dis-)services

Avian communities in agricultural landscapes provide both ecosystem services and disservices, with the relative densities of different functional groups influencing overall agroecosystem dynamics and thus agricultural productivity (Peisley et al. 2015; Gaston et al. 2018; Pejchar et al. 2018; Garcia et al. 2020). The density dynamics of the different guild-FD groups were complex and relatively uncertain, but broadly aligned with the observed yield changes as vegetation patch cover increased. Guild-FD groups likely providing yield benefits tended to be more abundant in landscapes with greater vegetation cover, echoing findings that these vegetation-rich landscapes benefit from enhanced bird-mediated pest suppression (Boesing et al. 2017). In particular, invertivores reached high, stable densities only above ~ 10% vegetation cover and vertivores had relatively high densities at medium levels of cover (10–20%), where both are known to contribute to natural pest control (Sekercioglu 2006, 2012; Dinesh et al. 2018; Díaz-Siefer et al. 2022). Below 10% vegetation patch cover, they may be insufficiently abundant to regulate agricultural pests effectively, and these services may be outweighed by any granivore-mediated crop and seed damage, possibly partially explaining the negative impact of vegetation patches on harvest-level yield at low levels of cover (see Supplementary Information 6 for an extended discussion). Nonetheless, we caveat that we did not directly measure avian-mediated ecosystem services or disservices, nor indeed any other biophysical mechanisms by which vegetation patches affect yield. Quantifying mechanisms not only increases the credibility of causality (Siegel and Dee 2025) but is also key to devising evidence-based management guidelines and we thus stress the need for future studies to do so (see Supplementary Information 6).

Conservation of forest and open-habitat birds

We found that the bird community increased in similarity to that of natural forests with increasing vegetation cover, as did the density of most medium-FD species and even some low-FD species. The ~ 10% threshold density response we found for some groups aligns with some previous studies that have shown a sharp decline in forest-affiliated bird species richness and occupancy of some species when habitat cover was below 10% (Radford et al. 2005; Betts et al. 2007). Nonetheless, the only species we recorded in the agricultural landscapes classed as being highly forest dependent was the Indian Golden Oriole (*Oriolus kundoo*), and even the communities in agricultural landscapes with the highest proportion of vegetation patches (25%) remained highly dissimilar to that of natural forests. A high cover, likely at least 30% to 60%, of woody vegetation is typically required to support the persistence and movement of forest-dwelling species in agricultural landscapes, albeit some highly sensitive forest specialist species, usually those of highest conservation priority, are restricted to natural forests (Betts et al. 2010; Zuckerberg and Porter 2010; Banks-Leite et al. 2014; Morante-Filho et al. 2015; Melo et al. 2018; Macchi et al. 2019; Arroyo-Rodríguez et al. 2020; Morante-Filho et al. 2021). As we have previously shown in our system (Berger et al. 2024), natural forests hold irreplaceable conservation value for forest birds.

Low- and non-FD birds exhibited mixed responses to vegetation patches, reflecting a preference for more open habitats. For example, low-FD vertivores had the lowest average densities at vegetation covers above around 20%, and the average non-FD invertivore and omnivore had the same density at high (15–20%) covers than in vegetation-free landscapes. These three groups predominantly constituted wading or waterbirds, and thus, did not benefit from tree-dominated vegetation patches. Conversely, increasing cover benefitted populations of other groups which may have competed with the former for resources, implying that increasing vegetation patch cover entailed a species turnover from open-habitat to forest birds—a trend consistently observed across the world (Lindell et al. 2004; Sekercioglu 2012; Bregman et al. 2014; Carrara et al. 2015; Morante-Filho et al. 2018, 2021; Hendershot et al. 2020; Wenzel et al. 2023). This highlights that balancing the needs of different species is challenging and outcomes for different functional groups or taxa must be considered simultaneously, with trade-offs explicitly examined and negotiated, if negative repercussions of landscape management are to be avoided.

Policy and management implications

Agricultural landscapes are increasingly becoming simplified, with vegetation patches rapidly disappearing across the world (Benton et al. 2003; Maron and Fitzsimons 2007; Gibbons et al. 2008; Brandt et al. 2024). There have been numerous calls to set minimum vegetation cover requirements, such as 20% (Garibaldi et al. 2020; DeClerck et al. 2023; Mohamed et al. 2024) or even 40% (Arroyo-Rodríguez et al. 2020). At the policy-level, a sub-indicator of Target 10 of the Global Biodiversity Framework has a criterion that at least 10% of landholding areas should be under 'natural or diverse vegetation' (CBD 2022; FAO 2023), and some countries have set national targets ranging from 5 to 25% (Garibaldi et al. 2020). However, the implications of different vegetation cover thresholds for ecological and social land system objectives remains globally poorly quantified.

Whilst India has not set such a target, there is strong policy enthusiasm for large-scale tree planting and agroforestry efforts as natural climate solutions (Chinnamani 1993; Pandve 2009; Borah et al. 2022). These have received ample criticism for poor implementation in the past (Coleman et al. 2021; Jose 2024), and thus far more research is needed on how vegetation patches can be effectively and equitably integrated into Indian agricultural landscapes, including in Andhra Pradesh which has comparatively high forest restoration potential (Gopalakrishna et al. 2022).

Notably, Andhra Pradesh's Zero Budget Natural Farming (ZBNF) programme, one of the largest agroecological transitions globally, encourages intercropping trees with non-woody crops and planting trees along field boundaries (APCNF 2020; ICRAF, 2021). However, in our study region, ZBNF was not associated with a higher cover of tree-dominated vegetation patches in comparison to agrichemical-based farming (Supplementary Figure 3). Further research to understand how the, possibly synergistic, interaction between vegetation patches and ZBNF (and other field-level agroecological management efforts) drives food and biodiversity outcomes is needed. Building on that, the ZBNF transition must be better aligned with policies and management efforts aimed at improving the multi-functionality and permeability of agricultural landscapes through the retention and restoration of woody elements, from individual trees to ecological corridors.

In our system, landscape-level yield was maximised when there were no vegetation patches embedded in the landscape, meaning that the protection or restoration of these patches comes at a cost to food production. Thus, realising the above-described targets will likely have perverse outcomes for agricultural production in certain contexts. Low levels (< 10%) of vegetation patch cover may incur costs to food production, perhaps because ecosystem services are ineffectively harnessed, and are still largely unsuitable for forest-dependent bird species; thus, arguably representing a poor management option. However, increasing non-crop vegetation cover from 10 to 20% did not significantly lower landscape-level yield, improved bird biodiversity outcomes, and is likely to have numerous other socio-ecological benefits, such as increased carbon sequestration and water regulation, and greater availability of items of economic and/or cultural value (e.g. timber, fuel, livestock fodder, complementary food, and medicinal and cultural plants) and maintenance of associated knowledge systems (Decocq et al. 2016; Chakravarty et al. 2019; Mohamed et al. 2024). In India, almost 90% of farmers are smallholders with less than 2 hectares of land (Ministry of Agriculture and Farmers Welfare, 2024), for whom farmland trees make a crucial contribution to their livelihoods (Sarath et al. 2023; Reang et al. 2024).

Conclusions

In summary, we show that native and semi-natural vegetation patches interwoven in agricultural landscapes have mixed effects on food production and bird abundance, with the direction and magnitude of impact hinging on the total cover of vegetation patches and bird species' diets and forest dependency. At low levels of cover, vegetation patches negatively affected harvest-level agricultural yield, and thus landscape-level yield declined more strongly than it would be expected if it was directly proportional to the area taken out of production. When the cover exceeded around 10%, the patches exerted a subtle positive effect on harvest-level yield and landscape-level yield did not significantly decline, possibly reflecting an increase in the densities of species known to fulfil natural pest control services. Nonetheless, our estimates were uncertain, and relationships between vegetation patches, biodiversity, and food production systems are likely to be highly context dependent. There remains substantial empirical work to characterise what optimal agricultural landscapes look like that minimize trade-offs, and a step-change in the number of studies that employ a similar approach to ours is needed to inform locally grounded land management and policy. We see a particular need to evaluate how the composition and configuration of vegetation patches drives yield and biodiversity outcomes, and how the effects of vegetation patches interact with those of field-level management interventions. This is especially important right now, as policies that incentivise or require specific thresholds for the proportion of native habitats in productive agricultural landscapes are likely being designed and implemented afresh, or existing ones being reinforced, in response to Target 10 of the Global Biodiversity Framework. Agri-environmental policy makers must take a holistic, multifunctional view of agroecosystems, carefully and equitably negotiating the needs of different species and land system actors.

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Author contributions I.B. and L.V.D conceived the project idea and designed the data collection; I.B., A.K., V.R., V.J, and S.R.N collected and processed the data; I.B. conducted the analyses with contributions from O.M. and L.V.D; I.B drafted the manuscript and all authors contributed to the revision of the manuscript.

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Data availability The interview and bird data that support the findings of this study will be deposited in Figshare.

Declarations

Conflict of interest The authors declare no competing interests, but we note for transparency that Rythu Sadhikara Samstha (the agency in charge of rolling out the ZBNF programme) provided us with information on where ZBNF is widely practiced. However, they had no influence on the final site selection and data collection process. L.V.D is a Board Member of Natural England, the UK Government's statutory nature conservation advisor for England.

Dual publication The field data underpinning this study is also part of another manuscript, entitled 'Agroecological transition delivers win–win outcomes for people and nature', that is currently under review in Nature Ecology & Evolution (preprint: https://www.researchsquare.com/article/rs-5138070/v1). Whilst both manuscripts are based on the same data, they address entirely different questions and involve completely different analyses. Thus, it does not constitute dual publication.

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