Journal of Applied Ecology

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Article type : Research Article

Editor : Júlio Louzada

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Rubber agroforestry in Thailand provides some biodiversity benefits without reducing yields

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2664.13530

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Abstract

1. Monocultural rubber plantations have replaced tropical forest, causing biodiversity loss. While protecting intact or semi-intact biodiverse forest is paramount, improving biodiversity value within the 11.4 million hectares of existing rubber plantations could offer important conservation benefits, if yields are also maintained. Some farmers practice agroforestry with high-yielding clonal rubber varieties to increase and diversify incomes. Here, we ask whether such rubber agroforestry improves biodiversity value or affects rubber yields relative to monoculture.
2. We surveyed birds, fruit-feeding butterflies and reptiles in 25 monocultural and 39 agroforest smallholder rubber plots in Thailand, the world's biggest rubber producer. Management and vegetation structure data were collected from each plot, and landscape composition around plots was quantified. Rubber yield data were collected for a separate set of 34 monocultural and 47 agroforest rubber plots in the same region.
3. Reported rubber yields did not differ between agroforests and monocultures, meaning adoption of agroforestry in this context should not increase land demand for natural rubber. Butterfly richness was greater in agroforests, where richness increased with greater natural forest extent in the landscape. Bird and reptile richness were similar between agroforests and monocultures, but bird richness increased with the height of herbaceous vegetation inside rubber plots.
4. Species composition of butterflies differed between agroforests and monocultures, and in response to natural forest extent, while bird composition was influenced by herbaceous vegetation height within plots, the density of non-rubber trees within plots (representing agroforestry complexity), and natural forest extent in the landscape. Reptile composition was influenced by canopy cover and open habitat extent in the landscape. Conservation priority and forest-dependent birds were not supported within rubber.
5. *Synthesis and applications.* Rubber agroforestry using clonal varieties provides modest biodiversity benefits relative to monocultures, without compromising yields. Agroforests may also generate ecosystem service and livelihood benefits. Management of monocultural rubber production to increase inter-row vegetation height and complexity may further benefit biodiversity. However, biodiversity losses from encroachment of rubber onto forests will not be offset by rubber agroforestry or rubber plot management. This evidence is important for developing guidelines around biodiversity-friendly rubber and sustainable supply chains, and for farmers interested in diversifying rubber production.

Keywords

bird; butterfly; diversification; *Hevea*; land sharing; reptile; sustainability; tropical forest

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Introduction

Demand for natural rubber, mostly for tyres, has driven sustained expansion of *Hevea brasiliensis* plantations across Southeast Asia (Warren-Thomas *et al.*, 2015) and tropical Africa (Assembe-Mvondo *et al.*, 2015). Global rubber area totalled 11.4 million ha in 2016 (FAO, 2018, **Fig. S1)**. Rubber expansion has caused forest and biodiversity loss, carbon emissions, and environmental degradation (Warren-Thomas *et al.*, 2015, 2018). Whether in smallholdings or agro-industrial estates, plantations are mostly monocultures of high-yielding clonal varieties, planted at densities of 400 – 550 stems ha^{-1}, that are usually intensively managed (Priyadarshan, 2011). Approximately two million ha of low-intensity 'jungle' rubber agroforestry also persist, particularly in Indonesia (forest-like systems containing multiple planted and native tree species with mixed rubber tree ages; Gouyon *et al.*, 1993; Joshi *et al.* 2002).

There is a trade-off between rubber yields, and biodiversity and ecosystem function (Clough *et al.*, 2016; Drescher *et al.*, 2016). At the two extremes, monocultural rubber yields are approximately double or triple those in 'jungle' rubber agroforests (Villamor *et al.*, 2014; Warren-Thomas *et al.*, 2015). However, yields in simpler agroforests containing only a few additional plant species, particularly those using clonal rubber varieties with even-aged trees, may not suffer this penalty. Evidence for non-linear relationships between livelihoods and biodiversity in other systems (Fischer *et al.*, 2011; Teuscher *et al.*, 2015) opens the question: could rubber production become more biodiversity friendly without reducing yields?

In Thailand, the world's largest rubber producer, much lowland forest has been converted to rubber, 90% of which is grown by smallholders (Somboonsuke and Wettayaprasit, 2013). Intensification of rubber production to monocultures was incentivised via the Office of Rubber Replanting Aid Fund (now the Rubber Authority of Thailand, RAOT, Romyen *et al.*, 2018). Over 85% of Thai rubber is now grown monoculturally using clonal planting material at standard planting densities (Simien and Penot, 2011). However, <15% is grown in agroforests: most commonly in relatively intensive systems combining modern rubber-cultivation methods with additional crops (Simien and Penot, 2011; Stroesser *et al.*, 2018), rather than jungle-type systems. In response to price fluctuations, incentives have recently shifted towards rubber conversion to fruit or oil palm, and a policy promoting diversification through rubber agroforestry was approved in 2014 (ORRAF, 2006; Stroesser *et al.*, 2018). However, rubber remains the dominant choice for smallholders in southern Thailand due to the well-established supply chain and local processing facilities, while further north, conversion to oil palm will be restricted by its intolerance of long dry seasons and cold (Warren-Thomas *et al.*, 2018). Although we are not aware of any biodiversity-specific

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policies relating to rubber agroforestry, farmer motivations to undertake agroforestry include receiving intercropping planting material from RAOT, anticipation of increased incomes, and awareness of environmental benefits for soils, water and climate (Romyen *et al.*, 2018). Rubber remains the main cash crop in such systems (Stroesser *et al.*, 2018). To our knowledge, no study has assessed the biodiversity value of intensive rubber agroforests relative to monocultures, while research assessing measures to improve biodiversity in rubber monocultures is also scarce.

Agroforests with greater diversity and density of non-rubber trees provide additional food resources (particularly fruits) and may have greater habitat suitability for forest specialists (Koh, 2007; Clough *et al.*, 2009; Teuscher *et al.*, 2015). Structurally-diverse jungle rubber in Sumatra supports frugivorous birds absent from monocultures, seven to 13 additional threatened species, and eight additional forest specialists (Beukema *et al.*, 2007; Prabowo *et al.*, 2016). Non-rubber trees also provide additional canopy cover that could influence species composition, particularly of ectotherms (Koh, 2007; Wanger *et al.*, 2010). Increasing height and density of the plantation understorey could also increase species richness, as shown for birds and butterflies (Aratrakorn *et al.*, 2006; Azhar *et al.*, 2011; Barbosa Cambui *et al.*, 2017). In Thailand, monocultures with vegetated understories had greater bird species richness than those without (Aratrakorn *et al.*, 2006). In Brazil, rubber plantations with 10–20 year old understorey supported four additional butterfly species, and were more similar in composition to forest fragments than intensive rubber (Barbosa Cambui *et al.*, 2017). Finally, biodiversity responds to land use at multiple spatial scales, and on-farm biodiversity is influenced by the wider landscape (Tscharntke *et al.*, 2005). In rubber monoculture-dominated landscapes of Southwest China, bird species richness was greater in landscapes with more forest cover (Zhang *et al.*, 2017) and richness may also increase in response to greater land-use diversity.

We investigated whether Thai agroforests can offer benefits for both rubber yields and biodiversity, using three contrasting taxa (birds, fruit-feeding butterflies and reptiles), selected because they are taxonomically resolved, relatively well-studied in other agroforestry systems, and likely to respond to different aspects of management. First, we examined whether yield, species richness and species composition differed between agroforests and monocultures. Second, whether richness and composition varied in response to understorey vegetation, and the types and densities of non-rubber crops and trees. Third, how richness and composition were influenced by landscape composition, and potential interactions with plot management.

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Materials and Methods

Study region

The study was conducted in southern Thailand (**Fig. S2**), where lowland landscapes are smallholder rubber dominated (farm sizes <1 ha to several ha), with smaller areas of oil palm, orchards, rice and forest. The largest forest fragments were ~320 ha of karst hilltop forest and 400 ha of secondary forest; others were small (~4 ha) and degraded. Three protected forests cover mostly upland areas (100-1,350 m asl). Rain is frequent May-December, with a dry season January-March (Phommexay *et al.*, 2011). Biodiversity data were collected March-June 2016, during unusually low rainfall and high temperatures linked to a strong El Niño-Southern Oscillation (**Fig. S3**).

Sampling plots

Biodiversity data were collected from 64 rubber 'plots' in Songkhla and Phattalung provinces. Plots were defined as even-aged units ≥1 ha (mean 1.92 ha, range 1.0-7.6 ha) at least 100x100 m in dimensions (measured using GPS and laser rangefinder), termed the 'biodiversity dataset'. Plots were categorised as monocultures (MO, n = 25) or agroforests (AF, n = 39). Plots were chosen by first locating an appropriately sized agroforestry plot with the help of local agroforestry groups, because agroforests are relatively rare in the landscape. Almost all agroforestry plots above the minimum size requirements were surveyed, and we then co-located monoculture plots in the vicinity of each agroforest. Clonal rubber trees were usually planted at 3 m intervals in rows 7 m apart in both systems (476 stems ha^{-1}, Phommexay *et al.*, 2011). Agroforests contained cultivated non-rubber tree, shrub or herbaceous plants, or naturally-regenerated wild trees, mostly in the inter-row (mean 162 ± 207 SD stems ha^{-1}). Complexity ranged from one or two cultivated species (**Fig. 1b**), to multiple native tree species (**Fig. 1d**). Three monocultures contained non-rubber crops at densities too low to be considered agroforests (e.g. a single bamboo clump, 17 ± 51 stems ha^{-1}). Latitude of biodiversity dataset plots ranged from 6.641374 to 7.602200 °N (76 km north-south) and elevation from 35.0 to 137.1 m asl.

Plots were clustered into 600 x 600 m 'blocks' (n = 23) for which landscape composition data was collected. Each block contained two or three plots with centroids 200-400 m apart (**Fig. 2a**). Agroforests and monocultures were represented in each block wherever possible, but five blocks contained only

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agroforests. Blocks were clumped within five 'districts' (not administrative districts, up to 127 km apart, **Fig. S2**), with plots <9.00 km apart within a district (**Fig. 2b**).

Biodiversity data

Biodiversity data were collected from up to nine agroforestry and monocultural plots each day, to control for potential weather and seasonal effects. The number of rainy days during sampling was recorded based on field or overnight observations (within 10 km of plot). Strong El Niño conditions during sampling could have influenced sampling by decreasing the suitability of relatively open habitats due to increased heat and decreased humidity (such as monocultures with lower canopy cover), or by forcing some species into cooler, wetter, refugia (e.g. stream beds).

Birds were surveyed by one experienced ornithologist (L.N.) on three consecutive mornings (06:00-09:30) in ten-minute point counts at each plot centre, alternating the order in which plots were visited (Gilroy *et al.*, 2014b). Birds within a 50 m radius (excluding fly-throughs) were identified to species using sight or sound, and number of detections recorded. A two-week pilot phase was used to familiarise L.N. with local species and the 50 m sampling radius. In the smallest plots (100 m x 100 m) the sampling radius reached the plot boundaries, and during the pilot phase these plots were used to check the location of calling birds: this experience was used to estimate the 50 m radius in larger plots. Sound recordings were made of each count, (Olympus LS-11 Linear Recorder), and sounds checked against existing recordings (Xeno-canto Foundation, 2017). Species' habitat associations (del Hoyo *et al.*, 2017) and conservation status (IUCN, 2016) were defined.

Reptile visual encounter surveys were conducted by one experienced herpetologist (W.J.) on four consecutive afternoons (13:00-18:00) in each plot (Crump and Scott, 1994), alternating the order in which plots were visited. A 200 m long "S" shaped path in the core of each plot, bounded by the butterfly traps (see below) was walked at a steady pace for 20 minutes while actively searching all microhabitats 5 m either side. Individuals were identified in the field, and taxonomy standardised to follow the IUCN Red List (IUCN, 2016). Reptiles were not captured or marked. To avoid re-counting across multiple sampling days the greatest number of detections on any single day was used in analyses. Reptile conservation status and habitat associations (Chan-ard *et al.*, 2015) were extracted.

Fruit-feeding butterflies (Nymphalidae) were sampled using non-lethal Van Someron-Rydon traps, 90 cm high and 30 cm in circumference, based on trap design #1 from Austin and Riley (1995). Five traps were

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set per plot, one at the centre and four 50 m away in cardinal directions, baited with two tablespoons of fermented banana mixture (750 ml ripe mashed bananas, one teaspoon quick action yeast, two tablespoons sugar, 1 tablespoon rum, fermented for 48 hours). Traps were set with the base 1.5 m from the ground. In plantation systems with simple canopy structures, this effectively samples butterflies from all strata (Barlow *et al.*, 2007). Traps were set on the first day and checked on four subsequent afternoons (13:00–18:00), replacing bait each day and discarding old bait away from the plot. Without trap loss or damage, this gave 20 trap-days per plot. Trapped butterflies were photographed (Canon 700D D-SLR, 105mm macro lens) and marked before release. No individuals were re-trapped across sampling plots. All analyses use presence-absence data, except where comparing total catch (as a proxy for total abundance across all species) between AF and MO, as the relative abundance of species is unlikely to be reflected in relative catches (Hughes *et al.*, 1998). Individuals were identified to subspecies following (Corbet and Pendlebury, 1992; Ek-Amnuay, 2012) and collections at Prince of Songkhla University. *Mycalesis* males were identified to species by O.B. based on unpublished taxonomic work. Identification of *Mycalesis* females requires dissection, so were omitted (only 4/49 plots containing *Mycalesis* contained no males).

Rubber plot management

Rubber plot management (and resulting vegetation structure) data were collected from each plot in the biodiversity dataset. Cultivated plant species names were recorded during a farmer interview. Vegetation structure was quantified through field measurements (**Fig. S4 and text**) giving plot-level values for herb height (cm), canopy cover (%), small stem density (ha^{-1}), non-rubber tree stem density (ha^{-1}), fruit tree stem density (ha^{-1}), and the number of agroforestry species.

Landscape composition

Landscape composition across each block was quantified by recording land covers with a GPS during semi-exhaustive surveys on foot (access and terrain permitting) resulting in a mean 139 ± 43 SD GPS points per block. The points were used to define land use at 100 m intervals along the block perimeter, once within each sampled plot, and once in the adjacent management units in each cardinal direction, giving 39 points per block (**Fig. 1**). Where sampled plots were adjacent (as in **Fig. 1**), land cover of the next management unit was recorded. Where only two plots were sampled within a block, land use was recorded in one additional management unit and its neighbours.

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Land cover was recorded as: rubber agroforestry (AF), rubber monoculture (MO), immature rubber, bare ground, scrub, urban (village, road or town), natural forest, fruit orchard, home garden, cassava, oil palm, rice paddy, timber plantation or coconut grove. Using Google Earth we mapped streams and rivers, and calculated riparian feature length per block. These data were summarised into six variables: percentage of the points (hereafter termed extents) in rubber (total AF and MO), open habitats (total of immature rubber, bare ground, cassava or rice paddy) and natural forest, the ratio of AF to MO, Shannon-Wiener diversity index of land uses (using point-frequency data), and riparian length.

This point-based sampling approach was validated by comparison with area-based measures of landscape composition, extracted from manual mapping of management units using Google Earth imagery for a subset of ten blocks, informed by all available GPS points for each block. Automated land-use classification was impossible due to the identical canopy characteristics of monocultures and agroforests. The two datasets correlated strongly (Pearson correlation, $r \geq 0.77$, $p \leq 0.05$, tested separately for each land cover type; **Fig. S5**), supporting the validity of the point-sampling approach to quantify land use.

Rubber yields

Rubber yield estimates were collected in 2016, via questionnaires with farmers, for a separate set of 47 agroforest and 34 monocultural rubber plots in Phattalung province with considerable spatial overlap to the 'biodiversity dataset' (**Fig. S2**). These data were collected as part of a wider study of farmer livelihoods and rubber agroforestry, which also included data on agroforestry species composition, and is termed the 'yield dataset' (full methods in Stroesser *et al.*, 2018). Annual rubber yields were either reported for latex (coagulated, reported as dry weight) or as 'cup-lump' values per plot (converted to dry weight assuming dry rubber content of 65%) to give yields in t ha^{-1} yr^{-1}.

Plot characteristics with the potential to affect rubber yield were compared between the yield and biodiversity datasets using generalised linear models and Mann-Whitney U tests. Rubber yields in Southeast Asia are affected by elevation, cold, and drought (Ahrends *et al.*, 2015). Mean latitude of yield plots was 7.473321°N (SD 0.199305°), and mean elevation (proxy for temperature and drought stress) was 98.2 m asl (range 42.0 – 164.0 m asl), differing trivially from the biodiversity plots (mean latitude difference: 47.2 km, 95% CI 38.2-55.6 km; elevation: 14.1 m, 4.3-24.0 m asl). All plots in both datasets contained high-yielding rubber clones, and mature rubber trees (7–30 years).

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There were no differences in cultivated plant species richness per plot, or the stem densities of rubber, fruit and timber trees respectively (stems ha^{-1}; **Fig. S6-S7**). The agroforestry systems are thus similar in both datasets, and any effects of structural complexity or intercropping density on yields and biodiversity are likely to be highly comparable.

Soil type may affect rubber yield. Soils for the region are defined as Acrisols (Food and Agriculture Organization of the United Nations, 2012), but according to a national-level soil survey, the plots fell within six soil types, dominated by Udults (freely-drained, humus poor, light soils, USDA, 1999; Department of Land Development, 2002). A greater proportion of yield plots had marginal "skeletal" soil types than biodiversity plots (53% versus 22%; **Table S1**). It is possible that soils in yield plots are generally poorer quality than biodiversity plots. However, within the yield dataset, 47% of plots were skeletal, of which 64% were agroforest, suggesting yield variation due to soil type is likely to be present within both agroforests and monocultures.

Support from RAOT during rubber planting/re-planting means farmers tend to follow standard practices for immature rubber, but experienced rubber farmers in southern Thailand have diverse ongoing management practices (e.g. fertilisation rates, tapping intensity) once trees are mature (Besson, 2002; Chambon *et al.*, 2017). However, we cannot conceive any reason why management practices would differ systematically between the yield and biodiversity datasets.

Analysis

All analyses were conducted in R separately for each taxon (R Core Team, 2017). Estimated rubber yields (t ha^{-1} yr^{-1}) were compared between AF and MO yield plots using a general linear model including plot type, soil type (loamy/clayey, skeletal or slope complex, **Table S1**) and their interactions. The AICc of this model was compared to a null model; where ΔAICc of the alternative model was ≥2 lower than the null, it was considered to be informative. Power analysis of the result was conducted using package pwr (Champely, 2018), to estimate the effect size (difference in yields) detectable with our sample.

Sampling completeness within each plot type (AF or MO) was calculated as the percentage of the estimated asymptotic species richness that was observed, based on four estimators (Jack1, Jack2, Bootstrap, and Mmean). These were compared between AF and MO using a Mann-Whitney U test. Cumulative species richness was compared between AF and MO using sample-based rarefaction extrapolated to the largest sample size (n = 39 for AF) using the iNEXT package (Chao and Colwell, 2014).

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Species richness and number of detections or catches per plot (proxies for abundance) were compared between AF and MO plots using generalised linear mixed models (GLMMs), fitted using maximum likelihood, with a Poisson distribution and log link function, using the lme4 package (Bates *et al.*, 2015). Block was included as an intercept-only random effect to account for the nested sampling design, with district and rainfall index additional intercept-only random effects for butterfly models, as these influenced butterfly species richness (**Fig. S8-S10**). The AICc of the full models were compared to a null model containing only random effects (Burnham and Anderson, 2002). Systematic spatial autocorrelation of model residuals, examined using a Monte-Carlo permutation test for Moran's I using package spdep with 1000 iterations (Bivand and Wong, 2018), was not found for any model. Residuals were tested for overdispersion, but theta (Pearson residuals/residual degrees of freedom) was <1 in all cases (Burnham and Anderson, 2002). Species composition response to agroforestry was investigated with a partial Redundancy Analysis (RDA) with Block as a conditional effect, using detection data for birds and reptiles (maximum individuals, or detections, recorded on one sampling day, divided by the variance of each species; Oksanen *et al.*, 2017) and presence-absence data for butterflies (Hughes *et al.*, 1998).

Species richness response to plot management was then investigated using multi-model inference (Burnham and Anderson, 2002). A global GLMM (containing all six vegetation structure variables, centred and standardised to zero mean and 0.5 SD so that effect sizes were on comparable scales; Grueber *et al.*, 2011), a null (intercept-only) model containing the random effects, and a candidate model set (comprising all possible model subsets with four or fewer variables, ensuring at least 15 observations for each candidate variable) were generated using the MuMIn package (Grueber *et al.*, 2011; Bartoń, 2016). The 57 candidate models were ranked according to AICc and weights using the bbmle package (Bolker and R Development Core Team, 2017). Models with a cumulative weight ≥95% were averaged by the full (zero) averaging method (Burnham and Anderson, 2002; Grueber *et al.*, 2011), using the MuMIn package (Bartoń, 2016). If the 95% confidence intervals of the averaged parameter estimate excluded zero, it was considered influential (Grueber *et al.*, 2011). Influential rubber plot management variables were included in the next step of analysis.

The same approach was used to generate a final set of candidate models for species richness responses. Explanatory variables were plot type (AF vs MO), influential rubber plot management variables, landscape composition variables, and two interaction terms (plot type and AF:MO ratio, plot type and natural forest). Model averaging was applied to the final model set. To estimate effect sizes and investigate interactions, species richness was predicted from the final averaged models for each taxon using the MuMIn package, holding all other continuous explanatory variables at the mean and including mean

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levels of random effects (Bartoń, 2016). Predictions made using standardised variables and log link function of the final model were back transformed, to visualise predictions relative to variables in their original units. The SE of predictions from the averaged model were not calculated, as tools to calculate prediction intervals for GLMMs using the lme4 package (Knowles and Frederick, 2016) cannot be applied to averaged models.

Species composition responses to rubber plot management and landscape composition were assessed using RDA. A global RDA model, including plot type and all plot management and landscape composition variables, was fitted using the vegan package (Oksanen *et al.*, 2017) without rare species (total detections/sum of presences <3; Barlow *et al.*, 2010). Block was not used as a conditional effect because landscape composition was measured at the block level. Systematic spatial autocorrelation in the global model, examined using an adaptation of the Mantel test in the vegan package (Wagner, 2004; Oksanen *et al.*, 2017), was not found for any taxon. Automatic backward model selection was performed on the global model (9999 permutations) with a threshold of $p > 0.05$ (a "pseudo-*F* " test statistic: ratio of constrained and unconstrained total inertia in the RDA, divided by their respective ranks) to drop terms from the model (Legendre *et al.*, 2011; Oksanen *et al.*, 2017). The significance of each term in the final model was examined using the same method.

Results

Rubber yields

Rubber yields did not appear to differ between AF (mean 1.34 t ha^{-1} yr^{-1} ± 0.61 SD) and MO plots (1.51 ± 0.54 t ha^{-1} yr^{-1}; **Fig. 3**), and soil type also had no effect (**Fig. S11**). With the sample size available (n = 77) power analysis showed that we would have been able to detect a difference in yield of 0.24 t ha^{-1} yr^{-1} (17% change relative to mean yields of all plots) given a power of 0.80. We would have required a sample of 117 plots to detect a difference of 0.14 t ha^{-1} yr^{-1} (i.e. a 10% change). It is therefore possible that we have failed to detect a real, but small, difference between the two systems. Yield variability of AF plots was slightly higher (SD of 0.61, range 0.05–2.78 t ha^{-1} yr^{-1}) than in MO plots (SD of 0.54, range 0.12–2.42 t ha^{-1} yr^{-1}), but both systems show considerable yield variability, suggesting that neither option necessarily reduces farmer risk in terms of yield variation.

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Rubber plot management and structure

AF plots in the biodiversity dataset had greater fruit and timber tree species richness (mean 6.6 ± 0.6 SE non-rubber tree species, 0.2 ± 0.1 in MO), greater density of timber, fruit and wild trees (162 ± 33 stems ha^{-1}, 17 ± 10 in MO), smaller rubber basal area (16.8 ± 1.0 m^2 ha^{-1}, 21.5 ± 1.7 in MO), and greater canopy density (76% ± 0.8, 71% ± 1.4 in MO), small stem density (2552 ± 522, 601 ± 224 in MO), and understorey density (index 6.6 ± 0.7, 4.3 ± 0.7 in MO; **Fig. S12**). However, mean herb height was similar between AF and MO, because understorey management varied among plots of both types**.** Three tree species recorded in agroforests are globally threatened, and a total of 37 plant species were recorded across all plots grown for a variety of uses including timber, fruit, and resin (**Table S2**).

Species richness and composition of birds, butterflies and reptiles in agroforests compared to monocultures

In total, 1,204 registrations of 69 bird species, 544 detections of 17 reptile species, and 809 individuals of 44 fruit-feeding butterfly species (excluding female *Mycalesis*), were recorded. Plot-level detections of each species are given in **Table S3**. Species richness estimators showed that ≥74% of species were detected, and sampling completeness did not differ between AF and MO (**Fig. S13**).

Agroforestry supported greater butterfly species richness, both at habitat level (cumulative species richness across all plots; **Fig. 4c**) and plot level **(Fig. 4f**). AF plots contained 6.1 ± 3.4 (mean ± SD) species, while MO contained only 3.6 ± 3.5. However, bird and reptile species richness did not differ between AF and MO, whether at habitat (**Fig. 4a-b**) or plot level (**Fig. 4d-e**). MO plots contained 11.9 ± 3.0 bird and 4.6 ± 1.7 reptile species, and AF 12.8 ± 3.1 bird and 4.3 ± 1.4 reptile species. Detections of birds and reptiles did not differ between AF and MO, but total butterfly catches were greater in AF **(Fig. S14)**. Species composition of all three taxa was unaffected by agroforestry (**Table S4**).

Species richness and composition of birds, butterflies and reptiles in response to agroforestry, rubber plot management and landscape composition

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Bird, butterfly and reptile species richness each responded to different combinations of plot type (AF or MO), plot management and landscape composition variables. Plot-level bird richness increased with greater herb height (**Fig. 5a**), but no other management variables affected richness **(Fig. 5b-d**). Predictions from the final averaged model showed that increasing herb height from 37 cm (25% quantile) to 98 cm (maximum), increased mean bird richness per plot from 11.8 (weighted across AF and MO) to 14.8 (**Fig. 6a**).

Butterfly richness was greater in AF than MO **(Fig. 4c and 4f)**, and was affected by an interaction between plot type (AF or MO) and forest extent, although we note that few plots were in landscapes with relatively high forest extent (**Fig. 5f**). Within AF, butterfly richness increased with natural forest extent, but not in MO (**Fig. 6b**). An agroforest in a block containing no forest (25% quantile) was predicted to contain 4.8 species, which increased to 11.2 species in a block containing 51% natural forest (maximum). In contrast, butterfly richness in MO remained at 4.1 and 4.0 respectively. Reptile richness was not related to any measured variables (**Fig. 5e**).

Bird species composition showed differing patterns to those of richness: herb height affected composition (as for richness), but non-rubber tree density and the surrounding extent of rubber, forest and open habitat in the block, were also influential: (**Fig. 7a; Table S5**). The RDA model explained 16% of total inertia (pseudo-*F* = 1.76, p = <0.001). The species most strongly associated with greater herb height were *Hemipus picatus* Bar-winged Flycatcher-shrike, *Leptocoma brasiliana* Van Hasselt's Sunbird, and *Orthotomus sutorius* Common Tailorbird. Although non-rubber tree stem density and forest extent were uncorrelated (**Fig. S15**) both had a similar influence on composition. Species strongly associated with greater forest extent and non-rubber tree density included small insectivores capable of using a range of habitats including scrub (*Arachnothera modesta* Grey-breasted Spiderhunter, *Macronus gularis* Pin-striped Tit Babbler, *Malacocincla abbotti* Abbott's Babbler, *Orthotomus atrogularis* Dark-necked Tailorbird and *Prionochilus maculatus* Yellow-breasted Flowerpecker) and an open-habitat species (*Merops viridis* Blue-throated Bee-eater).

Butterfly species composition altered in response to forest extent, the interaction between plot type and ratio of AF:MO in block, and canopy cover (**Fig. 7c**). This RDA model explained 15% of total inertia (pseudo-*F* = 1.95, p = <0.001; **Table S5**). To explore the interaction between plot type and the ratio of AF:MO, the RDA was re-run separately for AF and MO (**Fig. S16**), showing that composition only responded to the ratio of AF:MO within monocultures, with some species strongly associated with landscapes containing a greater proportion of agroforestry. Species composition in AF was also affected by forest extent, but not in monocultures, mirroring patterns in species richness.

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In contrast to both birds and butterflies, reptile species composition only changed in response to canopy cover (positive response to canopy openness by some species) and open habitat extent **(Fig. 7b; Table S5**). This model explained 14% of inertia (pseudo-*F* = 1.79, p = 0.005).

Only two bird species of conservation concern were recorded, both as singletons within AF plots (IUCN NT), while one forest-dependent species was recorded in both AF and MO (**Table S3**). Fifteen bird species were open-habitat specialists, but the majority were small generalist insectivores. The five reptile species with IUCN assessments were all LC (nine unassessed), and no forest specialists (**Table S3**) were associated with agroforestry, plot management variables, or landscape composition.

Discussion

Despite recent natural rubber price declines, and concomitant reductions in rubber area locally in parts of Southeast Asia (Zhang *et al.*, 2019), global rubber area continues to increase (FAO, 2018). Future rubber demand is likely to drive expansion and/or intensification of plantations, driving biodiversity and ecosystem loss (Warren-Thomas *et al.*, 2015). This generates a need for biodiversity-friendly but high-yielding cultivation methods. Clonal rubber agroforests in southern Thailand retained yields and benefitted butterfly species richness, while plot management (understorey plant height, non-rubber tree density) and landscape composition (proportion of rubber cultivation in agroforestry, natural forest extent) also increased species richness and altered composition of butterflies and birds. Our findings relating to forest extent must be interpreted in the context of a relatively small number of high-forest-cover landscapes, and further evidence for the importance of forest fragment cover on biodiversity in rubber is needed. We found no evidence that agroforests supported forest-dependent or conservation-priority species, but our findings suggest there is room for improvement of biodiversity within rubber plantations, without negatively impacting rubber yields.

Our finding that butterfly richness was greater in agroforests, and increased further with increasing forest extent (reflected in compositional change), suggests that agroforests may act as transitional habitat for fruit-feeding butterflies that can move several kilometres in a lifetime (Marchant *et al.*, 2015). Contrastingly, monocultures are relatively impermeable for butterflies (Scriven *et al.*, 2017). This corroborates findings of similar butterfly composition between forest fragments and structurally complex rubber in Brazil (Barbosa Cambui *et al.*, 2017). These patterns could be driven by increased food-plant availability, or microclimatic similarities between forest and agroforests (affecting flight ability or thermal

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tolerance; (Koh, 2007)). For example, *Euthalia evelina* uses *Anacardium occidentale* and *Garcinia* spp as larval food-plants, both found in agroforests (**Table S2**; (Ek-Amnuay, 2012)). Alternatively, the assertion from agroforestry farmers that herbicides were not used (used in around half of monocultures; S.B. pers. obs.) may influence butterflies via enhanced understorey plant diversity.

Unlike butterflies, bird richness was unaffected by agroforestry, but altered in agroforests with greater non-rubber tree density, and was similarly, but independently, influenced by greater natural forest extent around plots of either type. A similar conclusion was drawn for cacao, where distance to forest and shade tree density had independent but similar effects on bird richness and composition (Clough *et al.*, 2009), and corroborates findings of altered bird diversity and composition in response to increased tree diversity and/or forest area in monocultural rubber (Zhang *et al.*, 2017) and oil palm (Gilroy *et al.*, 2014a; Teuscher *et al.*, 2015).

Birds and butterflies using agroforests and forest fragments may differ functionally from forest-dependent or agriculture-tolerant species (Koh, 2007; Sekercioglu, 2012). Agroforests and forest fragments may therefore be refugia for species that cannot utilise monocultures (Bhagwat *et al.*, 2008), and their presence may increase landscape beta diversity (Faria *et al.*, 2007) and connectivity (Bhagwat *et al.*, 2008). However, this does not mean that agroforests support forest-dependent or threatened species. The lack of such species in rubber agroforests in our study echoes findings in polycultural oil palm (Azhar *et al.*, 2011, 2015), but contrasts with findings from industrial tree plantations of *Albizia* and *Acacia* (Sheldon *et al.*, 2010), highlighting the importance of gathering evidence on biodiversity responses to different plantation systems. Together, this suggests that conservation of contiguous forest (Edwards *et al.*, 2010; Barbosa Cambui *et al.*, 2017) or complex jungle rubber (Prabowo *et al.*, 2016), remains essential for forest-dependent and conservation priority birds and butterflies.

In addition to modest biodiversity benefits, rubber agroforests could provide additional ecosystem functions and services. Integration of native trees into rubber improves water infiltration, improving and stabilising soil (Langenberger, 2017), while reducing herbicide decreases runoff, soil erosion and loss of total organic soil carbon (Liu *et al.*, 2016). Maintenance of herbaceous vegetation in rubber could be a simple management tool to both modestly increase bird diversity (by up to three species) and protect soils. This could also improve soil macrofauna diversity and abundance, as found in oil palm (Ashraf *et al.*, 2018; Ashton-Butt *et al.*, 2018). Evidence from oil palm suggests that reduced herbicide use does not reduce soil fertility (Ashton-Butt *et al.*, 2018), but the potential effects of understorey plant competition for water and nutrients on rubber yields (Langenberger *et al.*, 2016), and the effect of understorey plant diversity on yields and birds, warrant further investigation. Further ecosystem services provided by more

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complex rubber agroforests could include enhanced pest control, pollination and decomposition (Tscharntke *et al.*, 2005; Maas *et al.*, 2016), climatic stability, and carbon storage (Clough *et al.*, 2016).

Reptile richness and composition were poorly explained by plot management, but composition was influenced by canopy openness and open habitat extent. This corroborates work in cacao, where open habitats and agroforests contained differing reptile assemblages to monocultures, and canopy heterogeneity affected composition (Wanger *et al.*, 2010). Other studies assessing reptile response to agroforest complexity (Deheuvels *et al.*, 2014), and forest cover around plantations (Faria *et al.*, 2007; Gilroy *et al.*, 2014a), have similarly failed to find effects. This may be because relevant variables were not measured, such as log piles, temperature, or leaf litter (Wanger *et al.*, 2010). Alternatively, reptile detectability could have been lower in agroforests due to increased habitat complexity. Similarly, arboreal reptiles (e.g. *Draco.* spp), that may be most likely to respond to agroforestry, are more difficult to detect than ground-dwelling species, meaning a real effect may have been missed.

Our finding of similar reported rubber yields in agroforests and monocultures is supported by existing empirical evidence that rubber tree growth is unaffected by inter-planting (Wibawa *et al.*, 2006). Our data were collected under strong El Niño conditions, resulting in higher temperatures and reduced rainfall than an average year, which may have reduced yields through drought stress. We cannot determine whether yields in agroforests or monocultures were relatively more resilient under these conditions, but this question is likely to become increasingly important as El Niño frequencies increase. Relationships between yields, agroforest structure, and biodiversity warrant further direct investigation, including in relation to climatic changes. As rubber is a canopy tree, and secondary plants grow either below the canopy or in shared canopy space, the relationship between yields and agroforest complexity may differ from other agroforestry systems.

Many factors affect the sustainability of agroforestry for farmers aside from rubber yields: shade-grown crops yield less than unshaded, and labour constraints can make additional crop cultivation unfeasible (Clough *et al.*, 2016; Langenberger *et al.*, 2016). However, in southern Thailand, simply structured high-yielding agroforestry not only improves incomes relative to monocultures, but also provides a social function by generating fruit crops to share within communities, and can provide as good or better return for labour (Romyen *et al.*, 2018; Stroesser *et al.*, 2018). Moreover, farmers with smaller plots were more likely to practice agroforestry, suggesting it provides additional benefits for poorer farmers (Romyen *et al.*, 2018). Despite concerns about economic viability of agroforestry in some regions of Asia (Langenberger *et al.*, 2016), appropriately designed rubber agroforestry seems to provide sustainable livelihood benefits while maintaining rubber yields in southern Thailand.

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Synthesis and applications

Overall, we found modest benefits for birds and butterflies in intensive-clonal rubber agroforests in southern Thailand, while yields were maintained. Increases in non-rubber tree density and understorey vegetation height enhanced bird diversity, while forest fragments were important at the landscape scale for birds and butterflies. Our findings echo those of studies in oil palm and cacao, and contribute further evidence to support sustainable intensification of tropical agriculture.

Small forest fragments may work synergistically with agroforestry for some taxa, such as butterflies, and should be retained, but conserving contiguous forest tracts is preferable for forest-dependent and threatened species (Edwards *et al.*, 2010). Biodiversity losses from continued encroachment of rubber onto protected forests in Thailand (Aratrakorn *et al.*, 2006) and elsewhere in mainland Southeast Asia (Warren-Thomas *et al.*, 2015) will not be mitigated by rubber agroforestry.

We need further empirical research on the yield outcomes of inter-planting non-rubber trees and maintaining understorey vegetation. Together with our study, such evidence could be used to develop guidelines for improving biodiversity value in rubber plantations. These could be applied to technical advice for smallholders (e.g. by RAOT in Thailand), the design of rubber sustainability standards, or to large-scale plantations to improve permeability large-scale monocultures, such in Cambodia (Warren-Thomas *et al.*, 2015) and developing in Africa (Assembe-Mvondo *et al.*, 2015). As demand for natural rubber continues to increase, it is essential that forests are protected against conversion, and that high-yielding biodiversity-friendly rubber cultivation methods, such as agroforestry, are given serious consideration.

Authors' contributions

EWT, PD, DPE conceived the ideas/methodology; EWT, LN, WJ collected biodiversity data; OB identified *Mycalesis*; LS, BC, EP, UT designed questionnaires; LS collected yield data; SB provided logistical support; EWT analysed data and led manuscript writing. PD, DPE, BC, EP, LN, SB, UT contributed to manuscript. All authors gave approval for publication.

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Acknowledgements

EWT was supported by NERC (NE/L50158X/1) and a Small Ornithological Research Grant from the British Ornithologists' Union. Werapun Pichpanus and staff, Nutjarin Petkliang, Tuanjit Sritongchuay and Rinmanat Waiyarat provided logistical support, and Natrada Plappleung provided access to the Princess Maha Chakri Sirindhorn Natural History Museum butterfly collection. Alain Brauman provided CIRAD connections. This research was only possible through the exceptional generosity of the rubber farmers, and their families, who participated in the study. We thank Dr Badrul Azhar and Dr Kevin Darras for constructive comments that improved the manuscript.

Data availability statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.bnzs7h464 (Warren-Thomas *et al.* 2019).

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Figure legends

Figure 1 – Smallholder rubber farms in southern Thailand. Monocultures (a, c) and agroforests (b, d), with minimal (a, b) or well-developed (c, d) understorey.

Figure 2 – Schematic of biodiversity sampling: a) survey plots (plot boundaries shown for reference) within a block, and b) three blocks within a 'district'. Google Satellite imagery accessed through QGIS in August 2019 (does not necessarily reflect land cover at time of sampling in 2016).

Figure 3 – Rubber yield of agroforest (AF) and monoculture (MO) plots. Boxes = 25% and 75% quartiles; thick lines = median; notches = 95% CI; diamonds = mean; whiskers = 1.5x interquartile range. ΔAICc is for the general linear model incorporating plot type (AF or MO), soil type (**Fig. S11**) and their interactions, relative to the null model (i.e. the null model has lower AICc). Yield is unaffected by plot type.

Figure 4 - Species richness of three taxa in rubber agroforest (AF, circles) and monoculture (MO, triangles), showing rarefaction and plot-level richness. Upper panels (a-c) show sample-based rarefaction and extrapolation of detection data for birds and reptiles, and presence-absence data for butterflies (excluding *Mycalesis* females). Dashed lines (a-c) show extrapolation of MO sample (n=25) to AF sample size (n=39), rescaled to number of individuals/detections (birds/reptiles) or plots (butterflies); grey shading shows 95% CI. Lower panels (d-f) show mean and 95% CI (whiskers) of species richness per plot; ΔAICc is for the alternative model incorporating plot type, relative to the null. The alternative model was no better than the null for birds and reptiles, but was best for butterflies (asterisks indicate support for difference between plot types).

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Figure 5 – Species richness response of three taxa to plot management and landscape context. Upper panels (a-c) show response to management, lower panels (d-f) to plot type (MO vs AF reference), influential structural/management variables (* in a-c) and landscape composition. Parameter estimates (predicted change in species richness with a one-unit change of the standardised predictor variable) are from full-model averaging across the 95% confidence set of models, each containing a maximum of four predictors. The central bar line shows the mean of parameter estimate and the bar encompasses 95% CI; those excluding zero are considered influential, marked *. Relative variable importance (proportion of models in set containing each predictor) shown above each bar. Structural/management variables: Can_Cov = canopy cover; Fru_stha = fruit trees stem density; Hrb_h = herb height; n_AF_spp = n agroforestry species; Non_rub_stha = non-rubber tree stem density; Sml_stha = small stem density. Landscape composition variables: AF_ratio = agroforest-monoculture ratio; Lduse_Shannon = Shannon diversity index of land covers; NF_prop = natural forest extent; Rub_prop = rubber extent; Stream = riparian feature length.

Figure 6 – Predicted species richness response to variables influential in averaged models of rubber plot management and landscape composition. Panels show: a) bird response to herb height (no interaction with plot type; line shows predicted effect in both plot types) and, b) butterfly response to natural forest extent, and interaction with plot type (dark grey line = AF, light grey line = MO). Original data points shown (black circle = AF plot, grey triangle = MO plot). Lines fitted to predicted species richness values (points not shown) with a linear model; CI not plotted as SE cannot be reliably computed for mixed effects models.

Figure 7 – Redundancy analysis for three taxa, relating species composition to rubber plot type, management and landscape composition. Panels for birds (a), reptiles (b) and butterflies (c), show plot scores (AF = black circles, MO = grey triangles). Predictors retained through backwards selection shown as arrows; predictors significantly affecting species composition marked *. Variables: AR = ratio of AF to MO; As = non-rubber tree density; Cc = canopy cover; Hh = herb height; LS = land-use Shannon diversity index; MO = plot type (MO vs AF); NF = natural forest extent; OP = open habitat extent; RB = total rubber extent.

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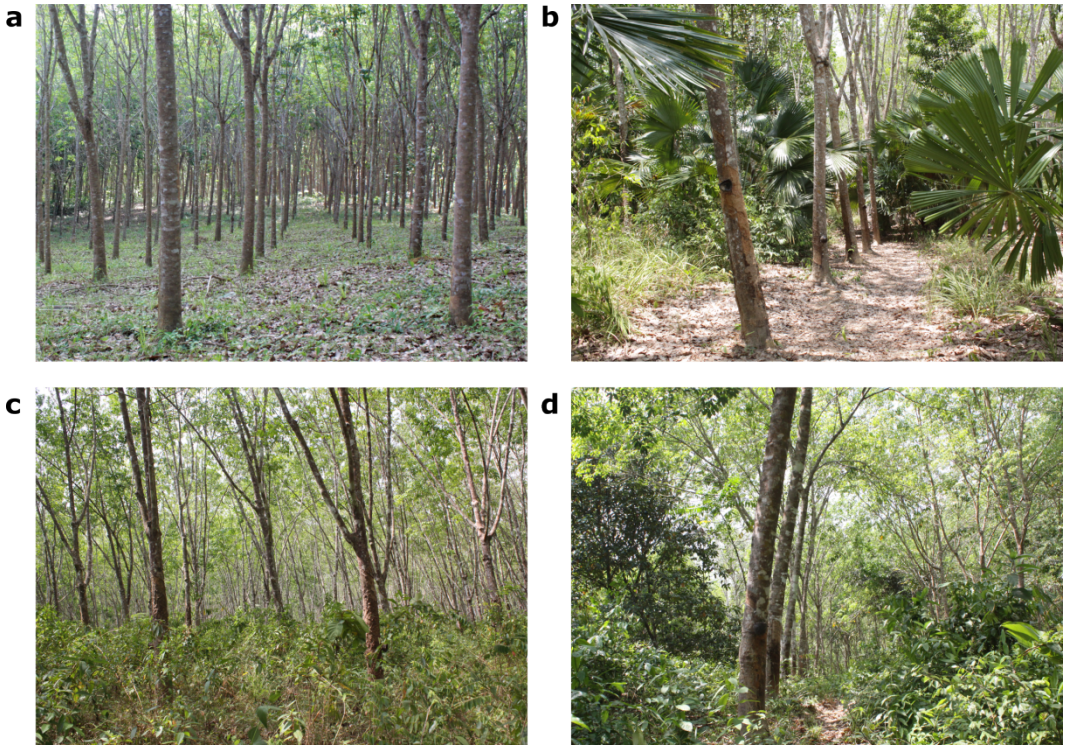

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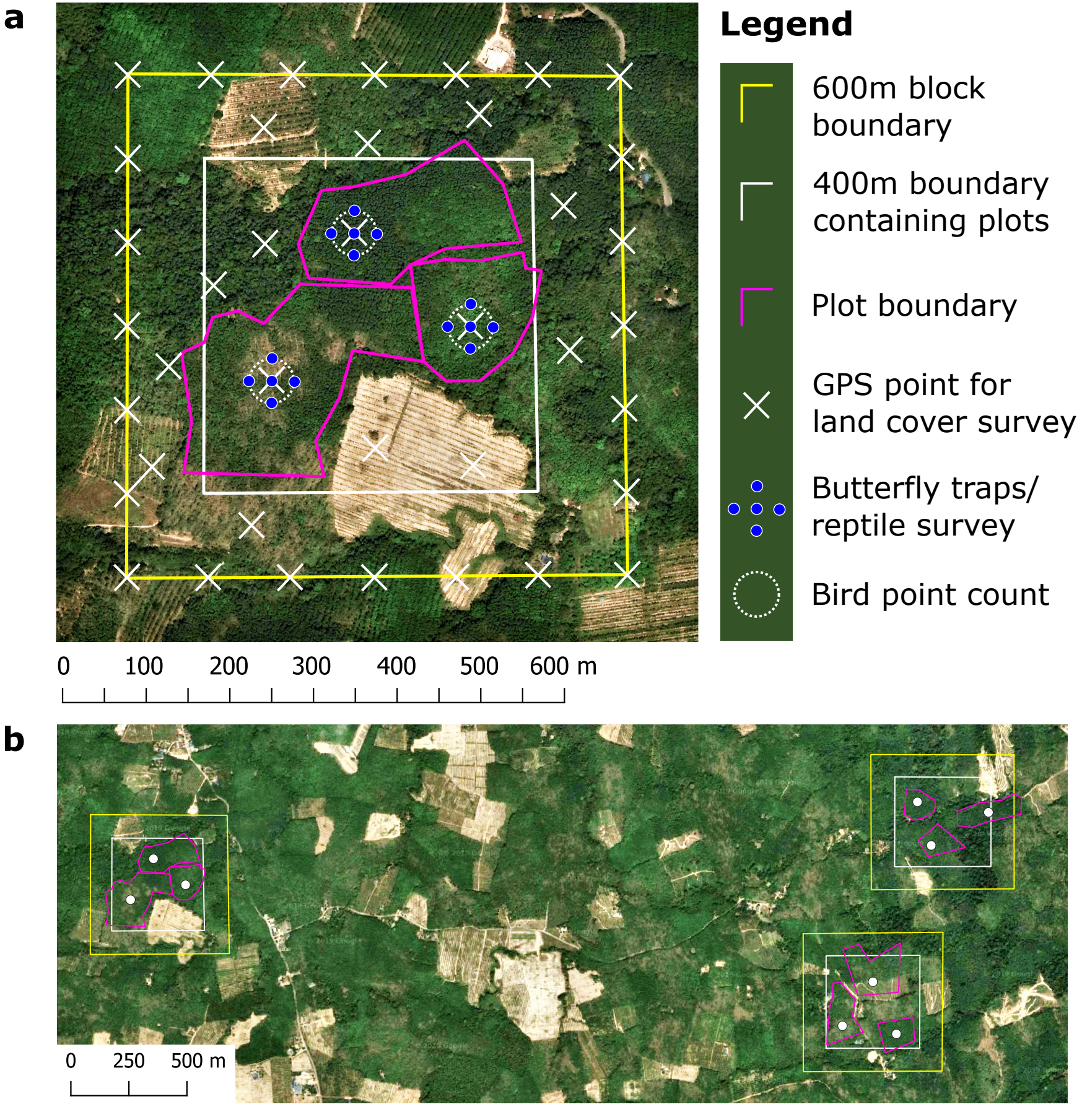
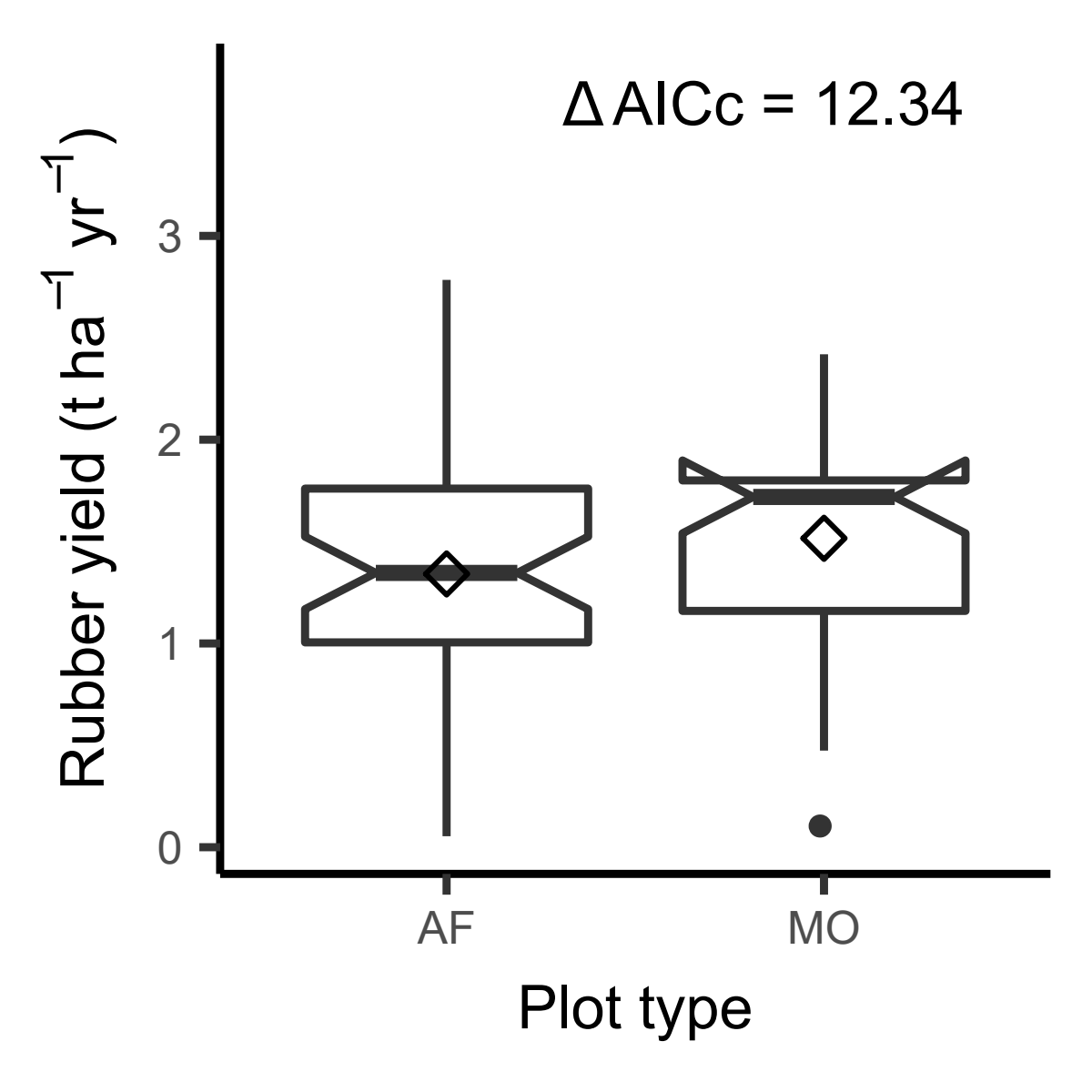
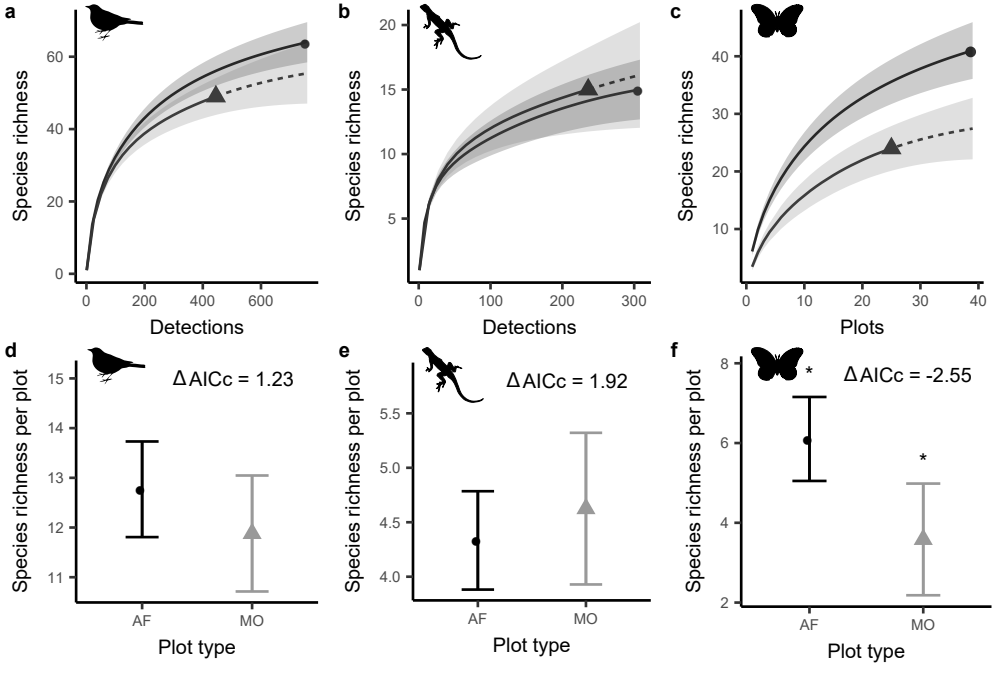
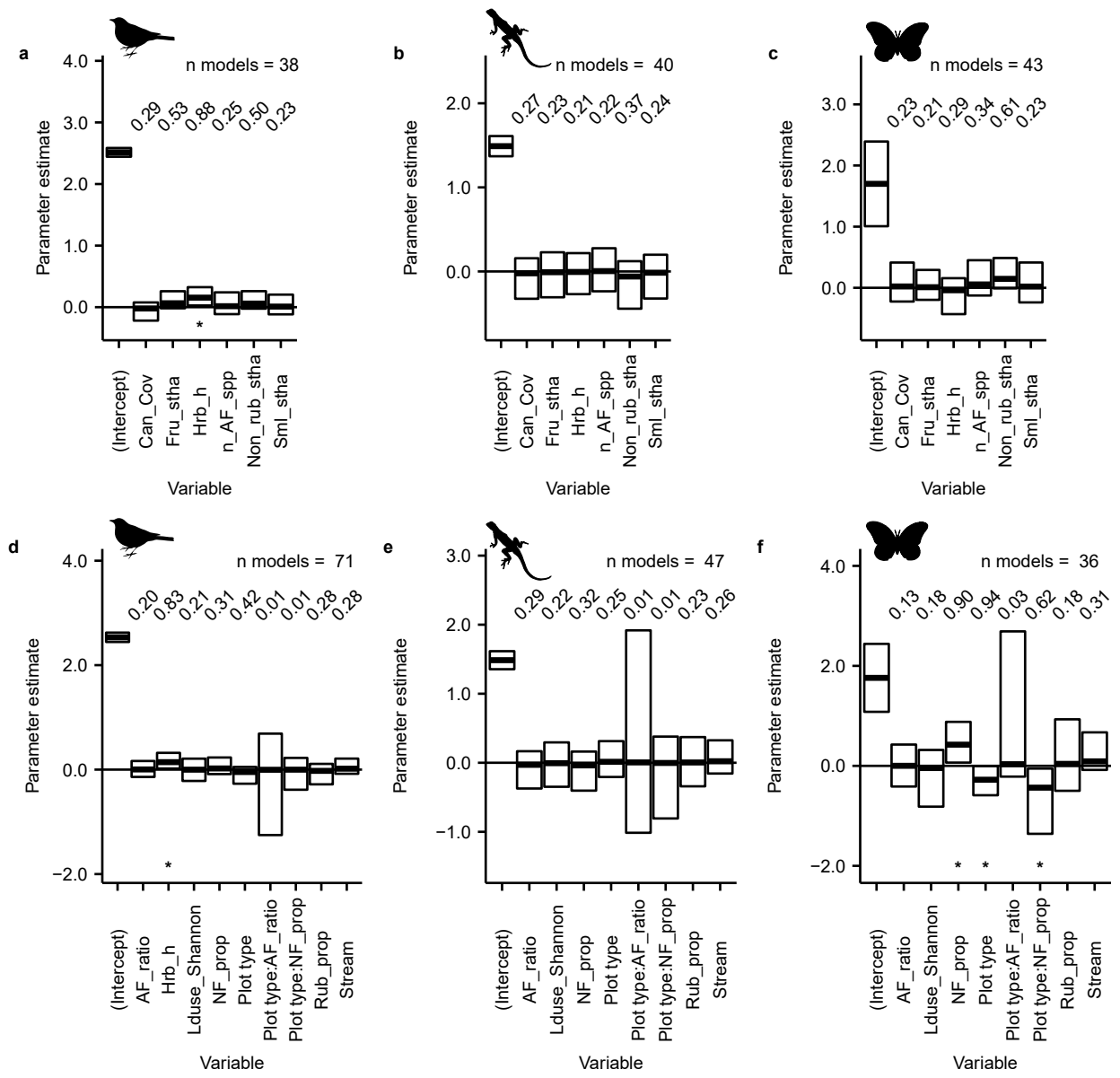
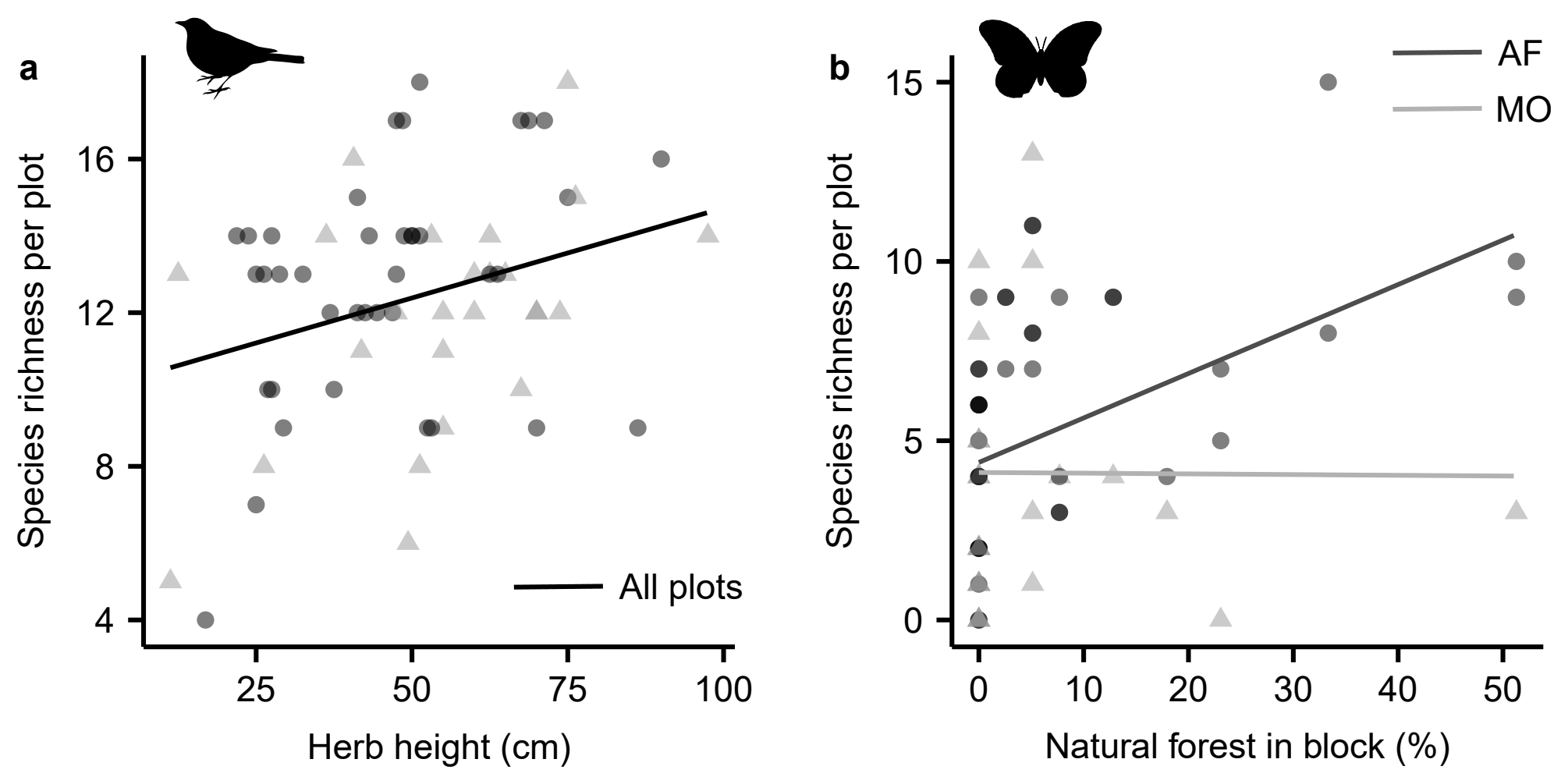
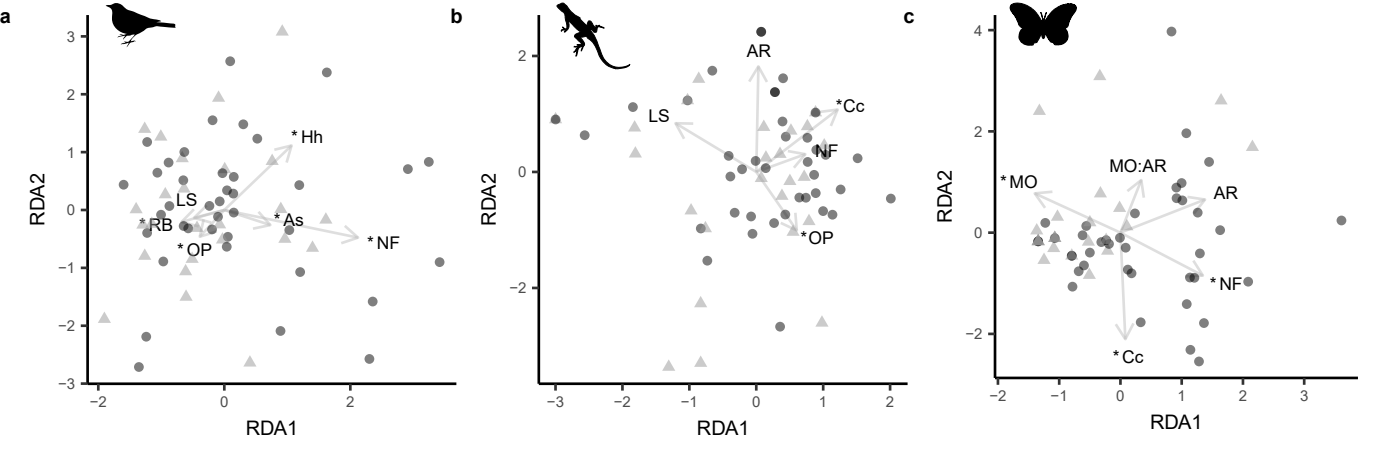

a
Legend
600m block boundary
400m boundary containing plots
Plot boundary
GPS point for land cover survey
Butterfly traps/ reptile survey
Bird point count
0 100 200 300 400 500 600 m
b
0 250 500 m


ΔAICc = 12.34
Rubber yield (t ha^{-1} yr^{-1})
3
2
1
0
AF
MO
Plot type


a
b
c
Species richness
Detections
Plots
d
e
f
Species richness per plot
ΔAICc = 1.23
ΔAICc = 1.92
ΔAICc = -2.55
AF
MO
Plot type


a
n models = 38
0.29 0.53 0.88 0.25 0.50 0.23
b
n models = 40
0.27 0.23 0.21 0.22 0.37 0.24
c
n models = 43
0.23 0.21 0.29 0.34 0.61 0.23
d
n models = 71
0.20 0.83 0.21 0.31 0.42 0.01 0.01 0.28 0.28
e
n models = 47
0.29 0.22 0.32 0.25 0.01 0.01 0.23 0.26
f
n models = 36
0.13 0.18 0.90 0.94 0.03 0.62 0.18 0.31
Parameter estimate
(Intercept)
Can_Cov
Fru_stha
Hrb_h
n_AF_spp
Non_rub_stha
Sml_stha
AF_ratio
Lduse_Shannon
NF_prop
Plot type
Plot type:AF_ratio
Plot type:NF_prop
Rub_prop
Stream
Variable


a
b
Species richness per plot
16
12
8
4
25
50
75
100
Herb height (cm)
All plots
15
10
5
0
0
10
20
30
40
50
Natural forest in block (%)
AF
MO


a
b
c
RDA2
RDA1
*Hh
LS
*As
*RB
*OP
*NF
AR
*Cc
NF
*OP
*MO
MO:AR
AR
*NF
*Cc