

Differential Spatiotemporal Distribution of Cryptic Intertidal Bangiales

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Morphologically similar but genetically distinct species have been termed cryptic and most have been assumed to be ecologically similar. However, if these species co-occur at a certain spatial scale, some niche differences at finer scales should be expected to allow for coexistence. Bladed Bangiales were identified and quantified across four intertidal elevations and four seasons for one year, at five rocky intertidal sites (between 39° S and 43° S) in southern Chile. Species determination was based on partial sequences of the mitochondrial cytochrome c oxidase 1 (COI) gene amplification. To assess species gross morphology, thallus shape, color, and maximum length and width were recorded. Hundreds of organisms were classified into nine Bangiales species belonging to three genera (i.e., *Fuscifolium*, *Porphyra*, and *Pyropia*), including five frequent (>97% of specimens) and four infrequent species. All species, except for *Pyropia saldanhae*, had been previously reported along the coasts of Chile. The thallus shape and color were very variable, and a large overlap of the maximum width and length supported the cryptic status of these species. Multivariate analyses showed that the main variable affecting species composition was intertidal elevation. Species such as *Py. orbicularis* were more abundant in low and mid intertidal zones, while others, such as *Po. mumfordii* and *Po. sp. FIH*, were principally observed in high and spray elevations. Despite all numerically dominant species being present all year long, a slight effect of seasonal variation on species composition was also detected. These results strongly support the existence of spatial niche partitioning in cryptic Bangiales along the Chilean rocky intertidal zone.

niche partitioning

environmental gradients

Chile

1. Introduction

The study of species co-occurring along environmental gradients allows us to improve the mechanistic understanding of biodiversity. For instance, cryptic species are commonly found co-occurring in organisms such as corals [1][2], nematodes [3], rotifers [4], and red algae [5][6] living in aquatic environments subjected to strong physical or chemical gradients (e.g., light intensity, desiccation stress, or salinity). Cryptic species have been classically defined as genetically distinct taxa that have been erroneously classified under a single nominal species name because they are, at least superficially, morphologically indistinguishable [7][8]. These cryptic taxa have been shown to be especially common in the marine realm [9]. Cryptic species that are morphologically similar have been assumed to be ecologically similar, which implies that they require very similar resources [7][8]. However, if these species are actually coexisting, some niche differences would be expected [1][2][9][10][11].

Contemporary coexistence theory predicts that niche partitioning allows for stable long-term coexistence of co-occurring species if their differences in competitive abilities (i.e., “fitness differences”) are not extremely large [12][13]. Therefore, cryptic species being truly ecologically similar and competing for the same resources should be observed in the same habitat only transiently [14][15]. Alternatively, Hubbell’s [16] unified neutral theory of biodiversity and biogeography posits that coexistence could be due to stochastic events of reproduction, death, and dispersal along with speciation but without any effect of niche partitioning or selection. Yet, such an extreme ecological equivalence between coexisting species has proven to be elusive in nature, and minor niche differences have been shown to underpin the slow competitive exclusion of inferior competitors (e.g., [17]). Cryptic species, despite largely similar morphologies, have been shown to exhibit subtle differential physiological tolerances, leading to niche partitioning and stable coexistence [4].

The rocky intertidal zone provides an ideal habitat to assess the association between the composition of cryptic species and environmental gradients over space and time. In the intertidal zone, stress increases with elevation, due to desiccation and sun exposure, favoring rapid vertical changes in community composition [18][19]. The strength of desiccation, jointly with other factors, such as the distribution of consumers, can affect the temporal and spatial distribution and composition of resource species (e.g., macroalgae [20][21]). Moreover, intertidal habitats in temperate biogeographic zones can be exposed to important seasonal variations in abiotic environmental conditions, affecting sessile invertebrate and macroalga performance and community structure [22][23][24][25][26].

Multiple macroalgae cryptic species have been identified co-occurring along rocky intertidal habitats. For example, cryptic species of the genus *Ectocarpus* (brown algae) show differences in attachment substrate and tidal zonation at a very small scale (i.e., a few meters [27][28]). Regarding other groups of cryptic macroalgae, such as bladed Bangiales (red algae), only a few studies have been performed along the intertidal gradient. In New Zealand, nine species were recorded along a three-year study in a single location, but no differences in seasonal growth or small-scale distribution were detected between the two most common species [29].

2. Responses of Bladed Bangiales to Vertical Stress Gradients in Intertidal Habitats

The results support the hypothesis that niche differences lead to distinct spatiotemporal patterns of cryptic bladed Bangiales in the southern part of the Chilean coast. Intertidal elevation accounted for most of the variation in species composition. Thus, and despite the observed overlaps in species abundances, the results support the existence of spatial niche partitioning in cryptic Bangiales along the intertidal zone.

The constant alternation of low and high tides determines that high intertidal elevations are characterized by strong physiological constraints for organisms living in intertidal habitats in terms of desiccation [30], high temperatures [31], nutrient shortages [32], and high UV radiation [33][34]. Thus, the upper distribution boundary of intertidal species is related to species physiological limits. Contrastingly, the lower limit of intertidal species distribution seems to be mainly regulated by biological interactions (e.g., consumption and competition) [35][36][37][38]. In southern Chile, for instance, small-sized grazers have been shown to strongly control the growth of intertidal macroalgae and sessile

invertebrates over succession [39][40]. Thus, the interplay of biotic and abiotic factors generates a sharp gradient of environmental conditions and a broad niche space in intertidal habitats [41][42][43].

Even though bladed Bangiales were morphologically very similar, some species occurred at different intertidal elevations. For example, while *Py. orbicularis* was mainly present at low/mid-intertidal elevations, both *Po. mumfordii* and *Po. sp. FIH* were distributed higher on the shore. These patterns were not detected in the previous studies focusing on the center part of the Chilean coast [44][45][46][47]. The species *Py. orbicularis* was first described as colonizing the upper and mid intertidal area of the Maitencillo beach (central Chile, [46]), but the species' abundance across intertidal elevations was not estimated in that study. In the same site, various studies also reported *Py. orbicularis* as commonly encountered in the high intertidal elevation [44][45]. It is possible that ecotypes with distinct preferences in intertidal elevations exist within *Py. orbicularis*, a species for which clear genetic differences have been detected between the samples from extreme south, south, central and north Chile [6].

3. Seasonal Variation in Intertidal Species Assemblages

Even if the effect of seasonal variation on species composition was much weaker than that imposed by intertidal elevation, the results show that seasonal changes affect bladed Bangiales communities in south Chile. For example, the distribution patterns observed for *Py. sp. CHJ* varied between seasons, with an increase in abundance from low to high intertidal elevations in spring and summer but a decrease along the same environmental gradient during autumn and winter.

Nonetheless, all the relatively abundant species observed in the study area were present across the four seasons sampled. In northern Atlantic populations of *Po. umbilicalis*, the production of spores (i.e., asexual spores or neutral spores) has been shown to be highly seasonal, with a higher spore release from fall to early spring [48][49][50]. These results are concordant with observations of the bladed Bangiales recruitment peak during autumn in New Zealand [29]. It is possible that most species of Chilean bladed Bangiales also reproduce during the colder periods, affecting the cover and biomass of Bangiales within each site but not necessarily the structure of the entire species assemblage [50].

4. Diversity and Biogeography of Bladed Bangiales

Measures of maximum blade width and length exhibited an overlap between the nine identified species. These results support the cryptic status of these species, at least at the level of gross morphology. Similar results were obtained for the bladed Bangiales species community located in central Chile, where only *Po. longissima* could be clearly differentiated morphologically from the rest of the bladed Bangiales, due to its long and thin blades [44]. At the study sites, *Po. longissima* was also characterized by long, thin, lanceolate thalli. However, *Po. longissima* shared these characteristics with some specimens from other species. A high level of variability in terms of thallus color, shape, and size was observed within species, probably due to phenotypic plasticity. A previous study conducted in central Chile detected clear phenotypic plasticity in *Po. mumfordii*, with specimens from the

high and mid intertidal habitats showing long, thin, lanceolate thalli, while the ones from the low intertidal habitats were characterized by much wider elongated rosettes [47]. Taken together, these results are in agreement with the previous studies that showed that morphological characters alone could lead to inaccurate species determination in bladed Bangiales [51][52][53][54]. In many taxa, most detected cryptic species represent recently diverged entities that still share the same gross morphology [55]. However, molecular studies have also revealed the existence of non-monophyletic complexes of cryptic species, and morphological similarities in these cases have been associated with evolutionary convergence, morphological stasis, or developmental constraints [55].

5. Conclusions

The observed differences in the occurrence and abundance of cryptic bladed Bangiales along the rocky intertidal zone in south Chile hint at niche partitioning within this assemblage. This, in turn, has probably favored the co-existence in time of these Bangiales species and indicates that they are not fully ecologically similar. Future research on physiological responses to biotic and abiotic environmental stress would help us to understand the mechanisms underpinning the observed spatial patterns. In bladed Bangiales, as in other species characterized by a complex life cycle, both the microscopic sporophyte (also known as the conchocelis phase) and the macroscopic gametophytic phases are important to study. Indeed, laboratory-based experimental studies have shown that the sporophyte and gametophyte phases respond differently to abiotic stresses (light and temperature [56][57]) and grazing pressure by intertidal mollusks [58].

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