Title: Fruit trees and herbaceous plants increase functional and phylogenetic diversity of birds in smallholder rubber plantations

Abstract

Rubber plantations are widespread in mainland South-east Asia. Intensive monocultural rubber cultivation practices predominate, which negatively impact biodiversity. Some plantations are managed as high-yielding agroforests, where the integration of fruit trees and other plant species marginally enhances crop diversity relative to monocultures, providing benefits for species richness of some taxa without compromising yields. A key question is whether these high-yielding agroforestry systems also support enhanced functional and phylogenetic diversity relative to monoculture. Focusing on birds in rubber monocultures and agroforests in two provinces of Southern Thailand, we study plantation habitat structure and wider landscape characteristics to identify effects on functional and phylogenetic diversity metrics. Functional diversity, phylogenetic diversity and evolutionary distinctiveness of birds were comparable between rubber monocultures and intensive agroforests. The density of fruit stems and taller herbaceous plants within agroforests positively influenced functional and phylogenetic diversity, and evolutionary distinctiveness. Functional and phylogenetic diversity was higher in landscapes with a greater proportion of fruit orchards, but was lower in landscapes with a greater proportion of degraded natural forest patches. Our study suggests that the integration of fruit trees and maintaining taller herbaceous plants within rubber plantations could help support bird diversity at evolutionary and functional levels. Small patches of degraded forest in areas dominated by agriculture may need time to generate positive spillover effects on the functional and phylogenetic diversity of birds within rubber plantations. Better management of existing rubber plantations could sustain higher diversity, whilst offering food security and alternative revenue streams.

Keywords

Rubber agroforestry, functional diversity, phylogenetic diversity, bird diversity

Introduction

The fate of biodiversity is becoming increasingly dependent on the state of farming landscapes (Frishkoff et al. 2014). *Hevea brasiliensis* rubber plantations threaten natural ecosystems (Warren-Thomas et al. 2015) and have expanded rapidly even into non-traditional growing areas (Ahrends et al. 2015), reaching a total area of 10.4 million hectares in 2017 in Asia (Lang et al. 2019). The expansion of rubber has occurred at the expense of forests in mainland Southeast Asia (Aratrakorn et al. 2006) and China (Sarathchandra et al. 2018), including within protected areas in Cambodia (Grogan et al. 2019), driving substantial biodiversity losses (Warren-Thomas et al. 2015; Wang et al. 2020).

Compared to traditional low-yielding rubber agroforestry systems with heterogeneous microhabitats that can support some forest-dependent biodiversity (Beukema et al. 2007), intensive rubber monocultures, which include the majority of rubber plantations globally (Warren-Thomas et al. 2019), substantially reduce the species richness and composition of faunal assemblages relative to forest (Aratrakorn et al. 2006; Liu et al. 2016; Prabowo et al. 2016; Sreekar et al. 2016). The integration of 'wildlife-friendly' habitat characteristics within farmlands, or the land-sharing approach (Cannon et al. 2019), is applicable in some countries (Murdiyarso et al. 2002; Grau et al. 2013). For instance, Sumatran jungle rubber better supported forest-dependent and frugivorous birds than did rubber monoculture (Prabowo et al. 2016), but yields in these systems are well below average (Villamor et al. 2014). Hence the debate on land-sharing versus land-sparing (where plantations are intensified for higher yields 'sparing' land elsewhere for nature (Cannon et al. 2019)) still continues (Luskin et al. 2018). However, intensive agroforestry systems, in which additional crop plant species are grown alongside normal densities of modern clonal rubber varieties, have comparable rubber yields to monocultures while supporting higher species richness of butterflies (but not birds or reptiles; (Warren-Thomas et al. 2019), offering an option for agroecological intensification (Tscharntke et al. 2012). Furthermore, a greater proportion of natural forest in surrounding landscapes tends to increase diversity of butterflies and birds within plantations, while taller herbaceous plants and a greater density of non-rubber trees in plantations positively influences the species richness and alters the composition of birds (Sekercioglu 2012; Azhar et al. 2013; Warren-Thomas et al. 2019).

Although the relationship between rubber production systems and species diversity is starting to be elucidated, a key remaining question is how functional diversity, phylogenetic diversity and evolutionary distinctiveness of species communities are impacted by rubber management. Functional diversity represents differences in functional traits among species in a community, capturing the extent of complementarity between species trait values (Petchey and Gaston 2002). It is a strong predictor of the productivity and vulnerability of an ecosystem (Schleuter et al. 2010), and an ecosystem is expected to be more stable and efficient when more functional traits are present (Cardinale et al. 2012). Functional diversity includes three different components: functional richness (the amount of niche space occupied by the species), functional evenness (whether there is a regular distribution of species traits) and functional divergence (variation of functions and positions of species clusters in trait space) (Schleuter et al. 2010). Measurements of functional diversity should ideally encompass these different aspects.

Phylogenetic diversity represents the patterns of genetic variation in a community and provides insights into evolutionary relationships between species (Faith and Baker 2007). Higher phylogenetic diversity leads to the preservation of a greater proportion of evolutionary history (Frishkoff et al. 2014; Jetz et al. 2014). By conserving phylogenetic diversity, the potential to lose unique ecological and phenotypical traits in a community decreases (Matos et al. 2017), while phylogenetically diverse communities are more stable and productive (Frishkoff et al. 2014) contributing to ecosystem function and stability (Matos et al. 2017). Phylogenetic richness (total evolutionary history of maximally distinct species lineages), divergence (phylogenetic distances among species pairs) and structure (whether taxa are phylogenetically clustered) characterise the components of phylogenetic diversity and are represented by different indices (Morante-Filho et al. 2018). Evolutionary distinctiveness, which indicates the extent to which species are closely related to other extant species, further supports conservation planning (Prescott et al. 2016a) and the conservation of a greater proportion of evolutionarily distinct species ensures the protection of unique ecological and phenotypic traits (Jetz et al. 2014).

In other tropical agricultural systems, such as oil palm and cattle pasture, forest conversion to cropland reduces functional diversity of birds and dung beetles (Edwards et al. 2013; Edwards et al. 2014; Cannon et al. 2019), but less so when more forest was retained nearby (Prescott et al. 2016b; Cannon et al. 2019). Similarly, avian phylogenetic diversity was lower in monoculture than in diversified agricultural systems in Costa Rica (Frishkoff et al. 2014) and higher in cattle pasturelands containing more wildlife-friendly features (Edwards et al. 2015). These studies also revealed that agriculture-affiliated species tend to be less phylogenetically diverse and less evolutionarily distinct than forest-affiliated species (Frishkoff et al. 2014), pointing to the importance of understanding how crop diversity, local habitat structure within plantations, and wider-scale landscape composition practices impact functional and phylogenetic diversity, and evolutionary distinctiveness.

In this study, we focus on Thailand, the biggest producer of natural rubber globally (Simien and Penot 2011), and on birds, which are a functionally diverse group that plays important ecological roles such as pollination, predation and seed dispersal (Sekercioglu 2012), and for which a complete phylogeny of all extant species is available (Jetz et al. 2012). Our three core objectives are to: (1) compare avian functional diversity, phylogenetic diversity, and evolutionary distinctiveness between rubber monocultures and agroforests; (2) identify how habitat structure within rubber plantations impacts functional diversity, phylogenetic diversity and evolutionary distinctiveness; and (3) understand how the surrounding landscape composition affects functional diversity, phylogenetic diversity and evolutionary distinctiveness.

Materials and Methods

Site description

In Thailand, the area occupied by rubber plantations is similar to the area occupied by forests (Phommexay et al. 2011). The majority (95%) of Thai rubber area is maintained by smallholder farmers, of which more than 90% is monoculture and the remaining is agroforestry, which may include jungle rubber systems or intensive agroforestry systems where rubber is intercropped with other crops such as fruits and vegetables (Simien and Penot 2011; Warren-Thomas et al. 2019).

The study area included two provinces in Southern Thailand (Figure S1-a), Songkhla and Phatthalung (Figure S1-b), where landscapes are mainly dominated by rubber plantations (Somboonsuke 2001; Stroesser et al. 2016). In addition, smaller areas of oil palm plantations, fruit orchards, rice fields and forest patches were also present. Forests closer to plantations were mostly fragmented and degraded secondary forests (largest fragmented forest patch was around 400 ha) while in upland areas three protected forests covered larger extents. The area has frequent rain in May-December and a dry season in January-March (Phommexay et al. 2011). In the plantations surveyed, rubber trees were planted with distances of three meters between trees and seven meters between rows.

Plantations categorised as ‘agroforest’ plots contained additional crops planted between the rows of rubber trees or multiple naturally occurring non-rubber plant species (Figure S2-a).

Sampling design

Bird diversity data collection was conducted in March-June 2016. Twenty-three sampling blocks (Figure S1-c) were demarcated in the study area with each block containing two or three sampling plots (64 plots in total) with plot central points 200-400 m apart (see supplementary methods; further methods detailed in (Warren-Thomas et al. 2019)). The plots (Figure S1-d) consisted of management units containing rubber trees with a uniform age distribution. Each plot was categorised as either monoculture (n=25) or agroforest (n=39). Except for five blocks with only agroforestry plots, the rest of the blocks contained both agroforestry and monoculture plots. The mean elevation of the plots was 82.6 m asl (35.0 - 137.1 m asl range). The minimum area of plots was ≥ 1 ha (100 m x 100 m).

Habitat structure of each sampling plot was recorded within subplots of 5-10 m radius (see supplementary methods). Measurements included height of herbaceous vegetation in centimetres referred to as herb height (Hrb_h), percentage canopy cover (Can_Cov), small stem density (Sml_stha), total density of planted agroforestry species and naturally regenerated trees; (Total_AF_Nat_st_ha), fruit tree stem density (including palms fruiting palms; Fru_stha) and the number of agroforestry species (counted across the entire plantation, not solely within subplots; n_AF_spp).

Land use for the 23 sampling blocks were recorded under 14 categories (see supplementary methods) for 39 points within and along the perimeter at 100 m intervals. These were further summarised into explanatory variables at the block level as: percentage of points that were agroforestry (AF_prop), percentage points in natural forest (NF_prop), percentage of points in immature rubber (IM_prop), percentage of points in fruit orchards (Fruit_prop) and the Shannon-Weiner diversity index of land uses (Lduse_Shannon). In addition, the distance from the centre of each point count location to the nearest contiguous forest area (to one of the protected forests), (For_dist), was measured using Google Earth Pro 7.1.5.1557.

Bird sampling

Bird sampling was performed according to a fixed-radius (50 m) point count method by a single experienced observer (LN), with point counts located at the centre of each plot (Warren-Thomas et al. 2019). Sampling plots from two or three blocks were surveyed for 10 minutes each on three consecutive days between 0600 and 0930, identifying birds to species level using both sight and sound, and recording the abundance of each species. All point counts were digitally recorded with an Olympus LS-11 Linear Recorder to verify unidentified vocalisations of birds using an online reference (www.xeno-canto.org). Individuals flying overhead or through the point count stations were excluded, while migratory and resident species were included in analyses.

Functional, phylogenetic, and evolutionary distinctiveness metrics

Functional traits of bird species were gathered using the *Handbook of the Birds of the World Alive* (del Hoyo et al. 2017). The functional traits considered were: mass (grams, largest reported); dietary guild (nectarivore, frugivore, insectivore, scavenger, granivore, predator, piscivore); foraging strata (open areas, forest terrestrial, forest understorey, forest midstrata, forest canopy, aquatic); and foraging substrate (soil/leaf litter, trunk/branch, foliage, aerial, sub-water-surface) (Prescott et al. 2016b; Cosset and Edwards 2017). These traits reflect the resource-use requirements of individuals

(Flynn et al. 2009). Apart from mass, all traits were categorical response variables. The trait matrix was used to calculate functional diversity metrics (Table 1).

We calculated five metrics relating to different aspects of functional diversity (Schleuter et al. 2010) to obtain a holistic understanding of the bird community. Functional diversity (FD) represents functional richness. Since FD is sensitive to species richness, the standard effect size of functional diversity (sesFD) was calculated to correct this (Table 1). The regularity of species traits is calculated by functional evenness (FEve). Functional divergence is represented by Functional dispersion (FDis; variability of traits) and Rao's quadratic entropy (Rao's Q) which calculates the abundance weighted variance of species pairs (see Table 1 for definitions of each metric). We calculated the FD metrics based on a distance matrix generated using extended Gower distance that could handle both continuous and binary variables. The functional dendrogram was built using the unweighted pair-group method with averaging (UPGMA) for hierarchical clustering which gave the highest co-phenetic correlation coefficient (Swenson, 2014). Since FD does not account for species abundances, we repeated the FD analysis omitting rare species (singletons and doubletons). We used the "trial-swap" method in the ses.pd function to calculate sesFD comparing observed FD to 999 scenarios where the number of species is held constant. For calculating the other metrics, FEve, FDis and Rao's Q, we used the dbFD function (Laliberté et al. 2014).

For calculating phylogenetic diversity, 500 phylogenetic trees based on the Hackett backbone (Hackett et al. 2008) were downloaded from http://birdtree.org/ (Jetz et al. 2012). Each tree represents a different hypothesis of bird species evolutionary relationships. Mean values at each sample point were used to calculate phylogenetic and evolutionary distinctiveness metrics (Table 1). For phylogenetic diversity aspects (PD), we calculated six metrics. For richness we calculated the phylogenetic diversity index (PD) and the standard effect size of phylogenetic diversity (sesPD). For phylogenetic divergence, the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) were used (Prescott et al. 2016a; Morante-Filho et al. 2018). Phylogenetic structure was represented by the standard effect size of MPD (sesMPD) and the standard effect size of MNTD (sesMNTD) (Morante-Filho et al. 2018). In addition, we obtained data for evolutionary distinctiveness (ED) and evolutionary distinctiveness rarity (EDR) (Prescott et al. 2016a). The definition for each metric is in Table 1.

For PD metrics, we used null communities generated using null models dependent on the "independent swap" algorithm. For sesPD, sesMPD and sesMNTD the observed community was compared to 999 null communities. This was performed for the 500 phylogenetic trees. ED and EDR values were obtained from a global phylogeny (Jetz et al. 2014), since it is more relevant to conservation, and the mean across all species was calculated for the community at each plot. All calculations for functional, phylogenetic and evolutionary distinctiveness metrics were performed in R version 3.6 using packages picante and FD (Kembel, 2010; Laliberté and Legendre, 2010; Laliberté, Legendre and Shipley, 2014; R Core Team 2019).

Data analyses

1. Effect of agroforest and monoculture on functional, phylogenetic and evolutionary distinctiveness metrics.

We compared all metrics between agroforestry and monoculture at the plot level. We constructed null models (with Block as a random effect) and habitat models (using only agroforest/monoculture as a fixed effect) for all dependent variables (Table S2) to test if functional and phylogenetic diversity at the plot level was explained by habitat management type (agroforest or monoculture). We used linear mixed-effects models and generalized linear mixed-effects models to identify the relationship between all FD and PD metrics and habitat management type (agroforest/monoculture). The lmer and glmer functions of the lme4 package (Bates et al. 2015) were used. FD and Rao's Q were compared between agroforestry and monoculture plots using sample-based rarefaction, using the R packages BAT (Cardoso et al. 2015) and iNEXT (Chao et al. 2014) since the sample sizes were different.

2. Effect of habitat structure on functional, phylogenetic and evolutionary distinctiveness metrics

We used linear mixed-effects models and generalized linear mixed-effects models to identify the relationships between FD, PD and ED metrics with habitat structure variables. For the dependent variables FD, sesFD and FEve, we used linear mixed-effects models considering the six habitat structure variables as explanatory variables. For FDis and Rao's Q, generalized linear mixed-effects models were used with a Gamma distribution and log-link function. For analyses where all PD and ED metrics were dependent variables, we used linear mixed-effects models. To account for the nested sampling design, we used 'Block' as a random intercept in all habitat structure models. We used an information theoretic approach to test our hypotheses and constructed a set of 45 models (Table S3). All explanatory variables were standardised and centered to make effect sizes comparable. We used the variance inflation factor (VIF) to test for multicollinearity between variables. A Monte Carlo permutation test for Moran's I was conducted with 1000 iterations to test for spatial autocorrelation. The models were tested for all dependent variables (FD, PD and ED metrics) and the best models for each were selected using the Akaike information criterion for small samples sizes (AICc). Averaged models were built using model sets that confirmed 95% confidence levels (Grueber et al. 2011).

To determine the impacts of habitat structure variables behaving differently in agroforestry and monoculture, we ran additional models in which we considered agroforestry and monoculture plots separately. We used a similar information theoretic approach using linear mixed-effects models and generalized linear mixed-effects models. In addition to the previous model set, we built a new set of 23 models containing only selected variables that were applicable to monoculture (Table S4). We used FD, PD and ED metrics separately as dependent variables and averaged the models that gave 95% confidence for each metric.

3. Effect of landscape composition on functional, phylogenetic and evolutionary distinctiveness metrics

We used a slightly different approach to test the effects of landscape composition. Since five of the landscape composition variables (except for distance to nearest contiguous forest) were measured at the Block level (23 blocks), we did not use 'Block' as a random effect as it creates confounding effects in the models with the landscape composition variables. Instead, we used linear models without any random effects (for FD, sesFD and FEve) and generalized linear models (for FDis and Rao's Q). Linear models were used for all PD and ED metrics as well. We used an information theoretic approach to test our hypotheses and built a set of 47 models (Table S5). A Monte Carlo permutation for Moran's I with 1000 iterations was carried out, which did not yield any evidence for the presence of spatial autocorrelation in model residuals. From the set of models, the best models were selected using AICc and averaged models were again built to yield 95% confidence levels.

Results

Sixty-nine species of birds spanning thirty-two families (within eight orders) were observed in total across all rubber plots, of which 64 and 49 species were recorded in agroforest and monoculture plots, respectively (Figure 1). Of the 22 rare species (singletons and doubletons), 15 were unique to agroforestry plots and five to monoculture plots (Figure 1, Table S1). Two of the rare species found in agroforests (*Eurylaimus ochromalus* and *Megalaima mystacophanos*) are Near Threatened according to the IUCN (2020). Twenty species were unique to agroforests, while five were unique to monoculture habitats. Species unique to agroforests or monocultures did not show strong clustering on the functional diversity dendrogram or phylogenetic tree (Figure 1). The majority of species recorded were insectivorous (N=64), of which 21 were obligate insectivores, with only three obligate nectarivores or frugivores. The avian community in both rubber monoculture and agroforestry plantations was dominated by passerines (46 species), with 13 non-passerines found only in agroforestry, and only one in monoculture. The families that dominated the phylogenetic tree were Cuculidae (N=7), Nectariniidae (N=7) and Pycnonotidae (N=6).

Effect of agroforests and monocultures on functional, phylogenetic and evolutionary distinctiveness metrics.

Functional diversity did not vary between agroforests and monocultures. However, sesFD was negative in agroforestry and positive in monoculture, indicating that observed FD is lower than expected in agroforestry and higher than expected in monoculture given the species richness (Table 1, Figure S3). FEve, FDis and Rao's Q did not significantly differ between habitats (Table 1, Figure S3). When rare species were omitted, the same pattern was observed between all FD metrics (Table 1); the full species list was therefore used for further analyses.

Phylogenetic diversity metrics did not vary between agroforest and monoculture, although sesMPD and sesMNTD were negative for agroforestry plots indicating that the observed values were lower than expected values (Table 1, Figure S4). Evolutionary distinctiveness did not differ between the two habitats (Table 1, Figure S4).

For each of the functional diversity metrics, including habitat management type as a fixed effect (agroforest or monoculture) in linear models did not improve model fit and null models were selected over habitat models in all cases (Table S2). Habitat models for phylogenetic diversity gave similar results (Table S2). This confirmed that the habitat management type could not explain the variation in functional and phylogenetic diversity between the different sampled plantations.

Effect of habitat structure on functional, phylogenetic and evolutionary distinctiveness metrics

Functional diversity metrics were significantly influenced by some habitat structure variables. The averaged model indicated a positive response of FD to increasing fruit tree stem density and herb height (Figure 2a and Table S6). There were no significant associations between sesFD, FEve, FDis and Rao's Q with habitat structure variables as main effects (Figures 2b-e). FDis and Rao's Q were however negatively related to the interaction effects between herb height and total agroforestry and natural stem density, and between herb height and number of agroforestry species (Figures 2d-e, figure S5, Table S6). Further, FDis was negatively associated to the interaction effect between canopy cover and small stem density (Figure 2d, Figure S5, Table S6).

When agroforestry plots were considered separately, fruit stem density positively influenced FD while small stem density and herb height negatively influenced FDis and Rao'sQ (Figure S6, Table S7). FD, sesFD, FDis and Rao's Q were positively influenced by natural stem density when only monoculture plots were considered (Figure S7, Table S7). Here, only the natural stem density has effect in monoculture plots (in the variable 'total agroforestry and natural stem density' in the models). Herb height positively influenced sesFD, but negatively influenced FDis and RaoQ. Further, small stem density was negatively associated with sesFD in monoculture plots (Table S7).

Phylogenetic diversity metrics were significantly influenced by some habitat structure variables. The averaged models indicated that fruit tree stem density and herb height had a positive influence on PD (Figure 3a), while herb height had a negative influence on sesPD, sesMPD and MNTD (Figures 3b-e respectively, Table S6). Small stem density had a negative effect on sesPD, MPD, sesMPD, MNTD and sesMNTD (Table S6). Fruit stem density and herb height had a positive influence on ED and EDR (Figures 3g-h; Table S6). The total agroforestry and natural stems also seemed to have a positive influence on PD and ED (Figures 3a, g).

We did not identify major differences in the responses of PD metrics when agroforestry plots were modelled separately (Figure S8, Table S7). In monoculture plots, the natural stem density (the variable 'total agroforestry and natural stem density' in the models) was positively influencing all PD metrics (Figure S9). In addition, the small stem density positively influenced EDR. Overall, more complex vegetation resulted in higher phylogenetic diversity and evolutionary distinctiveness of birds in the rubber plantations studied.

Effect of landscape composition on functional, phylogenetic and evolutionary distinctiveness metrics

The averaged models revealed that the proportion of fruit orchards positively influenced FD, FDis and Rao's Q (Figure 4a,d,e; Table S8), while proportion of degraded natural forest negatively influenced sesFD, FDis and Rao's Q (Figure 4b,d,e; Table S8). FEve was positively associated with the interaction effect between proportion of fruits and proportion of natural forest (Table S8).

The averaged models for phylogenetic diversity showed that the proportion of fruit orchards had a positive effect on PD, sesPD, MNTD and sesMNTD (Figures 5a, b, e, f; Table S8). The proportion of degraded natural forest had a significant negative effect on sesPD, MPD, sesMPD, MNTD and sesMNTD (Figures 5b-f; Table S8). MNTD and sesMNTD had a negative association with the distance to nearest contiguous forest (Figures 5e, f; Table S8). In contrast, the proportion of degraded natural forest had a positive relationship with ED and EDR (Figures 5g, h; Table S8). Overall, phylogenetic diversity was positively influenced by fruit orchards and negatively influenced by degraded natural forests in the landscape.

Discussion

Although overall functional and phylogenetic diversity metrics were comparable between intensive agroforestry and monoculture rubber systems, functional and phylogenetic diversity of birds was greater in plantations with greater densities of fruit tree stems and increased height of herbaceous plants. This suggests that management could enhance the habitat structure of rubber plantations to sustain more biodiversity at ecosystem functional and evolutionary scales. Since both intensive agroforest and monoculture plantation systems offer comparable rubber yields (Warren-Thomas et al. 2019), the presence of economically important fruits and herbs could also provide socio-economic benefits (Stroesser et al. 2018) in addition to biodiversity benefits.

We observed a strong clustering of functional traits on the functional dendrogram (Figure 1) due to the dominance of small-medium-sized insectivores. Insectivores dominate some agricultural habitats in the region (Azhar et al. 2013) although their presence is much lower in agriculture compared to forest habitats (Nájera and Simonetti 2010; Maas et al. 2016). The plantations we observed did not support a higher abundance of frugivores or nectarivores. This is similar to Sumatra where frugivores were absent in monoculture rubber but more abundant in traditional jungle rubber (Prabowo et al. 2016), which is more forest-like and not comparable to intensive agroforestry in Thailand. Nevertheless, we expected higher functional diversity in agroforests given their undergrowth, higher canopy cover and multiple plant species making them structurally more comparable to forests than monoculture rubber. However, negative sesFD in agroforestry plots indicated that the observed functional diversity in agroforestry was lower than expected for the species pool. This could be a consequence of the presence of functionally unique species in monoculture that prefer open foraging habitats, e.g. *Todiramphus chloris* and *Corvus macrorhynchos*.

Similarity in the functional roles played increases with species richness (Cooke et al. 2019), leading to higher functional redundancy (Flynn et al. 2009). Rubber agroforestry plantations had a higher species richness than monoculture (although not statistically significant) and, in turn, a higher functional redundancy, which may explain lower sesFD. For instance, in the Colombian Llanos, sesFD of species-rich remnant forests was lower than that of species-poor oil palm plantations or pasture (Prescott et al. 2016b). The results were comparable for functional divergence too, indicated by FDis and Rao's Q.

Phylogenetic diversity was comparable between intensive rubber agroforests and monocultures, supporting findings from diversified agriculture and intensive monocultures of different crops in Costa Rica (Frishkoff et al. 2014). When compared to natural forests, phylogenetic clustering is higher in agricultural habitats (Edwards et al. 2017) while phylogenetic diversity is much lower (Frishkoff et al. 2014), likely reflecting that sensitive forest species have been extirpated due to the initial forest loss (Prescott et al. 2016a). In the current study, species in agroforests appeared to be distributed among clades with more recent ancestors and with co-occurrence of more closely related individuals, as indicated by negative sesMPD and sesMNTD in agroforestry. This indicates that the agroforest bird community is more phylogenetically clustered than the monoculture community in the intra-familial or intra-generic levels (Prescott et al. 2016a).

Novel bird communities in diversified agriculture or monocultures contain bird communities with lower evolutionary distinctiveness compared to forest (Frishkoff et al. 2014). As agricultural habitats undergo multiple and frequent disturbances, they favour adaptable species. Previous research shows that monocultures contain younger species with rapid diversification rates (Frishkoff et al. 2014). In our study, the bird community in intense rubber agroforestry did not conserve a considerably greater evolutionary distinctiveness than monoculture habitats. This means that, compared to forests, facilitative interactions between bird species in these communities are less frequent, and that both these habitats are poor at providing a buffer against stressful environmental changes (Cadotte et al. 2012).

We identified that habitat structure in rubber plantations was associated with the functional and phylogenetic diversity of birds. Herbaceous plants influence the structural complexity of plantation habitats benefitting avifauna (Nájera and Simonetti 2010; Sheldon et al. 2010). Other studies in oil palm landscapes show that vegetation cover has a positive influence on bird foraging guilds (Azhar et al. 2013), while the presence of weed plants increases butterfly species richness (Koh 2008). However, functional divergence was positively correlated to the interaction effects between high herb height and low number of agroforestry species and low natural stem density. A similar relationship was observed with low canopy cover and high stem density suggesting that functional variations and resource differentiation between species is affected by these complex interactions. Another interesting finding was that functional, phylogenetic and evolutionary distinctiveness metrics were greater when the density of fruit tree stems increased. The presence and density of understory plant stems positively influences insectivorous birds in forests (Castaño-Villa et al. 2014) and bird abundance in Acacia plantations (Sompud et al. 2016). In monoculture, density of natural stems supported functional and phylogenetic diversity while small stems extracted a positive response in evolutionary distinctiveness rarity. The habitat complexity in monoculture rubber, explained by the presence of plant stems, supports biodiversity to some extent (Nájera and Simonetti 2010).

Functional and phylogenetic diversity metrics had a negative relationship with the proportion of surrounding natural forest. This could be because the natural forests patches in our study were fragmented, degraded, and located in an area dominated by rubber plantations (Prescott et al. 2016a; Ulrich et al. 2016). Further, phylogenetic richness of non-forest bird species could be negatively related to forest cover, indicating the importance of compensatory dynamics between forest and non-forest birds in agricultural habitats (Morante-Filho et al. 2018). By contrast, previous studies have found that avian phylogenetic diversity is positively related to natural forest area in agricultural habitats (Prescott et al. 2016a; Zhang et al. 2017). However, there are instances where phylogenetic metrics such as MNTD have decreased with increasing forest proportion (Prescott et al. 2016a) suggesting that interactions between species and landscapes are complicated. Further, MNTD and sesMNTD decreased with the distance to contiguous forest suggesting that the presence of nearby natural forest could support more distantly related bird species. Although our bird community only included a few frugivore species, the availability of fruits positively influenced bird diversity in our rubber plantations, similar to previous studies (Cosset and Edwards 2017).

The agroforest plantations we studied in Southern Thailand are high-yielding, intensive rubber agroforestry systems. These are not comparable to highly biodiverse jungle rubber systems present in countries like Indonesia, which are already de-facto land-sharing systems for biodiversity, at risk of intensification (Clough et al. 2016) without the protection of high-quality habitat that would form a land-sparing approach. In Thailand, intensively managed rubber plantations are already dominant in the landscape, and farmer livelihoods are strongly dependent on rubber yields, so it could be considered that a land-sparing approach has already been established (for example via protection of remaining forest fragments). However, diversifying these plantations to enhance habitat heterogeneity could deliver biodiversity benefits and increase connectivity between remaining forest fragments in surrounding landscapes (Swallow et al. 2006). Beyond the land-sparing -sharing debate, improving the hospitability of the cultivated matrix between patches of high-quality habitat is essential for biodiversity persistence in the long term (Grass et al. 2019).

The land-use history of these habitats could also play an important role as open habitat-derived agroforestry harbours less biodiversity compared to forest-derived agroforestry (Martin et al. 2020). The bird species assemblages of the Sundaic region, where this study took place, may have fewer species able to colonise simplified environments, such as plantations (Lambert and Collar 2002), than other regions with naturally open habitats, such as further north in Thailand. It would be interesting to consider effects of rubber agroforestry techniques closer to a deforestation frontier, to understand how the functional diversity, phylogenetic diversity, and evolutionary distinctiveness are shaped in these habitats.

Conclusions

Both agroforestry and monoculture rubber plantations can be managed to positively influence bird functional and phylogenetic diversity, as the height of herbaceous vegetation and the density of fruit tree stems have potential to enhance these metrics. Although a clear difference in overall functional diversity, phylogenetic diversity and evolutionary distinctiveness was not identified between monocultures and agroforests in Thailand, integration of fruits and herbs within rubber plantation habitats would benefit bird communities at ecosystem functioning and evolutionary scales. There is evidence that high-yielding agroforestry plantations provide additional socio-economic benefits to farmers, in particular, diversified income streams and food security. In the context of wider landscape management, better conservation and restoration of natural forest patches in the region could sustain more biodiversity, whilst offering enhanced spillover of species into rubber plantations. Agricultural policies should thus focus on the creative management and diversification of existing intensive rubber plantation systems, whilst maintaining yields. Such ecological intensification can support functionally and phylogenetically diverse bird communities, enhancing the landscape connectivity that is vital for movement of biodiversity under climate change (Senior et al. 2019).

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Table 1: Measures of functional diversity, phylogenetic diversity and evolutionary distinctiveness used for the analysis.

Diversity Metrics	**Description**
Functional Diversity (FD)	A tree-based metric, calculated by using a distance matrix of functional traits to create a functional dendrogram of the entire species pool across all samples, and then calculating the total branch lengths for samples of interest (Petchey and Gaston 2002).
Standard effect size of FD (sesFD)	FD is sensitive to species richness, so the standard effect size of FD (sesFD) was also calculated by randomizing species identities (across the entire species pool). Here, observed FD is compared to null communities of similar species richness with random species drawn from the species pool. More diverse communities would have positive values of sesFD (Prescott et al. 2016b).
Functional evenness (FEve)	A measure of the regularity of species abundances in functional space, calculated as the shortest minimum spanning tree that links all species within a community, and which can be interpreted as the degree of occupation of niches (Villéger et al. 2008).
Functional dispersion (FDis)	FDis is a measure of variability in functional traits in a community (Laliberté and Legendre 2010).
Rao’s quadratic entropy (Rao’s Q)	Rao’s Q calculates the abundance-weighted variance between of species pairs (Schleuter et al. 2010) and is closely related to FDis.
Phylogenetic diversity (PD)	PD represents the total sum of evolutionary history in a community and measures the phylogenetic richness (Prescott et al. 2016a).
Standard effect size of phylogenetic diversity (sesPD)	PD is positively correlated with species richness (Swenson 2014). SesPD is calculated by comparing the PD of null communities of equal species richness, which are created by drawing species at random from the regional species pool. Positive values of sesPD suggest that communities have higher PD values than expected for that given species richness and the opposite is true for negative values.
Mean pairwise distance (MPD)	The average phylogenetic distance between individuals in a community. Higher values suggest that species are distributed across a wide range of clades and low values suggest phylogenetic clustering (Prescott et al. 2016a). MPD is a measure of phylogenetic divergence (Morante-Filho et al. 2018).

Standard effect size for MPD (sesMPD)	MPD corrected for species richness. Positive values of sesMPD are found in communities with greater MPD than expected given the species richness, and vice versa for negative values. sesMPD is a measure of phylogenetic structure (Morante-Filho et al. 2018).
Mean nearest taxon distance (MNTD)	The average phylogenetic distance between an individual and the most closely related (non-conspecific) individual (Morante-Filho et al. 2018). High levels of MNTD suggest that closely related individuals do not co-occur in the community, and low levels suggest they do.
Standard effect size of mean nearest taxon distance (sesMNTD)	MNTD adjusted for species richness. Positive values of sesMNTD are found in communities with greater MNTD than expected given the species richness, and negative values for less than expected.
Evolutionary Distinctiveness (ED)	Measures the amount of unique evolutionary history contributed by a species to a phylogenetic tree. High values of ED are found in species that have no close extant relatives, and species with low values have closely related extant species. Thus, communities with high ED have more evolutionarily unique species (Prescott et al. 2016a).
Evolutionary Distinctiveness Rarity (EDR)	ED adjusted for species rarity. Range size was used as a measure of rarity, meaning species with high EDR has a high importance for the conservation of evolutionary diversity and an elevated extinction risk due to a small range size.

Table 2: FD, PD and ED metrics and their standard error values calculated for Agroforestry and Monoculture.

	Metrics	Agroforestry	Monoculture
Functional Diversity	FD	1.37 ± 0.04	1.37 ± 0.06
	sesFD	-0.04 ± 0.04	0.06 ± 0.05
	FEve	0.78 ± 0.01	0.81 ± 0.01
	FDis	3.32 ± 0.05	3.36 ± 0.07
	RaoQ	0.21 ± 0.01	0.22 ± 0.01
Functional Diversity metrics (excluding rarities)	FD	1.32 ± 0.04	1.33 ± 0.06
	sesFD	-0.07 ± 0.05	0.09 ± 0.07
	FEve	0.77 ± 0.01	0.80 ± 0.01
	FDis	3.45 ± 0.06	3.46 ± 0.08
	RaoQ	0.32 ± 0.01	0.32 ± 0.02
Phylogenetic Diversity	PD	537.37 ± 86.05	520.78 ± 104.16
	SESPD	0.04 ± 0.01	0.34 ± 0.07
	MPD	87.10 ± 13.95	88.00 ± 17.60
	SESMPD	-0.08 ± -0.01	0.16 ± 0.03
	MNTD	59.35 ± 9.50	63.21 ± 12.64
	SESMNTD	-0.10 ± -0.02	0.25 ± 0.05
Evolutionary Distinctiveness	ED	1.43 ± 0.23	1.34 ± 0.27
	EDR	0.003 ± 0.001	0.003 ± 0.001

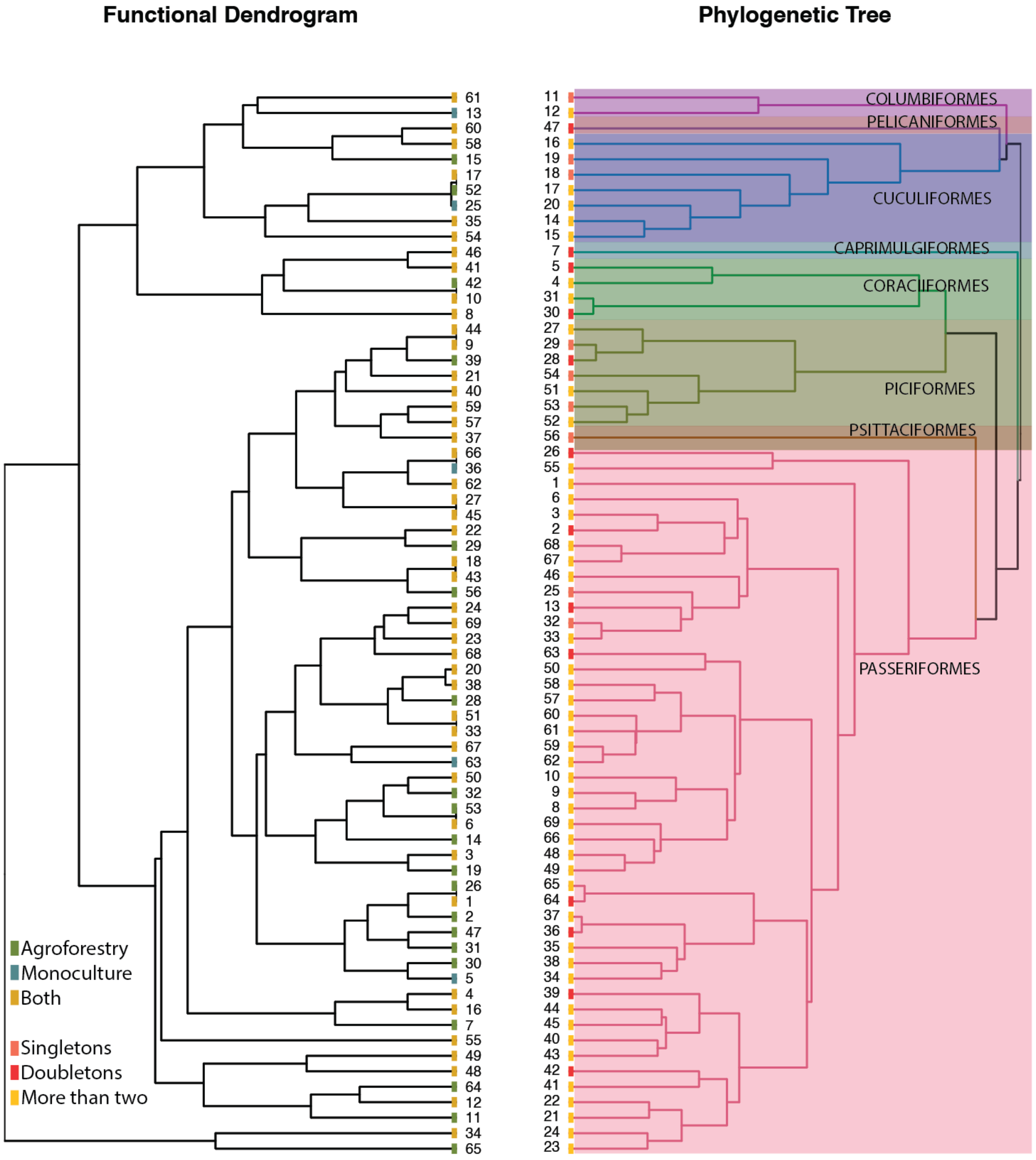

Figure 1: Functional dendrogram and phylogenetic tree for the 69 species observed during the study. The numbers relate to species names given in Table S1.

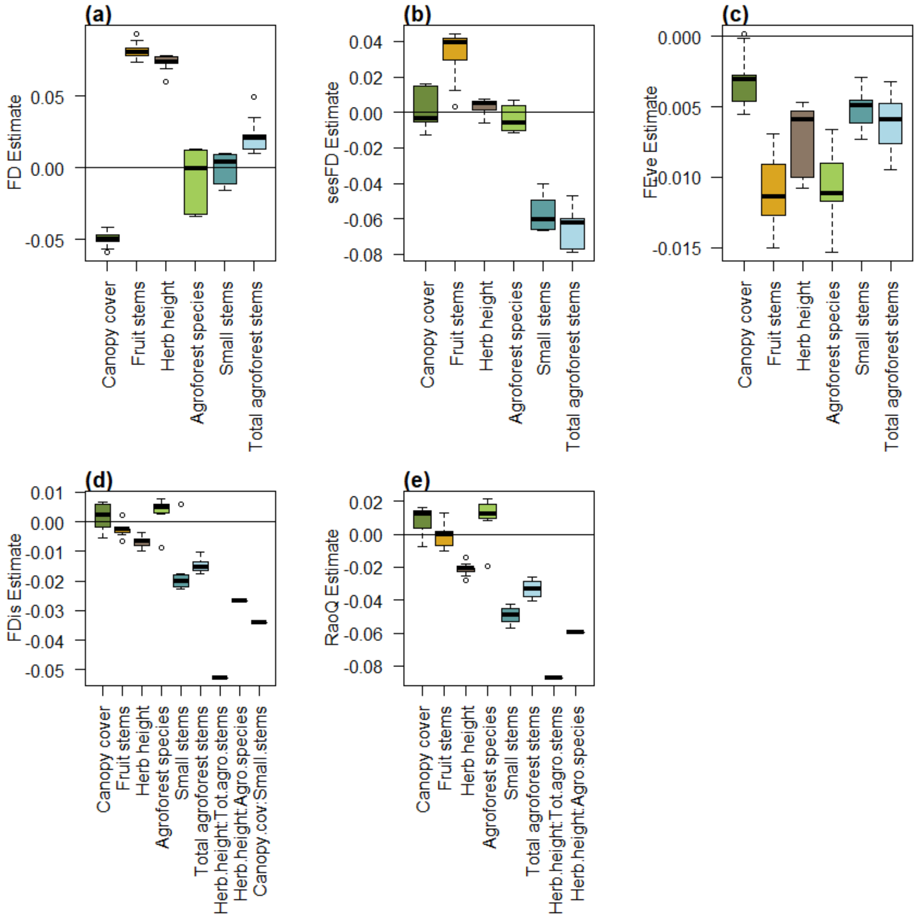

Figure 2: Estimates for FD metrics resulting from the averaged habitat structure models with above 95% cumulative confidence. The bold bars represent median; box bounds, the interquartile range and whiskers extend to 1.5*interquartile range. Outliers are represented by dots.

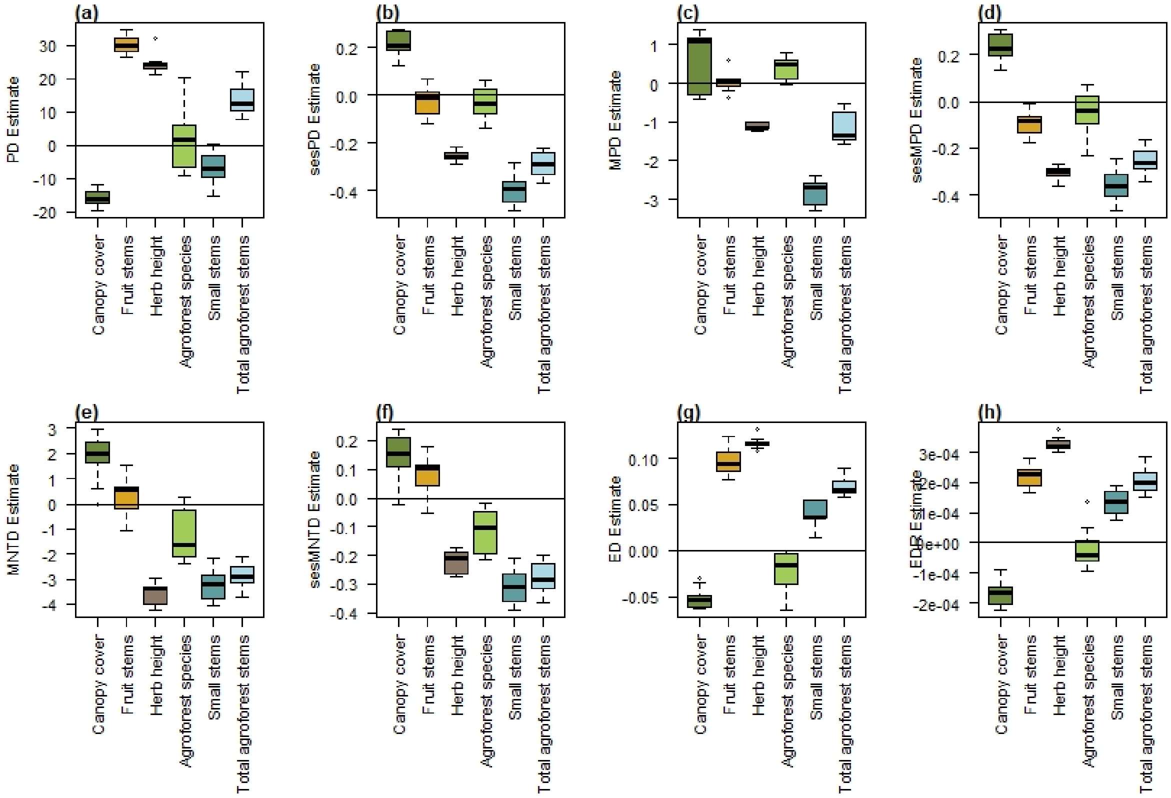

Figure 3: Estimates for the main PD and ED metrics resulting from the averaged habitat structure models with above 95% cumulative confidence. The bold bars represent median; box bounds, the interquartile range and whiskers extend to 1.5*interquartile range. Outliers are represented by dots.

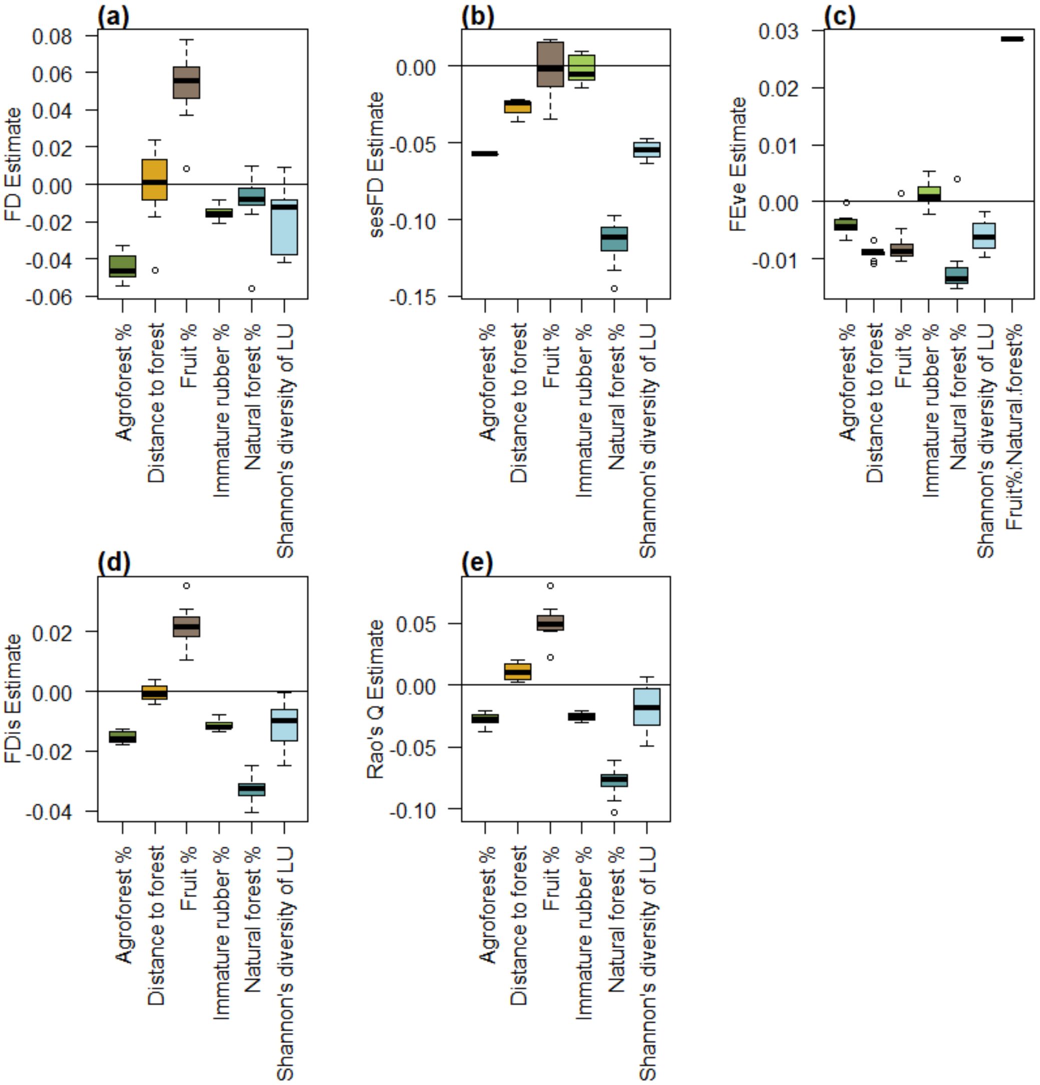

Figure 4: Estimates for the main FD metrics resulting from the averaged landscape composition models. The bold bars represent median; box bounds, the interquartile range and whiskers extend to 1.5*interquartile range. Outliers are represented by dots.

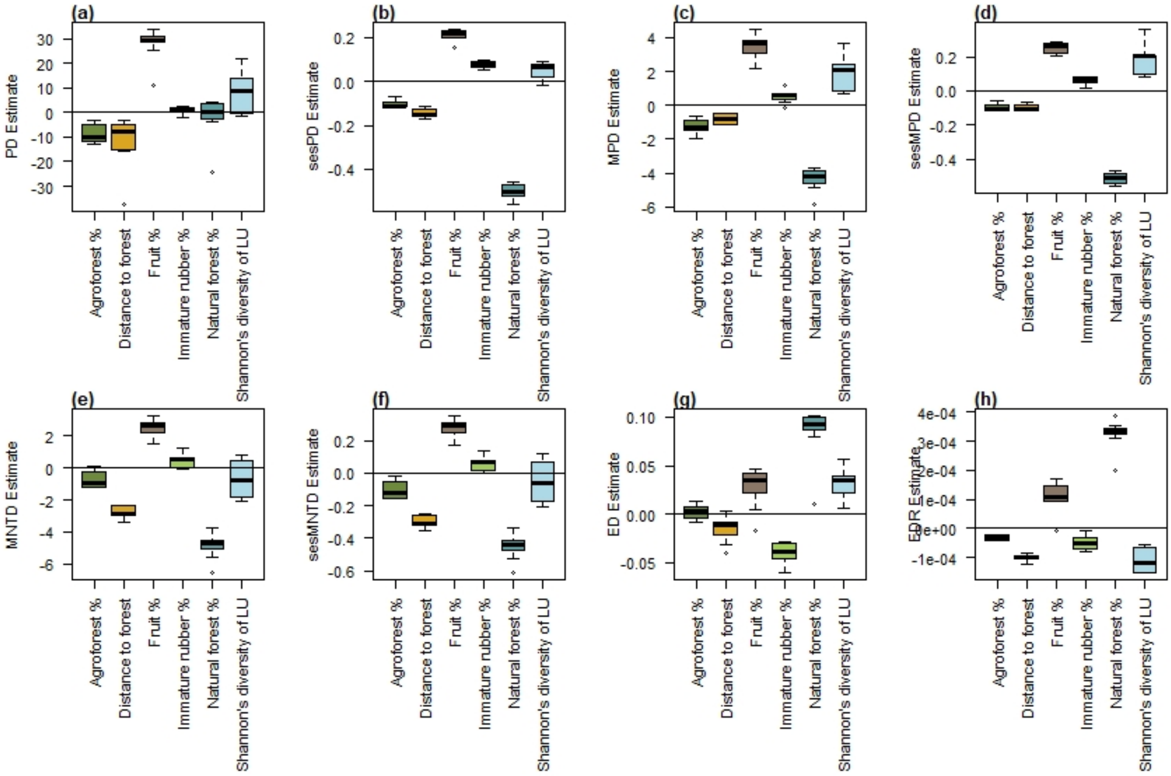

Figure 5: Estimates for the main PD and ED metrics resulting from the averaged landscape composition models. The bold bars represent median; box bounds, the interquartile range and whiskers extend to 1.5*interquartile range. Outliers are represented by dots.