RESEARCH ARTICLE

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Functionally diverse tree stands reduce herbaceous diversity and productivity via canopy packing

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Abstract

1. There is extensive experimental evidence for the importance of biodiversity in sustaining ecosystem functioning. However, such experiments typically prevent immigration by continuously removing non-target species, thereby questioning the generality of these findings to real-world ecosystems. This is particularly true in forest ecosystems where understorey herbaceous species are key biodiversity components but are usually weeded in tree diversity experiments. Consequently, little is known about how tree diversity influences the natural dynamics of understorey herbaceous layers.

2. We conducted a 3-year non-weeded tree diversity experiment composed of eight woody species differing widely in plant economic strategies. We examined how the functional diversity and identity of tree species mixtures drive the temporal dynamics of understorey productivity, functional diversity and composition through canopy packing (CP).

3. Tree mixtures with high functional diversity experienced increased CP over time, thereby decreasing understorey productivity and diversity. Furthermore, herbaceous communities were dominated by species with functional traits typical of low-light conditions [lower community-weighted mean (CWM) of maximum plant height, but larger CWM of specific leaf area] in response to increased CP.

4. Our results provide mechanistic insights into the role of tree functional diversity in shaping the dynamics of biomass, functional diversity and composition of the understorey herbaceous layer during the early successional period. It is expected that the effects of tree functional diversity would also be relevant over time due to the increasing usage of canopy space. This study highlights the significance of natural community processes in determining the effects of tree diversity on the temporal dynamics of previously neglected ecosystem structures and functioning.

KEYWORDS
biodiversity, ecosystem function, functional composition, functional dispersion, functional strategies, species interactions, stand age, tree mixture

1 | INTRODUCTION

One of the biggest challenges in ecology is to understand how changes in biodiversity affect ecosystem functioning (Cardinale et al., 2012; Hooper et al., 2005). Over the last three decades, numerous experiments involving the manipulation of plant diversity have been implemented in grassland and forest ecosystems to elucidate how plant species loss influences ecosystem functioning (Cardinale et al., 2007; Huang et al., 2018; Tilman et al., 2006; Zhang et al., 2012). One of the common features of such experiments is that species richness levels are maintained by continuously removing non-target species (Tilman et al., 2006; Veen et al., 2018). In forest ecosystems, many experiments have manipulated multiple aspects of plant diversity encompassing species richness, evenness, species identity, as well as genetic, functional and phylogenetic diversity. However, in these forest experiments, non-experimental understorey herbaceous plants were typically removed (Grossman et al., 2017; Grossman et al., 2018; Paquette et al., 2018; Tobner et al., 2016; Williams et al., 2017). Consequently, little is known regarding the consequences of tree species diversity on the natural dynamics of understorey herbaceous species.

Forests are the most important repositories of terrestrial biodiversity (FAO, 2020). Tree and herbaceous species are two essential components of plant diversity that together drive forest ecosystem functioning (Luo et al., 2019). Herbaceous plants contribute ~5% of above-ground net primary productivity and 20%–25% of the annual litterfall in forests, and play an important role in nutrient cycling (Gilliam, 2014). In particular, the interactions between tree and herbaceous species at the early successional stage are critical for the determination of community structures and dynamics (Ampoorter et al., 2015). Numerous studies have examined how climate change, soil properties and canopy layers influence herbaceous layer dynamics in natural forests (Depauw et al., 2020; Gilliam, 2014, 2019; Hart & Chen, 2008). However, the effects of tree diversity on natural herbaceous processes in experimental ecosystems remain not well understood.

Tree diversity influences herbaceous layer properties mainly through the modification of resource availability, especially for light (Davis et al., 1998; Hart & Chen, 2008; Reich, Frelich, et al., 2012). The quantity and quality of light resource reaching the forest floor are greatly modified by canopy structures (Messier et al., 1998). As one of the key characteristics of canopy structures during forest development, canopy packing (CP) is indicative of the light interception and space usage of tree species (Jucker et al., 2015; Morin et al., 2011). Increased CP has been proposed as one of the key mechanisms that drives positive tree diversity effects on forest productivity, as individual trees pack their crowns more densely and develop more structurally complex canopies in species mixtures in contrast to monocultures (Jucker et al., 2015; Sapijanskas et al., 2014; Williams et al., 2017). This variation in canopy structures may further determine the diversity, composition and functioning of the herbaceous layer by altering the space and light conditions of the understorey.

Functional diversity plays a key role in determining the effects of tree mixtures on the efficient usage of above-ground space (Williams et al., 2017). Tree species with variant crown architectures and economic strategies utilize different spatial positions in forests, thus resulting in the efficient partitioning and utilization of space and light resources (Huang et al., 2018; Jucker et al., 2015). Increased CP reduces the amount of light that reaches the understorey and stipulates understorey plants to use diffusive light (Bartels & Chen, 2010; Sapijanskas et al., 2014). The limited amount of light in the understorey favours shade-tolerant species, thereby resulting in the decline in herbaceous productivity and diversity (Bartels & Chen, 2010; Depauw et al., 2020; Hart & Chen, 2008). Concurrently, functional identity is also an important driver of the effects of tree diversity on exploring the above-ground space (Grossman et al., 2017; Tobner et al., 2016). Compared with conservative slow-growing species, fast-growing acquisitive species with higher specific leaf area (SLA) and leaf nitrogen content (LNC), shorter leaf life span, lower dry mass content and wood density (WD) express faster rates of resource acquisition and tissue turnover (Reich, 2014). Fast-growing tree species with efficient biomass investments in stems and leaves can rapidly develop crown architectures and occupy canopy positions (e.g. by overtopping; Van de Peer et al., 2018). Therefore, communities dominated by fast-growing tree species can eventually control herbaceous layer properties through the modification of microenvironmental conditions (Hart & Chen, 2008), by favouring conservative herbaceous species with a higher capacity of persistence against shaded environments.

The effects of diversity on ecosystem functioning may change over time due to shifts in species interactions (Hooper & Dukes, 2004; Weis et al., 2007). Several studies have revealed that the effects of diversity on productivity increased over time via increased interspecific complementarity and decreased functional redundancy (Cardinale et al., 2007; Reich, Tilman, et al., 2012). In forests, species with varying crown architectures and economic strategies are able to more efficiently utilize canopy space due to crown complementarity (Williams et al., 2017), where the accumulated usage of above-ground space is enhanced with stand age (Huang et al., 2018; Zhang et al., 2012). This diversity-dependent temporal shift in CP may indirectly drive the dynamics of herbaceous biomass production, diversity and functional composition (Germany et al., 2017; Hart & Chen, 2008).

Here, we examined how tree diversity influences the dynamics of understorey herbaceous species in experimental tree ecosystems. We quantified the temporal shifts of herbaceous layer properties over a 3-year non-weeded tree diversity experiment, composed of eight tree species that differed significantly in economic strategies and covering 17 scenarios of tree species compositions in subtropical China. Specifically, we tested whether (a) tree functional diversity and the community-weighted mean (CWM) of acquisitive traits influenced understorey productivity, functional diversity and composition via CP; (b) the effects of tree functional diversity on the herbaceous layer mediated by CP strengthened over time. We hypothesized that (a) the tree

functional diversity and CWM of acquisitive traits increase CP, thereby decreasing understorey productivity and diversity and increasing dominance of conservative functional composition; and (b) the effects of tree functional diversity on the herbaceous layer properties mediated by CP strengthen with stand age.

2 | MATERIALS AND METHODS

2.1 | Site description

The tree diversity experiment was conducted on Putuo Island, of the Zhoushan Archipelago (29°58′N, 122°23′E), in eastern China. This region features a subtropical monsoon climate, with a mean annual temperature of 16°C and mean annual precipitation of 1,358 mm. The experimental site is an original forest-transformed agricultural field with an area of 0.5 ha. The soils are sandy clay laterite, composed of 20%–40% sand and 10%–15% clay. The historic vegetation is coniferous and broadleaved mixed forests, with dominant species that include *Pinus massoniana*, *Liquidambar formosana*, *Cinnamomum camphora* and *Celtis sinensis* (Yan et al., 2018), which remain around the experimental site. The local people cleared the forest on our experimental site for planting vegetables 30 years ago; however, these agricultural activities were halted by the government 2 years before the experiment (i.e. 2016). We cleared up all the remaining crops, vegetables and weeds by the roots to set up the experiment. Subsequently, the surface soil (30–40 cm in depth) was ploughed using a land preparation machine. We did not kill the seed banks of herbaceous species using herbicides or other chemical agents to determine the role of herbaceous species in the tree diversity–ecosystem functioning relationship. We acknowledge that the herbaceous species regenerating from the seed bank of the abandoned agricultural fields are different from those in the matured natural forests. However, their interactions with tree species feature a typical process during the early stage of secondary forest succession in widespread applied forest restoration, as well as the natural regeneration of the deforested and abandoned agricultural fields worldwide. The tree diversity experiment and field measurements were permitted by the local government.

2.2 | Experimental design

The experiment was established in April 2018 to test how tree species with contrasting economic strategies affect ecosystem functions. We selected eight species that differ characteristically in economic strategies and are located in different positions of the 'fast–slow' economics spectrum (Figure 1a; Table S1). The species set included four evergreen tree species (*Schima superba*, *Cyclobalanopsis glauca*, *Neolitsea sericea* and *Machilus thunbergii*) and four deciduous species (*Sapium sebiferum*, *L. formosana*, *Koelreuteria bipinnata* and *Sapindus mukorossi*), which are common species for forest restoration in eastern subtropical China. These species were divided into four economic segments from the conservative to acquisitive side (two species per segment), according to their positions in the leaf and wood economics spectrum (Figure 1a).

The experiment contains four random blocks for buffering random environmental variations, in which each block contains 17 non-weeded plots (4.2 × 4.2 m). Within each block, the plots were assigned to one of 17 compositions: eight monocultures, four single-segment (two-species) mixtures, four two-segment (four-species) mixtures and one four-segment mixture including all eight species (Figure 1b). We used this design for the experiment as we focused on how functional diversity influenced ecosystem processes rather than disentangling the composition effects of species richness (Bruelheide et al., 2014). The plot distribution was randomized within each block, where each plot included sixty-four 1-year-old tree seedlings of the selected species (Table S2), which were planted at high density (0.6 m apart) to accelerate species interactions. Within each square plot, species in mixtures were planted at random locations with equal proportions but avoided having the eight nearest neighbours within 1.44 m^2 of each focal tree belong to the same species. This approach ensures diversity effects occur at the neighbourhood level in tree mixtures, as neighbouring tree individuals interact strongly and contribute to the diversity effects in forest communities (Grossman et al., 2017).

The plots were spaced 1 m apart to allow for movement, while minimizing inter-plot interactions. There were 4,352 tree individuals in 68 non-weeded plots, that is 64 individuals × 17 compositions × 4 replicates (blocks). Two months after the establishment of the experiment, any dead tree seedlings were replanted to mitigate planting shock. Thereafter, replanting, weeding and any other human interference were not carried out to allow the plots to develop naturally to test how tree species and herbaceous species interactively affect ecosystem functions. The total tree mortality after three growing seasons since plot establishment was 8%.

2.3 | Herbaceous layer survey

From 2018 to 2020, we conducted surveys of the herbaceous layer at the beginning of September for each year. Herbaceous layer species were defined as all non-woody vascular plants including forbs, grasses, sedges and ferns. To avoid edge effects, we conducted the surveys at the 3 m × 3 m areas of the plot centres. The per cent cover of each species was visually estimated according to the Braun-Blanquet method within each plot (Braun-Blanquet, 1964) for seven different classes (1%, 5%, 15%, 25%, 50%, 75% and 95%).

After surveying of the herbaceous species composition each year, the above-ground biomass was harvested from three randomly chosen quadrats (0.5 m × 0.5 m) within each plot. The herbaceous above-ground biomass, including both annuals and perennials, was harvested on an annual basis to estimate annual above-ground biomass production. Subsequently, all collected herbaceous samples
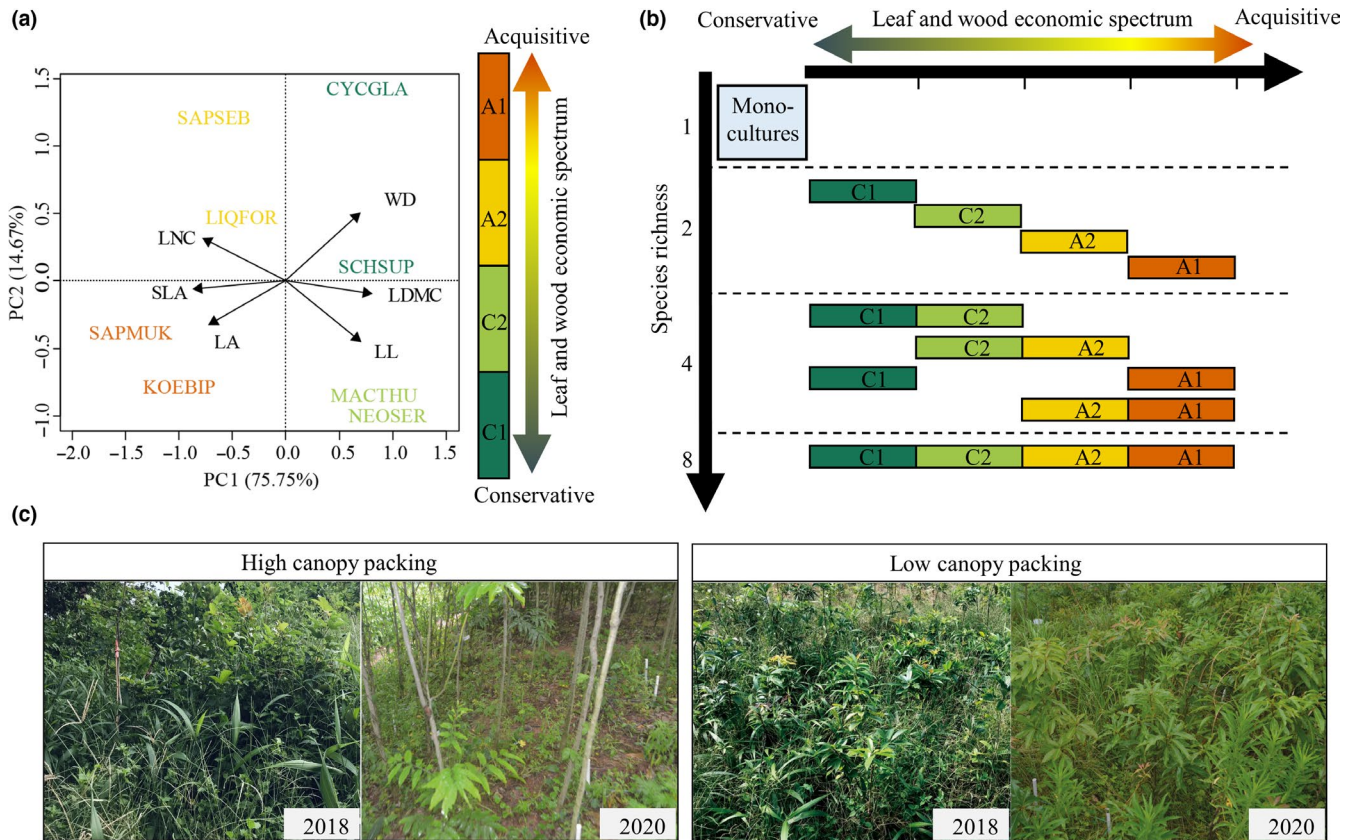
FIGURE 1 Experimental design and overview of herbaceous layer changes from 2018 to 2020. (a) Species are divided into four economic segments from the conservative to acquisitive side according to the species scores for the first two axes in principal component analysis. (b) Schematic representation of species richness (SR) and economic spectral segment mixtures in this study. Monocultures included all eight species. C1, C2, A1 and A2 represent the first and second conservative segments, the first and second acquisitive segments respectively. Abbreviations for each species are given in Table S1. (c) Contrasting herbaceous layers shifted between 2018 and 2020 in stands with both high and low canopy packing

were transferred to the laboratory from plastic to paper bags. They were then oven-dried for 72 hr at 70°C to a constant weight, at which point the dry biomass was weighed. The annual above-ground biomass production of the herbaceous layer of each plot was calculated by averaging the dry biomass collected from three quadrats (g/m^2).

2.4 | Tree crown measurement

We measured the tree crowns each September (the end of the growing season) from 2018 to 2020 when leaves were fully flushed. We used a steel tape to determine the overall height and the height of the lowest leaf on the first living branch of each tree. The maximum crown radii of the east–west and north–south directions were also measured. The crown depth (CD, m) was calculated by subtracting the height of the lowest leaf from the overall tree height. As all trees in this experiment are broadleaf species, we viewed the crown as spherical and determined the crown volume (CV; in m^3) of each tree according to Equation (1):

$$CV = \frac{4}{3}\pi \frac{C_a}{2}\frac{C_b}{2}\frac{CD}{2}, \tag{1}$$

where CV is the crown volume, C_a and C_b are the maximum crown radii from east–west and north–south directions, respectively, and CD is crown depth.

2.5 | Estimation of canopy packing

We summed the CVs of all individual trees as the total CV of a given plot, where individuals on the outermost row or column of each plot were excluded. As recommended (Jucker et al., 2015), we estimated CP at the plot level as the proportion of above-ground space available to trees that are occupied by crowns:

$$CP_i = \frac{\sum CV_i}{\text{Plot area} \times [H_{max\,i} - BH_{min\,i}]}, \tag{2}$$

where CP_i is the CP index of a plot in year i, $\sum CV_i$ is the sum of all individual tree CVs within a plot in year i, and $H_{max\,i}$ and $BH_{min\,i}$ are the maximum tree height and the lowest living branch recorded in a plot in year i respectively. The numerator defines the total CV of a plot, while the denominator defines the total canopy space that tree individuals might potentially utilize. Although there was a strong correlation

between the CP and total CV (Figure S1), CP reflects the efficiency of the utilization of canopy space by taking into account the changes in tree crown heights over time.

2.6 | Light intensity measurements

To assess whether increased CP decreases the light availability for herbaceous species, we measured the light intensity (lux) that reached the herbaceous layer of each plot using photometric sensors with an active spectrum of 380–730 nm (WS102, Wumi, China). In each plot, accurate measurements of the lux illuminance (0.5 m above the ground surface) were obtained three times per day when the plots were in direct sunlight. The measurements were conducted from June to September 2021. We estimated the light intensity that reached the herbaceous layer per plot as the mean of the daily measurements and found a significant negative relationship between CP and the light intensity that reached the herbaceous layer (Figure S2).

2.7 | Functional traits of tree and herbaceous species

Among the many plant functional traits linked with economic strategies, we chose leaf longevity (LL, month), SLA (cm^2/g), leaf area (LA, cm^2), leaf dry mass content (g/g), LNC (mg/g), and WD (g/cm^3) to quantify the functional diversity and identity of the tree species mixtures. These traits are key features of the plant leaf and wood economic spectra, which are strongly associated with resource capture and usage (Díaz et al., 2016; Reich, 2014). To estimate the LL of tree species, we selected five individuals for each species and recorded the number of fresh leaves that emerged on the newly extended shoots of each target individual. These individuals were selected from an open buffer area with high light conditions. Thereafter, we repeated field surveys every month to record the number of leaves that remained on the shoots of the target until all the leaves fell. LL for each species was calculated as the averaged duration from leaf expansion to falling off. We obtained the other species-level traits from a previous dataset in this region (Zhao et al., 2017) and an unpublished dataset that contained the functional traits of common species collected from multiple sites in this region. We used species mean trait values to quantify the functional diversity and identity of economic traits of tree species mixtures, similar to previous studies (Grossman et al., 2017; Huang et al., 2018).

To determine the functional traits of herbaceous species, we measured the SLA and maximum plant height (H_{max}, m), which are generally considered important for light competition and resource acquisition (Depauw et al., 2020). We collected mature and undamaged leaves of 50 randomly selected individuals per species in the experimental area to determine the SLA. We also recorded the plant height of these individuals and calculated the maximum plant height for each species. The species-level trait means reflect the acquisition strategies of plants as an outcome of evolutionary processes

(Roscher et al., 2018). Therefore, we used species mean of trait values to quantify the functional diversity and composition of the herbaceous layer.

2.8 | Calculation of functional diversity and identity

We used functional dispersion (FDis) to determine the functional diversity of each tree mixture. FDis calculates the distance of each species to the centroid of all species in the trait space (Laliberté & Legendre, 2010). The Gower dissimilarity matrix and species–species Euclidean distance matrix were employed to compute the multidimensional FDis and FDis of each single trait respectively. Even though the multidimensional- and single-trait dispersion were highly correlated (Table S3), the multidimensional trait axes characterized more types of resource niches (Villeger et al., 2008). We used multidimensional FDis to link tree diversity with CP and herbaceous properties.

We quantified the functional identity of tree mixtures using the CWM values of each trait, which were calculated as the averaged trait values of each species mixture. We performed principal component analysis with the CWM of six traits to obtain a comprehensive predictor of the combination of each tree mixture. Subsequently, we extracted the first principal component (CWM$_{PC1}$, representing 79.3% of total inertia) as a variable of the functional identity (Figure S3), where the high CWM$_{PC1}$ represents the acquisitive economic strategy of a tree mixture. We also calculated the herbaceous FDis and CWM of the SLA and H_{max} (weighted by the species abundance) to determine the functional diversity and composition of the herbaceous layer for each tree mixture. The FDis and CWM calculations were conducted using the FD package (Laliberté & Legendre, 2010).

2.9 | Statistical analysis

We used linear mixed effect models to examine the effects of tree functional diversity and identity on herbaceous properties. Each constructed model included FDis, CWM$_{PC1}$, stand age, and the interactions between FDis and CWM$_{PC1}$ with stand age as the fixed factors, and block and plot identity as random factors:

$$y_i \sim \beta_0 + \beta_1 \text{FDis} + \beta_2 \text{CWM}_{PC1} + \beta_3 \text{Age} + \beta_4 (\text{FDis} \times \text{Age})$$
$$+ \beta_5 (\text{CWM}_{PC1} \times \text{Age}) + \pi_{\text{Block}} + \pi_{\text{Plot.ID}} + \varepsilon, \tag{3}$$

where y_i are functional diversity, biomass production, CWM H_{max} and CWM SLA of the herbaceous layer, respectively; β_i are partial regression coefficients to be estimated; π_{Block} and $\pi_{\text{Plot.ID}}$ are the random effect factors of 'Block' and 'Plot identity'; and ε represents sampling errors.

We used partial regression coefficients to demonstrate the effects of each predictor on the response variables. To graphically show the effects of FDis or CWM$_{PC1}$ on the herbaceous properties

across stand ages, we calculated the age-dependent FDis or CWM_{PC1} effects as $\beta_0 + \beta_1 FDis + \beta_4 FDis \times Age$ or $\beta_0 + \beta_2 CWM_{PC1} + \beta_5 CWM_{PC1} \times Age$ in Equation (3) at the stand age of 1, 2 and 3 respectively. Subsequently, we tested the effects of tree FDis and CWM_{PC1} on CP using the same linear mixed effect model, in which CP was treated as a response variable. Further, we examined the relationships between the herbaceous properties with CP using similar linear mixed effect models with herbaceous properties as the response variables, CP, stand age and their interactions as the predictor variables. Prior to analysis, the herbaceous property variables were transformed by natural logarithm and the CP (proportional data) was transformed by logit function to achieve its values being linearly distributed between 0 and 1 (Hart & Chen, 2008; Jucker et al., 2015). All the explanatory variables were standardized (mean = 0, SD = 1) prior to comparing the coefficient estimates.

To mechanistically understand how tree functional diversity and the CWM of economics traits directly and indirectly influenced the temporal shifts of herbaceous layer properties through CP, we employed piecewise structural equation modelling (SEM). First, we built a SEM that included all paths from tree FDis, CWM_{PC1}, stand age and their interactions, as well as 'FDis × Age' and 'CWM_{PC1} × Age', to the herbaceous layer properties, both directly and indirectly via CP (Figure S4). The interactions between FDis and CWM_{PC1} with stand age in the SEM were obtained by constructing two new variables as the multiplication of stand age and FDis (FDis × Age) and CWM_{PC1} (CWM_{PC1} × Age), respectively, following Chen and Chen (2019). The direct effects of stand age on herbaceous properties were included, as the herbaceous components might change due to the time of colonization effects. This first model that included all the pathways was not a good fit based on Fisher's C statistic test ($p < 0.05$). We therefore removed the nonsignificant paths to improve the overall performance of the SEM model. As the final model, we selected the one with the lowest Akaike information criterion value (Table S4). We fitted SEMs by accounting for the random effects of 'Block' and 'Plot.ID' using the 'psem' function of the PIECEWISESEM package (Lefcheck, 2016).

We conducted a permutational multivariate analysis of variance (PERMANOVA) test to examine how tree mixtures affected the species composition of the herbaceous layer over time. In PERMANOVA, the Bray–Curtis (based on cover data) dissimilarity matrix was used to summarize the temporal changes in herbaceous species composition from 2018 to 2020. The significance of the compositional differences over the 3 years was tested by PERMANOVA by 999 permutations (Anderson, 2001). Moreover, we performed non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity measure to visualize how species composition among plots varied over time.

All linear mixed effect models, structural equation models and NMDS analyses were performed in R 4.0.3 (R Core Team, 2021).

3 | RESULTS

On average, the productivity, FDis and CWM H_{max} of the herbaceous layer did not change significantly with the tree FDis (Figure 2a–c;

Table S5), whereas the herbaceous CWM SLA increased marginally with the tree FDis ($p = 0.05$; Figure 2d). For the effects of tree functional identity on herbaceous properties, only the herbaceous CWM H_{max} decreased marginally with the tree CWM_{PC1} ($p = 0.07$; Figure 2g). The averaged influence of tree FDis and CWM_{PC1} on the herbaceous properties did not change with stand age (Figure 2a–h).

The positive effects of tree FDis on CP increased from 2018 to 2020 ($p = 0.001$; Figure 3a), whereas on average, the CP increased significantly with stand age ($p < 0.001$; Table S5). However, CP did not change with tree CWM_{PC1} and its interaction with stand age (Figure 3b). The herbaceous biomass decreased significantly with increasing CP, with more pronounced decreases as stands aged ($p < 0.001$; Figure 4a; Table S6). The herbaceous FDis consistently decreased significantly with CP across the three measurement years ($p = 0.001$; Figure 4b). Functionally, the herbaceous community shifted towards a higher dominance of species with shorter plant height (decreased CWM H_{max}; $p = 0.001$; Figure 4c) but higher SLA (increased CWM SLA; $p < 0.001$; Figure 4d) in response to increased CP. There was a significant species compositional shift in the herbaceous layer in response to increased CP through time; the dominant species shifted from grasses and sedges to forbs with increased CP over time (Figure S5).

The SEMs revealed that stand age and its interaction with FDis had positive direct effects on CP, while CP had a negative direct effect on the herbaceous biomass, which resulted in negative indirect effects of stand age and age-strengthened FDis (Figure 5a). Similarly, stand age and its interaction with tree FDis negatively influenced the herbaceous FDis via increasing CP (Figure 5b). Further, tree CWM_{PC1} had negative direct effects on the herbaceous CWM H_{max} (Figure 5c). The interactions between the tree FDis with stand age indirectly decreased the herbaceous CWM H_{max} via CP (Figure 5c), but increased the herbaceous CWM SLA (Figure 5d). Stand age had positive direct effects on the herbaceous CWM H_{max} but negative direct effects on the herbaceous CWM SLA (Figure 5c,d).

4 | DISCUSSION

As hypothesized, we found that the positive effects of tree functional diversity on CP increased over time, thus driving the temporal dynamics of herbaceous properties by decreasing productivity and functional diversity but increasing the dominance of conservative functional composition. These results suggest that trait diversity of tree mixtures drives temporal dynamics of the herbaceous layer at the early successional period of forest communities. Previous studies in natural or experimental stands confirmed the impacts of overstorey species richness and cover on herbaceous layers (Ampoorter et al., 2015; Germany et al., 2017; Hart & Chen, 2008; Reich, Frelich, et al., 2012). Our study emphasized how functionally diverse tree stands influence temporal processes of natural understorey herbaceous properties in experimental ecosystems.
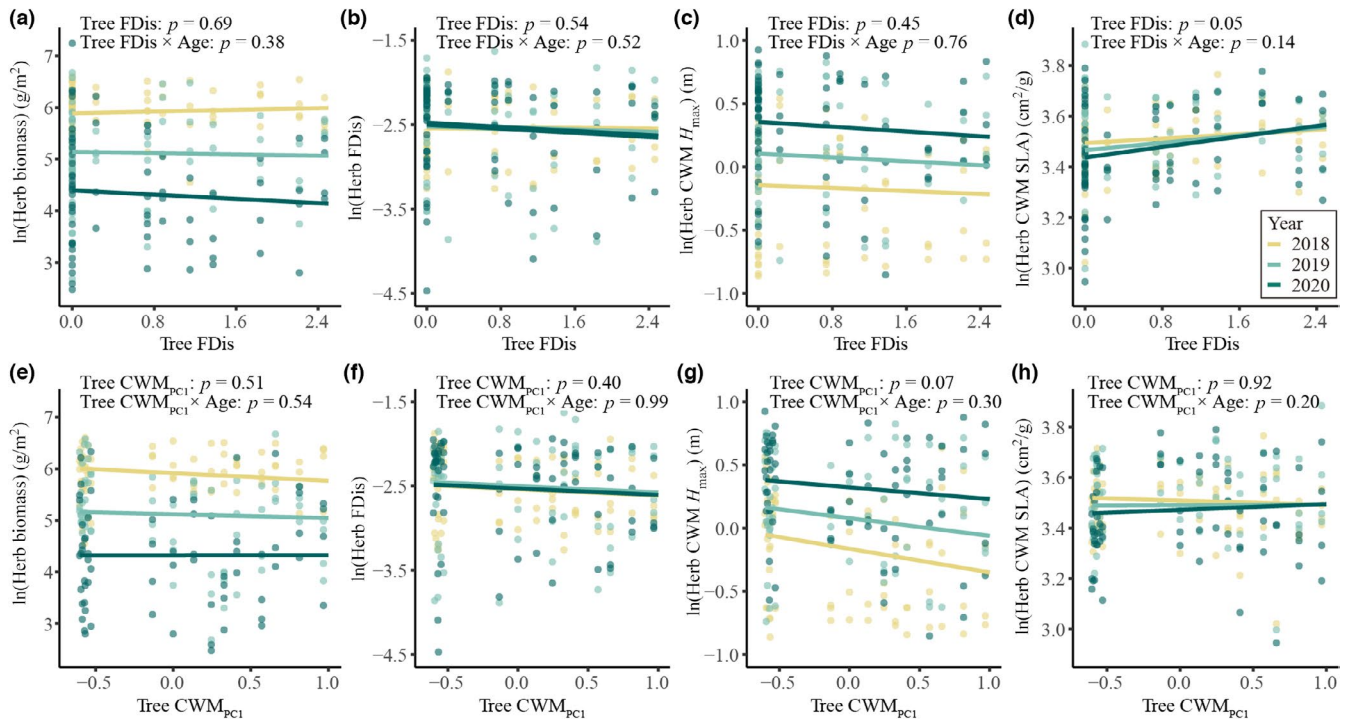
FIGURE 2 Relationships between herbaceous properties with tree functional diversity (FDis; a–d) and community-weighted mean of acquisitive economics traits (CWM$_{PC1}$; e–h) from 2018 to 2020. The response variables include herbaceous biomass production (Herb biomass), functional dispersion (Herb FDis), community-weighted mean of maximum plant height (Herb CWM H_{max}) and specific leaf area (Herb CWM SLA). All response variables were natural log-transformed
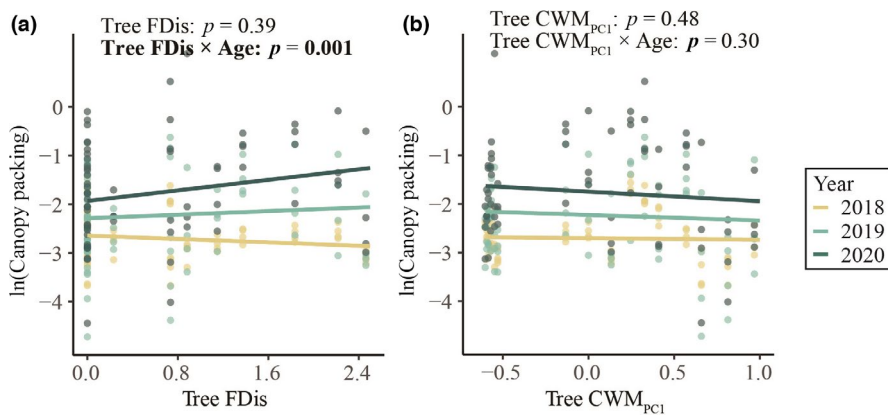
FIGURE 3 Relationships between canopy packing with tree functional diversity (FDis; a) and community-weighted mean of acquisitive economics traits (CWM$_{PC1}$; b) from 2018 to 2020. Canopy packing was logit-transformed

4.1 | Functional consequences of tree species mixtures on herbaceous properties

Over our 3-year study with the realistic interactions between experimental tree species and herbaceous species regenerating from the seed bank, there was a positive relationship between herbaceous CWM SLA and tree functional diversity, but a negative relationship between herbaceous CWM H_{max} and tree CWM$_{PC1}$, which represents resource acquisition strategies. In tree mixtures with high functional diversity, the efficient partitioning of space and light resources by tree species decreases light availability to the herbaceous layer (Hart & Chen, 2008; Reich, Frelich, et al., 2012). In a light-limited environment, herbaceous species typically possess large SLA to enhance light capture and improve carbon gains

(Gommers et al., 2013). Several studies revealed that rapidly occupied above-ground space by fast-growing tree species reduces the light resource availability for the understorey, which suppresses the growth of understorey plants (Bartels & Chen, 2010; Reich, Frelich, et al., 2012). However, in this study, we did not find a significantly negative correlation between the CWM$_{PC1}$ of acquisitive traits and the light intensity of the herbaceous layer (Figure S6). In addition to competition for light, tree species with fast economic strategies also exhibit a competitive capacity for nutrient and water resources by fine roots, which also suppress the growth of herbaceous plants (Gilliam, 2014).

Notably, in this study, there was no significant correlation between the tree functional diversity and the herbaceous biomass and functional diversity. Tree functional diversity affects herbaceous functional

FIGURE 4 Relationships between herbaceous properties with canopy packing from 2018 to 2020. The response variables include herbaceous biomass production (Herb biomass), functional dispersion (Herb FDis), community-weighted mean of maximum plant height (Herb CWM H_{max}) and specific leaf area (Herb CWM SLA). All response variables were natural log-transformed and canopy packing was logit-transformed
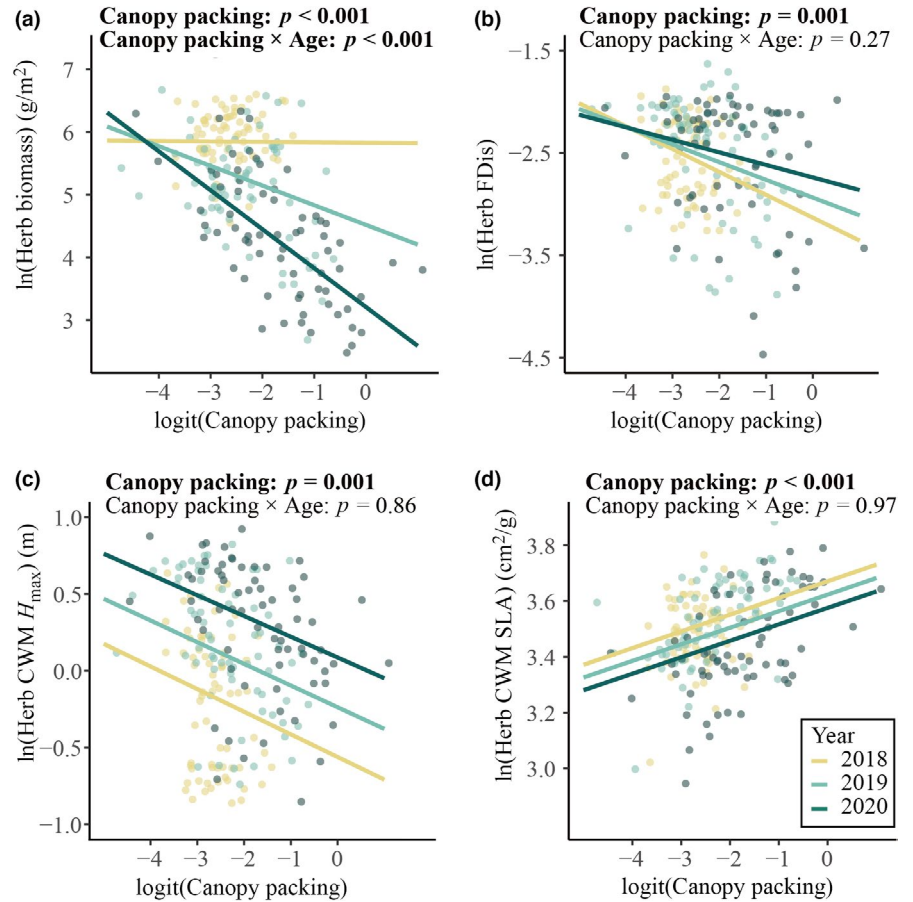
FIGURE 5 Structural equation models illustrating the influence of tree functional diversity (Tree FDis), community-weighted mean of acquisitive economics traits (CWM$_{PC1}$) and stand age (Age) via canopy packing on the herbaceous properties. Response variables include herbaceous biomass production (Herb biomass), functional dispersion (Herb FDis), community-weighted mean of maximum plant height (Herb CWM H_{max}) and specific leaf area (Herb CWM SLA). Black solid and grey dashed lines represent significant ($p < 0.05$) and nonsignificant regression paths respectively. Marginal (R^2_m; based on fixed effects) and conditional R^2 (R^2_c; based on both fixed and random effects) for the herbaceous properties and canopy packing are reported in the corresponding box
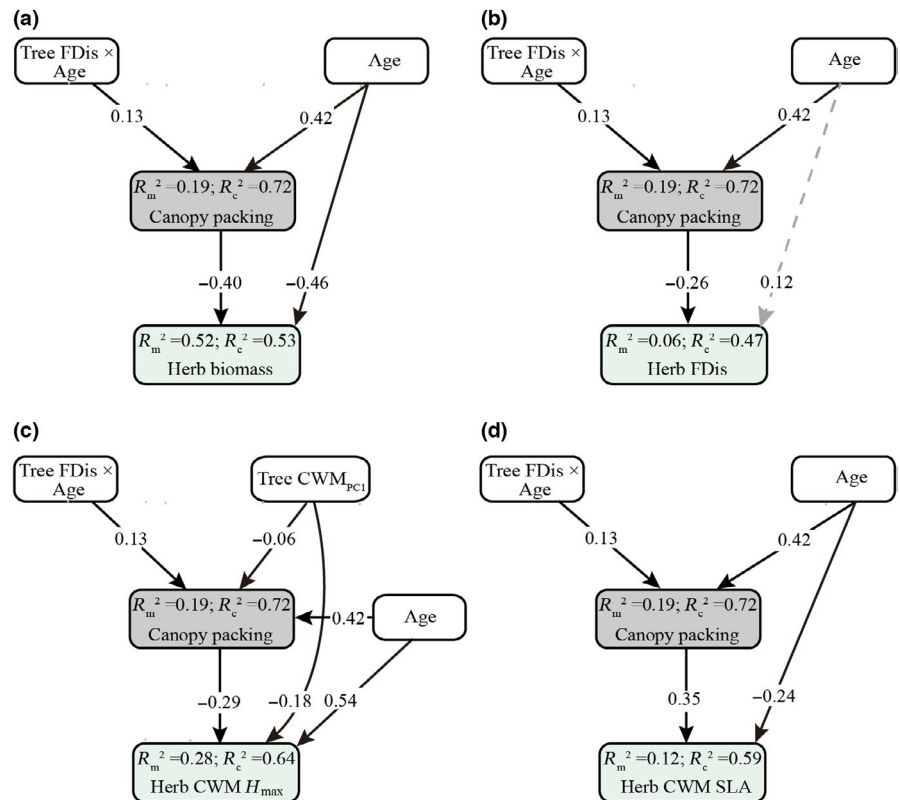
traits/diversity in complex, indirect ways rather than directly (Reich, Frelich, et al., 2012). Understorey biodiversity is determined by either resource quantity (Bartels & Chen, 2010; Stevens & Carson, 2002) or heterogeneity as plants specialize in variable light and soil resources (Bartels & Chen, 2010; Huston, 1979). Tree mixtures comprised of species with various strategies differ substantially in their influences on abiotic and biotic properties of the understorey, such as the quality and quantity of understorey light, leaf litter return, fine root turnover, soil water and nutrient status (Gilliam, 2014; Hart & Chen, 2008). Among these multiple drivers, light availability appears to be the main factor that controls variations in properties of herbaceous layers (Depauw et al., 2020; Reich, Frelich, et al., 2012). This was illustrated in this study via the indirect effects of tree mixtures through CP on the functional diversity and composition of herbaceous layers.

4.2 | Effects of tree mixtures on canopy packing over time

We found that the positive effects of tree functional diversity on CP increased significantly with stand age (Figure 3a). The age-dependent effects of tree functional diversity on CP indicate a strong complementarity effect through time (Cardinale et al., 2007; Weis et al., 2007). In tandem with the coupling of light and water resources, crown architecture plays a central role in structuring CP through mediating strategic trade-offs between resource acquisition, mechanical support and hydraulic functions across co-occurring species (Poorter et al., 2006). As stands develop, the interspecific interactions through crowns become more intense in functionally diverse communities, thus leading to more differentiated niche regarding the light interception and more optimized usages of canopy space (Jucker et al., 2015; Sapijanskas et al., 2014; Williams et al., 2017). Therefore, the accumulated complementary usages of canopy space and the other resources enhance positive diversity effects over time (Huang et al., 2018; Reich, Tilman, et al., 2012).

The effects of the functional identity of tree acquisitive traits (i.e. CWM_{PC1}) or its interaction with stand age on CP were weak. This might have been caused by the specific crown architectures of species, which develop either horizontally or vertically structured crown architectures for optimizing mechanical support and light capture (Poorter et al., 2006; Reich, 2014). In this study, communities dominated by fast-growing species with large LA, such as *L. formosana* and *S. sebiferum*, deployed wide and deep crowns, which packed a high degree of the canopy. In contrast, communities dominated by fast-growing species (*K. bipinnata* and *S. mukorossi*) deployed shallow crowns, and packed a low degree of the canopy. As forests aged, CP in evergreen–deciduous species mixtures increased significantly, compared with communities comprised of pure fast-growing species (Figure S7). The lack of tree CWM_{PC1} effects on CP over time suggests that the trait divergence of tree crowns (e.g. shade tolerance heterogeneity) plays an important role in the development of community structures (Jucker et al., 2015; Williams et al., 2017; Zhang et al., 2012).

4.3 | Tree mixtures promote dynamics of herbaceous layer properties through canopy packing

Our results demonstrate that variations in the CP of tree mixtures result in various temporal processes of herbaceous layer properties. Interestingly, we found significant declines in herbaceous biomass and functional diversity in response to the increased CP of tree mixtures. Declines in herbaceous productivity and functional diversity over time might be correlated with the diminution of resources for herbaceous species (Reich, Frelich, et al., 2012). Tree species with high functional diversity occupy more above-ground space as stands develop, thus reducing light availability and potentially other resource availability (i.e. soil nutrients and water) for herbaceous plants. As a result, stressful resource limitations eventually decrease the biomass and diversity of herbaceous species (Depauw et al., 2020; Germany et al., 2017; Kumar et al., 2018).

Our results also indicate that the CP of tree mixtures plays a strong role in shaping the successional shift of the herbaceous layer. In general, the enhanced degree of CP is associated with increasing canopy closure over time (Jucker et al., 2015; Morin et al., 2011; Williams et al., 2017). This induces herbaceous community reorganization and shifts the dominance from taller to shorter species (Depauw et al., 2020). Dominant species are also evident via the shift from tall competitive grasses and sedges to shorter forbs with increased CP in tree mixtures (Figure 1c; Figure S5). Given the typically higher SLA of forbs compared to those of grasses and sedges (Scharfy et al., 2011; Vile et al., 2005), the functional composition of herbaceous plants shifted from low to high SLA. The diffusive light penetration to herbaceous layers resulting from CP can alter light niche partitioning between herbaceous species (Ampoorter et al., 2015; Germany et al., 2017). In the low-light environments under the forest canopy, the deployment of the larger SLA of herbaceous species is a compensatory mechanism that allows plants to harvest diffusive light and to maintain net photosynthetic rates (Dwyer et al., 2014). However, a high SLA might negatively impact LL in shaded environments which is a trade-off between mass investment and resource conservation (Gommers et al., 2013). Producing a large LA at little construction cost to enhance carbon gains makes these leaves sensitive to mechanical stress (Reich, 2014). We note that intraspecific trait variation may also contribute to this temporal dynamics to tree diversity (Blondeel et al., 2020). For example, individuals of the same species exhibit higher SLA under low-light conditions for optimal light acquisition (Liu et al., 2016).

We regarded the lower CWM of H_{max} but higher CWM of SLA caused by increasing CP as the functional composition of a conservative functional strategy in the herbaceous layer. Meanwhile, the dynamics of herbaceous functional composition reflect an acquisitive–conservative trade-off associated with light availability (Reich, 2014; Sendall et al., 2016). Even though conservative functional strategies relate to relatively lower growth and competitive ability, they may perform well in a shaded environment due to low-light compensation points (Givnish, 1988). Acquisitive light-competing herbaceous species are competitive dominants when

light resources are sufficient, whereas shade-tolerant conservative herbaceous species are dominants in light-limited environments due to high light use efficiencies (Hart & Chen, 2008; Reich, Frelich, et al., 2012).

The results of this study suggest that the unequivocal effects of tree functional diversity on the dynamics of herbaceous layer properties appear even over a period of a few years. However, these observed patterns may not persist as forests are dynamic systems (Grossman et al., 2018). Self-thinning may occur subsequent to forest canopy closure, where the resulting reduction in CP may allow greater light penetration to the herbaceous layer (Gilliam, 2014). Afterwards, stands attain a steady state with more closed and denser CP, which causes more light-limited conditions for the herbaceous layer (Gilliam, 2014; Hart & Chen, 2008). Changes in canopy structure may alter the functional dominance of the herbaceous layer fluctuating between acquisitive and conservative species (Depauw et al., 2020). High-intensity intraspecific competition may induce higher mortality in low-diversity stands, whereas reduced interspecific competition via niche differentiation in high-diversity stands may alleviate self-thinning (Tatsumi, 2020). Therefore, we expect that the dynamics of herbaceous layer properties in functionally diverse tree stands would exhibit lower fluctuations in future successional stages, in contrast to low-diversity stands. Longer term experiments are required to better elucidate the dynamics of tree diversity effects on the herbaceous layer.

Moreover, the temporal dynamics of herbaceous properties could be further related to ecosystem processes such as productivity, stability and multifunctionality (Van der Plas, 2019). This indicates that the interactions between experimental tree species and non-experimental species may further drive the biodiversity–ecosystem functioning relationships under realistic situations (Jochum et al., 2020; Veen et al., 2018). Although our results come from young experimental plantations on abandoned fields, they have definite relevance for forest restoration or secondary forest regeneration (Williams et al., 2017). The choice of functionally diverse tree mixtures can prevent overgrowth by herbaceous vegetation, promote the dynamics of herbaceous layer properties in the early stage of forest restoration, and maintain stable structures for both tree and herbaceous layers during stand development process.

5 | CONCLUSIONS

Based on a 3-year non-weeded tree diversity experiment, our study demonstrates that tree mixtures with high functional diversity develop a higher degree of CP over time. This eventually leads to decreased biomass, functional diversity and CWM of H_{max}, but a higher CWM of SLA of herbaceous species. Our study adds a new dimension to research into the biodiversity–ecosystem functioning relationships by showing the ecological responses of herbaceous properties to tree species diversity across young tree communities. The consideration of realistic interactions between experimental and naturally occurring species is crucial for understanding how natural community

processes impact ecosystem functioning. Under natural conditions, the temporal dynamics of herbaceous species may impact the long-term patterns of community structures and functioning across functionally distinct tree species mixtures. We expect that the effects of tree functional diversity would also be relevant over time because of the increased complementary usage of canopy space. Thus, further studies across different biomes and ecosystems are needed to explore how tree diversity influences the long-term dynamics of the herbaceous layers. Our results provide an ecological perspective for maintaining biodiversity, structures, functioning and optimizing ecological restoration procedures in forest ecosystems.

CONFLICT OF INTEREST
The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS
E.-R.Y., L.-T.Z. and H.Y.H.C. designed the study; L.-T.Z. and D.-F.B. collected and analysed the data; L.-T.Z. wrote the first draft. All the authors revised and improved the manuscript.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.pg4f4qrrd (Zheng et al., 2022).

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