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The value of shifting cultivation for biodiversity in Northeast India

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Abstract

Aim: Shifting cultivation is a widespread land-use in many tropical countries that also harbours significant levels of biodiversity. Increasing frequency of cultivation cycles and expansion into old-growth forests have intensified the impacts of shifting cultivation on biodiversity and carbon sequestration. We assessed how bird diversity responds to shifting cultivation and the potential for co-benefits for both biodiversity and carbon in such landscapes to inform carbon-based payments for ecosystem service (PES) schemes.

Location: Nagaland, Northeast India.

Methods: We surveyed above-ground carbon stocks and bird communities across various stages of a shifting cultivation system and old-growth forest using composite carbon sampling plots and repeated point counts directly overlaying the carbon plots in both summer and winter. We assessed species diversity using species accumulation and rarefaction curves based on Hill numbers. We fitted a linear mixed-effect model to assess the relationship between species richness and fallow age. We also examined possible co-benefits between carbon and biodiversity from fallow regeneration in terms of relative community similarity to old-growth forest across carbon stocks.

Results: Farmland and secondary forests regenerating on fallowed land had similar bird species richness to old-growth forests in summer and relatively higher species richness in winter. Within regenerating fallows, we did not find any strong evidence that fallow age influenced bird species richness. Bird community resemblance to old-growth forest increased with secondary forest maturity, correlating also with carbon stocks in summer. However, bird community assemblage did not show a strong association with habitat types and carbon stocks during winter.

Main conclusions: This study underscores the important role of traditional non-intensive shifting cultivation in providing refuges for biodiversity within heterogeneous habitat mosaics. Effectively managing these landscapes is crucial for both biodiversity conservation and carbon sequestration in the subtropics.

KEYWORDS

bird diversity, carbon-biodiversity co-benefits, community composition, payment for ecosystem services (PES), species accumulation, swidden cultivation

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1 | INTRODUCTION

Shifting cultivation is an important land-use system in 64 tropical and subtropical countries (Li et al., 2014; van Vliet et al., 2012), spanning 280 million hectares worldwide (Heinimann et al., 2017). It is a traditional farming method that typically involves cycles of burning and clearing forests (primary or secondary), cropping for a short time, and subsequent abandonment of the site for vegetation regeneration (Ramakrishnan, 2007). Farmers grow up to 60 crops in a mixed cropping system in shifting cultivation (Nakro, 2011). The number and arrangements of farmland, successional stages of herbaceous and woody fallows, and old-growth forests and remnant trees or forest patches generate a highly complex mosaic landscape in this system (Padoch & Pinedo-Vasquez, 2010). As local human populations and thus food demand has expanded in these areas, there has been an increase in the frequency of shifting cultivation cycles of fallow clearing and cropping (i.e., shortening rotation time) likely impacting biodiversity and carbon stocks in such landscapes (Grogan et al., 2012). However, the understanding of biodiversity response to shifting cultivation with the changing patterns of fallow cycles is still limited (Mertz et al., 2021). Therefore, it is crucial to (a) assess the impact of this cultivation system on biodiversity and (b) formulate strategies for protecting biodiversity in such landscapes.

Species richness is typically lower in forests recovering from shifting cultivation than old-growth forests (review of 24 studies; Scales & Marsden, 2008), but not all taxa show consistent responses. Bird species richness, for example, follows this pattern in the Asia-Pacific region (Raman et al., 1998; Thiollay, 1995; Zhijun & Young, 2003) and Amazon (Andrade & Rubio-Torgler, 1994; Barlow et al., 2007; Borges, 2007), yet avian diversity was higher in recovering secondary forest than in primary forest in Costa Rica (Blake & Loiselle, 2001) and Indonesia (Jones et al., 2003) and similar in Costa Rica (Kormann et al., 2018). This inconsistency could arise from differences in landscape history, such as historical land-use change or cultivation intensity, or alternatively from differences in research methods, for example accounting for imperfect detection which can bias species richness estimates, especially in more diverse habitats (Mackenzie, 2005). Moreover, land-use change can alter community composition by benefiting generalist and wide-ranged species while reducing the populations of forest specialist and endemic bird species (Shahabuddin et al., 2021).

Our understanding of biodiversity responses across the entire cycle of shifting cultivation, i.e., from farmland to regenerating fallows and old-growth forests, is also limited (but see Raman et al., 1998). Determining the optimal strategy for biodiversity conservation in shifting cultivation landscapes depends on the rate of biodiversity recovery as secondary forest ages. Meta-analysis suggests that tropical secondary forests take at least 48 years to reach 80% of the species richness of old-growth forest, but with variation across taxa and locations (Norgrove & Beck, 2016). This average recovery time is much longer than the typical shifting cultivation cycle, which traditionally is around 20–30 years in most regions (Spencer, 1966) but has frequently been reduced to <5 years

(6–27 years in Nagaland; Borah et al., 2018) due to increasing human population densities and associated demand for agricultural land (Ramakrishnan & Patnaik, 1992; Schmidt-Vogt et al., 2009; Thong et al., 2018).

Carbon-based payments for ecosystem services (PES) schemes, including the Reducing Emissions from Deforestation and Forest Degradation (REDD+) program initiated by United Nations Framework Convention on Climate Change (UNFCCC), present an opportunity to protect old-growth and secondary forests from further clearing in shifting cultivation landscapes (Borah et al., 2018). These interventions can also potentially provide co-benefits for biodiversity by protecting the forest habitats to reduce carbon emissions (Gilroy et al., 2014; Matos et al., 2020). Possible biodiversity co-benefits from PES schemes are especially important given the limited direct funding available for biodiversity conservation (Waldron et al., 2017). PES schemes can potentially help to protect old-growth forest from conversion to shifting cultivation and can also promote permanent abandonment of older fallows to maximize carbon sequestration via recovery of secondary forest. Previous studies suggest that sparing old-growth forests from deforestation and intensifying cropping in the remaining area of shifting cultivation under REDD+ can maximize landscape-level carbon stocks while maintaining food production, and that in areas lacking old-growth forest, substantial carbon stocks can be stored by sparing old fallows for permanent forest regeneration (Borah et al., 2018).

Evidence of a positive relationship between carbon stocks and biodiversity across various taxa, including plants (Capellesso et al., 2021; Matos et al., 2020), dung beetles (Gilroy et al., 2014), birds (Gilroy et al., 2014), and amphibians (Basham et al., 2016), suggest a strong potential for PES schemes to provide co-benefits for biodiversity. However, the optimal strategy for conserving biodiversity will depend on whether priority species respond to the shifting cultivation cycle in a similar manner to the broader biodiversity measures assessed by previous work (e.g., Raman et al., 1998), and on the precise rate and pattern of biodiversity recovery as secondary forest regenerates (Prateep & Wangpakapattana Wong, 2017). For instance, forest-dependent priority species will likely respond positively to management focusing on conserving old-growth forests, whereas other species can benefit from sustainable management of shifting cultivation in a heterogeneous landscape.

Here, we assess bird species diversity and community composition recovery across fallow ages and the alignment of above-ground carbon and bird diversity co-benefits in a shifting cultivation-dominated landscape of Nagaland, Northeast India. Nagaland is of critical importance for global biodiversity conservation (Myers et al., 2000) and provides a strong potential for biodiversity co-benefits while mitigating climate change with a high emission mitigation potential under PES, as shown in a previous study (Murthy et al., 2013). Birds are important pollinators (Jing et al., 2015), predators, and seed dispersers (Sekercioglu, 2012), and thus are key indicators of ecosystem resilience to land-use change (Barlow et al., 2007), making them ideal to assess diversity recovery following shifting cultivation and the alignment of carbon-biodiversity co-benefits.

2 | METHODS

2.1 | Study area

We assessed carbon stocks and bird communities in three districts (Kiphire, Phek, and Kohima) in Nagaland, Northeast India across an altitudinal range of 1487–2652 m asl (see Appendix S1: Table S1 for plot details). These landscapes are within the Indo-Burma global biodiversity hotspot and specifically are part of the 'Fakim Wildlife Sanctuary and Saramati area' Important Bird Area (#IN421 Birdlife International, 2022). The major forest types of the sampling sites were subtropical broad-leaved wet hill forests (500–1800 m), subtropical pine forests (1000–1500 m), and montane wet temperate forests (>2000 m) (Champion & Seth, 1968). Annual rainfall varies from 1800 to 2500 mm (Statistical Handbook of Nagaland, 2013).

Shifting cultivation, locally referred to as '*jhum*', is a dominant cultivation system in Northeast India, covering an area of 19,820 km² and providing subsistence for about 443,336 families across Northeast India (Tiwari, 2007). Although the fundamental cultivation process is similar, shifting cultivation system differs across tribes in Northeast India in terms of land-tenure system, and crop and fallow management practices (Krishna, 2020). Across villages, farm plot sizes vary depending on the land-tenure system (Krug et al., 2013). Crops grown, cropping patterns, length of fallow cycles, and fallow management practices also vary across tribes (Bhuyan, 2019).

Shifting cultivation in Northeast India typically involves cycles of burning and clearing forests (primary or secondary), cropping for a short time and subsequent temporary abandonment of the site for vegetation regeneration (Ramakrishnan, 2007). Farmers start clearing land during November–December (Maikhuri & Gangwar, 1993). They usually prefer clearing secondary forests over primary forests as it involves less labour, easier burning of wood logs, and lower concentrations of allelochemicals in the soil (Singh, 2009). The clearing pattern varies depending on elevation and availability of soil nutrients (Ramakrishnan & Patnaik, 1992). At low elevation (100–1500 m asl), forest is clear cut and burnt to grow rice. However, at higher elevation (>1500 m asl), farmers generally retain the big trees in relatively less fertile site to facilitate regeneration (Mishra & Ramakrishnan, 1983).

Sowing typically takes place in March–April in Northeast India. Upland rice (*Oryza sativa*) and maize (*Zea mays*) seeds are sowed at regular intervals, whereas perennial crops such as ginger (*Zingiber officinale*), Colocasia (*Colocasia esculenta*), tapioca (*Manihot esculenta*), and castor (*Ricinus communis*) are sown intermittently throughout the growing season (Toky & Ramakrishnan, 1982) (See Appendix S1: Text S1 for a detailed list of crops grown in shifting cultivation landscapes in Northeast India). Cropping in Northeast India is predominantly done for 1 year in a cultivation cycle, rarely up to 3 years. Similarly, fallow period ranges from 6 to 27 years (Borah et al., 2018). Harvesting continues throughout the year as crops are sown at different times in a mixed-cropping system. The main crop (e.g., rice or maize) is usually harvested in September–October (Bhuyan, 2019).

2.2 | Sampling framework

2.2.1 | Locations

We assessed carbon stocks and bird communities across three main habitat types during January–May 2016: old-growth forest, secondary forests that regenerates on fallowed land (3–27 years [12.2 ± 6.9 (mean \pm SD)] after plot abandonment), and farmland (plots currently under cultivation, usually cultivated for 1 or 2 years and then left fallow to regenerate). For analysis, we categorized the regenerating secondary forests to very young fallow [1–6 years], young secondary fallow [7–14 years], and advanced fallow [15–29 years]. These were fallows at various successional stages and part of an active shifting cultivation cycle (Figure 1, Appendix S1: Text S2).

We selected thirty-six 400 m \times 400 m sampling squares across the three habitats in each of the three landscapes (15, 12 and nine squares in Kiphire, Phek, and Kohima, respectively; Appendix S1: Table S1). The sampling squares were placed at least 300 m apart between different habitats and 400 m apart within the same habitats. We took careful measures to ensure that the sampling points across habitats and the three landscapes were representative of the wider landscape. The sampling points in each habitat category fall across the full altitudinal range spanned by other habitats (Appendix S1: Table S1). We also chose sampling squares across similar topography (soil type, slope, and elevation) and vegetation types to account for potential confounding variables in the three landscapes.

2.2.2 | Birds

Within each square, three point-count stations were established, spaced 200 m apart from each other (a total of 108 point-count stations across three landscapes; Appendix S1: Figure S1). We sampled birds using repeat-visit point counts at each station between 04:45 and 12:30 avoiding sampling in rain or strong winds. We did so in the summer (April–May) breeding season and in winter (January–February) when Palearctic migrant bird species frequent the region. At each station, four point counts of 10 min duration were conducted on consecutive days. However, we were only able to make two visits during summer at nine of our point counts in Kohima landscape due to the early onset of the rainy season and associated flooding. Additionally, we were not able to conduct any point count survey in Kiphire landscape in winter season owing to a civil unrest. This resulted in a total of 414 point counts (108 point count stations) in summer and 252 counts (63 point count stations) in winter.

Any bird seen or heard during the point count duration was recorded with care taken to avoid double counting of the same individuals. To allow for interspecific variation in detection, we estimated different distance categories from the centre of the station as A = 0–25 m, B = 25–50 m, C = 50–100 m, and D = >100 m. At every point count station across different habitats, we recorded all species



FIGURE 1 Schematic representation of successional stages in regenerating secondary forests with farmland (a), 5 years old (b), 10 years old (c), and 20 years old (d) fallows within a shifting cultivation cycle and an adjacent old-growth forest (e) in Nagaland, Northeast India

detected within these distance categories. However, for analysis we chose a 50 m radius to avoid bias in detection across different habitats. Similar point count radii have been used in studies conducted in both primary and secondary forests (Bicknell et al., 2015; Gilroy et al., 2014; Socolar et al., 2019). The entire duration of each point count was recorded with a sound recorder (Olympus LS11) to allow unknown vocalizations to be subsequently identified using online reference material (xeno-canto.org) and assistance from regional experts. We randomized the sampling order of the plots to reduce bias due to survey time, while raptors and birds flying over the plots were excluded from the analysis. Nomenclature followed (Jetz et al., 2014) which was compiled from Birdlife International world list (version 3), Handbook of the Birds of the World (Del Hoyo et al., 1992) and IOC world list v2.7.

2.2.3 | Carbon

We sampled aboveground carbon stocks within 10×30 m sampling plots ($n = 108$; 3.24 ha sampled in total) that were directly overlaying with the point-count stations. In all three landscapes, to ensure unbiased selection of plots, we walked 100 m perpendicular (North) from the boundary between two distinct habitats into the focal habitat type. The resultant end point was used as the first corner of the 10 m×30 m carbon-sampling plot and as the centre of the point

count station for sampling birds. The second point for the carbon-sampling plot was located 30 m to the left (i.e., roughly 30 m parallel to the habitat edge). The other two axes of the rectangular plot were parallel to these two randomly selected points. We followed this methodology consistently for all plots. However, due to the small sizes of the shifting cultivation sites, 5 of the 36 sampling squares (four squares in Phek and one square in Kohima landscapes) also contained two different habitat types. We ensured that each of the three sampling plots within each square consisted of only one habitat type (Appendix S1: Figure S1). Within each sampling plot, we measured aboveground living biomass (trees and lianas) and dead biomass (deadwood and leaf litter) using a composite plot design and converted these biomass estimates to carbon stocks. For the detailed methods and estimation of carbon stocks, see Borah et al. (2018).

2.3 | Estimating species diversity across habitats

To estimate how representative the sites were of the local species pool, we calculated the Chao 2 estimator of species richness (Chao & Chiu, 2016) for each habitat type, i.e., farmland, very young fallow [1–6 years], young fallow [7–14 years], advanced fallow [15–29 years], and old-growth forest using the ‘SpadeR’ package in R (Chao et al., 2016). We also constructed species accumulation

curves using the 'vegan' package in R (Oksanen et al., 2007) to assess species diversity across the different habitat types. We built these separately for summer and winter seasons.

In addition, we analysed species diversity across the different habitat types by using rarefaction and extrapolation curves with Hill numbers as diversity indices (Chao et al., 2014). We computed the sample-based rarefaction/extrapolations based on presence-absence data and examined the Hill numbers of order 0, 1, and 2 (Species richness, Shannon's index and Simpson's index, respectively) using the 'iNEXT' package (Hsieh et al., 2016). Rarefaction was estimated as the mean of 50 replicate bootstrapping runs to estimate 95% confidence intervals.

We then fitted a linear mixed-effect regression (Lmer) model using the lme4 package (Bates et al., 2015) to examine differences in bird species richness across fallow age in regenerating secondary forests. We included age and elevation and an interaction term between age and elevation as fixed effects and 'square' nested within landscapes as random intercept in the model to control for multiple sites within each square in each landscape. 'Elevation' in the model was scaled by subtracting the mean and dividing by the standard deviation to facilitate model interpretation (Gelman & Hill, 2006). We conducted AICc-based multi-model inference using the function 'dredge' in the 'MuMIn' package in R (Barton & Barton, 2015) to run a complete set of models with all possible combinations of the fixed effects including their interaction terms. The function 'r.squared' in the same package was used to calculate marginal and conditional r-squared values for each model, which showed the percentage of variation explained by the fixed and random effects respectively. We used an information theoretical approach based on Akaike Information Criterion corrected for small sample sizes (AICc) for model selection. The model with the lowest AICc value was chosen as the best-fit model (Burnham & Anderson, 2002).

2.4 | Bird community composition across habitats

We evaluated community composition across the five habitat types using the raw data. We did so by calculating Bray–Curtis similarity indices for the presence-absence species matrix and using nonmetric multidimensional scaling (NMDS) (Legendre & Gallagher, 2001). To test for significant differences between habitat types, we employed multivariate analysis of variance via the ADONIS function (Anderson, 2001) at 1000 permutations. We then applied 'pairwiseAdonis' function to make multilevel pairwise comparison in community composition across habitat types and seasons.

2.5 | Above-ground carbon-bird diversity co-benefits

To investigate the correlation of above-ground carbon stock and bird diversity at point level, we assessed community similarity to

old-growth forest in relation to carbon stocks based on raw data for each corresponding habitat for both summer (April–May) and winter (January–February). We calculated community similarity as Bray–Curtis similarity index using the 'vegan' package during summer and winter across the five habitat types (farmland, very young fallow, young fallow, advanced fallow, and old-growth forest) (Chao, 2005). We then calculated differences in the mean pairwise similarity of each habitat types relative to old-growth forest for each posterior sample and inferred significant differences between habitats if the resulting 95% BCI excluded zero. We did this separately for summer and winter surveys.

3 | RESULTS

We made a total of 7790 detections of 277 species across all habitats representing 45 families (255 and 189 species in summer and winter, respectively; Appendix S1: Table S2). Among these, three species were Vulnerable (*Tragopan blythii*, *Paradoxornis flavirostris*, *Sitta formosa*), five were Near threatened (*Garrulax nuchalis*, *Psittacula finschii*, *Spelaeornis chocolatinus*, *Spelaeornis caudatus*, *Luscinia peccardens*) and the rest were Least Concern in the global IUCN red list of threatened species (BirdLife International, 2020).

3.1 | Species diversity across habitats

Our results showed significant variation in observed point-level species richness between young fallow (7–14 years) and old-growth forest in summer and between very young fallow (1–6 years) and old-growth forest in winter (Figure 2). Mean point-level species richness at farmland, very young fallow, young fallow, advanced fallow, and old-growth forests was 51.8%, 28.9%, 112.8%, 56.5%, and 57.6% higher in summer compared to winter. (Figure 2b). The Chao 2 estimator suggested that the number of species estimated for each habitat in summer and winter was, on average, 23.62% and 39.93% larger than the number of species observed in summer and winter, respectively (Appendix S1: Table S3, Figures S3 and S4). Species accumulation curves show similar levels of species richness in farmland, very young, young, and advanced fallows compared to old-growth forests in summer (Appendix S1: Figure S2). However, species richness was higher in young fallow and very young fallow compared to old-growth forest in the summer and winter, respectively (Figure 2a,b). However, sample-based rarefaction and extrapolation curves showed consistently increasing bird species diversity (Shannon and Simpson diversity) as regenerating secondary forest matured from farmland to advanced fallows, with old-growth forest retaining highest level of bird diversity in both summer (Figure 3c,e) and winter (Figure 3d,f).

The best-fit model for species richness included elevation as a fixed effect, with higher species richness with increasing fallow age (coefficient estimates \pm SD, 2.65 ± 1.30 ; marginal $R^2 = .09$,

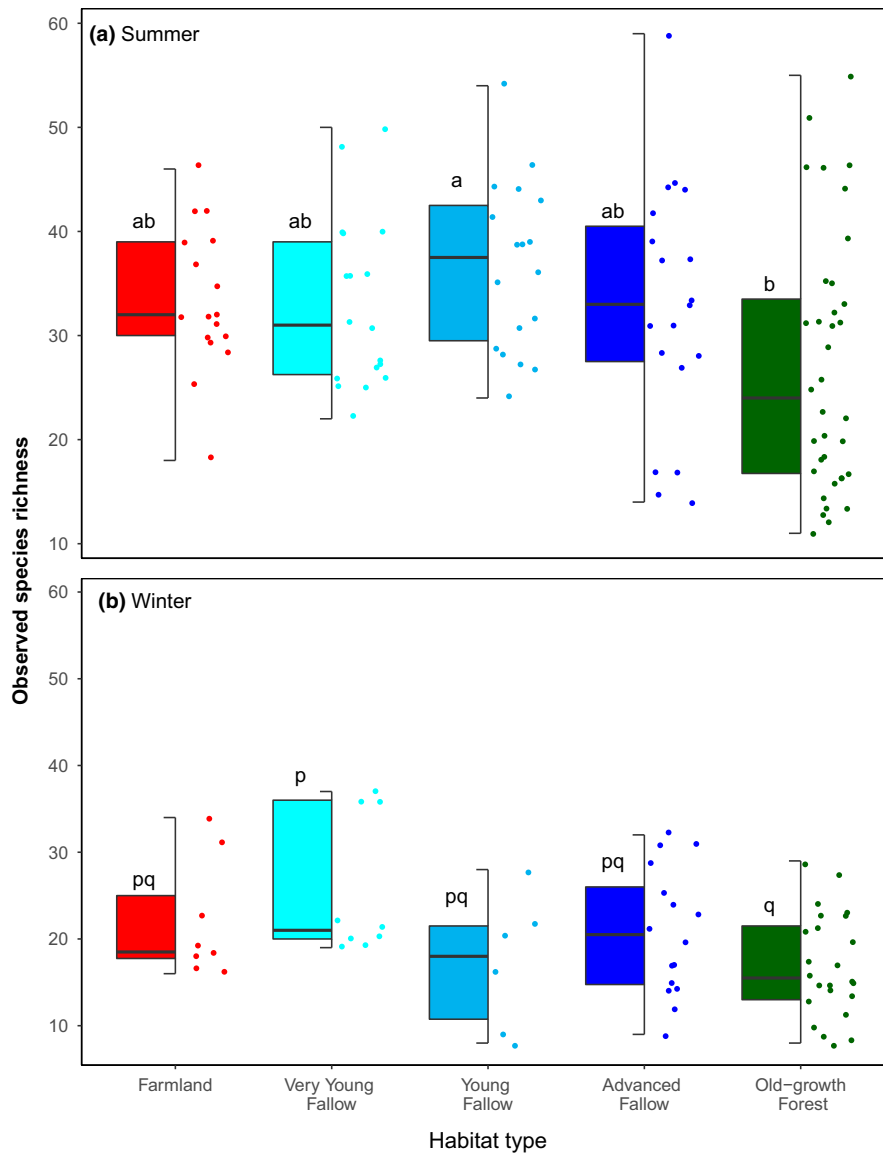


FIGURE 2 Observed point-level species richness across farmland, very young fallows (1–6 years), young fallows (7–14 years), advanced fallows (15–29 years) and old-growth forests in (a) summer and (b) winter in Nagaland, Northeast India. The black horizontal line represents the median for each habitat type, and the lower and upper hinges of each box correspond to the first and third quartiles. The upper and lower F whiskers indicate the inter-quartile range of the dataset. Letters indicate significant differences between habitat types based on pairwise Tukey's honest significance tests. (Numeric test results in Table S4)

conditional $R^2 = .43$) in summer. However, the best fit model for winter only included the intercept suggesting no significant response of species richness to fallow age or elevation.

3.2 | Bird community composition across habitats

The NMDS ordination plots suggested distinct community composition across habitats in summer (ADONIS: $r^2 = .14$, $df = 4$, $p < .001$), whereas bird communities were much more overlapped during winter (ADONIS: $r^2 = .09$, $df = 4$, $p = .005$) (Figure 4a,b). Species' assemblages were significantly different in old-growth forest from farmland and fallows in summer (Pairwise Adonis: old-growth forest vs. farmland: $r^2 = .13$, $p = .001$; vs. very young fallow: $r^2 = .09$, $p = .001$; vs. young fallow: $r^2 = .10$, $p = .001$ and vs. advanced fallow: $r^2 = .06$, $p = .001$). Within regenerating fallows, species composition did not vary across very young, young, and advanced fallows in both seasons suggesting that fallow age had little influence on community composition in regenerating forests (Figure 4).

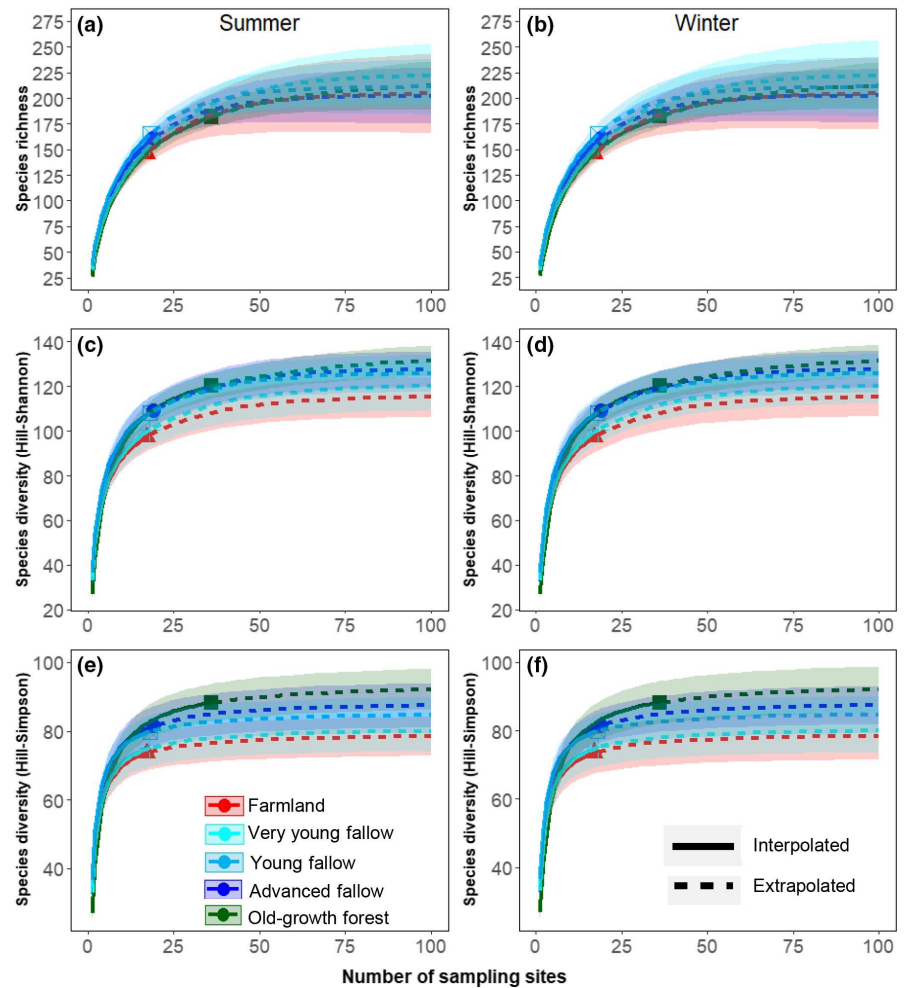
3.3 | Above-ground carbon-bird diversity co-benefits

Carbon stocks in secondary forest increased with fallow age towards old-growth stocks (Figure 5a), and this was reflected in both summer (Figure 5a) and winter (Figure 5b) biodiversity sampling points. During summer, birds showed a strong positive increase in similarity to old-growth forest communities with increasing carbon stocks, with communities closely resembling those of old-growth forests after 15–29 years of regeneration (Figure 5c). By contrast, bird communities did not show a strong association between similarity to old-growth and carbon stocks across habitat types during winter (January–February; Figure 5d).

4 | DISCUSSION

Understanding biodiversity responses to shifting cultivation is crucial in formulating conservation strategies. Focusing on a

FIGURE 3 Sample-based rarefaction (solid lines) and extrapolation curves (dashed lines) of bird species diversity based on the Hill numbers ($q = 0, 1$ and 2) for farmland (FA), very young fallow, young fallow, advanced fallow, and old-growth forest in summer and winter in Nagaland, Northeast India



biodiversity hotspot region within Northeast India, we find that farmland and naturally regenerating fallows sustained higher species richness than old-growth forests in shifting cultivation landscapes. However, old-growth forests harboured a distinct bird community of forest-dependent species, including internationally vulnerable and near-threatened species such as Naga wren-babbler (*Spelaornis chocolatinus*) and Grey-headed Parakeet (*Psittacula finschii*), particularly during the breeding season. Bird communities increasingly resembled old-growth forest in summer (but not in winter) as fallows regenerated and accumulated carbon stocks over time. These results suggest the high biodiversity value of shifting cultivation system. This finding can potentially contribute to achieving biodiversity co-benefits under carbon-based payments for ecosystem services, via protecting old-growth forests from deforestation and mature secondary forests from degradation.

4.1 | Bird community response to shifting cultivation

This study reveals that farmland and regenerating fallows had similar bird species richness to old-growth forests (Figure 2),

which is consistent with studies in multi-strata agroforestry systems in India (Elsen et al., 2017) and elsewhere (Buechley et al., 2015; Harvey & González Villalobos, 2007; Mulwa et al., 2012; Van Bael et al., 2007). However, previous studies in shifting cultivation have indicated that old-growth forest often supports higher species richness than farmland and regenerating fallows (Martin et al., 2021; Raman et al., 1998). Our results could be partly explained by the presence of large trees retained by farmers in farmed parts of the shifting cultivation system (here referred as farmland) and young regenerating fallows, which is typical of the shifting cultivation landscapes in our study region (Borah et al., 2018). These trees can facilitate both open habitat and forest-dependent species in farmlands and regenerating forests, thus increasing the species richness in farmland and young fallows (Sayer et al., 2017), especially in our study system where shifting cultivation creates a landscape mosaic of heterogeneous habitats with old-growth forests in proximity. Regenerating fallows might also harbour relatively higher species richness by providing resources for bird species from both open farmlands and old-growth forest suggesting a likely effect of the intermediate disturbance hypothesis (Osman, 2015). In addition, diversity measures, such as species richness, may underestimate the true extent of impacts of land-use change on biodiversity (Moullot

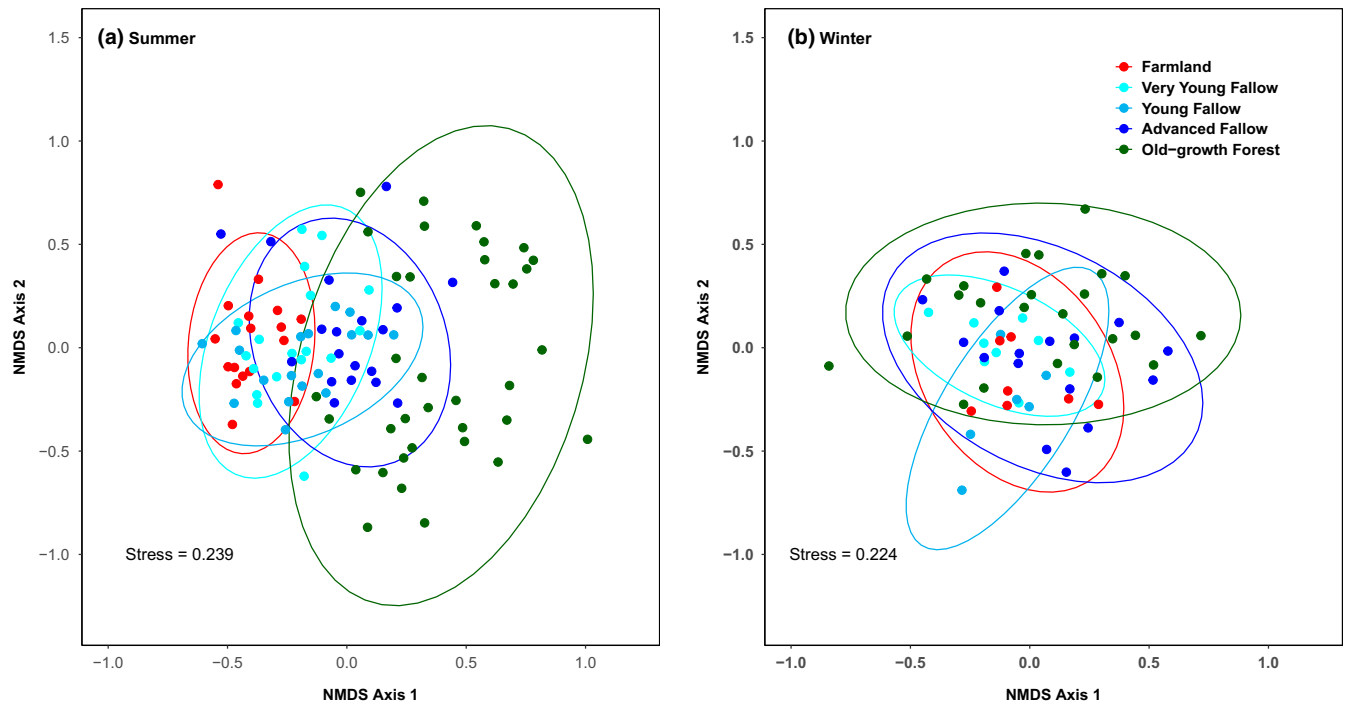


FIGURE 4 Ordination of point-level community composition using non-metric multidimensional scaling (NMDS) in summer (a) and winter (b) across farmland, very young fallow, young fallow, advanced fallow, and old-growth forest in Nagaland, Northeast India. The circles represent normal confidence ellipses for each habitat type calculated using `stat_ellipse()` function in R software. (Pairwise Adonis for summer: old-growth forest vs. farmland: $r^2 = .13$, $p = .001$; vs. very young fallow: $r^2 = .09$, $p = .001$; vs. young fallow: $r^2 = .10$, $p = .001$ and vs. advanced fallow: $r^2 = .06$, $p = .001$)

et al., 2013) as they fail to capture changes in communities' response in terms of ecological functions and evolutionary history (Edwards et al., 2014).

Within regenerating fallows, we did not find any strong evidence that fallow age influenced bird species richness in both summer and winter (Figure 3). This is also in contrast to biodiversity recovery patterns observed in shifting cultivation systems in Northeast India (Raman et al., 1998) and elsewhere (Blankespoor, 1991; Bowman et al., 1990; Marsden et al., 2006; Zhijun & Young, 2003) where bird species richness, abundance, and diversity tend to increase with successional age. Most of these studies, however, were conducted at lower elevations (<1000 m asl); but see (Zhijun & Young, 2003) than our study (1460–2600 m asl), and differences in avian resource use along altitudinal gradients can influence responses to land-use change (Dehling et al., 2014). It is also plausible that the retention of larger trees reduces the influence of fallow age on biodiversity as these trees are often key supporters of biodiversity (Lindenmayer et al., 2014) and will be present across the gradient in age. However, Shannon and Simpson diversity consistently increased as regenerating secondary forest matured from farmland to advanced fallow suggesting that fallow age positively influenced bird community evenness and dominance (Figure 3a–f).

Management decisions by local communities can influence the rate of fallow recovery in shifting cultivation, that in turn can lead to varying degrees of biodiversity recovery across sites (Borges &

Stouffer, 1999; Norgrove & Beck, 2016; Zhijun & Young, 2003). For example, repeatedly cultivated sites had a distinct bird species composition and lower species richness compared with fields cultivated once in the Brazilian Amazon (Borges, 2007). The three landscapes in our study site included land owned by seven local village communities, and the shifting cultivation system, including fallow management, varied across these communities. These varying management practices can influence plot-level bird species richness and diversity across landscapes. For instance, the two different clusters in very young fallow plots in winter showed relatively higher species richness in Kohima landscape compared to sites in Phek landscape (Figure 2b).

Community composition was distinct in farmland from regenerating and old-growth forest in summer (Figure 4a), mirroring findings from previous studies (Raman, 2001). In contrast to summer patterns, winter communities showed much weaker variation across habitats (Figure 4b). The weak relationship between bird community resemblance to old-growth forest and above-ground carbon stocks during winter (Figure 5d) suggests that heterogeneous landscapes with low-intensity subsistence agriculture and regenerating secondary forests can sustain high bird diversity in winter as evidenced in previous studies from the region (Elsen et al., 2017). The majority of bird species in the study region undergo seasonal migration (Rasmussen & Anderton, 2005) and thus may respond more strongly to elevational gradients than to habitats in winter. Farmland and regenerating fallows supported diverse winter bird communities, including

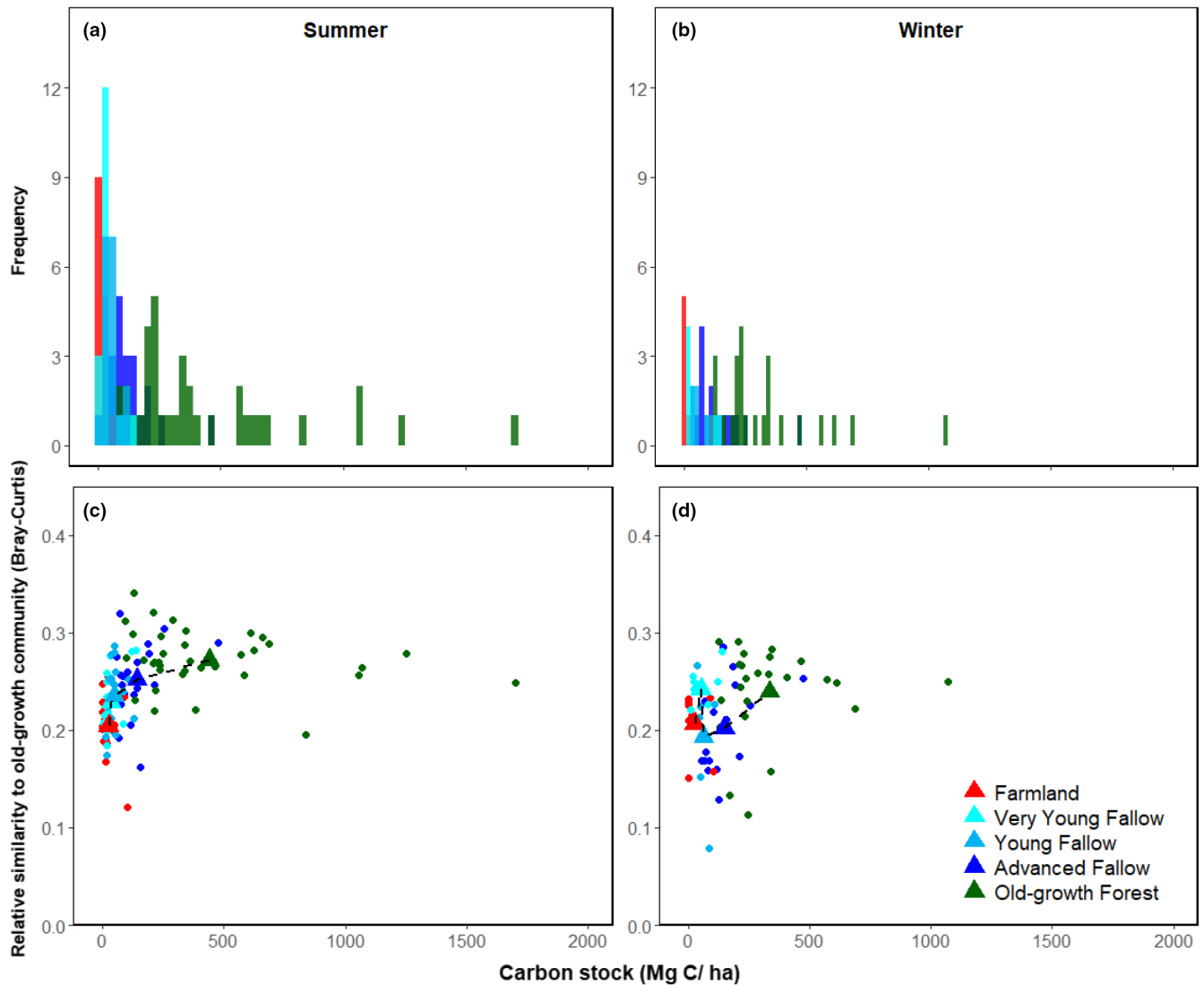


FIGURE 5 Above-ground carbon stocks (Mg C/ha) ((a) and (b)) and bird community similarity (Bray-Curtis index) to the mean similarity of old-growth forest based on raw data across farmland, very young fallow (1–6 years), young fallow (7–14 years), and advanced fallow (15–29 years) in relation to carbon stocks (Mg/ha) ((c) and (d)) in summer (April–May) and winter (January–February) in Nagaland, Northeast India. A Bray-Curtis index of 1 suggests most similar, 0 suggests least similar. The triangles show mean value for each habitat category

many species that are dependent on old-growth forest during the breeding season, such as Black-faced Warbler (*Abroscopus schisticeps*), Himalayan Cutia (*Cutia nipalensis*), and Black-eared Shrikebabbler (*Pteruthius melanotis*) (high forest dependency; Birdlife International, 2020), mirroring patterns elsewhere in the tropics (Elsen et al., 2017; Laiolo et al., 2004). In addition, although birds are good indicators, they are generally more resilient to land-use change compared to other taxonomic groups as evidenced in previous studies (Phalan et al., 2011; Williams et al., 2017).

4.2 | Impacts of management regimes and landscape configuration on bird responses

Biodiversity responses to shifting cultivation are strongly affected by management regimes and landscape configuration

(Norgrove & Beck, 2016). Shifting cultivation is a mosaic system with interspersed regenerating forest and old-growth forest providing heterogeneity of habitats. This can increase biodiversity through an accumulation of species associated with the different habitat types across the landscape (Borges, 2007; Devictor & Jiguet, 2007; Padoch & Pinedo-Vasquez, 2010). For instance, non-forest and open-habitat birds that colonize farmlands provide additional species richness in farmland and secondary vegetation as observed in India (Raman et al., 1998) and the Amazon (Andrade & Rubio-Torgler, 1994). This can be due to an increase in landscape complementation (Brottons et al., 2005; Dunning et al., 1992), with different habitat types preferred by birds at different times and providing complementary resources, such nest sites during summer and food during winter.

Landscape heterogeneity might also increase biodiversity by influencing interspecies interactions. For instance, increasing

compositional heterogeneity within landscapes can reduce dispersal rates between patches of the same habitat type, which can indirectly increase biodiversity by reducing competition (Fahrig et al., 2011). In addition, management decisions made by local communities can influence biodiversity recovery by determining the rate of fallow recovery in shifting cultivation (Borges & Stouffer, 1999; Norgrove & Beck, 2016; Zhijun & Young, 2003). For example, repeatedly cultivated sites had a distinct bird species composition and lower species richness compared with fields cultivated once in the Brazilian Amazon (Borges, 2007). Similarly, the various stages of the cultivation process, such as farm size, retaining certain trees while clearing, and distance to old-growth forest also vary across villages. These factors can lead to varying degrees of biodiversity recovery across sites.

4.3 | Importance of shifting cultivation for carbon and biodiversity co-benefits

Our study showed that old-growth forests held the highest amount of aboveground carbon (441.4 ± 60 Mg/ha) compared to other habitat types (i.e., farmland and regenerating forests) (for more details see Borah et al., 2018). Old-growth subtropical hardwood forests with minimal anthropogenic and environmental disturbances can accumulate very high levels of biomass as shown in tropical sites from South-East Asia (McEwan, 2011). The relatively high levels of carbon stocks in some of the young fallows were mainly due to the retention of a few large trees in those plots by the farmers. Farmers generally retain the big trees in relatively less fertile site to facilitate regeneration at higher elevation (>1500m asl) in Nagaland (Ramakrishnan & Patnaik, 1992). These large trees contribute disproportionately to the carbon stock in forests (Hu et al., 2015; Sist et al., 2014) and drive variation in aboveground carbon (Slik, 2013).

We found a positive relationship between carbon stock and community similarity to old-growth forests during the breeding season (summer) (Figure 5c), suggesting a strong potential for co-benefits in shifting cultivation landscapes in Northeast India. This can be achieved by protecting old-growth forest from conversion to farmland (avoided deforestation), permanent abandonment of mature secondary forests currently under shifting cultivation (avoided degradation), and enhancing carbon under natural forest regeneration within the shifting cultivation system (carbon enhancement), similar to those identified in secondary forest of the Tropical Andes (Basham et al., 2016; Gilroy et al., 2014), within degraded forests in the Brazilian Amazon (Lennox et al., 2018), and in fragmented forests in the Brazilian Atlantic Forest (Matos et al., 2020).

4.4 | Implications for carbon-based PES management and conclusions

A core mechanism for ensuring forest protection in shifting cultivation landscapes are carbon-based payments for ecosystem services

(UN-REDD, 2017). Carbon-based PES schemes, such as REDD+, hold potential for biodiversity co-benefits while protecting carbon stocks in shifting cultivation landscapes (Borah et al., 2018; Gardner et al., 2012), especially in tropical and sub-tropical mountainous regions with high levels of both carbon sequestration and biodiversity (e.g., Gilroy et al., 2014). Northeast India—a biodiversity hotspot with 66% of its total geographical area under secondary and old-growth forest cover—has immense potential to harness PES to reduce carbon emissions and biodiversity loss from shifting cultivation (Murthy et al., 2013).

There are potential barriers to harnessing win-wins for carbon and biodiversity. First, ~93% of forests in Nagaland are owned and managed by village councils (Bhupathy et al., 2013) and vary in their protection status. Incorporating mature secondary or old-growth forest areas in protected area networks co-managed with local communities can be effective in conserving forest cover (Oldekop et al., 2016; Sze et al., 2022) at minimal cost given that shifting cultivation is subsistence-based farming mainly practised in remote regions with low crop yields (Borrego & Skutsch, 2014; Morton et al., 2020). However, the opportunity costs of PES implementation to local communities could be high due to limited market access and structural barriers to adopting alternative livelihoods (e.g., Poudyal et al., 2016). Second, conservation interventions can displace land-use pressures outside the area of management (Boyle & Murphy, 2012). Such 'leakage' might occur when a transition away from shifting cultivation encourages food imports, driving agricultural replacement of forest elsewhere. Similarly, regulating timber extraction from fallow forest could increase pressure for timber production elsewhere. Evaluating the potential direct and indirect impacts of REDD+ actions across multiple spatial scales will help to avoid unintended leakage.

In conclusion, despite the global trend towards a transition from subsistence to commercial agriculture, shifting cultivation continues to be an important agricultural system in many remote areas in South and South-east Asia, and Africa, where multi-functional land uses remain the most suitable option to farmer's socio-economic life. Our results reveal that shifting cultivation modifies the landscape into habitat mosaics that harbour high levels of bird diversity. This study thus underscores the importance of shifting cultivation in providing co-benefits for both bird diversity and carbon stocks.

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CONFLICT OF INTEREST

The authors declare no competing or conflicts of interest.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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