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A functional-trait approach reveals community diversity and assembly processes responses to flood disturbance in a subtropical wetland

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Abstract Despite the strong effects of disturbance on plant community diversity and assembly, we do not fully understand how different aspects of taxonomic or functional diversity respond to disturbance or how different assembly processes change along a disturbance gradient. In this study, plant communities were sampled and the distributions of three functional traits were measured in 45 plots across a flood disturbance gradient in Poyang Lake wetland in China. We examined the within-community means, ranges, variances, kurtoses, and other parameters of trait values. Results showed that the effects of disturbance depended largely on the aspects of diversity considered. Along the flood disturbance gradient, taxonomic/functional richness did not change, while Shannon–Wiener diversity and evenness and functional evenness and dispersion showed significant unimodal patterns. Communities experiencing the highest disturbance levels tended to have significantly shorter shoot heights with lower specific leaf area (SLA). We also found a significant non-random functional trait distribution: a significant reduction in the range and variance of SLA and a more even distribution of the measured traits compared with the null model. Our results highlight that niche-based assembly processes play structuring roles in wetland plant community response to flood disturbance gradients and that both environmental filtering and limiting similarity can work on the same traits (e.g., SLA)

through hierarchical effects on the distribution of functional traits within communities.

Keywords Diversity · Assembly · Environmental filtering · Limiting similarity · Flood disturbance

Introduction

Understanding how plant community diversity responds to disturbance gradients is a longstanding pursuit in plant ecology that has important ramifications for the conservation and management of ecosystems (Huston 1979; Hooper et al. 2005; Houlihan et al. 2006). The effects of disturbance on plant diversity have been investigated for decades; however, such effects remain controversial. Species diversity usually peaks at intermediate levels of disturbance, as predicted by the intermediate disturbance hypothesis (IDH) (Connell 1978; Huston 1979). The IDH postulates that competitive exclusion reduces species richness at low levels of disturbance, whereas high levels exclude all but the most disturbance-tolerant species (Huston 1979). However, diversity–disturbance relationships are not consistently unimodal distribution. Mackey and Currie (2001) conducted a meta-analysis of empirical disturbance studies and found that increasing, decreasing, peaked, and U-shaped diversity–disturbance relationships (DDR) all exist. Moreover, numerous non-significant DDR have been reported (Mackey and Currie 2001), implying that neutral processes may also contribute to plant responses to disturbance.

The inconsistency in DDR among studies can be attributed to the different aspects of diversity (i.e., richness and evenness) considered (Violle et al. 2010; Hall et al. 2012). While the diverse DDR observed are mostly based on the effects of disturbance on taxonomic diversity, very little information exists on how disturbance affects functional diversity (Biswas and Mallik 2010; Carreño-Rocabado et al. 2012). Functional diversity characterizes the functional aspect of diversity

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and has been defined as the value, range, and relative abundance of functional traits in a plant community (Díaz and Cabido 2001). Functional diversity can be considered as an important indicator of processes governing community assembly and for predicting ecosystem functions (Hooper et al. 2005; Suding et al. 2005; Díaz et al. 2007a; Villéger et al. 2008; Pakeman 2011; Spasojevic and Suding 2012). Therefore, a functional-trait approach would improve our understanding of disturbance effects on plant communities and, thus, ecosystem performance.

Significant DDR are largely associated with the niche processes within/among communities (Mouillot et al. 2013), while neutral processes result in non-significant DDR. A functional-trait approach provides a promising way to distinguish between niche and neutral processes (Cornwell et al. 2006; Ackerly and Cornwell 2007; Kraft et al. 2008; Lebrija-Trejos et al. 2010; Mouillot et al. 2013) by identifying whether co-occurring plant species are distributed randomly across the functional trait space. Under neutral processes, all individuals, and thus all species, are ecologically identical, resulting in random patterns of species co-occurrence with respect to ecological strategy (i.e., functional trait axes) (Hubbell 2001). Niche-based assembly of plant communities is largely driven by two hierarchical processes (Keddy 1992; Weiher et al. 1998): (1) environmental filtering, which can restrict the range and variance of trait values in a particular habitat, leading to a more converged trait distribution among coexisting species within communities than expected by chance (Kraft et al. 2008; Cornwell and Ackerly 2009); and (2) limiting similarity, which can spread the spacing or volume of trait values within this restricted range and variance because of competitive exclusion, causing trait values to be more evenly distributed than under a null expectation (Kraft et al. 2008; Maire et al. 2012). The combined effects of environmental filtering and limiting similarity on specific functional traits may contribute to differences in community diversity patterns along a disturbance gradient (Cornwell and Ackerly 2009; Fu et al. 2014). Because we cannot reliably distinguish between niche and neutral processes in shaping the community responses to disturbance based solely on taxonomic diversity (Mouillot et al. 2013), functional diversity would be a better metric for assessing the effects of disturbance on plant community assembly.

In the present study, we used a functional-trait approach to examine the responses of community diversity and assembly along a flood disturbance gradient in a subtropical wetland. In particular, this study aimed to answer the following questions: first, how do taxonomic and functional diversity change across the flood disturbance gradient? Second, are neutral or niche processes responsible for the observed DDR? Third, if niche-based assembly processes exist, how do environmental filtering and limiting similarity affect specific functional traits along the flood disturbance gradient? We hypothesized that: (1) the diversity–disturbance relationship is largely dependent on the aspects of taxonomic and functional

diversity, which may not respond to disturbance gradients in a similar manner (Mackey and Currie 2001; Svensson et al. 2012); and (2) niche-based assembly processes help shape community responses to flood disturbance in this subtropical wetland, because neutral processes usually work in tropical forests at large scales (i.e., regional and global) (Hubbell 2001), while niche processes are more important in wetlands at local scales (Keddy 1989; Weiher et al. 1998; Wilson and Stubbs 2012).

Materials and methods

Study location

This study was conducted in Nanjishan Wetland Nature Reserve (NWNr, 28°52'21"–29°06'46"N, 116°10'24"–116°23'50"E), which is located at the southern end of Poyang Lake in Jiangxi Province, China. The floodplain in Poyang is subject to significant seasonal water-level fluctuations. The surface area of the lake shrinks to <1000 km² in the dry season (November–March) and can expand to >4000 km² in the wet season (April–October). The average and maximum depths are 8 and 23 m, respectively. As the largest freshwater lake in China and a wintering area for endangered Siberian, White-naped, and Hooded Cranes, Poyang Lake is an important site for crane conservation in China. Spanning an area of 333 km², NWNr was established in 2003 mainly to preserve wintering bird species, many of which are globally endangered. The coverage of the wetland plant community in NWNr is significantly influenced by the seasonal hydrological changes in Poyang Lake. NWNr also comprises many small disc lakes that connect with one another only in summer, when the water level is relatively high. All of the disc lakes and grasslands are submerged during the wet season, while wetland plant species sprout and grow during the dry season. NWNr also contains significant natural topographic gradients, from high dry land with a short flooding duration to low lake basin with prolonged flooding. Differences in flooding duration may greatly influence community diversity and assembly processes.

Field sampling and trait measurements

Forty-five 10 m × 10 m plots were positioned using a geographic information system (Arc-GIS; ESRI, Redlands, CA, USA) at three sites within the wetland plant communities in NWNr, with 15 plots in Donghu grassland, 19 in Baishahu grassland, and 11 in Fengwei grassland (Fig. S1). The three sampling sites were characterized by a typical topographical flooding gradient from low lake basin to high dry land. Based on different flooding durations (days) along a topographical gradient, the flood disturbance gradient was separated into eight classes: 1, >240 days; 2, >220 days; 3, >200 days; 4, >180 days; 5, >160 days; 6,

> 140 days; 7, > 120 days; and 8, < 100 days. The plots were randomly sampled along the topographical gradient in wetland plant dominated areas in each site. These plots were then grouped into the eight classes of flood disturbance based on bathymetric maps from the geographic information system and hydrological data from 2002 to 2011. The number of plots in each class ranged from 4 to 9. The disturbance classes were distributed unevenly across the sites because the three sites were at different elevations. Locations that were disturbed by recent human activities (e.g., mowing) were excluded from the sampling.

In each 100 m² plot, 10 quadrats with dimensions of 1 m × 1 m were used for analysis. All of the species in these plots were identified and recorded during fieldwork in November 2012. The relative abundance of each species was visually estimated using seven cover classes: I, 0–0.1 %; II, 0.1–0.9 %; III, 1–5 %; IV, 6–25 %; V, 26–50 %; VI, 51–75 %; VII, 76–100 %. The median coverage of each class was used as abundance data in the following statistical analysis. Two non-native species (*Daucus carota* and *Geranium carolinianum*), which are rare components of the wetland plant communities at NPNR (< 1 % of sampled individuals), were recorded. These species were excluded in the subsequent analyses because the statistical power considered to examine the assembly processes of invaders was very low.

Three functional traits, specific leaf area (SLA), leaf dry mass content (LDMC), and shoot height (SH), were selected to characterize the major functional niches of species. We measured these traits on 10–30 different individuals of each species found across the study area in accordance with the protocols outlined by Cornelissen et al. (2003). SLA is a part of the leaf economic spectrum and closely correlated with photosynthetic capacity, nitrogen content per mass, and leaf lifespan (Reich et al. 1999; Wright et al. 2004). LDMC reflects the fundamental tradeoff of investing resources in structural tissues versus liquid-phase processes. Therefore, LDMC has been considered the main variable governing correlations among traits in the leaf economic spectrum (Reich et al. 1999; Wright et al. 2004; Messier et al. 2010). We collected fully developed leaves, without signs of damage or senescence, at peak biomass. These leaves were stored in water-filled and sealed plastic bags and scanned to determine the area within 2 h of collection. The leaves were then dried at 60 °C for 4 days to determine leaf dry weight. Individual leaf area was calculated from the leaf scans by using Image-Pro Plus (IPP) 6.0 (Media Cybernetics, Rockville, MD, USA). SLA was calculated as the leaf area (cm²) per unit of leaf dry mass (g), and LDMC was the ratio of leaf dry mass to water-saturated mass (g g⁻¹). SH is often allometrically associated with overall plant size and light competition (Westoby et al. 2002). SH was calculated as the distance from the basal stem to the top of photosynthetic tissues. For each species, mean trait values were determined across the study area.

Trait metrics and the null model

Six metrics of trait distribution that were sensitive to environmental filtering and limiting similarity were compared to a null expectation. Community trait range and variance were used as measures sensitive to environmental filtering (i.e., a significant reduction in the range and variance of trait values) (Kraft et al. 2008; Cornwell and Ackerly 2009; Kraft and Ackerly 2010), because range can capture the “hard edge” effect of environmental filtering and variance may also be reduced by filtering processes. Measures sensitive to limiting similarity (trait values distributed more evenly than expected) were: the standard deviation of nearest-neighbor distance along the trait axes (SDNN, as defined by trait distances along univariate trait axes); SDNNr (SDNN divided by the observed trait range within a plot); SDNDr (the standard deviation of successive-neighbor distances along trait axes divided by range); and kurtosis (Kraft et al. 2008; Cornwell and Ackerly 2009; Kraft and Ackerly 2010). SDNN and SDNNr were calculated by identifying the most similar co-occurring species to each successive species in the community and are therefore conceptually linked to the classic concept of limiting similarity (Kraft and Ackerly 2010). SDNNr and SDNDr partially avoid the effects of environmental filtering by considering trait ranges (Kraft et al. 2008). SDNN, SDNNr, and SDNDr characterize how evenly co-occurring species are distributed across a trait axis. Under the effects of limiting similarity, kurtosis would be lower (i.e., more platykurtic) than the expected trait distribution within the community (Cornwell and Ackerly 2009).

In each plot, the observed metrics were compared to a null expectation generated by creating 9999 random communities of equal richness of species drawn at random from our entire trait database (i.e., species × trait matrix), weighted by their plot-wide frequencies of occurrence (number of plots in which the species was found, plot × species matrix), irrespective of trait values (Kraft et al. 2008; Kraft and Ackerly 2010). We used a fixed–fixed algorithm of plot–species occurrence as the randomization procedure for null models. We report the occurrence-weighted null in this study, as it produced the most conservative results compared with an abundance-weighted and a presence–absence null (Kraft et al. 2008). A standardized effect size (SES) was used to assess the significance of non-random patterns of trait distribution (Gotelli and Graves 1996). An SES was calculated for each metric: $SES = (\text{Metric}_{\text{obs}} - \text{Metric}_{\text{null}}) / \text{Metric}_{\text{SD}}$, where $\text{Metric}_{\text{obs}}$ is the value of the observed metric in the quadrats, $\text{Metric}_{\text{null}}$ is the mean value of the metric for quadrats in 9999 null communities, and $\text{Metric}_{\text{SD}}$ is the standard deviation of the metric for quadrats in 9999 null communities (Gotelli and Graves 1996). To assess the significance of each metric, we performed a Wilcoxon signed-rank test and examined whether the mean values of SES were significantly different from zero among the 45 plots (Gotelli 2000).

Two-tailed tests were used for trait means, since environmental filtering is expected to shift the means of the observed trait values above or below the null expectation (Jung et al. 2010). One-tailed tests were conducted on the basis of a priori predictions of environmental filtering and limiting similarity, since environmental filtering and limiting similarity are expected to shift the range, variance, SDNDR, and kurtosis of the observed trait values below the null expectation (Kraft et al. 2008).

Data analyses

All of the diversity metrics were calculated independently by pooling the data of 10 quadrats in each plot (45 plots total). Three metrics were used for taxonomic diversity: species richness (S), the Shannon–Wiener diversity index [$H = -\sum p_i \ln(p_i)$ where p_i is the proportional abundance for species i], and the Shannon–evenness index [$J = H/\ln(S)$] (Mackey and Currie 2001). The three other diversity metrics considered functional diversity based on multiple traits: functional richness, functional evenness, and functional divergence. Functional richness quantifies the convex hull volume of functional space occupied by a community; functional evenness represents the regularity of the distribution in abundance in this volume; and functional divergence represents the divergence in the distribution of species traits within the trait volume occupied (Villéger et al. 2008; Spasojevic and Suding 2012). Functional evenness and functional divergence scale from 0 to 1; a high value indicates more regularity and more deviation, respectively, in the distribution of abundance of individuals in this volume (Villéger et al. 2008). Standardized trait values were used to calculate functional indices, with a mean of 0 and standard deviation of 1.

Functional diversity can also be described by the community weighted mean (CWM) of a trait, which is defined as the mean value of a single trait in the community weighted by the relative abundance of taxa bearing each value (Lavorel et al. 2008). CWMs are widely used to describe the functional composition of plots (Garnier et al. 2004; Lavorel et al. 2008) and to assess community/ecosystem properties (Díaz et al. 2007b). CWM was computed for each trait in the database as (Garnier et al. 2004): $CWM = \sum_{i=1}^S PiTi$, where S is the total number of species, Pi is the relative abundance of the i -th species, and Ti is the trait value of i -th species.

Pearson correlation analysis was performed to evaluate the relationships among the six measures of diversity and CWMs for the three traits. To determine whether or not a trait shifted across the flood disturbance gradient at NWNR, we tested the correlation between the plot CWM trait value and the flood disturbance gradient. Site was not included in the regression analysis because there were no significant estimates on site in the general linear model with sites as a random factor. We also analyzed the effect of flood disturbance

on the coverage of each species using the six measures of diversity across the 45 plots by conducting a linear or polynomial regression analysis. We used the Akaike information criterion (AIC) to select the model that best explained the decomposition rate from among a set of candidate models (Burnham and Anderson 2002). To assess the relative roles of environmental filtering and limiting similarity across the flood disturbance gradient, we established a linear or polynomial regression model between disturbance gradients and SES values of each metric for the three traits.

All of the statistical tests were performed using R version 2.15 (R Development Core Team 2012). We used the FD package (Laliberté and Legendre 2010) to calculate CWM and functional diversity metrics, the vegan package (Oksanen et al. 2011) to calculate taxonomic diversity metrics, and the “trait_test. R” code (Kraft et al. 2008) to run null models.

Results

Fifteen native species were found in the 45 sampled plots across the flood disturbance gradient. Community species richness varied from four to nine species per plot. *Carex cinerascens* was the most dominant species, with the highest average coverage and occurrence frequency in the study area (Table 1). An increase in flood disturbance significantly increased the coverage of *C. cinerascens*, *Zizania latifolia*, *Phalaris arundinacea*, and *Polygonum hydropiper* (all $P < 0.01$). In contrast, *Phragmites australis*, *Triarrhena lutarioriparia*, *Artemisia selengensis*, and *Cynodon dactylon* significantly decreased in coverage (all $P < 0.01$). There were no significant changes in the coverage of other species along the gradient (all $P > 0.05$).

No significant correlations were observed between species richness and disturbance gradients (Fig. 1a, $P = 0.12$). Shannon–Wiener diversity and evenness displayed significant unimodal patterns along the f gradient (Fig. 1b, $F_{2, 42} = 25.15$, $r^2 = 0.52$, $P < 0.0001$ and Fig. 1c, $F_{2, 42} = 25.6$, $r^2 = 0.53$, $P < 0.0001$, respectively), with peak diversity and evenness under intermediate disturbance regimes.

No significant relationship was observed between functional richness and disturbance gradient (Fig 1d, $P = 0.65$). Functional evenness and functional dispersion showed significant unimodal patterns along the f gradient (Fig. 1e, $F_{2, 42} = 6.07$, $r^2 = 0.19$, $P = 0.004$ and Fig. 1f, $F_{2, 42} = 13.00$, $r^2 = 0.35$, $P = 0.0004$, respectively).

The trait values ranges of these species were 26.16–89.03 kg m⁻² for SLA, 0.11–0.36 g g⁻¹ for LDMC, and 5–118 cm for SH (Table 1). CWM varied significantly along the gradient for all traits except LDMC. Communities with the highest flood disturbance had significantly lower SLA (Fig. 2a, $r = 0.35$, $P = 0.022$) and shorter SH (Fig. 2c, $r = 0.37$, $P = 0.015$). The CWM of LDMC did not change

Table 1 Trait values (mean \pm SD), average occurrence frequency, and coverage (mean \pm SD) of each species across the flood disturbance gradient in Nanjishan Wetland Nature Reserve of Poyang Lake wetland

Species	SLA	LDMC	SH	Frequency (%)	Coverage (%)
<i>Artemisia selengensis</i> Turcz. ex Bess.	37.97 \pm 9.76	0.23 \pm 0.03	35.90 \pm 13.77	33.33	5.20 \pm 9.57
<i>Cardamine lyrata</i> Bunge	53.02 \pm 2.66	0.17 \pm 0.01	5.03 \pm 1.64	40.00	0.56 \pm 5.62
<i>Carex cinerascens</i> Kuntze	32.81 \pm 10.18	0.30 \pm 0.07	54.04 \pm 26.74	93.33	36.08 \pm 31.06
<i>Cynodon dactylon</i> (Linn.) Pers.	49.81 \pm 6.39	0.25 \pm 0.02	14.71 \pm 6.62	15.56	6.94 \pm 15.42
<i>Heleocharis valleculosa</i> Ohwi f. <i>setosa</i> (Ohwi) Kitagawa	26.16 \pm 2.69	0.22 \pm 0.01	30.33 \pm 6.43	15.56	2.64 \pm 7.99
<i>Oenanthe sinensis</i> Dunn	89.03 \pm 15.64	0.15 \pm 0.03	12.67 \pm 6.81	8.89	0.47 \pm 2.27
<i>Phalaris arundinacea</i>	56.03 \pm 9.35	0.23 \pm 0.03	38.43 \pm 14.73	48.89	8.46 \pm 14.67
<i>Phragmites australis</i> Trin. ex Steub	29.91 \pm 4.17	0.36 \pm 0.05	118.0 \pm 29.09	31.11	5.64 \pm 10.72
<i>Polygonum hydropiper</i> Linn	44.05 \pm 5.96	0.23 \pm 0.05	25.17 \pm 10.77	2.22	2.15 \pm 4.90
<i>Polygonum. posumbu</i> Buch.-Ham. Ex D. Don	52.33 \pm 3.96	0.21 \pm 0.003	8.18 \pm 3.69	26.67	0.79 \pm 1.93
<i>Polygonum orientale</i> Linn	37.45 \pm 4.39	0.30 \pm 0.01	80.71 \pm 5.88	60.00	0.21 \pm 0.96
<i>Polygonum sieboldii</i> Meisn.	59.46 \pm 11.86	0.22 \pm 0.02	11.15 \pm 7.61	11.11	0.41 \pm 1.69
<i>Rumex acetosa</i> Linn	66.00 \pm 22.78	0.11 \pm 0.02	12.28 \pm 6.88	28.89	0.65 \pm 2.25
<i>Triarrhena lutarioriparia</i> L.Liu	43.42 \pm 4.83	0.32 \pm 0.04	95.29 \pm 27.97	62.22	21.78 \pm 24.53
<i>Zizania latifolia</i> (Turcz.et Trin.) Hand	29.50 \pm 9.83	0.35 \pm 0.03	98.85 \pm 31.58	35.56	7.35 \pm 15.90

SLA specific leaf area, LDMC leaf dry mass content, SH shoot height

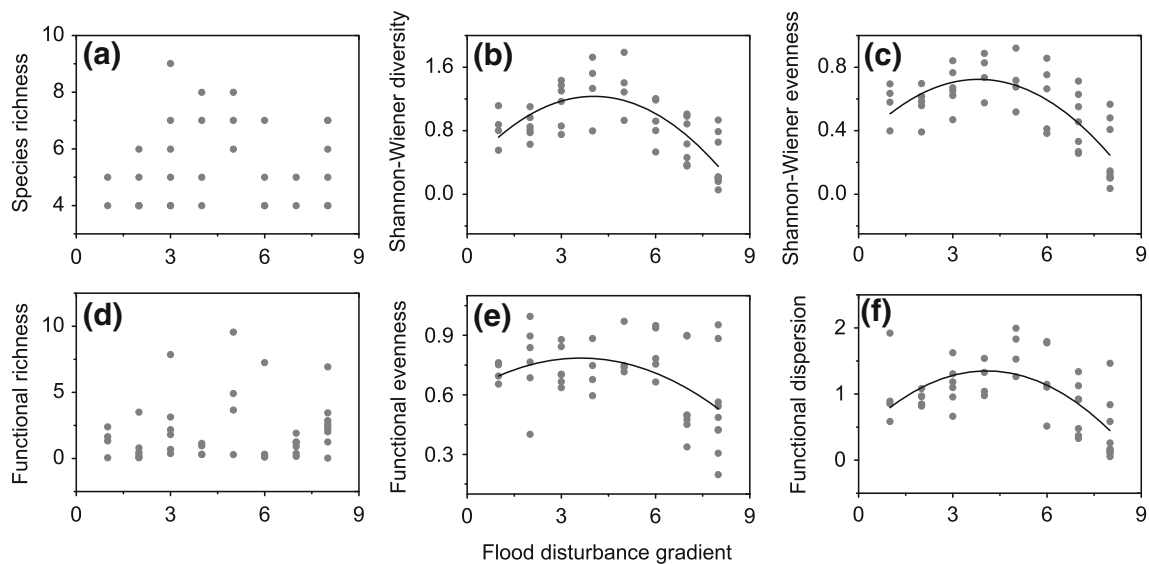


Fig. 1 Relationships between the flood disturbance gradient and six diversity indices: **a** species richness, **b** Shannon–Wiener diversity, **c** Shannon–Wiener evenness, **d** functional richness, **e** functional evenness, and **f** functional dispersion. Grey dots represent the 45 communities sampled. Regression lines drawn in

black are significant ($P < 0.05$). Based on different flooding durations (days) along a topographical gradient, the flood disturbance gradient was separated into eight classes: 1, > 240 days; 2, > 220 days; 3, > 200 days; 4, > 180 days; 5, > 160 days; 6, > 140 days; 7, > 120 days; and 8, < 100 days

significantly along the gradient (Fig. 2b, $r = 0.07$, $P = 0.15$). The CWM of LDMC was significantly positively correlated with the CWM of SH ($r = 0.84$, $P = 0.00006$) and significantly negatively correlated with the CMW of SLA ($r = -0.72$, $P = 0.0001$).

The mean values shifted significantly below the null expectation ($SES < 0$) for SLA and above the null expectation ($SES > 0$) for SH and LDMC (Table 2). Compared to the null model, a significant reduction was found in the range and variance of SLA, consistent with environmental filtering processes. The three traits were more evenly distributed than predicted. SLA also showed a more platykurtic distribution than the null

expectation. For all trait metrics of community assembly processes, the number of plots with significantly lower values than the null expectation ranged from 30 to 39 for SLA, from 22 to 33 for LDMC and from 22 to 40 for SH across the flood disturbance gradient.

Along the flood disturbance gradient, the standardized effect size of SDNNr and kurtosis exhibited a significant U-shaped distribution for SH (Fig. 3a, $F_{2, 42} = 10.60$, $r^2 = 0.30$, $P = 0.0002$ and Fig. 3b, $F_{2, 42} = 3.62$, $r^2 = 0.11$, $P = 0.035$). This result suggested that SH was more evenly distributed at intermediate disturbance levels than at the two ends of the gradient. However, the standardized effect sizes of the

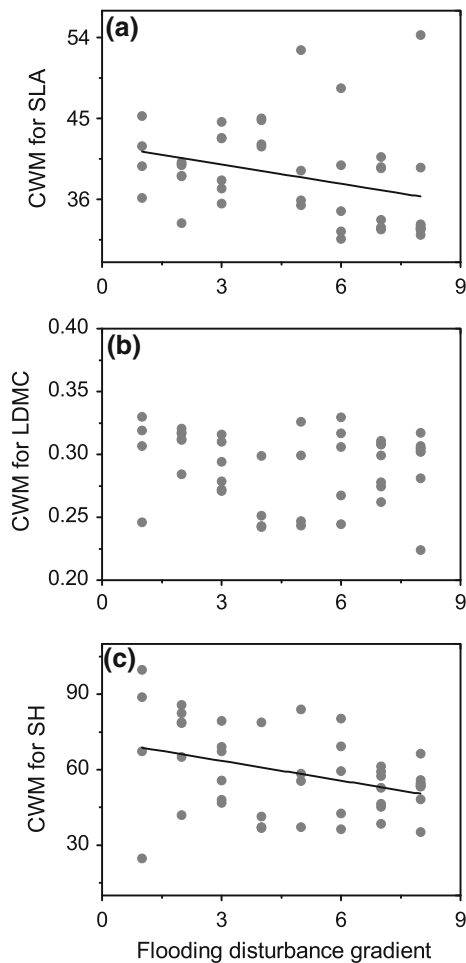


Fig. 2 Relationships between flood disturbance gradient and community weighted means (CWMs) for specific leaf area (**a**, SLA), leaf dry mass content (**b**, LDMC), and shoot height (**c**, SH). Grey dots represent the 45 communities sampled. Regression lines in black are significant ($P < 0.05$). Based on different flooding durations (days) along a topographical gradient, the flood disturbance gradient was separated into eight classes: 1, > 240 days; 2, > 220 days; 3, > 200 days; 4, > 180 days; 5, > 160 days; 6, > 140 days; 7, > 120 days; and 8, < 100 days

other metrics of the three traits did not significantly change with disturbance gradient (all $P > 0.05$).

Discussion

Taxonomic/functional diversity along the gradient

This study was conducted to evaluate the effects of a flood disturbance gradient on species/functional diversity and assembly processes in a subtropical wetland plant community. Significant effects of flood disturbance were observed on species coverage and community composition. Along the gradient, the wetland species in this study showed a zone distribution with a significant shift in dominant species. *Carex cinerascens* was the most dominant species, as expected based on its well-

developed rhizomes and roots, which enable this species to withstand long flood durations (high disturbance). *Carex cinerascens* also had the greatest coverage and was distributed across the entire topographical gradient of the Poyang Lake wetland during winter. This phenomenon supports the idea that stress-tolerators can also function as dominant competitors (Emery et al. 2001).

In present study, the diversity–disturbance relationship depended greatly on taxonomic/functional diversity (Fig. 1), which is found in many communities (Mackey and Currie 2001; Svensson et al. 2012). This result suggests that different aspects of diversity may not respond similarly to disturbance gradients. In this study, neither taxonomic nor functional richness was significantly affected by flood disturbance. Such non-significant DDR have also been observed in 35 % of published studies, as reviewed by Mackey and Currie (2001). Our results and those presented in other studies suggest that species richness and the volume of a functional trait space are conserved among communities. However, the non-significant changes observed in species and functional richnesses might be responsible for low richness and, thus, the low variation in this wetland.

The existence and shape of DDR has been the subject of much debate. After incorporating the relative abundance of species, we found that the Shannon diversity index and evenness showed significant unimodal patterns along the flood disturbance gradient; this finding is consistent with the predictions of the IDH (Huston 1979). Given that Shannon diversity indicates a mix of evenness and richness, these similar diversity–disturbance patterns suggest that evenness may be a major factor determining the response of Shannon diversity to flood disturbance. At a low level of disturbance, taxonomic diversity and evenness were low because competitors dominated and were most abundant during the brief inundation period; specifically, *C. dactylon*, *P. australis*, and *T. lutarioriparia* had a combined of 36–62 % coverage. At a high level of disturbance, many species were habitat-restricted by the long inundation, during which a few stress-tolerators could sprout and expand. Thus, *C. cinerascens* covered > 80 % of this area, with *Heleocharis valleculosa*, *Polygonum sieboldii*, and *Cardamine lyrata* as companion species; hence, low evenness may be observed. At intermediate flood disturbance, a balance is observed between competitive exclusion and loss of competitive dominants by disturbance (Roxburgh et al. 2004); this condition results in high evenness by reducing the abundances of competitors and tolerators.

Functional evenness and functional divergence also exhibited significant unimodal variation along the flood disturbance gradient (Fig. 1). This result may be largely attributed to changes in relative species abundance and may also be associated with taxonomic evenness along the gradient, because multi-trait functional diversity indices are determined after these values are weighted by abundance (Villéger et al. 2008). At an intermediate

Table 2 Standard effect sizes (SES, mean values), number of plots with values lower than expectation, and Wilcoxon signed-rank test for plot-wide trait-based tests of community assembly

	SLA			LDMC			SH		
	Mean SES	No. plots < expectation	Wilcoxon P	Mean SES	No. plots < expectation	Wilcoxon P	Mean SES	No. plots < expectation	Wilcoxon P
Environmental filtering									
Mean	-0.43	34	<0.0001	0.49	12	0.0002	0.48	13	0.0012
Range	-0.44	37	<0.0001	-0.06	28	>0.5	0.00	22	>0.5
Variance	-0.50	39	<0.0001	-0.13	33	>0.5	-0.11	25	>0.5
Limiting similarity									
SDNN	-0.53	38	<0.0001	-0.18	31	0.0200	-0.42	34	0.0039
SDNNr	-0.40	33	0.0011	-0.35	27	0.0060	-0.53	35	0.0002
SDNDr	-0.58	36	<0.0001	-0.37	32	0.0015	-0.80	40	<0.0001
Kurtosis	-0.32	30	0.0063	-0.12	22	>0.5	-0.14	25	>0.5

The mean test was two-tailed; all other tests were one-tailed
SLA specific leaf area, *LDMC* leaf dry mass content, *SH* shoot height, *SDNN* standard deviation of nearest-neighbor distance along the trait axes, *SDNNr* *SDNN* divided by the observed trait range within a plot, *SDNDr* standard deviation of successive-neighbor distances along trait axes divided by range

flood duration, high functional evenness indicates the maximum utilization of resources, and a high functional dispersion indicates strong competition for specific resources (Spasojevic and Suding 2012). This result suggests that inundation may function as a stressor reducing resource use efficiency in the plant community at both ends of the gradient.

A clear functional response of wetland plant communities occurred in the flood disturbance gradient; this result was indicated by the strong trends in CWMs observed in two of the three traits (Fig. 2). SLA is an important trait related to the resource-use and acquisition/conservation trade-off in leaf economics (Wright et al. 2004). As flood inundation increased, the CWM for SLA decreased; this result is associated with a gradual change in resource-use strategies from fast-growing and acquisitive species (*C. dactylon* and *T. lutticulariparia*) to slow-growing and conservative species (*C. cinerascens* and *Z. latifolia*) (Sterck et al. 2011). Furthermore, prolonged inundation promoted short species (i.e., with low competitive ability but high inundation resistance) while restricting taller species. This increase in the CWM of SH suggested that a high competitive ability for above-ground resources (e.g., light) and long dispersal distances were advantageous as flooding duration decreased (Pennings et al. 2005; Carreño-Rocabado et al. 2012). Long inundation at high disturbance levels could largely shorten the plant growing period and restrict a plant's ability to harvest light. This phenomenon may greatly reduce the relative abundances of species with high SLA and SH; as a result, low CWM was observed for these traits.

Community assembly processes along the gradient

The distributions of trait values within plant communities in the Poyang Lake wetland were strongly non-random, suggesting that niche-based assembly processes play a structuring role in shaping the community response to flood disturbance in this subtropical wetland. We found evidence of limiting similarity (as indicated by a more even distribution of trait values than expected) for SLA, LDMC, and SH, supporting the hypothesis that limiting similarity may be found throughout the flood disturbance gradient (Violle et al. 2010). Very few studies have reported limiting similarity in wetland plant communities compared with environmental filtering (Maire et al. 2012; Wilson and Stubbs 2012). Weiher et al. (1998) measured 11 morphological plant traits across a number of wetland habitats and found evidence for limiting similarity. Wilson and Stubbs (2012) also found clear evidence for limiting similarity in two of three saltmarsh plant communities with more evenly distributed traits related to canopy interactions than under a null expectation.

Wetland plant communities are usually characterized by high productivity and density associated with strong biotic interactions (Keddy 1989; Callaway and Walker

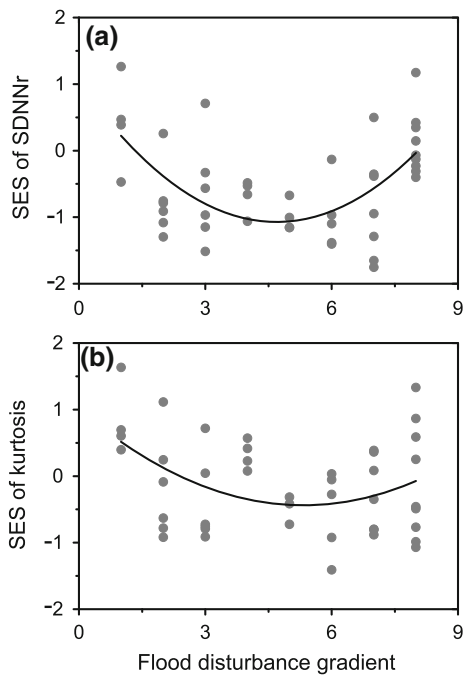


Fig. 3 Relationships between the flood disturbance gradient and standard effect sizes (SES) for SDNNr (a) and kurtosis (b) of shoot height. Grey dots represent the 45 communities sampled. Regression lines in black are significant ($P < 0.05$). SDNNr standard deviation of nearest-neighbor distance along the trait axes (SDNN) divided by the observed trait range within a plot. Based on different flooding durations (days) along a topographical gradient, the flood disturbance gradient was separated into eight classes: 1, > 240 days; 2, > 220 days; 3, > 200 days; 4, > 180 days; 5, > 160 days; 6, > 140 days; 7, > 120 days; and 8, < 100 days

1997; Minchinton and Bertness 2003; Pennings et al. 2005; Sokol et al. 2014). There is growing evidence that competition controls the distribution, abundance, and composition of these communities and affects plant zonation and species richness on shorelines (Keddy 1989; Weiher et al. 1998; Costa et al. 2003; Pennings et al. 2005; Hautier et al. 2009). Competition for a specific resource (i.e., water, nutrients, or light) can result in the differentiation of resource use among plant species with dissimilar traits in a particular community (Grime 1973; Hautier et al. 2009; Niinemets 2010), which might be the major factor causing an even distribution of the three traits related to light capture, photosynthetic rate, and plant construction cost. Our results strongly supported the existence of limiting similarity processes in wetland plant communities. In the case of SLA, we also observed a smaller range and variance than under a null expectation, supporting the presence of environmental filtering processes. Our results provided further evidence that a restricted range/variance and an even spacing of coexisting species can occur simultaneously for the same trait (Cornwell and Ackerly 2009). However, the possible mechanisms underlying this phenomenon remain unclear.

Based on our results from a seasonally-flooded wetland plant community, there was a significant flooding

duration gradient, and each disturbance level had unique light, water, and nutrient conditions. The significant clustering of SLA may be due to each disturbance level favoring a particular carbon capture strategy. The marked changes in community compositions (dominant species) along the flood disturbance gradient may further indicate the effects of environmental filtering. Our results clearly support the hypothesis that environmental filtering can occur throughout disturbance gradients. At high disturbance levels, plants with rapid growth rates and high nutrient-acquisition abilities were filtered out, as suggested by the reduced range and variance in SLA. Only conservative and disturbance-tolerant strategies (small, short plants with low SLA) could persist and cope with the stressful conditions.

Significant trends in the effects of environmental filtering along the flood disturbance gradient were only observed for SH, which was significantly different at intermediate disturbance levels from the two ends of the gradient. This result suggested that competition for light may be stronger under intermediate disturbance. The divergence of SH may represent the vertical partitioning of above-ground resource capture and the differences in dispersal distances (Bernard-Verdier et al. 2012; Fu et al. 2012). Previous studies suggested that competition increases with flood disturbance (Violle et al. 2010). Stronger competition also promotes resource use efficiency because of trait-based limiting similarity processes; thus, niche overlap and dominance decrease in the community. This condition may result in high evenness. The significant unimodal patterns between taxonomic/functional evenness and disturbance gradients might be largely attributed to changes in the relative roles of biotic interactions among species. For SLA and LDMC, however, the effects of environmental filtering and limiting similarity did not change significantly along the gradient, suggesting that the strength of assembly processes may vary widely in some specific traits but be relatively conserved in others, linking the intrinsic trade-offs among different sets of traits along the gradient.

In conclusion, the effects of disturbance on diversity were largely dependent on the aspects of diversity considered. Taxonomic/functional richness did not change with flood disturbance. In contrast, Shannon–Wiener diversity and evenness, functional evenness, and dispersion showed significant unimodal patterns along the flood disturbance gradient. Communities at the highest flood disturbance level exhibited significantly shorter SH with lower SLA. The functional spectrum of the community changed, therefore, from conservative and disturbance-tolerant species towards acquisitive and competitive species. Compared to the null model, a significant reduction was found in the range and variance of SLA. SLA also showed a more platykurtic distribution (i.e., lower kurtosis) than under a null expectation. The three traits were more evenly distributed than predicted. Our results provide further evidence that niche-based assembly processes play structuring roles in wetland plant community responses to flood

disturbance gradients and that both environmental filtering and limiting similarity can work on the same traits (e.g., SLA) through hierarchical effects on the distribution of functional traits within communities.

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