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## Species diversity patterns differ by life stages in a pine-oak mixed forest

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**Abstract:** Natural forests comprise trees of different species and sizes, constituting a “biotic framework”. Although examinations of diversity patterns at various spatial scales are frequently conducted, life stages are rarely accounted for. Pine-oak mixedwood forest is widely distributed around the world and constitutes main forest type in the Nanpan River Basin in southwest China. We established a fixed plot with an area of 100 m × 100 m in an undisturbed forest stand and classified trees according to five life stages based on their diameter at breast height (DBH) and height. Then, we calculated eight traditional diversity indices for each life stage. We found that species richness (R), abundance (N), and three diversity indices first increased and then decreased with increasing life stage. As sampling area increased, R, the Shannon-Wiener index (H') and Simpson's diversity index (D) first increased quickly, followed by a reduced rate of increase, whereas N showed a linear increase and three evenness indices showed gradual decreases. Global Moran's I values for each diversity index were small, indicating weak spatial autocorrelation. Both R and N of shrubs and saplings decreased sharply with life stage, with only large trees comprising the later life stages. Our results indicate that species diversity patterns in pine-oak forests, particularly in early successional stages, differ among life stages. The changes contribute to the understanding and conservation of forest biodiversity.

**Keywords:** Biodiversity, life stage, scale effect, secondary forest, spatial distribution.

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## Introduction

At the global scale, increases in extreme climate events (Franklin et al., 2007; Marimon et al., 2020), pest and disease outbreaks, alien species invasions (Dyderski & Jagodziński, 2020), and anthropogenic activity (Barlow et al., 2016; Gomes et al., 2019) have

damaged forest ecosystems, leading to biodiversity loss and widespread concern. Trees are the primary constituents of forests and thus the most relevant biodiversity measure at the stand scale (i.e., alpha diversity) (Lähde et al., 1999; Valbuena et al., 2012; Feroz et al., 2016). Generally, higher tree species richness (R) is associated with greater genetic diversity,

which promotes ecological variation and greater niche utilization (Hui & Pommerening, 2014). Tree species diversity has been a major focus of forest ecosystem research (Ma, 1994; Ma & Liu, 1994; Turner & Tjørve, 2005; Hwang & He, 2011; Ostertag et al., 2014) and is critical to sustainable development and forest management efforts (Barna & Bosela, 2015).

Trees of varying sizes, life stages, and species provide scaffolding promoting structural and species diversity in forests (Li et al., 2020a). Life stages vary morphologically among trees, but all follow a process of maturation from germination to saplings, adults, senescence and mortality. Many assessments of tree diversity in natural stands use permanent monitoring plots, wherein the recording of trees begins when they reach a diameter at breast height (DBH; 1.3 m) of  $\geq 1$  cm, following the standards proposed by the Center for Tropical Forest Science (He et al., 1996; 2002; Ostertag et al., 2014; Inman-Narahari et al., 2016; Shankar, 2019). Few studies have assessed trees with a DBH < 1 cm (Zhang et al., 2010), because these individuals are often grouped together under “regeneration” and assessed at lower vegetation strata (Barna & Bosela, 2015; Liira et al., 2017; Lin et al., 2017; Awasthi et al., 2020; Ray et al., 2021). However, variability in regeneration may not be well reflected in understory surveys (Clark et al., 1999). In reality, natural forests may show a reversed J-shaped distribution of tree diameter (Hui & Pommerening, 2014; Shankar, 2019; Li et al., 2020a). Therefore, large numbers of small individuals, namely germinants, seedlings, and saplings, are often neglected in species diversity assessments.

It is critical to account for space in species diversity analyses. Species diversity is closely related to the spatial scale of measurement, both within regions (e.g., climatic zones) and between them (Stein et al., 2014; Chisholm et al., 2018; Shankar, 2019). The relationships between R, abundance (N), and spatial scale have been well discussed, with much consideration of sampling methods, including quadrat shape and size (He et al., 1996; Turner & Tjørve, 2005; Hwang & He, 2011; Jin et al., 2019). Many studies have employed nested quadrats and assessed differences in R and N by grain size (He et al., 2002; Wang et al., 2007; Zhang et al., 2010). Others have explored relationships between different R, N, and spatial measures (Ostertag et al., 2014), or correlations with diversity across scale (Stein et al., 2014; Almoussawi et al., 2020). Generally, these assessments have aimed to understand tree and shrub species composition, habitat characteristics, or vegetation restoration processes (Tang et al., 2010; Chisholm et al., 2018). However, it remains unclear if relationships between species diversity and scale are consistent across life stages.

The majority of trees in natural forests originate from seeds. As trees grow, they are at high risk of mortality due to resource constraints (e.g., limited

soil resources, rainfall, and/or light), habitat heterogeneity/partitioning (e.g., karst topography and terrain gradients), competition from neighboring trees, predation, pests and diseases, and stochastic events (Coomes & Allen, 2007; Guo, 2021). Generally, the smaller individual, the lower capacity for adaptation to adverse conditions (Franklin et al., 1987; Laarmann et al., 2009; Hurst et al., 2012; Wang et al., 2017). Therefore, we hypothesized that earlier life stages would be more abundant, i.e., represented by a greater number of individuals, with higher R and higher diversity (i.e., hypothesis 1), and that spatial scale would have limited influence on young life stages, given that these small individuals require few habitat resources (i.e., hypothesis 2).

## Materials and Methods

### Study area

The study area was located in Guangxi Yachang Orchid National Nature Reserve, China (106°11'31"–106°27'04"E, 24°44'16"–24°53'58"N). The area is characterized by a mountainous transition zone between the Yunnan-Guizhou Plateau and rolling hills of Guangxi. Most of the mountainous terrain is typical karst landform, with numerous caves and some eolian deposits. The climate is mid-subtropical monsoon, with the majority of the region influenced year-round by both the Foehn effect and monsoon circulation. The average annual temperature is approximately 16.3 °C, with extreme highs of > 40 °C and extreme lows of –3 °C. The average annual rainfall is approximately 1,050 mm, most of which falls during the summer months. Droughts can be severe during the spring and winter, leading to distinct seasonal dry and wet periods (Li et al., 2017, 2020a, 2020b; Yu et al., 2018).

Within this area, the sampling plot was established at the Langquqan conservation station, near the town of Huaping (24°51'15.9"E, 106°19'4.2"N). This area was once dominated by a primary forest of *Pinus yunnanensis* var. *tenuifolia* (PY) that was completely burned by a wildfire in 1987. It was replaced by a natural secondary forest dominated by PY and several oak species, and showed no signs of additional disturbance and no clear vertical stratification. The stand is dense, with a high crown density (0.9). Other common species include *Keteleeria davidiana* (Bertr.) Beissn., *Rhus chinensis* Mill., *Schima wallichii* (DC.) Choisy, *Betula alnoides* Buch-Ham., *Meliosma veitchiorum* Hemsl., *Liquidambar formosana* Hance, *Myrica rubra* (Lour.) S. et Zucc., *Lyonia ovalifolia* (Wall.) Drude var. *elliptica*, *Eurya distichophylla* Hemsl., and *Wendlandia uvariifolia* Hance. There was obvious stratification of tree species with elevation within the plot. In the

understory, *Dicranopteris linearis* (Burm.f.) Underw. completely dominates the herb layer, with scattered *Miscanthus floridulu* (Labnll.) Warb and orchids. Oak species were predominant in the regenerating understory, with ample decaying coarse woody debris and snags (Li et al., 2017, 2020a, 2020b; Yu et al., 2018).

## Plot establishment

Pine-oak mixed forest is zonal vegetation in the Nanpanjiang River basin. Based on terrain and forest growth conditions, we established a fixed quadrat of 100 m × 100 m on an upper slope in 2016. Using a handheld GPS unit, we established the four outer boundaries of the quadrat and divided it into 25 20 m × 20 m sub-quadrats using a total station (NTS-372R10; South Group, Guangzhou, China). Plastic tubes were inserted into the soil at the corner of each sub-quadrat and then reinforced with rebar approximately 60 cm in length. We then determined the relative positions (x, y, and z) of all trees ≥ 10 cm in height (HT) in each sub-quadrat using the eccentric mode of the total station. Live trees with a DBH ≥ 5 cm were tagged with aluminum tags and their HT, DBH, and crown width were assessed. Any trees with a DBH < 5 cm and HT ≥ 10 cm were marked

with plastic plates, after which we measured their HT, DBH, and ground diameter. We also recorded the species and growth status (i.e., bent, bifurcated, withered, broken, reclined, or sprouting) (Li et al., 2017, 2020a, 2020b). In total, 2,391 trees with a DBH ≥ 5 cm, and 2,144 with DBH < 5 cm and HT ≥ 10 cm, were recorded, representing 24 species (Table 1). We also mapped the understory locations of herbaceous species. Due to nutrient-poor soils and slow tree growth, we intend to census the plot every 6 years to obtain temporal data.

Classifying trees, small trees, and shrubs is challenging due to overlap in size among species and unclear vertical stratification (Li et al., 2020a, 2020b). We used five size classes based on DBH and HT, as described in Table 1, and recorded the number of individuals of each life stage. Some species were represented in all life stages, whereas others were only represented in a single stage.

## Data analyses

We calculated eight species diversity indices: R, N, Shannon-Wiener index (H'), Simpson's diversity index (D), Fisher's alpha diversity index (Alpha), Pielou's evenness index ( $E_H$ ), Sheldon's evenness index

Table 1. Trees, small trees, and shrubs encountered in the 1 ha permanent monitoring plot. S1 (seedling) = 10 cm ≤ HT < 100 cm; S2 (sapling) = HT ≥ 100 cm and DBH < 5 cm; S3 (young trees) = 5 cm ≤ DBH < 10 cm; S4 (medium-sized trees) = 10 cm ≤ DBH < 20 cm; S5 (mature trees) = DBH ≥ 20 cm. Abundance indicates the number of individuals in each life stage category

Species	Abbreviation	Life form	Abundance				
			S1	S2	S3	S4	S5
<i>Albizia kalkora</i> (Roxb.) Prain	AK	Tree	44	19	0	1	0
<i>Betula alnoides</i> Buch-Ham	BA	Tree	0	6	49	22	1
<i>Cyclobalanopsis glauca</i> (Thunb.) Oerst.	CG	Tree	138	62	73	73	24
<i>Cyclobalanopsis glaucoides</i> Schotky	CGs	Tree	7	3	0	0	0
<i>Coriaria nepalensis</i> Wall.	CN	Shrub	0	0	0	1	0
<i>Craibiodendron stellatum</i> (Pierre) W. W. Smith	CS	Shrub	1	0	0	0	0
<i>Cerasus yedoensis</i> (Matsum.) Yu et Li	CY	Tree	1	4	1	0	0
<i>Diospyros kaki</i> Thunb. var. <i>silvestris</i> Makino	DK	Tree	2	0	4	1	0
<i>Eurya distichophylla</i> Hemsl.	ED	Small tree	12	101	75	10	0
<i>Eurya japonica</i> Thunb.	EJ	Shrub	65	31	5	0	0
<i>Gordonia kwangsiensis</i> Chang	GK	Tree	0	1	0	0	0
<i>Keteleeria davidiana</i> (Bertr.) Beissn.	KD	Tree	49	70	38	28	24
<i>Liquidambar formosana</i> Hance	LF	Tree	0	0	2	0	1
<i>Litsea glutinosa</i> (Lour.) C. B. Rob.	LG	Tree	0	1	0	0	0
<i>Lyonia ovalifolia</i> (Wall.) Drude var. <i>elliptica</i>	LO	Small tree	471	200	633	203	2
<i>Myrica rubra</i> (Lour.) S. et Zucc.	MR	Small tree	19	103	85	2	0
<i>Meliosma veitchiorum</i> Hemsl.	MV	Tree	3	0	0	0	0
<i>Pinus yunnanensis</i> Franch. var. <i>tenuifolia</i> Cheng et Law	PY	Tree	0	0	37	188	239
<i>Quercus variabilis</i> Bl.	QV	Tree	388	167	314	206	19
<i>Rhus chinensis</i> Mill.	RC	Tree	47	81	17	4	1
<i>Schima wallichii</i> (DC.) Choisy	SW	Tree	5	28	4	0	1
<i>Vaccinium bracteatum</i> Thunb.	VB	Shrub	0	1	0	2	0
<i>Viburnum cylindricum</i> Buch. -Ham. ex D. Don	VC	Small tree	0	1	0	0	0
<i>Wendlandia uvariifolia</i> Hance	WU	Small tree	7	6	1	0	0
Total			1,259	885	1,338	741	312

Table 2. Species diversity indices used to characterize tree species diversity at the stand level

Formula	Index	References
$R = \sum_{i=1}^S 1$	R – richness; S – number of species	Widely used
$N = \sum_{i=1}^S n_i$	N – abundance; $n_i$ – number of individuals of species $i$	Widely used
$H' = -\sum_{i=1}^S p_i \ln(p_i)$	H' – Shannon-Wiener index; $p_i$ – proportion of individuals belonging to the $i^{\text{th}}$ species	(Hui et al. 2011)
$D = 1 - \sum p_i^2$	D – Simpson's diversity index	(Hui et al. 2011)
$S = \alpha \ln(1 + \frac{N}{\alpha})$	$\alpha$ – Fisher's alpha diversity index	(Ma 1994)
$E_H = \frac{-\sum p_i \log p_i}{\ln S}$	$E_H$ – Pielou evenness index	(Ma and Liu 1994)
$E_s = \frac{\exp(-\sum p_i \ln p_i)}{S}$	$E_s$ – Sheldon evenness index	(Ma and Liu 1994)
$E_h = \frac{[\exp(-\sum p_i \ln p_i) - 1]}{(S - 1)}$	$E_h$ – Heip evenness index	(Ma and Liu 1994)

( $E_s$ ) and Heip's evenness index ( $E_h$ ). All indices were calculated for each sub-quadrat (Table 2). We then tested for differences in each index among life stages using Kruskal-Wallis (KW) tests. We assessed the degree of dispersion and spatial autocorrelation within

each index using the coefficient of variation (CV) and global Moran's I, respectively. We also analyzed the similarity among life stages using hierarchical clustering based on individual distances, and Venn diagrams based on species composition. Analyses were

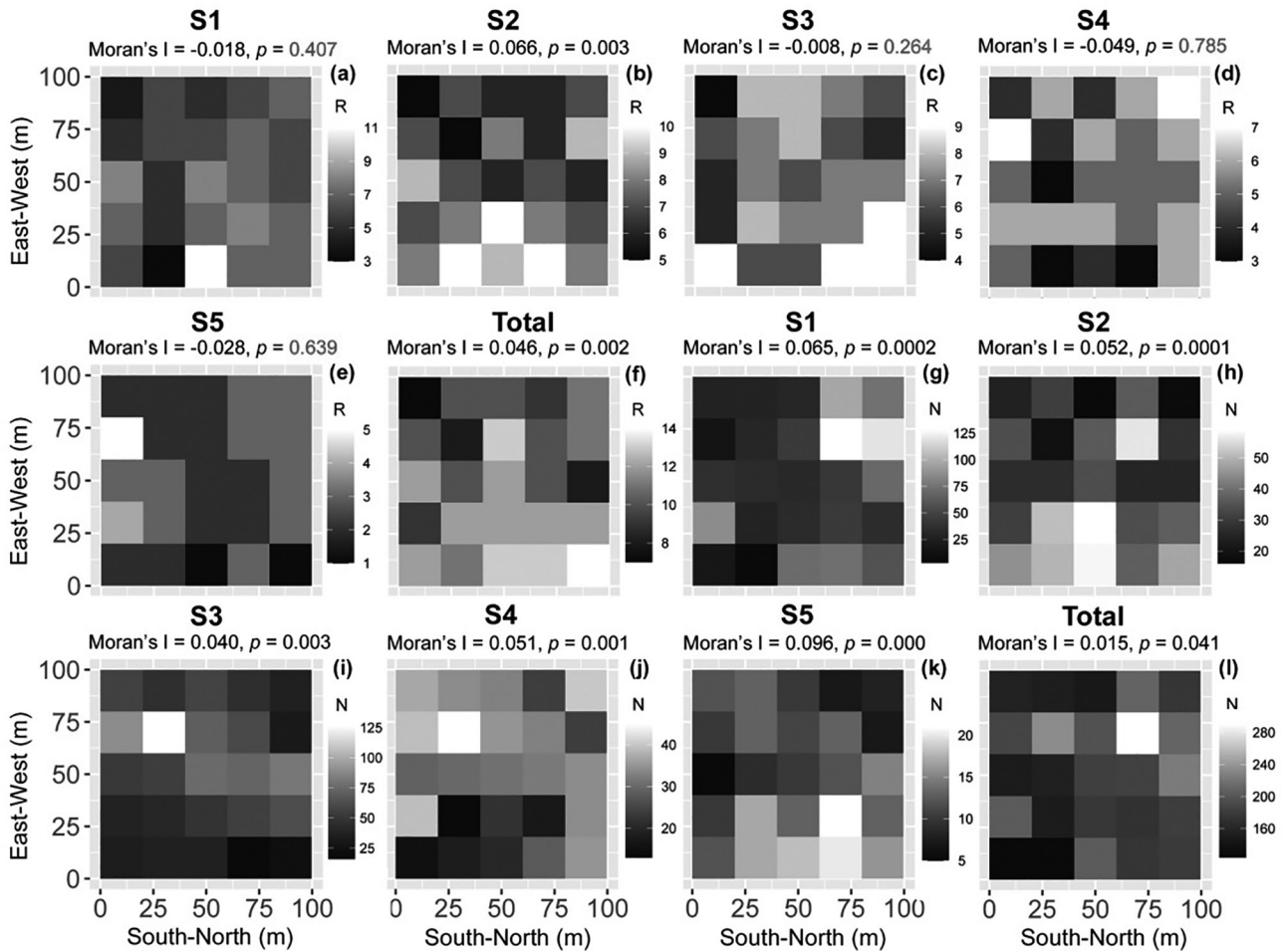


Fig. 1. Spatial patterns of species richness (R) and abundance (N) among five life stages and all trees in a pine-oak mixed-wood forest. Life stage descriptions are provided in Table 1



conducted in R software (<https://www.r-project.org/>) using the packages ‘vegan’ (Oksanen et al., 2019) and ‘ggplot2’ (Wickham, 2016). Finally, we assessed relationships between diversity indices and sampling area using EstimateS software (version 9.1.0; Colwell, 2019), and between sub-quadrats and species distributions, using non-metric multidimensional scaling.

## Results

### Patterns in species richness and abundance

There were differences between R and N within life stages (i.e., all species combined) among sub-quadrats (Fig. 1); their CVs were 0.198–0.345 and 0.285–0.637, respectively (Fig. 2). With increasing life stage, R first increased and then decreased (Fig. 3,  $p_{\text{KW}} < 0.01$ ), consistent with the results of the hierarchical cluster analysis (Fig. 2). By contrast, N first decreased and then increased, followed by a final decrease (Fig. 2,  $p_{\text{KW}} < 0.01$ ). This change in N was reflective of a change in species composition, with both R and N decreasing for small trees and shrubs with increasing life stage (Fig. 3).

Spatial autocorrelation in R was largely non-significant for all life stages (Moran’s  $I = 0.066$ –0.785,

Fig. 1). However, N was strongly autocorrelated for all life stages ( $p = < 0.001$ –0.04), with correspondingly low Moran’s  $I$  values (0.015–0.096). Increased sampling area was similarly related to R in all life stages; an initial rapid increase followed by a more gradual increase (Fig. 2). N showed a linear increase, following the pattern of  $S3 > S1 > S2 > S4 > S5$  (Fig. 2).

### Patterns in species diversity indices

Within life stage categories, diversity indices varied substantially (Fig. 4); the mean values of  $H'$ ,  $D$ , and Alpha ranged from 0.55–1.69, 0.33–0.77, and 1.94–3.05, with CVs of 0.09–0.67, 0.06–0.68, and 0.25–0.63, respectively. CVs generally increased with life stage. There were some significant differences in these diversity indices among life stages (Fig. 5). The majority of global Moran’s  $I$  values were small and not significant ( $p > 0.05$ ) within life stages (Fig. 4).

$H'$  values for each of the five life stage categories showed a similar trend, i.e., increasing with increased sampling area and approaching a constant value around 10 sub-quadrats. Among life stages, S2 and S5 had the highest and lowest  $H'$  values, respectively, whereas S1, S3, and S4 showed similar values (Fig. 5). Values of  $D$  were similar to those of  $H'$  for four of the life stages, excluding S5, where  $D$

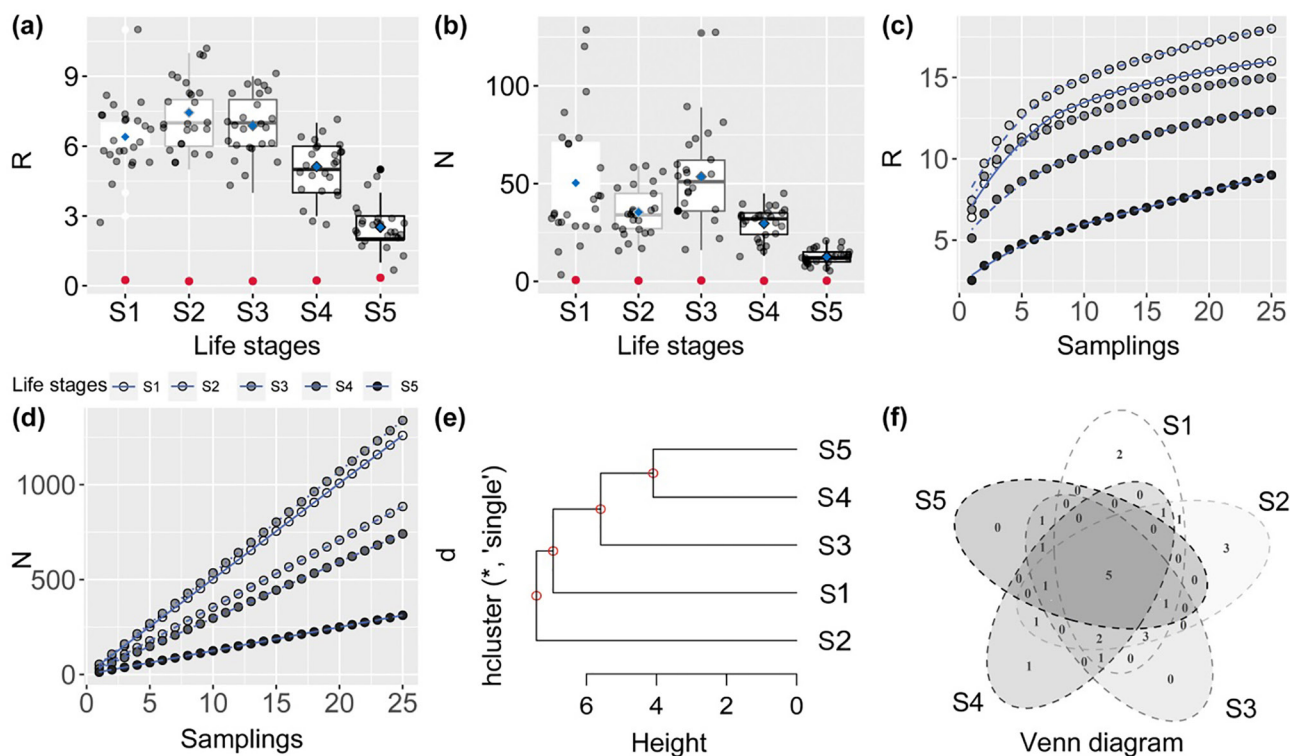


Fig. 2. Relationships of species richness (R) and abundance (N) with sampling area and life stage. Life stage descriptions are provided in Table 1. Red dots in the upper panels indicate the coefficients of variation (CV). The hierarchical cluster diagram (e) and Venn diagram (f) show similarity among life stages based on N and overlap in species composition, respectively.

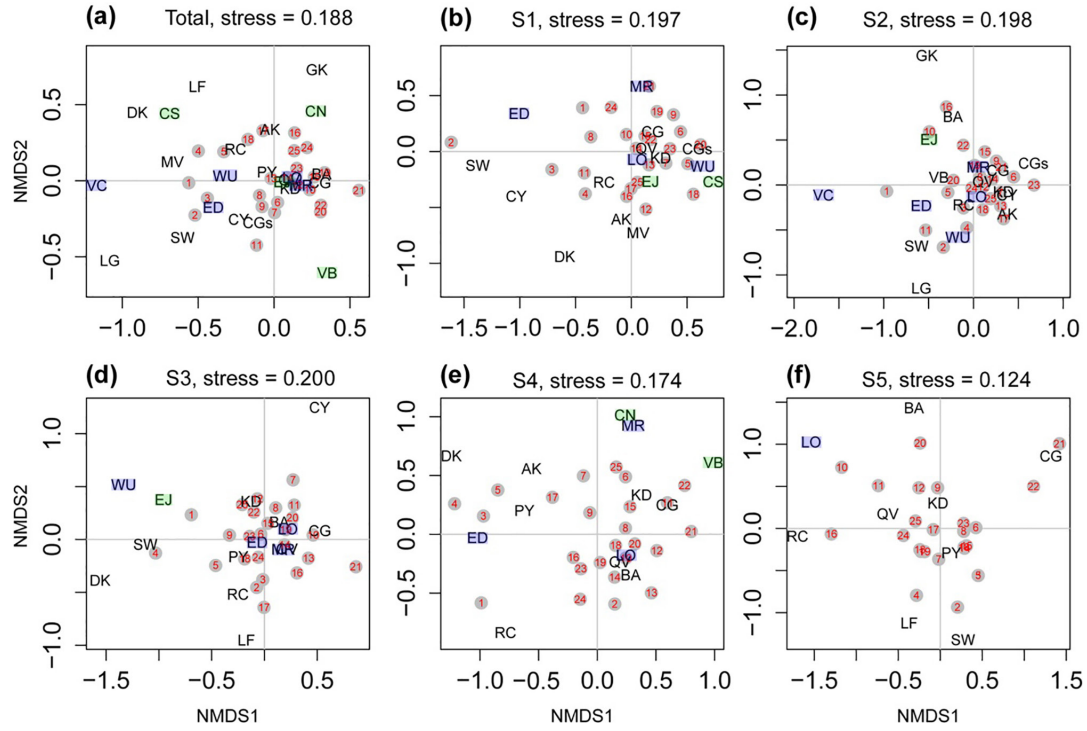


Fig. 3. Non-metric multidimensional scaling analysis of five life stages and all trees within the monitoring plot. Life stages are described in Table 1. Red numbers indicate sub-quadrat identities. The two letter codes without highlighting represent trees, those highlighted in light blue represent small trees, and those in light green represent shrubs. AK = *A. kalkora*, BA = *B. alnoides*, CG = *C. glauca*, CGs = *C. glaucoides*, CN = *C. nepalensis*, CS = *C. stellatum*, CY = *C. yedoensis*, DK = *D. kaki*, ED = *E. distichophylla*, EJ = *E. japonica*, GK = *G. kwangsiensis*, KD = *K. davidiana*, LF = *L. formosana*, LG = *L. glutinosa*, LO = *L. ovalifolia*, MR = *M. rubra*, MV = *M. veitchiorum*, PY = *P. yunnanensis*, QV = *Q. variabilis*, RC = *R. chinensis*, SW = *S. wallichii*, VB = *V. bracteatum*, VC = *V. cylindricum*, and WU = *W. uvariifolia*. Stress values are reported by panel, where stress represents the degree of fit in reduced dimensions (values < 0.1 are “great”, < 0.2 is “good/ok”, and < 0.3 indicates “poor representation”)

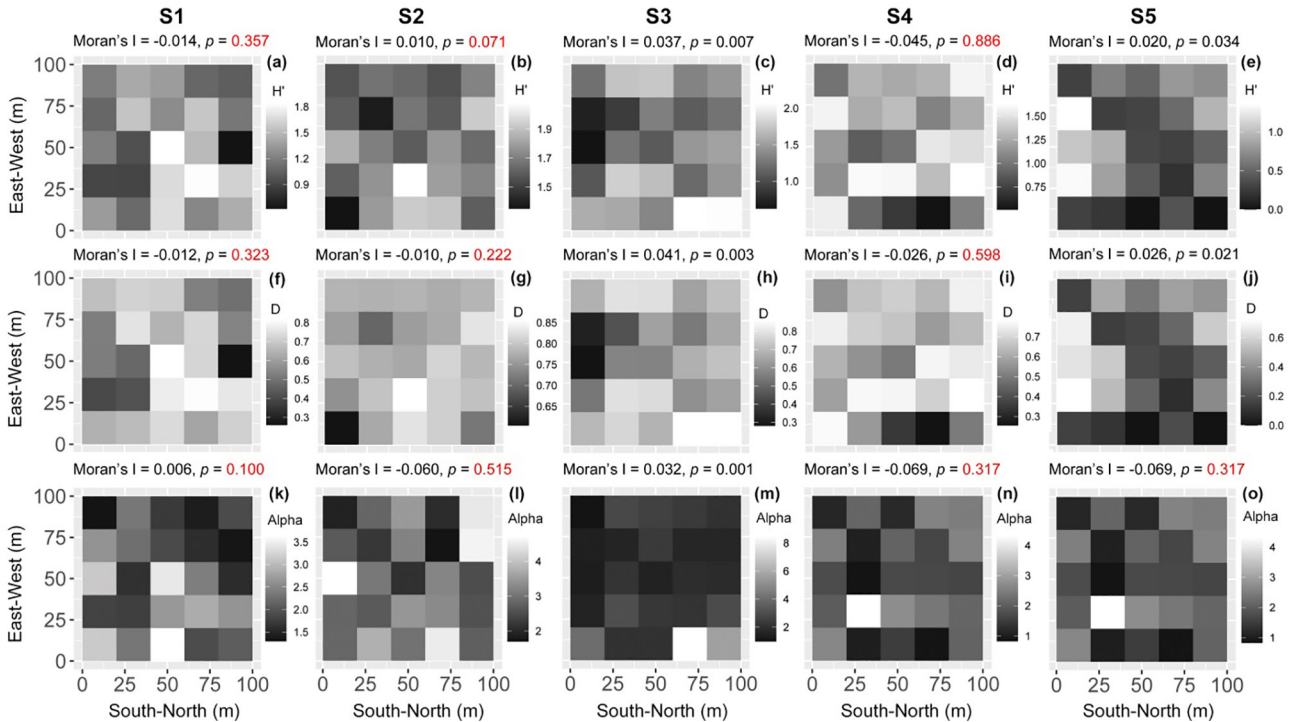


Fig. 4. Spatial patterns of species diversity indices for five tree life stages in a pine-oak mixedwood forest. H' = Shannon-Wiener, D = Simpson's, Alpha = Fisher's alpha

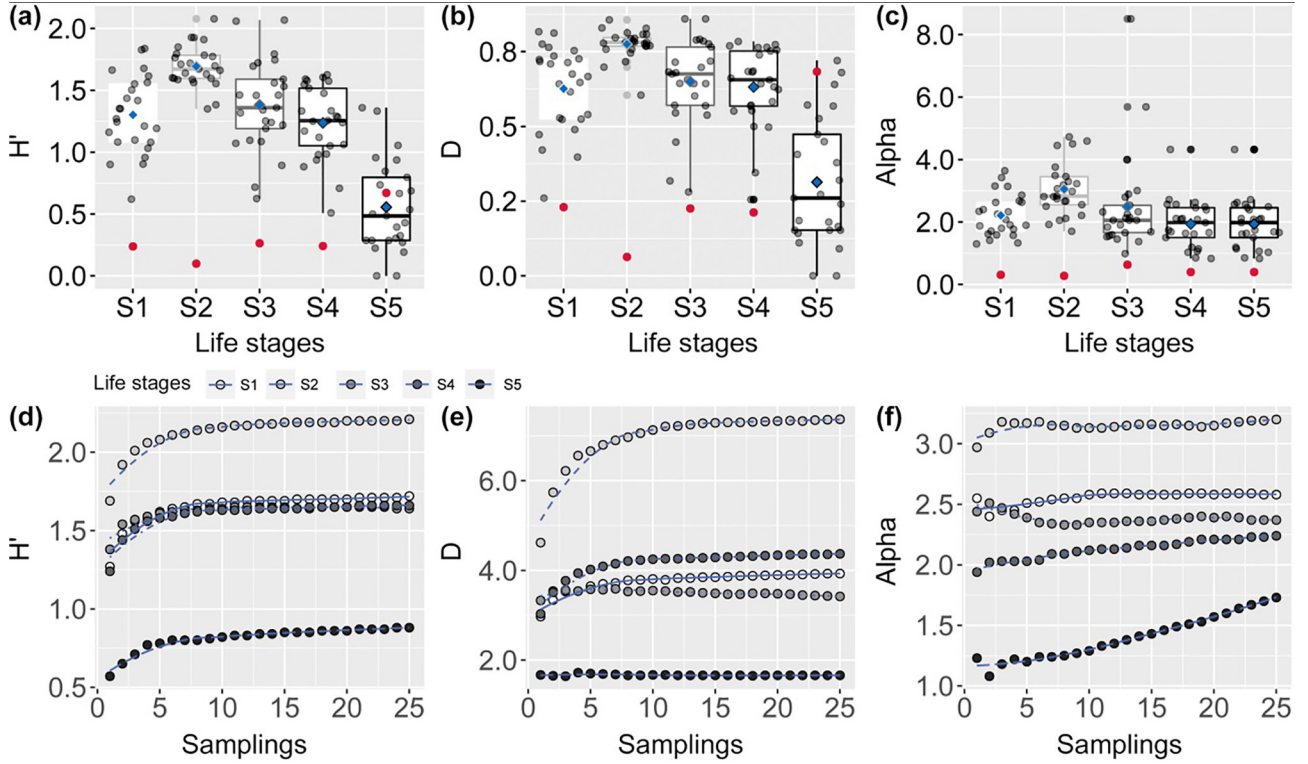


Fig. 5. Patterns of species diversity indices by tree life stage and sampling area. Red dots in the upper panels represent the coefficients of variation (CVs).  $H'$  = Shannon-Wiener,  $D$  = Simpson's,  $\alpha$  = Fisher's alpha

was low and nearly constant (Fig. 5). Values of  $\alpha$  were less consistent, with a slight change for S1 and S2 with increased sampling area, nearly linear increases for S4 and S5, and a strong decrease for S3 (Fig. 5).

### Patterns in species evenness

The similarity in the distributions of the three evenness indices ( $E_H$ ,  $E_s$ ,  $E_h$ ) within life stage categories was showed in Figure 6, and their means and

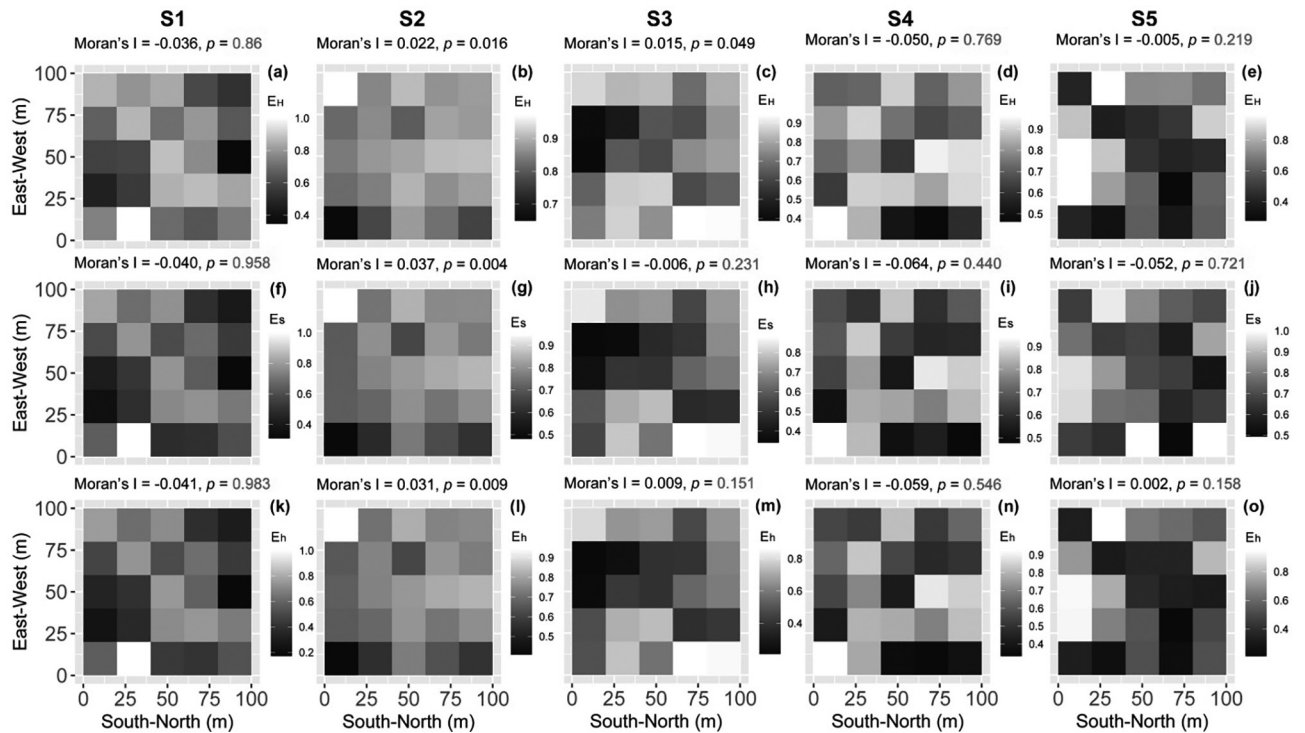


Fig. 6. Spatial patterns of species evenness indices among five tree life stages.  $E_H$  = Pielou's evenness index,  $E_s$  = Sheldon's evenness index,  $E_h$  = Heip's evenness index



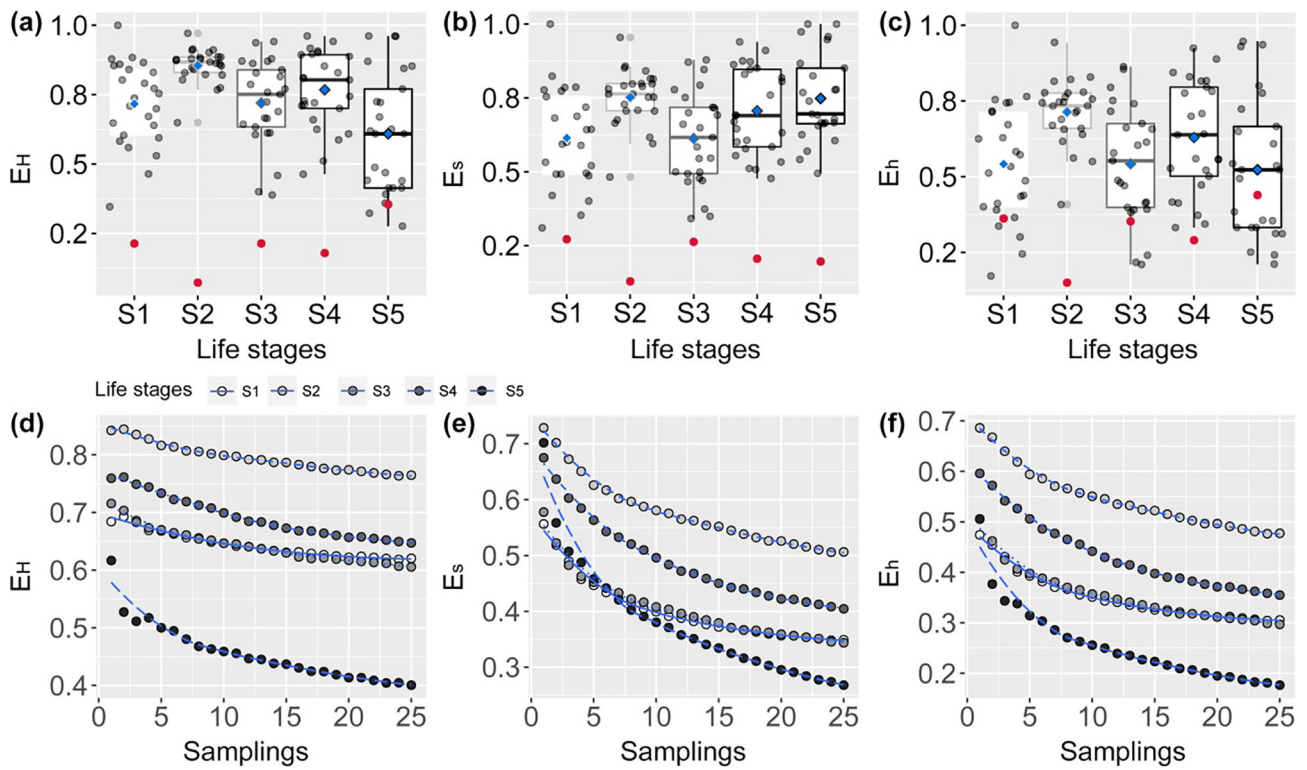


Fig. 7. Patterns in species evenness indexes by tree life stage and sampling area. Red dots in the upper panels represent the coefficients of variation (CVs).  $E_H$  = Pielou's evenness index,  $E_S$  = Sheldon's evenness index,  $E_h$  = Heip's evenness index

associated CVs (in parentheses) among sub-quadrats were 0.61–0.85 (0.07–0.35), 0.61–0.75 (0.19–0.27), and 0.52–0.71 (0.15–0.44), respectively. However, there were significant differences in the three evenness indices among life stages ( $p_{\text{KW}} < 0.01$ ). Excluding S2, all life stages had small, non-significant Moran's  $I$  values ( $p > 0.05$ ). Evenness indices gradually decreased within each life stage with increased sampling area. Generally, evenness indices were similar within S1 and S3, with larger values seen for S2 and S4, and smaller ones for S5 (Fig. 7).

## Discussion

### Species richness and abundance among life stages

R and N are among the oldest and most intuitive species diversity indices. The pattern of these indices between S1 and S2 seen in this study indicated low seedling survival rates. This is potentially a result of negative density dependence, wherein conspecific individuals die due to resource competition, disease, or pests, and the overall number of individuals decreases (Inman-Narahari et al., 2016; Lin et al., 2017; Li et al., 2020a). There was evidence of high intraspecific aggregation (clustering) in S1 for populations of *L. ovalifolia* (LO), *Q. variabilis* (QV), and *C. glauca*

(CG), and these three species combined accounted for nearly 80% of all individuals within this life stage. Variability in early life stages is common (Clark et al., 1999), as seedlings have limited ability to cope with adversity and many environmental factors, such as light limitation, substrate availability, and soil organic matter content, can reduce their R and N (Barna & Bosela, 2015; Liira et al., 2017; Lin et al., 2017; Dyderski & Jagodziński, 2020). The life stage categories that we used precluded shrubs and small trees from being classified as S5, as these plants rarely if ever enter the upper canopy layer. Results from natural forests in tropical and subtropical regions support our findings, in that R and N tend to decrease in the upper canopy (Feroz et al., 2016; Shankar, 2019). The progression from S3 to S5 is associated with increased competition and mortality, which can reduce both R and N (Li et al., 2019). Other factors, such as stand origin, floral and faunal communities, geography and climate, and disturbance may also influence the pattern and quantitative relationships of R and N among life stages (D'Amato et al., 2009; Ostertag et al., 2014; Jin et al., 2019; Ray et al., 2021).

R and N are tightly related to sampling area. The species-area curves documented here are consistent with those reported in a wide variety of natural forests in different regions (Hui et al., 2011; Ostertag et al., 2014; Feroz et al., 2016; Shankar, 2019); even some managed forest stands show similar patterns (Li et



al., 2021; Xi et al., 2021). Generally, small patches of uniform habitat may be suitable for many species, but limitations in carrying capacity mean that overall  $N$  is largely dictated by individual species densities (Preston, 1962). Although  $R$  is not additive,  $N$  is (He et al., 2002), which explains why  $R$  and  $N$  are highly correlated at small scales, but show only a weak or no correlation at large scales (He et al., 2002; Wang et al., 2007; Li et al., 2016). As sampling area further increases, there are fewer gains in niche space, so the rate of increase in  $R$  declines and the curve flattens (Turner & Tjørve, 2005; Li et al., 2016). We found that both  $R$  and  $N$  were determinants of the patterns in species-area and abundance-area curves, which contradicted our second hypothesis.

### Species diversity among life stages

Species diversity indices (e.g.,  $H'$ ,  $D$ , and Alpha) are widely used to assess diversity in many ecosystems. These indices assign different weights to common and rare species; some emphasize the former and others the latter (Hill, 1973; Hui et al., 2011; Hui & Pommerening, 2014).  $H'$ ,  $D$ , and  $R$  showed similar patterns across the five life stage categories in this study, reflecting the close relationships among these indices. Some natural forests have highly similar characteristics (Li et al., 2016; Shankar, 2019), but in some cases  $H'$  is nearly constant across vertical strata, which may be a product of decreased  $R$  and increased evenness (Feroz et al., 2016). Yue (1999) discussed a critical defect in  $H'$ ; that is, when  $p_i < 0.368$ ,  $H'$  increases with an increase in  $p_i$ ; otherwise,  $H'$  decreases with an increase in  $p_i$ . Therefore, differences in  $p_i$  preclude congruency among  $H'$  and other indices. Alpha is positively proportional to both  $R$  and  $N$  (Ma, 1994), and we found low variation in Alpha among life stages. Although Alpha is considered to be an excellent indicator of species diversity (Ma, 1994), we found it to be less sensitive than  $H'$  or  $D$  in our study, particularly for the adult stage (S5).

All three diversity indices increased with increased sampling area. Our rarefaction curve suggested that 90% of the species diversity in our 1 ha plot could be predicted from approximately 10 sub-quadrats (20 m  $\times$  20 m), and these diversity indices reached their maximum values much earlier than  $R$ . This highlights the importance of careful index selection when assessing stand-level species diversity. Although other studies have reported similar findings (Ostertag et al., 2014), still others found a decrease in  $H'$  with increased sampling area, and cautioned against its use for evaluating plant diversity from single or multiple plots with a small total area (He et al., 2002; Yang et al., 2012). The species-area curves of saplings (S2) and adults (S5) were distinct from those of the other life stages in this study. Our

results indicate that small-sized trees were the main drivers of species diversity at the stand-level, evidenced by greater  $R$  and few individuals per species within this class. Generally, understory species diversity is much greater than that of the upper canopy in subtropical forests, potentially reflecting secondary patterns of regional vegetation (Wu et al., 2010; Shankar, 2019). Population sizes in the S5 category showed a marked decline from preceding life stages. PY, a shade-intolerant colonizer of burned areas (Li et al., 2017; 2020a), dominated the canopy in our study area, with little representation of broad-leaved species (Li et al., 2020b). Our study forest of pine-oak mixedwood is in an early successional stage, so its diversity was much lower than that of old growth forests, particularly in tropical regions (He et al., 1996; 2002; Inman-Narahari et al., 2016; Shankar, 2019).

### Species evenness among life stages

Species evenness indices reflect  $N$  ratios. In our study, there were no clear patterns across life stages in  $E_H$ ,  $E_s$ , or  $E_H$ . This indicates that the balance in interspecific  $N$  may decline with declining  $R$ . This may be related to the dominance of a small number of species in each life stage, which may reinforce imbalances among species and reduce species diversity (Stein et al., 2014). Intraspecific competition is an important driver of succession in mixed stands (Li et al., 2020b). Evenness generally decreases with vertical stratification, reflecting patterns in older to younger life stages (Feroz et al., 2016; Shankar, 2019); this differs from our findings, where both biotic and abiotic factors may contribute to this pattern. However, we note that all three evenness indices displayed clear scale-dependency. This finding is consistent with results from a large (320.5 ha) rainforest monitoring plot in Uganda (Mwavu & Witkowski, 2015). One possible explanation for this pattern is that dominant populations, particularly of small-sized tree species in the understory, show highly clustered distributions (Li et al., 2020b), such that increasing scale (area) exacerbates the observed balance in interspecific  $N$ . In a report from the same study plot, Li et al (2020b) observed that some species dominated in the upper portion (upslope) of the plot, whereas others dominated in the lower slope. Horizontal distribution patterns may relate to species diversity patterns in the vertical plane (Feroz et al., 2016), which indirectly supports our findings.

### Conclusion

Species diversity reflects the heterogeneity of forests in terms of species composition, structure, function, and dynamics through space and time. Diversity

is also inextricably linked to scale. It is important to first understand the organization and structure of forest communities to in turn understand mechanisms promoting species coexistence. Here, we assessed spatial patterns of species diversity among five life stages in a secondary forest stand in the Nanpan River Basin in southwest China. We found that trees in different life stages may play different roles in the maintenance of species diversity at the stand scale. Generally, seedlings were highly affected by resource availability, and diversity varied substantially across space. The R and N of small-sized individuals (i.e., classes S2 and S3) were both high, reflecting a substantial contribution to stand-level diversity, but diversity and species stability was decreased in the adult life stage (S5). The scale dependency of species diversity varied among life stages. Therefore, it is important to use multiple indices to assess the full scope of diversity within forests. We noted significant variation in diversity among sub-quadrats and life stages, with weak spatial autocorrelation among sub-quadrats, indicating differences in ecological patterns and processes across space and time. The management and conservation of forest biodiversity should consider life stages in future.

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