



Phylogenetically diverse macrophyte community promotes species diversity of mobile epi-benthic invertebrates

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ABSTRACT

Various aspects of plant diversity such as species diversity and phylogenetic diversity enhance the species diversity of associated animals in terrestrial systems. In marine systems, however, the effects of macrophyte diversity on the species diversity of associated animals have received little attention. Here, we sampled in a subtropical seagrass-seaweed mixed bed to elucidate the effect of the macrophyte phylogenetic diversity based on the taxonomic relatedness as well as the macrophyte species diversity on species diversity of mobile epi-benthic invertebrates. Using regression analyses for each macrophyte parameter as well as multiple regression analyses, we found that the macrophyte phylogenetic diversity (taxonomic diversity index: Delta) positively influenced the invertebrate species richness and diversity index (H'). Although the macrophyte species richness and H' also positively influenced the invertebrate species richness, the best fit model for invertebrate species richness did not include them, suggesting that the macrophyte species diversity indirectly influenced invertebrate species diversity. Possible explanations of the effects of macrophyte Delta on the invertebrate species diversity were the niche complementarity effect and the selection effect. This is the first study which demonstrates that macrophyte phylogenetic diversity has a strong effect on the species diversity of mobile epi-benthic invertebrates.

1. Introduction

Various aspects of plant diversity including plant species diversity and plant phylogenetic diversity strongly impact ecosystem functioning such as primary production, carbon storage and nutrient cycling (Cardinale et al., 2012; Cadotte, 2013). Plant diversity also influences the species diversity of associated animals. In terrestrial systems, the species diversity of animals such as arthropods, birds and mammals have been shown to be positively correlated with plant species diversity and phylogenetic diversity (Lewinsohn and Roslin, 2008; Castagneyrol and Jactel, 2012; Dinnage et al., 2012).

In marine systems, the effects of macrophyte diversity on the species diversity of associated animals have received little attention. However, there are a few studies treating the effect of macrophyte species diversity and the macrophyte functional diversity on the invertebrate species diversity, but no or only a weakly positive relationship has been found (Parker et al., 2001; Bates and DeWreede, 2007; Gustafsson and Boström, 2009). Instead, the species diversity of associated

invertebrates is often correlated with the habitat abundance such as macrophyte biomass or surface area (Parker et al., 2001; Gustafsson and Boström, 2009; Best et al., 2014). The weak effect of macrophyte species diversity has been suggested to be due to most mobile epi-benthic invertebrates having lower host-specificities as compared to many arthropods in terrestrial systems (Stachowicz et al., 2007).

However, previous studies have shown that species composition of mobile epi-benthic invertebrates is different among macrophyte species (e.g. Taylor, 1998; Schmidt et al., 2011). Furthermore, there is evidence that mobile epi-benthic invertebrates have preferences for specific foods and habitats (McDonald and Bingham, 2010; Lürig et al., 2016). Superficially these findings seem to be inconsistent with the weak effect of macrophyte species diversity on species diversity of mobile epi-benthic invertebrates. But the preferences of mobile epi-benthic invertebrates may correspond to macrophyte relatedness. In other words, not the species diversity of macrophytes but macrophyte phylogenetic diversity may positively influence the species diversity of mobile epi-benthic invertebrates.

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Seagrass beds in subtropical areas are mainly formed on coral reef flats, where several species of seagrass grow (Short et al., 2007). In addition to bed-forming seagrass species, rhizophytic green algae such as *Avrainvillea* spp. and *Halimeda* spp. growing on sand and other macroalgae attaching to hard stable substrata are often found in seagrass beds (Heijs, 1985; Lewis, 1987; Davis and Fourqurean, 2001). As hard substrata such as the coral rocks and gravel are patchily abundant on the sandy bottom of the coral reef flats, the macroalgae can grow even within the seagrass beds, attaching to the hard substrata (Heijs, 1985). Consequently, several species of seagrass and seaweed form subtropical seagrass-seaweed mixed beds, where it is adequate to test the effect of macrophyte phylogenetic diversity on animal species diversity because there are both taxonomically close and distant macrophyte species occurring over small spatial scales. In the present study, we conducted a field survey designed to evaluate several indexes concerning the macrophyte diversity in a subtropical seagrass-seaweed mixed bed in Nagura Bay, Ishigaki Island, Japan, in order to assess the relationship between the invertebrate species diversity and the macrophyte diversity.

2. Materials and methods

2.1. Study site

This study was conducted in Nagura Bay, Ishigaki Island, Okinawa, Japan (24°23′ 23″ N; 124°08′ 05″ E; Fig. S1). The depth of the study site is about 0.2 m at the spring ebb tide. Sandy bottoms broadly occur in the study site and seagrasses such as *Thalassia hemprichii*, *Cymodocea rotundata* and *C. serrulata* are found all year round. Seaweeds such as *Tolypocladia glomerulata* and *Hydroclathrus tenuis* grow from winter to spring. Biomass of seaweed appeared to be influenced by the abundance of hard substrata, which were patchily located on the sandy bottom, so that the biomass of seaweed also showed a patchy distribution (Fig. S2).

2.2. Sampling procedure

Field samplings were conducted in April of 2014 and 2015, the month when the biomass of seaweeds reaches a maximum and is the best season to evaluate the effect of the macrophyte phylogenetic diversity because the variation of macrophyte phylogenetic diversity among points is the largest. Temperature and salinity were 24.2 °C and 33.8 in 2014, and 27.4 °C and 31.5 in 2015, respectively. Twelve quadrats (50 cm × 50 cm) were haphazardly put on the bed at the points where the degree of macrophyte heterogeneities were different from each other, ranging from where almost only seagrasses grew to where seagrasses and seaweeds were densely mixed. No distinct environmental clines (e.g. water temperature, salinity, depth) were observed. In each quadrat, seagrasses and seaweeds were cut with scissors at sheaths or rhizomes just above the sand bottom or at rhizoids, respectively, and then collected in a net (0.8 mm mesh) with coexistent mobile epi-benthic invertebrates. All the samples collected were immediately put in a cool box filled with seawater and seawater ice at the sampling site, and were carried to the Research Center for Subtropical Fisheries, Seikai National Fisheries Research Institute and immediately frozen at −20 °C for preservation. Mobile epi-benthic invertebrates retained on a 1 mm-mesh sieve were identified to the lowest possible taxonomic level.

Abundance, species richness, and Shannon-Wiener diversity index (H') for mobile epi-benthic invertebrates were calculated for each quadrat. Seagrasses and seaweeds were also classified to the lowest possible taxonomic level, and then dried at 60 °C for 24–48 h. Dry weight of each macrophyte species was measured for each quadrat; hereafter we refer to the dry weight as biomass. Species richness, Shannon-Wiener diversity index (H') for macrophytes was calculated for each quadrat. In addition, we used the taxonomic diversity index (Delta) as the index for phylogenetic diversity. Delta is empirically

related to H' , but has an additional component of taxonomic separation (Warwick and Clarke, 1995). As the difference in the taxonomic category (i.e. species, genus, family, order, class and phyla) among macrophyte species increases (i.e. greater taxonomic separation), higher Delta values are calculated. AlgaeBase (<http://www.algaebase.org> on January 15th, 2017) was used to confirm macrophyte taxonomic categories. Unidentified amphipods were excluded when calculating species richness and H' . Some macrophytes and invertebrates included multiple species (e.g. *Halimeda* spp. and Amphipodidae spp.) and each of them was treated as one species because preliminary analyses with the data from which those multiple species were excluded did not alter the general trends (Tables S1–S4). Rhodophyta sp.1 could not be identified below class and this species was excluded when calculating Delta because the values of Delta were almost unchanged (below 0.01) even assuming that Rhodophyta sp.1 was different from other macrophyte species in the highest taxonomic category level (i.e. different from other rhodophyte species in the class).

2.3. Statistical analysis

We compared the community structures of macrophytes as well as mobile epi-benthic invertebrates using the Bray-Curtis dissimilarity matrix calculated from square-root transformed macrophyte biomass or invertebrate abundance data to balance contributions from rare species. The macrophyte and invertebrate community structures were visualized using non-metric multidimensional scaling (nMDS) of metaMDS function in R version 3.3.2 packages vegan. Both of the stress values were below 0.2, which provide useful 2-dimensional ordinations (Clarke and Warwick, 2001).

We conducted regression analyses for macrophyte parameters to assess the effect of each macrophyte parameter, that is the macrophyte biomass, the macrophyte species richness, the macrophyte H' and the macrophyte Delta, on the abundance, the species richness and the H' of mobile epi-benthic invertebrates. Generalized linear mixed models (GLMMs) were used to analyze the abundance and the species richness of invertebrates. As these response variables are discrete data, Poisson distributions with log link functions were used. Random intercepts were included for each quadrat to account for environmental differences and to address overdispersion of residuals (Harrison, 2014). GLMMs were fitted using Gauss-Hermite quadrature, which is more accurate than the Laplace approximation in parameter estimation (Bolker et al., 2009). Generalized linear models (GLMs) were used to analyze H' of invertebrates with Gaussian distributions and identity link functions as H' are continuous data. Residuals for violations of normality and homoscedasticity were visually inspected. The results of nMDS showed that the community structure of macrophytes and invertebrates differed between 2014 and 2015, so that the relationships between each macrophyte parameter and respective invertebrate parameters may have differed between the two years. Therefore, we constructed three models for each macrophyte parameter: a model including only a macrophyte parameter as a predictor variable, a model including a macrophyte parameter and year as predictor variables and a model including a macrophyte parameter, year and the interaction between the two as predictor variables. Then, we compared Akaike's information criterion (AIC) of the three models and drew the fitted line using the lowest AIC model for each macrophyte parameter.

In addition to the above regression analyses, we conducted multiple regression analyses and model selections to assess the contribution of each macrophyte parameter to the respective invertebrate parameters. The macrophyte biomass, the macrophyte species richness, the macrophyte H' , the macrophyte Delta, year and interactions between the former four variables and year were included as predictor variables in the global models. GLMMs were used to analyze the abundance and the species richness of mobile epi-benthic invertebrates and GLMs were used to analyze H' of mobile epi-benthic invertebrates. Distributions and link functions were the same as the single regression analyses.

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