INTRODUCTION

How community assembly processes are driven by environmental factors and geographic distance remains a critical topic in ecology (Cottenie, 2005; Leibold et al., 2004; Socolar et al., 2016). The emergence of beta diversity concepts, representing spatiotemporal community dissimilarity from taxonomic or functional perspectives, has improved our understanding of biodiversity patterns (Baselga, 2012;
Legendre & De Caceres, 2013; Legendre et al., 2009; Podani et al., 2013). To identify changes in internal community composition, beta diversity can be divided into turnover and nestedness components (Baselga, 2010, 2012; Villéger et al., 2013). In turnover, the loss of a species or trait is replaced by the gain of other species or traits, whereas in nestedness, species or traits that occur in one location are considered a subset of those from another location (Baselga, 2010; Villéger et al., 2013). Taxonomic and functional dissimilarity can characterize the different facets of community composition among sites. For example, communities may have higher species turnover but lower functional turnover as species may be replaced by those with similar traits (Fu, Yuan, Jeppesen, Ge, Li, et al., 2019). Changes in taxonomic and functional beta diversity indices can also differ along environmental gradients for a particular community. For example, Bishop et al. (2015) found that with increasing elevational gradients, taxonomic community composition is driven by turnover while functional community structure is controlled by both turnover and nestedness patterns. Therefore, species-based beta diversity alone may include limited information on the compositional changes among sites (Villéger et al., 2008, 2011). Incorporating functional traits into beta diversity indices could provide a more detailed understanding of biodiversity patterns and processes (Carvalho et al., 2020; Chun & Lee, 2017; Villéger et al., 2013).

However, the magnitude of beta diversity and relative importance of turnover and nestedness may depend on spatial scale (Declerck et al., 2011; Fu, Yuan, Jeppesen, Ge, Li, et al., 2019). Generally, both local environmental filtering and regional spatial processes (dispersal limitation with increasing geographic distance) are important factors of community composition changes among sites (Alahuhta et al., 2015; Legendre et al., 2009; Soininen et al., 2007). Theoretically, turnover patterns are influenced by environmental filtering, competition, and historical events, whereas physical barriers across large geographic distances may lead to nestedness (Alahuhta et al., 2017; Baselga, 2010; Legendre, 2014; Melo et al., 2009). For example, small species such as fish and zooplankton do not exhibit nestedness patterns at the fine scale as they can sufficiently and freely disperse, that is, show low dispersal limitation (Cottenie et al., 2001; Erós et al., 2012). In this situation, environmental heterogeneity will screen out species with specific adaptive capacity (He et al., 2019). Thus, species distribution patterns may mirror environmental gradients and turnover is prevalent (Baselga, 2012; Legendre, 2014). At the broad scale, species distribution patterns can include large geographic gradients (e.g., latitude, altitude) and dispersal barriers (Viana et al., 2015). Thus, community composition changes may originate from environmental filtering and dispersal limitations, with turnover and nestedness both important components of beta diversity (Declerck et al., 2011; Legendre, 2014). However, lake environments may change dramatically at the small scale (e.g., soil pH, total nitrogen (TN), and total phosphorus (TP)), thus filtering species less tolerant to extreme environments (e.g., water depth, water transparency), which, in turn, causes species nestedness among sites (Fu et al., 2020).

In freshwater lakes, submerged macrophytes are an important trophic level and play a vital role in determining ecosystem stability and services (Fu, Yuan, Jeppesen, Ge, Zou, et al., 2019; Fu et al., 2015, 2018; Scheffer et al., 1993). Thus, understanding the beta diversity patterns, including the turnover and nestedness components, of submerged macrophytes at different scales is essential. Previous studies on the spatial variation mechanisms of macrophyte assemblages have primarily focused on the larger scale. For example, Alahuhta et al. (2017) reported that turnover accounts for most beta diversity due to the variability in elevational range at the global scale. Fu, Yuan, Jeppesen, Ge, Li, et al. (2019) found that at the regional scale, different drivers contribute to structural (mainly turnover) and functional (mainly nestedness) beta diversity patterns in macrophyte species in Chinese lakes, and both species turnover and functional nestedness decrease with increasing water TP. Zhang et al. (2018) concluded that habitat loss and fishery intensity can impact the taxonomic and functional nestedness patterns of macrophytes, whereas water quality is a weaker driver at the regional scale. Excessive attention to large-scale variation patterns of biodiversity will inevitably lead to a partial understanding of the generality of community organization and the drivers (e.g., water depth and transparency) that affect the distribution of submerged macrophytes on a fine scale will be ignored. Nonetheless, very few studies have examined taxonomic and functional beta diversity patterns in submerged macrophytes driven by environmental variables and geographic distance at the fine scale. In a small-scale subtropical reservoir, Boschilia et al. (2016) found that landscape configurations, local environmental conditions, and biotic interactions cause high beta diversity (mainly species turnover). In addition, aquatic macrophyte communities exhibit greater seasonal variation in community composition than terrestrial plants. Rooney and Kalff (2000) found that macrophyte colonization depth increases in the warm season, resulting in greater productivity and distribution of submerged macrophyte communities. Therefore, integrating multiple sampling approaches will help provide a clearer understanding of the dynamic beta diversity patterns of submerged macrophytes.

Here, we examined seasonal patterns in submerged macrophyte beta diversity based on taxonomic and functional approaches at the fine scale (ca. 10 km²) (Hongshan Bay of Erhai Lake). We seasonally sampled 189 plots (200 × 200 m intervals between adjacent plots) evenly over the bay and measured taxonomic and functional beta diversities (Sørensen coefficient) and their turnover (Simpson coefficient) and nestedness components. Previous studies have found that strong winds and waves occur on Erhai Lake for most of the year (Chu et al., 2014), which transport propagules and thus weaken the effects of spatial processes on community structure. We used the generalized dissimilarity model (GDM) (Ferrier et al., 2007) to disentangle the role of environmental and spatial (i.e., geographic distance) processes in determining beta diversity patterns across the four seasons. Firstly, we hypothesized that turnover would be the main component of beta diversity (both taxonomic and functional), with nestedness only accounting for a small proportion. This is because wind and wave action in Erhai Lake may endow submerged macrophytes with a higher dispersal ability (i.e., low nestedness) (Chu et al., 2014), and thus, environmental variables
will more strongly impact community structure (i.e., high turnover).
Secondly, we hypothesized that beta diversity, including the turn-
over and nestedness components, would change seasonally. For
example, beta diversity may be low in summer and high in winter
regardless of taxonomic or functional beta diversity. This is because
submerged macrophytes thrive in summer and species ecological
amplitude is broader, which may result in a more homogeneous
community structure in the bay (i.e., low taxonomic and functional
beta diversity). In contrast, species habitat ranges may contract in
winter, with only a few tolerant species able to survive the extreme
environmental conditions, thus leading to a divergent commu-
nity structure in the bay (i.e., high taxonomic and functional beta
diversity). Thirdly, we hypothesized that environmental variables
would be more important than geographic distance for taxonomic
and functional beta diversity because of obvious environmental
gradients (e.g., water depth) in the bay and weakened effects of
geographic distance caused by strong wind and wave action in Erhai
Lake (Wang et al., 2020).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in the northern Hongshan Bay of Erhai
Lake (25°52′N, 100°06′E), Yunnan Province, China. Erhai Lake be-
longs to the northern subtropical climate, with a rainy season be-
tween May and October and a harsh dry period between November
and the following April (Fu et al., 2013). Hongshan Bay is located
at the northern end of Erhai Lake, with a maximum depth of 10 m
and an area of 10 km$^2$. In recent decades, there has been an in-
crease in the external nutrient input in the lake with the develop-
ment of surrounding cities. Thus, the water quality of Erhai Lake
has changed from an oligotrophic state to a mesotrophic state (Lin
et al., 2020), which has, in turn, lead to a change in the submerged
macrophyte community from Potamogeton maackianus dominance
to Ceratophyllum demersum and P. maackianus codominance (He
et al., 2015) (Figure 1). The location of Erhai Lake and distribution of
sampling sites are shown in Figure 2.
2.2 | Data collection

The submerged macrophyte communities were sampled seasonally in 189 evenly sampling sites (mean intervals between adjacent plots of 200 × 200 m) across the bay. Sampling time occurred in April, July, and October 2018 and in January 2019, corresponding to spring, summer, autumn, and winter, respectively. In each survey, GPS coordinates were recorded using a GPS map 60CSx receiver at each site to calculate spatial variables. The submerged macrophyte communities were sampled three times at each sampling site with a rotatable reaping hook (area = 0.2 m²). Plants were washed and identified to species. In addition, TN, TP, chlorophyll-a (Chl.a), water transparency (SD), and water depth (WD) were determined at each site as environment variables, as per Wang et al. (2020).

Based on our previous research, we measured 12 functional trait indices for the submerged macrophytes, which are widely used to analyze environmental adaptation (Fu et al., 2012; Fu, Zhong, Yuan, Ni, et al., 2014, Fu et al., 2017), including specific leaf area (SLA), relative growth rate (RGR), leaf area ratio (LAR), leaf mass ratio (LMR), shoot height, stem diameter, leaf dry mass content, lamina thickness, stem dry mass content, flowering duration, ramet size, and leaf carbon/nitrogen (C/N) ratio.

2.3 | Data analysis

We used three complementary steps to investigate seasonal patterns in taxonomic and functional beta diversity of the submerged macrophytes. Firstly, taxonomic beta diversity (TBD) of submerged macrophytes was calculated using pairwise-site Sørensen coefficients ($p_{sae}$) based on presence–absence species data (Baselga, 2010; Baselga & Orme, 2012). Given that species turnover ($p_{ss}$) and nestedness ($p_{n}$) combine to equal beta diversity (dissimilarity) and similarity equals 1 − dissimilarity, we used a triangular graph to describe the distribution of turnover and nestedness, that is, similarity = (1 − beta diversity), according to Legendre (2014). Each side of the triangle represents one of the three components. For functional beta diversity (FBD), we used the Sørensen coefficient, as suggested by Villéger et al. (2013): 1) We calculated the functional distance matrix among species with original trait data using Gower’s distance (Gower, 1971); 2) principal coordinate analysis (PCoA) was used to create replaceable functional axes from the functional distance matrix, and we selected the first two axes as synthetic functional traits of submerged macrophytes because of long computation times; 3) finally, we used the “functional.beta.pair” function from the R package betapart (Villéger et al., 2013) to calculate the three functional dissimilarity indices: that is, beta diversity, turnover, and nestedness by combining species data and synthetic functional traits. We also used the triangular diagram mentioned above to represent functional beta diversity as well as its turnover and nestedness components.

3 | RESULTS

3.1 | Relative importance of turnover and nestedness in taxonomic and functional beta diversity

Both taxonomic turnover and nestedness and functional turnover and nestedness showed comparable contributions to variations in taxonomic and functional beta diversity across the four seasons. For taxonomic beta diversity (TBD), significant differences in taxonomic turnover and nestedness components were found in summer (p < .05) and in winter (p < .05), that is, in summer, on average, 58% of species were replaced between pairs of sites and 42% were lost/gained, while in winter, on average, 43% of species were replaced and 57% were lost/gained (Figure 3). In spring and autumn, taxonomic turnover and nestedness showed similar contributions (49% and 51%) to taxonomic beta diversity (p > .05). For functional beta diversity (FBD), only winter functional turnover (61%) was significantly higher than functional nestedness (39%), while functional nestedness had a higher or almost equal contribution relative to functional turnover in the other three seasons.

3.2 | Seasonal variation in taxonomic and functional diversity

In Hongshan Bay, there were obvious seasonal patterns in taxonomic and functional beta diversity as well as corresponding turnover and
In general, the functional dissimilarity index (beta diversity, turnover, and nestedness) was higher than the taxonomic dissimilarity index in Hongshan Bay in all seasons. This indicated more divergence in functional community composition than taxonomic composition in the bay. Moreover, taxonomic and functional beta diversity exhibited opposite patterns of seasonal change, with taxonomic beta diversity being highest in summer and lowest in winter, and functional beta diversity being highest in winter and lowest in summer. Taxonomic and functional turnover among pair sites presented similar patterns as taxonomic and functional beta diversity (Figure 4) (i.e., taxonomic turnover was highest in summer and lowest in winter, and functional turnover was highest in winter and lowest in the other three seasons). For the nestedness components, taxonomic nestedness was lowest in summer and highest in winter, while functional nestedness exhibited a lower state in summer.

3.3 | Role of environmental factors and geographic distance in taxonomic and functional diversity

Predominantly, across seasons, environmental factors were the main drivers of beta diversity, turnover, and nestedness, regardless of the taxonomic or functional diversity index (Table 1). Only in spring, pure spatial drivers had a similar impact as pure environmental drivers on functional beta diversity and nestedness components (Table 1). Environmental factors better predicted the functional
diversity index (i.e., beta diversity, turnover, and nestedness) than the taxonomic diversity index (Figure 5).

Of all predictors, Chl.a and SD were the most important environmental drivers for both taxonomic beta diversity and functional beta diversity across seasons (Figure 5, Figures S1 and S2). TP had an important influence on functional beta diversity and its turnover in autumn and winter. Importantly, the rate and magnitude of species and functional turnover or nestedness also changed along environmental gradients (Figures S1 and S2). For example, with increasing Chl.a concentration differences among sites in spring, taxonomic nestedness ($\beta_{sne}$) gradually increased. However, taxonomic beta diversity and turnover increased sharply when the changes in Chl.a concentration were small. When the Chl.a concentration changed over a certain value, the increase in taxonomic beta diversity and turnover slowed (Figure S1).

4 | DISCUSSION

We explored seasonal variation in taxonomic and functional beta diversity of submerged macrophytes at a fine scale, as well as the underlying mechanisms responding to environmental factors and
geographic distances. Firstly, our results indicated that both nest-
edness and turnover processes were important drivers of taxo-
nomic and functional dissimilarity among submerged macrophyte
communities in Hongshan Bay. Secondly, taxonomic and functional
beta diversity and the related turnover and nestedness components
showed significant seasonal patterns. Notably, taxonomic and func-
tional beta diversity showed the opposite patterns of change (i.e.,
taxonomic beta diversity was highest in summer and lowest in winter,
while functional beta diversity was lowest in summer and highest in
winter). Thirdly, in Hongshan Bay (fine scale), environmental filtering
of species and traits was the main process driving spatial variation in
submerged macrophytes, rather than dispersal limitations.

Both taxonomic turnover and nestedness as well as functional
turnover and nestedness showed comparable contributions to taxo-
nomic and functional beta diversity variations. This does not accord
with our first assumption that turnover would be the main compo-
nent of both taxonomic beta diversity and functional beta diversity.
Regarding aquatic plants at the fine scale, this is the first study to
observe that turnover and nestedness patterns had equally im-
portant effects on beta diversity. Compared to previous research,
Boschilia et al. (2016) only observed the prevalence of taxonomic
turnover in macrophyte beta diversity at the small scale (five arms
of Itaipu Reservoir) due to distinct environmental factors. This may
be because there was a wide magnitude of environmental gradi-
ents in Hongshan Bay; that id, environmental factors (Chl.a and SD)
may have had a strong effect on nontolerant species, resulting in a
decrease in the number of species from one site to another, thus
leading to community dissimilarity nestedness in Hongshan Bay (as
seen in Figure 5, Figures S1,S2). Similarly, da Silva et al. (2018) found
that higher elevation sites experience more extreme seasonal and
daily temperature variations, which may cause nestedness-related
temporal dissimilarity patterns. He et al. (2019) also reported that
 Vallisneria natans is dominantly colonized in sites with high basin
slope and moderate–high water depth, indicating that commu-
nity structure is simpler under extreme environmental conditions
(i.e., community assemblages become nested under extreme envi-
ronments). In the current study, however, we did not consider the
impact of species competition and other environmental factors (e.g.,
sediment nutrition, lake bottom topography) on nestedness pat-
terns. For example, interspecies competition in natural communities
can eliminate less competitive species, thereby shaping community
structure. Fu, Zhong, Yuan, Xie, et al. (2014) reported that niche
differentiation plays a structuring role in macrophyte community
assembly.

Our results add novel insights emphasizing the temporal vari-
ability of taxonomic and functional beta diversity patterns as well
as corresponding turnover and nestedness patterns. We found that
axonomic beta diversity was highest in summer and lowest in winter,
while functional beta diversity was highest in winter and lowest in
summer. This did not accord with our second hypothesis that both
axonomic beta diversity and functional beta diversity would be low
in summer and high in winter. Our results suggested that taxonomic
differentiation in community composition was greater in summer
than functional differentiation but exhibited the opposite pattern in
winter. This may be because submerged macrophytes prospered in
summer (e.g., increasing ecological range, wider distribution) but de-
clined in winter (e.g., shrinking spatial distribution), leading to spatial
dissimilarity patterns in species and traits among the four seasons.
Our results also demonstrated that species identity alone does not
provide reliable information about biodiversity patterns (Carvalho
et al., 2020), which is important for the protection and management
of biodiversity. Thus, the taxonomic and functional characteristics of
community organization patterns should be considered comprehen-
sively (Hill et al., 2019; Socolar et al., 2016).

The submerged macrophyte community in Hongshan Bay has
maintained a stable climax community dominated by Potamogeton
maackianus (>70%) from at least 2011 to 2018 (He et al., 2015;
Wang et al., 2020). We found that taxonomic beta diversity grad-
ually increased from spring to summer and decreased from summer
to autumn and winter (Figure 4), whereas functional beta diversity
demonstrated the opposite change (Figure 4). Thus, the submerged
macrophyte beta diversity patterns in Hongshan Bay may show
seasonally cyclic changes based on life history to ensure the long-
term stability of the community structure, as shown in Figure 6.

**FIGURE 6** Schematic of variation patterns in taxonomic and functional beta diversity of submerged macrophytes with season in a stable climax community
Taxonomic beta diversity decreased from summer to winter and increased from winter to summer, whereas functional beta diversity showed the opposite patterns. Similar seasonal patterns (or seasonal cyclical changes) may occur in other stable biological communities, but this requires further research. Thus, for slow population dynamics (e.g., terrestrial forest and grassland communities), single snapshot studies may be suitable to quantify the role of community assembly drivers at large spatial scales. In contrast, organisms in freshwater ecosystems experience considerable seasonal changes and are more easily affected by water environmental factors. As such, the temporal patterns of spatial variation should be considered over time (Erős et al., 2012).

Beta diversity will produce varied patterns under the different contributions of environmental and geographic distance across various spatial scales (Declerck et al., 2011; Fu, Yuan, Jeppesen, Ge, Li, et al., 2019; Mykrä et al., 2007). At the fine scale, species with different traits can disperse to suitable environments, thus increasing species replacement via species sorting (Gianuca et al., 2017). Different traits can disperse to suitable environments, thus increasing environmental filtering more greatly contributes to species and trait turnover. Boschilia et al. (2016) found that high beta diversity (due to spatial turnover) in aquatic macrophyte assemblages is correlated with local-scale environmental factors. Fu, Yuan, Jeppesen, Ge, Li, et al. (2019) also found that local and regional drivers (e.g., altitude, TN concentration, TP concentration) contribute to structuring species and functional beta diversity patterns (mainly due to species turnover and functional nestedness). However, when environmental factors change dramatically from suitable to extreme conditions, some tolerant species will be screened out to form nested communities (Bevilacqua & Terlizzi, 2020; da Silva et al., 2018). This process (turnover and nestedness driven by environmental factors) is in line with the catastrophic regime shifts that occur in shallow lakes, that is, when the water environment conditions change drastically, the structure, function, and stability of freshwater ecosystems also change (Scheffer & Carpenter, 2003; Scheffer et al., 2001).

5 | CONCLUSION

In conclusion, we studied seasonal taxonomic and functional beta diversity patterns in submerged macrophyte communities and found that both taxonomic turnover and nestedness as well as functional turnover and nestedness were important drivers of seasonal variations in taxonomic and functional beta diversity. Environmental variables rather than geographic distance dominated spatial variations in species and trait composition of submerged macrophytes across seasons at the fine scale. Using the trait-based approach to study the variation mechanisms underlying the community structure of submerged macrophytes, we confirmed the importance of niche-based processes in community assembly at a fine scale. Moreover, patterns of taxonomic and functional community structure varied across seasons, indicating the importance of considering functional traits over time to study community structure variation. These results provide a reference for future studies on aquatic plant communities, especially in the management and restoration of local habitats.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

Hao Wang: Data curation (equal); Investigation (equal); Methodology (equal); Writing-original draft (equal); Writing-review & editing (equal). Hui Fu: Funding acquisition (equal); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). Zhaoh Wen: Investigation (equal); Writing-review & editing (equal). Changbo Yuan: Investigation (equal); Writing-review & editing (equal). Xiaolin Zhang: Funding acquisition (equal); Project administration (equal); Supervision (equal); Writing-review & editing (equal). Leyi Ni: Project administration (equal); Resources (equal); Supervision (equal); Writing-review & editing (equal). Te Cao: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

Data used in this manuscript were submitted to Dryad and are preliminarily available at https://doi.org/10.5061/dryad.kwh70rz3c.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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