Different functional feeding groups of mangrove soil molluscs invoke unique co-occurrence patterns in response to a climate extreme

Guogui Chen | Xuan Gu | Yi Liu | Wenqing Wang | Mao Wang

Key Laboratory of the Coastal and Wetland Ecosystems (Xiamen University) Ministry of Education, College of the Environment & Ecology, Xiamen University, Xiamen, China

Correspondence
Wenqing Wang and Mao Wang, College of the Environment & Ecology, Xiamen University, South Xiang’an Road, CN-361102 Xiamen, Fujian, China. Emails: mangroves@xmu.edu.cn (W.W.); wangmao@xmu.edu.cn (M.W.)

Funding information
Fieldwork Funds for graduate students of Xiamen University, Grant/Award Number: 2020FG022; National Natural Science Foundation of China, Grant/Award Number: 42076161: 42176169; 31670490; Programs of Science and Technology on Basic Resources Survey for the Ministry of Science and Technology of China, Grant/Award Number: 2017FY100701

Editor: Luigi Maiorano

Abstract

Aim: Due to differences in community functional traits and composition, the response of communities to environmental changes can be variable, and thus an understanding of the mechanisms underlying differential functional group responses is necessary. We investigated a mangrove soil mollusc community before (in 2007) and after (in 2008 and 2009) an extreme cold event (ECE) to determine the effects of the ECE on co-occurrence patterns, spatiotemporal turnover and ecological processes in different functional groups (i.e. infaunal shelled deposit feeders [ISDFs] and hard-bodied, mobile scavenger/predators [MS/Ps]).

Location: Southeast coasts of China.

Method: We used network analysis and null models to test the co-occurrence patterns of the soil mollusc community. We used the analysis of distance and time decay to characterize the spatial turnover and temporal succession of the mollusc community based on presence/absence, relative abundance and biomass data. We performed random forest (RF), variation partitioning analysis (VPA) and Mantel tests to detect the effects of local environmental filtering and dispersal limitations on the soil mollusc community.

Results: We found a decrease in species richness and biomass and an increase in abundance after an ECE, reflecting a significant change in mangrove soil mollusc communities. The network modularization, divergent succession and geographical differentiation of the ISDFs increased from 2008 to 2009, but environmental filtering and regional dispersal limitations decreased. The temporal trends of the network modules, geographical differentiation and dispersal limitations of MS/Ps followed a hump-shaped pattern from 2008 to 2009, whereas the temporal trends of environmental filtering and temporal divergence exhibited an inverted hump-shape pattern. The ECE changed the main environmental drivers of ISDFs and MS/Ps from water salinity to meteorology and vegetation factors.

Main conclusions: Mangrove soil mollusc communities in different functional groups invoked different spatiotemporal turnover models and ecological processes to shape
1 | INTRODUCTION

Soil, as one of the most biodiverse habitats, contributes to many ecosystem functions and services (Thakur et al., 2020). Extreme climate events, such as extreme cold events (ECEs), influence soil ecosystems and are increasing in intensity, frequency and duration (IPCC, 2020). Therefore, uncovering the factors that make soil communities vulnerable to extreme climate change has become integral to the field of soil conservation biogeography (Coyle et al., 2017; Maxwell et al., 2019; Richardson & Whitaker, 2010). During ECEs, temperatures rapidly decrease to near freezing conditions and typically remain there for several weeks (Ross et al., 2009). Therefore, the threats posed by ECEs to soil-related systems will persist. To date, climate change vulnerability assessments that have included ECEs have predominantly focused on how the taxonomic diversity (e.g. species richness and abundance) of soil communities responds to extreme changes in climate (Chen, Wang, Zhang, et al., 2020; Liu et al., 2016). The findings of these studies suggest that community composition responses to ECEs (i.e. changes in richness and/or abundance) may be highly variable. In addition, in their response to diverse environmental changes, soil communities comprise different functional groups (Barnes et al., 2019; Dethier & Steneck, 1994). Although different functional groups coexist at local and regional scales, they impart different effects on soil community dynamics in response to environmental changes (Sundstrom et al., 2012; Voigt et al., 2007). However, knowledge concerning the mechanisms underlying the ecology, evolution and assembly of different soil functional groups in response to climate extremes, such as ECEs, remains limited (Voigt et al., 2007). Mangrove soil molluscs, as macroinvertebrates, are generally found on the surfaces and upper layers of mangrove soil, humus and sediment (Cannicci et al., 2008; Decaens, 2010; Lee, 2008; Thakur et al., 2014). Based on morphospecies of differing feeding types, mobility and skeletonization, mangrove soil molluscs are generally grouped into two functional groups according to how they affect mangrove soil structure and function: infaunal shelled deposit feeders (ISDFs) and hard-bodied, mobile scavenger/predators (MS/Ps) (Barnes et al., 2019). Recent studies have shown that ECEs influence species richness, abundance and biomass in the mollusc community (Chen, Wang, Zhang, et al., 2020; Liu et al., 2016; Reiss et al., 2006). The early development, juvenile growth, reproduction, physiological metabolism, mortality and distribution of intertidal soil molluscs are influenced by ECEs (Ansart & Vernon, 2003; Liu et al., 2016; Prather et al., 2013). Therefore, the community structure and function of mangrove soil molluscs in different functional groups should be influenced by ECEs.

Abundance-based and trait-based co-occurrence patterns can characterize the structure and function, respectively, of the soil community (Mouchet et al., 2010; Suding et al., 2005). Spatial turnover (i.e. spatial dispersal), temporal turnover (i.e. ecological succession) and local environmental filtering are critical ecological processes that shape the regional and biogeographical co-occurrence patterns of soil fauna (Ainsworth et al., 2020; Lv et al., 2014; Suurkuukka et al., 2012; Wu & Wang, 2019). Therefore, scale dependency, including environmental and spatiotemporal trends continues to be of pivotal importance to soil communities (Suurkuukka et al., 2012). Recent studies have increasingly emphasized the following points: both spatiotemporal turnover and local environmental filtering of communities are influenced by climate change; one of these processes may dominate depending on the particular case; and trade-offs exist between these processes (Araújo et al., 2011; Chen, Wang, Liu, et al., 2020). Therefore, climate disturbances, especially extreme climate changes, may influence the assemblages of soil communities by modulating both spatial and temporal processes (Stegen et al., 2013). In addition, the mixture of environmental filtering and spatial and temporal processes affecting communities indicates that assemblages with different properties or traits might respond to climate changes via different ecological strategies (Chen, Wang, Zhang, et al., 2020; Pandit et al., 2009). For instance, previous studies have shown that abundant arboreal mangrove mollusc taxa mainly increased divergent succession and spatial limitations to cope with ECEs; the rare assemblages maintained high levels of divergent succession but eroded spatial limits in response to ECEs (Chen, Wang, Zhang, et al., 2020). However, the limitations of taxonomic approaches (e.g. abundance based and species based) are obvious because species within different functional groups differ in their responses to environmental changes, such as climate change (Mouillot et al., 2013). Therefore, it is important to differentiate between the different functional groups to better understand the mechanisms underlying soil community functioning in response to extreme climate changes.

To address this knowledge gap, we studied soil mollusc (benthic mollusc) communities that involved five mangrove wetlands. The mangroves in our study system experienced an ECE in 2008 (Boucek et al., 2016; Chen, Wang, Zhang, et al., 2020), providing a unique opportunity to evaluate the effects of the ECE on the different functional groups of a soil community. We calculated the taxonomic and biogeographical co-occurrence pattern, divergent succession, extreme cold event, functional group, mangrove wetland, soil mollusc, spatial turnover
functional diversity of ISDF and MS/P sub-communities based on species identity, species abundance and body mass. We aimed to determine how the taxonomic and functional diversity of soil mollusc communities with different functional groups responded to the ECE, including changes in regional co-occurrence patterns, temporal succession, spatial turnover and environmental filtering. Low temperatures can affect the early development, juvenile growth, reproduction, physiological metabolism and mortality of coastal soil fauna (Reiss et al., 2006). Therefore, ECEs can dramatically affect the species’ richness, abundance and biomass of coastal invertebrate communities (Chen, Gu, Liu, Shi, et al., 2021; Chen, Wang, Zhang, et al., 2020; Liu et al., 2016) and then change the community composition, increase modules of the co-occurrence network pattern, enhance the spatiotemporal turnover of mangrove soil mollusc communities and break down the balance between deterministic and stochastic processes in mangrove soil mollusc communities (Chen, Gu, Liu, Shi, et al., 2021; Chen et al., 2021; Chen, Wang, Zhang, et al., 2020; Ferrenberg et al., 2015; Legras et al., 2019; Lundquist et al., 2018). Additionally, communities with different feeding types or mobility might respond to environmental disturbances (e.g. the ECE) via different mechanisms (Lundquist et al., 2018; Pandit et al., 2009; Voigt et al., 2007).

For example, species with a strong athletic ability can avoid cold waves by actively moving, while species with a weak athletic ability cannot (Coyle et al., 2017). In this study, we tested the following hypotheses: (I) ECEs increase the modularity of co-occurrence patterns of mangrove soil molluscs, and different changes are exhibited between ISDFs and MS/Ps; (II) the ECE increases the spatiotemporal turnover of community, and different changes occur between ISDFs and MS/Ps; and (III) the ECE is expected to break the balance between spatial processes and environmental filtering in the mollusc community, and different changes occur between ISDFs and MS/Ps.

2 | METHODS

2.1 | Study area

The study region comprised Qinglan Bay (QL), Dongzhai Bay (DZ), Techeng Island (TC), Yingluo Bay (YL) and Beilun Estuary (BL) in China (19.532–21.598°N, 107.996–110.849°E; Figure S1a). This region is located in the tropical and southern subtropical zones and has a warm and humid maritime climate, with an annual average air temperature of 23–24°C and annual average precipitation of 1500–1700 mm. The average air temperature in January (the coldest month) is generally 16–17°C. The daily average air temperature minima fall below 10°C on fewer than 7 days per year under normal circumstances. The annual average sediment temperature is 24.2°C.

Previous studies have shown that the soils (sediments) of mangrove forests in this region had the highest mollusc diversity of all mangrove wetlands in China (Chen, Wang, Liu, et al., 2020). In 2008, this region suffered an ECE that was characterized by daily minima below 10°C for more than 3 weeks (Figure S1b). During this event, the minimum air temperature at the adjacent weather station decreased to 3°C (Figure S1b). A mean air temperature of 12.6°C was found in January and February of 2008 (Figure S1b). The number of continuous days with abnormally low and/or freezing temperatures broke records that had been held in the region since the winter of 1954 (Chen, Wang, Zhang, et al., 2020; Liu et al., 2016).

2.2 | Sampling and environmental variables

Long-term seasonal sampling work started in March 2007 and ended in early January 2010. Seasonal sampling means the soil mollusc sample was taken according to the following schedule: spring sampling occurred March 1 through April 30; summer sampling occurred June 1 through July 31; autumn sampling occurred September 1 through October 31 and winter sampling occurred December 1 through the following year in early January. Thus, there were four seasonal samplings conducted before the ECE (2007) and eight seasonal samplings conducted after the ECE (2008 and 2009). During each season, soil molluscs were sampled from three to five parallel transects that were 100 m apart and along an intertidal gradient in each mangrove wetland (Figure S2a). That is, 15–25 transects were sampled among the five mangrove wetlands in each season. Each transect was 100–200 m long from landward to seaward and was divided into hypo-, meso- and hyper-tidal zones (Figure S2b). Three to six 25 cm × 25 cm duplicate sediment samples were taken at a depth of 30 cm within an area of 25 m² (5 × 5 m) in each tidal zone (Figure S2c). In other words, three to six replicates were sampled in each tidal zone within a transect (Figure S2c). In total, 640, 948 and 603 samples were collected in 2007, 2008 and 2009 respectively. Additionally, to reduce the effects of sampling activities on our results, the sampling transects of two adjacent seasons were 10–30 m apart (Figure S3). Sediment samples were wet sieved in the field through a 1 mm mesh sieve, after which living molluscs were collected and fixed in 4% formaldehyde. Within 3 days of fixation, specimens were washed with water and transferred to 75% ethanol. The following local environmental variables were measured immediately after taking biotic samples at each tidal zone within a transect during sampling seasons: water salinity (Sal) was measured using a hand-held refractometer (three to six replicates); vegetation types (VT) were determined by the dominant mangrove species and latitude and longitude (coordinates) were measured using a hand-held GPS. The seasonal average highest atmospheric temperature (HT), seasonal average lowest atmospheric temperature (LT) and seasonal average rainfall (Rain) for each site were based on data from the China Meteorological Data Sharing Service System (http://data.cma.cn/site/index.html). The tidal amplitude (Tide) for each study site was based on data from the National Marine Science Sharing Service Platform (http://mds.nmdis.org.cn). Taxonomic categories of molluscs were then identified using morphological differences (species identity), counted to determine abundance and measured to determine wet weight. In this study, species abundance (abundance) and species identity (species richness) were used to represent compositional features, and wet weight (biomass) was used to represent...
2.3 Statistical analyses

2.3.1 Definition of different functional groups

To assess whether different functional groups responded differently to the ECE, we constructed two non-overlapping functional groups (Dethier & Steneck, 1994). We categorized benthic molluscs into two functional groups, ISDFs and MS/Ps, without combining morphospecies of differing feeding types or mobility (Barnes et al., 2019).

2.3.2 Impact of ECE on the soil mollusc community

To detect the influences of the ECE on the soil mollusc community, we compared the annual species’ abundance, species’ richness and biomass before (in 2007) and after (in 2008 and 2009) the ECE. To compare these measures, a one-way analysis of variance (ANOVA) was performed in R v3.6.1 (R-Core-Team, 2019). Data were tested for homoscedasticity and normality using Levene’s test and the Shapiro–Wilks test, respectively; if normality assumptions were not met, non-parametric equivalent analyses were used (Kruskal–Wallis ANOVA and Mann–Whitney U tests). Bonferroni corrections were used to assess the p-values of the pairwise comparisons between years.

2.3.3 Effect of the ECE on the spatiotemporal dynamics of the soil mollusc community

Beta diversity has proved to be a useful approach to assess community response to disturbances, highlighting community responses by the loss and gain of taxonomic composition and functional traits (Baselga, 2010; Vanschoenwinkel et al., 2013). Therefore, Jaccard distance and Bray–Curtis distance were used to describe compositional turnover and trait replacement in the mollusc metacommunity. The Jaccard distance was calculated using the “SpadeR” package in R v3.6.1 based on the presence–absence matrix (R-Core-Team, 2019). The Bray–Curtis dissimilarities were calculated using the SpadeR package in R v3.6.1 based on the relative abundance and relative biomass data (R-Core-Team, 2019). To test the effects of ECE on the beta diversity of soil mollusc communities, a non-metric multidimensional scaling (NMDS) ordination was used to investigate the changes in the soil mollusc communities over time from 2007 to 2009. To evaluate the significant differences in mollusc communities between these years, we used the randomization/permutation procedure analysis of similarities (ANOSIM) and permutational multivariate analysis of variance (PERMANOVA) tests (Anderson, 2017). The global R of ANOSIM is calculated as the difference in between-year mean rank similarities; thus, it displays the degree of separation between years (Mo et al., 2018). R = 1 indicates a complete separation of the community, whereas R = 0 means no community separation (Mo et al., 2018). The significance level was assessed using a Bonferroni correction.

To detect whether and how the ECE affected the co-occurrence of the soil mollusc community, we calculated the Spearman
correlations for pairs of species based on abundance and biomass data. The calculated correlations were used to construct species co-occurrence networks from before (in 2007) and after (in 2008 and 2009) the ECE (Chen, Gu, Liu, Shi, et al., 2021; Mo et al., 2021). We also constructed sub-networks for the ISDF and MS/P mollusc sub-communities to uncover the difference between different functional groups. Higher network modularization indicates higher community complexity and stability (Grilli et al., 2016). To characterize the recovery strategies of mollusc communities after the ECE (i.e. more complex or simpler), the modularity of networks was measured (Grilli et al., 2016).

To determine how soil molluscs co-exist (i.e. random or non-randomly aggregated or non-randomly segregated) and to assess whether and how the ECE influenced the co-occurrence pattern, null models were further calculated in EcoSim v7.72 based on presence-absence, relative abundance and biomass data (Gotelli & Entsminger, 2001). The checkerboard score (C-score) was used as a matrix of mollusc co-occurrence. The observed C-score was calculated and compared with the C-scores calculated for 5000 randomly assembled null models based on the tail probability that the observed (O) index was larger or smaller than expected (E) by chance (Gotelli & Entsminger, 2001; Gotelli & McCabe, 2002). Values of O > E for the C-score indicate negative co-occurrence (Gotelli & Entsminger, 2001), suggesting that soil molluscs are non-randomly segregated, resulting in reduced rates of co-occurrence. Conversely, values of O < E for the C-score reflect a positive co-occurrence (Gotelli & Entsminger, 2001), suggesting that soil molluscs non-randomly aggregate with similar compositional and functional traits. Finally, values of O = E for the C-score suggest that molluscs randomly co-occur. To determine whether and how the non-randomness of the soil mollusc metacommunity varied in response to ECEs, we calculated the standardized effect size (SES) for each mollusc community metric as follows (Gotelli & McCabe, 2002):

\[
SES = (I_{obs} - I_{sim}) / S_{sim}
\]

where Iobs is the observed value, Isim is the mean simulated value and Ssim is the standard deviation of the simulated indices. The null hypothesis is that the average SES = 0, and that 95% of the Iobs values fall between 1.95 and −1.95 (Gotelli & McCabe, 2002).

2.3.5 | Effect of the ECE on the ecological factors of soil mollusc communities

To evaluate whether and how the ECE changes the environmental factors that influence the distribution of the soil mollusc community, random forest (RF) machine learning (Breiman, 2001) was performed to assess the major drivers of the mollusc community in R v3.6.1 based on species richness, abundance and biomass data. In the RF model, the percentage increase in the mean squared error (IncMSE%) was used to assess the importance of environmental variables (Breiman, 2001; Mo et al., 2021). Environmental factors with a high IncMSE% value are the most important factors. To assess the significance of the RF model, 5000 permutations of the response variable were performed within the “A3” package (Mo et al., 2021). The significance of each environmental factor was determined using the “rfPermute” package in R v3.6.1.

To evaluate whether and how ECE changes the environmental and spatial processes of beta diversity in the mollusc community, variation partitioning analysis (VPA) and Mantel tests were used to assess the relative contribution of these ecological processes. According to the longitude and latitude coordinates, principal coordinates of neighbour matrices (PCNM) analysis were used to generate the regional spatial variables in CANOCO v5 (Chen, Wang, Liu, et al., 2020; Šmilauer & Lepš, 2014). Based on the longest gradient lengths of detrended correspondence analysis (DCA), either a redundancy analysis (RDA) or canonical correspondence analysis (CCA) was selected to assess the relationship between mollusc communities and local environmental variables/regional spatial factors (Chen, Wang, Liu, et al., 2020; Šmilauer & Lepš, 2014). The longest gradient lengths were <3 for total, ISDF and MS/P communities, indicating that RDA was suitable for these communities. Before RDA analysis, forward selection was conducted to select the environmental variables and PCNMs with significant explaining factors (p < 0.05) for further analyses. Then, variation partitioning analysis (VPA) was used to evaluate the relative contribution of environmental filtering and regional dispersal process in shaping mangrove soil mollusc communities with adjusted R² coefficients based on RDA in CANOCO v5 (Chen, Wang, Liu, et al., 2020; Mo et al., 2018; Šmilauer & Lepš, 2014). The relative role of both components was explained by pure spatial factors (SIE), pure environmental factors (E) and the combined effects of both space and environment (S∩E). In this analysis, the residual proportion represents the unexplained variance. Furthermore, Mantel tests were conducted to identify relationships between mollusc community dissimilarity and environmental spatial distances (Mo et al., 2018). In the Mantel tests, the first two spatial components (i.e. PCNM1 and PCNM2) and the Euclidean distance of environmental factors were used for analysis.

3 | RESULTS

3.1 | The ECE influenced the soil mollusc community

The species richness (Figure 1a–c), abundance (Figure 1d–f) and biomass (Figure 1g–i) of ISDF, MS/P and total mollusc communities changed significantly (one-way ANOVA, p < 0.05) after the ECE, indicating that the ECE greatly influenced the regional soil mollusc community. Specifically, the species richness of ISDFs continued to decrease in the 2 years after the ECE (one-way ANOVA, p < 0.01; Figure 1a), while those of MS/Ps began to increase in the second year (2009) after the ECE (one-way ANOVA, p < 0.01; Figure 1b). The biomass of ISDFs increased in the second year (2009) after the
ECE (one-way ANOVA, \( p < 0.01; \) Figure 1g), while the biomass of MS/Ps continued to decrease in the 2 years after the ECE (one-way ANOVA, \( p < 0.05; \) Figure 1h). Interestingly, the abundance of ISDFs and MS/Ps increased in the 2 years after the ECE.

Multidimensional scaling plots showed that ECE had a significant influence on the soil mollusc community (ANOSIM test, ISDFs: \( R(2007 \text{ vs. } 2008) = 0.745, p = 0.001, R(2007 \text{ vs. } 2009) = 0.820-1.0, p = 0.001, R(2008 \text{ vs. } 2009) = 0.648-0.650, p = 0.001; \) MS/Ps: \( R(2007 \text{ vs. } 2008) = 0.743-0.745, p = 0.001, R(2007 \text{ vs. } 2009) = 0.649-0.819, p = 0.001, R(2008 \text{ vs. } 2009) = 0.638-0.679, p = 0.001; \) PERMANOVA test, ISDFs: \( F(2007 \text{ vs. } 2008) = 92.55-137.83, p = 0.001, F(2007 \text{ vs. } 2009) = 36.21-88.77, p = 0.001, F(2008 \text{ vs. } 2009) = 6.89-18.40, p = 0.001; \) MS/Ps: \( F(2007 \text{ vs. } 2008) = 3.21-45.55, p < 0.05, F(2007 \text{ vs. } 2009) = 50.26-154.05, p = 0.001, F(2008 \text{ vs. } 2009) = 47.95-189.21, p = 0.001; \) Figure 2; Table S1a and b). Particularly, the community patterns between ISDF and MS/P taxa were significantly different since the value of the global \( R \) of the ISDF community (ANOSIM test, \( R = 0.697-0.698, p = 0.001; \) Figure 2; Table S1) was greater than those of MS/P community (ANOSIM test, global \( R = 0.695-0.697, p = 0.001; \) Figure 2; Table S1a). These results indicate that the ECE had a great influence on the mollusc community, and that the effects of the ECE on ISDFs were different from those on MS/Ps.

### 3.2 The ECE affected the spatiotemporal turnover of the soil mollusc community

A positive relationship (Mantel test, Mantel’s \( r > 0, p < 0.01; \) Figure 3; Table S2) was observed between temporal distance and community dissimilarity of the total, ISDF and MS/P soil molluscs, indicating that divergent succession may be the general temporal dynamic of mangrove soil molluscs. The intensity of the divergent succession in ISDFs was greater than the strength of the divergent succession in MS/Ps, since the value of Mantel’s \( |r| \) in ISDFs (Mantel test, mean \( |r| = 0.42 \) was greater than that in MS/Ps (Mantel test, mean \( |r| = 0.22; \) Table S2; one-way ANOVA, \( F = 33.94, p < 0.001; \) Figure
After the ECE, Mantel’s $r$ of ISDFs increased by 60% (one-way ANOVA, $F = 759.45, p < 0.001$; Figure S4b), while in MS/P taxa, it decreased (one-way ANOVA, $F = 0.46, p = 0.65$; Figure S4c). This reflects that the ECE enhanced the divergent succession of ISDFs, while reducing the divergent succession of MS/Ps.

A positive relationship (Mantel test, Mantel’s $r > 0, p < 0.01$; Figure S5; Table S2) was found between geographical distance and community dissimilarity of all ISDF and MS/P taxa, reflecting the spatial differentiation of soil molluscs. The mean Mantel’s $r$ of ISDFs (0.4) was greater than that of MS/Ps (0.28), reflecting that the strength of spatial differentiation in ISDFs was greater than the strength of spatial differentiation in ISDFs (one-way ANOVA, $F = 11.05, p = 0.004$; Figure S6a). After the ECE, the mean Mantel’s $r$ of ISDFs increased significantly (one-way ANOVA, $F = 150.82, p = 0.001$; Figure S6b).
p < 0.001; Figure S6b), while that of MS/Ps decreased significantly (one-way ANOVA, F = 87.81, p < 0.001; Figure S6b). This indicates that the spatial differentiation of mangrove soil molluscs was influenced by the ECE; the spatial differentiation of ISDFs was enhanced by the ECE, while the spatial differentiation of MS/P taxa was reduced by the ECE.

### 3.3 Effects of the ECE on the co-occurrence patterns of soil mollusc communities

The observed C-scores and SESs of mangrove mollusc communities were greater than the null model (null model analysis, p < 0.05, SES > 1.95; Figure S7; Table S3), meaning that a segregated co-occurrence pattern may be a common pattern of the mangrove mollusc community. After the ECE, the SESs of ISDFs were reduced, while those of MS/Ps increased (null model analysis, Figures S7 and S8). Additionally, the modules of the total community network increased greatly after the ECE (Figure S9; Table S4), indicating that the network structure of the mollusc community was significantly influenced by the ECE. After the ECE, the network modules of ISDFs continued to increase, while those of MS/Ps decreased in the first year but then increased (Figure 4).

These results suggest the great effects of the ECE on the co-occurrence pattern of the mangrove soil mollusc communities, with different effects of the ECE on the co-occurrence pattern of ISDF and MS/P taxa.

### 3.4 Effects of the ECE on the driving factors of the soil mollusc community

We found that the hydrology (Tide and Sal), meteorology (LT, HT and Rain) and vegetation (FT) factors significantly affected species richness, abundance and biomass of all mangrove molluscs (RF analysis, p < 0.05; Figure 5). Before the ECE, Sal and LT were the most important variables for the total mollusc community (RF analysis, p < 0.05; Figure 5). After the ECE, these factors were replaced by meteorology (LT, HT and Rain) and vegetation (FT) factors (RF analysis, Figure 5). Among the ISDFs, Sal was the most important variable for predicting species richness, abundance and biomass before the ECE (2007) (p < 0.05; Figure 5). However, after the ECE, HT, LT and FT were the most important factors shaping the

![FIGURE 3](image-url)  
**FIGURE 3** The relationships between community dissimilarities and temporal distance before (2007) and after (2008 and 2009) the extreme cold event (ECE) based on the Mantel test and Spearman’s rank correlation. The community dissimilarities include the Jaccard dissimilarity of presence/absence data and Bray–Curtis dissimilarities of relative abundance and biomass data.
MS/P community ($p < 0.05$; Figure 5). These results indicate that the ECE changed the driving factors of the mangrove mollusc community. Different effects of the ECE on the ISDF and MS/P taxa were determined.

We found that the relationships between the driving factors of the mollusc communities changed after the ECE since Spearman’s $\rho$ changed greatly (Spearman correlation analysis, Figure 6; Figure S10). We observed a clear correlation between the community dissimilarities and driving factors, which were significant on all community scales (i.e. total, ISDFs and MS/Ps; Mantel test, $p < 0.05$; Figure 5; Figure S10). This reflects spatial and environmental processes that jointly influence the mollusc community. Importantly, the Mantel’s $r$ between the mollusc communities and driving factors changed greatly after the ECE (Figure 5; Figures S10–12). Specifically, among ISDFs, the absolute value of Mantel’s $r$ of the spatial factor (PCNM1-2), meteorological factors (LT, HT and Rain) and hydrological factors (Tide and Sal) were reduced in the 2 years after the ECE (one-way ANOVA, $p < 0.05$; Figure S12). However, Mantel’s $r$ of the spatial, temporal (PCNM1-2) and hydrological factors (Tide and Sal) in MS/Ps continued to decrease after the ECE (one-way ANOVA, $p < 0.05$; Figure S12).

Additionally, both the purely spatial (S/E) and environmental (E/S) variation significantly explained the total ISDF and MS/P communities (VPA analysis, $p < 0.01$; Table S5; Figures S13 and 14). The explained proportion of purely spatial (S/E) variation was greater than that of the purely environmental (E/S) variation (Table S5), indicating that the spatial process was more important than environmental filtering in shaping the mangrove soil mollusc community. Importantly, the relative importance of these processes was broken by the ECE. For instance, after the ECE in 2008, the explained proportion of purely environmental (E/S) variation was greater than that of the purely spatial (S/E) variation in the ISDF and MS/P groups (Table S5). In contrast, in ISDFs, the explained proportion of purely spatial (S/E) and environmental (E/S) variation decreased after the ECE in 2008 (Table S5), whereas in MS/Ps, the explained proportion of purely spatial (S/E) variation decreased, while that of purely environmental (E/S) variation increased after the ECE in 2008 (Table S5).

**4 | DISCUSSION**

**4.1 | Effects of extreme climate changes on different functional groups**

Our results suggest shifts in the functional composition with the ECE, causing great declines in functional groups representing ISDFs and MS/Ps. The decrease in species richness and biomass of particular functional groups of mangrove molluscs (ISDFs and MS/Ps) support broad generalizations about the negative effects of extreme climate changes on the ecosystem (Chen, Gu, Liu, Shi, et al., 2021; Maxwell et al., 2019). The decrease in ISDFs would...
reduce nutrient cycling, pollutant burial and mobilization and sediment stability (Lavelle et al., 2006; Lundquist et al., 2018). Declines in MS/Ps would reduce nutrient cycling and the redistribution of energy and affect disease transmission associated with decomposition (Cannicci et al., 2008; Decaens, 2010; Lundquist et al., 2018). Additionally, declines in biomass would result in a decrease in many ecosystem services, such as food production and carbon sequestration (Chen, Gu, Liu, Shi, et al., 2021). Decreasing marine food yield may lead to human malnutrition in some food-insecure regions (Chen, Gu, Liu, Shi, et al., 2021). The carbon shell of soil molluscs, as long-term carbon storers, would decrease after ECEs and influence the ecosystem services of climate warming alleviation (Barnes et al., 2019). An increase in abundance reflects that ECEs might cause further impacts on this ecosystem’s functions and services through species interactions (Bairey et al., 2016).

4.2 | Different functional groups may use different ecological strategies in response to extreme climate changes

Both theoretical and empirical studies suggest that the spatiotemporal dynamics of community turnover are often the key mechanism affecting the self-recovery of the community (Chen, Wang, Zhang, et al., 2020; Dethier & Steneck, 1994; Guo et al., 2018; Hortal et al., 2010). The ECE increased the divergent succession and spatial differentiation of the ISDF community, while decreasing those of the MS/P community, reflecting that ISDFs and MS/Ps utilized different strategies of spatiotemporal turnover in response to extreme climate events. As previous studies have found, communities with different properties (e.g. abundant vs. rare, generalist vs. specialist and different functional groups) have different successional patterns in response to environmental changes (Chen, Wang, Zhang, et al., 2020; Mo et al.,
Similarly, different functional groups (algal and herbivory) on Jamaica’s Discovery Bay reef have different spatiotemporal dynamics in response to hurricanes and mass mortality (Dethier & Steneck, 1994). Different dynamics of spatiotemporal turnover lead to distinct patterns of community structure. Therefore, this may be one of the explanations for the different co-occurrence patterns in ISDFs and MS/Ps. Additionally, increased differences in spatiotemporal turnover are expected to lead to an increase in the spatiotemporal heterogeneity of the community, thus improving the spatiotemporal stability and complexity of the community (Grilli et al., 2016; Yuan et al., 2021). This might be why we observed an increase in the network modules of the ISDF community in the 2 years after the ECE, while a decrease was observed in the MS/P community. Therefore, climate extremes may enhance the stability and complexity of the soil mollusc network and have a different effect on ISDFs and MS/Ps (Grilli et al., 2016; Yuan et al., 2021). Our results reinforce the view that communities with different properties (e.g. differently functional groups) might respond to disturbances, such as extreme climate events, via different mechanisms of spatiotemporal turnover.

Local (e.g. environmental filtering) and regional (e.g. dispersal limitation) ecological processes are two important factors that influence the geographical distribution of soil mollusc communities (Chase et al., 2011; Chen, Wang, Liu, et al., 2020; Gotelli & McCabe, 2002). We found that dispersal limitations and environmental filtering jointly affected the mangrove soil mollusc community, while the contribution of dispersal limitation was more important than that of environmental filtering. Notably, the balance of these ecological processes in the mangrove soil mollusc communities was broken by the ECE. For example, meteorological factors (LT, HT and Rain) and vegetation type (FT) replaced Sal as the most important variable for shaping soil mollusc communities after the ECE. Under normal circumstances, salt tolerance may be the main factor that influences intertidal species since the larval dispersal and genetic exchange of intertidal species can be influenced by changes in Sal caused by human activities, such as freshwater discharge (Dong et al., 2016). Climate changes may induce other tolerances in species, such as climate change-linked stress tolerance, which could influence their fitness and chances of survival (Yusefi et al., 2021). Furthermore, climate changes will probably impact coastal species through declines in primary productivity (Chen, Wang, Zhang, et al., 2020). Additionally, the initiation of dispersal (emigration) by a species, its subsequent movement (transfer) and its settlement decision (immigration) are influenced by local conditions. Therefore, climate changes, such as an ECE, may affect the dispersal ability of a community (Travis et al., 2013). This could explain why we observed a decrease in the dispersal limitation of mangrove soil molluscs.

We found different changes in these ecological processes (environmental filtering and dispersal limitation) between ISDFs and MS/Ps after the ECE. On the one hand, we found that Rain and Tide were the most important factors that shaped the ISDF community, while these factors were not important for MS/Ps. On the other hand, the explained proportion of purely environmental (E/S) variation in the
MS/P community increased after the ECE in 2008, while the explained proportion of E/S in ISDFs decreased. The reasons for these differences can be explained by the fact that different functional groups (ISDFs and MS/Ps) may differ in many fundamental features, such as environmental tolerance and dispersal characteristics. The divergent responses to climate change by trait-specific groups could lead to changes in the composition of ecosystems, calling the resilience and sustainability of various ecosystems into question (Fei et al., 2017; Voigt et al., 2007).

4.3 Implications for soil conservation biogeography

Soil biological conservation aims to maintain soil ecosystem functioning and services. The contribution of each soil species and taxon to soil ecosystem functioning relies on its functional properties, such as herbivory and nutrient cycling. Soil fauna are acknowledged as key components of soil health and soil ecosystem services (Delgado-Baquerizo et al., 2020; Lavelle et al., 2006). Environmental changes, such as extreme climate events, can negatively affect coastal soil management because changes in the structure and function of soil fauna jeopardize soil systems, such as the southern China mangrove soil, where the communities are already influenced by and responsive to anthropogenic-driven abiotic regimes (Boucek & Rehage, 2014; O’Connor et al., 2020). Based on the regional coastal soil mollusc community, a novel contribution of our study is the finding that different functional groups invoke different spatiotemporal turnover models and ecological processes (local environmental filtering and dispersal limitation) to shape their unique co-occurrence patterns in response to ECEs. Methods of dividing different functional groups allow researchers to identify the relative vulnerabilities of member functional groups and, more importantly, the vulnerabilities of their traits to specific stressors associated with environmental changes, such as ECEs. Identifying a quantifiable link between environmental stressors and different functional meta-communities responses greatly improves our predictive power concerning how an ECE may affect the metacommunity function impacted by climate change, potentially providing a powerful tool in soil biodiversity and biogeography conservation. Thus, under environmental changes, such as extreme climate events, a major challenge is to conserve various functional groups while preserving biodiversity, ecological functions and associated ecosystem services. Our results highlight the importance of identifying the responses of different functional groups to climate disturbances. We recommend the use of functional groups to develop indicators for soil conservation biogeography.

ACKNOWLEDGEMENTS

We thank Xiaofang Shi for her assistance during the revision. We also thank the reviewers for their general and specific comments on the manuscript. The authors acknowledge the financial support from the National Natural Science Foundation of China (No. 42076161, 42176169 and 31670490) and the Programs of Science and Technology on Basic Resources Survey for the Ministry of Science and Technology of China (No. 2017FY100701) and Fieldwork Funds for graduate students of Xiamen University (No.2020FG022).

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. All authors agreed to the submission of this manuscript. The material is original research, has not been previously published and has not been submitted for publication elsewhere while under consideration.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13467.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jsxksn0bh.

ORCID

Guogui Chen https://orcid.org/0000-0002-3931-079X
Mao Wang https://orcid.org/0000-0001-6550-2405

REFERENCES

Ainsworth, T. D., Hurd, C. L., Gates, R. D., & Boyd, P. W. (2020). How do we overcome abrupt degradation of marine ecosystems and meet the challenge of heat waves and climate extremes? Global Change Biology, 26(2), 343–354. https://doi.org/10.1111/gcb.14901
Anderson, M. J. (2017). Permutational multivariate analysis of variance (PERMANOVA). In Wiley StatsRef: Statistics Reference Online (pp. 1–15). https://doi.org/10.1002/9781118445112.stat07841
Ansart, A., & Vernon, P. (2003). Cold hardness in molluscs. Acta Oecologica-International Journal of Ecology, 24(2), 95–102. https://doi.org/10.1016/s1146-609x(03)00045-6
Araújo, M. B., Rozenfeld, A., Rahbek, C., & Marquet, P. A. (2011). Using species co-occurrence networks to assess the impacts of climate change. Ecography, 34(6), 897–908. https://doi.org/10.1111/j.1600-0587.2011.06919.x
Bairey, E., Kelsic, E. D., & Kishony, R. (2016). High-order species interactions shape ecosystem diversity. Nature Communications, 7, 12285. https://doi.org/10.1038/ncomms12285
Barnes, D. K. A., Sands, C. J., Richardson, A., & Smith, N. (2019). Extremes in benthic ecosystem services; Blue carbon natural capital shallower than 1000 m in isolated, small, and young Ascension Island’s EEZ. Frontiers in Marine Science, 6, 663. https://doi.org/10.3389/fmars.2019.00663
Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x
Boucek, R. E., Gaiser, E. E., Liu, H., & Rehage, J. S. (2016). A review of sub-tropical community resistance and resilience to extreme cold spells. Ecosphere, 7(10), e01455. https://doi.org/10.1002/ecs2.1455
Boucek, R. E., & Rehage, J. S. (2014). Climate extremes drive changes in functional community structure. Global Change Biology, 20(6), 1821–1831. https://doi.org/10.1111/gcb.12574
Breiman, L. (2001). Random Forests. Machine Learning, 45(1), 5–32. https://doi.org/10.1023/A:1010933404324
Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J. M. Diamond’s assembly rules model. Ecology, 83(8), 2091-2096. https://doi.org/10.1890/0012-9658(2002)083[2091;SCMA2.0.CO;2

Grilli, J., Rogers, T., & Allesina, S. (2016). Modularity and stability in ecological communities. Nature Communications, 7, 12031. https://doi.org/10.1038/ncomms12031

Guo, X., Feng, J., Shi, Z., Zhou, X., Yuan, M., Tao, X., Hale, L., Yuan, T., Wang, J., Qin, Y., Zhou, A., Fu, Y., Wu, L., He, Z., Van Nostrand, J. D., Ding, N., Liu, X., Luo, Y., Tiedje, J. M., ... Zhou, J. (2018). Climate warming leads to divergent succession of grassland microbial communities. Nature Climate Change, 8(9), 813–818. https://doi.org/10.1038/s41558-018-0254-2

Hortal, J., Roura-Pascual, N., Sanders, N. J., & Rahbek, C. (2010). Understanding (insect) species distributions across spatial scales. Ecology, 91(3), 51–53. https://doi.org/10.1111/j.1160.02009.06428.x

IPCC (2020). Climate change 2020: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change (Core Writing Team, R.K. Pachauri & L.A. Meyer eds.). Switzerland: IPCC.

LaVelle, P., Decaens, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., & Rossi, J. P. (2006). Soil invertebrates and ecosystem services. European Journal of Soil Biology, 42, S3–S15. https://doi.org/10.1016/j.ejsobi.2006.10.002

Lee, S. Y. (2008). Mangrove macrobenthos: Assemblages, services, and linkages. Journal of Sea Research, 59(1), 16–29. https://doi.org/10.1016/j.jsre.2007.05.002

Lee, S.-H., Sorensen, J. W., Grady, K. L., Tobin, T. C., & Shade, A. (2017). Divergent extremes but convergent recovery of bacterial and archaeal soil communities to an ongoing subterranean coal mine fire. ISME Journal, 11(6), 1447–1459. https://doi.org/10.1038/ismej.2017.11

Legras, G., Loiseau, N., Gaertner, J.-C., Poggiale, J.-C., Ienco, D., Mazouni, N., & Mérigot, B. (2019). Assessment of congruence between co-occurrence and functional networks: A new framework for revealing community assembly rules. Scientific Reports, 9(1), 19996. https://doi.org/10.1038/s41598-019-56515-7

Lepš, J., Rejmánek, M., Leps, J., & Rejmanek, M. (1991). Convergence or divergence: What should we expect from vegetation succession? Oikos, 62(2), 261–264. https://doi.org/10.2307/3545274

Liu, T., Guo, R., Ran, W., Whalen, J. K., & Li, H. (2015). Body size is a sensitive trait-based indicator of soil nematode community response to fertilization in rice and wheat agroecosystems. Soil Biology & Biochemistry, 88, 275–281. https://doi.org/10.1016/j.soilbio.2015.05.027

Liu, Y., Wang, M., Wang, W., Fu, H., & Lu, C. (2016). Chilling damage to mangrove mollusk species by the 2008 cold event in Southern China. Ecosphere, 7(6), e01312. https://doi.org/10.1111/ecs2.1312

Lundquist, C. J., Bowden, D., Cartner, K., Stephenson, F., Tuck, I., & Hewitt, J. E. (2018). Assessing benthic responses to fishing disturbance over broad spatial scales that incorporate high environmental variation. Frontiers in Marine Science, 5(405), 1–14. https://doi.org/10.3389/fmars.2018.00405

Lv, Y., Guo, X., & Zhang, W. D. (2014). The responses of soil nematode assemblages to disturbance in Liaohe estuary wetlands. European Journal of Soil Biology, 61, 6–11. https://doi.org/10.1016/j.ejsoilbi.2013.12.003

Maxwell, S. L., Butt, N., Maron, M., McAlpine, C. A., Chapman, S., Ullmann, A., Segan, D. B., & Watson, J. E. M. (2019). Conservation implications of ecological responses to extreme weather and climate events. Diversity and Distributions, 25(4), 613–625. https://doi.org/10.1111/ddi.12878

Mo, Y., Zhang, W., Wilkinson, D. M., Yu, Z., Xiao, P., & Yang, J. (2021). Biogeography and co-occurrence patterns of bacterial generalists and specialists in three subtropical marine bays. Limnology and Oceanography, 66(3), 793–806. https://doi.org/10.1002/lno.11643

Mo, Y., Zhang, W., Yang, J., Lin, Y., Yu, Z., & Lin, S. (2018). Biogeographic patterns of abundant and rare bacterioplankton in three subtropical
bays resulting from selective and neutral processes. ISME Journal, 12(9), 2198–2210. https://doi.org/10.1038/s41396-018-0153-6

Moretti, M., Dias, A. T. C., Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibáñez, S., Öckinger, E., Sousa, J. P., Ellers, J., & Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Functional Ecology, 31(3), 558–567. https://doi.org/10.1111/1365-2435.12776

Mouillot, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24(4), 867–876. doi.org/10.1111/j.1365-2435.2010.01695.x

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. Trends in Ecology and Evolution, 28(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology. Journal of Biogeography, 26(4), 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x

O’Connor, J. J., Fest, B. J., Sievers, M., & Swearer, S. E. (2020). Impacts of land management practices on blue carbon stocks and greenhouse gas fluxes in coastal ecosystems-A meta-analysis. Global Change Biology, 26(3), 1354–1366. https://doi.org/10.1111/gcb.14946

Pandit, S. N., Kolasa, J., & Cottenie, K. (2009). Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. Ecology, 90(8), 2253–2262. https://doi.org/10.1890/08-0851.1

Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, M., Bloch, C. P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T. A. S., Parsons, S., & Joern, A. (2013). Invertebrates, ecosystem services and climate change. Biological Reviews, 88(2), 327–348. https://doi.org/10.1111/bbrv.12002

R-Core Team (2019). R: A language and environment for statistical computing. Foundation for Statistical Computing.

Reiss, H., Meybohm, K., & Kroencke, I. (2006). Cold winter effects on benthic macrofauna communities in near- and offshore regions of the North Sea. Helgoland Marine Research, 60(3), 224–238. https://doi.org/10.1007/s10152-006-0038-3

Richardson, D. M., & Whitaker, R. J. (2010). Conservation biogeography – foundations, concepts and challenges. Diversity and Distributions, 16(3), 313–320. https://doi.org/10.1111/j.1472-4642.2010.00660.x

Ross, M. S., Ruiz, P. L., Sah, J. P., & Hanan, E. J. (2009). Chilling damage in a changing climate in coastal landscapes of the subtropical zone: A case study from south Florida. Global Change Biology, 15(7), 1817–1832. https://doi.org/10.1111/j.1356-2488.2009.01900.x

Šmilauer, P., & Leps, J. (2014). Multivariate analysis of ecological data using CANOCO 5 (2nd edn). Cambridge University.

Stegen, J. C., Freestone, A. L., Crist, T. O., Anderson, M. J., Chase, J. M., Comita, L. S., Cornell, H. V., Davies, K. F., Harrison, S. P., Hurlbert, A. H., Inouye, B. D., Kraft, N. J. B., Myers, J. A., Sanders, N. J., Swenson, N. G., & Vellend, M. (2013). Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. Global Ecology and Biogeography, 22(2), 202–212. https://doi.org/10.1111/1466-8238.2012.00780.x

Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Penningts, S. (2005). Functional and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America, 102(12), 4387–4392. https://doi.org/10.1073/pnas.0408648102

Sundstrom, S. M., Allen, C. R., & Barichievy, C. (2012). Species, functional groups, and thresholds in ecological resilience. Conservation Biology, 26(2), 305–314. https://doi.org/10.1111/j.1523-1739.2011.01822.x

Suurkuukka, H., Meissner, K. K., & Muotka, T. (2012). Species turnover in lake littorals: spatial and temporal variation of benthic macroinvertebrate diversity and community composition. Diversity and Distributions, 18(9), 931–941. https://doi.org/10.1111/j.1472-4642.2012.00889.x

Thakur, M. P., Berg, M. P., Eisenhauer, N., & van Langevelde, F. (2014). Disturbance-diversity relationships for soil fauna are explained by faunal community biomass in a salt marsh. Soil Biology & Biochemistry, 78, 30–37. https://doi.org/10.1016/j.soilbio.2014.06.021

Thakur, M. P., Phillips, H. R. P., Brose, U., De Vries, F. T., Lavelle, P., Loreau, M., Mathieu, J., Mulder, C., Van der Putten, W. H., Rillig, M. C., Wardle, D. A., Bach, E. M., Bartz, M. L. C., Bennett, J. M., Briones, M. J. I., Brown, G., Decaëns, T., Eisenhauer, N., Ferlian, O., ... Cameron, E. K. (2020). Towards an integrative understanding of soil biodiversity. Biological Reviews, 95(2), 350–364. https://doi.org/10.1111/brv.12567

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubis, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species’ responses to climate change. Oikos, 122(11), 1532–1540. https://doi.org/10.1111/j.1600-0766.2013.00399.x

van der Schatte Olivier, A., Jones, L., Vay, L. L., Christie, M., Wilson, J., & Malham, S. K. (2020). A global review of the ecosystem services provided by bivalve aquaculture. Reviews in Aquaculture, 12(1), 3–25. https://doi.org/10.1111/raq.12301

Vanschoenwinkel, B., Buschke, F., & Brendonck, L. (2013). Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. Ecology, 94(11), 2547–2557. https://doi.org/10.1890/12-1576.1

Voigt, W., Perner, J., & Hefin Jones, T. (2007). Using functional groups to investigate community response to environmental changes: Two grassland case studies. Global Change Biology, 13(8), 1710–1721. https://doi.org/10.1111/j.1365-2486.2007.01398.x

Wu, P., & Wang, C. (2019). Differences in spatiotemporal dynamics between soil macrofauna and mesofauna communities in forest ecosystems: The significance for soil fauna diversity monitoring. Geoderma, 337, 266–272. https://doi.org/10.1016/j.geoderma.2018.09.031

Yuan, M. M., Guo, X., Wu, L., Zhang, Y. A., Xiao, N., Shi, Z., Zhou, X., Wu, L., Yang, Y., Tiedje, J. M., & Zhou, J. (2021). Climate warming enhances microbial network complexity and stability. Nature Climate Change, 11(4), 343–348. https://doi.org/10.1038/s41558-021-00989-9

Yusefi, G. H., Safi, K., Tarroso, P., & Brito, J. C. (2021). The impacts of extreme climate change on mammals differ among functional groups at regional scale: The case of Iranian terrestrial mammals. Diversity and Distributions, 27(9), 1634–1647. https://doi.org/10.1111/ddi.13307

BIOSKETCH

Guogui Chen is a Ph.D. candidate at Xiamen University. His interests include coastal wetland ecology, macroecology, community ecology and biogeography.

Author contributions: Guogui Chen: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review and editing (equal). Xuan Gu: Data curation (equal); Formal analysis (equal); Investigation (equal). Yi Liu:
Data curation (equal) and Investigation (equal). Wenqing Wang: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing-original draft (equal); Writing-review and editing (equal). Mao Wang: Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Resources (equal); Writing-original draft (equal); Writing-review and editing (equal).

SUPPORTING INFORMATION
Additional supporting information may be found in the online version of the article at the publisher’s website.

How to cite this article: Chen, G., Gu, X., Liu, Y., Wang, W., & Wang, M. (2022). Different functional feeding groups of mangrove soil molluscs invoke unique co-occurrence patterns in response to a climate extreme. Diversity and Distributions, 28, 331–345. https://doi.org/10.1111/ddi.13467