Extreme cold events reduce the stability of mangrove soil mollusc community biomass in the context of climate impact

Guogui Chen, Xuan Gu, Yi Liu, Xiaofang Shi, Wenqing Wang* and Mao Wang* ©

Key Laboratory of the Coastal and Wetland Ecosystems (Xiamen University) Ministry of Education, College of the Environment and Ecology, Xiamen University, Xiamen CN-361102, Fujian, People’s Republic of China

* Authors to whom any correspondence should be addressed.
E-mail: mangroves@xmu.edu.cn and wangmao@xmu.edu

Keywords: extreme cold event, ecological stability, competitive interaction, spatiotemporal dynamic, benthic fauna, mangrove soil mollusc

Abstract

The frequency and intensity of climate extreme events are expected to increase with global warming in the future. Climate extreme events, such as an extreme cold event (ECE) will continue to influence the stability of soil fauna community biomass, since climate changes often cause a shift in community compositions and structures (e.g. biomass). Few studies, however, have addressed the effects of climate extreme events on the stability of soil fauna community biomass. A field investigation was conducted from 2007 to 2010 to assess the influence of an ECE on the biomass stability of the soil mollusc community across four mangrove wetlands (~450 km) in South China. Distance-decay and time-decay were used to test the spatiotemporal dynamics of the community biomass. Network analysis and null model were performed to detect the importance of competitive interactions in shaping the stability of the soil mollusc community biomass. The ECE reduced the biomass of the soil mollusc community but increased the complexity of the spatiotemporal patterns of the community biomass. The ECE increased divergent temporal succession and spatial segregation in the soil mollusc community biomass, reflecting the spatiotemporal dynamics of the soil mollusc community biomass influenced by the ECE. Importantly, the ECE decreased the biomass stability of the soil mollusc community by an average of 34.17%. An increase in the modularity of an interactive network (by 75%) and a rise in the intensity of species competition were found after the ECE, reflecting that the ECE enhanced the competitive interactions of the soil mollusc community. The changes in the biomass stability of the soil mollusc community potentially impact their ability to provide ecosystem functions and services such as food production and carbon sequestration for humans. In general, these findings provide valuable ecological insights concerning the effects of climate extremes on the stability properties of ecological soil communities, thereby providing potential applications for soil management and predicting climate changes.

1. Introduction

The stability of soil community biomass over time or across space is a fundamental soil ecosystem property (McCann 2000, Ives and Carpenter 2007). Uncovering the driving forces of soil ecological stability in a changing world is a central goal of soil ecology since stable ecosystems are important for providing sustainable ecological services to humanity (Oliver et al 2015, Ma et al 2017). It is estimated that the frequency and intensity of extreme temperature events such as extreme cold event (ECE) will continue to rise in response to greenhouse warming (Counou and Rahmstorf 2012, Cai et al 2014, Dosio et al 2018, Maxwell et al 2019, Qie et al 2019). The threats posed by ECEs to the stability of the soil community will persist (Coyle et al 2017, Chen et al 2021). Therefore, uncovering the mechanisms of the stability of
the soil community in response to extreme climate change is important for restoring soil biodiversity and functioning.

Soil fauna on land and in wetlands are acknowledged as key components of soil health and ecology (Cannicci et al. 2008, Lee 2008, Zeppilli et al. 2015). Mangroves are distributed in tropical and subtropical intertidal zones (Lee et al. 2014, Duke 2017, Friess et al. 2019). Currently, mangrove ecosystems have attracted the attention of global scientists and managers since their potential to mitigate climate change while achieving co-benefits, such as coastal protection, high biodiversity and food production (Lee 2008, Lovelock 2008, Friess et al. 2019, Lovelock and Duarte 2019, Macreadie et al. 2019). Mangrove soil molluscs, as macroinvertebrates in the mangrove ecosystems, which are generally found on the surfaces and upper layers of mangrove soil, humus and sediments (Cannicci et al. 2008, Lee 2008, Chen et al. 2021). The soil molluscs provide important ecosystem functions and services such as litter decomposition, food production, carbon stabilization, water purification, and nutrient cycling (Cannicci et al. 2008, Lee 2008, Penha-Lopes et al. 2009, Carrillo et al. 2011, de Vries et al. 2013). Many studies have confirmed that climate-driven environmental stresses, as well as ECEs and other temperature-related extreme climate events, can change the community compositions and structures of soil fauna communities in mangrove wetlands (Asbridge et al. 2015, Zeppilli et al. 2015, Bernardino et al. 2018, Harada et al. 2020, Chen et al. 2021). For instance, ECEs can decrease the community species richness, abundance and biomass of mangrove mollusc community (Liu et al. 2016, Chen et al. 2021). ECEs also influence the assembly process of mangrove molluscs (Chen et al. 2020b). Flooding and drought generally result in decreases in mangrove macrobenthos biomass (Grilo et al. 2011, de Oliveira Gomes and Bernardino 2020). Among these studies, negative ecological responses are the most commonly reported (Gerisch et al. 2012, Altwegg et al. 2017, Coyle et al. 2017, Maxwell et al. 2019).

Changes in community compositions and structures (e.g., dominant species, species richness, biomass and functional traits) are the main driving forces contributing to community and ecosystem stability (Hector et al. 2010, Loreau and de Mazancourt 2013). Therefore, the ECEs are expected to reduce the biomass stability of soil mollusc communities by altering soil biodiversity (Loreau and de Mazancourt 2013, Ma et al. 2017). Still, knowledge of whether and how the ECEs are impacting the stability of the soil mollusc community in mangrove ecosystems is limited (Hoegh-Guldberg and Bruno 2010, Cavanaugh et al. 2014). This is in part because long-term observations of changes in mangrove ecosystems are rare (Cavanaugh et al. 2014, Maxwell et al. 2019, Harada et al. 2020, Chen et al. 2020b).

Theoretical analysis suggests that an increasing role for biotic interactions in maintaining community temporal stability under environmental fluctuations has been proposed (Loreau and de Mazancourt 2013, Douda et al. 2018). Although reduced competition has been verified as one of the three main mechanisms that mediate ecosystem stability (Loreau and de Mazancourt 2013), biotic competition and the physical environment currently have been confirmed to jointly determine spatiotemporal features of communities (Wardle 2006, Loreau and de Mazancourt 2013, Gao et al. 2014, Bulleri et al. 2016, Chen et al. 2020b). For example, competitive interactions can regulate the influence of drought on community stability (Douda et al. 2018). Additionally, climate warming also alters the stability and species interactions of marine ecosystems (Griffith et al. 2018). Reduced competition enhanced community stability in a permanently dry environment (Douda et al. 2018). Although some advances have been made, the importance in relation to community stability of changes in competitive interactions has not been as well demonstrated especially in the context of extreme temperature changes. Competitive interactions may potentially affect the soil mollusc community in mangrove wetlands (Wardle 2006, Cannicci et al. 2018). Such interactions are also influenced by climate extremes (Wardle 2006, Cannicci et al. 2018, Chen et al. 2020b). Therefore, the effect of ECEs on the stability of the soil mollusc communities is expected to be mediated by changes in biotic competition.

This study focused on a mangrove soil mollusc community to examine whether and how climate extremes influence the spatiotemporal stability of community biomass at a biogeographical scale (~4.5 × 10^5 m²; Hortal et al. 2010) that suffered an ECE in January and February of 2008. During the 2008 ECE, the number of continuous days with low and/or freezing temperatures was more than three weeks, which broke the record that was recorded in the winter of 1954/1955 in the lower reaches of the Yangtze River Basin (Liu et al. 2016). Therefore, the 2008 ECE is a typical disturbance and opportunity to study the influence of extreme climate on the stability of the community. Three hypotheses were proposed for this study. This study first assumed that the ECE would reduce the biomass of the soil mollusc community and its stability. The study then assumed that the reduction of biomass stability would be mediated by changes in biotic competition. These changes were expected to reduce the ecosystem functions (e.g., carbon storage and food production) of the soil mollusc community. To address these questions, this study compared the spatiotemporal stability of community biomass and mechanisms of the soil mollusc meta-community before the ECE (April 2007–December 2007) and after (April 2008–January 2010).
2. Materials and methods

2.1. Study sites

The study region included four mangrove ecosystems in Qinglan Bay (QL), Dongzhai Bay (DZ), Yingluo Bay (YL), and Beilun Estuary (BL), China (19.532°–21.598° N, 107.996°–110.849° E; figure S1 (available online at stacks.iop.org/ERL/16/094050/mmedia)). This region contains the greatest mollusc richness of all the mangrove wetlands in China (Chen et al. 2020a). This region has a total of 23 mangrove tree species among 14 different genera, with several having different root types; including Sonneratia spp. (six species), Bruguiera spp. (three), Acanthus spp. (two), Acrostichum spp. (two), Xylocarpus (one), Nypa (one), Lumnitzera (one), Ceriops (one), Rhizophora (one), Excoecaria (one), Aegiceras (one), Avicennia (one), Kandelia (one), and Laguncularia (one). The region is located in the tropical and northern subtropical zone and has a maritime climate. The annual average precipitation is 1500 mm, and the annual average temperature is 23 °C. Under normal circumstances, daily mean temperatures and minima fall below 10 °C for less than one week per year. During the 2008 cold event, daily minima fell below 10 °C for more than 21 days (figure S2). The mean temperature in 2008 was lower than in 2007 (16.4 °C) and in 2009 (17.1 °C) (figure S2). During the 2008 cold event, about 30% of the mangrove trees in the study region died, and more than 50% of the foliage displayed leaf scorch (figure S1(b)).

2.2. Soil mollusc collection

Sampling was conducted during low tide from April 2007 to early January 2010. Samples were collected in spring, summer, autumn, and winter, and covered all tidal zones (the hypo-, meso-, and hyper-tidal zones). Spring samples were taken between March and April; summer samples were taken between June and early August; autumn samples were taken between September and early November, and winter samples were taken between December and early January of the following year. Four seasonal samplings were conducted before the ECE, and eight seasonal samplings were conducted after the ECE. Additionally, the samples of each year were kept separate for each season. During each seasonal sampling, soil molluscs were sampled in each mangrove wetland along three to five parallel transects 100 m apart along an intertidal gradient. In total, 15–25 transects were sampled each season. Each transect was 100–200 m long from landward to seaward and was divided into three tidal zones (the hypo-, meso-, and hyper-tidal zones). Five 25 cm × 25 cm duplicate sediment samples were collected at a depth of 30 cm in each tidal zone (figure S3). Sediment samples were wet sieved in the field through a 1 mm mesh sieve, after which mollusc samples were collected and fixed in 4% formaldehyde. Within three days of fixation, mollusc specimens were washed with water and transferred to 75% ethanol. Trapped molluscs were identified to the species or sometimes genus level (table S1; Xu and Zhang 2008, Huang and Lin 2012) and weighed to determine the fresh weight of body mass (biomass). To test the effects of the ECE on carbon regulation of the mangrove ecosystem, the dry shell weights of the molluscs were calculated based on the biomass and conversion factors from the literature for each species (see supplementary information text 1).

2.3. Statistical analyses

2.3.1. ECE impacts the spatiotemporal dynamics of mollusc community biomass

To characterize the effects of the ECE on seasonal dynamics of the soil mollusc community biomass, we compared the community biomass of each season before and after the ECE. Furthermore, we employed a generalized additive model (GAM) to examine whether the ECE indeed changed the temporal dynamics of the mollusc community biomass. GAM is a non-parametric regression technique not restricted by linear or nonlinear relationships that is flexible regarding the statistical distribution of the data (Murase et al. 2009). We conducted GAM regression using the mag package in R v4.0 to model temporal dynamics in the community biomass of mangrove soil molluscs (Trenkel et al. 2005). More information of GAM presented in supplementary information text 2a.

2.3.2. ECE impacts the temporal succession of community biomass

Beta diversity can assess how community biomass changes along a temporal or environmental gradient (Kuznetsova and Saraeva 2018). Using the community biomass data, the Bray–Curtis distances were calculated using the SpadeR package in R v4.0 (R-Core-Team 2019). To evaluate whether the ECE caused a divergent or convergent succession of the soil mollusc biomass, we employed generalized dissimilarity modelling (GDM) in R v4.0 using the ‘GDM’ package (Ferrier et al. 2007). More information of GDM presented in supplementary information text 2b.

2.3.3. ECE impacts the spatiotemporal dynamics of community biomass stability

The constancy of species biomass was used to characterize the stability of the community. Constancy measures the temporal stability of biomass of a species and is defined as

\[ C = \frac{\mu}{\sigma} \]

where \( \mu \) is the mean of the biomass over time and \( \sigma \) is the standard deviation (McCann 2000, Ma et al. 2017). Finally, the average of all the constancy values of species within a community was reported as
the constancy of the community before or after the climate extreme. Community biomass of each season and each sampling site were compared before and after the ECE to determine whether and how the ECE impacted the spatiotemporal dynamics of community biomass. Mann–Whitney U tests were used to analyse the differences in link constancy before and after the ECE.

2.3.4. Biotic interactions mediate the effect of the ECE on biomass stability of the soil mollusc community

To understand whether and how the ECE affected the stability of community biomass by changing species interactions, interactive network and Monte Carlo null models were used to characterize the species interactions of the soil mollusc community before (April 2007–December 2007) and after (April 2008–January 2010) the ECE. Based on biomass, Spearman relationships were used to calculate pairwise correlations between molluscan species (Mo et al 2021). Network visualization was generated with Gephi version 0.9.1. Each node was one molluscan species, and each edge represented the correlation between two species. To describe the changes in interactive networks, modularity values of both before and after networks were calculated and compared (Mo et al 2021).

A Monte Carlo null model was run on the software EcoSim 7.72 (Gotelli and Entsminger 2001) and used to decide whether the soil mollusc community biomass displayed non-random (non-random aggregated or segregated) or random occurrences (Gotelli and McCabe 2002). The C-score (Checkerboard score) and niche overlap indices were used as a metric of the co-occurrence of mollusc biomass. We calculated the niche overlap of mangrove molluscs using the Pianka index. The Pianka index (Gotelli and Entsminger 2001) represents niche overlap and is calculated as

\[ O_{ab} = O_{ab} = \frac{\sum_{i=1}^{n} P_{ai}P_{bi}}{\sqrt{\sum_{i=1}^{n}(P_{ai}^2 \times P_{bi}^2)}}, \]

where \( O_{ab} \) is Pianka’s index of niche overlap of species \( a \) with species \( b \); \( O_{ab} \) is the reciprocal overlap of \( b \) over \( a \); \( P_{ai} \) is the proportion of the \( i \)th resource used by species \( a \); \( P_{bi} \) is the proportion of the \( i \)th resource used by species \( b \), and \( n \) is the total number of resources. The observed C-score was calculated and compared with C-scores calculated for 5000 randomly assembled null models. More information presented in supplementary information text 2c.

A matrix with fixed rows and columns was used to calculate the C-scores, and an algorithm of RA3 was used to test the niche overlap (Gotelli and Entsminger 2001). To test whether non-randomness in the soil mollusc community varied among ECEs, we calculated the standardized effect size (SES) for the biomass matrix using the following equation (Gotelli and McCabe 2002):

\[ \text{SES} = (I_{\text{obs}} - I_{\text{sim}}) / \varepsilon_{\text{sim}}, \]

where \( I_{\text{obs}} \) indicates the observed value; \( I_{\text{sim}} \) is the mean simulated value, and \( \varepsilon_{\text{sim}} \) is the standard deviation of simulated indices. The null hypothesis is that the average SES = 0 and that 95% of \( I_{\text{obs}} \) will fall between 1.95 and -1.95 (Gotelli and McCabe 2002). The magnitude of the SES was interpreted as the strength of the signal of competitive interactions on the community (supplementary information text 2d).

To detect the relationship between species interactions and community biomass stability, a test based on Spearman’s correlation and simple linear regression was used to assess the relationship between SES and community biomass stability (Ma et al 2017). To detect the relationship between biodiversity (species richness and abundance) and community biomass stability, a test based on Spearman’s correlation and simple linear regression was used to detect the link between biodiversity and community biomass stability (Ma et al 2017). ANOVA (Analysis of Variance) was used to test whether the slopes of the linear regressions differed significantly before and after the ECE.

3. Results

3.1. ECE influenced the spatiotemporal dynamics of soil mollusc community biomass

The seasonal and spatial dynamics of community biomass reduced significantly after the ECE (one-way ANOVA, \( p < 0.05 \); figure 1; table S3). The GAMs showed that the effective degrees of freedom (edf) of the spatiotemporal patterns of soil mollusc community biomass increased after the ECE (figure S4; table S4), reflecting the spatiotemporal patterns of soil mollusc community biomass changed greatly after the ECE. These results indicated that the ECE not only resulted in a reduction of soil mollusc community biomass but also caused clear changes in the spatial and temporal patterns of the community biomass.

The GDM models showed that the maximum dissimilarity of the soil mollusc community biomass increased from less than 0.2 before the ECE to more than 0.8 after the ECE (figure 2). In addition, the maximum distance of the soil mollusc community biomass increased from 0.8 before the ECE to more than 0.95 after the ECE (figure 2). The shape of the temporal and spatial I-spline for the soil mollusc biomass became steeper after the ECE (figure 2), indicating that the segregated rate of community biomass with increasing spatiotemporal distance after the ECE were higher than those before the ECE. These results revealed that the ECE resulted in increases of
3.2. ECE influenced the stability of soil mollusc community biomass

The stability of the soil mollusc community biomass was reduced significantly after the ECE (figure 3(a)). Specifically, the stability of the community during spring was reduced by 35.67%–42.81% (figure 3(a)). The ECE significantly reduced the stability of mollusc biomass during the summer months by an average of 41.82% (figure 3(a)). Likewise, the ECE significantly decreased biomass stability during the winter months by an average of 49.50%, whereas the stability of the autumn community had a slight increase by an average of 13.18% after the ECE (figure 3(a)). Even so, the
stability of the mollusc biomass after the ECE had a clear decrease, by an average of 34.17% compared to before the ECE (figure 3(a)). The stability of the community biomasses at Dongzhai Bay (DZ), Qinglan Bay (QL) and Beilun Estuary (BL) were reduced significantly by averages of 36.60%, 14.33%, and 51.89%, respectively, after the ECE (figure 3(b)), whereas the biomass stability of the mollusc community at Yingluo Bay (YL) increased significantly by an average of 78.33% after the ECE (figure 3(b)). The stability of the mollusc community at the regional scale was reduced by an average of 22.40% after the ECE (figure 3(b)).

3.3. ECE changed biotic interactions of soil molluscs
Numbers of both nodes and edges in the entire network increased with the occurrence of the ECE (figure 4). The number of modules in the network increased by 75% after the ECE (figure 4). These findings revealed that the ECE had a strong influence on the interactions of molluscs.

After the ECE, the observed C-scores for all eight seasonal communities from 2008 to 2009 were clearly greater than those of the null model; the observed niche overlap values of these communities were significantly less than those of the null model (table S5).
Figure 5. ECE effects on the standardized effect size (SES) of seasonal soil mollusc communities. (a) Effects size for the C-score of each seasonal soil mollusc trait during the study. (b) Effects size for the niche overlap of each seasonal soil mollusc trait during the study. (c) SESs for annual community from 2007 to 2009. (d) SESs for communities before and after the ECE. The red dashed line indicates a standardized effect size of 1.95 and −1.95, which is the approximate 5% significance level \((p < 0.05)\). A mean SES >1.95 for the C-score but SES < −1.95 for the niche overlap indicate that traits are non-randomly segregated by competitive interactions. When the C-score’s SES < −1.95 but niche overlap’s SES >1.95, it means that traits are non-randomly aggregated by environmental filtering.

Before the ECE, only the SES for the summer community was greater than 1.95 but smaller than 2.5; only the SESs for spring and winter communities were smaller than −1.95 but greater than −3 (figures 5(a) and (b)). After the ECE, the SESs for C-scores of the eight seasonal communities were greater than 1.95, and the maximum SES value exceeded 6; the SESs for niche overlap of these communities were smaller than −1.95, and the minimum value was close to −7 (figures 5(a) and (b)). Both the mean SESs of C-score and niche overlap for mollusc communities in 2007 were between −2 and 2 (figure 5(c)). The mean values of SES of C-scores for soil mollusc communities in 2008 and 2009 were greater than 4, and the average SESs for niche overlap in 2008 and 2009 were close to 4 (figure 5(c)). Additionally, the mean SES of C-scores was smaller than 2, and the average SES of niche overlap was greater than −2 before the ECE (figure 5(d)). After the ECE, the mean SES of C-scores was close to 4, and the average SES of niche overlap was close to −4 (figure 5(d)). More importantly, linear regression revealed that community biomass stability was significantly negatively correlated with SES (Spearman’s \(r = −0.61\), \(p = 0.03\); figure 6), indicating that species interactions (e.g., competitive interactions) may have had a negative influence on the stability of community biomass. These results indicate that competitive interactions mediated the community biomass stability of mangrove soil molluscs in response to the ECE.

4. Discussion

4.1. Climate extremes reduced soil ecosystem stability and services

The community biomass of mangrove mollusc generally increases from a normal winter to spring in China (figures S11 and S12) (Yu et al 1997, Chen et al 2007, Zou et al 2008). However, the ECE not only reduced the mean biomass of the mangrove soil mollusc community but also decreased its stability in this study (figures 1 and 3), indicating that the ECE had a negative effect on the stability of the mangrove soil mollusc community. This study thus
Figure 6. Relationships between standardized effect size (SES) and community biomass stability.

represents a rare exploration of an ECE impact on biomass stability of a soil fauna community and reinforces the view that negative ecological responses are the most common phenomena in response to extreme climate events (Maxwell et al. 2019). On the one hand, the decrease in biomass stability of mangrove soil mollusc community after the ECE undoubtedly suggests that the stability of the mangrove soil ecosystem is mediated by the disturbance of climate extremes. Climate changes indeed mediate the stability of community biomass (Ma et al. 2017, de Oliveira Gomes and Bernardino 2020). The findings in this study reinforce these ideas. Cold temperature can influence biotic biomass by directly constraining the biological processes (e.g. growth, respiration, decomposition and nutrient cycling) of a community (Dolbeth et al. 2007, Galbraith et al. 2009, Rudgers et al. 2014, Liu et al. 2016, Ma et al. 2017). Additionally, low temperature affects community biomass by indirectly altering community composition (e.g. the stability of dominant species, the proportion of resistant species, and the degree of species asynchrony) (Ma et al. 2017). Similarly, this study found a positive link between community composition (species richness and abundance) and biomass stability; the intensity of the positive link was changed after the ECE (figure S8), reflecting the strong climatic dependency of the biodiversity–stability relationship in the mangrove soil ecosystem. Abnormal low temperature may also change community biomass by altering energetic structures and function since cold spell can reduce the availability of suitable resources for mangrove soil molluscs (e.g. mortality and leaf scorch in mangrove plants and algae mortality) (Harada et al. 2020, Chen et al. 2020b). Temperature-related disturbances such as ECEs can change overall sediment conditions by causing mangrove dieback and changing organic matter inputs and degradation of sediment organic matter (Atwood et al. 2017, Sippo et al. 2018, Harada et al. 2020) and consequently influence soil faunal assemblages (Bernardino et al. 2018, Chen et al. 2021).

On the other hand, the reduction of community biomass will reduce the soil ecosystem functioning and services that are provided by soil molluscs. Mangrove soil molluscs can provide many ecosystems services for humanity, including food production and carbon regulation (Cannicci et al. 2008, Lee 2008, Feller et al. 2010, Barnes 2017). The ECE resulted in a decrease of marine food yield, and such an event may contribute to human malnutrition in some food-insecure regions (Feller et al. 2010, Servino et al. 2018, Xu et al. 2020). Many previous studies have confirmed that extreme environmental changes will reduce the biomass of communities and then
weaken the productivity of ecosystems (Bai et al 2004, Servino et al 2018, Maxwell et al 2019, Xu et al 2020). Additionally, mangrove soil molluscs assist in carbon regulation not only by converting organic matter (i.e. dead branches and fallen leaves) into coastal soils but also by burying carbon within their shells (i.e. shell carbon) as long-term carbon storage (Barnes 2017, van der Schatte Olivier et al 2020). The shell carbon of soil molluscs in the polar sediment regions and aquaculture ponds have been studied in recent years, along with the consistency of their biomass (Barnes 2017, van der Schatte Olivier et al 2020). Therefore, the decrease in community biomass after the ECE is expected to reduce the carbon regulation of the mangrove soil ecosystem. Like the observation in this study, the ECE reduced the content of shell carbon of soil molluscs and changed its spatiotemporal dynamics (figures S6 and S7). Therefore, extreme climate events threaten the loss of ecosystem functions and services by impacting the stability of soil fauna communities.

4.2. Species competition mediates the response of soil mollusc community stability to climate extremes

Competitive interactions were verified to shape the observed dispersion pattern of soil mollusc community based on biomass data (figures 4 and 5). Generally, community dispersion could be considered as a proxy for the effect of increased competitive interactions and dispersal limitation on community (Gao et al 2014, Violle et al 2014, Ulrich et al 2017, Montano-Centellas et al 2020). However, the signal of dispersal limitation that influences the community biomass of mangrove soil mollusc was not found in this study (see supplementary information text S3; figure S9). In addition, methods based on diversity (e.g. species richness) seem to have difficulty detecting biotic interactions within a community, while methods based on functional traits (e.g. biomass) are able to detect competitive interactions (Liu et al 2013, Ulrich et al 2017, Blanchet et al 2020). Therefore, competitive interaction should be the driving forces that regulate the mangrove soil fauna community (Cannicci et al 2018).

Additionally, the competitive environments of species are expected to be altered by climate change, since climate change would affect the performance and relative abundance of their current competitors and introduce novel competitors (Gilman et al 2010, Alexander et al 2015). Indeed, competitive interactions of soil molluscs increased significantly after the ECE in this study (figure 5). The results of this study were not in accordance with the stress-gradient hypothesis (Bertness and Callaway 1994, Liancourt et al 2017). A possible explanation is that soil molluscs living in the sub-surface of the soil in mangrove ecosystems face regular abiotic disturbances (e.g. salinity and anoxic conditions) by the periodic sea water inundation (Thakur et al 2014), reflecting mangrove environmental conditions that may be inconsistent with those of the stress-gradient hypothesis (Bertness and Callaway 1994).

Environmental stresses such as low temperature can directly result in species extinctions and possibly change organismal and population parameters, and this can influence other members of a community via biotic interactions (Gilman et al 2010). For example, low temperature can change the metabolic rates and the energetic requirements of a species, which would affect individual growth and further shift body sizes and influence the outcome of biotic interactions (Vasseur and McCann 2005, Gilman et al 2010). Additionally, species extinctions would cause niche vacancies that would result in the establishment of novel competitors (table S1) (Chen et al 2020b). The compensation of new species with novel and resistant traits may alter biotic controls, causing an increase in the biotic regulation of the soil mollusc community (Boucek and Rehage 2014, Alexander et al 2015). Species extinctions and compensation are expected to result in species experiencing competition from new and functionally different migrants (Alexander et al 2015). For instance, an extreme flood lessened the biotic regulation of a rodent community in arid grasslands of the southwestern United States, resulting in a change in trait dominance (Thibault and Brown 2008). Like the rodent example, another ECE also lessened the biotic interactions of a fish community in South Florida (Boucek and Rehage 2014). In addition, compared with highly dispersal-limited soil animals living in terrestrial ecosystems (Gao et al 2014), water-mediated mangrove soil molluscs will have higher dispersal ability in highly connected intertidal wetlands (Cowen and Sponaugle 2009, Alvarez-Noriega et al 2020), which may cause their degree of niche overlap (figure S10) to be very high, resulting in strong competition (MacDougall and Turkington 2006). Obviously, extreme weather will directly or indirectly influence the biotic competition of mangrove soil mollusc community.

Theoretical research suggests that competitive interaction is one of the three main mechanisms of ecosystem stability, and that increased competition would reduce ecosystem stability under most conditions (Loreau and de Mazancourt 2013). This is consistent with the clear negative link between SES and biomass stability found in this study (figure 6). This suggests that biotic competition mediated the effect of the ECE on biomass stability of soil molluscs. The reduced biotic competition will enhance community stability due to a rising mean total biomass of the subordinate species (Loreau and de Mazancourt 2013). Similarly, a five-year mesocosm experiment that demonstrated the effects of interspecific interactions on the temporal stability of a riparian community across different drought-stress scenarios showed that the role of reduced competition was enhanced in a
permanently dry environment and increased community stability (Douda et al 2018). Contrary to the second hypothesis, a decrease in biomass stability (figure 5) but an increase in the intensity of competitive interactions (figure 5) after the ECE were observed in this study. The ECE triggered increased competition in the soil mollusc community and thus reduced the stability of the community biomass. These findings reflect the huge difference in response to disturbances between aboveground and belowground communities. Increased competition could enhance the negative effects of environmental stresses such as climate extremes on community stability (Isebúl et al 2009). We emphasize that the variation in interaction intensity after extreme environmental disturbances is important in generating the changes in the stability of soil communities at a biogeographical scale.

5. Conclusion

This study provides new insight that climate extremes can have a negative effect on soil fauna community biomass and its stability. The changes in mangrove soil mollusc community biomass would further increase the risk of lost ecosystem services such as food productions and carbon sequestrations provided by mangrove soil molluscs. These findings emphasize that it is necessary to conserve the biodiversity of soil fauna in mangrove ecosystems since it is a co-benefit of protecting mangrove soil biodiversity for mitigating climate change, food security and biodiversity conservation. Mangrove ecosystems experience high levels of environmental variability, including changing climates and hydrological regimes (Friess et al 2019). Understanding the mechanisms contributing to their stability will allow scientists and managers to better anticipate how, and to what extent, they will change under various environmental and climate change scenarios. The current study identified enhanced competitive interactions as the main reason why climate extremes reduced the stability of soil fauna community biomass. This finding suggests that a study that excludes consideration of the biotic interactions may not offer a realistic prediction of the effects of climate change on ecosystem stability and functioning. These findings may be important in systems such as the southern China mangrove soil or other systems where the soil has already been influenced by anthropogenic-driven abiotic regimes (e.g. environmental changes). Since the frequency and intensity of such extreme temperature events are expected to increase in the coming decades, policymakers should incorporate these ideas in the formulation of soil management strategies.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

Acknowledgments

We thank the editors and three reviewers for their suggestions and comments. The authors acknowledge the financial support from the Programs of Science and Technology on Basic Resources Survey for the Ministry of Science and Technology of China (No. 2017FY100701), the National Natural Science Foundation of China (Nos. 31670490 and 42076161) and Supported by the Fieldwork Funds for graduate students of Xiamen University (2020FG022).

ORCID iD

Mao Wang https://orcid.org/0000-0001-6550-2405

References

Alexander J M, Diaz J M and Levine J M 2015 Novel competitors shape species’ responses to climate change Nature 525 515–8
Altweeg R, Visser V, Bailey I D and Erni B 2017 Learning from single extreme events Phil. Trans. R. Soc. B 372 20160141
Alvarez-Noriega M, Burgues S C, Byers J E, Pringle J M, Wares J P and Marshall D J 2020 Global biogeography of marine dispersal potential Nat. Ecol. Evol. 4 1196–203
Asbridge E, Lucas R, Accad A and Dowling R 2015 Mangrove response to environmental changes predicted under varying climates: case studies from Australia Curr. For. Rep. 1 178–94
Atwood T B et al 2017 Global patterns in mangrove soil carbon stocks and losses Nat. Clim. Change 7 523
Bai Y F, Han X G, Wu J G, Chen Z and Li L 2004 Ecosystem stability and compensatory effects in the Inner Mongolia grassland Nature 431 181–4
Barnes D K A 2017 Polar zoobenthos blue carbon storage increases with sea ice losses, because across-shelf growth gains from longer algal blooms outweigh ice scour mortality in the shallows Glob. Change Biol. 23 5083–91
Bernardino A F, Gomes L E D O, Hadlíc H L, Andrades R and Correa L B 2018 Mangrove clearing impacts on macrofaunal assemblages and benthic food webs in a tropical estuary Mar. Poll. Bull. 126 228–35
Bertness M D and Callaway R 1994 Positive interactions in communities Trends Ecol. Evol. 9 191–3
Blanchet F G, Cazelles K and Gravel D 2020 Co-occurrence is not evidence of ecological interactions Ecol. Lett. 23 1050–63
Boucek R E and Rehage J S 2014 Climate extremes drive changes in functional community structure Glob. Change Biol. 20 1821–31
Bulleri F, Bruno J F, Silliman B R and Stachowicz J J 2016 Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning Funct. Ecol. 30 70–78
Cai W et al 2014 Increasing frequency of extreme El Nino events due to greenhouse warming Nat. Clim. Change 4 111–6
Cannicci S et al 2018 Interference competition as a key determinant for spatial distribution of mangrove crabs BioMed Cent. Ecol. 18 1–12
Cannicci S, Burrows D, Fratini S, Smith T J, Offenberg J and Dahdouh-Guebas F 2008 Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review Aquatic Bot. 89 186–200
Carrillo Y, Ball B A, Bradford M A, Jordan C F and Molina M 2011 Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil Soil Biol. Biochem. 43 1449–9
Cavanaugh Y, Kellner J R, Forde A J, Gruner D S, Parker J D, Rodriguez W and Feller I C 2014 Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events Proc. Natl. Acad. Sci. 111 723–7
Chen G-C, Ye Y and Lu C-Y 2007 Changes of macro-benthic faunal community with stand age of rehabilitated Kandelia candel mangrove in Jiujiangjiang Estuary, China Ecol. Eng. 31 215–24

Chen G et al 2020a Uncovering the relative influences of space and environment in shaping the biogeographic patterns of mangrove mollusc diversity Int. Council Explor. Sea J. Mar. Sci. 77 30–39

Chen G, Gu X, Liu Y, Wang W and Wang M 2021 Responses of a soil mollusk community to an extreme cold event Appl. Soil Ecol. 167 104067

Chen G, Wang W, Zhang Y, Liu Y, Gu X, Shi X and Wang M 2020b Abundant and rare species may invoke different assembly processes in response to climate extremes: implications for biodiversity conservation Ecol. Indic. 117 107616

Counoud D and Rahmstorf S 2012 A decade of weather extremes Nat. Clim. Change 2 491–6

Cowen R K and Sponaugle S 2009 Larval dispersal and marine population connectivity Ann. Rev. Mar. Sci. 1 443–66

Coyle D R et al 2017 Soil fauna responses to natural disturbances, invasive species, and global climate change: current state of the science and a call to action Soil Biol. Biochem. 110 116–33

de Oliveira Gomes L E and Bernardino A F 2020 Drought effects on tropical estuarine benthic assemblages in Eastern Brazil Sci. Total Environ. 703 134907

de Vries F T et al 2013 Soil food web properties explain ecosystem services across European land use systems Proc. Natl Acad. Sci. 110 14296–301

Dolbeth M, Cardoso P G, Ferreira S M, Verdelhos T, Raffaelli D and Pardal M A 2007 Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period Mar. Pollut. Bull. 54 576–85

Dosio A, Mentaschi L, Fischer E M and Wyser K 2018 Extreme heat waves under 1.5 °C and 2 °C global warming Environ. Res. Lett. 13 054006

Douda J, Doudova J, Hulik J, Hlavodova A and Boublik K 2018 Reduced competition enhances community temporal stability under conditions of increasing environmental stress Ecology 99 2207–16

Duke N C 2017 Mangrove floristics and biogeography revisited: further deductions from biodiversity hot spots, ancestral discontinuities, and common evolutionary processes Mangrove Ecosystems: A Global Biogeographic Perspective: Structure, Function, and Services ed V H Rivera-Monroy, S Y Lee, E Kristensen and R R Twilley (Cham: Springer) pp 17–33

Feller I C, Lovelock C E, Berger U, Mcke K L, Joyce S B and Ball M C 2010 Biocomplexity in mangrove ecosystems Ann. Bot. 106 395–417

Ferrier S, Manion G, Elith J and Richardson K 2007 Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment Divers. Distr. 13 252–64

Friess D A, Rogers K, Lovelock C E, Krauss K W, Hamilton S E, Lee S Y, Lucas R, Primavera J, Rajkaran A and Shi S 2019 The state of the world’s mangrove forests: past, present, and future Annu. Rev. Environ. Resour. 44 89–115

Galbraith H S and Vaughan C C 2009 Temperature and food interact to influence gastropod growth in freshwater mussels Hydrobiologia 636 35–47

Gao M, He B, Zhang X, Liu D and Wu D 2014 Relative roles of spatial factors, environmental filtering and biotic interactions in fine-scale structuring of a soil mite community Soil Biol. Biochem. 79 68–77

Gerisch M, Agostinelli V, Henle K and Dixo F 2012 More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity Oikos 121 508–15

Gilmans S E, Urban M C, Twesbury J, Gilchrist G W and Holt R D 2010 A framework for community interactions under climate change Trends Ecol. Evol. 25 325–31

Gotelli N J and Entsminger G L 2001 EcoSim: null models software for ecology, Version 7.0 Acquired Intelligence Inc. & Keesey-Bear

Gotelli N J and McCabe D J 2002 Species co-occurrence: a meta-analysis of J. M. Diamond’s assembly rules model Ecology 83 2091–6

Griffith G F, Strutton P G and Semmens J M 2018 Climate change alters stability and species potential interactions in a large marine ecosystem Glob. Change Biol. 24 490–100

Grilo T F, Cardoso P G, Dolbeth M, Bordalo M D and Pardal M A 2011 Effects of extreme climate events on the macrobenthic communities’ structure and functioning of a temperate estuary Mar. Pollut. Bull. 62 303–11

Harada Y, Fry B, Lee S Y, Maher D T, Sippo J Z and Connolly R M 2020 Stable isotopes indicate ecosystem restructuring following climate-driven mangrove dieback Limno. Oceanogr. 65 1251–63

Hector A et al 2010 General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding Ecology 91 2213–20

Hoehg-Guldberg O and Bruno J F 2010 The impact of climate change on the world’s marine ecosystems Science 328 1523

Hortal J, Roura-Pascual N, Sanders N J and Rahbek C 2010 Understanding (insect) species distributions across spatial scales Ecol. Evol. 3 51–53

Huang Z and Lin M 2012 An Illustrated Guide to Species in China’s Seas (Beijing: Ocean Press) (In Chinese)

Isbell F I, Polley H W and Wilsey B J 2009 Biodiversity, productivity and the temporal stability of productivity: patterns and processes Ecol. Lett. 12 443–51

Ives A R and Carpenter S R 2007 Stability and diversity of ecosystems Science 317 58–62

Kuznetsova N A and Saravka A K 2018 Beta-diversity partitioning approach in soil zoology: a case of Collombola in pine forests Geoderma 332 142–52

Lee S Y 2008 Mangrove macrobenthos: assemblages, services, and linkages J. Sea Res. 59 16–29

Lee S Y et al 2014 Ecological role and services of tropical mangrove ecosystems: a reassessment Glob. Ecol. Biogeogr. 23 726–43

Liancourt P, le Bagousse-Pinguet Y, Rixen C and Dolezal J 2017 Beyond biogeography: a forward looking approach in soil zoology: a case of Collombola in pine forests Geoderma 332 142–52

Liu J, Soininen J, Han B-P and Declerck S A J 2013 Effects of connectivity, dispersal directionality and functional traits on the metacommunity structure of river benthic diatoms J. Biogeogr. 40 2234–48

Liu Y, Wang M, Wang W Q, Fu H and Lu C 2016 Chilling damage to mangrove mollusk species by the 2008 cold event in Southern China Ecosphere 7 e01312

Loreau M and de Mazancourt C 2013 Biodiversity and ecosystem stability: a synthesis of underlying mechanisms Ecol. Lett. 16 106–15

Lovelock C E 2008 Soil respiration and belowground carbon allocation in mangrove forests Ecosystems 11 342–54

Lovelock C E 2017 Dimensions of blue carbon and emerging perspectives Bioll. Lett. 15 521

Ma Z, Liu H, Mi Z, Zhang Z, Wang Y, Xu W, Jiang L and He J-S 2017 Climate warming reduces the temporal stability of plant community biomass production Nat. Commun. 8 15378

MacDougall A S and Turkington R 2006 Dispersal, competition, and shifting patterns of diversity in a degraded oak savanna Ecology 87 1831–18

Macreadie P I et al 2019 The future of blue carbon science Nat. Commun. 10 3998

Maxwell S L, Butt N, Maron M, Mc Alpine C A, Chapman S, Ullmann A, Segan D B and Watson J E M 2019 Conservation implications of ecological responses to extreme weather and climate events Divers. Distr. 25 613–25
McCann K S 2000 The diversity–stability debate Nature 405 228–33
Mo Y, Zhang W, Wilkinson D M, Yu Z, Xiao P and Yang J 2021 Biogeography and co-occurrence patterns of bacterial generalists and specialists in three subtropical marine bays Limnol. Oceanogr. 66 793–806
Montano- Centellas F A, McCain C and Loiselle B A 2020 Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients Glob. Ecol. Biogeogr. 29 232–45
Murase H, Nagashima H, Yonezaki S, Matsukura R and Kitakado T 2009 Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill: a case study in Sendai Bay, Japan ICES J. Mar. Sci. 66 1417–24
Oliver T H, Isaac N J B, August T A, Woodcock B A, Roy D B and Bullock J M 2015 Declining resilience of ecosystem functions under biodiversity loss Nat. Commun. 6 10122
Penha-Lopes G, Bartolini F, Limbu S, Cannicci S, Kristensen E and Paula J 2009 Are fiddler crabs potentially useful ecosystem engineers in mangrove wastewater wetlands? Mar. Pollut. Bull. 58 1694–703
Qie L, Telford E M, Massam M R, Tangki H, Níluis R, Hector A and Ewers R M 2019 Drought cuts back regeneration in logged tropical forests Environ. Res. Lett. 14 045012
R-Core Team 2019 R: A Language and Environment for Statistical Computing (Vienna: Foundation for Statistical Computing)
Rudgers J A, Kivlin S N, Whitney K D, Price M V, Waser N M and Harte J 2014 Responses of high-altitude graminoids and soil fungi to 20 years of experimental warming Ecology 95 1918–28
Servino R N, Gomes I, E D O and Bernardino A F 2018 Extreme weather impacts on tropical mangrove forests in the eastern Brazil marine ecoregion Sci. Total Environ. 628–629 233–40
Sippo J Z, Lovelock C E, Santos I R, Sanders C J and Maher D T 2018 Mangrove mortality in a changing climate: an overview Estuar. Coast. Shelf Sci. 215 241–9
Thakur M P, Berg M P, Eisenhauer N and van Langevelde F 2014 Disturbance-diversity relationships for soil fauna are explained by faunal community biomass in a salt marsh Soil Biol. Biochem. 78 30–37
Thibault K M and Brown J H 2008 Impact of an extreme climatic event on community assembly Proc. Natl Acad. Sci. USA 105 34110–5
Trenkel V, Pinnegar J K, Dawson W A, du Buit M H and Tidd A N 2005 Spatial and temporal structure of predator-prey relationships in the Celtic Sea fish community Mar. Ecol. Prog. Ser. 299 257–68
Ulrich W, Jabot F and Gotelli N J 2017 Competitive interactions change the pattern of species co-occurrences under neutral dispersal Oikos 126 91–100
van der Schatte Olivier A, Jones L, Vay L L, Christie M, Wilson J and Malham S K 2020 A global review of the ecosystem services provided by bivalve aquaculture Rev. Aquacult. 12 3–25
Vasseur D A and McCann K S 2005 A mechanistic approach for modeling temperature-dependent consumer-resource dynamics Am. Nat. 166 184–98
Violle C, Reich P B, Pacala S W, Enquist B J and Kattge J 2014 The emergence and promise of functional biogeography Proc. Natl Acad. Sci. USA 111 13690–6
Wardle D A 2006 The influence of biotic interactions on soil biodiversity Ecol. Lett. 9 870–86
Xu F and Zhang S 2008 An Illustrated Bivalvia Mollusca Fauna of China Seas (Beijing: Science Press) (In Chinese)
Xu H, Xiao J and Zhang Z 2020 Heatwave effects on gross primary production of northern mid-latitude ecosystems Environ. Res. Lett. 15 074027
Yu R-Q, Chen G Z, Wong Y S, Tam N F Y and Lan C Y 1997 Benthic macrofauna of the mangrove swamp treated with municipal wastewater Hydrobiologia 347 127–37
Zeppilli D et al 2015 Is the meiofauna a good indicator for climate change and anthropogenic impacts? Mar. Biodiversity 45 505–35
Zou F, Zhang H, Dahmer T, Yang Q, Cai J, Zhang W and Liang C 2008 The effects of benthos and wetland area on shorebird abundance and species richness in coastal mangrove wetlands of Leizhou Peninsula, China For. Ecol. Manage. 255 3813–8