

REPORT

Foundation species canopies affect understory beta diversity differently depending on species mobility

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Abstract

Beta diversity measures the spatial variation in species composition. Because it influences several community attributes, studies are increasingly investigating its drivers. Spatial environmental heterogeneity is a major determinant of beta diversity, but canopy-forming foundation species can locally modify environmental properties. We used intertidal communities dominated by the canopy-forming alga *Mazzaella laminarioides* as a model system to examine how a foundation species affects spatial environmental heterogeneity and the resulting beta diversity. Since canopies were found to reduce the spatial variation of temperature and desiccation during low tides, we hypothesized that canopies would decrease understory beta diversity, which we tested through a field experiment that contrasted canopy removal with presence treatments over 32 months. The beta diversity of sessile species was always lower under canopies, but canopies never affected the beta diversity of mobile species. The observed responses for sessile species may result from their abundance being more dependent on spatial abiotic variation than for mobile species, which can occur in stressful areas while temporarily foraging or in transit to other areas. These responses may likely apply to other systems exhibiting canopy-forming foundation species hosting sessile and mobile species assemblages.

KEYWORDS

beta diversity, canopy, foundation species, intertidal, mobile species, sessile species

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INTRODUCTION

Beta diversity refers to the spatial variation in species composition (Magurran, 2004). It is an important metric because it can inform our understanding of biodiversity change and its consequences for communities and ecosystems (Mori et al., 2018). For example, beta diversity can increase the capacity of communities to withstand natural or anthropogenic disturbances that affect certain species more than others (Ferrigno et al., 2016). Overall, beta diversity has been associated with changes in the productivity (Silva Pedro et al., 2016; Wang et al., 2021), multifunctionality (Hautier et al., 2018), and resilience (Appolloni et al., 2017) of communities. Therefore, beta diversity is being increasingly considered in regional conservation planning (Socolar et al., 2016; Suurkuukka et al., 2012). While studies continue to address the consequences of beta diversity, additional efforts are focusing on the mechanisms that drive beta diversity changes (Maxwell et al., 2022; McDevitt-Irwin et al., 2021; Mitchell et al., 2022).

Several explanations have been proposed for the variation observed in beta diversity patterns, including dispersal limitation, predation, anthropogenic activities, and heterogeneity of abiotic conditions (Catalán et al., 2020; Gianuca et al., 2017; Legendre et al., 2005; Qian & Ricklefs, 2007). Spatial environmental heterogeneity increases beta diversity by increasing the variety of environmental conditions that species encounter across space, which directly or indirectly affects their abundance (Alahuhta et al., 2017; Corte et al., 2017; Heino et al., 2015; Lawrence et al., 2022; Silliman & He, 2018). Because spatial environmental heterogeneity is ubiquitous in nature, it is likely one of the major drivers of beta diversity patterns.

The physical attributes of the environment (e.g., soil properties, topography) are primary determinants of the magnitude of spatial environmental heterogeneity. However, such heterogeneity can in turn be influenced by biological factors. An example is given by foundation species, which are organisms that typically form extensive canopies. These organisms dominate many terrestrial and aquatic communities and can be either primary producers (e.g., trees and algae) or consumers (e.g., corals and mussels; Catalán et al., 2021; Ellison et al., 2019; Stachowicz, 2001). By limiting abiotic stress in understory environments, these canopies often increase local species richness, or alpha diversity (Altieri & van de Koppel, 2014; Ellison, 2019; Watt & Scrosati, 2013). More importantly for this study, canopies may also decrease the spatial variation in abiotic conditions in understory environments despite spatial variation in substrate properties and wind or water flow above the canopies (Helmuth et al., 2006; Ørberg et al., 2018; Stevens et al., 2015; von Arx et al., 2012).

This knowledge suggests that canopy-forming foundation species might limit beta diversity in natural communities. Such effects should be more pronounced for the sessile species than for the mobile species in the associated community, since sessile species depend more on local conditions given their inability to move away after their reproductive propagules (e.g., spores, seeds, larvae) have settled. This article evaluates these notions experimentally using intertidal species as a model system.

We initially show how a dominant canopy-forming seaweed decreases the spatial variation in temperature and desiccation during low tides, which are key factors affecting intertidal life (Benedetti-Cecchi & Trussell, 2014). We then test the hypothesis that canopy removal increases beta diversity through a field experiment, which we ran for 32 months to determine the temporal consistency of the effects. Because sessile species (algae and filter-feeders) were expected to be more responsive than mobile species (grazers and predators) to spatial environmental variation (Allen et al., 2018; Valdivia et al., 2014), we tested our hypothesis separately for sessile and mobile species, predicting stronger canopy effects on beta diversity for the sessile species. To evaluate whether the level of ecological information could influence the results, we examined beta diversity responses using data on species occurrence (presence/absence) and abundance.

MATERIALS AND METHODS

We conducted this study in rocky intertidal habitats on the Pacific coast of Chile that are dominated by the red alga *Mazzaella laminarioides* (*Mazzaella* hereafter; Broitman et al., 2001; Santelices, 1990). This seaweed inhabits middle and low intertidal elevations on this coast between 28° S and 56° S (Hoffmann & Santelices, 1997). It produces many foliose fronds up to 35 cm long (Jara & Moreno, 1984) that often form extensive canopies that limit thermal and desiccation extremes at the understory (Hoffmann & Santelices, 1997; Moreno & Jaramillo, 1983; Nielsen & Navarrete, 2004), thereby providing a suitable habitat for small species (Jara & Moreno, 1984).

To evaluate the ability of *Mazzaella* canopies to reduce spatial abiotic variation, we conducted a mensurative experiment at Chaihuín (39.94° S, 73.58° W). At the mid-intertidal zone on bedrock areas, patches fully covered by *Mazzaella* canopies are interspersed with patches without canopy cover. At low tide during summer, we measured temperature and desiccation on random substrate areas underneath canopies and on uncovered areas. We took 66 temperature measurements under canopies and 80 on uncovered areas with an infrared thermometer

(ITF 5, PCE Instruments, Palm Beach, FL, USA). We measured desiccation using 22 cotton pads (6 cm in diameter) for canopy-covered areas and 23 pads for uncovered areas. We first submerged all pads in seawater until they reached constant mass. Then we placed the pads on the substrate under either full canopy cover or no canopy cover at low tide. After 1 h of field deployment, we collected all pads and weighed them to calculate the amount of water loss as a measure of desiccation. We calculated the spatial variation in temperature and desiccation as the coefficient of variation (CV) for pairs of randomly selected observations from each treatment. We tested for canopy effects through two-sample testing.

To evaluate the effects of *Mazzaella* canopies on beta diversity, we did a manipulative experiment using rocky intertidal habitats with a similar substrate rugosity and slope, sea surface temperature, and species composition (Valdivia et al., 2013, 2015) found between Limarí (30.75° S, 71.70° W) and Punta Talca (30.93° S, 71.68° W). We used mid-intertidal bedrock areas excluding large cracks and tide pools. On substrate areas fully covered by *Mazzaella*, we randomly established 16 permanent plots (30 cm × 30 cm), marking their position with screws. Using half of the plots selected at random, we created a canopy removal treatment by removing all *Mazzaella* thalli (holdfasts and fronds) with a knife with care to avoid disturbing understory species (we also removed surrounding *Mazzaella* fronds that could lay over these plots). The other half of the plots were not altered and, thus, served as controls. We started this experiment in January 2015 and ended it in August 2017 (32 months). Any *Mazzaella* recruits found during this period in canopy removal plots were removed.

Every 3 months at low tide, we measured the abundance of each species (>5 mm) found in each plot. For the entirety of each plot, we measured percent cover for each sessile species and density (number of individuals per square meter) for each mobile species, as is normally done in intertidal studies (Broitman et al., 2011; Freilich et al., 2018; Menge et al., 2017). We identified most taxa to the species level, with a few identified at higher levels due to morphological unclarities, as is often done in non-destructive community studies (Broitman et al., 2001; Kimbro & Grosholz, 2006; Russell et al., 2006). We used Oliva and Castilla (1992), Hoffmann and Santelices (1997), Espoz et al. (2004), and Zagal and Hermosilla (2007) as identification guides. All scientific names are given in Appendix S1 and conform to the World Register of Marine Species (WoRMS, 2022).

We calculated beta diversity for each treatment and sampling date using species data from pairs of plots selected at random on each sampling date. We quantified beta diversity through the Jaccard and Bray–Curtis dissimilarity indices (Clarke & Warwick, 2001; Stevens, 2009). The Jaccard

index measures compositional dissimilarity between plots based only on differences in species occurrence (presence/absence). It ranges between 0 (when both plots have the same species) and 1 (when the plots do not share any species). The Bray–Curtis index measures compositional dissimilarity between plots based on differences in species abundance. It ranges between 0 (when both plots have the same species with equal abundances) and 1 (when the plots do not share any species). We calculated these indices separately for sessile and mobile species.

We used generalized additive mixed models (GAMMs) to evaluate the effect of *Mazzaella* canopy (two levels: canopy and no canopy) on beta diversity and whether its temporal trend depended on canopy presence (Wood, 2017) using an “ordered factor smooth interaction” approach (Simpson, 2017). We chose this technique to be able to examine curvilinear trends in the responses. We ran a separate model for each beta diversity index for sessile and mobile species. Appropriate smoothness for each applicable model term was determined through maximum likelihood (Wood, 2011). Model validation was also examined. All models were fitted using a Gaussian error distribution. Then, for each beta diversity index and for sessile and mobile species separately, we plotted the difference between the smoothed temporal trend of the no-canopy and canopy treatments (van Rij et al., 2017). If the mean and 95% confidence interval of the contrast were both above zero, we interpreted this as meaning that the no-canopy treatment had a positive effect on beta diversity. We did these statistical analyses with the *vegan* (Oksanen et al., 2018), *mgcv* (Wood, 2017), and *itsadug* (van Rij et al., 2017) packages in R version 3.6.1 (R Core Team, 2019). All of the data on species abundance used for this study are freely available from the *figshare* online repository (Catalán et al., 2023).

RESULTS

The spatial variation (CV) in temperature was, on average, 43% lower ($t_{71} = 2.8$, $p = 0.007$) under *Mazzaella* canopies (10.4 ± 1.4 ; mean \pm SE) than on uncovered substrate areas (18.1 ± 2.2), while the spatial variation in desiccation was on average 48% lower ($t_{20} = 2.2$, $p = 0.020$) under *Mazzaella* canopies (38.5 ± 7.6) than on uncovered substrate areas (74.3 ± 14.4).

During the 32 months of the experiment, we identified a total of 43 taxa (Appendix S1), including 27 sessile and 16 mobile taxa. In total, we found 36 taxa (24 sessile and 12 mobile) for the no-canopy treatment and 42 taxa (26 sessile and 16 mobile) for the canopy treatment.

For sessile species, beta diversity was higher overall for the no-canopy treatment than for the

canopy treatment based on both the Jaccard index (41% higher on average, $t_{87} = 4.609$, $p = 0.001$) and the Bray–Curtis index (40% higher on average, $t_{87} = 6.648$, $p = 0.001$). The temporal trend in beta diversity throughout the study period was statistically

similar between both treatments based on the Jaccard index ($F_{0.001,10} = 0.001$, $p = 0.568$) and the Bray–Curtis index ($F_{1,1} = 0.192$, $p = 0.662$). The confidence band for the difference between both smoothed temporal trends revealed that the increase in beta diversity caused by

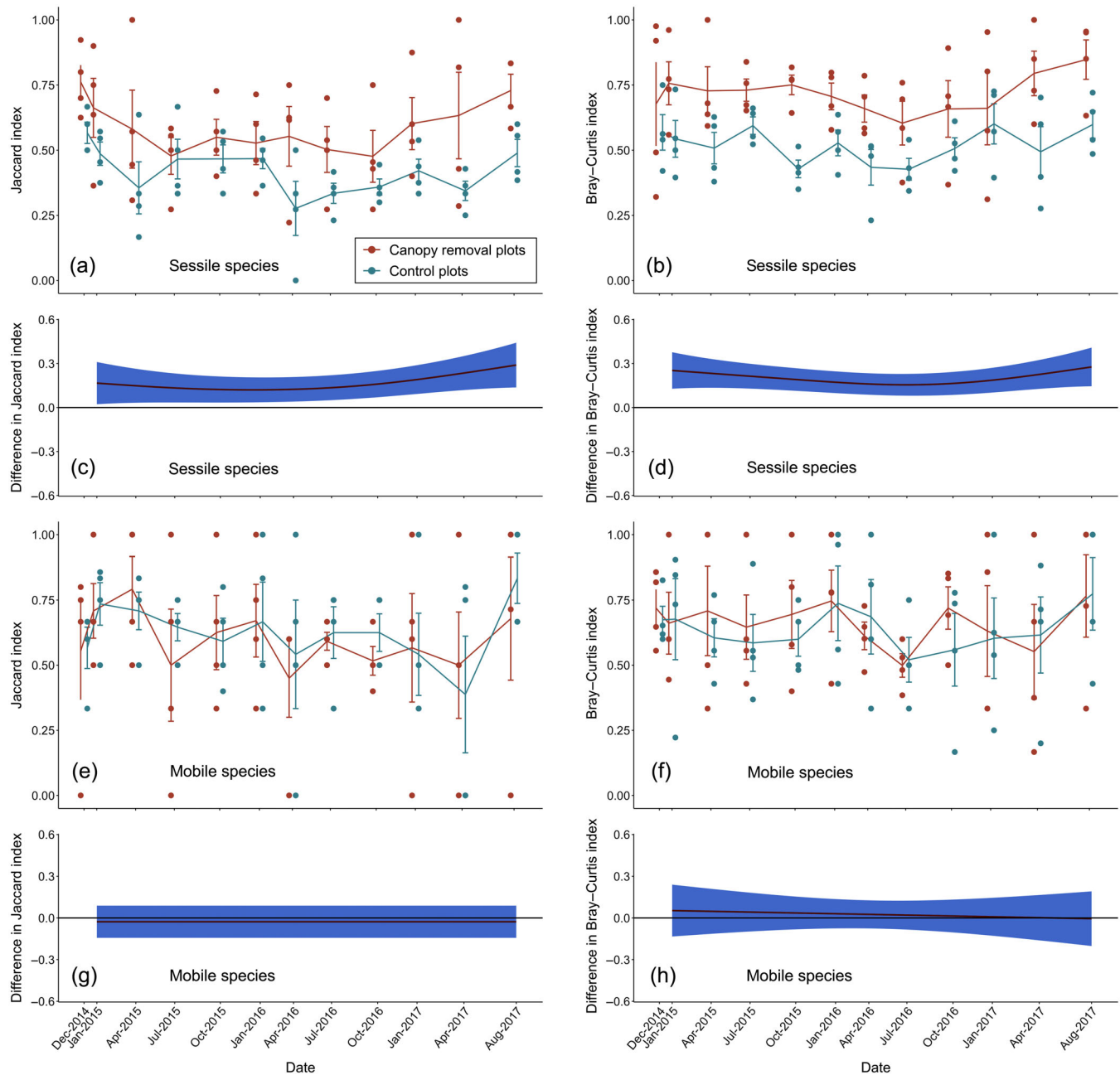


FIGURE 1 (a, b) Beta diversity of sessile species expressed as (a) the Jaccard index and (b) the Bray–Curtis index for the no-canopy (canopy removal) and canopy (control) treatments across the 12 studied dates (the line for each treatment connects the corresponding means and the error bars depict standard error, while the dots depict the values of each replicate plot). (c, d) Difference between the smoothed temporal trends of beta diversity for the no-canopy and canopy treatments for sessile species based on (c) the Jaccard index and (d) the Bray–Curtis index, showing in both cases the 95% confidence band. (e, f) Beta diversity of mobile species expressed as (e) the Jaccard index and (f) the Bray–Curtis index for the no-canopy (canopy removal) and canopy (control) treatments across the studied dates (the line for each treatment connects the corresponding means and the error bars depict standard error, while the dots depict the values of each replicate plot). (g, h) Difference between the smoothed temporal trends of beta diversity for the no-canopy and canopy treatments for mobile species based on (g) the Jaccard index and (h) the Bray–Curtis index, showing in both cases the 95% confidence band.

canopy removal was persistent over time based on both dissimilarity indices (Figure 1).

For mobile species, however, neither the Jaccard index ($t_{87} = 0.465$, $p = 0.643$) nor the Bray–Curtis index ($t_{87} = 0.484$, $p = 0.630$) differed significantly overall between the two canopy treatments. The temporal trend in beta diversity was also statistically similar between both treatments based on the Jaccard index ($F_{0.001,10} = 0.001$, $p = 0.487$) and the Bray–Curtis index ($F_{1,1} = 0.081$, $p = 0.777$). The confidence band for the difference between both smoothed temporal trends included zero persistently over time based on both dissimilarity indices (Figure 1).

DISCUSSION

In intertidal habitats, crevices, ridges, and rugosity create heterogeneity in temperature and desiccation across the substrate during low tides (Aguilera et al., 2019; Chapman & Bulleri, 2003; Lam et al., 2009; Mazzucco et al., 2020), but *Mazzaella* canopies reduce such environmental heterogeneity. It is then likely that, after canopy removal, abiotic filtering eliminated sessile species lacking physiological adaptations to extreme conditions in some plots (Crowe et al., 2013), increasing their occurrence-based beta diversity. The increase in their abundance-based beta diversity after canopy loss could have additionally resulted from reduced abundances in stressful plots in species that can tolerate stressful conditions but that do not thrive in them. Indeed, spatial variation in assemblage composition often results from species-specific responses to environmental gradients, with locations (plots in our case) with similar conditions often hosting similar assemblages (Catalán et al., 2020; López-Delgado et al., 2020).

Species mobility influenced beta diversity responses, however, since the beta diversity of mobile species was not affected by canopy removal. Mobile organisms exhibit dynamic spatial distributions (Schmitz, 2008), so they can be found in stressful habitats in patchy environments while foraging or in transit to other places, since they can reach benign habitats with relative ease (Amarasekare & Nisbet, 2001; Barua & Heckathorn, 2004; Marini et al., 2012). This property of mobile species is thus what might explain the absence of canopy effects on their beta diversity. In support of this notion, the temporal synchrony of species abundance changes between no-canopy plots (Pearson's correlation) was, on average, 0.32 for sessile species but only 0.15 for mobile species, revealing a higher degree of asynchrony for mobile species consistent with an active mobility of organisms across space. The influence of species mobility on beta diversity patterns is

increasingly attracting research attention (Soininen et al., 2018). This study shows for the first time that species mobility influences the effects of foundation species on beta diversity.

Monitoring biodiversity across space and time is critical to obtaining a more complete and realistic view of how natural and anthropogenic disturbances influence ecological communities (Socolar et al., 2016). This study demonstrates that the loss of a canopy-forming foundation species increased the beta diversity of sessile, but not mobile, assemblages. In addition, we linked these responses to changes in spatial environmental heterogeneity associated with the presence of canopies, information that is highly desirable for beta diversity research (Soininen et al., 2018). Also, the effects (or lack thereof) of canopy removal on beta diversity were consistent over almost 3 years. Overall, our study contributes novel insights into the mechanisms that shape beta diversity by demonstrating that canopy loss can increase the biological heterogeneity of the landscape.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Catalán et al., 2023) are available in Figshare at <https://doi.org/10.6084/m9.figshare.21953552.v1>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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