

Land use and elevation interact to shape bird functional and phylogenetic diversity and structure: Implications for designing optimal agriculture landscapes

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Abstract

1. The conversion of rainforests into agriculture resulted in massive changes in species diversity and community structure. Although the conservation of the remaining rainforests is of utmost importance, identifying and creating a biodiversity-friendly agriculture landscape is vital for preserving biodiversity and their functions.
2. Biodiversity studies in agriculture have often been conducted at low elevations. In this study, we compared the functional diversity (FD), phylogenetic diversity (PD) and community structure of birds along an interacting gradient of land use (protected rainforest, reserve buffer and agriculture) and elevation (low, middle and high) in Sri Lanka. Then, we measured the compositional change by identifying how ecological traits (dietary guild, vertical strata, body mass and dispersal ability) and conservation characteristics (forest dependence and threatened status) responded to land use types.
3. Elevation and land use interacted with each other to shape bird FD. Depending on the elevation, FD in agriculture was either higher or similar to forest. However, PD was similar across all elevation and land use types. Bird community structure in forest was functionally and phylogenetically clustered in comparison to agriculture. Insectivorous birds declined from forest to agriculture, and so did understory and middle-storey birds. But frugivorous and canopy birds did not change across land use types, while nectarivores, granivores and carnivores proliferated in agriculture. Forests were dominated by birds with low dispersal abilities, but birds in agriculture had more evenly distributed dispersal abilities. About half of all the individuals in agriculture were composed of forest species, several of which were threatened.
4. *Synthesis and applications.* Most farmers in Sri Lanka practice agriculture on small farms (c. 2 ha) and rely on services (e.g. pest control and pollination) provided by

biodiversity for their livelihoods. Our results underline the important role of these heterogeneous agriculture landscapes in maintaining high functional diversity (FD) and harbouring several threatened species. While FD in agriculture was comparatively high, conservation decisions based on land use alone cannot be reliable, because land use effects were elevation dependent. Thus, priority setting exercises aimed at designing optimal agriculture landscapes should consider landscape features, in combination with elevation, to benefit both people and wildlife outside protected areas.

KEYWORDS

community structure, ecosystem services, environmental filtering, functional diversity, optimal agriculture, phylogenetic diversity

1 | INTRODUCTION

Large areas of tropical rainforests are fast being converted into agriculture landscapes, increasing the risk of species extinctions and the loss of associated ecosystem services (Hughes, 2017). Although the protection of the remaining rainforests is of utmost importance for biological conservation, determining the biodiversity capacity of agriculture and designing optimal agriculture landscapes to boost their adaptability are also a priority (Arroyo-Rodriguez et al., 2020; Garibaldi et al., 2021). High levels of biodiversity in agriculture increase the range of ecological services (Dainese et al., 2019). It is therefore critical to identify, conserve and design functionally diverse agriculture landscapes to improve positive interactions between biodiversity conservation and agricultural production. However, a bias towards estimating species diversity in agriculture at low elevation sites is quite evident (Chapman et al., 2018). Higher elevations harbour many narrow-ranged endemic species that also provide many ecosystem services (Pigot et al., 2016) and are increasingly threatened by expanding agriculture and exotic timber plantations (Goodale et al., 2014). Recent studies showed that the response of ecosystem functions to land use change depends on the elevation (climatic) gradient (Peters et al., 2019; Santillan et al., 2019). Therefore, in this study, we determine the responses of bird functional and phylogenetic diversity (FD and PD) along an interacting gradient of elevation and land use.

There are two well-known patterns that previous studies have already established. First, FD and PD generally decline from forest to agriculture, because the homogeneous nature of agriculture often translates to environmental filtering of a few specific traits and lineages (Cannon et al., 2019), resulting in functionally and phylogenetically redundant species thriving in human-dominated landscapes. Second, FD and PD reduce with increasing elevation in tropical mountains (Dehling et al., 2014; Montano-Centellas et al., 2020), because specialized environments at high elevations with lower oxygen, temperature and biomass filter species with specific traits and lineages (Dehling et al., 2014; Sam et al., 2019). The interaction between these two well-known patterns has, however,

been less studied. Santillan et al. (2019) showed negative effects of forest fragmentation on FD at low elevations, but positive effects at high elevations. The interaction effect suggested that higher elevation habitats could be naturally more ecologically adapted to disturbance. Like fire-related disturbances that maintain community assemblages in savannas, wind- and frost-related disturbances appear to be important in high elevations (Joshi et al., 2020; Werner & Balasubramaniam, 1992). Therefore, in comparison with low elevation communities, many high elevation species may be naturally adapted to some amount of disturbance to forests.

Environmental filtering is expected to be an important process driving species assemblages if species are more functionally or phylogenetically clustered than random communities because specific environments select for certain traits (Webb et al., 2002). On the other hand, competitive exclusion could be the dominant process if species are more functionally or phylogenetically over-dispersed than species from randomly assembled communities because inter-specific competition does not allow species with similar traits (niche use) to co-exist (Webb et al., 2002), given the assumption of niche conservatism (Davies, 2021). In this study, along with FD and PD, we will also examine which process (environmental filtering or competitive exclusion) is important for structuring bird communities across an interacting gradient of land use and elevation.

Sri Lanka is a mountainous biodiversity hotspot with an agricultural countryside that evolved over a millennium and has been maintained with similar practices for more than a century (Goodale et al., 2014; Sreekar, Sam, et al., 2021), much longer than relatively recent agricultural expansion in other tropical regions. In many locations, the value (\$/hectare) of agricultural land may reduce with increasing elevation (Zhang et al., 2018). But in Sri Lanka, agriculture land value remains relatively constant across elevations because higher elevations produce high-value tea and many of country's vegetables. Agriculture lands in Sri Lanka are relatively small (c. 2 ha; FAO, 2018) and often chequered with landscape features like forests associated with temples (sacred groves), large isolated keystone tree species like figs, natural forest strips that act as windbreaks for tea plantations and corridors for wildlife, home gardens with diverse

fruiting and flowering crops, and multiple diverse agriculture crops like rice, tea, coffee and rubber (Goodale et al., 2014).

Many recent studies discussed the importance of designing optimal agricultural landscapes for a robust post-2020 framework to improve biodiversity, climate regulation and livelihoods (Arroyo-Rodríguez et al., 2020; Garibaldi et al., 2021). From our previous study, we already know that bird species richness in agriculture lands of Sri Lanka is similar to forests, and species richness decreases with increasing elevation (Sreekar et al., 2015). In this study, we aim to estimate bird FD and PD and community structure in agriculture lands to understand birds' conservation values and its contribution to ecosystem services, and help conserve and design environmentally friendly agricultural landscapes. Specifically, we examine:

1. Whether elevation and land use interact to drive bird FD and PD, after accounting for variation in species richness (Figure 1). We hypothesized that high elevation communities are less affected by agricultural disturbance because they are regularly disturbed by strong winds and occasional frost (Joshi et al., 2020; Werner & Balasubramaniam, 1992). Therefore, at high elevations, agriculture may be as functionally/phylogenetically diverse as forest, causing a land use–elevation interaction effect.
2. Such, dependent and threatened interactions can also be important for conservation management because it can help predict elevation-dependent disturbance tolerance in bird communities. We hypothesized proportionally fewer forest and threatened bird species in agriculture at lower elevations when compared to higher elevations.
3. Whether ecological processes that structure bird communities differ according to the combination of elevation and land use type. Agriculture communities are homogeneous across elevation

in comparison to forests (Sreekar et al., 2017). Hence, we hypothesized community structure in agriculture to be comparatively clustered and evenly distributed across the entire elevation gradient, while we expected changes in forest (Dehling et al., 2014), again causing an interaction effect (Figure 1).

4. The effect of individual functional traits across these two interacting environment gradients.

Knowing the answers to these questions is crucial for improving agricultural policies, maintaining traditional agricultural practices and increasing ecosystem services performed by some (dietary) groups (e.g. insectivores and frugivores), while mitigating disservices produced by other groups (such as granivores; Horgan & Kudavidanage, 2020).

2 | MATERIALS AND METHODS

2.1 | Study sites

The island nation of Sri Lanka can be biogeographically divided into two main climatic zones, namely the dry zone (<2 m rainfall per year) and the wet zone (>2 m rainfall per year). The wet zone is located in the south-west corner of the country, and all the 34 Sri Lanka endemic birds occur in that region. Therefore, it is the most important region in the country for biological conservation. In this study, we sampled the full elevation (90–2,180 m) and land use (protected rainforest to agriculture) gradients in the wet zone.

We sampled birds in the low elevation (90–799 m) habitats of Sinharaja western sector, middle elevation (800–1,499 m) habitats of Sinharaja eastern sector and high elevation (>1,499 m) habitats of

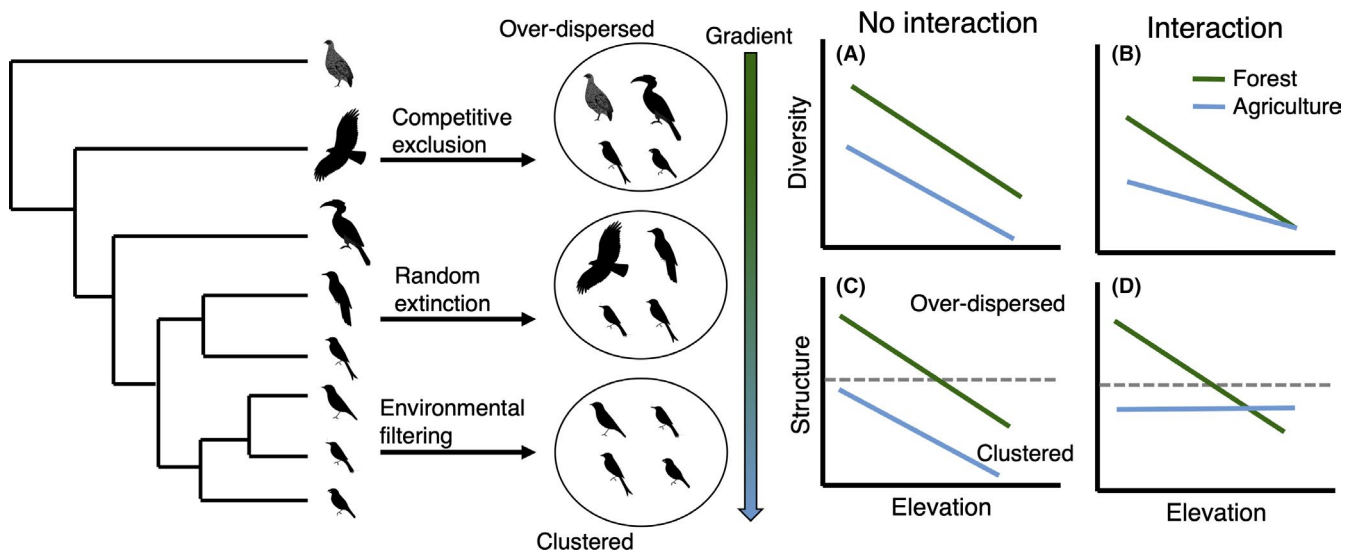


FIGURE 1 A conceptual representation of functional and phylogenetic community structure across gradients of elevation and land use. We illustrate a functional and/or phylogenetic tree and three hypothetical mechanisms driving bird community assembly across a gradient of increasing disturbance and elevation. We predict diversity and community structure patterns in non-interaction (A and C) and interaction scenarios (B and D). See hypotheses in introduction for more information. Bird silhouettes were built upon L. Shyamal's images through Wikimedia Commons (<https://creativecommons.org/licenses/by-sa/3.0/>)

Nuwara Eliya region between December 2006 and December 2007 (twenty-four 2-km transects; see Figure S1). Later, between January 2008 and January 2009, we sampled the full elevation gradient from the Gillimale Forest reserve to Horton Plains reserve (seventeen 1-km transects; Goodale et al., 2014; Figure S1). See Appendix S1 for details on study design.

2.2 | Data collection

Two observers walked all 41 transects at a pace of *c.* 1 km/hr, and each transect was revisited 7.2 ± 4.0 ($M \pm SD$) times across 1 year. Each day the observers conducted one transect in the morning (8:00–10:00) and another in the afternoon (15:00–17:00). The time of day for any transect was rotated throughout the sampling period, so that sampling was balanced between the two time periods. All observed or heard birds were counted and their distance to the transect was noted with a 100 m limit on either side. We then used the distance and bird count measures to estimate species abundance in each transect after accounting for differences in detection, using the distance sampling method (half normal models). See Goodale et al. (2014) for more details. In this study, we followed Clements et al. (2019) taxonomy, and categorized forest and threatened species using Billerman et al. (2020). See Appendix S2 for details on the construction of phylogenetic and functional trees.

2.3 | Data analyses

2.3.1 | Phylogenetic and functional diversity

All analyses in this study were conducted using the statistical software R 3.6.1 (R Core Team, 2019). To determine the changes in phylogenetic diversity and structure across a full gradient of elevation and land use, we calculated Faith's PD and the abundance-weighted mean pairwise phylogenetic distance (MPD), using the functions *pd* and *mpd* functions in the R package *PICANTE* respectively (Kembel et al., 2010). PD is the sum of the total phylogenetic branch length of species within each transect (Faith, 1992). The MPD calculates the sum of all intervening branch lengths between two taxa (pairwise distance) and averages the values of all possible pairs in each transect (Webb et al., 2002). Lower values of MPD indicate species within communities are phylogenetically closely related. In this study, we used quantitative abundance-weighted MPD values instead of qualitative presence-absence MPD values because abundance is more important for ecosystem functioning than mere presence.

We used the same *pd* and *mpd* functions to calculate FD and abundance-weighted mean pairwise functional distance (MFD). These are functional equivalent indices of PD and MPD, and therefore comparable. We used Pearson correlation tests to determine the correlation between PD and FD, and MPD and MFD.

2.3.2 | Null models

Species richness is highly correlated with FD and PD metrics (Cadotte et al., 2019). To account for the influence of species richness on these metrics, we used 'tip-shuffling' null model approach that compared observed values with values from random communities (Webb et al., 2002). We generated 999 null communities by randomly shuffling species on the tips of both phylogenetic and functional trees. Shuffling just the species names retains the structure of these trees (Zhao et al., 2020). We then calculated standardized effect sizes (SES) for metrics by calculating the difference between the observed value and mean value of null communities, and then divided the obtained value by the standard deviation of null communities.

Positive SES values of MPD and MFD indicate that the bird community is phylogenetically and/or functionally over-dispersed, while negative SES values indicate that the community is phylogenetically and/or functionally clustered, relative to random communities. Values between -1.96 and 1.96 indicate that the structure of the observed community is not significantly different from that of random communities (Webb et al., 2002). We used linear models to determine the effects of elevation and land use on PD and FD, and zero-inflated GLMMs to determine the effects on individual traits (see Appendix S3 for details).

3 | RESULTS

A total of 27,234 bird individuals of 125 species were observed in 41 transects along the full elevation gradient (90–2,180 m) and three land use types. All four functional traits (diet type, vertical strata, body mass and hand-wing index) had significant phylogenetic signal ($p < 0.001$), indicating that they were phylogenetically conserved.

3.1 | Effects of elevation and land use on FD and PD

Bird functional and phylogenetic diversity (SES.FD and SES.PD) metrics showed different trends with increasing elevation and disturbance. The SES.FD was affected by the interaction between elevation and land use ($F = 3.78$, $p = 0.012$), but SES.PD was not ($F = 2.47$, $p = 0.065$; Figure 2). In contrast to our expectations, SES.FD and SES.PD in agriculture were either higher than forest or similar to it across elevation gradients (Figure 2).

3.1.1 | Elevation effects

We found that the SES.FD in low elevation forest was lower than middle elevation and high elevation, but middle elevation forest had similar SES.FD as high elevation (Table S1; Figure 2). The SES.FD in buffer and agriculture habitats was similar across elevation gradients

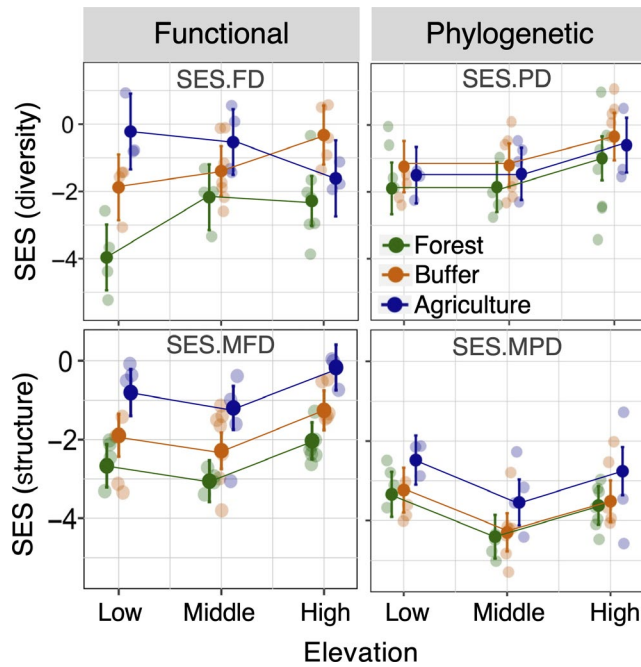


FIGURE 2 Line plots showing variation in bird functional and phylogenetic diversity and structure across an interacting gradient of elevation and land use. Elevation and land use interacted to shape functional diversity (SES.FD), but not phylogenetic diversity (SES.PD). Bird communities were functionally and phylogenetically clustered (negative values of SES.MFD and SES.MPD). Clustering was highest in middle elevation and forest land use. Significant differences can be visually estimated by examining the overlap between mean and 95% confidence intervals. See results and Tables S1–S7 for details

($p > 0.05$; Figure 2). The SES.PD was similar across all elevation gradients ($F = 3.23$; $p = 0.052$; Figure 2).

3.1.2 | Land use effects

We found that at low elevation the SES.FD in forests was lower than buffer and agriculture, and buffer had similar SES.FD as agriculture (Table S2; Figure 2). At middle elevation, the SES.FD in all land use types were similar ($p > 0.05$; Figure 2). At high elevation, the SES.FD in forest was lower than buffer, but agriculture had similar SES.FD as forest and buffer (Table S3; Figure 2). The SES.PD in all land use types were similar ($F = 1.48$, $p = 0.240$).

3.2 | Effects of elevation and land use on community structure

The metrics of functional and phylogenetic structure (SES.MFD and SES.MPD) were similar to each other. We did not find a significant interaction between elevation and land use ($p > 0.05$), suggesting that they independently affected phylogenetic and functional structure. The null modelled values of phylogenetic

community structure (SES.MPD) in all transects except one in agriculture were below -1.96 , indicating that bird communities were significantly clustered. The values of functional community structure (SES.MFD) varied from 0.03 to -3.79 ($M = -1.82$), among which 20 transects (49%) had values below -1.96 , indicating that they were significantly clustered, while the bird communities in the other 21 transects could not be distinguished from random communities.

3.2.1 | Elevation effects

The SES.MFD values in low elevation were similar to middle and high elevations, but SES.MFD in middle elevation was lower (more clustered) than high elevations (Table S4; Figure 2). The SES.MPD values in middle elevation were lower than low and high elevation, but SES.MPD values in low elevation were similar to high elevation (Table S5; Figure 2).

3.2.2 | Land use effects

The SES.MFD in forest was lower than buffer and agriculture, and SES.MFD in buffer was lower than agriculture (Table S6; Figure 2). The SES.MPD in agriculture was higher than forest and buffer, but SES.MPD values in forest were similar to buffer (Table S7; Figure 2).

See Appendix S4 for FD and PD and structure results without accounting for variation in species richness.

3.3 | Effects of elevation and land use on species traits

3.3.1 | Dietary guilds

We used insectivore, frugivore and others as three dietary guilds for analysis. We clumped nectarivore, granivore and carnivore into 'others' guild, because there were few species in the dataset that belonged to these individual dietary categories. We observed a triple interaction between dietary guilds, elevation and land use ($\chi^2 = 18.51$, $p = 0.017$). At low elevation, frugivores had higher abundances in agriculture habitats (Figure 3). Other dietary guilds also had high abundances in low elevation agriculture (Figure 3), primarily driven by nectarivores (specifically purple sunbird; Figure S2). At middle elevation, frugivore abundances were similar in all land use types, and others had higher abundances in agriculture. At high elevation, frugivore abundances were similar between forest and agriculture, but frugivores in buffer habitats had lower abundances than in forest (Figure 3). The abundances of other guilds at high elevation were highest in agriculture, primarily driven by high abundances of granivores (specifically House Sparrow; Figure S2). Insectivore abundances reduced from forest to buffer and agriculture at all elevation types (Figure 3).

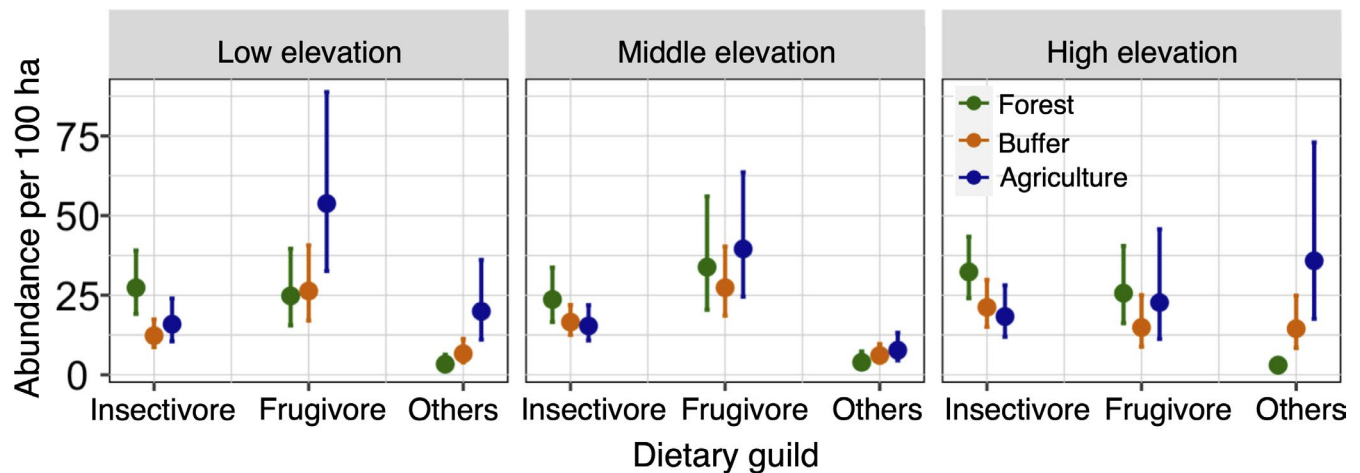
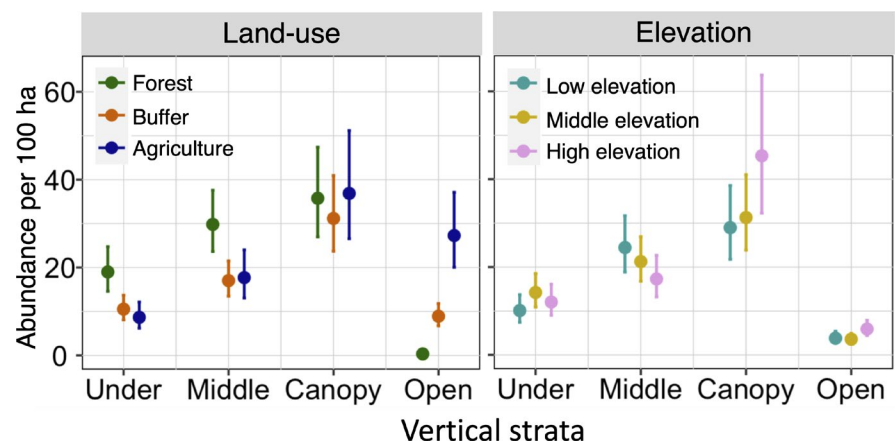


FIGURE 3 Variation in abundances of bird dietary guilds across an interacting gradient of land use and elevation. Dots are average model fits and bars are their 95% confidence intervals

FIGURE 4 Plots showing variation in vertically stratified bird abundances across land use (left) and elevation (right) gradients. Dots are average model fits and bars are their 95% confidence intervals



3.3.2 | Vertical strata

We observed interactions between vertical strata and elevation ($\chi^2 = 18.40$, $p = 0.005$), and vertical strata and land use ($\chi^2 = 380.07$, $p < 0.001$). Canopy birds were the most abundant species in the landscape, across all elevation and land use gradients (Figure 4).

The abundances of understory birds were highest at middle elevation and were higher than low elevation. The abundances of middle-storey birds were highest at low elevation and were higher than high elevation. The abundances of canopy birds were highest at high elevation and were higher than low and middle elevations. The abundances of open landscape birds were also highest at high elevation and were higher than low and middle elevations (Figure 4).

The abundances of understory birds were highest in forests and were higher than buffer and agriculture. Similarly, the abundances of middle-storey birds were highest in forests and were higher than buffer and agriculture. The abundances of canopy birds were similar in all land use types. The abundances of open landscape birds were highest in agriculture, much higher than buffer and forest (Figure 4).

3.3.3 | Body mass

We observed a triple interaction between body mass, elevation and land use ($\chi^2 = 10.79$, $p = 0.029$; Figure 5). At low elevation, body mass did not affect bird abundances in all land use types. But at middle elevations, abundances were higher for smaller birds in all land use types (Figure 5). At high elevation, body mass interacted with land use to affect bird abundances: (a) smaller birds had higher abundances in forests and declined steeply with increasing body mass, (b) bird abundances also declined with increasing body mass in buffer, but less steeply than forests and (c) body mass did not affect bird abundance in agriculture (Figure 5).

3.3.4 | Hand-wing index (HWI)

We observed interactions between HWI and elevation ($\chi^2 = 7.58$, $p = 0.022$), and HWI and land use ($\chi^2 = 8.03$, $p = 0.018$; Figure 6). Birds with lower dispersal abilities (lower HWI) were the most abundant birds in the landscape. Bird abundances did not change with increasing HWI at low elevation, but abundances were higher for birds with

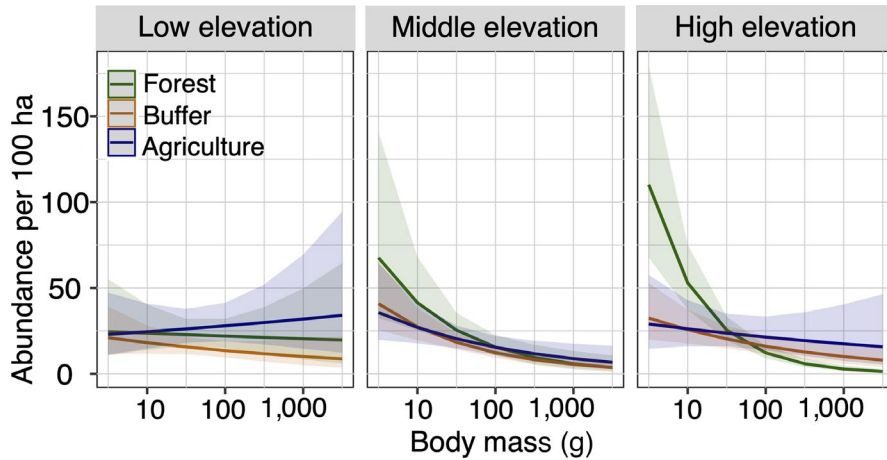


FIGURE 5 Variation in mass–abundance relationships across an interacting gradient of land use and elevation. The relationship becomes steeper with increasing elevation, especially in forests. Lines are average model fits, and the surrounding polygons are their 95% confidence intervals

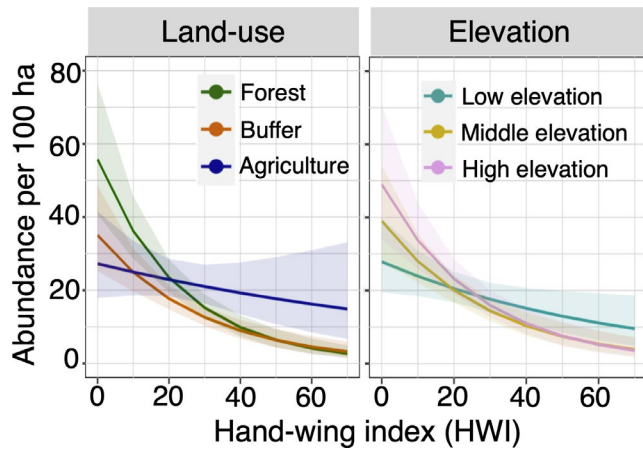


FIGURE 6 Relationship between bird abundance and hand-wing index (HWI) across land use (left) and elevation (right) gradients. The slopes of the relationships were comparatively even in agriculture and at low elevation. Lines are average model fits, and the surrounding polygons are their 95% confidence intervals

lower HWI at middle and high elevations (Figure 6). Bird abundances did not change with increasing HWI in agriculture, but abundances were higher for birds with lower HWI in buffer and forests (Figure 6).

3.4 | Forest and threatened birds across elevation and land use types

Land use and elevation did not interact to shape the richness and abundance of forest birds ($p > 0.05$), but the two variables had separate effects ($p < 0.001$). Agriculture retained c. 58% of the forest species in low and middle elevations, but only c. 44% in the high elevation (Figure 7; Table S8). Forests had a significantly higher proportion of forest species than buffer and agriculture at all elevations (Figure 7; Table S9). About 40% of the bird abundance in agriculture habitats at low and high elevation were forest species, but middle elevation had significant higher percentages of forest bird abundance in agriculture (c. 58%; Figure 7). Like richness, forests had a significantly higher percentage of forest bird abundances in all elevations (Figure 7).

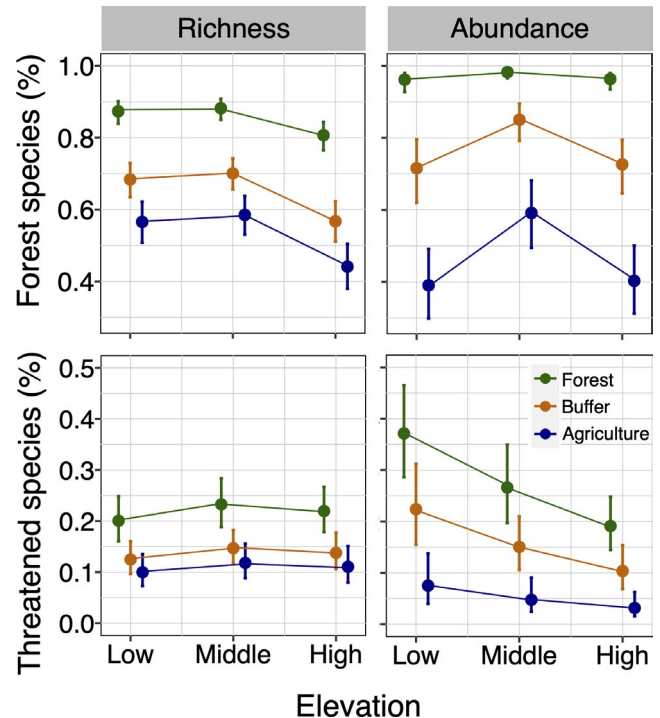


FIGURE 7 Proportion of bird species richness (left) and abundance (right) represented by forest (top) and threatened (bottom) species across an interacting gradient of land use and elevation. Dots are average model fits and bars are their 95% confidence intervals (CIs)

Land use and elevation did not interact to shape the richness and abundance of threatened species ($p > 0.05$). Elevation also did not affect the proportion of threatened species richness in a bird community ($X^2 = 1.41, p = 0.49$). Land use by itself, however, did have significant effects ($X^2 = 26.07, p < 0.001$). Agriculture and buffer had similar proportion of threatened species at all elevations (c. 12.5%), but forests had significantly higher percentages (c. 22%; Figure 7; Table S10). In contrast, the proportion of bird abundance represented by threatened species was affected by both land use and elevation separately ($p < 0.001$). They declined from low to high elevation (Table S11) and from forests to agriculture (Figure 7; Table S12).

4 | DISCUSSION

Although several studies have determined the variation in FD and/or PD and structure across land use or elevation types, few studies have explored the interaction between them. In this study, we showed that depending on the land use type, bird FD in the wet zone of Sri Lanka either increased with elevation or remained the same. In contrast, bird PD did not show any significant interaction effect and remained similar across elevation gradients in all land use types (Figure 2). Importantly, we showed higher FD in agriculture than forest, except for at high elevations where they had similar FD. The low dispersal ability of birds in high elevation areas (Figure 6) hints towards the mechanism behind the interaction effect and highlights the importance of connectivity in agricultural land-management strategies at high elevations. About half of the birds in agriculture were composed of forest species, and c. 10% represent threatened species. Our results emphasize the need to consider elevation along with the structural elements within agriculture for designing highly functional agricultural landscapes (Arroyo-Rodriguez et al., 2020).

4.1 | Functional structure across ecological gradients

Forests filtered understorey, insectivorous birds, and those with low dispersal abilities, but functional structure in agriculture lands was comparatively even (less filtered) across different functional traits (Figures 3, 4, and 6). The agriculture landscape had similar numbers of frugivores and nectarivores as forests, which may help maintain seed dispersal and pollination services (Hanle et al., 2021). This is especially important for the decade of ecosystem restoration (2021–2030), which aims to restore native habitats even in production landscapes for higher food security, ecosystem services and biodiversity conservation (Garibaldi et al., 2021). But lower number of insectivores suggest lower pest control services (Nyffeler et al., 2018). Lower number of insectivores can also be directly related to lower insect biomass in agriculture, when compared to rainforests. Further experimental studies should be conducted to better understand the pest control services, especially in understudied and biodiversity-rich regions like Sri Lanka.

The influence of environmental filtering processes on bird functional and phylogenetic structure was lowest at low and high elevations, and highest at middle elevation (Jarzyna et al., 2021). Middle elevation filtered (reduced abundances) species with distinctive functional traits like large frugivores (e.g. Sri Lanka grey hornbill, Sri Lanka myna) and large insectivores (e.g. red-faced malkoha, Sri Lanka Drongo) from low elevation. In contrast, lower environmental filtering at high elevations could be because of higher rate of species replacement (turnover), along with loss from low and middle elevations. Although high elevations supported fewer species, most functional guilds were present, including large frugivores (Sri Lanka wood pigeon) and insectivores (Sri Lanka whistling thrush). Our results are

similar to Pigot et al. (2016), which showed 80% similarity in trait space between low and high elevations.

4.2 | Management implications

The findings of this study indicate that the wet zone of Sri Lanka might be an appropriate setting for wildlife-friendly agricultural practices, which in turn produce ecosystem services that are important for small-holder farmers (Garibaldi et al., 2021). For Sri Lanka, these landscape elements can include forest fragments near temples, home gardens (Hanle et al., 2021) and isolated fig trees (Peabotuwage et al., 2019). We found that birds in agriculture lands have high FD (Figure 3), albeit with changes in functional composition and the loss of some threatened endemic species (Sreekar, Sam, et al., 2021; Sreekar et al., 2015). Agriculture still harboured 13 of the 18 threatened species (72%) recorded in the study, of which Alexandrine parakeet, dull-blue flycatcher, Legge's Flowerpecker, orange-billed babbler, spot-winged thrush, Sri Lanka myna and yellow-eared bulbul were regularly recorded in them. Disproportionately diverse bird functional traits in agriculture reflect a broad range of ecosystem services like seed dispersal, invertebrate and vertebrate pest reduction, carrion removal and pollination, which collectively improve agriculture production and livelihoods (Dainese et al., 2019). Although agriculture had lower insectivore richness and abundance, some insectivores were still found there, which are undoubtedly important for pest control (Nyffeler et al., 2018). Pollinators such as the specialist sunbirds were abundant in agriculture and are known to increase the pollination of some plants of commercial importance in Asia (Corlett, 2004; Sun et al., 2017). Frugivores were also abundant in agricultural lands, especially in the lowlands (Figure 3; Figure S2), and they can be important for regeneration and reforestation of small patches in buffer and riparian areas that can retain connectivity with larger, protected areas of natural forest (Pejchar et al., 2008). However, it should be noted that high FD also includes traits that are associated with ecosystem disservices. For example, some carnivores in agriculture such as corvids (e.g. Andren, 1992) and coucals (e.g. Li et al., 2019) may cause adverse effects on other bird species through nest predation. More importantly to farmers, some granivores can reduce yield. While parakeets (Kotagama, 1982) and munias can be considerable pests on rice at low elevations, the highest abundances of granivores in agricultural habitats within our study area were at high elevations (Figure S2), primarily dominated by a single species, the house sparrow. Therefore, future studies should carefully study the ecosystem disservices of this species at high elevations, as this species can also provide crucial ecosystem services like pest control during the breeding season when it feeds its young with insects (Billerman et al., 2020). For government agencies, then, the objectives are both to make management decisions and to advise farmers for mitigating yield losses without diminishing ecosystem services (Horgan & Kudavidanage, 2020).

Our results also underline the importance of elevation-dependent effects, as we showed comparatively lower FD in higher

elevation agriculture (Figure 2), which can be attributed to lower dispersal ability in that gradient (Figure 6). Hence, connectivity should be a priority when designing optimal agricultural landscapes in high elevations. This result points to the use of windbreaks that retain or restore natural vegetation and can act as corridors for wildlife in agriculture and help reduce soil erosion and wind damage in agriculture lands (Sreekar et al., 2013). In conclusion, keystone landscape structures like windbreaks, sacred groves and single trees within Sri Lankan agriculture landscape should be a conservation priority, and conversion into monoculture landscape should be regulated, like elsewhere in the tropics (Hughes, 2017).

4.3 | Study limitations

Many studies in the tropics have shown collapses in FD from forests to agriculture (Bregman et al., 2016; Cannon et al., 2019; Edwards et al., 2014). Contrasting results in our study could be because of two main reasons: (a) It should be noted that our agriculture transects were in close proximity to forest or buffer land use types. Therefore, some amount of spillover effect is expected, and results may be different when comparing with agriculture sites away from forests (>5 km). Indeed, wildlife-friendly agricultural practices may be particularly effective in areas close to the forest (Cannon et al., 2019; Gilroy et al., 2014). (b) The evolutionary history of the Western Ghats–Sri Lanka biodiversity hotspot may also play an important role in such assemblages because many forest bird species in this hotspot are known to show some degree of tolerance towards agriculture (Sreekar et al., 2013, 2015). Therefore, along with landscape elements in Sri Lanka agriculture, biogeography and study design may have also played a role to increase FD and structure in agriculture land use. We highlight the need of additional studies in landscapes with small-scale agriculture (<2 ha) to better understand the design of optimal agricultural landscapes that can effectively conserve biodiversity and their functions.

5 | CONCLUSIONS

The four important findings from our study are as follows: (a) changes in bird FD across land use types are dependent on the elevation gradient, (b) higher functional clustering of communities at middle elevation, and not at high elevation, (c) higher FD and lower clustering of communities in agriculture lands, and not in rainforests and (d) about 50% of birds in the Sri Lankan agriculture landscapes we studied are composed of forest species, which includes several threatened species. Therefore, priority setting exercises aimed at designing optimal agriculture landscapes should consider elevation-dependent effects to benefit both farmers and biodiversity. Although it may not be possible for agriculture landscapes to achieve the compositional similarity of natural habitats, we show that at least similar FD is achievable and could be set in the future biodiversity targets. Given that FD indices largely obscure the responses of separate traits, we propose

that FD analysis should be supported by separate trait analysis, and by keeping specific ecosystem services and disservices (if any) in perspective, to better understand land use change implications on ecosystem resilience (Bregman et al., 2016).

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AUTHORS' CONTRIBUTIONS

R.S., K.S., J.L., S.D. and E.G. designed the study; E.G., U.G. and S.K. acquired the data; R.S. and X.S. analysed the data; R.S. led the writing of the article and all the authors revised it critically and approved for publication.

DATA AVAILABILITY STATEMENT

Raw data are available for download from Dryad Digital Repository <https://doi.org/10.5061/dryad.jwstqjq8p> (Sreekar, Si, et al., 2021).

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SUPPORTING INFORMATION

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