Research article

Assessing the recovery in species, size and location diversities of a lowland tropical rainforest after shifting cultivation by multiple indices at stand and neighborhood scales

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ABSTRACT

Tropical forests are rapidly being converted for agricultural use, but abandoned agricultural lands can recover naturally through secondary succession. However, comprehensive knowledges of how species composition, size structure and spatial patterning (represented by species, size and location diversities) change during recovery at multiple scales are still lacking. Our aim was to explore these change patterns to understand the underlying mechanisms of forest recovery and propose corresponding solutions for restoring regrowing secondary forests. Here, twelve 1ha forest dynamics plots (4 plots each in young-secondary forests (YS), old-secondary forests (OS) and old-growth forests (OG) from a chronosequence of tropical lowland rainforest after shifting cultivation) were used to assessed the recovery in species, size and location diversity of trees at stand (plot) and neighborhood (focal tree and its neighbors) scale by using 8 indices. The relative recoveries of YS and OS were quantified by dividing each of the indices in YS and OS to those in OG. Results showed that species and size diversity increased while location diversity decreased with the recovery process. The relative recovery of location diversity was higher than those of species and size diversity in both YS and OS, while species diversity was only higher than size diversity in YS. The relative recovery of species diversity at neighborhood scale was higher than that at stand scale in OS, while there were no differences between scales in size and location diversity. Additionally, using only the Shannon index and Gini coefficient at two scales can provide consistent insights into the recovery patterns of diversity as indicated by the 8 indices. Our study demonstrated that recovery rates of secondary forests relative to old-growth counterparts could be comprehensively quantified using multiple diversity indices in three types at two scales. This quantitative assessment on the relative recovery of disturbed forests could be helpful in applying appropriate management activities and selecting rational approaches to speed up restoration process of degraded forest ecosystems.

1. Introduction

Tropical forests are critical to biodiversity conservation and climate change mitigation (Brancalion et al., 2019). However, the rapid growth of the population and demand for food have resulted in the destruction and conversion of large areas of old-growth tropical forests into agricultural lands (Poorter et al., 2021a). Abandoned agricultural lands can naturally regenerate through secondary succession (Poorter et al., 2021b), and these regrowing secondary forests (SFs) now occupy a significant proportion of tropical forests (Chazdon et al., 2016; Powers and Marín-Spiotta, 2017). However, the rate and trajectory of SFs

recovery varies greatly across regions (Chave et al., 2020; Poorter et al., 2021b), highlighting the need for quantitative assessments of the recovery process in each area (Poorter et al., 2016, 2021a). In tropical Asia, most studies have focused on the recovery of forests during fallow periods (Sovu et al., 2009; Tongkoom et al., 2018; Wangpakapattanawong et al., 2010), while few have investigated the long-term recovery of abandoned lands (Ding et al., 2012; Tian et al., 2022).

To date, studies on the recovery of tropical SFs on the abandoned lands have mainly focused on species diversity (Rozendaal et al., 2019; Sovu et al., 2009), forest structure (Mukul et al., 2020; Peña-Claros, 2003), functional traits (Chazdon et al., 2016; Poorter et al., 2021b), and

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abiotic environment (Ayala-Orozco et al., 2018). Recently, a global study has quantified the multidimensional recovery of these SFs by using 12 attributes from all four aspects, indicating the species richness, structural heterogeneity and maximum tree size can better reflect the capacity of secondary forest ecosystem to recover (Poorter et al., 2021a). All of these three indices fall under the category of diversity, highlighting its central role in the recovery process. A comprehensive knowledge of the recovery process of diversities during succession is a prerequisite for the rapid restoration and fulfillment the ecological functions of SFs (Cardinale et al., 2012; De Boeck et al., 2006; Hui et al., 2019).

The diversities of trees in a forest community can be grouped into three types: species diversity, size diversity, and location diversity (Gadow and Hui, 2002; Neumann and Starlinger, 2001; Pommerening, 2002). Common measures of species diversity include the species richness (Fisher et al., 1943), Shannon index (Shannon, 1948), and Simpson index (Simpson, 1949). Measures of size diversity include the Shannon index (Buongiorno et al., 1994), coefficient of variation (Montes et al., 2005), and Gini coefficient (Gini, 1921). Measures of location diversity include the Pielou index (Pielou, 1959) and Clark-Evans index (Clark and Evans, 1954). These indices have been tested by numerous studies since they were proposed and have proved to be effective indices for monitoring diversity (Lexerød and Eid, 2006; Peña-Claros, 2003; Poorter et al., 2021a; Rozendaal et al., 2019). However, these metrics are almost limited to the stand scale, and the spatial relationship information at neighborhood scale are often ignored (Fichtner et al., 2018; Man and Yang, 2015).

In forest ecosystems, the basic ecological processes are strongly influenced by intraspecific and interspecific interactions (competitive or facilitation) between neighboring trees (Chen et al., 2016; Fichtner et al., 2017; Forrester and Bauhus, 2016; Glatthorn, 2021). Therefore, indices such as Mingling, Size Differentiation, and Uniform angle index (Aguirre et al., 2003; Gadow and Hui, 2002) were developed to evaluate neighborhood-scale diversity, as they can reflect the neighboring interactions and enable multi-scale analysis (not only at neighborhood scale, but can upscale to species or stand scale) (Glatthorn, 2021; Hui et al., 2019). It is worth noting that Man and Yang (2015) applied the Shannon index to neighborhood scale, allowing for diversity comparison between stand and neighborhood scales using the same index. Despite this, these neighborhood indices have not been well applied in the study of secondary forest recovery.

Although comprehensive research on various diversity characteristics at different scales can provide us with a more accurate understanding of ecological mechanism behind complex forest community dynamics, there is a lack of quantitative assessment on the recovery in different facets of diversity during secondary forest succession. The complex structure of biodiverse tropical forests makes them an ideal object for studying variations in the three types of diversity at both stand and neighborhood scales during the recovery process. Here, based on a chronosequence of tropical lowland rainforest in Hainan Island, China, we quantified the relative recovery rates of three types of diversity (species diversity, size diversity, and location diversity) by multiple indices at two scales (stand and neighborhood scale) during the secondary recovery process of a lowland rainforest after shifting cultivation. The objective of this study was to understand the underlying mechanisms of forest recovery by exploring the variation patterns among different diversity types and scales with the recovery process, and ultimately proposing comprehensive and targeted solutions for restoring diversity in secondary forest ecosystems.

2. Material and methods

2.1. Study site and data collection

This study was carried out in the Bawangling Forest Region (18°52' – 19°12' N, 108°53' – 109°20' E), situated on Hainan Island, China. The region boasts a diverse topography, with elevations ranging from 100 to 1654 m asl. Being under the influence of the tropical monsoon, the region experiences a seasonal distribution of precipitation, with the wet season from May to October, and the dry season (monthly rainfall less than 100 mm) from November to April. The mean annual temperature and precipitation reach 22.5 °C and 2553 mm, respectively, at elevations of 600 m asl (Zang et al., 2010). The dominant vegetation types in this region include lowland rainforest, mountain rainforest, mountain evergreen forest, and alpine dwarf forest. The tropical lowland rainforests are mainly located at altitudes below 800 m and were primary subject of shifting cultivation (Zang et al., 2010). Most of these rainforests were subject to extensive (more than 80%) extraction of wood volume and at least five cycles of shifting cultivation, with ca. 15–20 years fallow periods, except for a few old-growth forests that were reserved (Ding et al., 2012). Since the 1950s, numerous agricultural lands have been abandoned after multi-cycle shifting cultivation, leading to the formation of secondary forests of different ages through secondary succession (Ding and Zang, 2021).

Between 2009 and 2010, twelve forest dynamics plots (FDPs) were established in tropical lowland rainforests with three distinct recovery stages in Bawangling Forest Region according to the standard of Center for Tropical Forest Science (CTFS). Four FDPs were randomly distributed in forests at each of the three recovery stages: the young secondary forests (YS, ca. 24 years old), the old secondary forests (OS, ca. 60 years old) and the old-growth forests (OG), respectively. The old-growth forests have a recovery history of nearly 500 years without obvious human disturbance (Tian et al., 2022), which can be served as a reference for calculating the relative recovery of secondary forests. Each plot measured 1-ha (100 m × 100 m) and was further divided into 25 subplots (20 m × 20 m) to record the tag, species, diameter at breast height (DBH), height and coordinates of trees with DBH ≥ 1 cm. In this study, only trees with DBH greater than 5 cm were used to calculate diversity indices.

2.2. The quantification of diversity

In this paper, diversity was quantified by multiple commonly used indices in species diversity, size diversity and location diversity at stand and neighborhood scales (Man and Yang, 2015; Pommerening and Grabarnik, 2019). Each diversity type consists of three categories of indices: one for stand scale, another for neighborhood scale, and the third can be applied to both scales. This allowed for comparison of diversity across different scales. To ensure comparability among diversity types, indices selected under the same category had better be the same or have similar nature. Finally, eight indices were chosen and twelve values were calculated to quantify diversities (Table 1). Each diversity type contains 2 values at stand scale and 2 values at neighborhood scale.

The indices at stand scale are constructed based on the information of the whole stand (usually represented by a sample plot). While the indices at neighborhood scale are constructed based on the information of local neighborhood (structural unit, a focal tree and its k neighboring trees, and the abbreviations will mark with capital "U"). We set the parameter k of neighborhood scale equal to 6 because we found the 6 neighboring trees (the average and largest proportion number) can represent the neighborhood of a focal tree in most cases (Fig. S1) by established Voronoi diagram with tree coordinates of each plot (Brown, 1965). Indices at neighborhood scale were summarized into the mean of the plot for comparison with indices at stand scale.

Except for Clark-Evans index, all indices that have higher values indicate greater diversity. In addition, the value of Clark-Evans index from 0 through 1 to 2.1491 and of Uniform angle index from 1 through 0.5 to 0 indicate a shift in spatial pattern from aggregate through random to regular and the decrease of location diversity (Ehbrecht et al., 2017; Glatthorn et al., 2021; Neumann and Starlinger, 2001; Parrott, 2010; Ziegler et al., 2017). All indices that need to judge the neighbor require the edge correction (Pommerening and Stoyan, 2006), include

Table 1
The equations of diversity indices.

Indices	Formulae		Descriptions
Species diversity			
Species richness (Fisher et al., 1943)	$N\_sp = s$	(1)	s - number of species in plot.
Shannon index (Shannon, 1948)	$H\_sp = -\sum_{i=1}^{s} p_i \, ln(p_i)$	(2)	p_i - proportion of ith species in plot.
Shannon index	$H\_Usp = -\sum_{i=1}^{t} p_j \, ln(p_j)$	(3)	p_j - proportion of jth species in structural unit, t - number of species in structural unit.
Mingling index (Gadow and Hui, 2002)	$M\_Usp = \frac{1}{k}\sum_{j=1}^{k} v_j$	(4)	v_j equal to 1 when the species of focal tree is the same as its jth neighbor tree, and 0 otherwise; k - number of neighbor trees for the focal tree.
Size diversity			
Diameter range (Pretzsch et al., 2016)	$Rng\_dm = \max(d) - \min(d)$	(5)	d - DBHs of trees in plot.
Gini coefficient (Gini, 1921)	$GC\_dm = \frac{\sum_{i=1}^{n}(2i - n - 1)d_i}{\sum_{i=1}^{n} d_i(n-1)}$	(6)	d_i - ith DBH in plot, i - rank of the value in plot in ascending order, n - number of trees in plot.
Gini coefficient	$GC\_Udm = \frac{\sum_{j=1}^{m}(2j - m - 1)d_j}{\sum_{j=1}^{m} d_j(m-1)}$	(7)	d_j - jth DBH in structural unit; j - rank of the value in structural unit in ascending order; m - number of trees in structural unit.
Diameter differentiation index (Gadow and Hui, 2002)	$T\_Udm = \frac{1}{k}\sum_{j=1}^{k}\left(1 - \frac{\min(d_i, d_j)}{\max(d_i, d_j)}\right)$	(8)	d_i and d_j - DBHs of focal tree i and its neighbor tree j;
Location diversity			
Clark-Evans index (Clark and Evans, 1954)	$R\_pd = \frac{\overline{r_A}}{\overline{r_E}} = \frac{\frac{1}{n}\sum_{i=1}^{n} r_i}{1/2\sqrt{n/A}}$	(9)	r_i - distance of the ith focal tree to its nearest neighbor; $\overline{r_A}$ - observed average distance; $\overline{r_E}$ - expected average distance under a random tree distribution pattern; A - plot area.
Gini coefficient	$GC\_pd = \frac{\sum_{i=1}^{y}(2i - y - 1)t_i}{\sum_{i=1}^{y} t_i(y-1)}$	(10)	t_i - ith distance among neighboring trees in Voronoi diagram of plot. y - number of distances in plot.
Gini coefficient	$GC\_Upd = \frac{\sum_{j=1}^{k}(2j - k - 1)t_j}{\sum_{j=1}^{k} t_j(k-1)}$	(11)	t_j - distance between focal tree and its jth neighbor tree.
Uniform angle index (Gadow and Hui, 2002)	$W\_Upa = \frac{1}{k}\sum_{j=1}^{k} z_j$	(12)	z_j equal to 1 when the jth angle α_j, formed by the focal tree and its two adjacent neighbors, is bigger than $360°/(k + 1)$, and 0 otherwise;

Note: Indices underlined indicate that they are calculated at neighborhood scale, otherwise they are calculated at stand scale. The parameter descriptions for different indices are universal, meaning that once a parameter is defined in the description of one index, it also applies to the subsequent indices. The indices of species diversity are based on tree species (_sp), reflect the abundance (Species richness, N_sp), proportional abundance (Shannon index, H_sp and H_Usp) and spatial mixing (Mingling index, M_Usp) of tree species populations. The indices of size diversity are based on tree diameters (_dm), reflect the distribution range (Diameter range, Rng_dm), dispersion degree (Gini coefficient of diameter, GC_dm and GC_Udm) and spatial differentiation (Diameter differentiation index, T_Udm) of tree sizes. The indices of location diversity are based on angles of positions (_pa) or position distances (_pd), reflect the inhomogeneity of tree locations (spatial pattern from regular though random to clustered; Clark-Evans index, R_pd, and Uniform angle index, W_Upa) or of distances among trees (Gini coefficient of position distance, GC_pd and GC_Upd).

the Clark-Evans index, Gini coefficient of position distance and other indices at neighborhood scale. A buffer zone of 5 m was set to all plots at their boundary to reduce the estimation error from the edge effects, only the trees in the 90 m × 90 m core area (focal trees) were used to calculate these indices.

2.3. Data analysis

The Kruskal-Wallis test and Wilcox rank sum test were used to assess differences in mean recovery values among different stages, types, scales and indices. All the values within each diversity type were used to evaluate the differences between types, while only the values from the indices that applied at both stand and neighborhood scales (i.e., Shannon index and Gini coefficient) were used to evaluate the differences between two scales.

To allow for direct comparisons across indices, the recovery of diversity indices in YS and OS was normalized as relative recovery (%) in comparison to OG. The relative recovery (%) indicates how closely the diversity values of YS and OS match those of OG (Poorter et al., 2021a). Before calculating the relative recovery, each index needs to conduct forward standardization. For indices that increase with recovery, the theoretical minimum value of the index should be subtracted from the value of all plots (including the old-growth forests). For indices that decrease with recovery, the theoretical maximum value of the index should be used to subtract the values of all plots. After standardization, the relative recovery of various indices Rel_{recov} (%) can be calculated using the following equation (Poorter et al., 2021a):

$$Rel_{recov} = e^{-|ln(SF/\overline{OG})|} \times 100 \tag{13}$$

Where, SF is the value of index in a secondary forest plot. $\overline{OG}$ is the average value of the corresponding index in the old-growth forest plot. The maximum value of the relative recovery is 100%. To determine whether the index of secondary forest had restored to the state of the old-growth forest, we used a relative recovery threshold of 90% as the standard for the complete recovery (Poorter et al., 2021a).

To examine the intrinsic correlation of diversity indices during the recovery process, we calculated the Pearson correlation coefficient between indices using the relative recovery values obtained from the YS and OS stages.

To determine whether partial indices can accurately reflect diversity recovery patterns and capture recovery differences among types or scales. We chose the indices of Shannon index in species diversity (H_sp, H_Usp), Gini coefficient in size diversity (GC_dm, GC_Udm) and location diversity (GC_pd, GC_Upd) that can apply to both stand and neighborhood scales. The sensitivity analysis was conducted by evaluating whether the use of these partial indices alone is consistent with the use of 8 overall indices in terms of capturing the recovery rates of diversity types and recovery differences among types or between scales. All statistical analysis were performed using R v4.1.3 (R Core Team, 2022).

3. Results

3.1. Variation patterns of diversity indices across recovery stages

All types of diversity indices changed gradually from young secondary forest (YS) through old secondary forest (OS) to old-growth forest (OG). Species diversity and size diversity indices increased, while location diversity indices decreased (Fig. 1). There were significant differences in all indices among the recovery stages ($P < 0.05$). However, the differences between YS and OS in N_sp, H_sp, Rng_dm, GC_Upd and between OS and OG in R_pd, GC_Upd were not significant ($P \geq 0.05$).
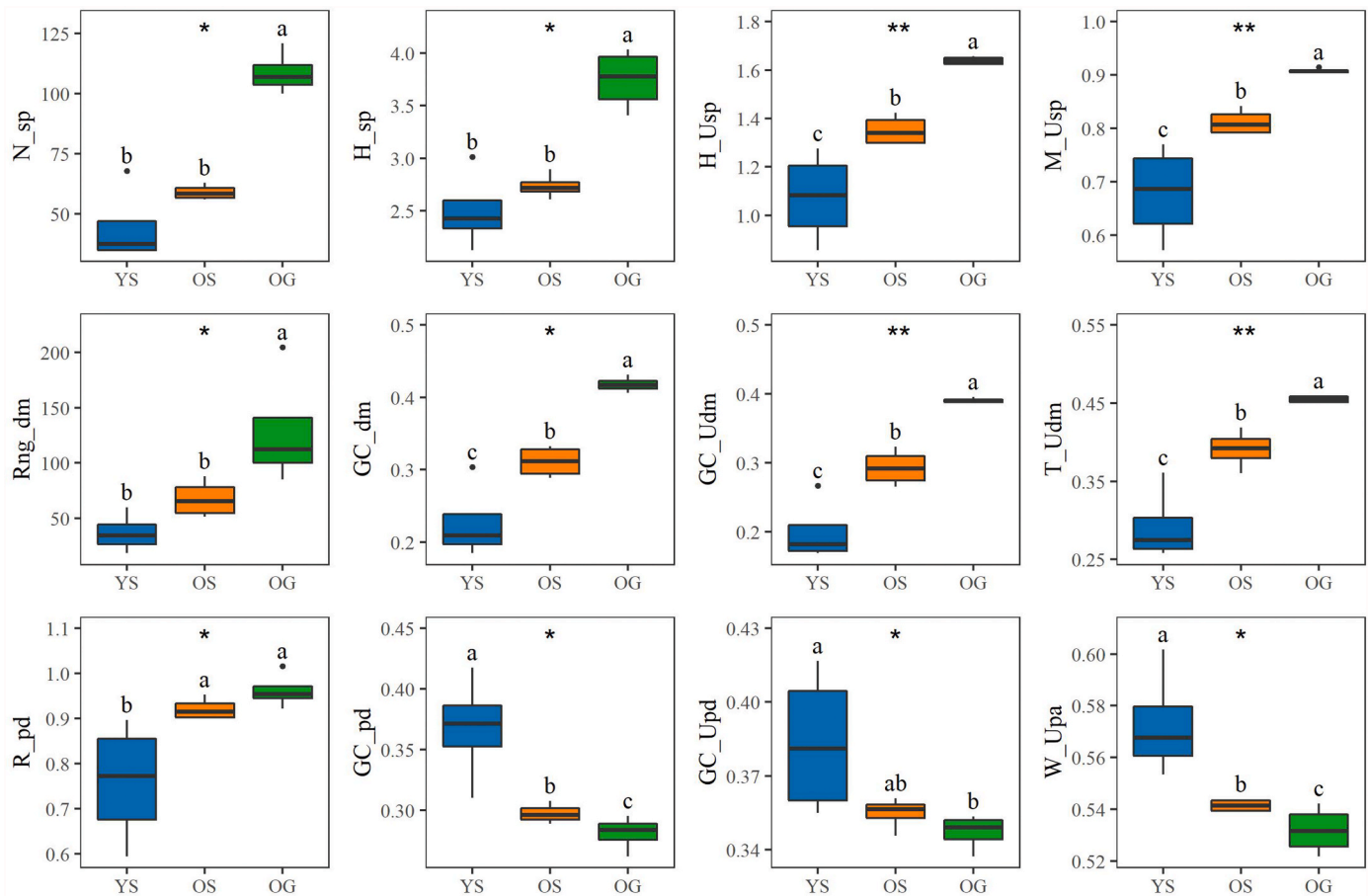
Fig. 1. Recovery of diversity indices across recovery stages. YS, young-secondary forests; OS, old-secondary forests; OG, old-growth forests. Asterisks above the graph indicate significant differences among the recovery stages: "*", $P < 0.05$; "**", $P < 0.01$. Completely different of lowercase letters indicated significant difference between two recovery stages ($P < 0.05$).

3.2. Relative recovery of diversity indices across different types

The lowest and highest relative recovery values for species diversity, size diversity, and location diversity in YS were 40.9%, 28.5%, 78.9% and 74.8%, 64.2%, 94.5% (Fig. 2a), while in OS the corresponding values were 54.3%, 52.4%, 95.8% and 89.4%, 85.9%, 98.7% (Fig. 2b). The relative recovery of location diversity was significantly higher than that of species diversity and size diversity in both stages ($P < 0.05$). However, the relative recovery of species diversity was only significantly higher than that of size diversity in YS (Fig. 2a, $P < 0.05$).

3.3. Relative recovery of diversity indices at different scales

The differences among the stand and neighborhood scale indices were not significant in location diversity (Fig. 2, $P \geq 0.05$) but significant in species diversity and size diversity ($P < 0.05$) in both stages. Specifically, the relative recoveries of M_Usp and T_Udm (neighborhood scale indices) were significantly higher than those of N_sp and Rng_dm (stand scale indices) in both stages, respectively (Fig. 2, $P < 0.05$). However, only the Shannon index (H_Usp and H_sp) showed a significant difference between the same index at two scales in OS (Fig. 2b, $P < 0.05$).

3.4. Correlation of different diversity indices based on relative recovery

In both stages (Fig. 3), most indices of same diversity type showed a strong positive correlation with each other. However, there were no significant correlations among the indices of species diversity at stand

scale (N_sp and H_sp) and the neighborhood scale (M_Usp and H_Usp) in YS (Fig. 3a, $P \geq 0.05$), and the diameter range (Rng_dm) did not correlate with the other three indices of size diversity (GC_dm, GC_Udm and T_Udm) in OS (Fig. 3b, $P \geq 0.05$).

Among the indices of different diversity types in YS (Fig. 3a), the species diversity at stand scale (N_sp and H_sp) and at neighborhood scale (M_Usp and H_Usp) were strongly positively correlated with size diversity and location diversity, respectively. However, there was no significant positive correlation between size diversity and location diversity ($P \geq 0.05$). In OS (Fig. 3b), the correlations among the three diversity types were not significant ($P \geq 0.05$), although the correlations of location diversity with species diversity and size diversity had changed from positive to negative.

3.5. Sensitivity analysis of using partial indices to detect the diversity recovery patterns

There is no significant difference between the mean values of partial indices and overall indices for each diversity type, whether it is YS or OS ($P \geq 0.05$, Fig. 4a and b). The results obtained from partial indices (Fig. 5a and b) were consistent with those obtained from overall indices (Fig. 2a and b) in detecting recovery differences in diversity between scales and among types.
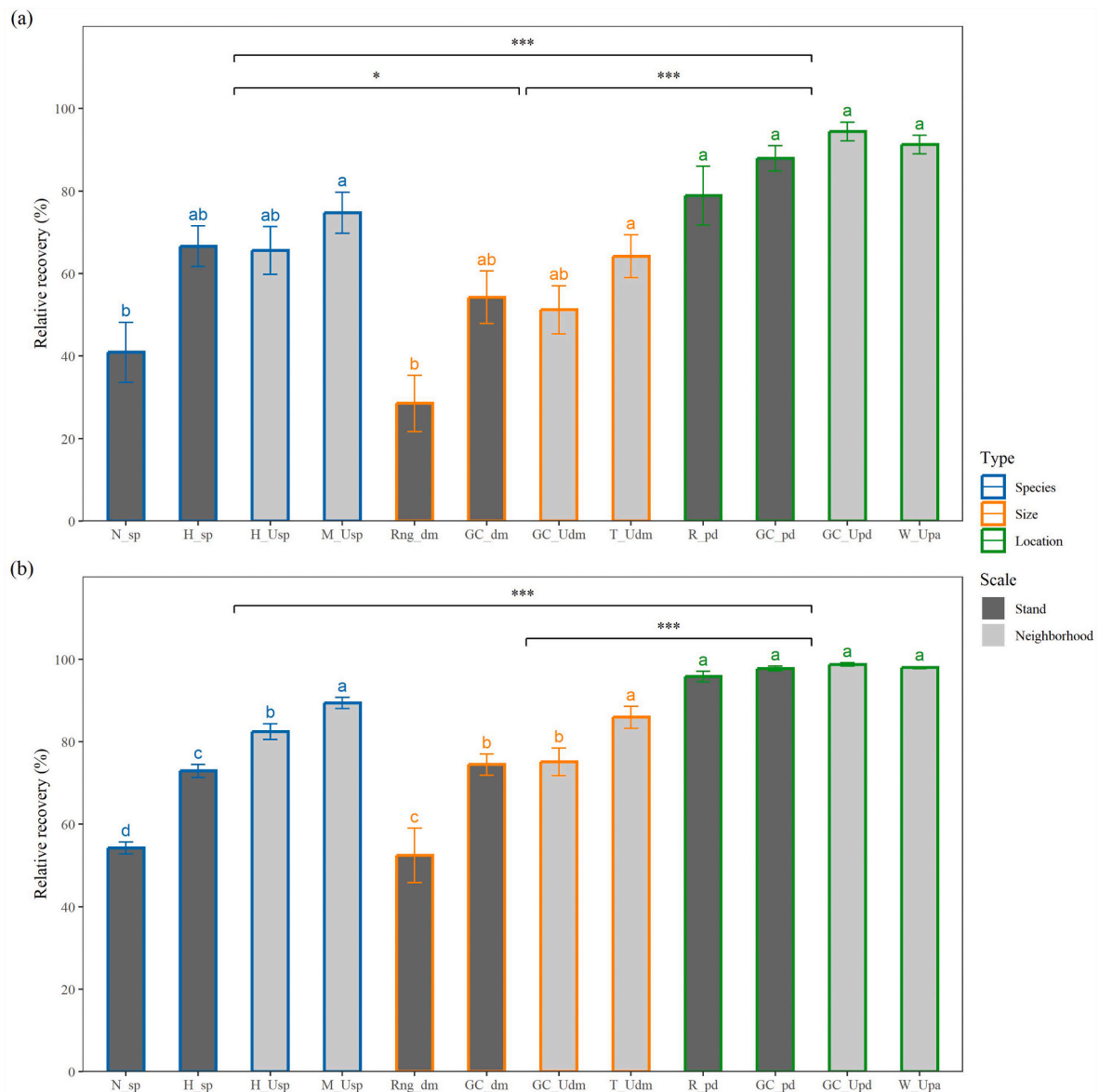
Fig. 2. Relative recovery (%) of diversity indices in YS (a) and OS (b). Completely different of lowercase letters indicated significant difference among indices within the same diversity type ($P < 0.05$). Asterisks above the solid line indicate the significant differences among the types ("*", $P < 0.05$; "**", $P < 0.01$; "***", $P < 0.001$).

4. Discussions

4.1. The species diversity and size diversity increased, while location diversity decreased during the recovery process

The gradual recovery trend observed in all diversity indices from YS through OS to OG (Fig. 1) supports the theory of predictable successional pathways (Norden et al., 2015; Rees et al., 2001). Consistent with most previous studies on Species richness (Dupuy et al., 2012; Wang-pakapattanawong et al., 2010), Gini coefficient of diameter (Poorter et al., 2021a), and Spatial pattern (Moustakas et al., 2008) at the stand scale, our findings showed an increase in species and size diversity, and a decrease in location diversity (from aggregation to random) during the recovery of secondary forests (Fig. 1).

The abandoned shifting cultivation lands were successively colonized by various tree species through seed rain and seed bank, resulting in an increase in species diversity (Chazdon, 2008). As time passed, the differentiation in tree size due to various niches or asymmetric competition led to an increase in size diversity (Ali et al., 2019). The Jansen-Connell effect and competitive exclusion resulted in the

separation of tree positions from aggregation, leading to a decrease in location diversity (Moustakas et al., 2008; Szmyt, 2012; Wang et al., 2021).

4.2. Location diversity recovers faster than species and size diversity

The recovery of species, size, and location diversity are impacted by three fundamental processes: recruitment, growth, and mortality (Gadow et al., 2012; Pretzsch, 2009). Recruitment, influenced by dispersal limitations and environmental filtering, brings about new random tree positions, small diameter trees, and potential new species (Chazdon, 2008), which can decrease location diversity (Pommerening, 2002) and increase species and size diversity (Wolf, 2005). Mortality, driven by asymmetric competition and the Jansen-Connell effect, eliminates tree with old positions and certain sizes, and relieved the aggregation of the same species (Gadow et al., 2012), which can decrease location diversity (Moustakas et al., 2008) but increase species and size diversity (Zhou et al., 2022). However, the growth process, driven by time and site conditions, only accelerates the differentiation of tree size and the rise of size diversity, but has little direct effect on
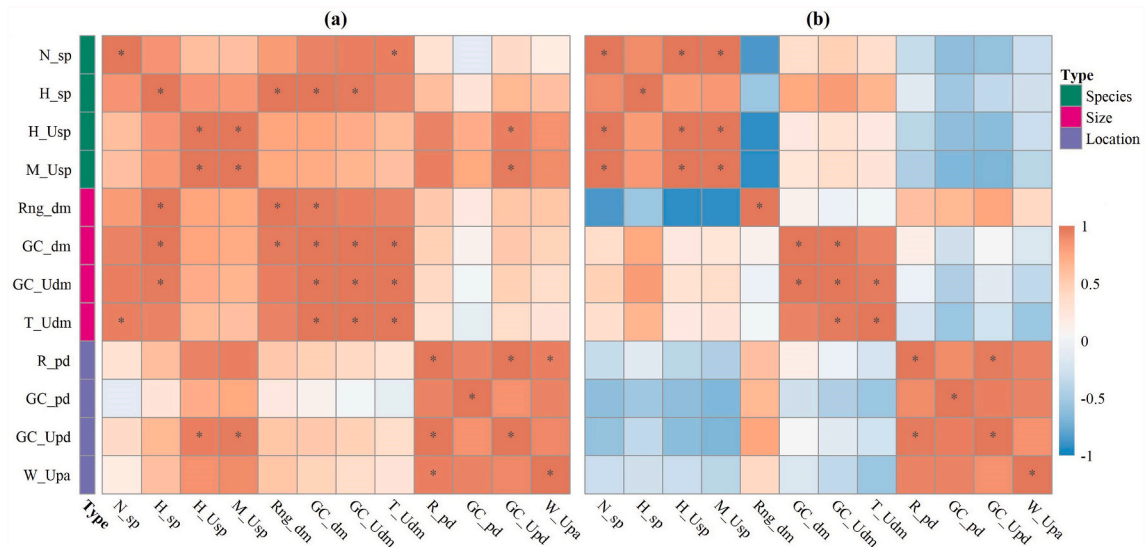
Fig. 3. Correlation matrix of diversity indices based on relative recovery in YS (a) and OS (b). Significant correlations ($P < 0.05$) are denoted with the symbol "*".
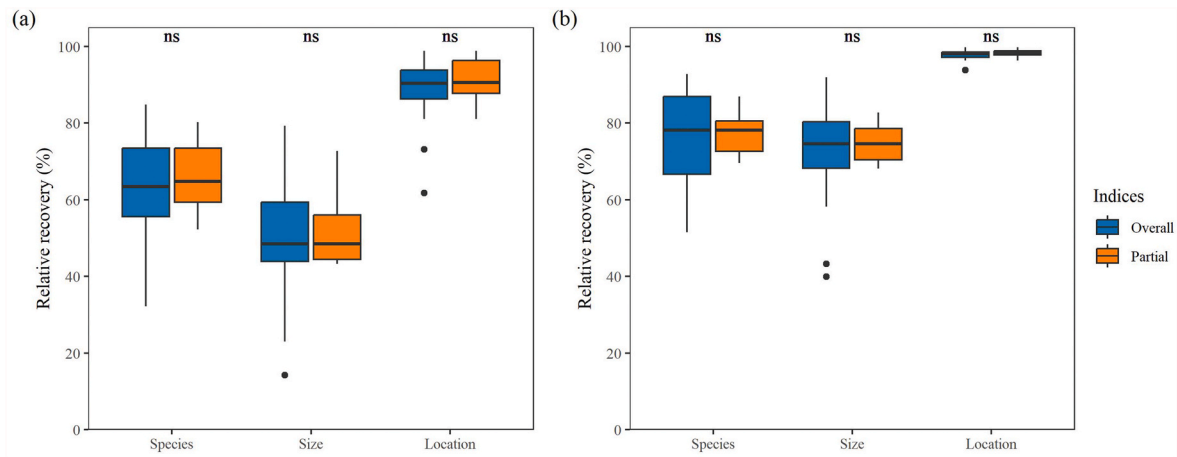

Fig. 4. Relative recovery (%) of each type of diversity using overall and partial indices in YS (a) and OS (b). "ns" indicated no significant difference ($P \geq 0.05$).
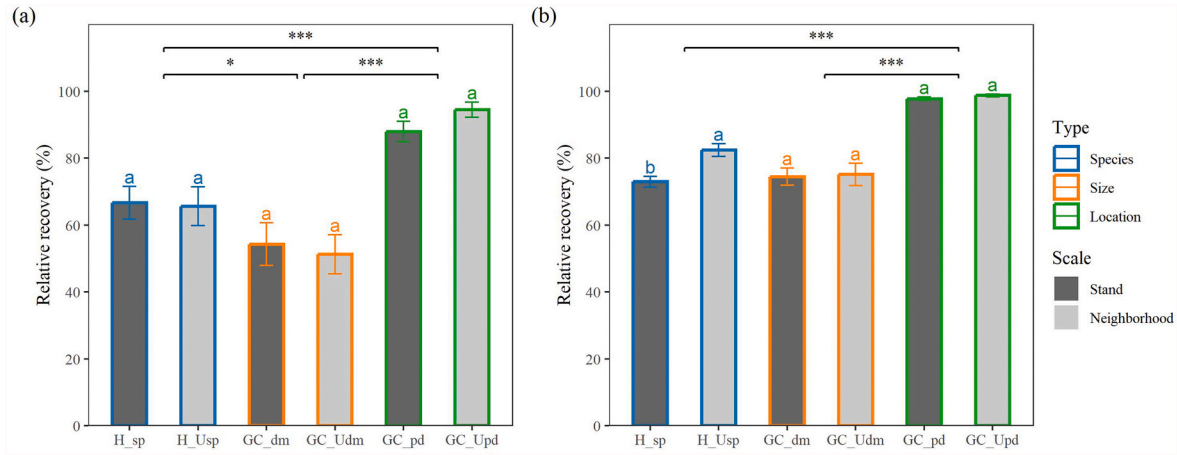

Fig. 5. Relative recovery (%) of partial indices in YS (a) and OS (b). Completely different of lowercase letters indicated significant difference of diversity indices at different scales under the same type ($P < 0.05$). The asterisks above the solid line indicate the significant differences among the types ("*", $P < 0.05$; "**", $P < 0.01$; "***", $P < 0.001$).

location and species diversity (Franklin and Van Pelt, 2004).

We found that location diversity recovered faster than size and species diversity both in YS and OS (Fig. 2a and b). This is because frequent mortality and recruitment process strongly influenced the recovery of location diversity, while they had a moderate effect on species diversity. On the other hand, size diversity was mainly driven by the slow growth process. Our results indicate that some location diversity indices had reached complete recovery (above 90%) in both stages, while none of the indices in size and species diversity had reached complete recovery in either stage. Murdjoko et al. (2022) and Tongkoom et al. (2018) have also both pointed out that the complete recovery of species diversity and forest structure may take longer in regrowing secondary forests.

Furthermore, our findings indicate that species diversity recovered faster than size diversity in the early stage of recovery (YS, Fig. 2a) but slowed down in the later stage, leading to no significant difference with size diversity (OS, Fig. 2b). The accelerated recovery of species diversity in the early stage may due to the rapid recruitment of new tree species, while the slowdown in the later stage may due to propagule restrictions and species replacement (Chazdon, 2008). This pattern is supported by a study on the recovery of forest diversity and structure in the Philippines (Mukul et al., 2020) but differ from studies in the Neotropics and West Africa (Poorter et al., 2021a), possibly due to the preservation of large diameter trees during shifting cultivation.

4.3. The relative recovery between stand and neighborhood scales was only discrepant in species diversity

We compared the same index (Shannon index, Gini coefficient of diameter or Gini coefficient of point distance) between the neighborhood and stand scales to determine whether the recovery varied by scale while avoiding the potential influence of differences in indicator construction methods. The results revealed that the relative recovery at neighborhood and stand scales was discrepant only in species diversity, while the differences were not significant in size diversity and location diversity (Fig. 2).

The relative recovery of species diversity at neighborhood scale (H_Usp) did no differ from that at stand scale (H_sp) in YS (Fig. 2a) but was significantly higher in OS (Fig. 2b). This pattern indicated that the recovery of species diversity at stand scale were slower than that at neighborhood scale. The interval from YS to OS corresponds the conversion from stem exclusion phase to understory reinitiation phase (Chazdon, 2008). The replacement of pioneer species by later-successional species and propagule restriction of new species may have contributed to the slower recovery of species diversity at stand scale (Oliver and Larson, 1996). However, the recovery of species diversity at neighborhood scale benefited from the abundance of species in tropical secondary forests, and a focal tree could easily meet a different species of trees in the neighborhood, thus minimizing the impact of species replacement and propagule restriction.

There was no significant difference in relative recovery of size diversity between two scale (GC_dm and GC_Udm) in both stages (Fig. 2a and b). Lexerød and Eid (2006) showed that the Gini coefficient of diameter was not sensitive to the scale. This may suggest that although asymmetric competition of individual trees at neighborhood scale created size diversity, size differentiation developed synchronously in practically every location of the stand throughout the recovery.

The difference in relative recovery of location diversity between two scales (GC_pd and GC_Upd) was also not significant in both stages (Figs. 2a and 3b). This was probably because location diversity was strongly affected by frequent mortality and recruitment process in the stand initiation phase and stem exclusion phase (Chazdon, 2008), and almost fully recovered in YS and OS.

4.4. The interrelations among diversity types have changed during the recovery

Species diversity at stand scale was strong positive correlated with size diversity in YS (Fig. 3a), while the correlation became insignificant in OS (Fig. 3b). The niche differentiation hypothesis suggests that higher species diversity at stand scale leads to the coexistence of tree species with different growth rates and maximum height, thereby promoting the development of size diversity. This, in turn, creates a diverse living environment that facilitates the survival of new tree species and promotes an increase of tree species diversity during the early recovery phase (Ali et al., 2019; Tetemke et al., 2021). However, propagule restriction and species replacement during the later recovery phase may retard the recovery of species diversity at stand scale (Chazdon, 2008), leading to a change in the correlation to insignificance.

There was a strong positive correlation between species diversity at neighborhood scale and location diversity in YS (Fig. 3a), while the correlation became insignificant and even negative in OS (Fig. 3b). Dispersal limitations and environmental filtering (Seidler and Plotkin, 2006; Shen et al., 2013) suggest that conspecific trees tend to cluster at neighborhood scale during the early recovery phase. The Janzen-Connell (Connell, 1971; Janzen, 1970) and herd protection effects (Wills et al., 1997) describe how species-specific pests and pathogens impair the performance of conspecific neighbors while facilitating the coexistence of heterospecific neighbors, thereby promoting the synchronous recovery of species diversity at neighborhood scale and location diversity. However, as the recovery progresses, the death and fall of pioneer species trees create space that allowed the aggregated regeneration of later-successional species (Chazdon, 2008). This may lead to the regressive recovery of location diversity and a negative correlation with species diversity at neighborhood scale.

4.5. Implications for biodiversity monitoring and restoration of tropical lowland rainforests

Our study suggests that a thorough comparative analysis of diversity recovery in secondary forests should be conducted, taking into account species, size, and location diversity at both stand and neighborhood scales, instead of evaluating diversity at a single scale. Adopting this approach led to some intriguing findings that can improve biodiversity monitoring techniques and provide targeted guidance for restoring secondary forests during their recovery process.

In this study, we examined how diversity recovery varies across different types and scales by using the same number and category indices. However, we needed to carefully consider the details when selecting these indices. For instance, we refrained from using the Shannon index to measure the continuous variable such as DBH and distance since it is not intended for such variables. Instead, we chose the Gini coefficient to quantify size and location diversity, which is specifically designed for continuous variables and can be standardized to calculate relative recovery, even if it decreased with recovery. Similarly, we selected the Shannon index to measure species diversity as it is better suited for categorical variables and captures the changes in recovery better than the Simpson index.

It is worth highlighting that our sensitivity analysis has shown that using Shannon index (H_sp, H_Usp) and Gini coefficient (GC_dm, GC_Udm, GC_pd, GC_Upd) can provide consistent insights into the recovery patterns of diversity, as indicated by using overall indices. These partial indices exhibit a moderate level of relative recovery in their respective diversity types (Fig. 2) and highly correlated with other indices of the same diversity type and scale (e.g., H_sp and N_sp, GC_Udm and T_Udm, Fig. 3). Therefore, we recommend these partial indices as preferred tools for analyzing the recovery differences of diversity types and scales in future biodiversity monitoring.

Current researches on tropical secondary forest management has concentrated on species composition or neighborhood competition

([Ding and Zang, 2021](#); [Swinfield et al., 2016](#)), with few studies integrating species, size, and location diversity at both stand and neighborhood scales ([Dieler et al., 2017](#); [Dong et al., 2022](#)). Our findings suggest that management measures for the forests in early recovery phase (stand initiation phase and stem exclusion phase) should prioritize size diversity, which recovers slowly. Thinning could be implemented on trees with low size differentiation at neighborhood scale, especially those with low species mixing and close to their nearest neighbor ([Li et al., 2014](#); [Pommerening and Grabarnik, 2019](#)). In contrast, for the forests in later recovery phase (understory reinitiation phase), management should focus on species diversity, which may have been retarded by propagule restriction and species replacement. Thinning should be implemented on trees of pioneer and mid-successional species at stand scale ([Ding and Zang, 2021](#)), and an appropriate amount of artificial regeneration (replanting) of later-successional species should also be considered if they were absent due to dispersal limitation ([Pommerening and Grabarnik, 2019](#)). Additionally, efforts should also be prioritized, such as protecting existing old-growth forests and legacies within stands (e.g. trees with large diameter and rare species) to speed up the natural restoration of secondary forests ([Rozendaal et al., 2019](#); [Van der Putten et al., 2000](#)).

5. Conclusions

This study revealed the recovery patterns of three types of diversity after the abandonment of shifting cultivation in the tropical lowland rainforest on Hainan Island, China. Our findings show that location diversity recovered faster than species diversity and size diversity, with species diversity only recovered faster than size diversity in the early recovery phase. The relative recovery of species diversity at neighborhood scale was higher than that at stand scale in later recovery phase, while there were no differences between scales in size diversity and location diversity. The relative recoveries of species diversity at stand scale and neighborhood scale were strongly correlated with size diversity and location diversity respectively in the early recovery stage, while these interrelations changed to no significance with the forest recovery. Additionally, our study found that using only Shannon index and Gini coefficient can provide consistent insights into the recovery patterns of diversity, as indicated by the 8 overall indices. Our study demonstrated that recovery rates of secondary forests relative to their reference old-growth counterparts could be quantified by using multiple indices of diversities belonging to three types characterizing community features at different scales. This kind of quantitative assessment on the relative recovery of disturbed forests could be helpful in applying appropriate management activities and selecting rational approaches for speeding up restoration process of degraded forest ecosystems.

Credit author statement

Chaofan Zhou: Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. Yi Ding: Methodology, Data curation, Investigation, Writing – review & editing. Runguo Zang: Conceptualization, Methodology, Writing – review & editing, Supervision, Validation.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.118089.

References

Aguirre, O., Hui, G., Gadow, K.V., Jiménez, J., 2003. An analysis of spatial forest structure using neighbourhood-based variables. For. Ecol. Manag. 183, 137–145. https://doi.org/10.1016/S0378-1127(03)00102-6.

Ali, A., Lin, S., He, J., Kong, F., Yu, J., Jiang, H., 2019. Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests. For. Ecol. Manag. 432, 823–831. https://doi.org/10.1016/j.foreco.2018.10.024.

Ayala-Orozco, B., Gavito, M.E., Mora, F., Siddique, I., Balvanera, P., Jaramillo, V.J., Cotler, H., Romero-Duque, L.P., Martínez-Meyer, E., 2018. Resilience of soil properties to land-use change in a tropical dry forest ecosystem. Land Degrad. Dev. 29, 315–325. https://doi.org/10.1002/ldr.2686.

Brancalion, P.H., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F.S., Almeyda Zambrano, A.M., Baccini, A., Aronson, J., Goetz, S., Reid, J.L., 2019. Global restoration opportunities in tropical rainforest landscapes. Sci. Adv. 5 https://doi.org/10.1126/sciadv.aav3223 eaav3223.

Brown, G.S., 1965. Point Density in Stems Per Acre. New Zealand Forestry Service Research Notes, Wellington, p. 12.

Buongiorno, J., Dahir, S., Lu, H.-C., Lin, C.-R., 1994. Tree size diversity and economic returns in uneven-aged forest stands. For. Sci. 40, 83–103. https://doi.org/10.1093/forestscience/40.1.83.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148.

Chave, J., Piponiot, C., Maréchaux, I., De Foresta, H., Larpin, D., Fischer, F.J., Derroire, G., Vincent, G., Hérault, B., 2020. Slow rate of secondary forest carbon accumulation in the Guianas compared with the rest of the Neotropics. Ecol. Appl. 30, e02004 https://doi.org/10.1002/eap.2004.

Chazdon, R.L., 2008. Chance and determinism in tropical forest succession. In: Carson, W.P., Schnitzer, S.A. (Eds.), Tropical Forest Community Ecology. Wiley-Blackwell, Oxford, pp. 384–409.

Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M., Bongers, F., Zambrano, A.M.A., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H., 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Sci. Adv. 2, e1501639 https://doi.org/10.1126/sciadv.1501639.

Chen, Y., Wright, S.J., Muller-Landau, H.C., Hubbell, S.P., Wang, Y., Yu, S., 2016. Positive effects of neighborhood complementarity on tree growth in a Neotropical forest. Ecology 97, 776–785. https://doi.org/10.1890/15-0625.1.

Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35, 445–453. https://doi.org/10.2307/1931034.

Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in forest trees. In: Boer PJ, G. (Ed.), Dynamics of Populations. PUDOC, Wageningen, pp. 298–312.

De Boeck, H.J., Nijs, I., Lemmens, C.M., Ceulemans, R., 2006. Underlying effects of spatial aggregation (clumping) in relationships between plant diversity and resource uptake. Oikos 113, 269–278. https://doi.org/10.1111/j.2006.0030-1299.14257.x.

Dieler, J., Uhl, E., Biber, P., Müller, J., Rötzer, T., Pretzsch, H., 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. Eur. J. For. Res. 136, 739–766. https://doi.org/10.1007/s10342-017-1056-1.

Ding, Y., Zang, R., 2021. Effects of thinning on the demography and functional community structure of a secondary tropical lowland rain forest. J. Environ. Manag. 279, 111805 https://doi.org/10.1016/j.jenvman.2020.111805.

Ding, Y., Zang, R.G., Liu, S.R., He, F.L., Letcher, S.G., 2012. Recovery of woody plant diversity in tropical rain forests in southern China after logging and shifting cultivation. Biol. Conserv. 145, 225–233. https://doi.org/10.1016/j.biocon.2011.11.009.

Dong, L., Bettinger, P., Liu, Z., 2022. Optimizing neighborhood-based stand spatial structure: four cases of boreal forests. For. Ecol. Manag. 506, 119965 https://doi.org/10.1016/j.foreco.2021.119965.

Dupuy, J.M., Hernández-Stefanoni, J.L., Hernández-Juárez, R.A., Tetetla-Rangel, E., López-Martínez, J.O., Leyequién-Abarca, E., Tun-Dzul, F.J., May-Pat, F., 2012. Patterns and correlates of tropical dry forest structure and composition in a highly

replicated chronosequence in Yucatan, Mexico. Biotropica 44, 151–162. https://doi.org/10.1111/j.1744-7429.2011.00783.x.

Ehbrecht, M., Schall, P., Ammer, C., Seidel, D., 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agric. For. Meteorol. 242, 1–9. https://doi.org/10.1016/j.agrformet.2017.04.012.

Fichtner, A., Haerdtle, W., Li, Y., Bruelheide, H., Kunz, M., Oheimb, G., 2017. From competition to facilitation: how tree species respond to neighbourhood diversity. Ecol. Lett. 20, 892–900. https://doi.org/10.1111/ele.12786.

Fichtner, A., Härdtle, W., Bruelheide, H., Kunz, M., Li, Y., Von Oheimb, G., 2018. Neighbourhood interactions drive overyielding in mixed-species tree communities. Nat. Commun. 9, 1144. https://doi.org/10.1038/s41467-018-03529-w.

Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 42–58. https://doi.org/10.2307/1411.

Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. Current Forestry Reports 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2.

Franklin, J.F., Van Pelt, R., 2004. Spatial aspects of structural complexity in old-growth forests. J. For. 102, 22–28. https://doi.org/10.1093/jof/102.3.22.

Gadow, K.v., Hui, G., 2002. Characterizing Forest Spatial Structure and Diversity. Materiały Konferencyjne IUFRO, Lund, Sweden.

Gadow, K.v., Zhang, C., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., Myklush, S., Hui, G., Kiviste, A., Zhao, X., 2012. Forest Structure and Diversity, Continuous Cover Forestry. Springer, Berlin, pp. 29–83. https://doi.org/10.1007/978-94-007-2202-6_2.

Gini, C., 1921. Measurement of inequality of incomes. Econ. J. 31, 124–125. https://doi.org/10.2307/2223319.

Glatthorn, J., 2021. A spatially explicit index for tree species or trait diversity at neighborhood and stand level. Ecol. Indicat. 130, 108073 https://doi.org/10.1016/j.ecolind.2021.108073.

Glatthorn, J., Annighöfer, P., Balkenhol, N., Leuschner, C., Polle, A., Scheu, S., Schuldt, A., Schuldt, B., Ammer, C., 2021. An interdisciplinary framework to describe and evaluate the functioning of forest ecosystems. Basic Appl. Ecol. 52, 1–14. https://doi.org/10.1016/j.baae.2021.02.006.

Hui, G., Zhang, G., Zhao, Z., Yang, A., 2019. Methods of forest structure research: a review. Current Forestry Reports 5, 142–154. https://doi.org/10.1007/s40725-019-00090-7.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528. https://doi.org/10.1086/282687.

Lexerød, N.L., Eid, T., 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. For. Ecol. Manag. 222, 17–28. https://doi.org/10.1016/j.foreco.2005.10.046.

Li, Y., Ye, S., Hui, G., Hu, Y., Zhao, Z., 2014. Spatial structure of timber harvested according to structure-based forest management. For. Ecol. Manag. 322, 106–116. https://doi.org/10.1016/j.foreco.2014.02.042.

Man, R., Yang, H., 2015. Construction of neighbourhood diversity indices with stem mapping data. Can. J. For. Res. 45, 1137–1141. https://doi.org/10.1139/cjfr-2015-0108.

Montes, F., Sánchez, M., del Río, M., Cañellas, I., 2005. Using historic management records to characterize the effects of management on the structural diversity of forests. For. Ecol. Manag. 207, 279–293. https://doi.org/10.1016/j.foreco.2004.10.031.

Moustakas, A., Wiegand, K., Getzin, S., Ward, D., Meyer, K.M., Guenther, M., Mueller, K.-H., 2008. Spacing patterns of an Acacia tree in the Kalahari over a 61-year period: how clumped becomes regular and vice versa. Acta Oecol. 33, 355–364. https://doi.org/10.1016/j.actao.2008.01.008.

Mukul, S., Herbohn, J., Firn, J., 2020. Rapid recovery of tropical forest diversity and structure after shifting cultivation in the Philippines uplands. Ecol. Evol. 10, 1–23. https://doi.org/10.1002/ece3.6419.

Murdjoko, A., Brearley, F., Ungirwalu, A., Djitmau, D.A., Benu, N., 2022. Secondary succession after slash-and-burn cultivation in papuan lowland forest, Indonesia. Forests 13, 434. https://doi.org/10.3390/f13030434.

Neumann, M., Starlinger, F., 2001. The significance of different indices for stand structure and diversity in forests. For. Ecol. Manag. 145, 91–106. https://doi.org/10.1016/S0378-1127(00)00577-6.

Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., Van Breugel, M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. Proc. Natl. Acad. Sci. USA 112, 8013–8018. https://doi.org/10.1073/pnas.1500403112.

Oliver, C.D., Larson, B.A., 1996. Forest Stand Dynamics, Update Edition. John Wiley & Sons, New York.

Parrott, L., 2010. Measuring ecological complexity. Ecol. Indicat. 10, 1069–1076. https://doi.org/10.1016/j.ecolind.2010.03.014.

Peña-Claros, M., 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon1. Biotropica 35, 450–461. https://doi.org/10.1111/j.1744-7429.2003.tb00602.x.

Pielou, E., 1959. The use of point-to-plant distances in the study of the pattern of plant populations. J. Ecol. 607–613. https://doi.org/10.2307/2257293.

Pommerening, A., 2002. Approaches to quantifying forest structures. Forestry 75, 305–324. https://doi.org/10.1093/forestry/75.3.305.

Pommerening, A., Grabarnik, P., 2019. Individual-based Methods in Forest Ecology and Management. https://doi.org/10.1007/978-3-030-24528-3.

Pommerening, A., Stoyan, D., 2006. Edge-correction needs in estimating indices of spatial forest structure. Can. J. For. Res. 36, 1723–1739. https://doi.org/10.1139/x06-060.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P.H., Broadbent, E.N., Chazdon, R.L., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214. https://doi.org/10.1038/nature16512.

Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F., Chazdon, R.L., Farrior, C.E., Kambach, S., Meave, J.A., 2021a. Multidimensional tropical forest recovery. Science 374, 1370–1376. https://doi.org/10.1126/science.abh3629.

Poorter, L., Rozendaal, D.M., Bongers, F., Almeida, d.J.S., Álvarez, F.S., Andrade, J.L., Arreola Villa, L.F., Becknell, J.M., Bhaskar, R., Boukili, V., 2021b. Functional recovery of secondary tropical forests. Proc. Natl. Acad. Sci. USA 118, e2003405118. https://doi.org/10.1073/pnas.2003405118.

Powers, J.S., Marín-Spiotta, E., 2017. Ecosystem processes and biogeochemical cycles in secondary tropical forest succession. Annu. Rev. Ecol. Evol. Syst. 48, 497–519. https://doi.org/10.1146/annurev-ecolsys-110316-022944.

Pretzsch, H., 2009. Forest Dynamics, Growth, and Yield: A Review, Analysis of the Present State, and Perspective, Forest Dynamics, Growth and Yield. Springer, Berlin, pp. 1–39. https://doi.org/10.1007/978-3-540-88307-4_1.

Pretzsch, H., del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., 2016. Mixing of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) enhances structural heterogeneity, and the effect increases with water availability. For. Ecol. Manag. 373, 149–166. https://doi.org/10.1016/j.foreco.2016.04.043.

R Core Team, 2022 (Vienna, Austria). R: a Language and Environment for Statistical Computing, 4.1, p. 3. http://www.r-project.org.

Rees, M., Condit, R., Crawley, M., Pacala, S., Tilman, D., 2001. Long-term studies of vegetation dynamics. Science 293, 650–655. https://doi.org/10.1126/science.1062586.

Rozendaal, D.M., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J.M., Bentos, T.V., Brancalion, P.H., Cabral, G.A., 2019. Biodiversity recovery of Neotropical secondary forests. Sci. Adv. 5 https://doi.org/10.1126/sciadv.aau3114 eaau3114.

Seidler, T.G., Plotkin, J.B., 2006. Seed dispersal and spatial pattern in tropical trees. PLoS Biol. 4, e344. https://doi.org/10.1371/journal.pbio.0040344.

Shannon, C.E., 1948. A mathematical theory of communication. The Bell system technical journal 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.

Shen, G., He, F., Waagepetersen, R., Sun, I.-F., Hao, Z., Chen, Z.-S., Yu, M., 2013. Quantifying effects of habitat heterogeneity and other clustering processes on spatial distributions of tree species. Ecology 94, 2436–2443. https://doi.org/10.1890/12-1983.1.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688. https://doi.org/10.1038/163688a0.

Sovu, Tigabu, M., Savadogo, P., Odén, P.C., Xayvongsa, L., 2009. Recovery of secondary forests on swidden cultivation fallows in Laos. For. Ecol. Manag. 258, 2666–2675. https://doi.org/10.1016/j.foreco.2009.09.030.

Swinfield, T., Afriandi, R., Antoni, F., Harrison, R.D., 2016. Accelerating tropical forest restoration through the selective removal of pioneer species. For. Ecol. Manag. 381, 209–216. https://doi.org/10.1016/j.foreco.2016.09.020.

Szmyt, J., 2012. Spatial structure of managed beech-dominated forest: applicability of nearest neighbors indices. Dendrobiology 68, 69–76.

Tetemke, B.A., Birhane, E., Rannestad, M.M., Eid, T., 2021. Species diversity and stand structural diversity of woody plants predominantly determine aboveground carbon stock of a dry Afromontane forest in Northern Ethiopia. For. Ecol. Manag. 500, 119634 https://doi.org/10.1016/j.foreco.2021.119634.

Tian, L., Letcher, S.G., Ding, Y., Zang, R., 2022. A ten-year record reveals the importance of tree species' habitat specialization in driving successional trajectories on Hainan Island, China. For. Ecol. Manag. 507, 120027 https://doi.org/10.1016/j.foreco.2022.120027.

Tongkoom, K., Marohn, C., Piepho, H.-P., Cadisch, G., 2018. Ecosystem recovery indicators as decision criteria on potential reduction of fallow periods in swidden systems of Northern Thailand. Ecol. Indicat. 95, 554–567. https://doi.org/10.1016/j.ecolind.2018.07.061.

Van der Putten, W., Mortimer, S., Hedlund, K., Van Dijk, C., Brown, V., Lepä, J., Rodriguez-Barrueco, C., Roy, J., Diaz Len, T., Gormsen, D., 2000. Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. Oecologia 124, 91–99. https://doi.org/10.1007/s004420050028.

Wang, H., Huang, S., Zhang, S., Peng, H., Cao, K., 2021. Localized neighborhood species mingling is correlated with individual tree size inequality in natural forests in South China. Ann. For. Sci. 78, 102. https://doi.org/10.1007/s13595-021-01111-x.

Wangpakapattanawong, P., Kavinchan, N., Vaidhayakarn, C., Schmidt-Vogt, D., Elliott, S., 2010. Fallow to forest: applying indigenous and scientific knowledge of swidden cultivation to tropical forest restoration. For. Ecol. Manag. 260, 1399–1406. https://doi.org/10.1016/j.foreco.2010.07.042.

Wills, C., Condit, R., Foster, R.B., Hubbell, S.P., 1997. Strong density-and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proc. Natl. Acad. Sci. USA 94, 1252–1257. https://doi.org/10.1073/pnas.94.4.1252.

Wolf, A., 2005. Fifty year record of change in tree spatial patterns within a mixed deciduous forest. For. Ecol. Manag. 215, 212–223. https://doi.org/10.1016/j.foreco.2005.05.021.

Zang, R., Ding, Y., Zhang, Z., Deng, F., Mao, P., 2010. Ecological Foundation of Conservation and Restoration for the Major Functional Groups in Tropical Natural Forests on Hainan Island. Science Press, Beijing.

Zhou, C., Liu, D., Chen, K., Hu, X., Lei, X., Feng, L., Zhang, Y., Zhang, H., 2022. Spatial structure dynamics and maintenance of a natural mixed forest. Forests 13, 888. https://doi.org/10.3390/f13060888.

Ziegler, J.P., Hoffman, C., Battaglia, M., Mell, W., 2017. Spatially explicit measurements of forest structure and fire behavior following restoration treatments in dry forests. For. Ecol. Manag. 386, 1–12. https://doi.org/10.1016/j.foreco.2016.12.002.