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Contrasting Structural Changes in Two Benthic Invertebrate Communities After an Extraordinary Rainfall Event in Liuqiu Island, Taiwan

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This study compared the changes in benthic community structures of the Shanfu (SF) and Duozaiping (DU) coral reef intertidal zones of Liuqiu Island between 2020 and 2022 after a prolonged precipitation event between late July and early August 2021. The trend of extreme rainfall on the island was also explored using the Standardized Precipitation Index (SPI) for coastal management use. The adjacent study sites of SF and DU have areas of 16,203 and 31,930 m^2, respectively. Variations in the diversity indexes between sites (SF and DU) and years (2020, 2021, and 2022) were determined by two-way ANOVA tests. SF and DU differed significantly in species density, richness, dominance, diversity, and evenness indexes. Site factor had a more significant effect than year on these indices. The benthic community at DU was distinctly clustered into before, after, and 1-year after rainfall groups, but this was not the case for SF. Echinodermata was the taxon primarily responsible for the differences. Based on the meteorological data from 1997 to 2022, the

SPIs varied from -1.83 (severe drought) to +1.90 (severe precipitation). Temporally, precipitation intensity and frequency increased during 2016–2021 compared with 2000–2006, with a peak precipitation event of 1,168 mm rainfall over 14 days in 2021. The broader reef flat at DU may have resulted in thermal and salinity stresses lasting longer for stenohaline echinoderms than at SF. Results from this island highlighted the differential vulnerability of the benthic communities from different sites to natural disturbances for the first time, allowing policymakers and stakeholders to formulate effective regional management strategies to minimize the impact of extreme climate events.

Keywords: Diversity index, Standardized Precipitation Index, SPI, Climate change, Low salinity, Echinoderms

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BACKGROUND

Climate-induced disturbances to marine ecosystems are expected to increase over the next few decades, posing threats such as elevated temperature, ocean acidification, sea level rise, and increasing storm frequency and severity (IPCC 2022). These effects can have short- or long-term consequences and vary depending on the ecosystem. In 2021, the Emergency Event Database recorded 432 natural disasters worldwide (CRED 2022), with 223 of these events (51.6%) being classified as flooding.

Taiwan's climate tends to be warm and humid, with a southwestern wind in summer and cool and dry with a northeastern prevailing wind in winter (Wu and Kuo 1999; Henny et al. 2021). Rainfall occurs mainly between May and September, depending on the frontal systems of the Mei-Yu season (Chen and Chen 2003) in May and June, with typhoons in July and August. In the Mei-Yu and typhoon seasons, rainfall is weighty over the southwest mountain slopes (Henny et al. 2021). Studies analyzing extreme precipitation trends have shown that extraordinary rainfall events in Taiwan have increased markedly between 1960 and 2015, particularly since 2000, in all seasons except fall. Moreover, studies have shown that rainfall has become more intense and unpredictable from 2003 onwards (Tung et al. 2022). In southwestern Taiwan, there has been an overall increasing trend in both the intensity and frequency of extreme rainfall alongside total annual precipitation.

Short bursts of excessively heavy rainfall generally result in flooding and landslides which are considered Taiwan's most significant natural hazard.

Extreme climate events, such as heatwaves, cold snaps, droughts, and intense rainfall, impact various marine ecosystems and adversely affect Taiwan's fishing industry (Hsieh et al. 2008; MOA 2020). In Penghu, an extreme cold in the coral reef ecosystem was related to a two-week low water temperature (minimum 11.7°C) in 2008 (Hsieh et al. 2008). Records show that 183 fish species in 58 families suffered significant mortality. Deaths of macroinvertebrates, including echinoderms, crustaceans, mollusks, and corals, were mentioned, but no further qualitative or quantitative descriptions were available of these dead animals. Another study reported losses of more than 73 tons of wild fish and an 80% mortality rate among caged aquaculture fish (Chang et al. 2013). It took 53 months for the wild fish stocks to recover (Chen et al. 2020).

A 96-hour rainfall of 2058 - 2888 mm was recorded in southern Taiwan when Typhoon Morakot hit Taiwan in early August 2009 (Central Weather Administration (CWA), Republic of China (ROC)). This record reached the average annual precipitation level of 2500 mm in the plains of Taiwan. Pond culture and coastal fishery losses were estimated at NT$4.7 billion, as reported by the Ministry of Agriculture (MOA 2020). However, no assessment was made of the impact on wild marine fauna.

Although heavy rainfall or flooding is rare, their impacts on coral reefs can be severe and last more than a decade (Jokiel et al. 1993; van Woesik et al. 1995; Jones and Berkelmans 2014). The responses of benthic fauna to hyposaline conditions vary by location and taxa. For example, exceptional rainfall with heavy flooding occurred in the inner Gulf of Thailand between July and December 2011 (Sangmanee et al. 2012). At Khang Khao Island, the density of the sea urchin *Diadema setosum* decreased from 9.5 in July 2010 to 5.2 individuals/m^2 in August 2011. Low salinity also killed more than 60% of corals on the island. Conversely, the mortality rate of the thorny oyster *Spondylus* cf. *versicolor* and the sea cucumber *Holothuria leucospilota* was less than 5%. In the Urbinu Lagoon, France, exceptional rainfall occurred between October 31 and November 1, 1993 (Fernandez et al. 2006). The salinity dropped to 23 psu over three days, and the sea urchin *Paracentrotus lividus* population was reduced by 50% between 1990 and 1994. Low salinity, turbidity, and siltation might have caused the population crash, and it would take six years to recover completely.

Floodwaters associated with tropical cyclones affecting coral communities were reported at Keppel Island, Australia, in 1990 and 2011 (van Woesik et al. 1995; Jones and Berkelmans 2014) and in Hervey Bay in 2010 and 2013 (Bulter et al. 2015) and Hawaii (Banner 1968; Jokiel et al. 1993). Regarding Hawaii, the re-occurrence of freshwater "killing" events were documented in Kaneohe Bay in May 1965, January 1988, July 2014, and April 2018 (Banner 1968; Jokiel et al.

1993; Bahr et al. 2015a b; Rodgers et al. 2021). Mass mortality events from the intertidal zone to 2 m depth were reported, including corals, sea cucumbers, crabs, and fishes (Jokiel et al. 1993). As smaller organisms rotted away quickly, evidence of the "killing event" was most apparent in corals and larger invertebrates. The highest mortality rates were near the estuary mouth, then declined to zero within 1 km. In contrast to the subtidal zones, however, there were no mortality events or adverse effects on fish and other organisms. For example, littorinid snails, periwinkle snails, hermit crabs, limpets, and barnacles remained in good condition. In 2018, at Pilaʻa and Haʻena on the island of Kauaʻi, a flooding event caused an increase in coral bleaching (55%). It decreased in sea urchin and fish populations (34–48% and 58%, respectively, Rodgers et al. 2021) and changed the community structure of corals.

In 2021, many extreme climate events occurred worldwide, including extraordinarily high temperatures caused by heatwaves across the Americas and the Mediterranean, which were accompanied by devastating wildfires. Extraordinary levels of rainfall were experienced in China and parts of Europe, causing severe flooding, numerous casualties, and economic losses (WMO 2021). In early August 2021, within 123 hours, Tropical Storm Lupit brought in 1218–1638 mm of rainfall in southern Taiwan (CWA, ROC).

Currently, our knowledge of the influence of extreme climate events on coral reef ecosystems is mainly restricted to corals and fish (Jones and Berkelmans 2014; Bahr et al. 2015a, b; Butler et al. 2015; Rodgers et al. 2021; Xie et al. 2020). Excessive precipitation is also expected to impact intertidal benthic invertebrate communities on coral reefs. However, studies of these impacts remain limited. This study used data from a regular monitoring program on benthic invertebrates at two coral reef sites on Liuqiu Island in southern Taiwan. The responses of the benthic invertebrate communities at Shanfu (SF) and Duozaiping (DU) were compared before and after the August 2021 rainfall event over a three-year investigation (2020–2022).

MATERIALS AND METHODS

Study area and sampling methodology

Liuqiu Island, also known as Xiao Liuqiu, Siaoliouciou, and Sio Liu-khiu, is located 14 km off southwestern Taiwan and has approximately 13,000 residents. It is a tropical island fringed with coral reefs, with a land area of 6.8 km^2 (Tourism Administration, Ministry of Transportation and Communications, ROC) and 12 km of coastline. The coast is a popular tourist attraction because of its scenic views and marine biodiversity. The monthly mean sea surface temperatures of the island range from 25.0 to 30.0°C (2004–2023) (CWA, ROC).

We investigated the benthic invertebrate communities between 2020 and 2022 during low tide at the adjacent sites of SF and DU (Fig. 1). The reef flats of the surveyed sites were 16,203 and 31,930 m^2, respectively. We set up two transect lines at each site with a 1 x $1m^2$ quadrat at 5-m intervals between the high and low tide levels. We counted the total number of invertebrates (> 5mm) in the quadrats, which included crustaceans, mollusks, annelids, and echinoderms. Specimens were identified in the field or the lab using a magnifier or a microscope. Species identification was undertaken using reference studies for invertebrates in general (Lo 2013), crustaceans (Miyake 1982; Chen and Lo 2014), annelids (Fauchald 1977; Ge et al. 2018), sipunculas (Cutler 1994), mollusks (Okutani 2000; Chen et al. 2012; Chiu and Su 2019, 2020; Jie 2019; Chiu et al. 2021), echinoderms (Chao 1998, 2018; Chao and Su 2009), and sponges (Hooper et al. 2002). The designation of species name follows the WoRMS taxonomic system (http://www.marinespecies.org/).

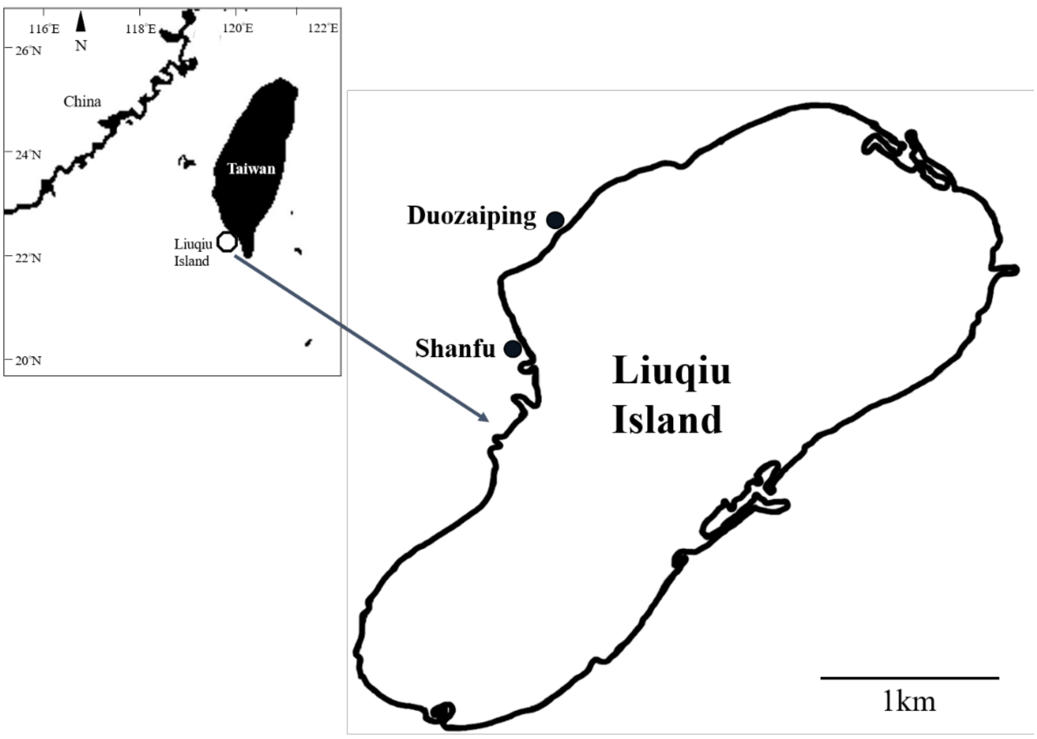

Fig. 1. The study area and sampling sites in Liuqiu Island, Taiwan.

Data analysis

We analyzed the data regarding K-dominance curves, density, and diversity indexes to obtain quantitative estimates of the spatial and temporal variability of the benthic communities at SF and DU. A K-dominance plot was applied to visualize the cumulative species abundance distribution pattern. Diversity indexes measure species richness (total number of species), evenness (relative abundance of each species), and composition (the identity of species) within a specific area. We used Margalef's Richness index (R), Shannon's Diversity index (Ho), Pielou's Evenness index (J_0), and Simpson's Dominance index (D) (Clarke and Warwick 2001).

We used two-way analyses of variance (ANOVAs) to separately evaluate the effects of site (SF and DU) and year (2020, 2021, and 2022) on the density and diversity indexes of the benthic communities. The Kolmogorov-Smirnov test was used to check data normality before the analyses. Whenever the ANOVA showed significant differences, the Tukey post hoc test was conducted to explore the differences in the interested factors.

Temporal variations of the benthic communities at SF and DU were analyzed separately by cluster analyses of the Bray-Curtis similarity (BCS) indices (Primer 6.0) to investigate the influence of precipitation (Clarke and Warwick 2001). The contribution of each species to the cluster was further determined by principal component analysis (PCA). All statistical analyses were run on the Primer 6.0 software package (Primer-E Ltd., Plymouth, UK).

Rainfall records of Liuqiu Island

The heaviest rainfall on Liuqiu Island occurred between July 28 and August 10, 2021. The rainfall trend was investigated using the Standardized Precipitation Index (SPI) based on precipitation records from the CWA, ROC. The data included monthly total precipitation amount (mm), annual maximum consecutive precipitation days, and annual precipitation amount (mm). The SPI was calculated at a time scale of 12 months using precipitation data from 1997 to 2022 to explore the climate change trend on Liuqiu Island. The SPI was developed by McKee et al. (1993) to define and monitor drought events at multiple time scales (1-, 3-, 6-, 12-, and 24-months). The World Meteorological Organization (WMO) recommended the SPI as an index for describing meteorological droughts (Svoboda et al., 2012). It categorizes climate conditions ranging from extreme wetness $\geq +2$ SPI to extreme drought ≤ -2 SPI; -1 to $+1$ as a normal regime; $+1$ to $+1.5$ and $+1.5$ to $+2.0$ as moderate and severe precipitation, respectively (McKee et al. 1993; Seiler et al. 2002). Conversely, moderate and severe drought are characterized by the same SPI ranges but with negative values.

RESULTS

Species composition and diversity indexes of the benthic communities at SF and DU

The total number of benthic invertebrate species at SF and DU varied among sampling months in 2020–2022, *i.e.*, 39–69 vs. 27–71, respectively (Table 1). The shape of the cumulative species dominance plots (K-dominance curves) had gentle slopes at SF contrasting at DU (Fig. 2). Echinoderms comprised 25.8–49.3 individuals/m^2 at DU, and 3.8 to 19.7 individuals/m^2 at SF (Fig. 3). Mean densities, Margalef's Richness index (R), Shannon's Diversity index (Ho), Pielou's Evenness index (J_0), and Simpson's Dominance index (D) at SF and DU were 17–41 vs. 31–59 (individuals/m^2), 7.8–16.9 vs. 17.6–27.8, 2.2–3.1 vs. 2.0–2.6, 0.66–0.83 vs. 0.54–0.70, and 0.08–0.25 vs. 0.14–0.23, respectively (Table 1).

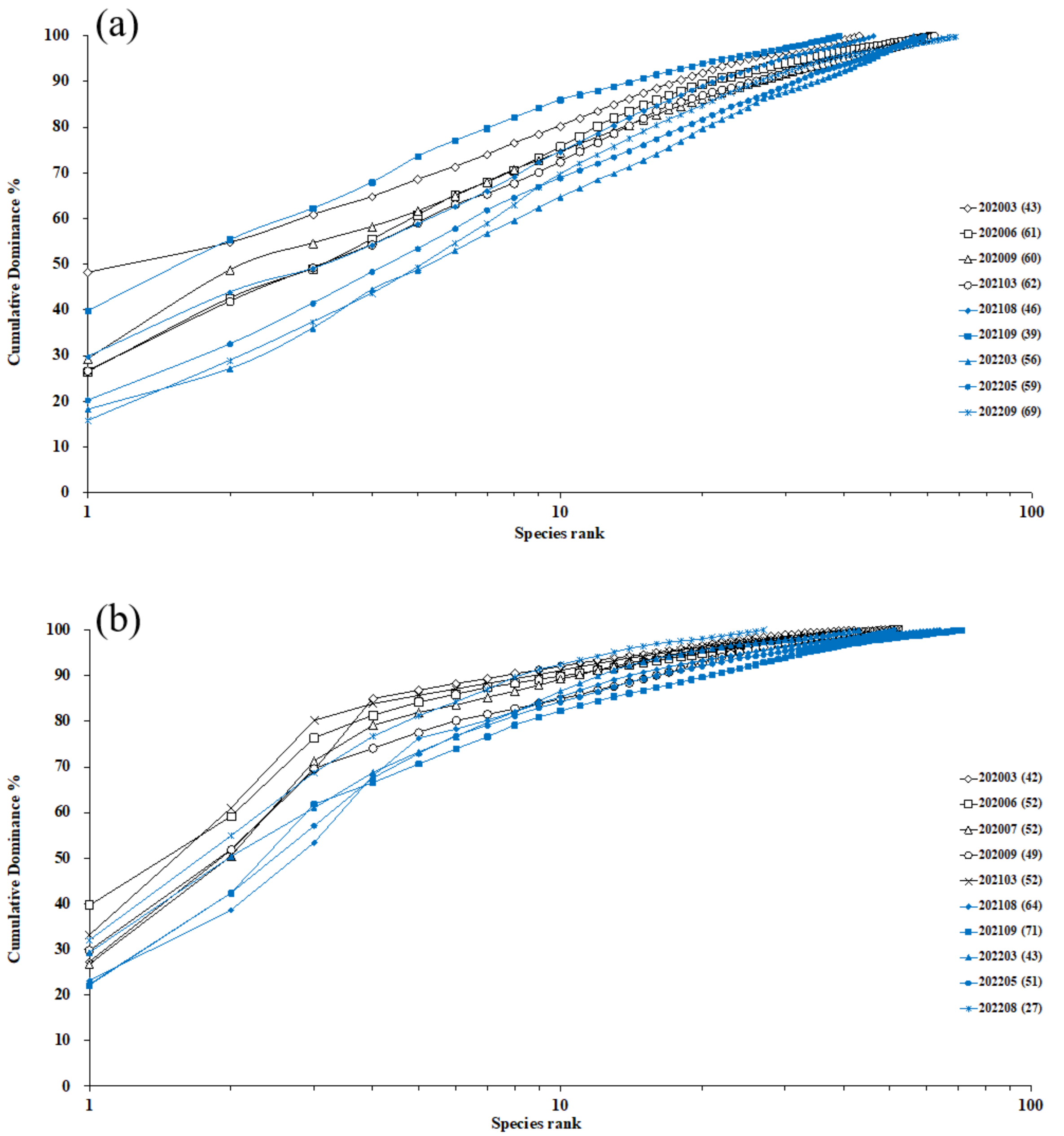

Fig. 2. K-dominance curves of the benthic communities at (a) Shanfu (SF) and (b) Duozaiping (DU) in 2020–2022. (n): the number of species.

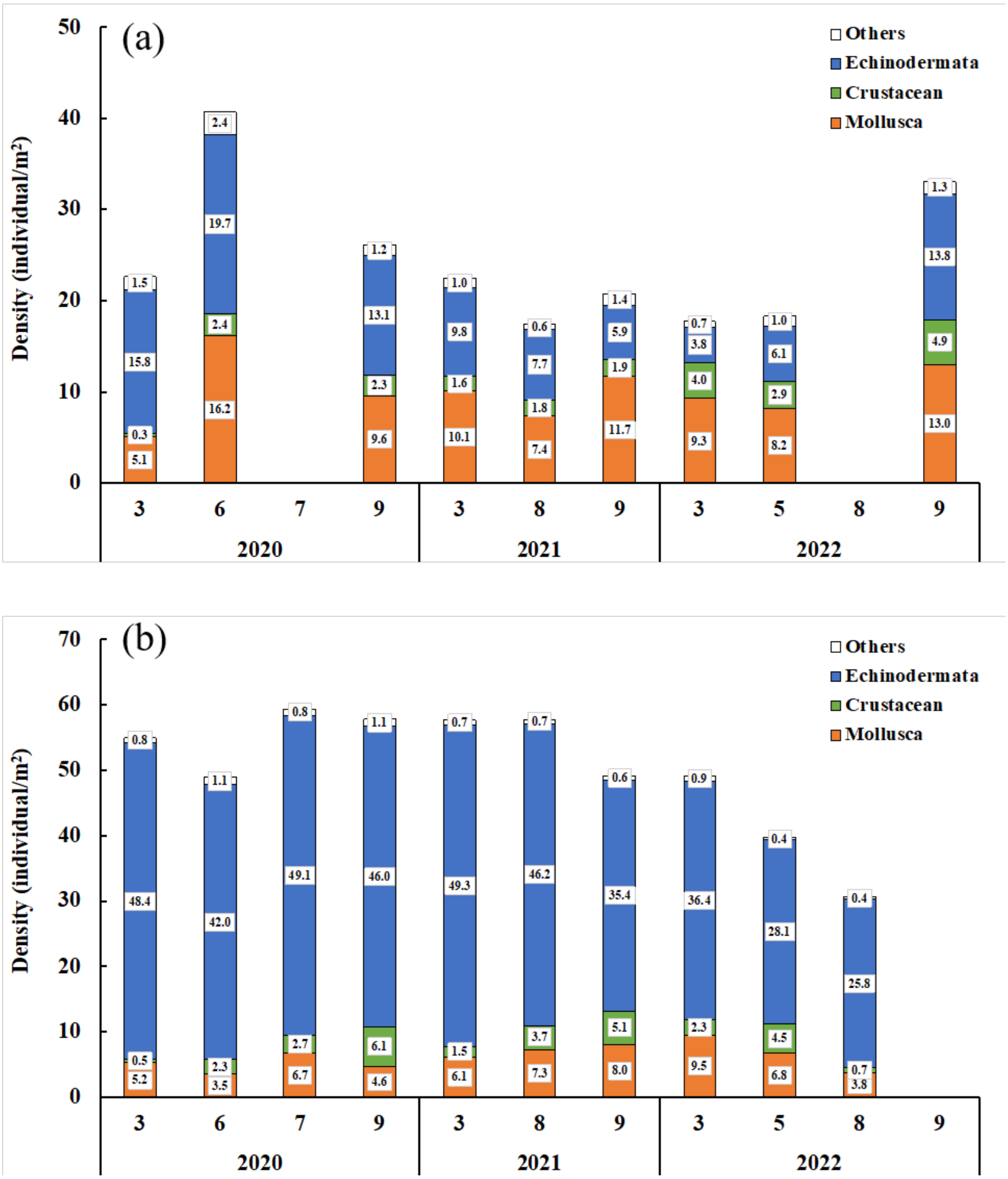

Fig. 3. The composition and density of invertebrate taxa at (a) Shanfu (SF) and (b) Duozaiping (DU) in 2020–2022.

Table 1. Diversity indices listed for the benthic communities of Shanfu (SF) and Duozaiping (DU). Density (no./m^2); R: Margalef's Richness index ; Ho: Shannon's Diversity index; J_0: Pielou's Evenness index; D: Simpson's Dominance index

Shanfu	2020			2021			2022			
Month	3	6	9	3	8	9	3	5	9	
Species	43	61	60	62	46	39	56	59	69	
Density	22.7 ± 3.3	40.7 ± 28.5	26.1 ± 6.4	22.4 ± 6.5	17.4 ± 5.2	20.8 ± 13.9	17.8 ± 6.7	18.3 ± 0.9	33.1 ± 7.8	
R	11.7 ± 1.6	16.9 ± 10.0	11.4 ± 2.5	10.0 ± 2.0	9.0 ± 1.5	11.1 ± 4.6	7.8 ± 2.5	8.7 ± 0.1	13.1 ± 2.8	
Ho	2.24 ± 0.44	2.61 ±0.18	2.63 ± 0.29	2.76 ± 0.18	2.62 ± 0.41	2.19 ± 0.10	2.92 ± 0.24	2.93 ± 0.02	3.10 ± 0.01	
J_0	0.66 ± 0.12	0.71 ± 0.02	0.71 ± 0.02	0.75 ± 0.00	0.77 ± 0.03	0.68 ± 0.12	0.83 ± 0.03	0.81 ± 0.00	0.79 ± 0.01	
D	0.25 ± 0.11	0.14 ± 0.03	0.15 ± 0.05	0.12 ± 0.02	0.14 ± 0.06	0.22 ± 0.09	0.09 ±0.03	0.09 ± 0.01	0.08 ± 0.01	
Duozaiping	2020				2021			2022		
Month	3	6	7	9	3	8	9	3	5	8
Species	42	52	52	49	52	64	71	43	51	27
Density	55.0 ± 8.5	48.9 ± 13.9	59.3 ± 14.0	57.8 ± 15.3	57.7 ± 9.9	57.8 ± 28.3	49.1 ± 10.4	49.2 ± 11.5	39.8 ± 1.1	30.7 ± 13.2
R	27.8 ± 4.2	24.2 ± 5.7	27.6 ± 5.3	25.9 ± 4.9	27.8 ± 5.7	25.0 ± 10.2	21.5 ± 7.1	22.0 ± 4.6	17.7 ± 0.5	17.6 ± 3.5
Ho	1.96 ± 0.08	2.03 ± 0.18	2.16 ± 0.01	2.27 ± 0.24	1.96 ± 0.21	2.48 ± 0.05	2.57 ± 0.50	2.34 ± 0.04	2.41 ± 0.08	1.99 ± 0.06
J_0	0.57 ± 0.01	0.56 ± 0.07	0.59 ± 0.03	0.62 ± 0.03	0.54 ± 0.05	0.65 ± 0.02	0.65 ± 0.11	0.69 ± 0.03	0.69 ± 0.01	0.70 ± 0.09
D	0.22 ± 0.03	0.23 ± 0.04	0.18 ± 0.01	0.18 ± 0.03	0.23 ± 0.04	0.14 ± 0.00	0.15 ± 0.07	0.16 ± 0.01	0.15 ± 0.01	0.20 ± 0.01

The two-way ANOVA tests showed that the site had a much more significant effect than year on density and diversity indexes, except for dominance (Table 2). Moreover, density and all the diversity indexes differed significantly between sites (2-way ANOVAs; *d.f.* = 1; F = 43.8, $P < 0.001$ for density; F = 73.1; $P < 0.001$ for richness index). DU had greater values than SF for density, richness, and dominance. By contrast, DU's diversity and evenness values were lower than SF's. There were no significant differences in density among 2020, 2021, and 2022. Diversity and Evenness indexes differed yearly in descending order of 2022 > 2021 > 2020 (2-way ANOVAs; *d.f.* = 2; F = 4.4, $P < 0.001$ for diversity index), while the richness and dominance indexes increased from 2020 to 2022 (2-way ANOVAs; *d.f.* = 2; F = 4.7, $P < 0.05$ for richness index).

Table 2. Summary of two-way ANOVA results for the variables of density and diversity indices

Variable	Factor	DF	MS	F	Sig.	
Density						
	Site	1	6177.41	43.81	**< 0.001**	DU^{a}, SF^{b}
	Year	2	395.89	2.81	> 0.05	2020^{a}, 202^{a}, 2022^{a}
	Site * Year	2	238.63	1.69	> 0.05	
R						
	Site	1	1433.96	73.05	**< 0.001**	DU^{a}, SF^{b}
	Year	2	92.28	4.70	**< 0.02**	2020^{a}, 2021^{ab}, 2022^{b}
	Site * Year	2	24.26	1.24	> 0.05	
Ho						
	Site	1	1.81	24.86	**< 0.001**	SF^{a}, DU^{b}
	Year	2	0.32	4.35	**< 0.001**	2022^{a}, 2021^{ab}, 2020^{b}
	Site * Year	2	0.23	3.13	> 0.05	
J_0						
	Site	1	0.12	43.06	**< 0.001**	SF^{a}, DU^{b}
	Year	2	0.04	15.34	**< 0.001**	2022^{a}, 2021^{b}, 2020^{b}
	Site * Year	2	0	0.04	> 0.05	
D						
	Site	1	0.01	5.54	**< 0.03**	D^{a}, SF^{b}
	Year	2	0.01	5.18	**< 0.01**	2020^{a}, 2021^{ab}, 2022^{b}
	Site * Year	2	0	1.71	> 0.05	

Density (no./m2); R: Margalef's Richness index ; Ho: Shannon's Diversity index; J0: Pielou's Evenness index; D: Simpson's Dominance index. Different letters indicate that the values significantly differ (Tukey's test; $p < 0.05$).

Spatial-temporal patterns of community structure at SF and DU

The Bray-Curtis similarity analyses showed that the benthic community at DU was separated into three groups: before, after, and 1-year after rainfall (Fig. 4). At DU, the five principal components (PC1–PC5) accounted for 53.3, 21.4, 11.1, 6.6, and 4.1% of the total variance, respectively. The separation was mainly contributed by PC1, including species of *Breviturma brevipes* (-0.594), *Echinometra mathaei* (-0.568), *Ophiocoma scolopendrina* (0.488), *Ophiocoma* sp. (-0.242), and *Holothuria atra* (-0.109), respectively (Fig. 5). In contrast, the clustered groups at SF did not correlate with the level of rainfall (Fig. 4). PC1−PC5 for SF comprised 58.8, 25.5, 5.7, 3.3, and 2.0% of the total variance, respectively. The major contributors of PC1 were *E. mathaei* (-0.931), *Calcinus latens* (0.171), *Nerita albicilla* (-0.142), *Stomopneustes variolaris* (-0.138), and *Porites lobate* (-0.103) (Fig. 5). The DU cluster demonstrated a year-long influence of rainfall on the benthic community.

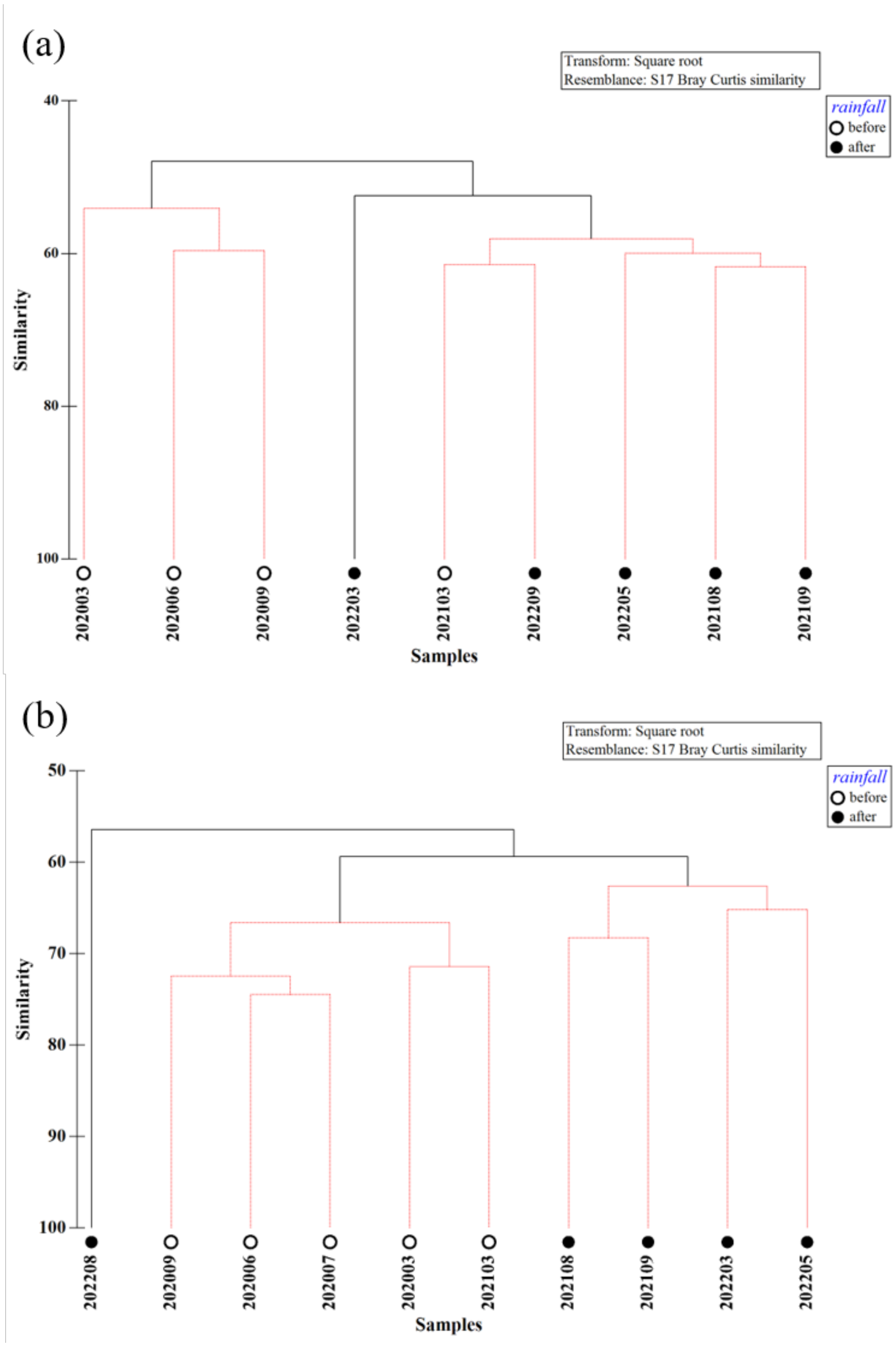

Fig. 4. Dendrograms of the hierarchical clustering of the benthic communities based on Bray-Curtis similarities at (a) Shanfu (SF) and (b) Duozaiping (DU) in 2020–2022.

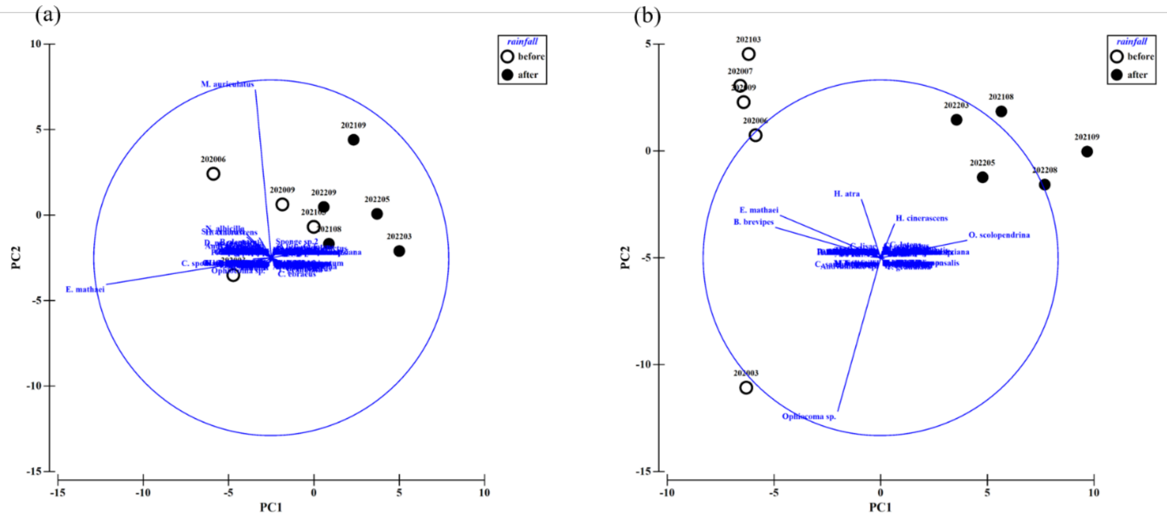

Fig. 5. The contribution of each species in the benthic communities of (a) Shanfu (SF) and (b) Duozaiping (DU) to the first and second principal component scores in 2020–2022.

Rainfall records of Liuqiu Island

The precipitation records for Liuqiu Island between 1997 and 2022 showed that the lowest annual precipitation occurred in 2002 (833.5 mm) (Fig. 6), and the highest occurred in 2016 (2,682 mm). The yearly maximum consecutive precipitation days were 14, with four records that fell in August−September 2001 (225 mm), June 2016 (404.5 mm), June 2021 (644 mm), and July−August 2021 (1168.5 mm). In 2021, the extreme rainfall lasted from July 28 to August 10, with the most rain falling on August 1 (272.5 mm).

The 12-month SPI values are shown in Fig. 7, along with the monthly total precipitation records for Liuqiu Island. Extreme precipitation and drought as ≥ +2 and ≤ −2 SPI were not observed. Severe rainfall occurred in 2016 and 2021 with SPI values of +1.81 and +1.90; conversely, severe drought occurred in 2002 (-1.83). The 2021 extreme rainfall matched the highest value of +1.90. Most of the consecutive positive SPI values of > +1 occurred after 2016. There seems to be a tendency for wetter than average periods since then.

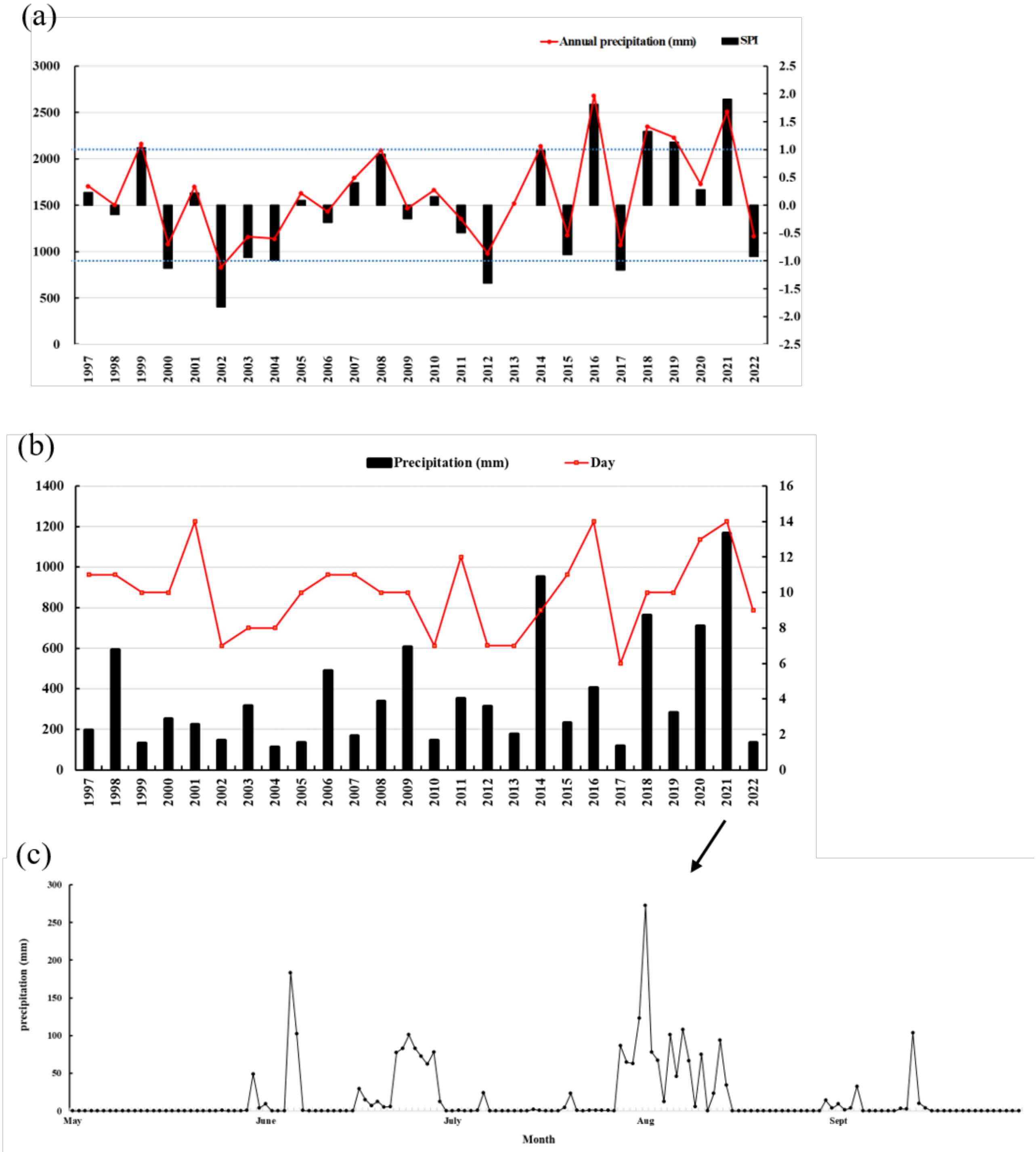

Fig. 6. The precipitation records in Liuqiu Island from 1997 to 2022. (a) Annual precipitation (mm) and SPI (standardized precipitation index) values; (b) annually maximum consecutive precipitation days and its total precipitation (mm); (c) daily precipitation (mm) from May to December in 2021. Data source: Central Weather Administration, ROC.

DISCUSSION

A 14-day extreme precipitation event (1,168 mm) was recorded in July/August 2021 (CWB, ROC), the highest level since 1997. Additionally, SPI values have shown that Liuqiu Island has experienced increasingly severe precipitation since 2016. The total number of species in the two benthic communities varied from 39 to 69 at SF and 27 to 71 at DU between 2020 and 2022. Site factor (SF and DU) had a more significant effect than year (2020, 2021, and 2022) on indexes of density, richness, dominance, diversity, and evenness. The benthic communities at DU were characterized by before, after, and 1-year after rainfall groups, chiefly comprising brittle stars (*B. brevipes*, *O. scolopendrina*, *Ophiocoma* sp.), sea urchins (*E. mathaei*), and sea cucumbers (*Holothuria atra*). Extreme precipitation in coastal areas had a year-long effect on benthic communities at DU but not at SF. The broader reef flat at DU, which contained more stenohaline echinoderms, suffered greater thermal and salinity stresses during low tide than SF, which may explain the difference.

Abiotic factors, such as flow direction and nutrient load, also govern the vulnerability of benthic communities to natural disturbances. Regarding global synthesis and meta-analysis of the contributions of coral reefs to coastal hazard risk reduction, Ferrario et al. (2014) reported that wave energy and wave height were attenuated significantly across more expansive reef flats. Conversely, as in the case of our study at DU and SF, large reef flats retain desiccation, thermal, and salinity stresses longer.

Regarding salinity tolerance of benthic invertebrates, Echinodermata is a stenohaline group compared with other invertebrates. Based on the experimental and observational estimates in the North Sea (Geburzi et al. 2022), the salinity tolerances of benthic crustaceans (13 spp.), echinoderms (3 spp.), molluscs (3 spp.), and polychaetes (1 sp.) were reported as 0.1–55, 18–36, 4–60, and 0.5–45 psu, respectively. Another study investigated the effect of salinity fluctuations on echinoderm and mollusc communities at Caye Cochons (CC) and Cap du Corbeau (CdC) in the northern Gulf of St. Lawrence (Drouin et al. 1985). Sites of CC and CdC differed markedly in the amplitude of salinity fluctuations, *i.e.*, 10–30 vs. 24–30 psu, respectively. In the intertidal area to 2 m deep, five echinoderms distributed at CdC, i.e., an urchin (*Strongylocentrotus droebachiens*), two ophiuroids (*Ophiopholis aculeata* and *Ophiura robusta*), two starfishes (*Asterias vulgaris* and *Leptasterias polaris*). However, at CC, *O. aculeata* and *O. robusta* were less abundant, and there was no *A. vulgaris*. The situation was different concerning mollusc species. The abundance of five molluscs was similar at both sites, including a chiton (*Tonicella marmorea*), a limpet (*Acmaea testudinalis*), a snail (*Buccinum undatum*), and two clams (*Hiatella arctica* and *Mytilus edulis*). Meanwhile, there was less chiton of *Tonicella rubra* at CC. There was a striking difference in the echinoderm diversity between CC and CdC but not molluscs. This discrepancy was likely due to the lower salinity tolerance of echinoderms than molluscs. Consistent with these studies, our results showed a higher proportion of stenohaline echinoderms in the benthic invertebrate communities at

DU (72–88%) than at SF (22–68%).

Heavy rainfall or flooding is rare, and their impacts on benthic coral reef communities primarily focus on corals and fish. For example, the flooding associated with Tropical Cyclone Joy affected nearshore coral communities in the Keppel Islands of Australia from December 23, 1990, to January 7, 1991 (van Woesik et al. 1995). Coral mortality reached 85% on leeward reefs, particularly affecting *Acropora* spp., *Pocillopora damicornis,* and *Seriatopora hystrix*. Subsequently, the community composition shifted to more flood-resistant species. Moreover, Tropical Cyclone Tasha caused flooding in Keppel Bay in 2011 (Jones and Berkelmans, 2014). This time, coral mortality reached 100% to 2 m depth. Based on the previous flood in 1991, coral recovery is expected to take 10–15 years. In another study in Hervey Bay, Australia, flooding in 2010 and 2013 caused coral mortality of 28% and 40%, respectively (Bulter et al. 2015), while changes in water quality parameters and salinity in submarine groundwater lasted for six and ten months, respectively. A study in Hong Kong showed that a minimum five-year mean salinity of 26.4 psu is required to sustain hard coral communities based on 24 water quality parameters and surveys of benthic fauna at 41 sites (Yeung et al. 2021).

This study showed that the structural changes in the DU benthic community were associated with extreme rainfall resulting from Tropical Storm Lupit and seasonal southwest monsoon flows. This event also caused NT$ 619 million loss to the aquaculture and fishing industries (MOA 2022). Extreme climate-related weather events are expected to increase in frequency and severity based on the IPCC's sixth assessment report (IPCC 2021), with Taiwan facing increasingly extreme levels of drought and precipitation (NSTC 2022). The coastal ecosystems of Taiwan will likely be severely impacted by climate variability in the future, which may result in either a shift in benthic invertebrates to hardier species or a complete collapse of the benthic communities (Hoegh-Guldberg and Salvat 1995). Even though Liuqiu Island is small, the response of the benthic community differs between the intertidal zones of SF and DU. Much of the economic activity of this island is associated with the burgeoning tourism industry. Understanding the responses of the ecosystem to climate change is vital if the regional government is to formulate effective management strategies for ensuring their ongoing protection. To fulfill the limitations of this study, we recommend further examination of the influence of reef flat size on inhabiting macrobenthos and environmental parameters, such as salinity and water temperature, with site replicates. Moreover, based on the study on the composition of benthic foraminifera at Dongsha Atoll, the results revealed that most survey sites are unsuitable for coral growth and reef recovery (Chen and Lin 2017). Since foraminifera is one of the most abundant shelled microorganisms in coral reefs, it provides an alternative approach to evaluating the health of coral reefs.

CONCLUSIONS

This study documented a 14-day rainfall episode with an accumulated precipitation record (1,168mm) in Liuqiu Island, Taiwan, in 2021. The benthic invertebrate communities at DU (but not at SF) were clustered into before, after, and 1-year-after rainfall groups. Echinoderms were the main taxa that contributed to the separation, and the event's impact still affected DU one year later. Based on the annual SPI, extreme precipitation events have increased in intensity and frequency since 2016, which aligns with the predictions of the Intergovernmental Panel on Climate Change (IPCC) and the National Science and Technology Council, ROC, in 2022. Our study of the differential responses of benthic fauna in Liuqiu Island provides a basis for policymakers to formulate effective regional management strategies to minimize the foreseeable impact of extreme climate events.

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REFERENCES

Bahr KD, Jokiel PL, Toonen RJ. 2015a. The unnatural history of Kaneʻohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. PeerJ **3:**e950. doi:10.7717/peerj.950.

Bahr KD, Jokiel PL, Rodgers KS. 2015b. The 2014 coral bleaching and freshwater flood events in Kaneohe Bay, Hawaiʻi. PeerJ **3:**e1136. doi:10.7717/peerj.1136.

Banner AH. 1968. A freshwater “kill” on the coral reefs of Hawaiʻi. Hawaiʻi Institute of Marine Biological Technology Report **15:**1–29.

Butler IR, Sommer B, Zann, Zhao JX, Pandolfi JM. 2015. The cumulative impacts of repeated heavy rainfall, flooding and altered water quality on the high-latitude coral reefs of Hervey Bay, Queensland, Australia. Mar Pollut Bull **96:**356–367. doi:10.1016/j.marpolbul.2015.04.047.

Chang Y, Lee MA, Lee KT, Shao KT. 2013. Adaptation of fisheries and mariculture management to extreme oceanic environmental changes and climate variability in Taiwan. Mar Policy **38:**476–482. doi:10.1016/j.marpol.2012.08.002.

Chao, SM. 1998. Shallow-water sea cucumbers of Taiwan. National Museum of Natural Science, Taichung, Taiwan, ROC. (in Chinese)

Chao SM. 2018. The Assemblage of Shallow-Water Holothurians (Echinodermata: Holothuroidea) from Hsiao Liouciou Island off Southwestern Taiwan. Collection and Research **31:**91–99.

Chao SM, Su Y (eds). 2009. Sea stars of Taiwan: Ecology and diversity. National Museum of Natural Science, Taichung, Taiwan, ROC. (in Chinese)

Chen CS, Chen YL. 2003. The rainfall characteristics of Taiwan. Mon Weather Rev **131:**1323. doi:10.1175/1520-0493.

Chen H, Chen CY, Shao KT. 2020. Recovery and variation of the coastal fish community following a cold intrusion event in the Penghu Islands, Taiwan. PLoS ONE **15:**e0238550. doi:10.1371/journal. pone.0238550.

Chen C, Lin HL. 2017. Applying benthic foraminiferal assemblage to evaluate the coral reef condition in Dongsha Atoll lagoon. Zool Stud **56:**20. doi:10.6620/ZS.2017.56-20.

Chen WJ, Tseng CF, Lo LC. 2012. The marine Mollusca from Siaoliouciou, Taiwan. Pingtung County Government, Pingtung, Taiwan, ROC. (in Chinese)

Chen WJ, Lo LC. 2014. Some brachyura and anomura fauna from Siaoliioucious, Taiwan. Pingtung

County Government, Pingtung, Taiwan, ROC. (in Chinese)

Chiu YW, Su CY. 2019. Marine mollusks in Kenting 1–Marine snails. Kenting National Park, Pingtung, Taiwan, ROC. (in Chinese)

Chiu YW, Su CY. 2020. Marine mollusks in Kenting 2–Sea slugs. Kenting National Park, Pingtung, Taiwan, ROC. (in Chinese)

Chiu YW, Guo HL, Su CY. 2021. Marine mollusks in Kenting 3–Bivalves, chitons and cephalopods. Kenting National Park, Pingtung, Taiwan, ROC. (in Chinese)

Clarke KR, Warwick RM. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, second Ed, Primer-E, Ltd., Plymouth Marine Laboratory, Plymouth, UK. Available at: http://www.primer-e.com/. Accessed 2017.

Cutler EB. 1994. The Sipuncula: Their systematics, biology and evolution. Cornell University, Ithaca, New York, USA.

CRED. 2022, 2021. Disasters in numbers. Brussels: Centre for Research on the Epidemiology of Disasters (CRED). Available at: https://www.un-spider.org/news-and-events/news/cred-publication-2022-disasters-numbers. Acessed 21 Mar 2023.

Drouin G, Himmelman JH, Béland P. 1985. Impact of tidal salinity fluctuations on echinoderm and mollusc populations. Can J Zool **63:**1377-1387. doi:10.1139/z85-207.

Fauchald K. 1977. The polychaete worms: Definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Science Series **28**, Los Angeles Calif, USA.

Fernandez C, Pasqualini V, Boudouresque CF, Johnson M, Ferrat L, Caltagirone A, Mouillot D. 2006. Effect of an exceptional rainfall event on the sea urchin (*Paracentrotus lividus*) stock and seagrass distribution in a Mediterranean coastal lagoon. Estuar Coast Shelf Sci **68:**259–270. doi:10.1016/J.ECSS.2006.02.020.

Ferrario F, Beck MW, Storlazzi CD, Micheli F, Shepard CC, Airoldi L. 2014. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nat Commun **5:**1–9. doi:10.1038/ncomms4794.

Ge ML, Xu QZ, Fan SL, Wang ZX, Zhang XL. 2018. Taxonomy at order and family levels of the benthic groups of Polychaeta in the coastal waters of China. Biodiv Sci **26:**998–1003. (in Chinese with English abstract)

Geburzi J C, Heuer N, Homberger L, Kabus J, Moesges Z, Ovenbeck K, Brandis D, Ewers C. 2022. An environmental gradient dominates ecological and genetic differentiation of marine invertebrates between the North and Baltic Sea. Ecol Evol **12:**e8868. doi:10.1002/ece3.8868.

Henny L, Thorncroft CD, Hsu HH, Bosart LF. 2021. Extreme rainfall in Taiwan: seasonal statistics and trends. J Clim **34:**4711–4731. doi:10. 1175/JCLI-D-20-0999.1.

Hoegh-Guldberg O, Salvat B. 1995. Periodic mass-bleaching and elevated sea temperatures:

bleaching of outer reef slope communities in Moorea, French Polynesia. Mar Ecol Prog Ser **121:**181–190. doi:10.3354/meps121181.

Hooper JNA, Van Soest RWM, Willenz P. 2002. Systema Porifera: A guide to the classification of sponges. Springer, Boston, Massachusetts, US. doi:10.1007/978-1-4615-0747-5_1.

Hsieh HJ, Hsien YL, Tsai WS. 2008. Tropical fishes killed by the cold. Coral Reefs **27:**599. doi:10.1007/s00338-008-0378-3.

IPCC. 2021. Summary for policymakers. *In:* Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R, Zhou B (eds) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 3−32. doi:10.1017/9781009157896.001.

IPCC. 2022. Summary for policymakers. *In:* Pörtner HO, Roberts DC, Poloczanska ES, Mintenbeck K, Tignor M, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (eds) Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jie WB. 2019. Sea Slugs of Taiwan. National Museum of Marine Biology and Aquarium, Pingtung, Taiwan, ROC. (in Chinese)

Jokiel PL, Hunter CL, Taguchi S, Watarai L. 1993. Ecological impact of a fresh water “reef kill” in Kaneohe Bay, Oahu, Hawai‘i. Coral Reefs **12:**177–184. doi:10.1007/BF00334477.

Jones AM, Berkelmans R. 2014. Flood impacts in Keppel Bay, southern Great Barrier Reef in the aftermath of cyclonic rainfall. PLoS One **9:**e84739. doi:10.1371/journal.pone.0084739.

Lo LC. 2013. Recreational Impact on Biodiversity and Spatial Distribution of Populations in the Intertidal Zones of Liuchio Hsu. J Geogr Sci **69:**25–46. (in Chinese)

McKee TB, Doesken NJ, Kleist J. 1993. The relationship of drought frequency and duration to time scales. *In:* The 8^{th} conference on applied climatology, American Meteorology Society, Boston, pp 179–184.

Miyake S. 1982. Japanese crustacean decapods and stomatopods in Color. Vol. 1: Macruca, Anomura and Stomatopoda. Hoikusha Publishing, Osaka, Japan. (in Japanese)

MOA. 2020. The 2020 Agricultural statistics yearbook. Ministry of Agriculture (MOA), Taiwan, ROC.

MOA. 2022. The 2022 Agricultural statistics yearbook. Ministry of Agriculture (MOA), Taiwan, ROC.

NSTC. 2022. Scientific key summary of the IPCC sixth assessment report on climate change and the updated information on climate change in Taiwan. National Science and Technology Council (NSTC), Taiwan, ROC. (in Chinese)

Okutani T. 2000. Marine mollusks in Japan. Tokai University Press, Japan. (in English and Japanese)

Rodgers KS, Stefanak MP, Tsang AO, Han JJ, Graham AT, Stender YO. 2021. Impact to coral reef populations at Hāʻena and Pilaʻa, Kauaʻi, Following a record 2018 freshwater flood event. Diversity **13:**66. doi:10.3390/d13020066.

Sangmanee K, Sutthacheep M, Yeemin T. 2012. The decline of the sea urchin *Diadema setosum* affected by multiple disturbances in the inner Gulf of Thailand. *In*: Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, pp. 9–13.

Seiler RA, Hayes MJ, Bressan L. 2002. Using the standardized precipitation index for flood risk monitoring. Int J Climatol **22:**1365–1376. doi:10.1002/joc.799.

Svoboda M, Hayes M, Wood DA. 2012. Standardized precipitation index user guide. World Meteorological Organization, Geneva, Switzerland.

Tung YS, Wang CY, Weng SP, Yang CD. 2022. Extreme index trends of daily gridded rainfall dataset (1960–2017) in Taiwan. Terr Atmos Ocean Sci **33:**8. doi:10.1007/s44195-022-00009-z.

van Woesik R, De Vantier LM, Glazebrook JS. 1995. Effects of cyclone Joy on nearshore coral communities of the Great Barrier Reef. Mar Ecol Prog Ser **128:**261–270.

WMO. 2021. State of climate in 2021: Extreme events and major impacts. World Meteorological Organization. Available at: https://public.wmo.int/en/media/press-release/state-of-climate-2021-extreme-events-and-major-impacts. Accessed 31 Oct. 2021.

Wu CC, Kuo YH. 1999. Typhoons affecting Taiwan: Current understanding and future challenges. Bull Am Meteor Soc **80:**67–80. doi:10.1175/1520-0477(1999)080<0067:TATCUA>2.0.CO;2.

Xie JY, Yeung YH, Kwok CK, Kei K, Ang Jr P, Chan LL, Cheang CC, Chow WK, Qiu JW. 2020. Localized bleaching and quick recovery in Hong Kong's coral communities. Mar Pollut Bull **153:**110950. doi:10.1016/j.marpolbul.2020.110950.

Yeung YH, Xie JY, Kwok CK, Kei K, Ang Jr P, Chan LL, Dellisanti W, Cheang CC, Chow WK, Qiu JW. 2021. Hong Kong's subtropical scleractinian coral communities: Baseline, environmental drivers and management implications. Mar Pollut Bull **167:**112289. doi:10.1016/j.marpolbul.2021.112289.