**Habitat stability modulates temporal β-diversity patterns of seagrass-associated fauna across biogeographical scales**

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**Abstract.**

Aim

Identifying drivers that shape biodiversity across biogeographical regions is important to predict ecosystem responses to environmental changes. While beta diversity has been widely used to describe biodiversity patterns across space, the dynamic assembly of species over time has been comparatively overlooked. Insights from terrestrial and marine studies on temporal beta diversity has mostly considered environmental drivers, while the role of biotic mechanisms has been largely ignored. Here, we investigated patterns of temporal variation in beta diversity of seagrass-associated animals (amphipods, as model organisms).

Location

We conducted a study in three biogeographical regions across a temperate to subtropical latitudinal gradient (approximately 2,000 km, 13º of latitude). In each region, we randomly selected three C. nodosa meadows, totalling nine meadows sampled seasonally (i.e., four times per year) from 2016 to 2018.

Methods

We partitioned temporal beta diversity into its turnover (i.e. species replacement) and nestedness (i.e. differences in species composition caused by species losses) components and addressed the relative influence of both temporal variation in habitat structure (i.e., biotic driver) and environmental conditions on such patterns.

Results

Our study revealed high temporal beta diversity of amphipod assemblages across the three biogeographical regions, denoting significant fluctuations in species composition over time. We identified species turnover as the primary driver of temporal beta diversity, strongly linked to temporal variability in local habitat structure rather than regional climatic drivers. Subtropical Atlantic meadows with high structural stability over time exhibited the largest turnover rates compared with temperate Mediterranean meadows, under lower structural stability, where nestedness was a more relevant component of temporal beta diversity.

Main conclusions

Our results highlight the crucial role of habitat stability in modulating temporal beta diversity patterns on animals associated with seagrasses, stressing its importance for developing management plans and restoration actions in the context of diversity loss and fragmentation of ecosystems.

**Keywords:** Amphipods, community assembly, ecosystem engineers, environmental stability, nestedness, species turnover,

1. **Introduction**

Understanding patterns in variation of biological assemblages and underlying processes has been, for many decades, at the core of ecological research (Brown, 1995; Gaston et al., 2008; Gotelli, 2009; Bosch et al., 2021). The distribution of biota, with some taxa occurring at certain sites and times but not at others, has significant implications for biodiversity conservation and the maintenance of ecosystem functions (Cardinale et al., 2006; Clare et al., 2022). Sites hold varying abundances of different species because of abiotic and biotic filters, which coexist to create a biological community (Brown, 1984). As a result, communities across spatial and temporal scales can range from being nearly identical (i.e., when they host the same species) to entirely distinct (i.e., when they harbour completely different species) (Baselga and Rodríguez, 2019). A key question remains then on how to measure biodiversity to understand the processes that generate such variation in ecological pattern. For example, beta diversity, often defined as variation in species composition across sites within a geographic area, has been widely used to establish a connection between local (i.e., alpha) and regional (i.e., gamma) diversity patterns (Whittaker, 1960; Anderson et al., 2011; Gaggiotti et al., 2018). Despite this spatial approach provides critical information about the structure of communities to inform conservation planning (Socolar et al., 2016), it often overlooks the highly dynamic assembly of species resulting from varying processes that occur over time (Legendre, 2019).

In recent years, several studies have adopted a temporal perspective to examine beta diversity (Baselga et al., 2015; Legendre, 2019; Magurran et al., 2019), fuelled by the ongoing rapid reorganization of biological assemblages in the Anthropocene (Hillebrand et al., 2018; Blowes et al., 2019; Bosch et al., 2022). This approach evaluates variation in relative abundances and community composition over time and determines whether these differences arise from changes in the identity of species (i.e., replacement or turnover), or from times of fewer species being subsets of times with higher species richness (i.e., nestedness) (Baselga, 2010). Most insights of temporal trends in beta diversity, considering its partition into turnover and nestedness components, have been derived from terrestrial ecosystems (Baselga et al., 2015; Uchida and Ushimaru, 2015; Legendre and Condit, 2019; Crabot et al., 2020; Lindholm et al., 2021; Wu et al., 2022). In marine ecosystems, however, these studies remain scarce and have primarily focused on pelagic organisms, such as bacteria (Hatosy et al., 2013), phytoplankton (Guelzow et al., 2014), and zooplankton (Lopes et al., 2019). Unlike pelagic, the dynamics of benthic ecosystems are more strongly shaped by the interplay between abiotic and biotic drivers, particularly for fauna living in close association with the benthos that rely on habitat structural properties. Yet, studies to date on fishes (Magurran et al., 2015; Zeni et al., 2020; Alabia et al., 2021; Camara et al., 2021) has mostly used environmental conditions (e.g., nutrient concentration, temperature, depth) to infer drivers of temporal variability in beta diversity, therefore ignoring variability in the benthic habitat structure. This reflects the existing gap in our comprehension of biotic drivers influencing temporal beta diversity in marine ecosystems (i.e., turnover and nestedness components), and questions whether these findings can be generalised to animals with lower mobility and higher dependence on habitat properties.

Benthic marine ecosystems exhibit a high degree of dynamism through both spatial and temporal dimensions (Underwood and Fairweather, 1989; Coma et al., 2000). This is particularly evident for diversity patterns of fauna associated with habitats created by “ecosystems engineers” (e.g., kelps, rhodoliths, seagrasses, etc.), because associated biotas are intrinsically linked to variation in the structural properties of their habitats (Jacobucci et al., 2009; Machado et al., 2019; Navarro-Mayoral et al., 2020; Pérez-Peris et al., 2023). In this regard, seagrasses provide a unique environment for studying species assemblages over both space and time, because of their notable variability in distribution, e.g., fragmentation across space, and extent throughout time, i.e., seasons and years (Edgar, 1990; Boström and Bonsdorff, 1997; Guidetti et al., 2002). In general, these marine plantsshow a marked seasonal variation, with more vigorous meadows in spring and summer, compared to winter and autumn, where they reach minimum vitality (Tuya et al., 2006; Máñez-Crespo et al., 2020). Moreover, seagrass meadows provide substantial support for epiphytes (Orth, 1984; Hall and Bell, 1988), which experience temporal fluctuations in abundance and composition, influenced by a range of abiotic (e.g., temperature variations; Borowitzka et al., 2006) and biological factors (e.g., intensity of herbivory; Tomas et al., 2005). This makes seagrass meadows one of the marine ecosystems with highest structural and biological heterogeneity (Böstrom et al., 2006).

Epifauna living on seagrasses typically display large seasonal variation in both abundance and species richness (Moore and Hovel, 2010; Leopardas et al., 2014), including mollusks, polychaetes, and crustaceans (e.g., Gambi et al., 1992; Scipione et al., 1996; Nakaoka et al., 2001). Amphipods, in particular, are one of the most abundant and diverse animal groups associated with seagrasses (Hyndes and Lavery, 2005; Vázquez-Luis et al., 2009; Michel et al., 2015; Sweatman et al., 2017). These crustaceans are a key group of organisms contributing to energy transfer in marine systems, acting as a link between primary producers and secondary consumers (Myers and Heck, 2013). The distribution and diversity of amphipods are influenced by a range of factors, including both habitat structure and environmental processes. For instance, changes in salinity and/or temperature can alter reproduction and survival of amphipods (Welton and Clarke, 1980; Sainte-Marie, 1991; Reynolds et al., 2018). However, the structural attributes of the habitat can play an equally, if not more, crucial role than climatic conditions (Fraser et al., 2020; Navarro-Mayoral et al., 2023). Structural elements of seagrass meadows (e.g., shoot densities) and the availability of secondary substrates (e.g., epiphyte biomass) can profoundly influence the distribution and diversity of amphipods. In other words, these habitat-related factors interact with climatic conditions over time to shape the community dynamics of amphipod assemblages (Navarro-Mayoral et al., 2023). Therefore, it is important to consider the temporal component of changes in species composition (i.e., beta diversity) to improve our understanding of how biotic communities respond in non-stationary environments. Contrary to marine taxa living in more homogenous environments (e.g., plankton) and with higher dispersal abilities (e.g., fishes), amphipods represent an ideal model taxon due to two key aspects of their ecology: (i) their direct development and (ii) low dispersal (Kolding and Fenchel, 1981; Sainte-Marie, 1991; Fernandez-Gonzalez et al., 2021). Their direct development means they reproduce without a dispersive larval phase, which enhances the stability and local persistence of their populations (Highsmith and Coyle, 1991; Fernandez-Gonzalez et al., 2021). Additionally, their limited dispersal restricts their spatial movement, heightening their sensitivity to changes within their local habitat (Munguia et al., 2007). Consequently, they serve as perfect indicators of the temporal variability of beta diversity in these ecosystems.

This study aims to investigate patterns and drivers of variation in beta diversity of seagrass *Cymodocea nodosa*-associated amphipods over two years across a wide biogeographical range across the Atlanto-Mediterranean region, i.e., 2,000s of km. The distribution of *C. nodosa* encompasses different ecoregions, subjected to varying climatic conditions and landscape configurations (Tuya et al., 2019; Máñez-Crespo et al., 2020). This provides an ideal case-study to partition the influence of both habitat structural attributes and climatic conditions on temporal compositional changes of seagrass-associated amphipods. In particular, we investigated (1) how beta diversity varies in amphipod assemblages over time, at 9 times through 2 years at 9 meadows from three different marine ecoregions, (2) whether these changes result from the turnover or nestedness components, and (3) which drivers typifying meadow structure and climatic conditions majorly contributed to explain such patterns in temporal beta diversity. In brief, the goal of this study is to examine temporal changes in beta diversity of amphipods to identify underlying causes.

1. **Materials and methods**
   1. *Study areas and sampling design*

*Cymodocea nodosa* (Ascherson, 1869) is a dominant seagrass in subtidal zones across the Mediterranean Sea and the adjacent Atlantic Ocean, including southern Portugal, Mauritania, Senegal, the Canary Islands and Madeira (Tuya et al., 2021). We conducted a study in three biogeographical regions across a temperate to subtropical latitudinal gradient (*ca.* 2,000 km, 13º of latitude; Fig. 1). This distribution covered the eastern Iberian Peninsula (Alicante [AL], 38º N), the Balearic Sea (Mallorca Island [ML], 40º N), both regions in the Western Mediterranean, and Macaronesia (Gran Canaria Island [GC], 28º N) in the northeastern Atlantic Ocean (Fig. 1).In each region, we randomly chose three nearshore *C. nodosa* meadows, each separated by at least 4 km, to capture variations in meadow structure and environmental conditions within each biogeographical region. At each meadow, seagrass structure and amphipod assemblages were sampled seasonally (i.e., 4 times a year) throughout 2016 to 2018, for a total of 9 temporal collections at each of the 9 meadows.

* 1. *Collection of amphipod assemblages*

At each time, we collected 5 random samples of vegetation and associated epifauna, separated by *ca.* 5 m from each other (Edgar and Robertson, 1992). We used a fine mesh bag (250 μm) affixed to a quadrat (25 x 25 cm2) placed over the seagrass canopy (0.0625 m2 of total area), which was then cut at the sediment surface level. We used this specific mesh size to effectively capture all amphipods, given their typical size range of 500 μm to 1 mm (Hughes and Ahyong, 2016). Sample bags were transported to the laboratory, where amphipods were separated using a mesh, and then identified and counted under a stereomicroscope (Ruffo, 1998). For each sample, we determined species abundances (expressed as number of individuals per m2).

* 1. *Habitat structure and climatic context*

For each sampling time and meadow, seagrass cover was *in situ* estimated by deploying on the bottom a 25 m-long fiberglass transect, and subsequent annotation of the total distance covered by the seagrass; final values were then expressed in percent cover. Plant biomass was measured by taking n = 10 cores (20 cm inner diameter, 50 cm depth) haphazardly located within each meadow. In the laboratory, sediment was removed from the cores, and above-ground biomass was separated and dried (60ºC at 48 h). Seagrass leaf biomass data was standardized to the core area and expressed as g DW cm-2. Seagrass density was estimated by counting the number of shoots in a 20 x 20 cm2 quadrant (n = 10) haphazardly allocated at each meadow and time. In addition, 20 shoots were randomly collected by hand at each meadow and sampling time. In the laboratory, we quantified the number of leaves per shoot, as well as the length and width (mm) of all leaves. Macroscopic epiphytes were removed using a razor blade and epiphytes and leaves were subsequently oven-dried to estimate epiphytic load (i.e., dry weight, DW, of epiphytes per DW of leaf biomass). Total leaf area (Seagrass Surface Area; SSA) was obtained as the sum of all the individual leaf areas of all leaves per shoot (cm2/shoot), and the Leaf Area Index (LAI) was estimated by multiplying the total leaf area per shoot by the mean shoot density per meadow and time. Epiphytic loads were expressed as g DW of epiphytes per g DW of leaf. These data were already presented in Máñez-Crespo et al. (2020).

To describe spatial and temporal variability in ocean climate, monthly data of Sea Surface Temperature (SST) and Photosynthetically Active Radiation (PAR) intensity were obtained through the entire study period (2016-2018), as in Máñez-Crespo et al. (2020), from the Moderate Resolution Imaging Spectroradiometer facility (MODIS-Aqua), using the Nasa Giovanni system (https://giovanni.gsfc.nassa.gov/giovanni/). The spatial resolution of all data collected was a 4 x 4 km2 grid that included each of the nine surveyed meadows. For each time, we calculated the mean SST and PAR.

* 1. *Statistical analyses*
     1. *Temporal beta diversity of amphipod assemblages*

Differences in the composition and structure of amphipod assemblages were assessed, for each meadow over the 9 times, using the 'betapart' R package (Baselga and Orme, 2012). For species composition, we used the 'beta.multi' function (Baselga, 2010) with the “Sørensen” family of dissimilarity (βSOR; Equation (1). This approach partitioned temporal beta diversity into its turnover (βSIM: turnover component of Sørensen dissimilarity; Equation (2)) and nestedness (βSNE: nestedness component of Sørensen dissimilarity; Equation (3)) components. When considering abundances, the 'beta.multi.abun' function was used, with the Bray-Curtis dissimilarity family specified. Hence, total dissimilarity for each meadow through time was studied by considering abundance data in addition to composition. The equations to calculate indices of temporal beta diversity for multiples times, considering the composition and structure data were the following:

Equation (1). Sørensen dissimilarity for multiple times:

βSOR = (1)

where Si is the total number of species in time *i*, ST is the total number of species at all times and *bij*, *bji* are the number of species exclusive to times *i* and *j*, respectively, when compared by pairs.

Equation (2). Similarity component of species turnover for multiple times:

βSIM =  (2)

Equation (3). Similarity component for species nestedness for multiple times:

ΒNES = βSOR – βSIM (3)

* + 1. *Drivers of temporal beta diversity*

Univariate Generalized Linear Models (GLMs) explored the relative contribution of predictor variables, typifying temporal variation (via coefficients of variation) in the habitat structure and environment of each seagrass meadow, on variation in the components of temporal beta diversity of amphipod assemblages (i.e., Sørensen, turnover, nestedness and Bray Curtis index). Prior to implementation of the models, correlations (Spearman coefficients) among each pair of predictor variables were tested and visualized using the ‘corrplot’ R package (Wei et al., 2017). To limit the inclusion of overly correlated predictors in the models, we chose those with a larger biological significance among those predictors that were correlated (Spearman correlation coefficient with r2 > 0.6; see Appendix S1 in Supporting Information) (Bolker, 2008). This analysis led to the selection of four predictors: seagrass leaf biomass, seagrass cover, seagrass shoot density and epiphytic loads, as descriptors of habitat (seagrass meadow) structure, and mean seasonal SST within a meadow as a descriptor of ocean climate. After modelling, Variance Inflation Factors (VIFs) among predictors was calculated using the ‘car’ R package (Fox et al., 2012), were always < 5, indicating that multicollinearity was not a concern (Quinn and Keough, 2002).

Model selection was performed to identify those predictors, or combinations, that better explain variation in the components of temporal beta diversity of amphipod assemblages. First, we used the ‘MASS’ R package (Venables and Ripley, 2002) to perform a backward stepwise approach, by iteratively removing from the full model the predictor variable with the lowest contribution, until obtaining the most parsimonious model according to the Akaike Information Criterion corrected for small sample sizes (AICc). Then, we used the ‘MuMIn’ R package (Barton and Barton, 2015), with the aims of (i) to validate the previous model (stepwise) selection by constructing a full set of candidate models (i.e., models containing all combinations of 1, 2, 3, 4 or 5 predictors), ranking models according to the AICc; and (ii) to estimate the relative importance of each predictor variable. For all fitted models, diagnosis plots of residuals and Q-Q plots were used to visually inspect their appropriateness, while assumptions of homogeneous variance were checked using the Breusch-Pagan heteroscedasticity test.

1. **Results**
   1. *Temporal beta diversity of amphipods*

In total, 6,794 amphipods were counted, including 81 taxa (73 identified at the species level and 8 at the genus level; see Appendix S2). We found a high dissimilarity in amphipod composition through time across all three regions, with the Sørensen index displaying high values irrespective of the seagrass meadow (i.e., βSOR; Table 1). Turnover (βSIM) was the main contributor to beta diversity across all meadows, while the nestedness component contributed considerably less to overall compositional differences, even being negligible in some meadows (e.g., GC, < 0.1, Fig. 2; Table 1). This implies that, in most meadows, the composition of species significantly varied over time, with replacement (turnover) of species as the primary driver of beta diversity. GC showed the highest turnover and the lowest nestedness, with a βSIM of 0.73 ± 0.03 (mean ± SD) and a βSNE of 0.08 ± 0.01. In AL, meadows showed the lowest turnover (βSIM of 0.56 ± 0.02), and the highest nestedness (βSNE of 0.22 ± 0.06). ML displayed intermediate values for turnover and nestedness (βSIM = 0.63 ± 0.02 andβSNE = 0.14 ± 0.01, respectively).

* 1. *Drivers of temporal beta diversity*

The overall beta diversity in amphipod composition (i.e., Sørensen index; Table 2) was primarily determined by seagrass cover, accounting for ca. 25 % of the variance (Table 3). Seagrass leaf biomass was the predictor majorly determining variation in turnover and nestedness in amphipod composition, accounting for 64 and 85% of the variance, respectively (Table 3). However, in the case of turnover, seagrass cover also contributed to explain additional variation, according to the multi-model averaging (Table 3). Overall, a distinct pattern emerged among regions; meadows with a lower coefficient of variation for both seagrass leaf biomass and cover exhibited higher turnover values (Table 1), as in GC (Table 1; Fig. 3g and h). None of the environmental (climatic) predictor variables were significant in explaining variability in beta diversity components or total assemblage abundance.

When considering abundances, all meadows from each region exhibited values of the Bray Curtis index close to 1 (Table 1), which reflects a high variability in species’ abundances over time. The primary predictor accounting for observed variation was the epiphytic loads, which explained ca. 55% of the total variance (Table 3). In particular, we found greater fluctuations in assemblage structure over time in those regions with larger variation in epiphytic loads (i.e., ML and AL; Table 1), in contrast to GC, which exhibited the smallest differences in assemblage structure and the lowest coefficient of variation in our study (Table 1; Fig. 3i).

1. **Discussion**

We found that amphipod assemblages displayed large temporal beta diversity in each meadow across the three biogeographical regions. Species turnover was the main process contributing to temporal beta diversity, which exhibited higher values in subtropical relative to more temperate meadows. Importantly, this disparity in temporal beta diversity of amphipod assemblages was more linked to local structural properties of meadows than climatic regional drivers (Figure 4).

Amphipod turnover typically follows seasonal variation in environmental conditions (e.g. temperature, photoperiod), but also in food resources (e.g. macrophyte quality and quantity, in the case of herbivorous amphipods) and energetic requirements directly connected with the habitat structure (Neuparth et al., 2002; Maranhão and Marques, 2003). In this sense, it is widely known that spatial variation in environmental conditions and ecological resources filter species in local communities (Heino and Tolonen, 2017; García-Llamas et al., 2019), leading to high rates of species turnover across space. In our case, we assume that, in seagrass meadows, where fluctuations in growth and expansion (i.e., vitality) in the seagrass occur throughout seasons and years (Máñez-Crespo et al., 2020), similar processes would be occurring to generate temporal patterns in beta diversity of amphipod assemblages. Thus, temporal variation in structural properties of the habitat affects the diversity of microhabitats and the availability of resources (e.g. epiphytes, detritus and organic material), filtering amphipod species to be present at different times (Bologna and Heck, 1999). For example, during periods of high epiphyte productivity, herbivorous species can proliferate (Michel et al., 2015), whereas in times of greater detritus accumulation, detritivores species can become dominant (Zimmerman et al., 1979).

Comparing our findings on the temporal variability in beta diversity of seagrass-associated amphipods with other studies focusing on this animal group is difficult; only Cereghetti and Altermatt (2023) have explored this with freshwater amphipods, employing a different methodological framework. Contrary to our results, they did not identify turnover as the main driver of temporal beta diversity patterns in amphipods. Rather, they found a temporally consistent coexistence of species, with some fluctuations in certain taxa that were mainly due to different uses and intensity of agricultural land uses surrounding streams. Nonetheless, our temporal pattern in beta diversity across all meadows (i.e., turnover > nestedness) appears to be ubiquitous in nature (i.e., freshwater, marine and terrestrial realms). For example, according to Soininen et al. (2018), turnover is typically more than five times larger than nestedness. Still, our findings diverge from the usual drivers of these patterns, as higher turnover rates in marine environments are typically associated with increased environmental variability, rather than the reverse pattern (this study). In this regard, studies with marine groups such as microbes (Hatosy et al., 2012), or zooplankton (Lopes et al., 2019) also found species turnover as the primary driver of temporal beta diversity, which was otherwise attributed to temporal fluctuations in nutrient concentrations and climatic conditions. In terrestrial habitats, temporal beta diversity of ant communities was also driven by replacement of certain species by others over time. However, higher turnover rates were again linked to fluctuations in environmental factors, such as temperature, humidity, and resource availability (Nunes et al., 2020; Neves et al., 2021).

We found that the contribution of species turnover to dissimilarity over time was somehow not consistent across regions. These inter-regional differences were mainly explained by temporal variation in the structural attributes of the meadows, specifically seagrass leaf biomass and cover. Of these, seagrass leaf biomass was the most influential variable, explaining *ca.* 64% in variation of species turnover. In this sense, the highest turnover values were found in the subtropical region (contributing on averaged *ca.* 73%), coinciding with the lowest coefficient of variation of seagrass leaf biomass. In contrast, temperate regions presented lower turnover on averaged (*ca.* 66% in ML and ca. 57% in AL), coinciding with greater temporal variability in the structure of these meadows. On the other hand, the contribution of nestedness was low across all meadows, except for TAB meadow (AL region), where the value was high, coinciding with the highest temporal variability of seagrass leaf biomass. Interestingly, these results indicate that more stable meadows over time (i.e., with lower coefficient of variation in their structural attributes) drove higher turnover values. These findings stress the importance of temporal variability in local habitat structure in mediating beta diversity patterns of animal assemblages, a key element that has been overlooked, to the best of our knowledge, in terrestrial (Cook et al., 2018; García-Llamas et al., 2019; Zeni et al., 2020; Wu et al., 2021) and marine (Hatosy et al., 2013; Guelzow et al., 2014; Lammy et al., 2015; Alabia et al., 2021) studies conducted to date. Previous works have demonstrated that the contribution of species turnover to spatial beta diversity is greatest in those regions under stable climates (Baselga et al., 2012, Dobrovolski et al., 2012). For example, amphibian assemblages in “unstable areas” were dominated by “nested” species losses that lead to high nestedness-resultant dissimilarity, while species replacements that lead to high spatial turnover were the predominant process in “stable areas” over evolutionary timescales (Baselga et al., 2012). However, in contemporary timescales, decreased compositional stability (i.e., high turnover rates) has been associated with an increase in environmental instability (La Sorte et al., 2008; Hillebrand et al., 2010; He et al., 2024). Our findings diverge from the patterns described in the literature, likely because we focused on the role of biotic mechanisms in temporal beta diversity rather than on abiotic factors. The increased nestedness rates observed in temperate meadows suggest that temporal variation in the structural properties of habitats can act as a filter, impacting the persistence of certain species and potentially leading to the loss of rare species (Davies et al., 2004). Rare species, characterized by their low abundance and limited regional occupancy, can be particularly vulnerable to these environmental changes (Foden et al., 2019). This vulnerability may lead to the persistence of dominant competitive species in unstable areas, with rare species potentially being replaced by opportunistic counterparts. In contrast, in more stable environments like the subtropical meadows, both dominant and rare species experience changes, contributing to a heightened turnover rate (Setubal and Bozelli, 2021).

We also found an inter-regional pattern in temporal beta diversity when considering abundances, which was driven by variation in epiphytic loads. In this case, the temperate meadows showed greater dissimilarity over time, coinciding with the greater temporal variability of epiphytes. This result was expected, since the availability of food resources (e.g., epiphytes) stands out as one of the most influential factors that shape amphipod abundances (Cook et al., 2011; Michel et al., 2015). It is known that epiphytes usually respond to environmental changes more quickly than the seagrasses themselves (Borum 1985; Frankovich et al., 2009). Thus, climate stability in the subtropical region leads to lower temporal variation of epiphytes on *C. nodosa* leaves, providing a stable resource that positively influences various aspects, such as space availability (Osman, 1997; Leite et al., 2007), food sources (Edgar, 1990; Buzá-Jacobucci and Pereira-Leite, 2014), refuge provision (Leber, 1985; Tuya et al., 2011), and predator-prey dynamics (Orth et al., 1984; Alexander et al., 2012). In contrast, the dynamic nature of temperate meadows, subjected to higher fluctuations of temperatures and light regimes, produces greater variations in the epiphytic load (Balata et al., 2007), which increased demands of certain species (e.g., herbivorous amphipods) reliant on epiphytes for survival.

1. **Conclusions**

Our study is, to the best of our knowledge, the first to directly examine the effect of temporal changes in habitat structure on temporal beta diversity of associated fauna. Results highlight that temporal beta diversity of amphipod assemblages is sensitive to variability in the structure of the habitat provided by the seagrass *Cymodocea nodosa*. We evidenced that species turnover emerges as the primary process driving temporal beta diversity, with a higher prevalence in subtropical meadows under large structural habitat stability. Given that, to date, most studies have linked the replacement of some species by other to environmental instability, more studies are necessary to understand the crucial role of habitat stability in sustaining both long-term resident species (i.e., specialized species) and transient species, mainly in a context of loss of diversity and fragmentation of ecosystems.

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**Conflict of interest statement**

The authors declare no conflict of interest.

**Data accessibility statement**

Data available from the figshare repertory: 10.6084/m9.figshare.26303875

**Authorship**

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**Biosketch**

This work is part of Sandra-Navarro Mayoral’s doctoral project, which focuses on the drivers of biodiversity in different engineered ecosystem. She aims to use species taxonomy and genetics to understand the specialization processes occurring in different ecosystems across various latitudes. Her research is grounded in conservation ecology. All authors involved have extensive experience in seagrass conservation, naturalistic studies, and conservation biology.