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Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Sucessional trajectories of bird assemblages in amazonian secondary forests: Perspectives from complementary biodiversity dimensions

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ARTICLE INFO

Keywords:

Ecological succession
Taxonomic diversity
Functional diversity
Phylogenetic diversity

ABSTRACT

Secondary forests occupy extensive areas in tropical regions, providing an opportunity to investigate their relevance to biodiversity restoration. However, determining the conservation value of secondary forests and evaluating their successional trajectories depends on how biodiversity is measured. Here, we explore different biodiversity dimensions to understand how bird assemblages recover from forest disturbance caused by small scale farmers in the Amazon. We sampled bird species through standard visual and auditory censuses in 24 small plots of 1-hectare distributed in a paired design of old growth forests and secondary forests from different age categories (early, middle and late succession). We used 12 biodiversity metrics to explore the taxonomic, functional, and phylogenetic dimensions of bird diversity. Total species richness and evenness was similar between secondary and old growth forests. In contrast, the number of passerine species and disturbance-vulnerable species were higher in the controls of old growth forests compared to secondary forests. The relative abundance of birds with distinct functional traits consistently differed between the secondary forests of different age categories and their old growth forest counterparts. Functional evenness and divergence increased with canopy height and basal area through forest regeneration. In contrast, bird phylogenetic diversity in secondary forests was higher compared to those found in old growth forests while accounting for forest types and age categories of secondary forests. Bird species tolerant to disturbances partially compensate the loss of avian taxonomic and phylogenetic diversity during the conversion of undisturbed forests to agricultural fields. Changes in functional evenness and functional divergence suggest that resources used by birds are altered along the secondary succession and that the niche complementarity among species is reduced in more intensively managed sites. Ecological succession can be highly complex in terms of taxa identity, their functional roles and evolutionary history. Therefore, measurements that explore distinct biodiversity dimensions are fundamental to understanding how species are organized in assemblages across time and space.

1. Introduction

Secondary succession refers to the sequence of events in the regeneration of plant assemblages after natural or human-induced disturbances (Shugart, 2004). Ecological succession extends the concept of secondary succession, focusing on how entire biological communities (not only plants) re-assemble following environmental disturbances (Chang and Turner, 2019). Recently, the study of secondary and ecological succession has gained renewed impetus (Chang and Turner, 2019), influenced by new analytical approaches (e. g. phylogenetic

metrics) and by the importance of secondary forests for carbon stocks around the world (Poorter et al., 2016). Moreover, secondary forests occupy extensive areas in tropical regions (Chazdon, 2008a, Aide et al., 2013, Chazdon, 2014). In the Brazilian Amazon, for instance, regenerating forests cover more than 17 million hectares (Almeida et al., 2016).

The relevance of Amazonian secondary forests as repositories of biological diversity has long attracted attention (Terborgh and Weske, 1969, Novaes, 1973, Saldarriaga et al., 1988, Uhl et al., 1988). These studies demonstrate that the effect of converting old growth forests to secondary forests on local biodiversity depends on: i) the taxonomic

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<https://doi.org/10.1016/j.foreco.2020.118731>

Received 28 August 2020; Received in revised form 19 October 2020; Accepted 20 October 2020

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group investigated (Barlow et al., 2007); ii) the landscape context of studied regions, especially the proximity of large tracts of undisturbed forests (Gilroy et al., 2014, Arévalo-Sandi et al., 2018); and iii) the type and intensity of the disturbance and posterior management of the vegetation (Borges and Stouffer, 1999, Mesquita et al., 2015, Jakovac et al., 2015). Even though there is a considerable variability in how biodiversity reacts to successional processes, there is a consensus among researchers that secondary forests are vital for biological conservation, especially if associated with large tracts of old growth forests (Chazdon et al., 2009, Gilroy et al., 2014, see also Kormann et al., 2018, Acevedo-Charry and Aide, 2019).

Biodiversity is a multifaceted concept (Ricotta, 2005), and determining the conservation value of secondary forests or evaluating their successional trajectories depends on how it is measured. The majority of the biodiversity studies use the number of species and species composition as proxies for biodiversity. Although these metrics are fundamental to documenting biological patterns (Magurran, 2004), they underestimate the role of species traits in the ecosystems/communities functioning and the evolutionary history of lineages (Cavender-Bares et al., 2009, Cadotte et al., 2011). Recently, new metrics that incorporate the functional and phylogenetic aspects of biological diversity have been used to advance our understanding of how assemblages react to environmental disturbance and subsequent regeneration in Amazonian forests (Santos et al., 2014, Edwards et al., 2017, Rocha et al., 2018, Arévalo-Sandi et al., 2018). At the same time, the temporal and spatial context of forest regeneration are highly variable in the Amazon (Mesquita et al., 2015, Jakovac et al., 2016, Carvalho et al., 2019) and needs to be considered for an adequate interpretation of biodiversity dimensions.

The principal deforestation agents in the Amazon are farmers acting at different scales (Godar et al., 2012, Fearnside, 2017). Small scale or familiar agriculture normally uses the traditional technique of slash and burn of small parcels (1–2 ha) of old growth or secondary forests to implement agricultural fields (Pedroso et al., 2008). These parcels are abandoned after the productive cycles of plant cultivation, allowing natural vegetation to regrow (Jakovac et al., 2015, Jakovac et al., 2016). Usually the same family keeps several small parcels in different regeneration phases, providing an opportunity to investigate how the different dimensions of biodiversity are affected by forests regeneration.

Studies of avian assemblages have been instrumental to understand the effects of forest regeneration in tropical biodiversity, including recent analyses that take in account its functional and evolutionary aspects (Sayer et al., 2017, Hughes et al., 2020, Matuoka et al., 2020). Indeed, as birds are a taxonomically diverse group that affect numerous aspects of ecosystem functioning (i. e. seed dispersal, herbivory), they are well suited to an integrative perspective on investigating changing biodiversity (Sekercioglu, 2006, Sekercioglu, 2012, Jetz et al., 2012, Maas et al., 2016). In addition, successional trajectories of plants and animal assemblages do not necessarily result in convergent patterns (Grass et al., 2015), which emphasizes the need to evaluate the responses of different taxa to have a broad perspective of ecological succession. Finally, understanding the different aspects of animal assemblage recovery could be potentially relevant to determine management strategies of secondary forests in tropics (e.g. assisted versus unassisted regeneration).

Here we simultaneously explore the taxonomic, functional, and phylogenetic diversity of bird assemblages to understand how they recover from forest disturbance caused by small scale agriculture in an Amazon forest. In a previous analysis, we identified a gradual increase in bird species richness along a chronosequence of regenerating forests and an increasing similarity in species composition between secondary forests of different ages and old growth forests (Borges, 2007). We broaden the Borges (2007) results by incorporating new metrics of biodiversity to answer the following questions:

- i) How are taxonomic, functional, and phylogenetic metrics related each other? We predict that utilizing a range of diversity metrics will reveal different aspects of bird diversity.
- ii) Does analysis of subsets of species groups with particular attributes reveals distinct patterns of species diversity? Decomposed bird species richness in groups composed only by Passeriformes and species with low tolerance to disturbance could reveal patterns that are not detected when considering total species richness.
- iii) How does the conversion of forests to agriculture fields affect taxonomic, functional and phylogenetic bird diversity? We expected that the magnitude and direction of the effects of habitat disturbance in bird diversity could be dependent on the biodiversity dimension considered.
- iv) Do distinct biodiversity dimensions show convergent temporal patterns in secondary forests? Given the complexity of ecological succession we do not expect convergent patterns in all biodiversity dimensions.

2. Material and methods

2.1. Study area and design

Birds were sampled in the Jaú National Park, one of the largest amazonian protected areas with approximately 2.2 million hectares. The Jaú National Park has been inhabited since its creation in 1980, although the antiquity of human presence in the region is documented by archaeological evidence (Lima, 2014). The natural resources in the Park are utilized by resident families through extractive activities and small scale agriculture (Borges et al., 2004, Pezzuti et al., 2004).

The land management of agriculture in the region is based on cutting and burning the vegetation patches of old growth or secondary forests, and planting of agricultural cultures, especially the manioc (*Manihot esculenta*) for flour production (Borges et al., 2004). After continuous cultivation for 2–3 years, soil nutrients are depleted leading to a diminished of production and the site is abandoned. This system results in small parcels of 1–2 ha per family of secondary forests in different regeneration stages distributed along the rivers. Secondary forests managed by local dwellers were located in a low-disturbed landscape dominated by large extensions of seasonal flooded forests and upland forests (Borges, 2007).

We interviewed local farmers to characterize the agricultural management at each site and to determine the approximate age of secondary forests. Since the ages of sites were quantified with variable accuracy by the farmers, we decided to classify the secondary forests parcels in broader age categories: i) young secondary forests (<than seven years); ii) mid-age secondary forests (7–15 years of abandonment); and iii) old-secondary forests (20–35 years).

We implemented four sampling sites for each age category, with each secondary forest site paired with a control site in the adjacent old-growth forests within 200 to 300 m. We looked for most possible homogeneous parcels and avoiding tracts of secondary forests with different ages and management history. However, two sites in young secondary forests were cultivated more than once resulting in lower canopy height and higher canopy openness compared to other sites (Borges, 2007). The full sampling design consists of 12 replicates in secondary forests (four for each age category) and 12 replicates in the neighbored old growth upland forests.

2.2. Methods for sampling birds and vegetation

In each sampling site, we established two intercrossed trails of 100 m. Bird surveys following the line transect method and were conducted on a scale of 1-ha to adjust the sampling units to the same scale of land parcels managed by farmers. During the bird censuses, the observer (SHB) moved through the trails counting birds detected by observation

or vocalizations. The censuses were taken from 06h00min to 10h00min on one occasion for each site focusing on diurnal birds. In each plot we recorded only birds detected inside a band of 50-meters each side of the trails. With this procedure we avoided counting birds from neighboring agricultural fields or secondary patches with different ages than the target sampled plot.

Variation in bird behavior (e. g. flying activities) and vegetation structure (e. g. canopy height) could affect the visual detection of birds. However, most species were detected by vocalizations (Borges, 2007) and we assumed that most individuals could be heard within 50-meters from the observer, an assumption supported by field work in temperate and neotropical regions (Schieck, 1997, Herzog et al., 2002). The observer made efforts to avoid double counting the same individuals, especially for fast-moving species such as hummingbirds, and woodcreepers. For these species, we considered that more than one individual was inside the plot only if they were detected simultaneously by voice or visually.

In each sampling site we defined a 10 × 5 m plot, where we measured: i) canopy height estimates in four points in the plot using an two meter stick as reference, ii) eight measures of canopy cover using a sphero-densimeter, iii) circumference of all trees larger than 30 cm at breast height (transformed in diameter for analysis). More details in the field work procedures are found in Borges (2007).

2.3. Biodiversity dimensions

Taxonomic diversity was represented by the number of species, and equitability quantified using the Pielou index (Magurran, 2004). We used the approach recommended by Marquet et al. (2004) to split the total species richness in a smaller subset of species with particular attributes. For this we used taxonomic (all species and only Passeriformes) and ecological (vulnerability to habitat disturbance) categories. For the latter, we follow categorization of Stotz et al. (1996) that ranks the vulnerability of bird species to disturbance as high, medium or low. Here, we considered only the number of species with high vulnerability to disturbance in each replicate.

We used continuous and categorical traits to calculate functional diversity indices (Table S1). The continuous morphometric traits refer to size, dispersal ability, and food manipulation. The categorical traits represent the i) foraging habitat: the main vertical forest stratum where birds taken its food; ii) diet: the main food items in the birds diet; and iii) social behavior: refers to degree of species sociability (Table S1). Most morphometric data were obtained during field work in the study region, complemented in few cases with measurements taken from specimens deposited in the National Institute of Amazonian Research (INPA) Bird Collection. Foraging habitat, diet and social behavior data were taken from Karr et al. (1990) and Cohn-Haft et al. (1997). The database used for calculations of functional indices is available as supplementary material 1.

Out of the innumerable indices of functional diversity (Mouchet et al., 2010, Mouillot et al., 2013) we selected functional richness (Frich), functional evenness (Feve), functional divergence (Fdiv) and functional dispersion (Fdis). These commonly used indices represent complementary aspects of functional diversity (Mason et al., 2005, Kuerbbing et al., 2018). Detailed descriptions of calculations and interpretation of these indices are found in Mouchet et al. (2010), Mouillot et al. (2013), and Kuerbbing et al. (2018).

For the functional diversity analysis, we organized matrices containing data on bird relative abundance and functional traits described above. All morphometric data were standardized by body mass. Gower transformations were applied before analysis since the functional matrix contains categorical and continuous data. The functional space was represented by a principal component analysis (PCA), and from this functional matrix we calculated the functional metrics (Frich, Feve, Fdiv and Fdis) for each replicate using the R package FD (Laliberté et al. 2014).

We calculated two metrics of phylogenetic diversity (Webb, 2000) using phylogenetic data from Jetz et al. (2012): mean pairwise distance between all species in a site (MPD), and phylogenetic diversity (PD). These metrics were standardized against the corresponding species richness at each site. We calculated both metrics using the R package PhyloMeasures (Tsirogianis and Sandel, 2015). As the phylogeny proposed by Jetz et al. (2012) had low confidence in the relationships among some species we supplemented the phylogenetic metrics of diversity by using the taxonomic structure as a proxy of evolutionary relationships (Heino et al., 2015, Cai et al., 2018).

For this, we used the bird taxonomic ranks proposed by the Brazilian Committee of Ornithological Records (CBRO) (Piacentini et al., 2015). Taxonomic structure is useful to understanding the evolutionary relationships among species since the decisions of CBRO ornithologists are based on careful revision of molecular and morphology-based phylogenies continuously available in the ornithological literature.

We used metrics of average taxonomic distinctness, calculating with abundance (Delta*) or presence or absence data (Delta⁺), as recommended by Clarke and Warwick (1998) and Clarke and Warwick (2001). These indices were applied only to Passeriformes birds families since more detailed taxonomic data is provided for these lineages in Piacentini et al. (2015). The taxonomic ranks used to calculate Delta* and Delta⁺ were species, genus, subfamily, family, parvorder, suborder, and order. A general description of all metrics used in this study is available in supplementary material 2.

2.4. Analysis

We used a Pearson's product moment correlation to quantify the relationships among the metrics calculated in the three biodiversity dimensions (taxonomic, functional and phylogenetic). For this study we considered coefficient of correlation (r-Pearson) superior of 0.70 as an evidence of strong correlation between metrics (Dormann et al., 2013).

To test the hypothesis that our different indices were significantly different between secondary forests and old growth forests we applied factorial analysis of variance (Factorial ANOVA). The effects of blocks (forest types: secondary vs old growth forests) and treatments (the three age categories of secondary forests) were treated separately. Complementary to this, we performed simple linear regressions between each diversity indices and the continuous variables of vegetation structure. We prefer using simple linear regressions to more sophisticated analysis (e. g. GLM with model selection) because the low number of environmental variables measured in field. We excluded canopy cover from analysis since it is significantly correlated with canopy height ($R^2_{adj} = 0.77$, $p < 0.001$) and basal area ($R^2_{adj} = 0.33$, $p = 0.002$). Two sites in young secondary forest were used more intensively, resulting in lower canopy height (see above), and we performed regression analysis with and without these two sites. Simple linear regressions were run using SAM package (Rangel et al., 2010).

3. Results

3.1. Diversity metrics relationships

During the censuses were counted 1150 individuals representing 150 bird species (Supplementary material 1). Correlational analysis among the 12 biodiversity metrics resulted in 66 paired combinations, of which only six produced coefficients of correlation (r-Pearson) above 0.70, suggesting that most indices represent unique and complementary aspects of diversity (Table 1).

The number of passerine bird species (Passeriformes) was highly correlated with total number of species (r-Pearson = 0.89, $P < 0.001$). Also, the number of species with high vulnerability to habitat disturbance was correlated with number of passerine species (r-Pearson = 0.73, $P < 0.0001$). No appreciable relationships were observed among functional diversity metrics with exception of a significant correlation

Table 1
Correlation coefficients (r-Pearson) between different biodiversity indices used in this study.

	Only Passeriformes	Pielou (J)	Vulnerable species	Frich	Feve	Fdiv	Fdis	Delta +	Delta *	PD Faith	MPD
All species	0.89	-0.09	0.68	0.76	-0.14	0.45	0.23	-0.29	-0.38	0.01	-0.14
Only Passeriformes		-0.02	0.73	0.61	0.01	0.4	0.03	-0.44	-0.51	-0.33	-0.54
Pielou (J)			-0.13	-0.11	-0.37	-0.45	-0.5	0.33	0.2	-0.06	0.02
Vulnerable species				0.51	0.23	0.47	0.08	-0.59	-0.71	-0.39	-0.51
Frich					-0.09	0.45	0.56	-0.01	-0.06	0.17	0.07
Feve						0.25	0.14	-0.38	-0.25	-0.27	-0.4
Fdiv							0.38	-0.46	-0.41	-0.08	-0.2
Fdis								0.2	0.33	0.37	0.34
Delta +									0.93	0.51	0.67
Delta *										0.57	0.66
PD Faith											0.84

among functional richness and total number of species (r-Pearson = 0.76, $P < 0.001$).

Phylogenetic diversity based in quantitative (Delta*) and presence or absence (Delta⁺) data were highly correlated (r-Pearson = 0.93, $P < 0.001$). Interestingly, average taxonomic distinctness (Delta*) and the number of disturbance-vulnerable species were negatively correlated (r-Pearson = -0.71, $P = 0.001$) indicating that assemblages with high phylogenetic diversity were composed by species more tolerant to disturbance. The mean pairwise distance (MPD) and phylogenetic diversity (PD) were also correlated each other (r-Pearson = 0.84, $P < 0.001$). For simplicity, we exclude functional richness (Frich), phylogenetic diversity (PD) and Delta + from some of the further analyses due their high correlation with other metrics.

3.2. Taxonomic diversity

Total species richness was not affected by forest types (F blocks = 2.75, GL = 1.18, $P = 0.11$) or secondary forest age (F treatments = 1.45, GL = 2.18, $P = 0.26$) (Fig. 1). Species evenness measured by Pielou index, was also similar between forest types (F blocks = 0.51, GL = 2.18, $P = 0.51$) and age categories of secondary forests (F treatments = 0.60, GL = 2.18, $P = 0.56$) (Fig. 1).

No effect of secondary forest age was observed in Passeriformes species richness (F treatments = 2.69, GL = 2.18, $P = 0.09$), although fewer species were found in young and old age secondary forests compared with their old growth controls (Fig. 1). This may lead to the higher number of Passeriformes species in the old growth forests compared to secondary forests combined (F blocks = 9.85, GL = 1.18, $P = 0.006$) (Fig. 1).

Old growth forests had higher number of disturbance-vulnerable species than secondary forests (Fig. 1) accounting for the effects of forest types (F blocks = 32.58, GL = 1.18, $P < 0.001$) and age of secondary forests (F treatments = 5.19, GL = 2.18, $P = 0.01$).

3.3. Functional diversity

Birds with distinct functional traits consistently differ in relative abundance between the secondary forests within age categories and their old growth control sites. Canopy species were more abundant in old growth secondary forest compared to young secondary forests, and a reverse pattern was observed with terrestrial bird species (Fig. S1).

Omnivores and nectivores/invertebrates (mostly hummingbirds) were proportionally more abundant in secondary forests compared to old growth forests in all three age categories (Fig. S1). In contrast, birds

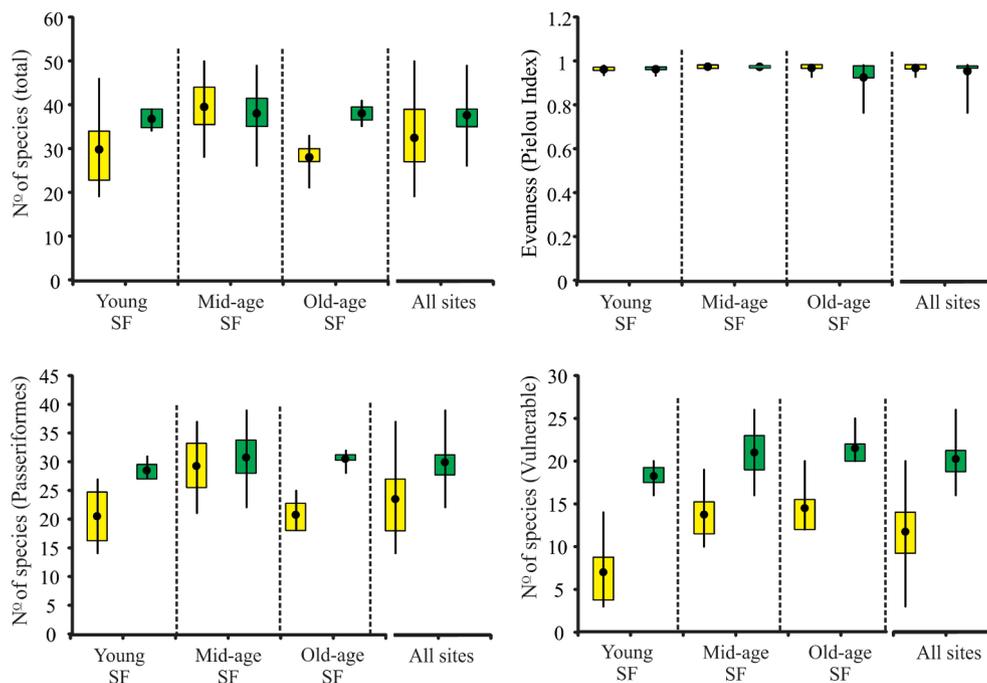


Fig. 1. Bird species richness and equitability in secondary forests (yellow boxes) and old growth forests (green boxes). Black points represents the mean, the vertical lines the minimum and maximum values and the boxes the quartiles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that eat invertebrates were more abundant in old growth forest compared to young secondary forests, but this difference diminished with secondary forests age (Fig. S1). Frugivore birds were more abundant in old growth forest only in comparison with old-age secondary forests (Fig. S1).

Birds that joined in heterospecific flocks were more abundant in old growth forests compared to secondary forests but these differences declined with age of the secondary forests (Fig. S1). Homospecific flocks were more abundant in mid-age secondary forests compared to control sites, but this pattern was also reversed in old-age secondary forests (Fig. S1). Solitary birds were apparently more common in young and old secondary forests compared to their old growth forests controls (Fig. S1).

Despite these differences in abundance of the functional groups between forests, the effects of forest types and age of secondary forest on the functional diversity indices were, at best, marginal significant. Functional divergence (Fdiv) was not different among forest types (F blocks = 1.92, $P > 0.05$) or secondary forest ages (F treatments = 0.38, $P > 0.05$). A marginal significant effect of secondary forest ages was observed in functional evenness (F treatments = 3.65, GL = 2.18, $P = 0.04$) and functional dispersion (F treatments = 3.62, GL = 2.18, $P = 0.04$) (Fig. 2). However, the effects of age of secondary forests on these components of functional diversity were not consistent among categories. Functional evenness, for instance, was lower in young and mid-age secondary forests, but higher in old-age secondary forests compared with its old growth forest controls (Fig. 2).

3.4. Phylogenetic diversity

The phylogenetic diversity of Passeriformes (Delta*) was higher in secondary forests compared to old growth forests considering forest types (F blocks = 15.07, GL = 1.18, $P = 0.001$) and age categories (F treatments = 6.42, GL = 2.18, $P = 0.008$) (Fig. 3). Also, the mean pairwise distance (MPD), which considers all bird species sampled, was also higher in secondary forest than in old growth forest with a significant effect of forest types (F blocks = 15.93, GL = 1.18, $P = 0.001$) and a marginal effect of age categories (F treatments = 2.94, GL = 2.18, $P = 0.07$) (Fig. 3).

3.5. Diversity metrics and vegetation structure

The three dimensions of biodiversity were affected by variation in the vegetation structure, represented by canopy height and basal area. Total number of bird species remained unchanged along a gradient of increasing canopy height and basal area (Table 2). In contrast, the number of passerine species increases with canopy height and basal area only if all sites are considered in the analysis (Table 2). We did not observe effects of structural components on the number of Passeriforme species, when the two high-disturbed sites in young secondary forest were excluded from analysis (Table 2). The number of

disturbance-vulnerable species increase with canopy height (Fig. 4) and basal area, but the effects of these structural elements are substantially diminished when excluding the two highly disturbed young secondary forests sites (Table 2).

Canopy height or basal area does not affect functional richness or dispersion, but these vegetation components positively affect the functional evenness (Fig. 4, Table 2). Functional divergence also increases with canopy height only when the two high-disturbed secondary forests sites are included in the analysis (Table 2).

Phylogenetic diversity represented by Delta* and MPD are also related with vegetation structure. However, contrary to taxonomic and functional diversity, phylogenetic diversity is higher in sites with lower canopy height and basal area (Fig. 4, Table 2).

4. Discussion

4.1. Bird diversity and ecological succession

Ecological succession involves the grouping of individuals and species into assemblages after habitat loss or degradation. This process can be highly complex in terms of taxa identity, their functional roles and evolutionary history (Finegan, 1996, Chazdon, 2008b, Letcher, 2009, Letcher et al., 2012). Therefore, measurements that explore distinct dimensions of biodiversity are important to understanding how species are organized in assemblages across time and space (Purschke et al., 2013, Chai et al., 2016, Mi et al., 2016). The biodiversity measurements applied here reveal complementary, although not necessarily convergent, patterns of bird assemblage during ecological succession.

Species richness was substantially higher in old growth forests among the passerine birds and species vulnerable to habitat disturbance. Total number of species, in contrast, was not affected by forest types or by secondary forest age. The species loss promoted by conversion of old growth forests to agricultural fields is partially compensated by the colonization of secondary forests by birds tolerant or favored by habitat modification, especially from non-Passeriformes lineages.

This compensatory mechanism had been documented in other studies (Supp and Ernest, 2014, Morante-Filho et al., 2015, Russildi et al., 2016). The loss of some amphibian species in disturbed landscapes in southeastern Mexico, for example, was compensated by colonization of other species, maintaining the abundance and richness relatively stable across sites with different disturbance intensities (Russildi et al., 2016). Similarly, richness and abundance of total bird species (forest plus non-forest birds) in the Brazilian Atlantic forest remains unchanged in landscapes with variable forest coverage (Morante-Filho et al., 2015). However, assemblages of forest-dependent birds were negatively affected by the availability of forests in the landscape (Morante-Filho et al., 2015). Both studies indicate that species with higher tolerance to habitat disturbance (e. g. edge and open area species) partially compensate the loss of primary forest species. Compensatory dynamics

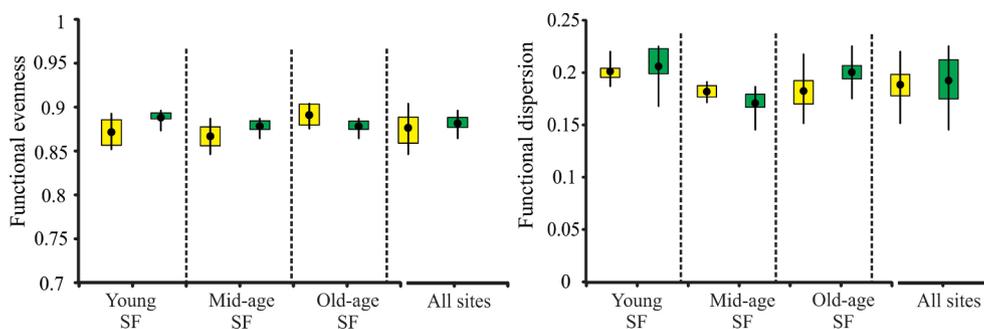


Fig. 2. Bird functional evenness and dispersion in secondary forests (yellow boxes) and old growth forests (green boxes). Black points represents the mean, the vertical lines the minimum and maximum values and the boxes the quartiles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

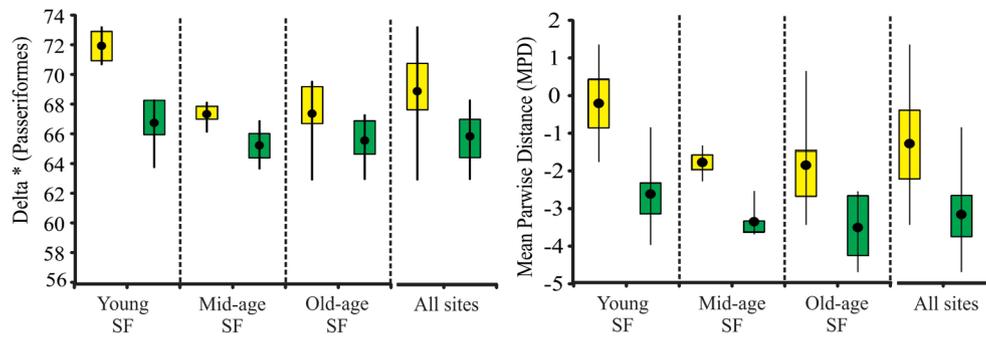


Fig. 3. Bird phylogenetic diversities represented by Delta* considering only Passeriformes taxa and mean pairwise distance (MPD) using all species sampled in secondary forests (yellow boxes) and old growth forests (green boxes). Black points represents the mean, the vertical lines the minimum and maximum values and the boxes the quartiles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Relationships between biodiversity metrics and canopy height and basal area of studied sites. Values are coefficients of determination (R^2 adjusted) and number inside parentheses are from regression analyses where two highly used sites were excluded (see Results). Values in bold are statistically significant and P values are denoted by asterisks as following: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Biodiversity dimensions	Metrics	Canopy height (R^2 adj)	Basal area (R^2 adj)
Taxonomic	Total number of species	0.102 (−0.050)	0.05 (−0.03)
	Number of Passeriformes species	0.26** (0.02)	0.18* (0.06)
	Evenness (Pielou index)	0.045 (−0.04)	0.12 (0.18)
	Vulnerable species	0.52*** (0.23**)	0.45*** (0.34**)
	FRic	0.038 (−0.05)	0.028 (−0.049)
Functional	FEve	0.14* (0.17*)	0.21* (0.17*)
	FDiv	0.27** (−0.042)	0.08 (−0.04)
	FDis	0.045 (−0.04)	0.04 (−0.04)
Phylogenetic	Delta*	0.47*** (0.17*)	0.56*** (0.48**)
	MPD	0.41*** (0.31**)	0.40*** (0.32**)

such as these can be efficiently detected using the richness deconstruction approach, as employed here (Marquet et al., 2004, see also Terribile et al., 2009).

The distribution of individuals among species (evenness) was similar between secondary and old-growth forests, but the bird species composition changes along the gradient of succession (Borges, 2007). Interestingly, the abundance distribution among species did not change

even during the succession. This result contrasts with plant assemblages whose evenness increase during the succession. Indeed, the first stages of regeneration are highly dominated by a small group of pioneer plant species that are replaced by more shade tolerant species in advanced successional stages (Finegan, 1996, Kou et al., 2016).

In contrast with taxonomic diversity, we find subtle differences in the bird functional diversity between forest types, indicating elevated levels of functional redundancy along the ecological succession. Similarly, bird functional diversity does not differ among burned and unburned forests in eastern Amazon (Hidasi-Neto et al., 2012). However, when forest regrowth is represented by continuous data of vegetation structure, some components of functional diversity are altered along forest succession.

Bird functional evenness is higher in secondary forests compared to primary forest in tropical regions (Sayer et al., 2017, Matuoka et al., 2020), and also increases with canopy height and basal area in our secondary forests sites. These patterns suggests that the resources available in secondary forests are used more efficiently by birds, especially in the latter phases of the forest regeneration (Mason et al., 2005, Mouillot et al., 2013, Kuerbbing et al., 2018). The niche space is underutilized in young secondary forests with functionally redundant species being more abundant. In Malaysia, bird functional evenness was gradually reduced from old growth forests to oil palm plantations indicating that changes in relative abundance affect the combination of functional traits (Edwards et al., 2013).

Functional evenness increased but taxonomic evenness remains relatively unchanged along the forest succession in our study sites. Contrasting patterns of taxonomic and functional evenness indicate that the relative abundance of individuals is not equally distributed among functional groups. Indeed, the relative abundances of birds with distinct traits (e. g. nectar-feeding, heterogeneous flocks) clearly changed along

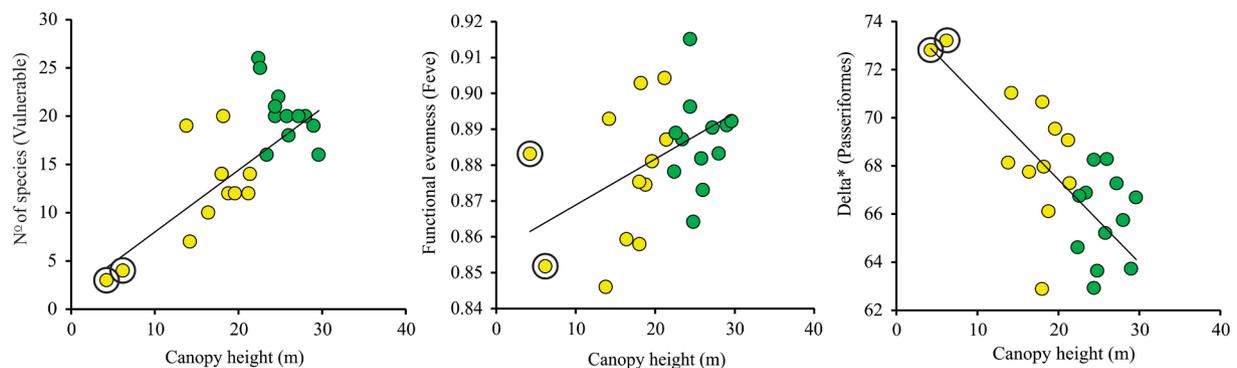


Fig. 4. Relationships among canopy height and taxonomic, functional and phylogenetic bird diversity in secondary forests (yellow points) and old growth forests (green points). Circled points are the secondary forest sites subjected to more intensive use. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the forest regeneration (Fig. S1, see also Borges, 2007) suggesting that resources provided by secondary forests also change along forest regeneration, favoring distinct functional groups. Indeed, interpretation of functional diversity could be substantially different for different bird functional groups across multiple land uses (Luck et al., 2013, Bregman et al., 2016). Therefore, the interpretation of functional evenness as a surrogate of resource utilization depends on the nature and quantity of those resources provided by different habitats.

Functional divergence also was positively related to canopy height and basal area when all sites were analyzed together. However, this relationship was not present after excluding two sites more intensively used for cultivation. This suggests that, in sites subject to more intense use, bird relative abundance is distributed among species with low functional divergence (Mouillot et al., 2013). Similarly, loss of functional divergence was documented in plant assemblages of secondary forests resulting from intensive cycles of land-use for agriculture in western Amazon (Jakovac et al., 2015, Jakovac et al., 2016). However, responses of bird functional divergence to land-use intensification can be highly variable (Luck et al., 2013). Therefore, further improvements in the number of sites with distinct levels of land-use intensification are necessary to make strongest predictions about the functional divergence of bird species in secondary forests.

The most surprisingly result of our study was the higher phylogenetic diversity in secondary forests compared to old growth forests. In most studies, plant phylogenetic diversity is lower in the initial stages of the succession (Purschke et al., 2013, Norden et al., 2012, Chai et al., 2016, Satdichanh et al., 2019). Similarly, bird phylogenetic diversity (measured with MPD) increases with secondary forest ages in Colombian agriculture landscapes, although no difference in phylogenetic diversity between secondary and old growth forests was observed (Edwards et al., 2017). In Costa Rica, the phylogenetic diversity of birds was much lower in diversified agricultural systems and monoculture compared to primary forests (Frishkoff et al., 2014). Also, in a recent review of phylogenetic diversity of tropical birds assemblages (including the database analyzed here), Hughes et al. (2020) found similar levels of phylogenetic beta diversity in primary and secondary forests. Interestingly, MPD decreases with age of secondary forests in New World tropics in a similar way as reported here (Hughes et al., 2020), a result in part explained by the overlap in data used in the analysis.

Higher phylogenetic diversity of birds that colonize the secondary forests in our study sites is likely explained, in part, by the fact that the species tolerant or favored by disturbance represent distant evolutionary lineages and, therefore, increase the phylogenetic diversity of the assemblages (see Santo-Silva et al., 2018 for examples in plant assemblage). Apparently there is a kind of phylogenetic compensatory effect (Morante-Filho et al., 2018) in disturbed habitats similar to those reported in taxonomic diversity (see above). Indeed, the phylogenetic diversity of non-forest birds had a substantial contribution to the total bird phylogenetic diversity in severely deforested Atlantic forest (Morante-Filho et al., 2018). It is also important to emphasize that, although these “weed” species had low conservation value, they performing a key role in forest restoration through seed dispersal (Cardoso da Silva et al., 1996, Carlo and Morales, 2016).

Additionally, distinct bird clades specialized in different habitats may increase the phylogenetic diversity of birds colonizing the secondary forests. For example, we recorded in the same secondary forest site the distant related Dusky antbird (*Cercomacroides tyrannina* - Thamnophilidae) and Marbled Wood-Quail (*Odontophorus gujanensis* - Odontophoridae), two species typically found in flooded forests and *terra firme* forests, respectively. In our study sites, a variety of habitats including flooded forests, open habitats and old growth forests serve as source for birds that colonize secondary forests, especially in the earlier phases of regeneration (Borges, 2007).

Patterns in phylogenetic diversity have also been used to infer the relative importance of abiotic filtering and biotic interactions among species during the ecological succession (Letcher, 2009, Chai et al.,

2016). Previous work suggested that abiotic filtering is more influential in the early stages of succession, resulting in a predominance of closely related species in the assemblages (phylogenetic clustering). In latter stages of succession, as well as in primary forests, the assemblages will be more affected by biotic interactions (e. g. competitive exclusion) and contains higher number of species less related to each other (phylogenetic overdispersion or evenness). Plant studies along gradients of succession in tropical and temperate ecosystems gave broad support to these expectations (Letcher et al., 2012, Whitfeld et al., 2012, Purschke et al., 2013, Satdichanh et al., 2019).

Contrary to this, our results show a trend from overdispersion to phylogenetic clustering along the gradient of successional forests to old growth forests. Assuming that secondary forests presents a different set of environmental conditions, our results suggests that the abiotic filtering promotes phylogenetic dispersion among bird species, just the opposite trend reported in plant assemblages. Being sessile organisms, plants may be more susceptible to strong environmental modification in the early stages of successions resulting in more phylogenetic impoverished assemblages (Grass et al., 2015). In contrast, the dispersive abilities of birds allowing them to move among patches of different habitats, favoring the mixture of species from distinct lineages (Grass et al., 2015). In this sense, how environmental filtering and biotic interactions affects species differ among animal and plant assemblages along ecological succession, a hypothesis that deserves further investigation.

Our data was collected in landscapes composed mostly of large blocks of continuous low-disturbed forests with small patches of secondary forests resulted from small scale agriculture. This ecological context contrasts with landscapes in other amazonian regions (e.g. eastern Amazon) where large-scale deforestation affects extensive areas of low-disturbed forests, and secondary forests are continuously degraded by recurrent deforestation and burning (Carvalho et al., 2019, Nunes et al., 2020). In such highly-degraded landscapes, habitat disturbance negatively affected the functional and taxonomic diversity of birds (Bregman et al., 2016). Even so, our results are broadly applicable since familiar agriculture is a common practice in most part of the Amazon basin that still is covered by vast extensions of continuous rainforest (Cruz et al., 2020).

4.2. Conclusions

Bird taxonomic and functional diversity, as well as their phylogenetic relationships, exhibit complex changes during forest regeneration, even in small scale agricultural landscape. Given this complexity, the use of measurements that represents complementary biodiversity dimensions helps to improve our understanding the assemblage dynamics through ecological succession. Overall, old growth forests harbored higher diversity of disturbance-vulnerable species, but with similar functional roles and less phylogenetic diversity than secondary forests. Our results also show that species tolerant to disturbance have an important contribution in restoring bird diversity by compensating the loss of avian taxonomic diversity during the conversion of undisturbed forests to agricultural fields. In similar way, these ecologically flexible species enrich the phylogenetic history of birds in disturbed landscapes. Additionally, functional evenness and divergence suggest that resources availability and their use by birds are altered along the secondary succession and that niche complementarity among species apparently is reduced in more intensively used sites. As secondary forests intensively disturbed lose their biodiversity and ecosystem values (Jakovac et al., 2015, Carvalho et al., 2019, Nunes et al., 2020), assisted regeneration management such as planting fast-growing species, could increase recovery rates in secondary forests (Jakovac et al., 2015) and may also favor the functional dimension of bird assemblage.

CRediT authorship contribution statement

Sérgio Henrique Borges: Conceptualization, Formal analysis, Funding acquisition, Methodology, Validation, Visualization, Writing - original draft, Writing - review & editing. **Tarcísio do R.S. Tavares:** Conceptualization, Formal analysis, Writing - review & editing. **Nicholas M.A. Crouch:** Formal analysis, Writing - review & editing. **Fabricio Baccaro:** Conceptualization, Formal analysis, Visualization, Writing - review & editing.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

Acknowledgements

We are grateful to the traditional farmers of Jau National Park for kindly share their valuable knowledge about traditional agriculture. Eduardo and Antenor Anicácio helped with the field work. Permits to work in Jau National Park were provided by ICMBIO, institution responsible to manage the Park. Financial and logistic support for this study came from WWF Brazil, Fundação Vitória Amazônica, and CAPES. During the execution of the analysis, the first author received a grant from Fundação de Amparo à Pesquisa do Amazonas (FAPEAM) (Fixam program, Edital no. 017/2014). We also appreciate the institutional support from Zoology Graduate Program of Federal University of Amazonas and Coordination for the Improvement of Higher Education Personnel (CAPES). FF FBB is continuously supported by CNPq grant (#309600/2017-0). Suggestions of two anonymous reviewers greatly improve the clarity and readability of the text.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118731>.

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