Local effects of spatial environmental heterogeneity on ecosystem structure and functioning in rocky shores

Jordi Sola Codina (MSc.)

Department of Biosciences

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To my mum, and the many gifts she has left behind.

Per a la meva mare, gràcies per deixar-me somiar.

Thesis summary

Ongoing anthropogenic and climate change impacts result in habitat loss around the world, removing complex physical structures with negative consequences for biodiversity. At the local scale (i.e., the scale at which species interact), spatial environmental heterogeneity originates from biotic and abiotic complex physical structures such as canopies and substrate rugosity and is a key local factor promoting species diversity. However, more recent assessments have found substantial variability in Heterogeneity-Diversity Relationships (HDRs) across plots, sites, and studies. Such variability may originate from the role of external environmental factors, limited temporal (e.g., <5 time points) and spatial ($<1m^2$ or within plot) scales considered in heterogeneity studies. This thesis aims at expanding our knowledge of heterogeneity effects on the structure and functioning of ecosystems by a) assessing how heterogeneity effects on the diversity, structure and functioning of species communities vary across environmental contexts worldwide and b) explores mechanisms (i.e., ecological causes) explaining how heterogeneity effects on species communities are maintained at larger temporal and spatial scales. Using rocky reef literature, I found that positive saturating heterogeneity effects on diversity and abundance were generally common and changed across several context-dependent variables from the type of heterogeneity considered (i.e., heterogeneity facet) and substrate to organismal group, ecological process, latitude, and depth (intertidal and subtidal). Second, using experimental data over three years from an intertidal rocky shore, I found that despite positive heterogeneity effects on community diversity and structure, heterogeneity did not increase temporal cover stability within the species community due to several counteracting mechanisms (e.g., increasing mean temporal population stability but decreasing temporal species asynchrony) and even reduced temporal compositional stability. Finally, also using the experimental data, I found that local and landscape heterogeneity effects competed to promote landscape or regional (gamma) diversity through effects on local (alpha) richness and species turnover, respectively. In addition, they presented combined effects that helped maintain community cover and diversity across seasons and species groups. Overall, results help reveal the key role that environmental context has in determining the strength of heterogeneity effects and uncovers temporal and spatial mechanisms that maintain heterogeneity effects over time and space. Given that heterogeneity effects on ecosystems are not as linear and straightforward as previously thought, improving our understanding of the mechanisms behind heterogeneity effects is crucial to better predict when and where heterogeneity will benefit ecosystems and help mitigate for habitat loss.

Authorship Statement

Chapter I:

Writing was conducted by Jordi Sola (JS), with feedback from John Griffin (JG).

Chapter II:

JS conceived the idea for the research, with contributions from JG. Literature review, analysis and writing were all conducted by JS with guidance from JG.

Chapter III:

JS and JG conceived the idea. Sampling, analysis, and writing was conducted by JS, with guidance and feedback from JG. Jim Bull (JB) provided statistical advice during data collection and analysis.

Chapter IV:

JS conceived the idea with feedback from JG. Sampling, analysis and writing was conducted by JS, with feedback and guidance from JG. JB provided statistical advice during data collection and analysis.

Chapter V:

Writing was conducted by JS, with feedback from JG.

DECLARATION

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree

Signed [redacted] . (candidate)

Date 01-May-2024……………………

STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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STATEMENT 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for interlibrary loan, and for the title and summary to be made available to outside organisations.

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Date 01-May-2024……………………

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1. Introduction

1.1. Habitat loss and spatial environmental heterogeneity

Habitat loss is a main anthropogenic and climate change driver of biodiversity loss through the removal of valuable habitats and ecosystems (Thrush et al. 2008). The loss of ecosystems such as forests due to deforestation, kelp forests from ocean warming, or coastal development promoting simplified harbour systems all reduce the presence of complex structures from the environment that are necessary for the maintenance of species-rich communities (Giam 2017; Todd et al. 2019; Smale 2020). Such physical structures, or habitat complexity, help reduce abiotic and biotic constraints on the community by increasing the range of environmental conditions locally available (i.e., present within a locality, habitat, or plot; which in this thesis is considered the scale at which organisms interact). Habitat complexity can reduce abiotic stress from factors like temperature, desiccation, storm disturbance or water currents by creating environments that act as refugia against stress and disturbance (e.g., Emslie et al. 2014). Within the community, habitat complexity also prevents exclusion events by reducing competition among species (Almany 2004), predation (Almany 2004) and grazing (Arcoverde et al. 2018) and allows for facilitation cascades (Fairchild et al. 2023) and more complex cascading events among species (e.g., Grabowski 2004). Thus, to better understand and mitigate for habitat loss impacts on biodiversity, it is crucial that we understand the effects of these complex structures within ecosystems.

Fundamentally, habitat complexity effects on species communities originate from the diversity of environments that complex structures create within an ecosystem, and such diversity of environments can be defined as spatial environmental heterogeneity. Spatial environmental heterogeneity, or heterogeneity, is an ecosystem property that defines the spatial distribution of environmental conditions within (e.g., Loke & Chisholm 2022). Heterogeneity can originate from the spatial variation of abiotic conditions such as temperature, humidity, salinity, and light due to the presence of physical structures in the environment. Heterogeneity can also cause variability in grazing and predatory pressure, or the presence of dominant species (e.g., Griffin et al. 2009). The variation in each one of these environmental variables allows for more species to find an environment where they can grow quicker than the other species, find refuge from stressors, disturbance, and species interactions: the species ecological niche (Grinnell 1917; Elton 1927; Hutchinson 1958). Thus, heterogeneity is a fundamental ecosystem property that explains the effects of habitat loss on species communities and can be used to promote the presence of more species (i.e., higher species diversity) locally.

1.2. Heterogeneity effects on species communities

Heterogeneity has been linked to more diverse species communities, despite more recent accounts showing higher variability in the Heterogeneity-Diversity Relationship (HDR). At first, evidence showed that the presence of more heterogeneous environments leads to higher species diversity (Peterson 1918; Shelford 1918). Later, heterogeneity was quantified and linked to the increase in diversity due to niche availability and niche partitioning events (e.g., MacArthur & MacArthur 1961). However, heterogeneity could also attract more individuals locally due to increased overall recruitment and survivability (e.g., Cheminee et al. 2016), leading to higher productivity, and thus increasing species diversity (Connell & Orias 1964). Other more recent hypotheses considered a trade-off between heterogeneity increasing niche availability and reducing area available for each individual environment (Allouche et al. 2012; Ben-Hur & Kadmon 2020b) or producing inaccessible environments for organisms and changing the mean effect of environmental factors (Tamme et al. 2010; Laanisto et al. 2013). These two trade-offs would suggest that heterogeneity effects are not always positive on species diversity and predict a humped HDR. Lastly, heterogeneous environments may benefit more from the arrival of new species (i.e., species dispersal) than from niche partitioning since the arrival of more individuals leads to richer species communities (Loke & Chisholm 2023). Thus, despite initial support for positive heterogeneity effects on species diversity, the continuous proposition of new hypotheses suggests that there is no consensus on the predominant shape of the relationship or the mechanisms (i.e., ecological causes; e.g., Pâslaru 2017) behind heterogeneity effects on species communities.

Beyond its effects on species diversity, heterogeneity effects on communities are very varied, from structural to functional effects (Bell et al. 1991; Soukup et al. 2022). This can help explain the substantial variability in HDRs and some of the mechanisms behind heterogeneity effects on species communities. Heterogeneity can affect the presence of species like grazers and consumers, by increasing or reducing their access to resources (e.g., Gotceitas & Colgan 1989; Beck 2000). Such changes in consumer density have cascading effects on the productivity and composition of lower levels of communities (e.g., Grabowski 2004; Vandvik et al. 2005; Grabowski et al. 2008). Alternatively, heterogeneity can also promote bottom-up cascading dynamics concerning facilitation interactions with foundation species (i.e., species providing habitat to other species; Ellison 2019), which may allow for the recruitment of other secondary foundation species and develop into facilitation cascades (Thomsen et al. 2022; Fairchild et al. 2023). More generally, heterogeneous environments have also been linked with larger trophic networks and with higher biomass, which suggests that heterogeneity may allow for more trophic interactions, more productivity and higher overall ecosystem functioning (Carey et al. 2010; Kovalenko et al. 2012; Alsterberg et al. 2017; Hall et al. 2018; the second definition of ecosystem functioning in Jax 2005: the sum or amount of processes within a system defining its trajectory). In the last decades, multiple reviews and syntheses have summarised these and other heterogeneity effects to improve the understanding of the mechanisms and factors behind the variability in HDRs and other heterogeneity effects on species communities (Tews et al. 2004; Temmy et al. 2010; Kovalenko et al. 2012; Stein et al. 2014; Agra et al. 2023).

1.3 Heterogeneity effects across environments, temporal and spatial scales

To find more general HDR patterns, the variability among HDRs and other community responses (e.g., abundance, biomass, grazing, recruitment) to heterogeneity needs to be unravelled. To do so, reviews and synthesis have looked at the variability in heterogeneity effects on communities from a qualitative (e.g., Tews et al. 2004; Kovalenko et al. 2012; Ben-Hur & Kadmon 2020a) and quantitative way (e.g., August 1983; Lawton 1983; Currie 1991; Kerr & Packer 1997; Kallimanis et al. 2008; Hortal et al. 2009; Stein et al. 2014; Agra et al. 2023). From a qualitative perspective, heterogeneity can originate from a variety of substrates and result in a wide range of spatial patterns or heterogeneity facets, from substrate 3D amount (e.g., canopy height), substrate 2D amount (e.g., canopy cover), feature richness (e.g., algae richness) to substrate complexity (e.g., fractals) and others (e.g., McCoy & Bell 1991; Heidrich et al. 2020; Loke & Chisholm 2022; Agra et al. 2023). In addition, heterogeneity can occur from millimetres to metres, and comprise variables difficult to measure (e.g., variation in predation within turf algae; Thrush et al. 2011). For this reason, many reviews have resolved for quantifying heterogeneity as differences in the physical substrate (i.e., habitat complexity). In turn, different community components may respond differently to heterogeneity, as shown by studies observing differences across trophic groups (Heidrich et al. 2020), synthesis looking at different environmental contextual variables (Stein et al. 2014), and other studies looking at heterogeneity effects on biomass stocks and a range of ecological or ecosystem processes within the community (e.g., decomposition, pollination, productivity; Albercht et al. 2021; with ecological processes being defined as ‘the interactions between living and non-living systems, including movements of energy, nutrients and species' as per e.g., Bartolo et al. 2018) and exploring mechanisms behind latitudinal patterns (Bracewell et al. 2018). Despite individual efforts, no studies have so far tried to apportion the importance of each one of these contextual factors in the variability of heterogeneity effects across community responses (e.g., diversity, abundance across taxa).

The mechanisms (i.e., ecological causes) behind community responses to heterogeneity also need to be understood to increase our predictive power on when and where heterogeneity will be most beneficial for species communities. Recent work has highlighted the relevance of heterogeneity for the scaling up of biodiversity assessments, and the importance of considering heterogeneity for conservation purposes (Tamme et al. 2010; Thompson et al. 2021). Despite this empirical and theoretical work, current research efforts are usually constrained to limited temporal and spatial coverage. Studies looking at heterogeneity effects over time focus on disturbance-response dynamics and consider small temporal scales (e.g., < 5 time points; e.g., Boddy & McIntosh 2021) or specific interactions within the community (e.g., Ward et al. 2023). Very few studies have considered the effects that heterogeneity may have on the temporal cover stability of communities, understood as the reduced temporal variability in the overall biomass or cover of species communities (e.g., Brown et al. 2003, 2007; Brown & Lawson 2010). Beyond reducing disturbance effects on communities, the mechanisms behind the effects of heterogeneity on temporal community stability remain poorly understood (Mintrone et al. 2024; also notice that temporal community stability in terms of biomass has been previously considered a dimension of ecosystem as per e.g., Grman et al. 2010). Similarly, despite research on local and landscape heterogeneity having been performed, not many studies have looked at their interactive roles within the same system (Katayama et al. 2014). In particular, few studies have looked at how the different effects that local and landscape heterogeneity may interact to promote diversity at the landscape or regional level (i.e., gamma diversity). For example, local heterogeneity may provide refugia against storms and grazing, while landscape heterogeneity may provide more specialised niches for other species. As more studies look at the effect of local heterogeneity across temporal and spatial scales, understanding the mechanisms behind heterogeneity effects at wider scales is crucial to identify whether scaling up local heterogeneity is beneficial for biodiversity.

1.4. A model system: the intertidal rocky shore

In this thesis, rocky shores are a good test system to propose hypothesis and ask questions around the generality of community responses (e.g., species diversity, abundance) to heterogeneity, and explore mechanisms (i.e., ecological causes) behind heterogeneity effects on species communities (Hawkins et al. 2020). Rocky shores are tractable marine systems that can be easily accessed, and scientists have accumulated a wealth of knowledge around rocky shore community structure, functioning and biotic interactions across a range of environmental settings along the intertidal stress gradient. Lots of studies in rocky shores have also quantified the effects of heterogeneity on species communities, in the form of e.g., substrate rugosity and complexity, boulder size, canopy size, algae cover, rockpool size or algae richness (e.g., Kovalenko et al. 2012). Many of these studies are conducted along the intertidal stress gradient, which determines low desiccation stress and high species richness in the low shore and increasing stress and reduced richness in the high shore. This provides with a breath of literature and a flexible, varied and diverse experimental system to understand the mechanisms behind local heterogeneity effects in rocky shores and help interpret the outcomes of the proposed studies in this thesis.

1.5. Aims and initial hypotheses

This thesis aims at expanding our understanding of heterogeneity effects on the structure (i.e., species diversity and community structure) and functioning (i.e., ecological processes defined above and temporal community stability) of ecosystems. First, by identifying environmental factors introducing variability in HDRs, and the response of multiple species groups and ecological processes to heterogeneity. Second, we explore new mechanisms that help maintain heterogeneity effects at larger temporal and spatial scales. In particular, using Structural Equation Modelling we look at the causal pathways (i.e., mechanisms) that link heterogeneity to temporal community stability, and the interactions between local and landscape heterogeneity. The following list summarises the hypotheses that were answered across the chapters of the thesis:

1) Local heterogeneity metrics and terms in the literature can be summarised into heterogeneity facets by defining the underlying spatial patterns they represent (Chapter 2).
2) Local heterogeneity will generally increase diversity and functioning (i.e., ecological processes) of ecosystems across studies in the literature as predicted by several hypothesis

referring to increases in niche availability, niche partitioning, local productivity, and benefits from species dispersal despite negative effects due to heterogeneity limiting the available area per individual environment (Chapter 2).

3) Local heterogeneity will promote community stability as heterogeneity diminishes disturbance effects on ecological communities (Chapter 3).
4) Local and landscape heterogeneity will present interactive effects, with local heterogeneity effects decreasing as landscape heterogeneity increases, since they may both provide niches for the same species within the community (Chapter 4).

2. Resolving the context-dependency of heterogeneity - diversity relationships: insights from rocky reefs worldwide

2.1. Abstract

Heterogeneity, spatial variation of environmental features and conditions, has long been assumed to promote biodiversity by providing varied niches and ameliorating environmental stress. However, recent theoretical debate and empirical evidence suggests substantial variability in this relationship. Resolution of heterogeneity's effects requires considering both the various ways that heterogeneity is conceptualised and measured, and the potential modulating roles of environmental context and organismal group. Using rocky reefs as a test system, I first developed a novel framework to organise heterogeneity studies into five main facets, before synthesising heterogeneity's effects on community responses and evaluating key moderators. Metaregression revealed generally positive saturating responses of richness and abundance, with three-dimensional structures generating the strongest responses of all facets. Organismal group emerged as a key moderator; microinvertebrates and fish benefitted the most – and macroinvertebrates the least – from heterogeneity. Community responses also increased towards the equator, on intertidal rocky reefs and on macroalgal substrates. Finally, heterogeneity further mitigated grazing and enhanced recruitment, helping explain effects on biodiversity. Our results highlight the importance of multiple context-dependent sources of variability on determining heterogeneity's effect. Future consideration of heterogeneity facets, organismal groups and environmental context will further expand our understanding of heterogeneity's role structuring communities.

2.2. Introduction

The influence of local environmental heterogeneity on community structure remains a central and debated topic in ecology (e.g., Heidrich et al. 2020; Borland et al. 2021; Agra et al 2023). At local scales, heterogeneity generated by abiotic (e.g., substrate topography) or biotic (e.g., canopy- and reef-forming organisms) elements mediates interactions between organisms (Chang & Todd 2023) and with their microhabitats (e.g., De Frenne et al. 2019) and has been shown to exert various influences on abundance, diversity, and ecological processes (e.g., Stein et al. 2014; Alsterberg et al. 2017; Albercht et al. 2021). After many decades of study since MacArthur & MacArthur (1961), the form and generality of heterogeneity-diversity relationships (HDR) remains contentious (e.g., Allouche et al. 2012; Heidrich et al. 2020). Meta-analysis of HDR in well-studied systems provides a way to resolve ongoing uncertainty in the general form of the local HDR and uncover the moderators (i.e., covariates promoting or reducing heterogeneity effects) of this relationship. Yet, to date, synthesis of heterogeneity effects are lacking a focus on the local scale (Stein et al. 2014; Agra et al. 2023), where we may find more variability in the form and strength of HDRs across environmental contexts and responding groups (Tamme et al. 2010).

Current uncertainty in the local HDR stems from differing theoretical expectations, variability among empirical findings, and unresolved moderators. Classically, heterogeneity has been thought to promote diversity through increases in niche availability (Ben-Hur & Kadmon 2020a), or by enhancing productivity potential (Connell & Orias 1964; Danescu et al. 2016). Additional mechanisms generating HDR include heterogeneity-provisioned resources and refugia from physical stress or biological interactions such as grazing and predation (e.g., Lee 2006; Wernberg et al. 2013; Castro-Sanguino et al. 2016). Yet, other recent theory argues that highly heterogenous environments excessively divide individual habitats, reducing diversity (Allouche et al. 2012; Carnicer et al. 2013; Ben-Hur & Kadmon 2020b). Moreover, while positive HDRs are often assumed (Ben-Hur & Kadmon 2020a), weak or negative effects are also common (e.g., Tamme et al. 2010; Bar-Massada & Wood 2014; Borland et al. 2021; Heidrich et al. 2020), further questioning the universality of HDRs.

Arriving at generalities for HDRs may crucially depend on elucidating sources of variability among studies. As heterogeneity frequently creates refugia from environmental stress, it is possible that HDRs will grow stronger in stressful conditions (Yang et al. 2015), such as at high altitude, low rainfall, or – in marine systems – under high desiccation levels in the intertidal (e.g., Navarro-Barranco et al. 2022). Differences in traits such as body size and locomotion type indicate that some organismal groups are more likely to benefit from local and small-scale variability in features such as microtopography and canopy structures (e.g., Jung et al. 2012). Heterogeneity effects across organismal groups may also depend on specific ecological processes such as grazing (e.g., for grazing macroinvertebrates; Griffin et al. 2009), predation (e.g., for fish; Chang & Todd 2023) or, more generally, recruitment (e.g., Cheminee et al. 2016). As more factors influencing the heterogeneity-diversity response are discovered, synthesis across studies becomes necessary to find generalisable patterns and identify consistent sources of variability.

Another issues preventing the synthesis of heterogeneity effects is the various ways that heterogeneity is conceptualised and quantified (e.g., >100 potential terms; McCoy & Bell 1991). Heterogeneity is inherently muti-faceted, with each heterogeneity facet being a different dimension of heterogeneity defined by fundamentally different spatial distributions of resources and refugia (e.g., number of branches, branch size, canopy cover, canopy volume), and variability across multiple physical (e.g., two versus three-dimensional variability) and conceptual (e.g., variability versus information) dimensions (e.g., Halley et al. 2004; Tews et al. 2004; Kovalenko 2012; Tokeshi & Arakaki 2012; Loke & Chisholm 2022; Borland et al. 2021; Agra et al 2023). Such heterogeneity facets are likely to differentially influence organism – environment interactions and, ultimately, diversity responses. For example, vertical structures such as tree or seaweed canopies often greatly increase local surface area, enhancing settlement substrate and resource availability (e.g., Shelamoff et al. 2020), while horizontal variation in environmental features may modify access to resources (e.g., Deza et al. 2010), and the sizes of such features determines which organisms can access these environments. Heterogeneity facets are generated by different sources (e.g., biotic vs. abiotic), and are quantified in empirical studies by multiple metrics (e.g., three-dimensional structure by height, volume or surface area). While recent syntheses have organised studies according to heterogeneity source and the types of metrics or metric proxies used (e.g., Stein et al. 2014; Agra et al 2023), synthesis stands to be further strengthened by using clearly defined - and internally consistent (i.e., that are not confounded with one another or by other external factors such as substrate type) - heterogeneity facets as an overarching organising framework.

Rocky reefs provide an archetypal system to apply such a framework and advance general understanding of local heterogeneity effects on ecological communities. Rocky reefs are distributed around the word's coastlines, span intertidal and subtidal environments, and provide key services to local communities such as coastal defences, fisheries provision, nutrient filtration, carbon sequestration and cultural services (e.g., Miloslavich et al. 2016). Physical structures within reefs are highly varied and translatable to other systems as canopy (e.g., algae canopy and kelp forests; Schmidt & Scheibling 2006), topographic features (e.g., rockpools, walls and reefs; La Mesa & Vacchi 2005), microscale features (e.g., rugosity and microtopography; Chapman 2000) and patch scale features (e.g., algae cover, cover diversity; Ferreira et al. 2001). Since rocky reef studies have been conducted considering multiple facets of heterogeneity and organismal response groups, this body of literature provides a valuable opportunity to improve our understanding of HDRs and key sources of context-dependency.

Here, I synthesise HDRs for rocky reef communities worldwide across explicitly defined heterogeneity facets. My principal aim is to elucidate the general patterns and context-dependency in the nature and form of HDRs. Beyond diversity, I further aim to determine how heterogeneity influences other related properties and processes, including the abundance of organisms, and the rates of ecological processes such as recruitment and grazing. My objectives are to 1) evaluate and compare the strength and form of heterogeneity effects on community responses across facets (a), organismal groups (b) and ecological processes (c); and 2) identify key biogeographical and environmental sources of variation in HDRs. I hypothesise that HDRs will respond more strongly to facets that represent three-dimensional habitat variability, where there is greater environmental stress, increasing the importance of heterogeneity-driven amelioration, and for smaller animal groups, as they are better able to capitalise on small-scale environmental variation. My results contribute towards resolving the general form of HDRs and reveal key sources of context-dependency.

2.3. Methods

2.3.1. Study selection

I performed a systematic search for studies looking into heterogeneity effects on diversity, community structure and ecological processes on intertidal and subtidal rocky reefs around the world. I performed a topic search in ISI Web of Science, including all studies before June

2021. I built a search string in three sections. I searched for ‘rock* shore*’, ‘rocky reef’ and ‘intertidal’. I included 70 different heterogeneity terms such as ‘habitat structure’, ‘microhabitat diversity’, ‘topographic complexity’, ’shore heterogeneity’ or ‘seafloor relief’. I defined the response variables using terms like ‘diversity’, ‘richness’, ‘Simpson’, ‘abundance’, ‘biomass’, ’rate’, ’recruitment’, or ’predation’. This study did not include terms such as ‘kelp’, ‘macroalgae’ and ‘coral’, or any derived system (e.g. ‘kelp forest*’, ‘coral reef*’). Searched studies were evaluated and refined to ensure targeting as many studies addressing heterogeneity effects on rocky reefs as possible. A total of 6192 studies were obtained.

For the screening process, I divided the selection process into multiple steps. An initial step to filter studies not targeting the marine environment and/or rocky reefs was done by examining titles. Subsequently, I included studies following pre-defined criteria: 1) study examined heterogeneity effects on rocky reefs; 2) study provided observational or experimental data; 3) heterogeneity was considered quantitatively or qualitatively, and study used adequate heterogeneity surrogates (e.g., number of seaweed branches); 4) examined abundance, diversity and/or ecological processes as responses; and 5) presented a clear *a priori* aim to address heterogeneity effects. I excluded studies that showed differences in area and isolation across plots to avoid confounding changes in heterogeneity with area or configurational effects across studies. Fragmentation variables were also excluded, as they were few (n = 2) and were considered a special case of substrate complexity (i.e., substrate 2D amount x feature size in Figure 1). I selected a total of 145 studies for data extraction (PRISMA workflow in Supplementary Materials 1).

2.3.2. Data extraction

For each study, I extracted information on: 1) location: geographic coordinates, biogeographical region, depth; 2) methodology: plot size, sampling date and season, type of study; 3) heterogeneity: heterogeneity metric, substrate type; 4) taxon: taxonomic group, trophic group; 5) community structure: diversity or community metric, units; and 6) ecological processes: metric and units. Data were extracted as observations, means and – wherever possible - raw data on community structure and diversity were extracted from tables and supplementary materials to avoid targeting only statistically significant and strong effects. Data were aggregated in HDR groups consisting of data from the same site, date, and substrate. For example, if a study examining the effects of heterogeneity (e.g., number of holes in a rock) on fish richness quantified heterogeneity and richness at sites A, B and C, during times 1, 2 and 3, a total of nine HDRs would be obtained. If insufficient replicates were found ($n<3$) within individual sites/dates/substrates, comparisons were made across sites, dates, or substrates, following the comparisons made by the authors of the study. This occurred in 19% of all studies (see section *Overall approach to modelling HDRs* for how these cases were dealt with).

Studies were then classified into different heterogeneity facets based on the heterogeneity variables quantified. An initial framework was built by defining five heterogeneity facets, and these were linked to metrics of heterogeneity used in the literature (Figure 1). Some of these facets have been previously defined in the literature (McCoy & Bell 1991; Tokeshi & Arakaki 2012; Loke & Chisholm 2022). I put together five heterogeneity facets that aimed to describe all the possible spatial differences within a plot, and defined substrate complexity as the interaction of two or more of these facets (e.g., Thrush et al. 2011; Gestoso et al. 2013; Loke & Chisholm 2022; Agra et al. 2023). Heterogeneity facets included substrate 3D amount, which considered the total amount of surface area, volume, or biomass within a plot (e.g., Beck 2000). Another facet was substrate 2D amount, defined as the relative amount of surface area or the density of elements within a plot (e.g., Koivisto et al. 2010). Feature size indicated the mean surface area, volume, height and even biomass of features within a plot (e.g., Beck 2000). Feature variation concerned the variation (e.g., standard deviation) of surface area, volume, biomass, or identity of features within a plot (e.g., Ferreira et al. 2001). When multiple feature classes existed (e.g., species or structure typology), feature richness quantified the number of classes present (e.g., Janiak & Whitlatch 2012). In addition, two or more of these facets could interact with one another in the form of substrate complexity (e.g., Kostylev & Erlandsson 2005). Complexity could be quantified explicitly, by combining multiple metrics representing different facets into one metric, or implicitly through fractal indices which accounted for, among other things, surface area and feature variation. All these steps and definitions ensured an internally consistent and comprehensive definition of facets that was not confounded by other factors (e.g., substrate type; Heidrich et al. 2020).

To make the framework operational, I linked each facet and complexity to existing metrics in the literature. Each facet and complexity were linked to specific heterogeneity metrics, which were later grouped into parsimonious categories. For example, metrics considering substrate 3D amount were grouped into dimensional metrics (e.g., rock contour perimeter, length, or surface area) and ratio metrics (i.e., dimensional metrics standardised to a unit metric). Most studies quantified metrics belonging to one or two facets (>90%; Supplementary Materials 2), but studies quantified up to 5 facets. When multiple facets were quantified within a single study, data describing HDRs relating to the distinct facets were included in the database as they represented distinct ways to conceptualise heterogeneity and may therefore result in distinct HDRs. For example, if a study on the effects of canopy macroalgae structure on invertebrate richness considered both the canopy's 3D amount and its complexity, two HDRs would enter the database. Furthermore, some studies (23%) quantified more than one metric within the same facet. For the previous example, suppose that canopy 3D amount was quantified both as biomass and as surface area. In such cases, we considered the metrics as largely capturing the same information and thus selected the most frequently used metric across studies within the metanalysis (e.g., biomass), while discarded the other (e.g., surface area). This was done to avoid statistically inflating the influence of studies that used many similar metrics to quantify the same heterogeneity facet.

Figure 1. Heterogeneity encompasses multiple facets and metrics across the literature. At the top, the conceptual and graphical definition of each heterogeneity facet and complexity. At the bottom, the link of each definition with the metrics found in the literature. Note that for fractal metrics, the interaction between facets is implicit, and potentially also considers configurational differences and carries some additional ambiguity (see Loke & Chisholm 2022; Madin et al. 2023; Loke & Chisholm 2023 for a discussion on the topic). References for metric examples = 1: Beck 2000, 2: Jacobi 1996, 3: Machado et al. 2019, 4: Gunnill 1982, 5: Kelaher 2003, 6: Falace & Bressan 2006, 7: Dean & Connell 1987, 8: Machado et al. 2019, 9: Koivisto et al. 2010, 10: Lathlean & McQuaid 2017, 11-13: Ferreira et al. 2001, 14-16: e.g. Ramirez & Haroun 2014; Ferrari et al. 2018, 17: Janiak & Whitlatch 2012, 18: Kostylev & Erlandsson 2005, 19: Ape et al. 2018, 20: e.g. Hills et al. 1999, 21: e.g. Thrush et al. 2011; Gestoso et al. 2013, 22: Raffaelli 1979.

2.3.3. Quantification of heterogeneity – diversity relationships (HDRs)

I transformed both heterogeneity and community response variables and calculated effects sizes to standardise for differences in methodologies and other study- and plot-level noise.

For each heterogeneity-response group, I normalised heterogeneity data to the 0-1 range by using the following formula

$$z_i = \frac{x_i - \min(x)}{\max(x) - \min(x)}$$

where x_i is any given heterogeneity value, min (x) is the minimum heterogeneity value, and max(x) is the maximum heterogeneity value. Following the same 0-1 scale, a variable between 0 and 1 was created for studies presenting heterogeneity discrete descriptors. The number of levels included (e.g., 0 and 1; 0, 0.5 and 1, etc.) was adjusted to the levels defined by the study (e.g., present vs. absent, low vs. medium vs. high).

Response variables includeds number of species (species richness), Shannon diversity, Pielou species evenness, abundance and biomass, and metrics linked to recruitment, grazing, predation and body size (more information on metrics used in Supplementary Materials 3). For response variables, community responses and ecological processes responses were quantified using a natural logarithmic response ratio (LRR), calculated as

$$LRR_i = \ln\left(\frac{yi}{\text{mean}(\min(\text{y}))}\right)$$

where y_i is any given response value and mean(min(y)) is the mean of all the response values when normalised heterogeneity is zero (e.g., Cardinale et al. 2013). For discrete heterogeneity variables, I adapted the LRR formula by comparing response values (y_i) to the mean response value from the treatment representing the lowest heterogeneity level.

2.3.4. Overall approach to modelling HDRs

I used linear mixed-effects models to test whether diversity, abundance and ecological processes (e.g., grazing and predation; see section 2.3.7 for more details) depended on heterogeneity. Heterogeneity was included as a fixed effect following a quadratic function so that HDRs were allowed to change from almost-linear, to saturating and humped relationships – following the multiple possible responses to heterogeneity (Bar-Masada & Wood 2013). Every fixed effects or covariate was excluded if only one level was present, or if replication across levels of the moderator was very unbalanced. Besides heterogeneity, fixed effects included season, substrate type, depth, and other moderators described in Supplementary Materials 4. Interactions across moderators were included following *a priori* expectations, and non-significant interactions were later excluded (Zuur et al. 2010). Random effects included study ID and plot ID, and captured the random variation of HDR slope and intercept across studies (e.g., Craven et al. 2018) and within each study (e.g., O'Connor et al. 2017). All model formulas, including a description of all moderators and random effects used in models, are shown in Supplementary Materials 4.

In each model, assumptions were graphically checked using q-q plots and residual vs predicted plots (Hartig 2020). Some studies did not assess heterogeneity effects within a single site, date and substrate type and could have therefore confounded heterogeneity effects with site, date or substrate type effects (14% of cases accounting for site comparisons and 5% for within-site, date, and substrate comparisons). To avoid such confounded heterogeneity effects, sensitivity tests were run by removing potentially confounded studies from the models, and after re-running the models, retaining the studies if significant coefficients were still the same. To make small and large heterogeneity changes comparable within the 0-1 scale, I computed the coefficient of variation (CV) for each heterogeneity descriptor. For example, given a study that obtained macroalgae canopy cover between 1% and 15%, and another study that obtained cover valued between 1% and 40%, CV allows to account for the disparate cover ranges in each study despite both metrics ranging between 0 and 1 after transforming heterogeneity metrics before the metanalysis.This factor was included in the model in interaction with heterogeneity and units used in each instance, and the interaction and added terms were removed when non-significant. This model specification allowed to standardise heterogeneity effects to their degree of change and compare this change across metrics of the same units. Since for discrete descriptors CV was zero or very small, I included an additional variable separating discrete and continuous descriptors, which was excluded if not significant. Publication bias was assessed adding two more fixed effects into the mixed-effects models: sample size and publication year. Accounting for sample size allowed to test for effects linked to sample variation and uneven sample size across studies, while considering publication year allows to test whether heterogeneity effects increased or decreased since the first publication due to non-ecological reasons (Nakagawa et al 2022). These two fixed effects were removed if not significant or driven by single-study effects (i.e., studies with lots of data or set apart in time), particularly in models presenting less data.

2.3.5. Objective 1a: Evaluating differences in heterogeneity effects on diversity and abundance across facets in benthic invertebrate-dominated communities using mixed-effects linear models

To evaluate the differences in HDRs across heterogeneity facets, I selected a dataset that contained data across all heterogeneity facets so that heterogeneity effects could be estimated across multiple sources of variability. For that, I grouped benthic invertebrate-dominated community data focusing on macro- and microinvertebrate studies (Objective 1a in Figure 2). For abundance, I included a fixed factor indicating whether the study considered one, less than five, or more species. Since I considered multiple organismal groups (macro- and microinvertebrates), I included organismal group as a fixed effect to control for potential differences. I also split the analysis by modelling each heterogeneity facet separately, as a single model for all facets became too complex, was not possible to fit, and the lack of data in some facets forced big extrapolations across factors that would compromise the comparisons across facets.

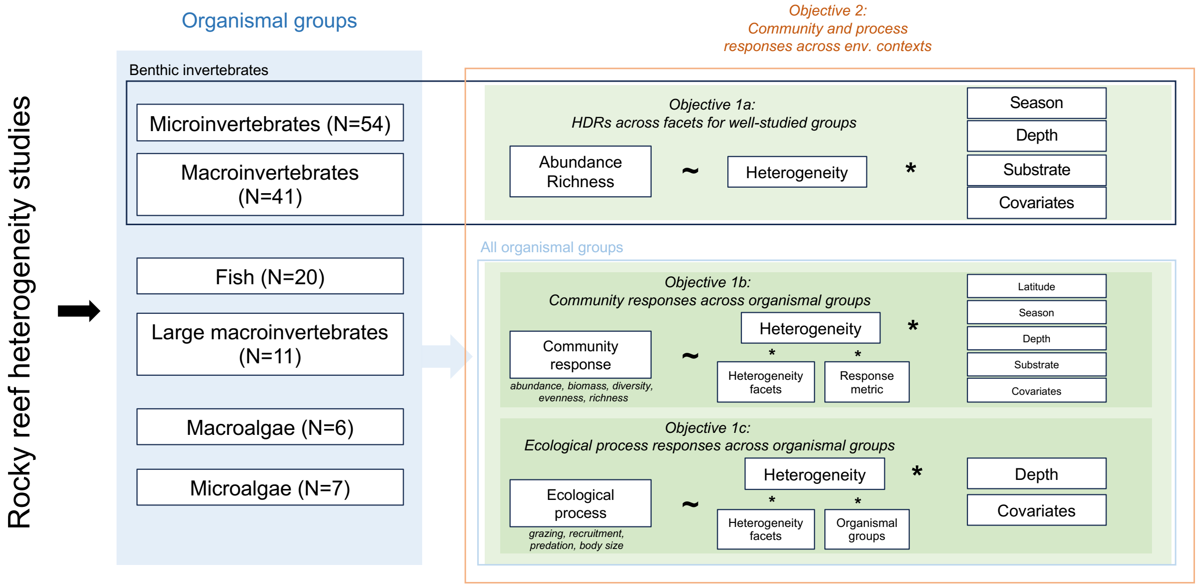

Figure 2. Data and models used for each one of the objectives in this study. An initial dataset was created from rocky reef heterogeneity studies and consisted of data across six organismal groups. For Objective 1a, a model with only data microinvertebrates and macroinvertebrates were used, while for Objectives 1b and 1c data for all organismal groups were used for each model. For Objective 2, fixed effects concerning biogeographical and environmental effects were included. Covariates refer to other variables that were used to allow comparability across studies (i.e., coefficient of variation across heterogeneity metrics, sample size, publication year). Abbreviations: N = number of studies.

2.3.6. Objective 1b: Evaluating differences in heterogeneity effects across organismal groups using mixed-effects linear models

No single response metric was consistently found across all organismal groups, as some metrics were used in some groups and not in others (e.g., abundance for fish and biomass for macroalgae). To make comparisons across groups possible, I considered multiple community responses to heterogeneity (e.g., abundance, biomass, richness, diversity) alongside one another, and included response metric type as a fixed factor (Objective 1b in Figure 2). Heterogeneity facets were also included as fixed effects, as even though comparisons across facets were not robust due to low replication within some facets (i.e., no data or less than three studies) – and therefore any significant value should be cautiously considered -, they helped account for variability across studies. Again, I split the analysis by modelling each organismal group separately, for reasons stated above.

2.3.7. Objective 1c: Evaluating differences in heterogeneity effects across ecological processes using mixed-effects linear models

I identified four ecological processes and proxy for ecological processes – grazing, predation, recruitment, body size – with sufficient data (i.e., more than three studies) in my dataset (Objective 1c in Figure 2). Body size was included as an indirect indicator or proxy of potential processes given its strong ecological effects (Brown et al. 2004). After initial exploration of predictors, I only included heterogeneity facet, organismal group, depth and the interaction between heterogeneity and depth, as other moderators showed highly unbalanced representation across levels. In the recruitment model, I also included the interactions between heterogeneity and facet, and heterogeneity and organismal group – as more data were available. And as previously indicated, non-significant interactions were later removed. Again, I split the analysis by modelling each ecological process separately, for reasons stated above.

2.3.8. Objective 2: Evaluation of biogeographical and environmental effects across heterogeneity facets, organismal groups and ecological processes using mixed-effects linear models

The inclusion of biogeographical and environmental moderators depended on the availability of data across models and were based on previous expectations (Objective 2 in Figure 2) and therefore not all fixed effects could be included in all models (Supplementary Materials 4). The interaction between season and latitude was included as seasonality effects were expected to decline closer to the equator. The interaction between season and depth was also included, as seasonal changes in e.g., temperatures were expected to be larger in the intertidal where conditions are more extreme. The interactions between substrate and depth and substrate and season were included as e.g., algae may develop smaller structures in harsher environments (e.g. intertidal). As per above, non-significant interactions were excluded (Zuur et al. 2010). In addition, some groups presented low representation of some moderators (e.g., latitude) or interactions across moderators, and after assessment I excluded such moderators and interactions in the final model.

2.4. Results

2.4.1. Geographical distribution and amount of included studies

A total of 145 studies were included in our analysis, distributed across all biogeographical regions except the Arctic and Southern Ocean (Figure 3a). A large proportion of studies quantified Substrate 3D and Substrate 2D amount, and in particular Substrate 3D amount presented more HDRs than the rest of the facets combined (Figure 3b-c). Data across organismal groups was similarly distributed, with microinvertebrates, macroinvertebrates, fish and mixed (i.e., benthic macro- and micro-invertebrates) presenting more studies, and microinvertebrates showing more than three times more heterogeneity-response groups than the second largest group (i.e., macroinvertebrates; Figure 3d-e). For ecological processes, the distribution of studies was less skewed, although there were overall few studies, with recruitment presenting ten studies, and predation and grazing five (Figure 3f-g). Again, these differences were increased when examining within-study groups, with recruitment showing three times more groups than the lowest group (i.e., predation; Figure 3g).

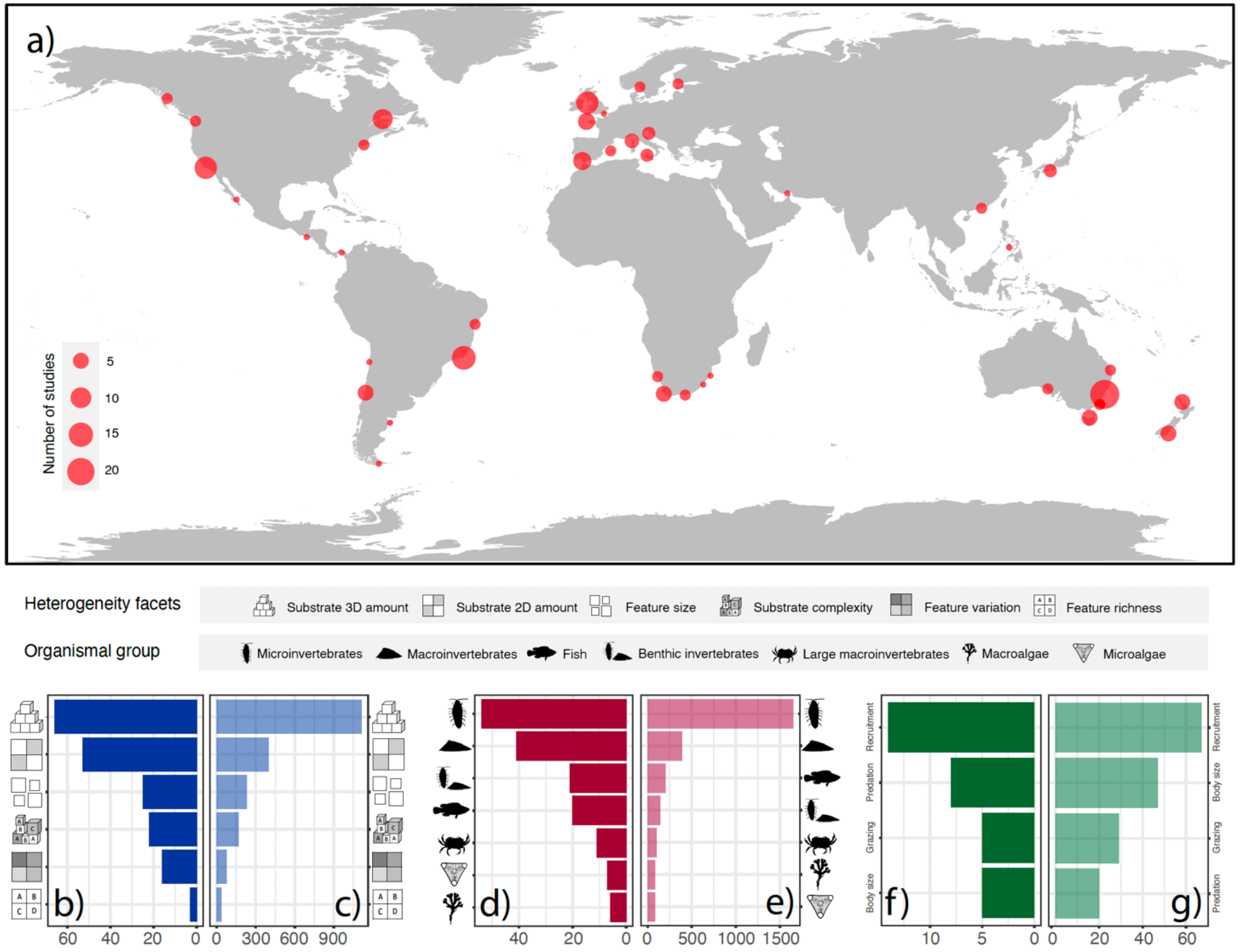

Figure 3. Geographical distribution and number of studies included in the metanalysis. At the top, a) the distribution of studies, with bubble size indicating the number of studies found in each location. At the bottom, b) the number of studies and c) HDRs quantifying heterogeneity effects across heterogeneity facets for richness and abundance in benthic macro- and micro-invertebrates, d) the number of studies and e) HDRs quantifying heterogeneity effects across organismal groups, and f) the number of studies and g) HDRs quantifying heterogeneity effects across ecological processes.

2.4.2. Objective 1a: Effects of different heterogeneity facets on benthic invertebrate richness and abundance

I first used the most highly represented organismal group (benthic macro- and micro-invertebrates) to address diversity and abundance responses to specific facets of heterogeneity (see Methods, and Figure 4). Heterogeneity promoted benthic invertebrate-dominated community richness and abundance following a saturating response, but the response varied across facets (Figure 4m-n). For richness, four of the six facets showed positive HDRs, with richness most strongly increasing with 3D amount (substrate 3D amount: $t_{x,20}$= 9.11, P<0.001; $t_{x^2,3074}$= -13.68, P<0.001; Figure 4a), moderately increasing with 2D amount (substrate 2D amount: $t_{x,101}$= 4.19, P<0.01; $t_{x^2,1135}$= -3.04, P<0.01; Figure 4b), and weakly increasing with substrate complexity ($t_{x,180}$= 2.41, P<0.05 ; $t_{x^2,983}$= -1.57, P>0.05; Figure 4c) and feature size ($t_{x,85}$= 2.19, P<0.05; $t_{x^2,850}$= -2.02, P<0.05; Figure 4d). On the other hand, only two of the six heterogeneity facets showed positive abundance HDRs: abundance strongly increased with 3D amount ($t_{x,37}$= 3.69, P<0.001; $t_{x^2,4215}$= -15.69, P<0.001; Figure 4g) and less strongly with 2D amount ($t_{x,24}$= 2.21, P<0.05; $t_{x^2,1380}$= -2.15, P<0.05; Figure 4h). Not only did substrate 3D amount show the most rapid increase, but also the most pronounced saturation and humped shape, as indicated by the strongest negative quadratic term for substrate 3D amount in both richness and abundance models (Figure 4n). For all facets, confidence intervals were greater for abundance than for richness (Figure 4m-n).

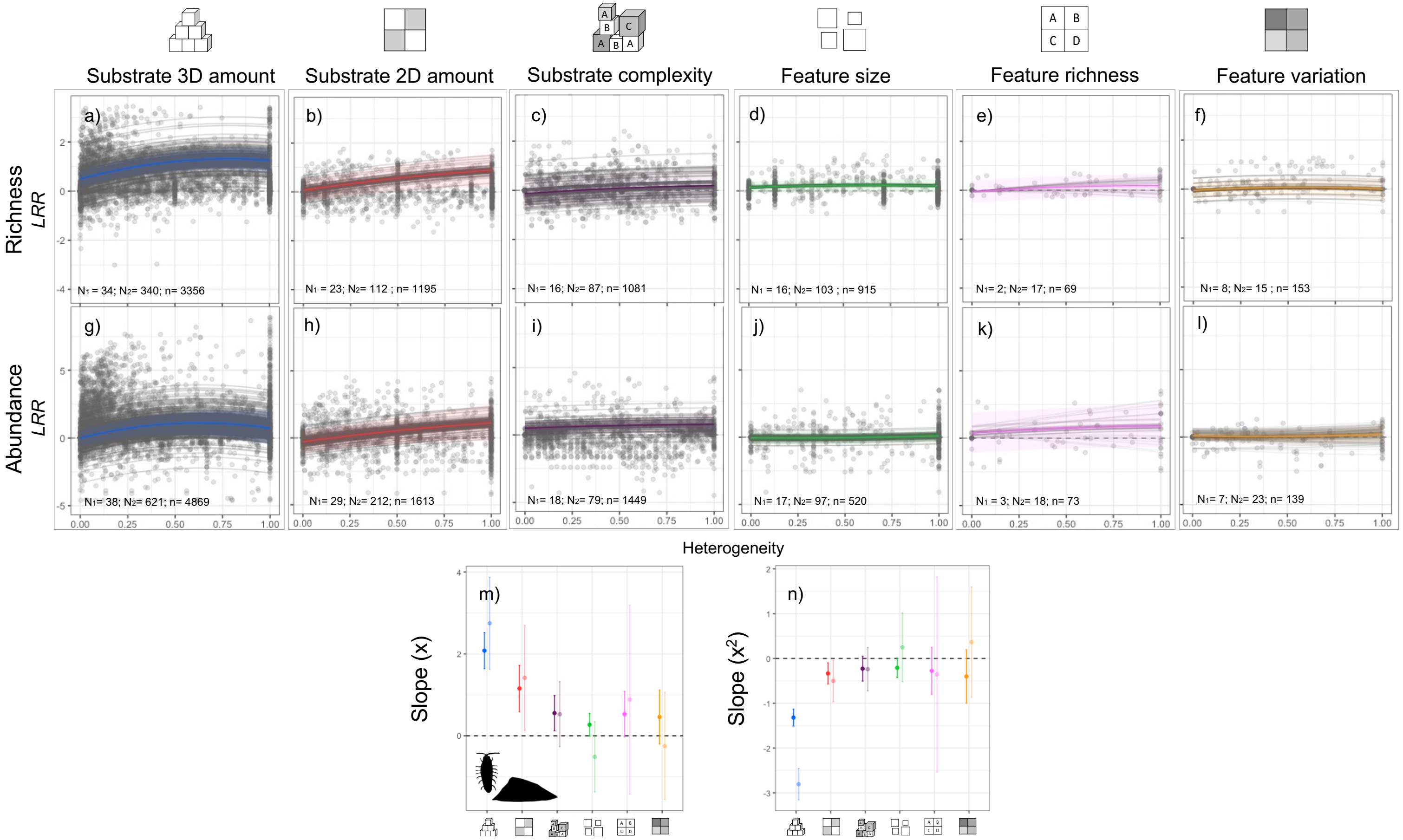

Figure 4. Heterogeneity effects on species richness and abundance across heterogeneity facets. Results from mixed-effects linear models for richness and abundance of benthic invertebrate-dominated communities for each heterogeneity facet. At the top, heterogeneity effects on species richness for a) substrate 3D amount, b) substrate 2D amount, c) substrate complexity, d) feature size, e) feature variation, f) feature richness; and heterogeneity effects on abundance for g) substrate 3D amount, h) substrate 2D amount, i) substrate complexity, j) feature size, k) feature variation, and l) feature richness. At the bottom, summary of the estimated m) linear (i.e. x; mean ± C.I.) and n) quadratic (i.e., x^2; mean ± C.I.) term of the quadratic function across heterogeneity facets for species richness (solid) and abundance (transparent). For (a-l) plots, N_1= number of studies included in the model, N_2= number of heterogeneity-response groups, and n= number of observations in total. The interpretation of the linear and quadratic terms of the quadratic function were done based on simulations in the Supplementary Materials 5.

2.4.3. Objective 1b: General effects of heterogeneity on community responses across organismal groups

To ascertain whether heterogeneity has differential effects across organismal groups, I considered all heterogeneity facets and responses in a single analysis for each group (see Methods; Figure 5a-f). Across organismal groups, microinvertebrates ($t_{x,72}$= 9.41, P<0.001; $t_{x^2,12610}$= -17.75, P<0.001) and fish ($t_{x,98}$= 6.06, P<0.001 ; $t_{x^2,1332}$= -4.58, P<0.001) presented the strongest community response to heterogeneity, while macroinvertebrates ($t_{x,86}$= 0.90, P>0.05 ; $t_{x^2,2496}$= 0.50, P>0.05) – and large macroinvertebrates ($t_{x,17}$= 1.60, P>0.05 ; $t_{x^2,1173}$= -0.56, P>0.05) – presented the weakest response (Figure 5g). In turn, microalgae ($t_{x,8}$= 3.16, P<0.05; $t_{x^2,213}$= -2.53, P<0.05) and macroalgae ($t_{x,18}$= 3.07, P<0.01; $t_{x^2,847}$= -2.40, P<0.05) presented positive responses at intermediate level between the top (microinvertebrates) and bottom (macroinvertebrates) groups. Microinvertebrates, in particular, showed the most pronounced saturating or humped response, as they presented the most negative quadratic term (Figure 5h). Differences across organismal groups remained largely consistent regardless of heterogeneity facet (Figure 5i).

Organismal group effects seemed largely robust across community response metrics, despite abundance responses generally tending to be slightly stronger (Figure 5j). In particular, abundance responses were larger than richness responses in microinvertebrates, and larger than any diversity responses in fish and large macroinvertebrates. Biomass was larger than diversity responses in macroalgae

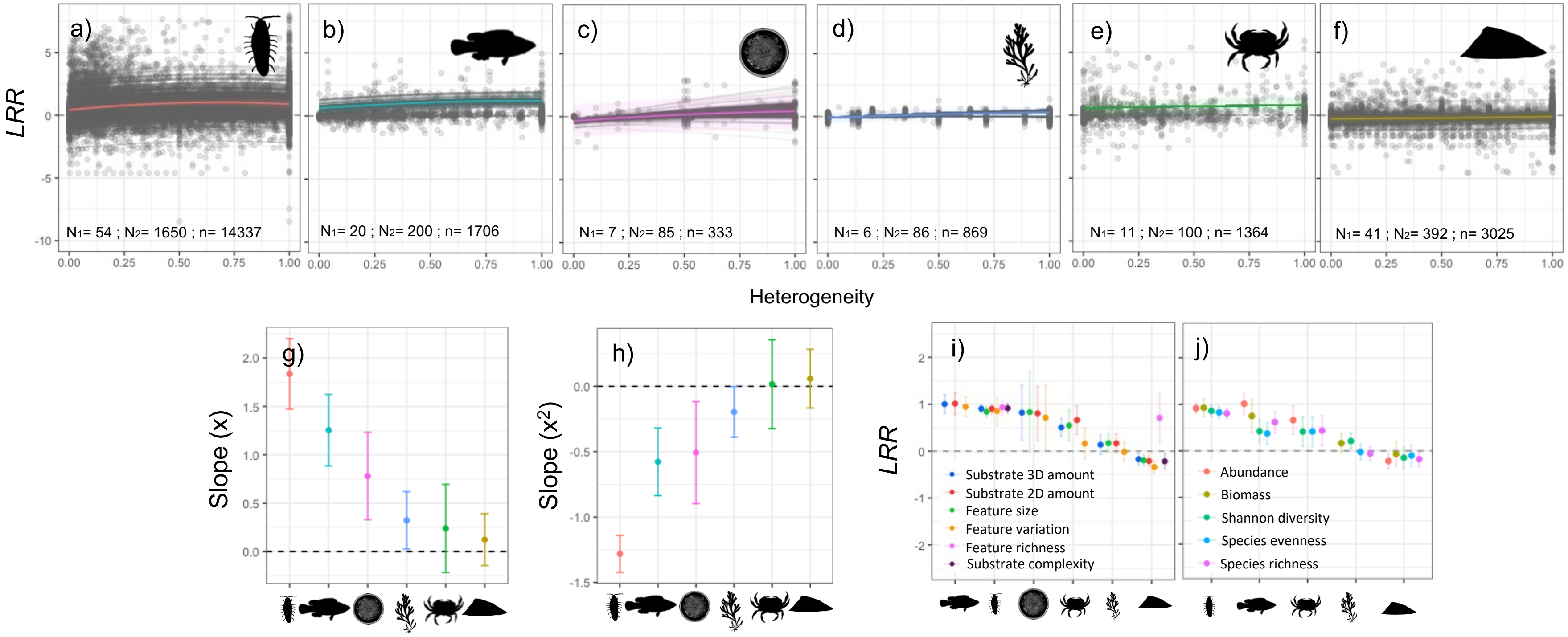

Figure 5. Heterogeneity effects on community responses across multiple organismal groups. Results from mixed-effects linear models for diversity, abundance, and biomass across organismal groups. At the top, heterogeneity effects on (a) microinvertebrates, (b) fish, (c) microalgae, (d) macroalgae, e) large macroinvertebrates, and (f) macroinvertebrates. At the bottom left, summary of the estimated g) linear (i.e. x; mean ± C.I.), and h) quadratic (i.e., x^2; mean ± C.I.) term of the function. Also shown are heterogeneity effects across organismal groups and both (i) heterogeneity facets and (j) response variables. For plots a to f, N_1= number of studies included in model, N_2= number of heterogeneity-response groups, n= number of observations in total.

2.4.4. Objective 1c: Heterogeneity effects on grazing, recruitment, predation and body size across substrate, organismal group and heterogeneity facets

Heterogeneity clearly affected grazing and recruitment and had no clear effect on predation and body size (Figure 6a-f), but note the limited sample size for grazing, predation, and body size models (Supplementary Materials 6). Grazing showed a negative response to heterogeneity ($t_{x,10}$= -2.01, $P>0.05$; $t_{x^2,10}$= 3.18, $P<0.01$), although these studies exclusively addressed macroinvertebrate grazing (Figure 6a). Recruitment was positively affected by heterogeneity ($t_{x,\ 58.03}$= 3.91, $P<0.001$; $t_{x^2,646}$= -2.73, $P<0.01$), presenting a saturating response (Figure 6b). For predation, a humped relationship was marginally significant ($t_{x,\ 115}$= 1.67, P=0.05-0.1; $t_{x^2,101}$= -1.76, P= 0.05-0.1; Figure 6c), and no differences were found across substrate, organismal or facet groups (Figure 6h-j). Heterogeneity effects on body size were non-significant ($t_{x,\ 398}$= 1.22, $P>0.05$; $t_{x^2,t371}$= -1.24, $P>0.05$; Figure 6d), and no differences were found across heterogeneity facets and organismal groups (Figures 6g-h), but mean effects were significantly larger on fish than on macroinvertebrates (Figure 6h).

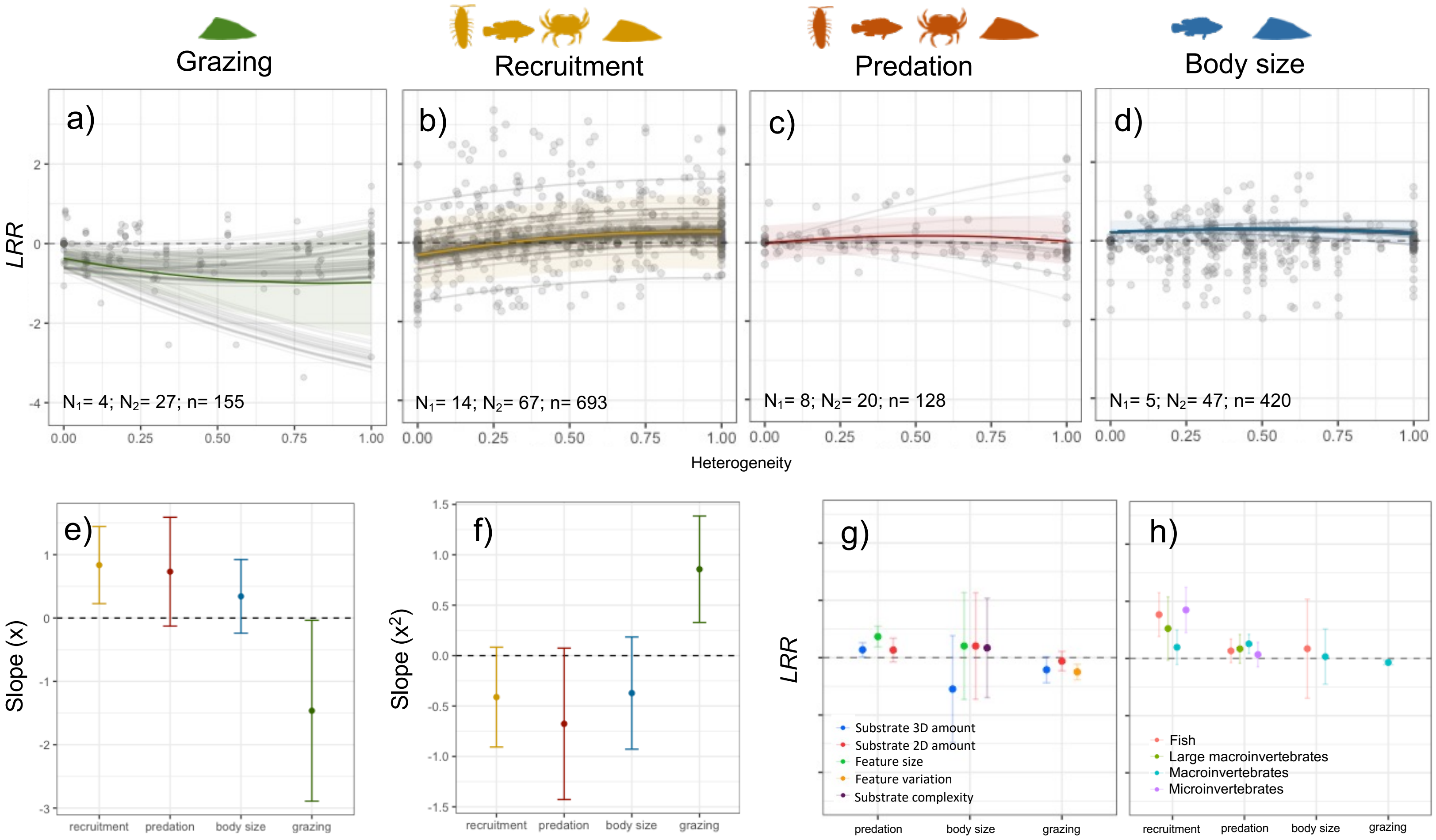

Figure 6. Heterogeneity effects on ecological processes across organismal groups and heterogeneity facets. Results from mixed-effects linear models for ecological processes (a-d). At the top, heterogeneity effects on a) grazing, b) recruitment, c) predation and d) body size. At the bottom, summary of the estimated e) linear (i.e. x; mean ± C.I.), and f) quadratic term of the function (i.e., x^2; mean ± C.I.) across ecological processes. At the bottom right, heterogeneity effects across g) heterogeneity facets, and h) organismal groups. For plots a to d, N_1= number of studies included in model, N_2= number of heterogeneity-response groups, n= number of observations in total.

2.4.5. Objective 2: Biogeographical and environmental patterns in heterogeneity effects across facets, organismal groups, and ecological processes

Latitude effects were intertwined with season and varied considerably across organismal groups. Patterns across latitudes were found for microinvertebrates in interaction with season, with stronger heterogeneity responses near the equator in winter, but an attenuation of this latitudinal effect in summer (Latitude: $F_{3301}= 3.32, P=0.05-0.1$; Latitude * Season: $F_{3931}= 5.52, P<0.001$; Figure 7a). Similarly, latitude also decreased the response of macroinvertebrates to heterogeneity, although in this case the effects were robust across seasons (Latitude: $F_{413}= 11.34, P<0.001$; *Latitude * Season:* $F_{450}= 2.02, P=0.05-0.1$; Figure 7b). Large macroinvertebrates showed the opposite pattern, with stronger responses to heterogeneity in temperate zones and did not present any seasonal differences (Latitude: $F_{1294}= 2.14, P<0.05$; Figure 7c). No latitudinal trends were found for fish (Latitude: $F_{186}= 0.88$, $P>0.05$; Figure 7d), macroalgae (Latitude: $F_{1294}= 1.94, P=0.05-0.1$; Figure 7e) and microalgae (Latitude: $F_{84}= 0.88$, $P>0.05$; Figure 7f), despite the latter two showing a slight non-significant increase in their response at higher latitudes. The limited latitudinal and data coverage for macroalgae, microalgae and seasonal coverage for fish could have affected the reliability of the patterns observed for these groups (Figures 7d-f).

Differences between the intertidal and subtidal systems occurred across heterogeneity facets, organismal groups, and ecological processes (Figures 7g-j). Amongst the six significant comparisons between the intertidal and the subtidal environments, five comparisons showed larger heterogeneity effects on the intertidal and one comparison showed the opposite trend (Figures 7g-i). No significant effects were found within the subtidal, and four comparisons showed intertidal differences (Figures 7g,j). Three of these significant comparisons occurred within species richness models across heterogeneity facets, with two of the three models presenting larger heterogeneity effects in the high intertidal (Figure 7g). In addition, heterogeneity effects supressing grazing were much larger in the low intertidal (Figure 7j).

Differences in heterogeneity effects across substrates (biogenic vs. rocky) only showed significant effects in the most populated models: species richness for the substrate 3D amount model, and community response in the microinvertebrates model (Figures 7k-m). In both cases, biogenic substrates (i.e.., macroalgae and reef-forming organisms) presented larger heterogeneity effects than rock substrate.

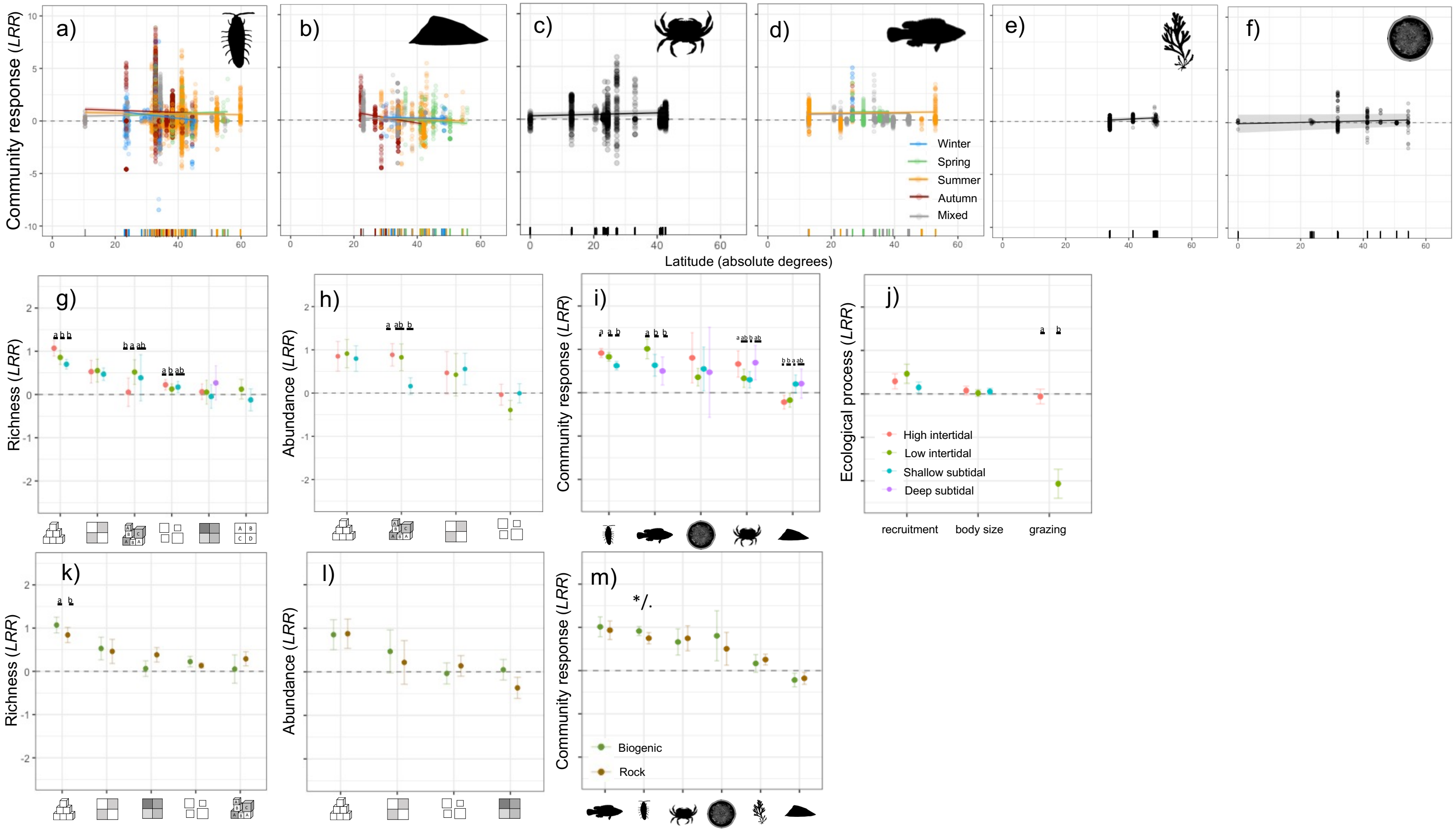

Figure 7. Biogeographical and environmental context alters patterns found across heterogeneity facets, organismal groups and ecological processes. Results from mixed-effects linear models for community responses across latitudes for (a) microinvertebrates, (b) macroinvertebrates, (c) large macroinvertebrates, (d) fish, (e) macroalgae and (f) microalgae. In the mid row, intertidal and subtidal depth effects (mean ± C.I.) on g) species richness across heterogeneity facets, h) abundance across heterogeneity facets, i) organismal groups and j) ecological processes. In the bottom row, substrate effects (mean ± C.I.) on k) species richness across heterogeneity facets, l) abundance across heterogeneity facets and m) organismal groups. Results of post-hoc tests are indicated with letters on the graphs.

2.5. Discussion

In this study, the developed framework allowed to test the effects of heterogeneity facets, environmental context and the targeted organismal group and ecological process within the umbrella of heterogeneity-diversity and community relationships. Showing mostly saturating effects, heterogeneity relationships were maximised when focusing on heterogeneity generated by 3D substrates and influencing microinvertebrates and fish. In contrast, the provision of substrate features (i.e., mean feature size, feature variation or feature richness), and effects on macroinvertebrates and large macroinvertebrates yielded the weakest effects. Heterogeneity effects also tended to increase towards the equator, in the intertidal system (vs. subtidal) and on biogenic (vs. rock) substrates. Such results may help prioritise management actions in favour of those heterogeneity facets capable of generating the largest effects (i.e., substrate 3D and 2D amount), and highlight the need to consider the targeted organism as well as the environment in which these occur.

Heterogeneity substrate 2D, and particularly 3D amount, promoted invertebrate diversity and abundance more strongly than the modification of substrate features. These 2D and 3D substrates (e.g., macroalgae canopy, boulder, rockpool) were highly correlated with features like topographic variation, mean frond length and algae richness (e.g., Jacobi & Langevin 1996; Supplementary Materials 7). This could be explained by larger 3D structures like macroalgae canopy simultaneously allowing for more space and attachment surface on larger fronds, stipes, and holdfast surface area for recruiting organisms (e.g., Raimondi 1990; Cheminee et al. 2016), and more refugia and resources under fronds and holdfast to find food and escape predators, storm effects and desiccation (e.g., Johnson et al. 1998; Kemppainen et al. 2005; Clemente et al. 2013). Simultaneously increasing substrate amount and features also helps explain the inferior substrate complexity effects, which despite accounting for multiple interacting facets, do not strictly promote both substrate amount and features per unit increase. Therefore, the double substrate and niche availability effect would make substrate amount effects optimal for invertebrates in natural rocky shores.

Differences between organisms depended on locomotory style and species interactions, highlighting the role of species traits and cascading effects in heterogeneity effects. Like in terrestrial systems (Flores-Abreu et al. 2014), swimming organisms in this study (microinvertebrates and fish) better capitalised 3D structures (macroalgae canopy or boulder fields). With higher mobility, small fish and microinvertebrates could find hiding from generalist predators in between boulders and search for food among macroalgae fronds (e.g., Martin-Smith 1993), but also develop into obligate specialised associations with specific substrates (e.g., tube-forming amphipods and macroalgae hosts; Hughes & Gliddon 1991). Despite their sessile nature, micro- and macroalgae also benefited from heterogeneity possibly due to the provision of more attachment substrates (e.g., Medrano et al. 2020) and reduction of macroinvertebrate grazing (e.g., Chapman 2020). Indeed, results indicated that heterogeneity reduced macroinvertebrate grazing by hindering their movements and creating grazing refugia that allowed algae to proliferate (Chapman 2020). Rock and macroalgae structures would have also prevented the movement of mobile benthic macroinvertebrates (e.g., Liversage & Benkendorff 2017) and recruitment of sessile macroinvertebrates (e.g., Benedetti-Cecchi & Cinelli 1992), resulting in some negative effects that produced the neutral effects in this study. Heterogeneity effects, thus, are dependent on the traits presented by species and the cascading effects through species interactions.

However, inconclusive effects were common across ecological processes and may indicate intricate mechanisms through which heterogeneity affects organismal groups. Increased recruitment, particularly of fish and microinvertebrates, could have originated from the association of these organismal groups with larger structures like rockpools or macroalgae canopy (e.g., Gunnill 1982; White et al. 2015). In contrast, heterogeneity reduced grazing and had mixed effects on predation, may indicative some refugia effects (e.g., Chapman 2020). However, data across organismal groups, environmental contexts, and better insight into the mechanisms at play in these heterogeneity effects are needed to be able to elucidate more from these relationships (e.g., Gonzalez-Rivero et al 2017; Oakley-Cogan et al. 2020; Reynolds et al. 2018; Chang & Todd 2023). It is also possible that both grazers and producers become more abundant in more heterogeneous and productive areas due to more resources available, further complicating this relationship (e.g., Gilson & McQuaid 2023). Low replication could also explain the inconclusive heterogeneity results on body size. It could indicate that heterogeneous substrates (e.g., canopy height) present intricate links with body sizes (Wardhaugh et al. 2013), while other types of heterogeneity (e.g., number of fronds in turf algae) may limit the size of the organisms living within (e.g., Kostylev et al. 2005). Overall, the data scarcity and multiple possible mechanisms make heterogeneity effects on ecological processes more difficult to decipher.

Across facets, organisms and ecological processes, heterogeneity effects on richness, abundance and other community responses were mostly positive. Most heterogeneity-response relationships also followed saturating trends, and in a few cases humped shapes. Saturating trends are common across systems and communities, indicating a reduction in the number of niches available or space available as heterogeneity increases, or that local richness is close to species pool richness (McCoy & Bell 1991). Only three cases visually showed a humped shape (substrate 3D amount for richness and abundance, and microinvertebrates), which coincided with the largest effects across models for each group of models. These humped patterns have been linked to heterogeneity creating environments that are too little and create small populations vulnerable to stochastic effects (Allouche et al. 2012) but could also mean that these environments are more inaccessible and harder to find and navigate for organisms – thus increasing mortality and reducing colonisation (Laanisto et al. 2013). In any case, humped patterns were much less common and possibly linked to stronger heterogeneity effects, indicating that saturating responses were the most common and explained by either reduced niche and space availability, or by decreasing species pool effects.

My initial hypothesis on increasing heterogeneity effects with increasing environmental stress received mixed support. Initially, overall heterogeneity effects increased in low latitudes and in the intertidal rocky shore. This suggests that organisms in the intertidal benefit from heterogeneity-mediated stress amelioration against e.g., desiccation, and specially in low latitudes where heat is more intense (e.g., Lima et al. 2016). However, the larger heterogeneity effects towards the equator could also indicate that higher species richness is correlated with larger heterogeneity effects (Ron et al. 2018). In addition, observed positive latitude effects over 20º indicated that biogenic structures can mask and 'reduce' rock substrate effects in lower latitudes (Bracewell et al. 2018), agreeing with my results indicating larger biogenic substrate effects and suggesting that latitude effects here could also be the result of biogenic substrate effects. The observed stronger latitude effects in autumn and winter would further support this, as during these seasons temperate areas are less productive and there would be less biogenic structures and overall fewer species around to respond. Consequently, despite the patterns across latitudes, intertidal/subtidal and substrate types are to some extent revealing, more experimental and survey work is needed to separate stress, richness, and productivity effects.

Overall, results show widespread positive heterogeneity effects across facets, organisms, and ecological processes in the local marine rocky shore environments from subtidal low latitudes to intertidal high latitudes. Both the heterogeneous substrate, the responding organismal group, and the context in which the relationship occurs can determine the magnitude of heterogeneity effects. Such relationships occur in the form of ecological processes and – more broadly – functions, of which I characterised the four most common in the literature. To be able to identify mechanisms behind these patterns, more quantitative and qualitative syntheses are needed targeting specific ecological processes, systems, and environmental contexts (e.g., Chang & Todd. 2023).

3. Unravelling the mechanisms of the heterogeneity-stability relationship on a rocky shore

3.1. Abstract

Spatial environmental heterogeneity is well known to influence the composition and diversity of communities, but whether and how these effects further cascade to influence temporal cover stability (i.e., the coefficient of variation in total community cover) is largely unknown. Heterogeneity may theoretically increase or decrease temporal cover stability, as it may drive stabilising (e.g., diversity, asynchrony) and destabilising (e.g., promoting disturbance-prone species) mechanisms. I tested the effects of heterogeneity on community composition, diversity and stability using experimental substrates replicating topographic heterogeneity that I distributed along the emersion gradient on a rocky shore and regularly surveyed over 3 years. My results showed that despite clear effects on species diversity and composition, heterogeneity only weakly influenced temporal cover stability along the gradient of environmental stress due to the presence of multiple counteracting mechanisms. On the one hand, heterogeneity promoted temporal cover stability by: i) providing refugia that increased mean temporal population stability; and ii) increasing species richness that in turn increased temporal species asynchrony and temporal statistical averaging. On the other hand, heterogeneity simultaneously suppressed temporal cover stability by iii) reducing consumer effects, which in turn reduced temporal statistical averaging and temporal compositional stability; and iv) reducing the abundance of a dominant species and in turn asynchrony and temporal statistical averaging, particularly in the mid and high shore. Some of these mechanisms responded to the variation in environmental conditions, decreasing with increasing environmental stress, and could also be linked to decreased background species diversity and excessive disturbance effects. These results reveal that heterogeneity effects on species diversity should not be assumed to translate into greater stability due to the complex interplay of multiple countervailing mechanisms.

3.2. Introduction

Recent decades of ecological research have yielded substantial evidence linking biodiversity and community composition to the temporal cover stability (i.e., the coefficient of variation in total community cover) of ecological communities across a wide range of environments (e.g., Grman et al. 2010; Hou et al. 2023). Much less frequent has been the evidence reporting habitat heterogeneity and spatial environmental heterogeneity effects on temporal cover stability, and the assessment of the mechanisms involved in these heterogeneity effects across environments despite studies focusing on disturbance response dynamics (e.g., Fuhlendorf et al. 2006). However, beyond individual responses to disturbance, heterogeneity holds a promising role promoting temporal cover stability by increasing biodiversity and reducing disturbance effects across communities and environments (e.g., Brown 2007). Understanding the mechanisms explaining such heterogeneity-stability links and how widespread this relationship is can reveal the importance of a potential third actor underpinning biodiversity-stability relationships.

Community temporal cover stability is a fundamental property of communities that is linked to variability at the level of component species' populations, and incorporates community responses to disturbance over a period of time. Temporal cover stability measures the relative variation in overall or aggregate community properties over time (e.g., biomass, cover; e.g., Bulleri et al. 2012; Yang et al. 2017). These aggregate properties are important because they relate to ecosystem state, as well as processes and services that are supplied to associated species as well as humans (Kremen 2005). Temporal cover stability is measured simply as the inverse of the coefficient of variation in an aggregate property over time (e.g., Lehman & Tilman 2000). Therefore, unlike other measures of ecological stability such as resistance or resilience, which address community responses to specific perturbations, temporal cover stability provides an integrated and often long-term measure of variability in response to all sources of variability, both internal to the community (e.g., individual species' life history events) and external (seasonality, disturbances, extreme weather events) (Tilman et al. 2006).Temporal cover stability may be determined by mean temporal population stability, the relative variation among populations, if a community is dominated by species with stable population dynamics (La Bella et al. 2023). However, the joint variability of multiple species population can also crucially affect temporal cover stability by different means. Where populations are highly asynchronous, the fall of one will be compensated by the rise in another and generate temporal cover stability. Meanwhile, just the random variation among multiple populations can also confer stability at the aggregate level. Communities may also undergo shifts in species composition over time, with different sets of species conferring temporal cover stability to aggregate properties (Hillenbrand et al. 2018). Deciphering the various pathways and mechanisms linking variation in community composition and diversity to temporal cover stability has been a major focus in modern ecology (Loreau et al. 2001; Griffin et al. 2009; Craven et al. 2018). Despite this sustained attention, however, the potential effects of heterogeneity on temporal cover stability have been largely overlooked.

Temporal cover stability may be linked to heterogeneity via its influences on individual species' populations, species composition, and diversity. First, heterogeneous environments often include refugia (e.g., rock crevices) which should reduce the impact of perturbations and increase the stability of individual species' populations (stabilising). Yet, second, by reducing the dominance of individual stress-resistant species, which have inherently more stable populations and whose competitive interactions may generate asynchronous dynamics, heterogeneity may have destabilising effects (e.g., Sasaki & Lauenroth 2011). Third, by increasing the range of environmental conditions and providing additional feeding, settling and reproduction opportunities (e.g., Arriero et al. 2006; Bartels & Chen 2010), heterogeneity tends to promote species richness (Stein et al. 2014; but see Allouche et al. 2012). These increases in richness are expected to buffer individual species variation through temporal species asynchrony (e.g., Schnabel et al 2021) and temporal statistical averaging (e.g., Zhao et al. 2022). Fourth, heterogeneity often mitigates consumer impacts which may further influence stability in multiple ways; consumers have been shown to enhance population fluctuations and reduce asynchrony in some systems (e.g., Sun et al. 2023) but may alternatively create free space that increases recruitment of diverse species (Connell 1978), which may be stabilising. Therefore, heterogeneity's multitudinous impacts on communities are expected to have complex and potentially cascading effects on temporal cover stability. Since these pathways can be both stabilising and destabilising, empirical tests are needed to decipher the relative importance and net effects on temporal cover stability.

The intertidal rocky shore provides a model system in ecology and is a suitable testbed for investigating heterogeneity effects on communities and temporal cover stability. Therein, heterogeneity widens suitable environmental conditions for organisms by increasing the variation in substrate with structures such as holes and crevices along the intertidal emersion stress gradient. These structures provide refuge against desiccation, wave disturbance and grazing (e.g., Chapman 2000), while also providing settlement sites for spores and larvae (e.g., Hills et al. 1999). At low shore, where there is low emersion stress, wave energy and grazing are the main sources of disturbance (e.g., Boaventura et al. 2002), while at high shore longer emersion time increases desiccation and thermal stress (e.g., Zamir et al. 2018). Along this gradient of increasing stress, the number of species able to withstand the levels of stress present decreases, resulting in a reduction in background species diversity (Scrosati et al. 2011). Although numerous accounts of heterogeneity effects on diversity exist on rocky shores (Kovalenko et al. 2012), few studies have linked these effects to the emersion stress gradient (e.g., Meager et al. 2011), and researchers have yet to link heterogeneity effects on diversity and community composition to temporal cover stability.

Here, I assessed the effects of heterogeneity on temporal cover stability, temporal stability dimensions, as well as multiple underlying mechanisms, along a gradient of increasing environmental stress and decreasing disturbance and species diversity (see Table 1 for the description of stability metrics used). I deployed a three-year field experiment consisting of replicated pairs of tiles that represented different levels of substrate heterogeneity and were set along a rocky shore emersion stress gradient. I used this experimental set up to test the following: 1) whether and how heterogeneity changes community diversity and composition along the emersion gradient; 2) how heterogeneity affects temporal cover stability along the emersion gradient; and 3) how heterogeneity effects on temporal cover stability are generated; specifically, how heterogeneity-driven changes in community composition and diversity influence stabilising mechanisms (e.g., mean temporal population stability, temporal statistical averaging), compositional temporal cover stability, and ultimately temporal cover stability.

Table 1. Stability-related metrics quantified in this study, their quantification, definition and interpretation.

Metric	Quantification	Definition	Interpretation
Temporal cover stability	$\frac{\mu_{tot}}{\sigma_{tot}}$	The averaged sum of species cover across the community (μ_{tot}) across temporal points or dates, divided by the temporal squared-root variance for the community (σ_{tot}). [4]	Quantifies the stability of aggregate properties of the community. Also referred to as aggregate or functional stability.
Mean temporal population stability	$\frac{\sum_{i,k}\mu_{i,k}}{\sum_{i,k}\sqrt{v_{ii,kk}}}$	The sum of tmean cover (μ_{ik}) per species across time points within the community k; divided by the sum of the square root of species ® variance (ν_{ii}) within community k. [1]	More stable populations increase temporal cover stability.
Temporal species asynchrony	$-\sum_i\left[p_i r\left(A_i, \sum_{j\neq i} A_j\right)\right]$	The sum of the correlation coefficient®) between non-consumer species cover i and j, weighted by the relative cover of species i (p_i) in the community, multiplied by (-1). [2]	Asynchrony buffers summed cover over time, thus increasing temporal cover stability.
Temporal statistical averaging	$\frac{\sum_i \sigma_i}{\sqrt{\sum_i \sigma_i^2}}$	The sum of individual standard deviation per species cover i, divided by the squared root of the sum of the variance per species cover i. [3]	Temporal statistical averaging indicates more random fluctuations over time, which buffers summed cover over time, thus increasing temporal cover stability.
Temporal compositional stability	$\frac{\sum_{ijk} 1-\beta_{BCijk}}{n_k}$	The sum of beta-Bray **similarity** $(1-\beta_{BC})$ on unweighted cover data between any given date (i) and its successive date (j) per tile (k), divided by the number of dates per tile (n_k). [4]	Changes in species composition may indicate additional temporal fluctuations within the community such as the overall reduction in community cover.

Liang et al. 2021[1]; Blüthgen et al. 2016[2]; Donohue et al. 2016[3]; Hilderbrand et al. 2018[4]

3.3. Methods

3.3.1. Study Site

The experiment was set up in a semi-sheltered rocky shore at Bracelet Bay, Swansea, Wales, UK (51.566, -3.971; Figure 1a-b). Topography along the shore consisted of a gentle slope along a limestone platform at low shore, divided by channels that followed up to high shore, where a much more pronounced slope was found. Between channels, areas of exposed rock were dominated by communities of barnacles at high shore, which transitioned into communities more dominated by grazers and mussels in the mid shore and eventually shifting to macroalgae and grazer dominated communities at low shore.

3.3.2. Experimental design

Between May 2019 and April 2022 (35 months) 35 pairs of experimental limestone tiles representing two levels of heterogeneity were deployed across the rocky shore and sampled seasonally resulting in 11 time points per tile (Figure 1c-e). Heterogeneous tiles were created by drilling a set of large, medium, and small holes following a standardised configuration, while non-heterogeneous tiles consisted of flat tiles without any holes. These experimental units were attached to exposed rock using 8mm screws on each corner of the tile, in 35 stations evenly distributed across five transects (orientated from low to upper shore) along the intertidal gradient. In each station, heterogeneous and non-heterogeneous treatments were established by deploying two square tiles corresponding to each heterogeneity treatment. Notably, due to random variation in tile basal size (as they were hand cut), there was no difference in the mean 3D modelled surface area of tiles across heterogeneous and non-heterogeneous treatments (Fairchild 2019).

Such experimental heterogeneity units and substrate heterogeneity modifications have been widely used over a variety of hard substrate natural and artificial substrates to modify local conditions including temperature, moisture, wave disturbance, and grazing (e.g., Airoldi & Cinelli 1997; Bulleri 2005; Hawkins et al. 2020). I placed the experimental units on exposed rock, thus avoiding rockpools, and transects were within 20 metres of one another to reduce other effects such as differential wave exposition. In addition, neighbouring fucoid and large red canopy algae were regularly removed to avoid adding statistical noise with the arbitrary

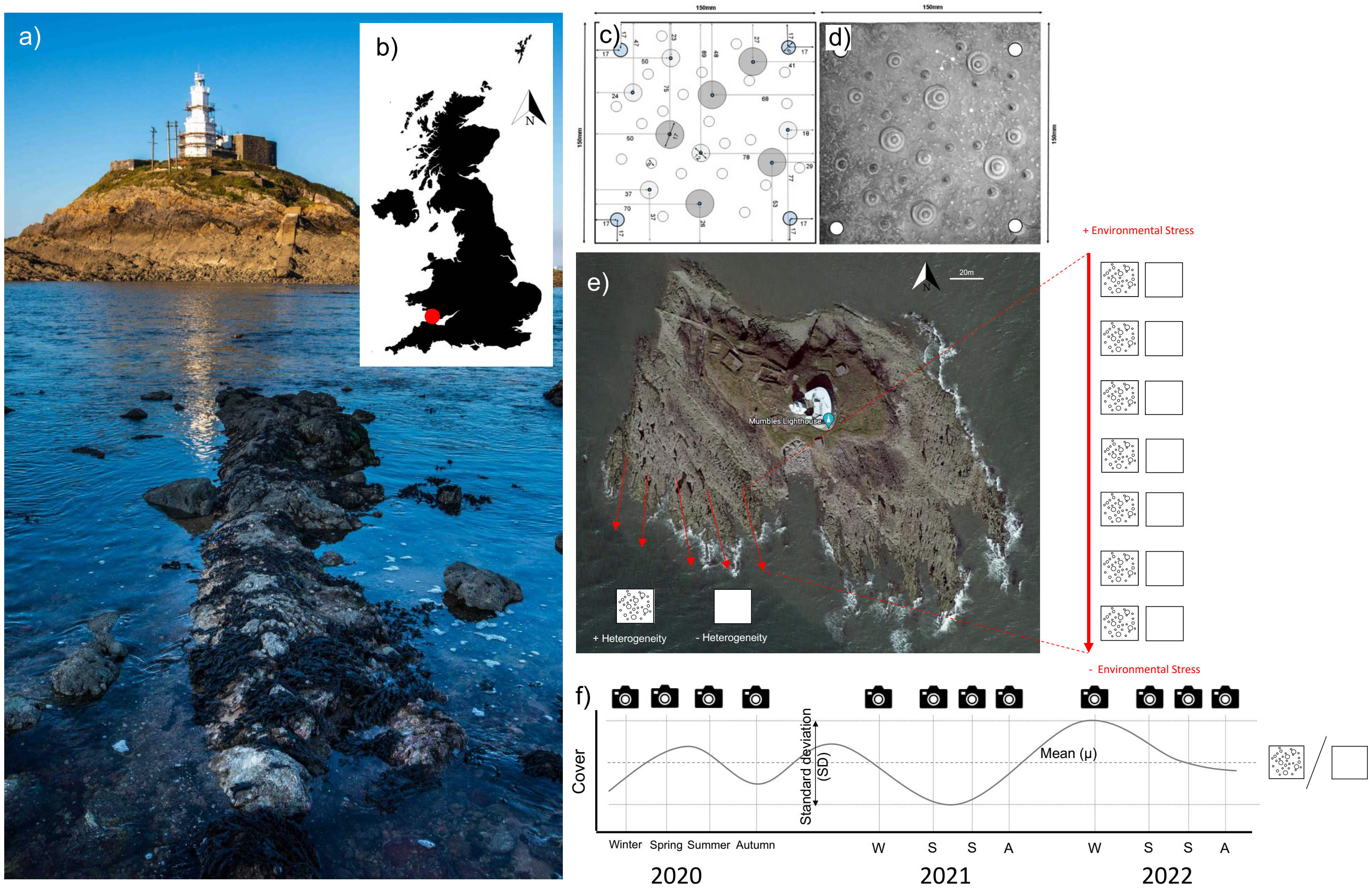

Figure 1. Overview of the experimental set-up testing the effects of heterogeneity on temporal cover stability. In an intertidal experimental site in Bracelet Bay, Swansea, Wales, UK (a, b), heterogeneous tiles (c, d), with a standardised set of holes of various sizes and configuration, were deployed alongside non-heterogeneous controls. The experiment was deployed along 5 transects on the shore (e) where each transect moved from the high shore (high emersion stress) to the low shore (low emersion stress). Each tile was sampled seasonally (f) using a camera and temporal cover stability (μ/SD) was quantified using cover as a proxy for biomass. Within each transect, 7 stations consisting of a tile representing the heterogeneous treatment (as per figures c and d) and a smooth tile representing the non-heterogeneous treatment were established. Tile schematics in figures c and d are from Fairchild (2019).

coverage of the tile which could act as a temperature buffer, wave attenuation factor or to increase whip-lash disturbance (Petrowski et al. 2016).

3.3.3. Data collection

Tiles were sampled using stratified image analysis – separating the canopy and understorey strata. Tile pictures were taken in two steps: the canopy stratum was pictured when arriving to the site without moving any organism, and the understorey stratum was pictured after carefully moving canopy organisms to the side. Multiple understorey pictures were taken when the understorey could not be captured with only one picture. Images without canopy were then trimmed to only include organisms falling within the 110 x 110 mm central area of the tile to avoid edge effects. Point Count Estimation (PCE; 500 points) subsampling was used for understorey sessile organisms within this area, identifying all organisms falling underneath each point. This avoided underestimating cover and diversity due to the exclusion of overlapping organisms in each point. The percentage cover of rare sessile species, mobile species and canopy was quantified directly (Photoshop 2020). All organisms found were identified to the lowest taxonomic level possible, and a conservative approach was applied where image resolution could limit identification accuracy. Three tiles did not present enough time points to be included in the study, reducing the sample size from 70 to 67, as these where very low in the shore and thus hard to access.

I applied corrections for two potential biases in the PCE dataset. First, I corrected for proximity to corners, where the four bolts fixing the tiles to the ground created topography that could be confounded with heterogeneity. To do so, I divided the tile image into four equal square corners, and delimited the area of influence to the four rows of PCE points closest to each bolt. Using binomial models, I tested whether proximity to bolt changed tile organism occurrence in each square corner, respectively. I repeated the test after sequentially removing each delimited row of PCE points until the binomial test was non-significant. Second, I corrected for missing PCE points inside holes in heterogeneous tiles due to image quality or canopy cover. For instance, heterogeneity effects are based on the identification of organisms in 120 points, resulting in 24% of the PCE points falling within the holes. However, if due to missing points this percentage fluctuated, heterogeneity effects would be over- or underestimated. To correct for this bias, I calculated the ratio of points within and outside holes for each heterogeneous tile image, and applied a weighting factor obtained by dividing the obtained ratio by the expected ratio for both points within and outside holes.

Annual percentage emersion time (i.e., emersion rate) was obtained from shore height, and the amount of time tiles were emersed within a tide was quantified to provide a proxy of emersion stress that accounts for non-linearity and temporal variation in tidal cycles. Shore height elevation was obtained for each tile using a RTK GPS (Trimble Catalyst DA1), and tile emersion times were obtained by using waterproof temperature loggers (HOBO MX2203) deployed for 24 hours. Local water height from the British Oceanographic Data Centre (BODC) buoy station at Mumbles was matched with the emersion times per tile and extrapolated to the proportion of time (between 0 and 1) that each tile was emersed for the entire experimental period. To allow assessment of heterogeneity effects under different levels of emersion stress (within Structural Equation Modelling multigroup analysis, see *Question 3*, below), emersion rate was split into three categories (i.e., low, mid, high) with each containing the same number of tiles.

In an *ex-situ* experiment, I linked emersion rate to environmental factors associated with emersion stress (e.g., Brown 1987; Silliman et al. 2011; Lathlean & Minchinton 2012). Emersion rate in the intertidal rocky shore has been linked to cellular stress responses (Collins et al. 2023) and previous authors have formulated the ‘environmental-stress hypothesis’ by which increasing abiotic stress (i.e., defined here by the decrease in community productivity or overall biomass by a given abiotic variable) increases the frequency of facilitation and decreases that of competition (Maestre et al. 2009). We exposed heterogeneous and non-heterogeneous tiles to temperature and desiccation during a total of three hours, after which all tiles dried out. To do so, briefly, tiles were submerged in seawater overnight, then exposed to air on a hot and sunny day, and surface temperature and water cover were measured, using a thermal camera (FLIR E5-XT) and image analysis, every 10 minutes until dry. This trial showed that increasing emersion rate led to reduced water cover ($t_{het} = -3.02$, $P<0.01$; $t_{het \times time} = -2.70$, $P<0.01$; Figure 2a) and increased temperature ($t_{het} = -3.96$, $P<0.001$; $t_{het \times time} = 0.77$, $P>0.05$; Figure 2b). However, while heterogeneity increased water cover as expected, it also slightly increased mean rock surface temperature (Figures 2 a-b).Thus, on the experimental tiles and in the absence of colonising organisms, heterogeneity seems to potentially mitigate desiccation stress, but potentially slightly compound thermal stress.

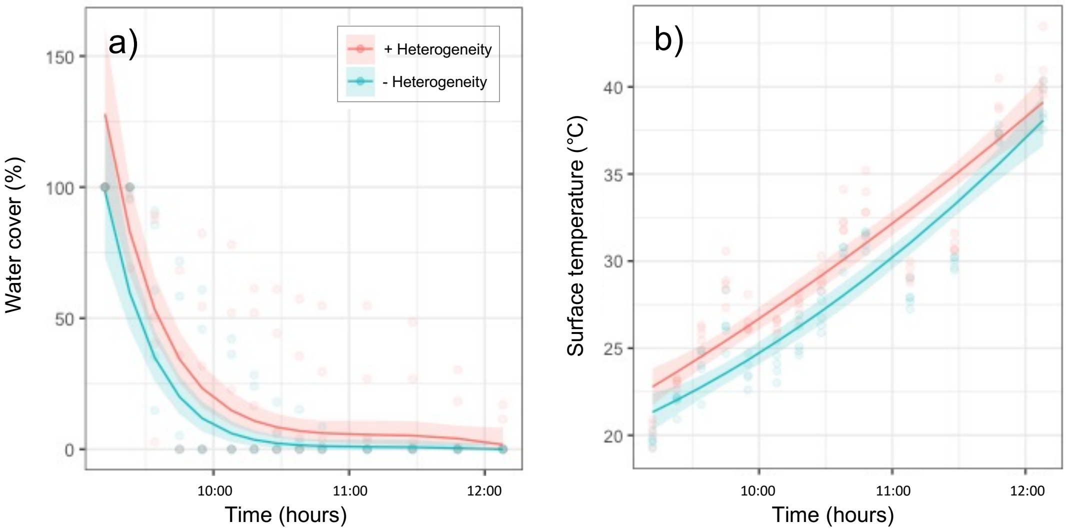

Figure 2. Heterogeneity effects on indicators of potential local desiccation stress and thermal stress. Linear model estimates (mean ± SE) and raw observations from the experiment comparing a) water percentage cover and b) average surface temperature across heterogeneity treatments for the experimental tiles. Mixed-effects linear models were used to fit the models. Square-rooting (water cover) and log-transforming (surface temperature) the response variable allowed to meet model assumptions. Time was z-transformed, and the interaction heterogeneity x time was included. Random effects included the station, where each pair of heterogeneous and non-heterogeneous tiles were located. Model assumptions were checked by visually examining Dharma residuals (Hartig 2020). Within graphs, t-statistic value for coefficients for heterogeneity (het) and the interaction between heterogeneity and time (het x time) and significance level. Models used to test this relationship are included in Supplementary Materials 8.

3.3.4. Question 1: Heterogeneity effects on community diversity and composition along the emersion gradient

I tested for heterogeneity effects on community diversity and composition, and the interactive effects with the emersion gradient. Using mixed effects linear models following a normal distribution (Bates et al. 2009), I tested effects of heterogeneity, emersion rate and their interaction on species richness and species evenness (Pielou Index) as the main diversity descriptors. For emersion rate, first, second and third order polynomial model specifications were assessed, and the model with the lowest Akaike Information Criterion (AIC) was selected. Fixed factors were z-transformed so that all variables were on a similar scale. I also included the random effects transect, and station nested within transect, since each station only occurred within one transect. Model diagnostics, including normality and heteroscedasticity of residuals for all linear models hereon, were checked visually (Hartig 2020). When needed, data were log-transformed or square-rooted to meet assumptions.

Using the same modelling approach, I tested for heterogeneity effects on the most abundant species or species groups, since dominant species are known to have strong effects on temporal cover stability (Sasaki & Lauenroth 2011). Groups were broadly defined based on ecological function and are hereon termed ‘species groups’. The invasive barnacle *Astrominius modestus* was considered separately due to its dominant and seasonal occurrence, while native barnacles such as *Semibalanus balanoides*, *Chthamalus montagui*, *Balanus* spp. and *Perforatus perforatus* were put together in another group. Aside from barnacles, other suspension feeders were considered together, a group which included *Mytilus edulis*, *Sabellaria alveolata, Pomatoceros* spp and other suspension feeders that are not barnacles. In the low shore, macroinvertebrate consumers such as *Patella* spp. and *Nucella lapillus* were grouped together, while the opportunistic seaweeds *Ulva* spp., *Cladophora* sp. and *Porphyra* sp. were considered within the same group.

I also assessed how heterogeneity changed community composition overall to understand how the individual heterogeneity effects on species groups were reflected more broadly across the community. First, compositional differences across communities were quantified using Bray-Curtis dissimilarities (Baselga et al. 2018) and plotted using Principal Coordinate Analysis (PCoA; Oksanen et al. 2007). A PCoA is an ordination technique similar to Principal Component Analysis (PCA) that allows to compute non-Euclidean distances such as Bray-Curtis dissimilarities. A k-means algorithm (Oksanen et al. 2007) was used to cluster communities into six groups that represented the minimum number of clusters with near-maximum Harabasz & Karonski (1974) scoring (cascadeKM in Oksanen et al. 2007). Second, these groups were described as community types based on the species groups (introduced above) present within. Then, the development and change in community composition of each tile was plotted over time to visually assess the identity and variability in their predominant community type. To aid interpretation, these community types were qualitatively ranked based on ‘community complexity’, with communities containing more species/groups or more highly differentiated groups ranking more highly. Finally, I used Permutational Multivariate Analysis of Variance (i.e., PERMANOVA; Oksanen et al. 2007) to assess whether community composition varied across heterogeneity, emersion rate, date and the interaction across the three factors. Note that the PERMANOVA analysis was based on the original community matrix and did not rely on the community types. All models are described in Supplementary Materials 8.

3.3.5. Question 2: Heterogeneity effects on temporal cover stability and temporal stability dimensions along the intertidal gradient

I quantified five ecological stability-related metrics including temporal cover stability and temporal stability dimensions (Table 1) for the whole community assemblage, using cover as a non-destructive community descriptor used in previous stability studies (e.g. Valencia et al. 2020). Temporal cover stability was calculated with and without detrending, by regressing total cover against experimental month and calculating the standard deviation of the residuals of each regression (Craven et al. 2018). Then, detrended temporal cover stability was calculated as the mean total cover divided by the detrended standard deviation. Detrending is a technique by which temporal data is transformed so that after detrending it does not show long-term temporal trends, and can thus be used to look at temporal fluctuations independent from other monotonic temporal patterns. Heterogeneity effects along the emersion gradient on temporal cover stability, as well as the underlying mechanisms of mean temporal population stability, temporal species asynchrony, temporal statistical averaging, and temporal compositional stability (Baselga et al. 2018), were assessed using mixed-effects linear models and the same modelling approach as in Question 1.

3.3.6. Question 3: Mechanistic pathways explaining heterogeneity effects on temporal cover stability

I built a multigroup piecewise Structural Equation Model (pSEM; Lefcheck 2016) to identify and quantify the mechanistic pathways linking heterogeneity and temporal cover stability. First, I formulated a hypothetical causal model based on *a priori* stability theory as well as knowledge of how heterogeneity affects rocky shore communities (Supplementary Materials 9). I included direct paths from heterogeneity to temporal cover stability and indirect paths through species groups and temporal stability dimensions. Partial bivariate correlations were added following *a priori* expectations and when d-separation tests indicated missing relationships. The multigroup analysis allowed to test how pSEM paths changed along the emersion gradient (defined in three groups: low, mid and high emersion stress). All models within the pSEM were fit using mixed-effects linear models following the modelling approach in Question 1. For each individual pSEM encompassing the multigroup pSEM analysis, tests of directed separation were used to check the fit of the pSEM model, and missing paths were identified and included, or added as bivariate correlation when not relevant. A Fisher's test was then used to check whether there were any paths missing in the multigroup pSEM analysis. To reduce multigroup pSEM degrees of freedom and thus allow for model convergence, only mixed-effects linear models were replaced for linear models when this change did not affect qualitatively the results. Lastly, I summed standardised path coefficient values to compare heterogeneity effects across species groups, temporal stability dimensions and emersion stress levels to account for both direct and indirect effects on temporal cover stability.

3.4. Results

3.4.1. Question 1: Heterogeneity effects on community diversity and composition along the emersion gradient

Heterogeneity increased both species richness (t_{het} = -4.25, P<0.001; $t_{emersion}$ = -1.95, P=0.05-0.1; $t_{het\ x\ emersion}$ = 3.64, P<0.001) and species evenness (t_{het} = -2.75, P<0.01; $t_{emersion}$ = -0.54, P>0.05; $t_{het\ x\ emersion}$ = 2.43, P<0.05) at low emersion stress, and these effects gradually decreased until disappearing at high emersion stress (Figures 3a-b). Dominant species and species groups, however, showed differential responses to heterogeneity and the emersion stress gradient. Heterogeneity benefitted other (i.e., non-barnacle) suspension feeders in the low shore, where they were generally more abundant, and had diminishing effects with increasing emersion stress (t_{het} = -4.19, P<0.01; $t_{emersion}$ =-0.74, P>0.05; $t_{het\ x\ emersion}$ = 3.43, P<0.05; Fig. 3c). In contrast, heterogeneity decreased the cover of Austrominius modestus, which reached high cover on non-heterogeneous tiles and in the upper shore (t_{het} = -1.38, P>0.05; $t_{emersion}$ = 2.32, P<0.05; $t_{het\ x\ emersion}$ = 2.18, P<0.05; Figure 3d). Although not significantly different, heterogeneity also seemed to reduce the cover of macroinvertebrate consumers throughout the emersion gradient (t_{het} = 1.05, P>0.05; $t_{emersion}$ = 2.23, P<0.05; $t_{het\ x\ emersion}$ = -0.69, P>0.05; Figure 3e). The other abundant groups comprising native barnacles (t_{het} = -0.26, P>0.05; $t_{emersion}$ = -3.01, P<0.01; $t_{het\ x\ emersion}$ = 0.25, P>0.05; Figure 3f) and ephemeral macroalgae (t_{het} = 0.41, P>0.05; $t_{emersion}$ = -3.84, P<0.001; $t_{het\ x\ emersion}$ = -0.23, P>0.05; Figure 3g) were not affected by heterogeneity and tended to dominate at high and low emersion stress levels, respectively.

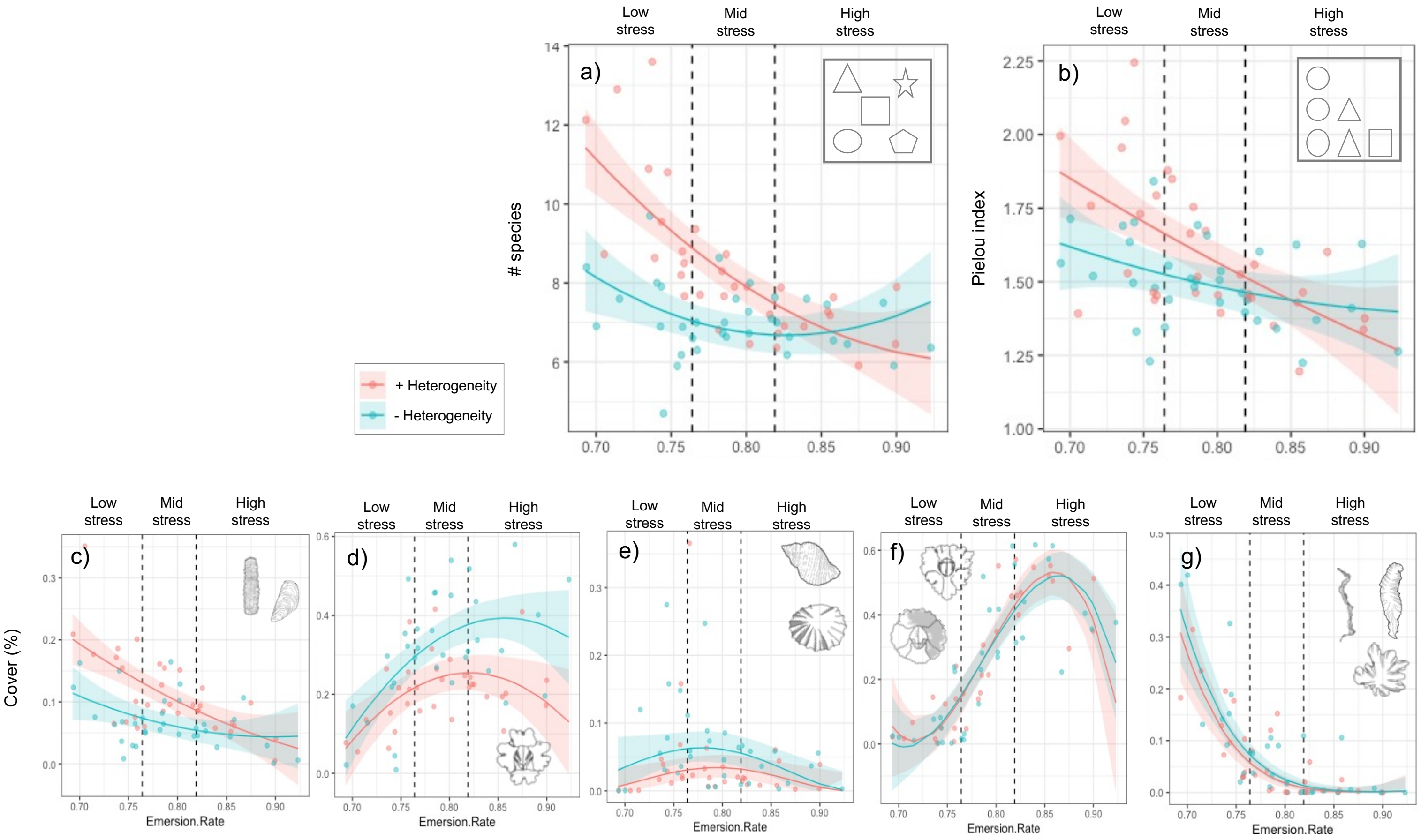

Figure 3. Heterogeneity effects on measures of diversity and the abundance of species groups of rocky shore communities along the emersion gradient. Results from linear models indicating original data and linear model estimates (mean ± SE) testing heterogeneity effects along the emersion gradient for a) species richness, b) Pielou species evenness, c) other suspension feeders (i.e., *Mytilus edulis, Sabellaria alveolata, Pomatoceros spp.* and other non-barnacles suspension feeders), d) *Austrominius modestus*, e) macroinvertebrate consumers, f) native barnacles and g) ephemeral macroalgae. Points in each graph are the mean of all observations across dates per tile. Lines are the predicted response obtained from the mixed-effects models used to test emersion rate and heterogeneity effects using the ggpredict function in ggeffects R package. Around lines, standard error is indicated with shaded color corresponding to each heterogeneity treatment. Further details and justification on the use of environmental stress and emersion rate please refer to section 3.3.3.

Aside from affecting individual groups, heterogeneity changed community composition overall along the emersion gradient ($F_{1,655} = 194.43$, $P<0.001$) and across dates (Figure 4a, b-e; $F_{10,655} = 20.45$, $P<0.001$; additional PERMANOVA results in Supplementary Materials 10). Supporting PERMANOVA results, heterogeneous tiles tended to represent different community types over time at high and mid emersion stress (Figure 4f-i). These heterogeneous communities tended to be dominated by communities with native barnacles (high shore) and macroalgae (mid and low shore), while non-heterogeneous tiles presented communities dominated by *A. modestus* in the high shore, and only in the low shore by macroalgae. In addition, communities that developed early in the experiment on heterogeneous tiles did not tend to appear until later in the experiment on non-heterogeneous tiles (Figures 4f-k). For example, early in the experiment heterogeneous tiles at low emersion stress tended to be macroalgae-dominated and non-heterogeneous tiles tended to be barnacle-dominated, while late in the experiment, communities for both treatments were macroalgae-dominated (Figures 4j-k).

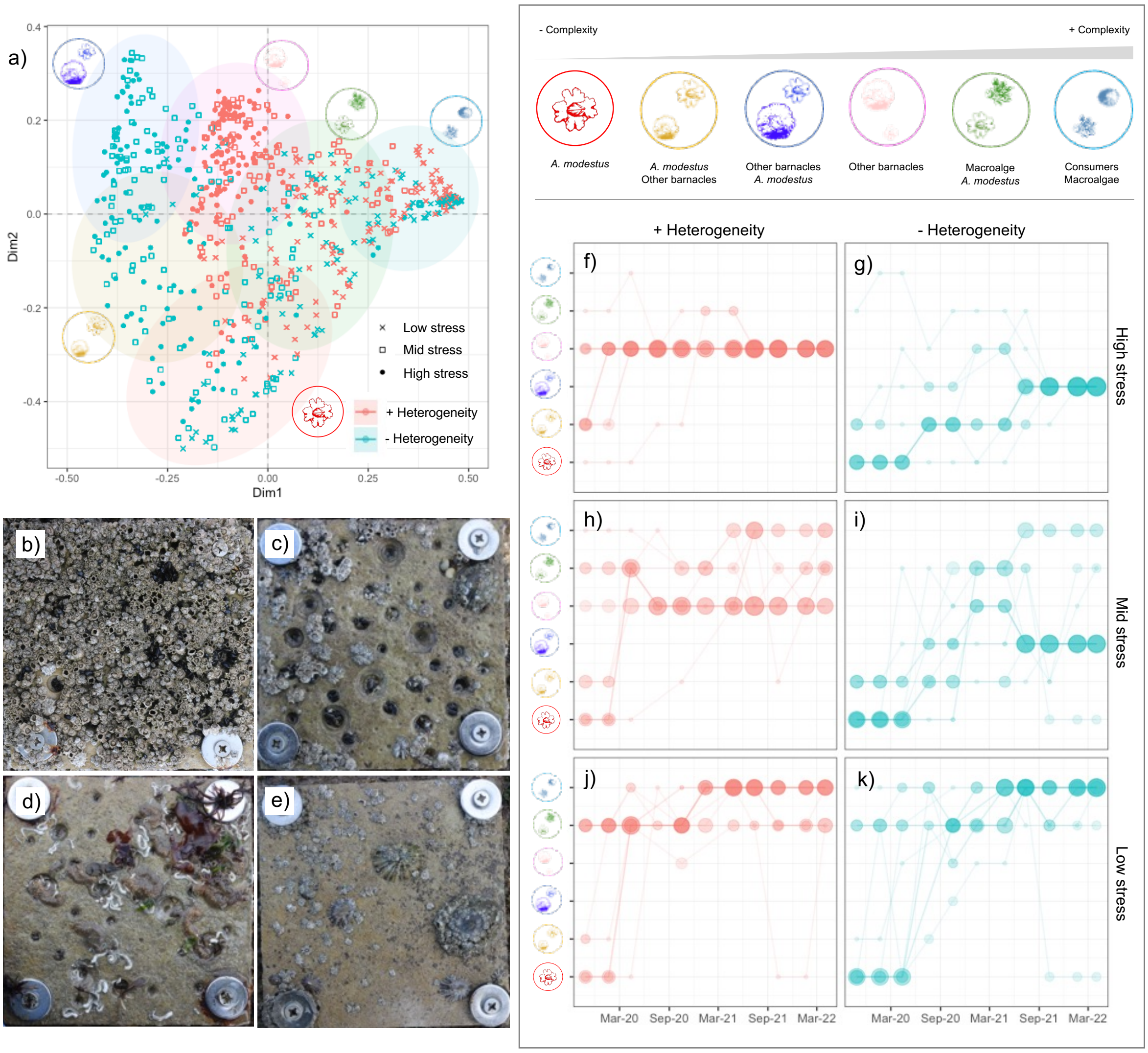

Figure 4. Heterogeneity effects on community composition. Results summarizing differences in community composition within the experiment across a) six mean community types. Examples of these communities are in pictures b-e), showing native-barnacles community in a heterogeneous tile, c) consumer-dominated community on a heterogeneous tile, d) macroalgae-dominated community in a heterogeneous tile and e) consumer-dominated community on a non-heterogeneous tile. Differences in community composition are also shown in terms of the community types defined within the PCoA space (f-k). In panels f-k, dot size and transparency increase with the number of tiles present belonging to a particular community type. Thus, the community type(s) and number of tiles per community type are shown per date, along the emersion gradient and across heterogeneity treatments.

3.4.2. Question 2: Heterogeneity effects on temporal cover stability and temporal stability dimensions along the emersion gradient

Heterogeneity did not increase temporal cover stability along the emersion gradient ($t_{het} = -1.95$, P=0.05-0.1; $t_{emersion} = -2.62$, P<0.05; $t_{het\ x\ emersion} = 1.17$, P>0.05; Figure 5a). Instead, temporal cover stability strongly and non-linearly responded to emersion stress, peaking in the lower part of the upper shore, but declining rapidly as emersion stress increased further. Heterogeneity had a marginal non-significant effect on mean temporal population stability in the high shore (t_{het} = -1.64, P>0.05; $t_{emersion}$ = -3.22, P<0.01; $t_{het\ x\ emersion2}$ = -1.69, P=0.05-0.1; Figure 5b), had no clear effect on temporal species asynchrony (t_{het} = -0.88, P>0.05; $t_{emersion}$ = -0.93, P>0.05; $t_{het\ x\ emersion}$ = 0.81, P>0.05; Figure 5c), and increased temporal statistical averaging at low and mid emersion stress (t_{het} = -2.67, P<0.05; $t_{emersion}$ = -2.82, P<0.01; $t_{het\ x\ emersion}$ = 2.43, P<0.05; Figure 5d). Among these mechanisms, mean temporal population stability followed the most similar pattern to temporal cover stability. Emersion stress tended to decrease temporal species asynchrony and temporal statistical averaging for heterogeneous tiles, compared to non-heterogeneous tiles. Lastly, heterogeneity did not modify temporal compositional stability in a meaningful way, as despite a statistically significant interaction between heterogeneity and emersion, both heterogeneity treatments similarly increased temporal compositional stability with emersion stress (t_{het} = -2.17, P<0.05; $t_{emersion}$ =-1.17, P>0.05; $t_{het\ x\ emersion}$ = 2.14, P<0.05; Figure 5e).

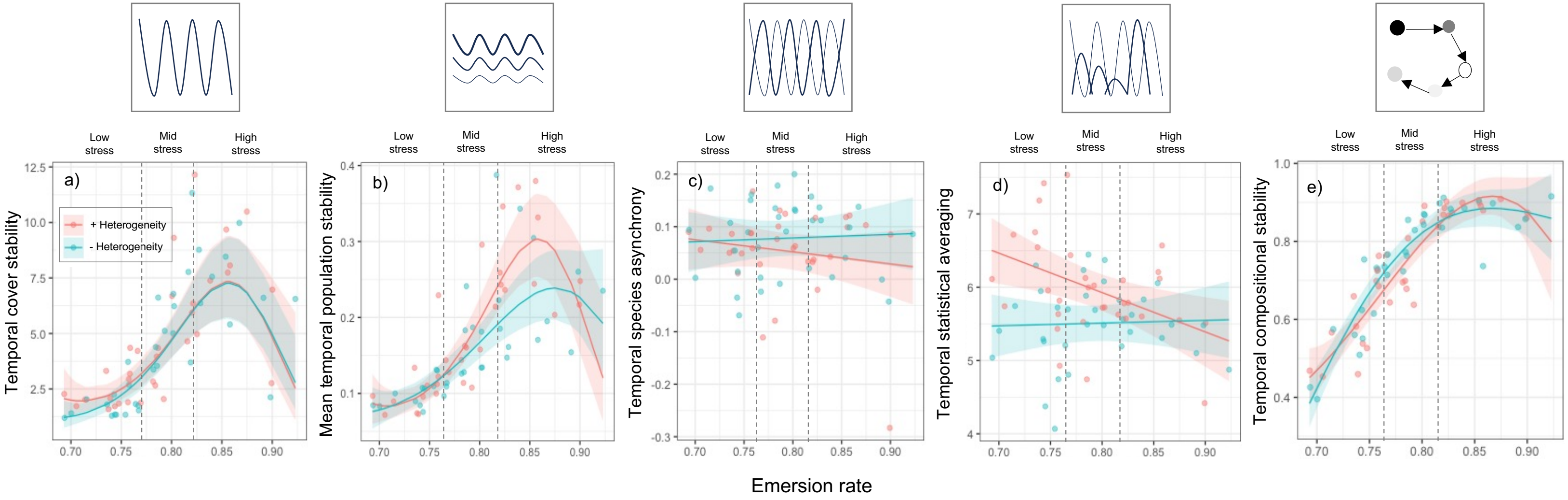

Figure 5. Heterogeneity effects on temporal cover stability and temporal stability dimensions along the emersion gradient. Results from linear models indicating original data and linear model estimates (mean ± SE) for a) temporal cover stability, b) mean temporal population stability, c) temporal species asynchrony, d) temporal statistical averaging and e) temporal compositional stability along the intertidal emersion gradient. Points in each graph are the mean of all observations across dates per tile. Lines are the predicted response obtained from the mixed-effects models used to test emersion rate and heterogeneity effects using the ggpredict function in ggeffects R package. Around lines, standard error is indicated with shaded color corresponding to each heterogeneity treatment.

3.4.3. Question 3: Mechanistic pathways explaining heterogeneity effects on temporal cover stability

Although heterogeneity had no net effects on temporal cover stability, further investigation revealed this could be explained by its effects on temporal stability dimensions. These occurred along four main pathways, which varied across emersion stress levels (Table 2; Figures 6a-c and Figures 6d-h). First, although not evident in the overall relationships shown in Fig. 5b, once accounting for indirect effects and covariates in the pSEM model, it emerged that heterogeneity directly promoted mean temporal population stability (Figure 6d). At low emersion stress, these positive effects were partially counteracted by the indirect negative effects from other suspension feeders (Table 2). The pathway via mean temporal population stability thus helped promote temporal cover stability along the emersion gradient, and particularly at mid and high stress (Figure 6h).

Table 2. Differences in multigroup *pSEM* mediator effects across emersion stress levels. Response and Predictor variables for the significantly different links across any of the emersion rate groups (high stress, mid stress and low stress).

Response	Predictor	p-value
Other suspension feeders	Heterogeneity	0.014
Species richness	Heterogeneity	0.001
Consumer	Emersion rate	0.004
Austrominius modestus	Emersion rate	0.047
Native barnacles	Emersion rate	<0.001
Other suspension feeders	Emersion rate	0.009
Ephemeral macroalgae	Emersion rate	0.010
Temporal statistical averaging	Native barnacles	0.047
Temporal compositional stability	Native barnacles	0.020
Temporal compositional stability	*Austrominius modestus*	0.013
Temporal statistical averaging	Species evenness	0.032

Second, heterogeneity promoted temporal species asynchrony and temporal statistical averaging by increasing species richness and other suspension feeders, while the positive effects on temporal species asynchrony were negated by species evenness and negative heterogeneity effects on *Austrominius modestus* abundance (Figure 6e). As a result, heterogeneity had positive net effects on temporal species asynchrony and temporal statistical averaging at low stress due to large species richness effects, and other suspension feeder effects on temporal statistical averaging. However, increasing heterogeneity also had negative effects at low stress, reducing temporal compositional stability. Heterogeneity effects were quickly reduced further up the shore, which caused overall negative heterogeneity effects on temporal species asynchrony at mid and high stress levels, contributing to reduced temporal cover stability (Table 2; Figure 6h).

A third pathway consisted of consumer effects on temporal statistical averaging and temporal compositional stability, which were accentuated with increasing stress levels (Figure 6f-h). Heterogeneity reduced consumer abundance, and decreased consumer effects on other suspension feeders, which in turn allowed to increase temporal statistical averaging. However, by reducing the abundance of consumers, their direct positive effect was also reduced and thus resulted in an overall decrease in temporal statistical averaging (Figure 6f). Similarly, the reduction in consumer abundance also reduced their positive effect on temporal compositional stability (Figure 6g), both directly and indirectly by reducing ephemeral macroalgae, causing a negative effect of heterogeneity on temporal cover stability (Figure 6h).

Despite the different heterogeneity-promoted mechanisms on temporal and temporal compositional stability across stress levels, there were other mechanisms with larger effects in the experiment (Table 2; Figures 6i-j). Mechanisms originating from emersion stress (even within low, mid, and high zones) and from the abundance of other barnacle species, which were unaffected by heterogeneity, tended to influence temporal cover stability much more than heterogeneity. The combination of these two additional drivers would have then contributed to obscure heterogeneity effects along the emersion gradient (Figure 5a).

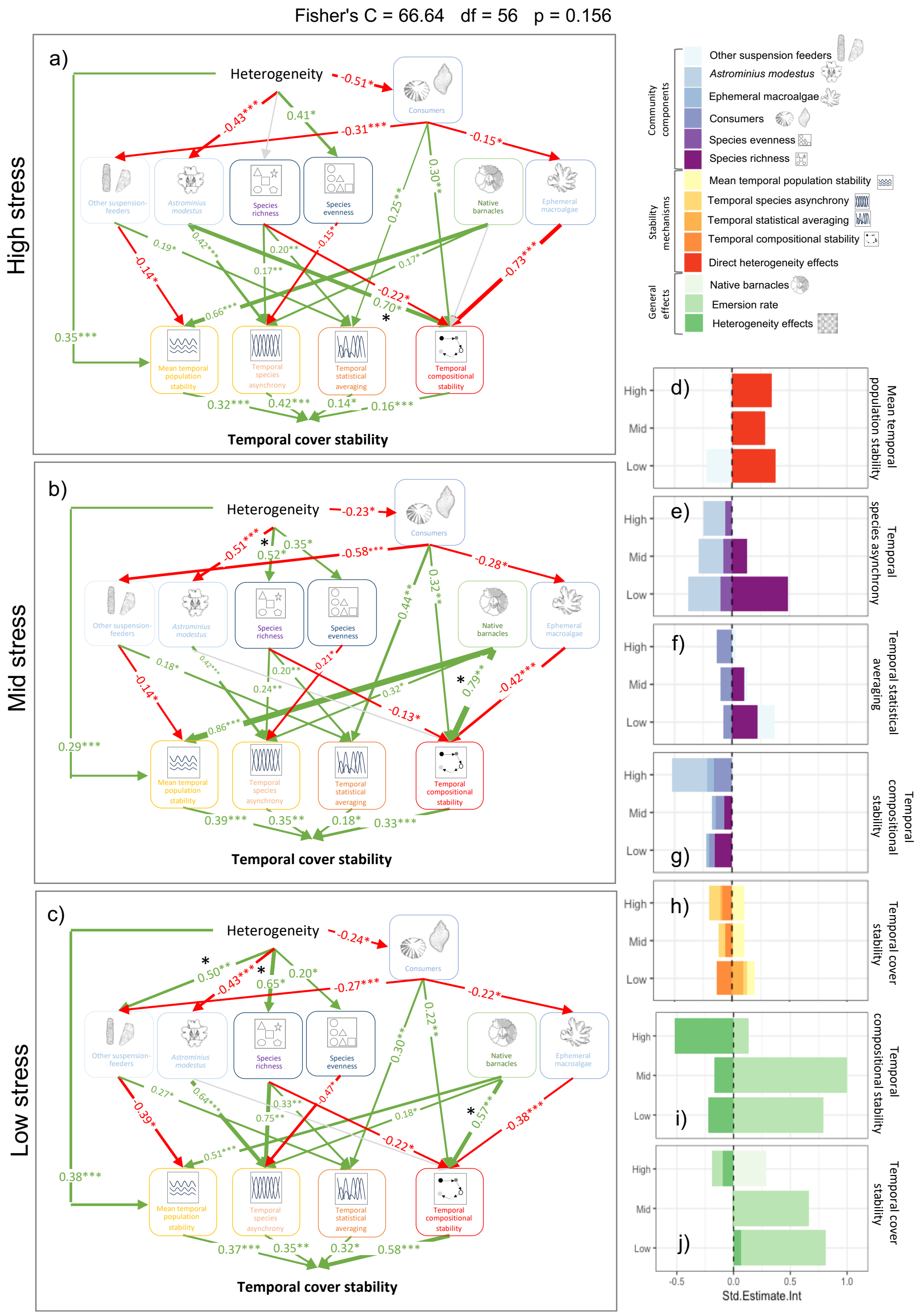

Figure 6. Heterogeneity effects on compositional and temporal cover stability explained through mechanistic pathways within the community. Piecewise SEM results for temporal and temporal compositional stability. At the left, multigroup pSEMs showing the effects of heterogeneity on temporal cover stability, and indirect effects across community components (e.g., species richness) and temporal stability dimensions (e.g., temporal species asynchrony) (a-c). Green and red lines indicate positive and negative significant (P<0.05) effects, respectively. Numbers on lines indicate the standardised path coefficients (SPC). At the right, the sum of SPCs representing heterogeneity effects on mean temporal population stability (d), temporal species asynchrony (e), temporal statistical averaging (f), temporal compositional stability (g) and temporal cover stability (h), as well as the sum of the co-occurring effects (i.e., heterogeneity, emersion gradient and native barnacles) on temporal compositional stability (i) and temporal cover stability (j). Colour coding indicates the source of SPCs across community components, temporal stability dimensions and general effects. Significance coding: . = 0.1 – 0.05, * = <0.05, **= <0.01, ***= <0.001. Black asterisks indicate paths that were significantly different across stress levels in the multigroup pSEM analysis.

3.5. Discussion

Biodiversity and dominant species traits have been traditionally considered the two focal drivers of local temporal cover stability, with environmental properties such as heterogeneity usually poorly studied. Despite results indicating minor net effects of heterogeneity on temporal cover stability, the effects of heterogeneity on diversity, composition, and the mechanisms underpinning temporal cover stability were in some cases much larger. Results revealed that heterogeneity simultaneously both promoted and undermined temporal cover stability, through four different mechanisms. First, heterogeneity increased temporal cover stability by promoting mean temporal population stability, presumably through the provision of refugia that buffered species from perturbations. Second, heterogeneity promoted diversity-dependent compensatory mechanisms. Third, heterogeneity reduced stabilising effects of a dominant species. Fourth, heterogeneity reduced consumer effects, with negative effects on temporal statistical averaging and temporal cover stability. Identifying the counteracting ways in which heterogeneity can affect stability allows us to link heterogeneity and stability theory.

The first stage of my analysis revealed clear heterogeneity effects on community composition and diversity. Heterogeneous tiles appeared to develop complex communities more rapidly, hold higher levels of richness and evenness, and influence composition by reducing the dominance of a non-native barnacle species while increasing the abundance of a diverse suite of suspension feeders including mussels. Observations in the field suggested that these effects occurred due to heterogeneity providing new environments that subdominant species (e.g., mussels) could colonise and escape dominant species (e.g., *Austrominius modestus*). These environments also allowed for less-resistant species with larger physical structures (e.g., macroalgae) that would have been otherwise removed by storms and wave action (Wernberg & Connell 2008). Notably, heterogeneity effects were dependent on the shore zone, with stronger effects on diversity lower on the shore where more species were available in the species pool, and on the dominant non-native barnacles (*A. modestus*) higher on the shore where it reached higher abundances. These results add further support to the evidence base that heterogeneity enhances diversity, reduces the presence of dominant species and further illustrates the important effects on species composition in the rocky shore system. Despite the clear effects on diversity and composition, heterogeneity effects did not seem to cascade down to affect temporal cover stability and stability-related mechanisms. The disconnect between heterogeneity effects on diversity and composition and heterogeneity effects on stability could have been explained by several counteracting mechanisms.

The first major mechanism revealed from the SEM analysis was the influence of heterogeneity on mean temporal population stability. Initially, heterogeneity did not seem to have net effects on mean temporal population stability, but after accounting for covariates and indirect effects in the SEM, it was possible to find direct stabilising and indirect destabilising effects on mean temporal population stability. Direct positive heterogeneity effects on mean temporal population stability occurred throughout the shore and were not mediated by species groups, but rather by species observed to occupy the space inside the holes which included *Semibalanus balanoides*, *Nucella lapillus* and *Fucus* spp. Such results align with general refugia effects from heterogeneity, whereby heterogeneity provides with spaces with ameliorated conditions that allow species to survive stress and disturbance (e.g., Keppel et al. 2012). Indirect negative heterogeneity effects were caused by the proliferation of other suspension feeders inside the holes in the lower shore. According to literature, species like mussels would have colonised in the milder months only to die off in the harsher months (e.g., Seed 1996). More broadly, this would indicate that heterogeneity refugia effects are not always effective and may depend on how resistant the species is and how large disturbance events are (e.g., Lancaster 2000). Overall, heterogeneity effects on mean temporal population stability reflect the potential for heterogeneity to increase resistance to disturbance (e.g., Selwood et al. 2015), but may not always be effective due to species traits and disturbance magnitude.

Second, more variable heterogeneity effects occurred on temporal species asynchrony and temporal statistical averaging, shifting from positive in the low shore to negative in the high shore. Heterogeneity increased species richness, which had strong effects on temporal species asynchrony by differential response to environmental variation (De Mazancourt et al. 2013; Loureau et al. 2021), and by increasing density-dependant competition inside and outside the holes, respectively (e.g., Lancaster & Ledger 2015). More arriving species, and particularly more other suspension feeder species, also increased the independent random fluctuation beyond responses to environmental variation and competition, further increasing temporal cover stability through temporal statistical averaging (Tilman et al. 1998). Heterogeneity effects on temporal species asynchrony and temporal statistical averaging may have depended on species traits and background species richness, as both effects decreased in the higher shore where less species arrived to the tile from neighbouring environments and there were resistant species that varied less with environmental fluctuation (e.g., *Austrominius* modestus and other barnacles; Anil et al. 2012). Collectively, these effects reflect the importance of heterogeneity-diversity effects for stability, and also reveal the role of recovery dynamics in heterogeneity-stability relationships as species replacements maintain stability after disturbance.

Third, the increase in diversity presented a trade-off, which was the reduction of dominant species abundance, and the subsequent decrease in temporal species asynchrony potentially due to a reduction in competition. Heterogeneity reduced the abundance of *Austrominius modestus* and other dominant species – as indicated by the increase in species evenness (Hillebrand et al. 2008). Negative effects of species evenness on temporal species asynchrony or stability are rarely reported and may depend on the specific traits of dominant species and the presence of insurance effects (e.g., Lazaro et al. 2022). *A. modestus* was a relevant dominant species in the community with a relevant role in the community as an invasive barnacle species that competed with native barnacles such as *S. balanoides,* other suspension feeders such as mussels, and any other encrusting organism (e.g., O'Riordan et al. 2020), and stabilised community composition in the high shore due to its stress- and disturbance-resistant traits (e.g., Beerman et al. 2013). The reduction in *A. modestus* abundance inside the holes, observed on the field, would have led to decreased competition in the overall community. This reduced temporal species asynchrony, as a result of niche partitioning (e.g., Durr & Wahl 2004), and allowed mussels to escape competition with *A. modestus* by finding refuge inside the holes. In contrast, the described increases in species richness would have promoted density-dependent competition both inside and outside holes (e.g., Lancaster & Ledger 2015). Overall, persistent negative heterogeneity effects on dominant species resulted in temporal species asynchrony only benefiting temporal cover stability when enough species were present, and revealed a mechanism which would have limited recovery after disturbance.

Fourth and last, heterogeneity also reduced macroinvertebrate consumer abundance and effects on temporal cover stability, possibly by hampering their movement and creation of home scars, and particularly of the limpet *Patella* spp. (Griffin et al 2009). Here, heterogeneity reduced consumers' ability to promote temporal statistical averaging, possibly through the creation of free spaces that would have increased species colonisation and thus temporal statistical averaging (Townsend & Gouhier 2019). Reduced consumer movement would also explain the reduced temporal compositional stability, as consumers tend to reduce the abundance and fluctuations of less-resistant species (e.g., ephemeral macroalgae; Jonsson et al. 2006; White et al. 2017). Surprisingly, lower consumer abundance did not increase species competition, which would have been reflected in increased temporal species asynchrony. This could have been due to a combination of reasons: competition happening inside holes, seasonality effects masking consumer effects (i.e., spring and autumn bloom effects), or excessive consumer pressure (e.g., bulldozing effects; Menge et al. 2010) wiping out most organisms outside holes and thus weakening any asynchronous dynamics. Consumer effects did decrease temporal statistical averaging, potentially due to dominant species occupying most of the surface area on the tile and left no opportunities for new species to colonise and generate random fluctuations (Bertness 1989). Thus, heterogeneity effects reducing consumers could have been cornerstone to the overall stability dynamics of the community, reducing resistance by allowing the growth of ephemeral species and reducing recovery by limiting temporal statistical averaging.

Environmental stress and disturbance played an important role in modulating the four described heterogeneity-stability mechanisms. As environmental stress increased, background species richness decreased as described by many rocky shore studies indicating lower species richness in the high shore (e.g. Thyrring & Peck 2021). Increased stress would have also selected for species more resistant to stress and disturbance (i.e., more barnacles, less ephemeral macroalgae) and could have accentuated the need for refugia (although no increased heterogeneity effects were found here). Field observations indicated that excessive disturbance, when *Patella* spp. dominated the community in the low shore, created barren spaces where no populations could survive outside holes (e.g., Fletcher & Underwood 1987) and this could have nullified heterogeneity effects on stability mechanisms. It was also noted that the excessive arrival of mussels and ephemeral macroalgae during spring and summer would have grown on top of existing organisms, causing their die-off and later leave a barren community due to their seasonal die-off (e.g., O’Neill 2016) which would have also negated heterogeneity effects on stability mechanisms. These observations would indicate that heterogeneity-stability mechanisms tend to decrease with environmental stress, and under excessive disturbance (although it may need minimal disturbance levels for heterogeneity effects to take place).

Overall, this study shows how counteracting mechanisms can yield net neutral heterogeneity effects on temporal cover stability. Even with strong heterogeneity effects on species richness (i.e., low shore), we cannot assume that these effects will translate into temporal cover stability, and it is possible that heterogeneity may have negative effects on stability. Results here are one of the only existing tests for heterogeneity-stability relationships (Supplementary Materials 11), and the only one that explicitly considers the relationship among multiple stability mechanisms, across multiple trophic levels and environmental settings based on stress levels, and over a term long enough to allow multiple mechanisms to play out (e.g., effects on consumers). This mechanistic understanding integrates resistance (i.e., mean temporal population stability) and resilience (i.e., temporal species asynchrony and temporal statistical averaging) dynamics over multiple disturbance events and complements such information with other compositional effects. However, information on community responses to individual disturbance, the role of individual species (e.g., different roles across consumer species; White et al. 2017), the effects of heterogeneity over larger gradients including more than two heterogeneity levels or the effect to account for non-linearities could help further our understanding of heterogeneity-stability dynamics. In addition, the consideration of separate heterogeneity facets (e.g., substrate 3D amount and substrate 2D amount) would allow to explore separate pathways in which heterogeneity can affect temporal cover stability.

4. Local and landscape heterogeneity combine and interact to promote gamma diversity

4.1. Abstract

Local and landscape heterogeneity promote regional (gamma) diversity by enhancing local (alpha) diversity and species turnover, respectively. Here, I test how local and landscape heterogeneity effects combine and interact to drive gamma diversity, and further explore how the mechanisms behind these effects change across seasons and species groups. Using artificial landscapes built by resampling experimental rocky shore community data, I found that local heterogeneity effects were reduced at high landscape heterogeneity due to decreased species turnover in locally heterogeneous landscapes. Local and landscape heterogeneity had positive, through differential effects across seasons, with local heterogeneity effects increasing in cold months, potentially due to the need for refugia, and landscape heterogeneity effects increasing in warm months potentially due to provision of more specialised niches. Local and landscape heterogeneity also had mostly positive effects across species groups, and these positive effects were magnified through cascading effects across groups (particularly for local heterogeneity effects). These results highlight the need to integrate the interactions between local and landscape heterogeneity in biodiversity management.

4.2. Introduction

Habitat loss reduce local and landscape heterogeneity, highlighting the pressing demand to understand its interactive and combined consequences on biodiversity (McKinney et al. 1999; Thrush et al. 2006; Hewitt et al. 2010). Despite studies having shown that heterogeneity promotes diversity at local and landscape scales (Kovalenko et al. 2012; Stein et al. 2014), little is known about how changes in heterogeneity at both scales combine to affect gamma diversity. Within a landscape, local heterogeneity effects generally promote local diversity, while landscape heterogeneity increases differences across communities over space (e.g., Veech & Crist 2007). Interactions across local and landscape heterogeneity may occur as, for example, the increase in mean local diversity (i.e., alpha diversity) may curtail or accentuate spatial community compositional differences (i.e., species turnover), and *vice versa*. Local-landscape heterogeneity effects on species communities may further change across seasons due to the fluctuation in environmental stressors, disturbance, and species interactions. Community responses to heterogeneity across scales will also depend on the species traits and interactions. For example, local heterogeneity may promote certain species groups, such as those that would be otherwise excluded by competitors or grazers, while increasing landscape heterogeneity may exclude others, such as those negatively affected by the presence of more extreme environmental conditions. Understanding how local-landscape heterogeneity interactions work is thus key to predict habitat loss effects and to promote conservation and restoration efforts both at the local and landscape scales to optimise heterogeneity positive effects on biodiversity.

Across systems, local and landscape heterogeneity modify different features in the environment, but both tend to promote diversity by increasing the range of conditions available for species (e.g., Arellano et al. 2017; Blubaugh et al. 2022). Landscape heterogeneity increases the large scale spatial variation of features like substrate or vegetation cover type or topography (e.g., Fahrigh et al. 2011), which in turn promote the spatial variation in community composition across environments (i.e., spatial species turnover; e.g., Veech & Crist 2007). The higher the landscape heterogeneity, the lower the effect of dominant landscape features (e.g., tree or algae canopy) on gamma diversity, the more extreme are the conditions that can be found therein, and the more specialised the niches present within the landscape (e.g., Perovic et al. 2015). At the local scale, structures such as macroalgae and tree canopies help increase heterogeneity and the variety of local conditions that promote alpha diversity (e.g., August 1983). Local heterogeneity increases niche provisioning by providing food, physical space, breeding sites (e.g., Grenouillet et al. 2002; Felderhoff et al. 2023), but also refugia that reduce effects from species interactions (e.g., competition, grazing; Grabowski et al. 2008), abiotic stressors (e.g., seasonality, temperature; McAfee et al. 2022) and disturbance (e.g., waves, wind; Sebens 1991). Landscape context (i.e., here defined as the proximity to landscape features such as macroalgae canopy) helps link the two heterogeneities, as local heterogeneity effects may be affected by the presence of landscape features like the proximity to a stand of trees, hillside, or aquatic habitat patch such as a rockpool that can increase or decrease the harshness of the environment, the number of specialised niches, arriving propagules and species (e.g., Wang et al. 2023). Despite this connection, local and landscape heterogeneity work at different scales, affect diversity through different processes, and are often generated by different features.

Yet, landscape and local heterogeneity effects may interact and combine as both promote gamma diversity, while potentially acting through different mechanisms across seasons and species groups. For example, as local heterogeneity often provides species with refugia from environmental stress, it may buffer external environmental variability and allow similar sets of species to persist across varied landscape contexts (heterogeneous landscape), thus reducing community compositional differences across communities and therefore the effects of landscape heterogeneity on gamma diversity (i.e., antagonistic effects). In contrast, landscape heterogeneity may increase alpha diversity by providing more specialised niches, and local heterogeneity may allow more of these species to capitalize on more varied local environmental conditions (i.e., synergistic effects; e.g., Bracewell et al. 2018). The role of local and landscape heterogeneity may also change across seasons, with local refugia needed in the cold months to escape inclement conditions such as storm effects, and landscape heterogeneity providing environments that – although too extreme in the cold months – allow for more specialised niches in the warm months (e.g., Duflot et al. 2014; Perovic et al. 2015). Some species groups may benefit from the increase in harsh conditions and specialised niches (Villeger et al. 2008) found across heterogeneous landscapes, while other species groups may need locally heterogeneous environments to find refugia against species interactions or disturbance (e.g., Keppel et al. 2012). For example, in rocky intertidal systems in the NE Atlantic, barnacles tend to be more resistant to water movement and desiccation found at high landscape heterogeneity but are easily outcompeted by large brown macroalgae (fucoids), which need more humid and calm environments away from grazing that are more commonly provided by local heterogeneity (e.g., Kordas & Dudgeon 2009). Accordingly, across seasons and species groups, landscape and local heterogeneity may combine to drive gamma diversity and the abundance of different species groups; these effects may be additive (local and landscape effects are both positive or negative), such that together they more strongly influence diversity or a species group or opposing (one positive and one negative) such that they together may yield net neutral effects (Figure 1).

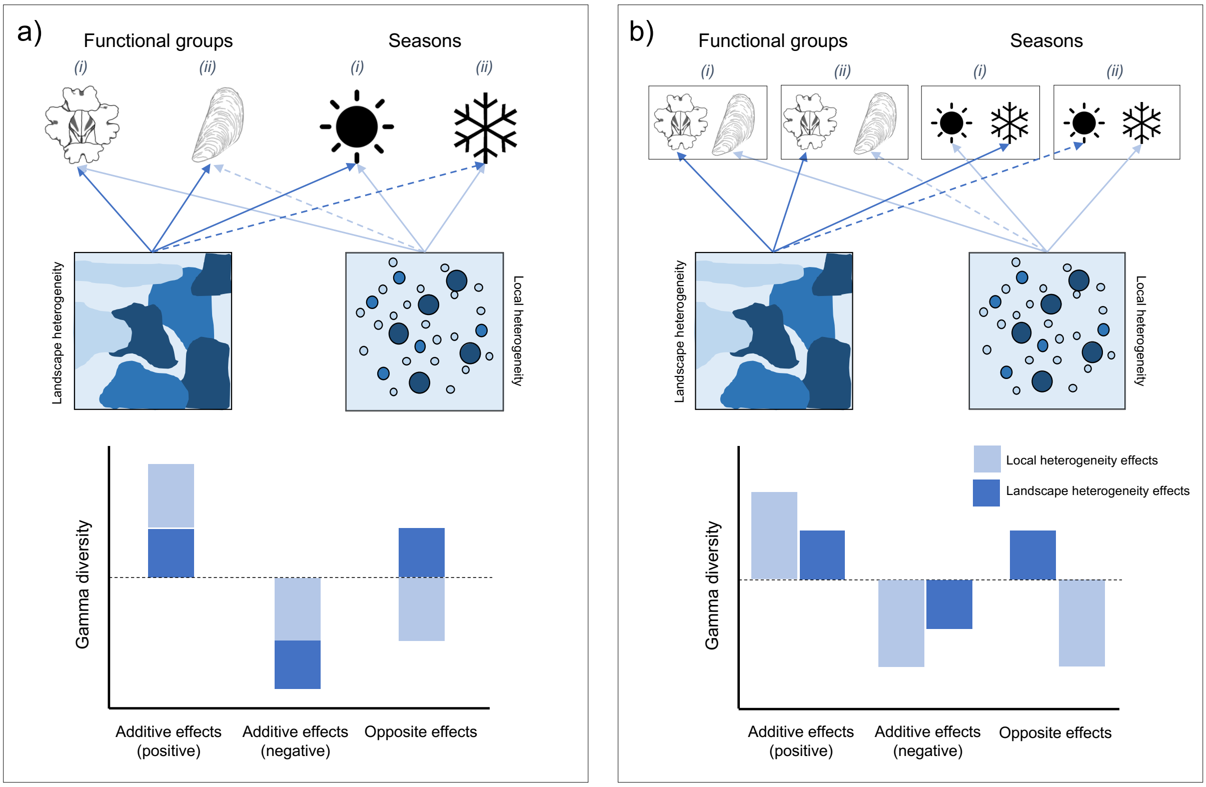

Figure 1. Hypotheses on the combined local and landscape heterogeneity on species groups and on gamma diversity across seasons. Combined effects may occur a) within species groups and seasons, with (i) both local and landscape heterogeneity effects being either positive or negative (additive effects) or (ii) with one positive and one negative effect (opposite effects). For example, local and landscape heterogeneity effects on gamma diversity may be both positive in the warm months but show opposite effects in the cold months. Combined effects may also occur b) between species groups and seasons, and again with (i) additive, or (ii) opposite effects. For instance, local heterogeneity effects may both promote different species groups (additive effects), or local heterogeneity can promote a group and landscape heterogeneity decrease another group (opposite effects). Alternatively, local heterogeneity effects on gamma diversity may be positive and occur in the warm months, while landscape heterogeneity effects on gamma diversity may still be positive (additive effects) or negative (opposite effects) but occur during the cold months. In the figure, dashed arrows indicate cases in which the effect shows the opposite sign in comparison to its paired effect.

To assess interactive and combined landscape and local heterogeneity effects, I formulated a series of hypotheses divided in three sections: the interplay between landscape context and local heterogeneity effects, the interaction between local and landscape heterogeneity effects, and the exploration of mechanisms explaining combined local and landscape heterogeneity effects across seasons. First, I hypothesised that 1) landscape context (i.e., here defined as the proximity to the different landscape features) would be a relevant factor for the structuring of communities and would influence local heterogeneity effects as different landscape features will interact with local heterogeneity to determine alpha richness. Second, I further hypothesised that 2) local heterogeneity effects would increase (synergistic effects) or decrease (antagonistic effects) with increasing landscape heterogeneity (i.e., here defined as the between-plot environmental dissimilarity, with the environment per plot [i.e., plot also referred to as tile in this experiment] being defined by the proximity to each one of the landscape features), depending on whether local heterogeneity would reduce species turnover or landscape heterogeneity would increase alpha richness, for the reasons explained above. Thirdly, I hypothesised that this relationship would 3) vary across seasons, since in cold months local refugia may be more needed and landscape heterogeneity may be decreasing diversity by providing more extreme environments (i.e., which wipe out organisms during the cold months), while in warm months landscape heterogeneity may help promote diversity by providing more specialized niches. I also hypothesized that 4) local and landscape heterogeneity will promote and suppress different species groups, depending on whether these are affected by the local or landscape environmental conditions provided by heterogeneity. Across seasons and species groups, effects of local and landscape heterogeneity may be additive or oppose one another either within or between species groups and seasons (Figure 1).

4.3. Methods

4.3.1. Study Site and sources of landscape heterogeneity

The experiment was set up in a semi-sheltered rocky shore at Bracelet Bay, Swansea, Wales (51.566, -3.971). This shore provided a slope with a large gradient of environmental conditions originating from the amount of time that organisms spent emersed during a low tide. This emersion gradient change community composition from high stress and low diversity to low stress and high diversity (e.g., Scrosati & Heaven 2007). Along this gradient, rockpools provide havens where environmental stress is partially reduced, and diversity was increased (e.g., Martins et al. 2007). Channels have the opposite effect, where additional to the emersion stress, water current and wave action generated disturbance for species (e.g., Endean et al. 1956). In turn, all these three landscape features (i.e., emersion gradient, rockpools, channels) have been observed to affect the presence of macroalgae canopy and limpet barrens (e.g., Hobday 1995; Martinez et al. 2012). Macroalgae canopy in the intertidal is mostly formed by fucoids, which harbour a high diversity of epibionts and benthic organisms as it reduces desiccation stress and wave action (Bertness et al. 1999). Limpet barrens have the opposite effect, increasing desiccation stress and wave action (e.g., Little et al. 2017). Barrens also increase the dispersal of limpets and grazers to surrounding areas, increasing grazing effects there (e.g., Little et al. 2017).

4.3.2. Experimental design

Between May 2019 and April 2022 (35 months) 35 pairs of experimental limestone tiles were deployed across the rocky shore and sampled seasonally. These experimental units were attached to exposed rock using 8mm screws on each corner of the plot, in 35 stations evenly distributed across five transects along the intertidal gradient. Transects were separated by roughly 20 metres from one another to reduce effects from differential wave exposure. Within each station, heterogeneity and non-heterogeneity treatments were placed by deploying two square tiles corresponding to each heterogeneity treatment (see Chapter 3 for a description of heterogeneity treatments). These tiles were placed on exposed rock, thus allowing to assess the effect of landscape features such as rockpools, channels fucoid canopy and limpet barrens by quantifying the proximity to these features. Fucoid and large red algae canopy was regularly removed from the immediate surrounding of the plot to avoid adding statistical noise from the arbitrary coverage of the whole plot by neighbouring algae which could act as temperature buffer or wave attenuation factor, or increase whip-lash disturbance (e.g., Kiirikki 1996). Since tiles surrounded by macroalgae canopy still presented canopy <1m distance after removal, and other tiles at similar shore heights were >10m away from canopy algae we concluded that removing neighbouring canopy did not affect the variable ‘proximity to canopy’.

4.3.3. Data collection

Tiles were monitored seasonally using stratified image analysis on 63 tiles and 11 time points per tiles, and seven tiles were not included in this study due to lack of accessibility to four stations down the shore and some tiles missing due to storm effects (see Chapter 3 for a description of the sampling conducted). This resulted in 661 community data points – after removing images that did not allow adequate sampling. I also measured emersion rate (an estimate of the proportion of time a plot is emersed over a year) from plot elevation, short-term measurements of plot emersion time and local water height measurements (see Chapter

3 for a description of the process to obtain emersion rate data). Data on the other landscape variables were obtained in the field by measuring the distance of each plot to the closest canopy, limpet barren grounds, rockpool and channel. Distance to canopy was the distance between the plot and the closest fucoid stipe that was larger than 20 cm long. Distance to barren grounds was the distance between the plot and the closest barren patch containing limpets (e.g., Firth et al. 2023) that was at least 20 cm wide. Distance to rockpool was the distance between the plot and the water edge of the closest rockpool that was at least 20 cm wide or 10 cm deep. Distance to channel was the closest distance between the plot and the vertical substrate connecting with a channel that was at least 50 cm wide. After all the data were collected, each distance-based variable was z-transformed and inverted so that each indicated proximity to a landscape features.

4.3.4. Data resampling

I recreated artificial landscapes by aggregating heterogeneous and non-heterogeneous tiles, *in silico*, separately. I used artificial landscapes since they have been successful in demonstrating landscape heterogeneity effects on the structure and functioning of communities (Wiersma 2022). More importantly, since the experiment was set at one shore, resampling allowed for replicated landscapes with tiles distributed across the shore, exposed to differing local conditions, and grouped into 'landscapes' with multiple levels of landscape heterogeneity. To obtain these artificial landscapes, I first chose landscapes to be composed of five tiles or plots since it was calculated that this allowed the maximum number of unique combinations of tiles and thus impose less constrains on the subsequently used resampling techniques. I then resampled the experimental dataset of 661 community data points to create a set of 20,000 unique combinations of five tiles that were from the same time point and either only heterogeneous or non-heterogeneous (Figure 2). To ensure that increasing the dataset above 20,000 data points did not qualitatively change the results of this study, I run a sensitivity analysis by re-running all tests with a dataset with 200,000 data points and qualitatively comparing results with the original analyses. Mean alpha richness and Jaccard-based species turnover (Baselga et al. 2018) were calculated, and after pooling together species cover data for all tiles, gamma richness was calculated.

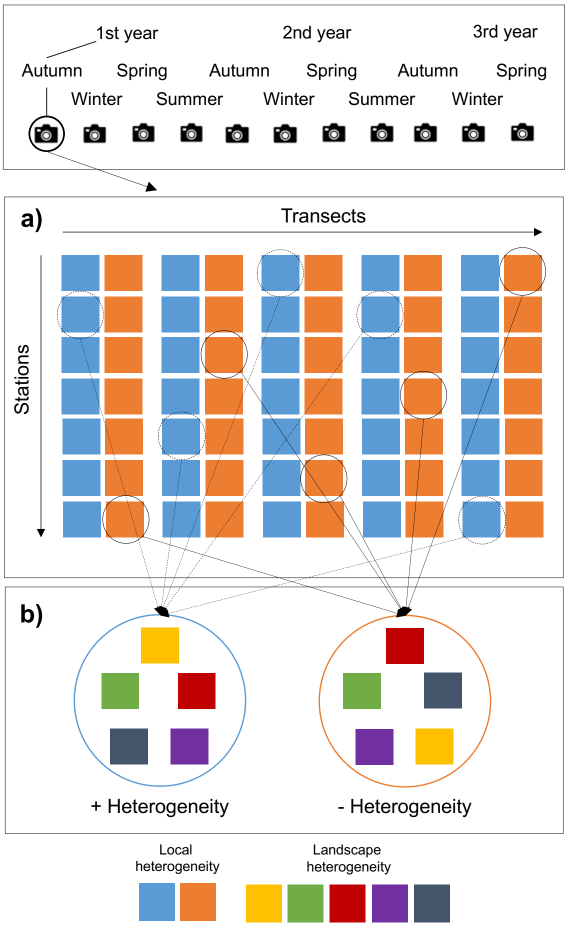

Figure 2. An example of one permutation during the resampling process per date to obtain the artificial landscapes. At the top, a) the experimental design with the 70 tiles down the shore, distributed across 5 transects. At the bottom, b) the random drawing process involved in each permutation of the resampling process to obtain a replicate of an artificial landscape for both locally heterogenous and non-heterogeneous communities per date. Sets of tiles were sampled from those surveyed within a single time point.

To calculate landscape heterogeneity, I calculated pairwise dissimilarities between tiles within each artificial landscape using data from the five measured landscape features (i.e., emersion rate, proximity to canopy, proximity to limpet barren, proximity to rockpool and proximity to channel) and defined heterogeneity as the mean distance among all tiles within an artificial landscape (e.g., Albertch et al. 2021). I computed a Bray-Curtis dissimilarity matrix (Oksanen et al. 2007) across all tiles in the original dataset using the five z-transformed landscape feature variables, to capture non-linear relationships across variables and not give more weight to any variable, respectively. For each artificial landscape, I plotted the obtained dissimilarities in an NMDS plot using only the data for the five tiles within each landscape, and the MDS1 and MDS2 coordinates were obtained per tile as a relative measure of their environmental distinctivenes. After each resampling iteration, landscape heterogeneity was quantified as the mean Euclidean distance across MDS coordinates within each artificial landscape.

To account for differences in the prevailing environmental conditions across sets of tiles and to test the individual effect of landscape features on local heterogeneity effects, the mean values of each landscape feature were also obtained per group of five tiles. Eight different species groups were defined within the community to test how the effects of each type of heterogeneity varied among groups. Species groups were defined by trophic group, and body size and the resistance of each group to thermal stress and dislodgement. Considering trophic group helped establish species interactions across the community, body size was indicative of the overall importance for ecosystem functioning (e.g., Hildrew et al. 2007), and how resistant each species was to thermal stress and dislodgment helped determine how species would respond to harsh environments (e.g., Anderson 1993; Dethier 1994; Collins et al. 2023).

Filter-feeding species were separated into barnacles, which presented resistant traits, other suspension feeders, which presented less-resistant traits, and other encrusting organisms which tended to settle on top of other organisms. Consumers grouped all macroinvertebrate grazers and predators, while other invertebrates grouped the smaller consumers that often lived on top of other organisms. Ephemeral macroalgae constituted highly seasonal and short-lived algae such as *Ulva* sp. *and* other macroalgae were the rest of more perennial algae such as *Osmundia* sp. or *Fucus* sp. The mean richness and mean cover for each species group was calculated per group of tiles.

4.3.5. Hypothesis 1: Landscape context effects on community composition and local heterogeneity effects

To assess landscape context effects, I first explored relative effects of landscape features and local heterogeneity on community composition, and later tested for individual interactive effects between landscape features and local heterogeneity. First, I used distance-based redundancy analysis (db-RDA; Oksanen et al. 2007) with abundance-weighted Bray-Curtis dissimilarities. Redundancy analysis is an ordination method that constrains the ordination data resulting from Principal Coordinate Analysis (PCoA) performed on species community following a set of environmental metrics and allows to use non-Euclidean distance measures (Oksanen et al. 2007). I also included season and year to account for context-dependency within the db-RDA, and run a Permutational Analysis of Variance to test wether local heterogeneity and landscape featues were related in any way (Oksanen et al. 2007). Then, I tested for landscape feature effects on alpha richness across local heterogeneity treatments to see if there were any interactions between landscape feature effects and local heterogeneity effects. I used a mixed-effects linear model (Bates et al. 2009) that included all landscape features, and each of their interactions with local heterogeneity. For each landscape feature, their effect and their interaction with local heterogeneity were included as fixed effects. I added season and year as covariates to control for context-dependency. I also included the random effects transect, and station nested within transect, since each station only occurred within one transect. Model diagnostics – as well as for all linear models hereon – including normality and heteroscedasticity were checked visually using Dharma diagnostics (Hartig 2020). Richness data were log-transformed to meet assumptions – rather than using a Poisson-family generalised mixed-effects linear model since it was estimated that doing so would have hampered comparability across model coefficients. All models are defined in Supplementary Materials 12.

4.3.6. Hypothesis 2: The interaction between local heterogeneity effects and landscape heterogeneity

Using linear regression models without random effects, I tested for landscape heterogeneity effects on gamma richness, mean alpha richness and mean species turnover across local heterogeneity treatments. In this case, each model was built using the landscape heterogeneity index calculated, local heterogeneity, season, and year. The interaction between landscape heterogeneity, local heterogeneity, season and year was also included to capture interactions that can help explain the general pattern. Anova was applied on the resulting linear model to obtain a general test for season effects.

4.3.7. Hypothesis 3 & 4: Combined local and landscape heterogeneity effects across seasons and species groups

I built a multigroup piecewise Structural Equation Model (pSEM; Lefcheck 2016) to identify and quantify the paths through which local and landscape heterogeneity affected gamma richness across cold (winter and spring) and warm (summer and autumn) months. First, I formulated a hypothetical causal model based on gathered *a priori* knowledge of how local and landscape heterogeneity affected rocky shore communities (Supplementary Materials

13). I included direct paths from local and landscape heterogeneity to gamma richness, and multiple indirect paths. For local heterogeneity, indirect paths included indirect effects through the richness and cover of individual species groups and through mean alpha richness and turnover. For landscape heterogeneity, effects on the richness/cover of species groups could be direct, or indirect through landscape features. Further indirect effects on gamma richness could be through richness/cover of species groups and through mean alpha richness and turnover. Associations among species groups were included, as well as interdependencies between landscape features (i.e., emersion rate, channel and rockpool proximity affecting the proximity of canopies and limpet barren). Partial bivariate correlations were added following *a priori* expectations and when d-separation tests indicated missing relationships. A pSEM was fit using linear models following the modelling approach used to test landscape heterogeneity effects. Tests of directed separation were used to check the fit of the pSEM model, and missing paths were identified and included, or added as bivariate correlation when not relevant.

To summarise multigroup pSEM results, I summed standardised path coefficient values to compare local and landscape heterogeneity effects across seasons to account for both direct and indirect effects on gamma richness. To that end, I summarised pSEM results in two different sets of figures to assess direct and indirect effects on gamma richness across seasons, and to assess indirect effects on alpha richness and species turnover through species groups. For the figure summarising direct and indirect pSEM results, I grouped all effects on species group cover and richness, and all effects on landscape features together, respectively, creating a variable called ‘species groups’ for the former and a variable called ‘landscape features’ for the latter. A second figure was used to group local and landscape heterogeneity on each individual species group, in terms of both percentage cover and species richness, and included both direct heterogeneity effects on each group and indirect effects through associations with other species groups (i.e., cascading effects). Finally, a third figure grouped indirect local and landscape heterogeneity effects on alpha richness and species turnover, which were mediated by the species richness found within each species group and the associations across species groups in terms of both percentage cover and species richness (i.e., cascading effects). Indirect effects were calculated as the sum of all the indirect effects. Each indirect effect consisted of the product of all Standard Path Coefficients (SPC) included in each indirect link from landscape and local heterogeneity to alpha richness and species turnover. For example, an indirect link could be quantified as the effect of local heterogeneity on consumer % cover (SPC1) * effects of consumer % cover on barnacles % cover (SPC2) * effects of barnacles % cover on other invertebrate % cover (SPC3) * effects of other invertebrate % cover on alpha richness (SPC4) = SPC1 * SPC2 * SPC3 * SPC4.

4.4. Results

4.4.1. Hypothesis 1: Landscape context effects on community composition and local heterogeneity effects

Local heterogeneity and landscape features contributed along with seasonality and year to the 40% variation in community composition (db-RDA$_{10,650}$: F=29.34, p=0.001, R^2=0.40; Figure 3a). The variation in the first axis was mainly explained by proximity to canopy and emersion rate (46.25% of all constrained variance; Figure 3b), while the second axis was explained by a combination of year and other landscape predictors such as proximity to barren, channel and rockpool (32.05% of all constrained variance; Figure 3c). Local heterogeneity had almost no contribution to the first db-RDA axis and was the fifth most contributing factor in the second axis. In addition, PERMANOVA results indicated that local heterogeneity and landscape features were not statistically linked ($F_{1,61} = -0.02$, $P>0.05$).

Despite the small effect of local heterogeneity on community composition, local heterogeneity interacted with several landscape components (Figure 3d-h). Local heterogeneity increased the response of alpha richness to (lower) emersion rate ($t_{local(630)} = -6.51$, $P<0.001$; $t_{emersion(64)} = -5.67$, $P<0.001$; $t_{het\ x\ emersion(64,655)} = 5.57$, $P<0.001$; Figure 3e), proximity to canopy ($t_{canopy(60)} = -0.74$, $P>0.05$; $t_{het\ x\ canopy(60,652)} = 3.43$, $P<0.05$; Figure 3f) and proximity to barren grounds ($t_{barren(57)} = 2.41$, $P<0.05$; $t_{het\ x\ barren(57,639)} = -2.92$, $P<0.01$; Figure 3g). Alpha richness response to proximity to rockpool ($t_{rockpool(146)} = -1.58$, $P>0.05$; $t_{het\ x\ rockpool(146,618)} = 1.25$, $P>0.05$; Figure 3h) and channels ($t_{channel(68)} = -2.09$, $P<0.05$; $t_{het\ x\ channel(68,642)} = 1.03$, $P>0.05$; Figure 3i) in heterogeneous communities was not different from non-heterogeneous ones, and both heterogeneity treatments showed a decrease in alpha richness at closer proximity to rockpools and channels (Figure 3h-i).

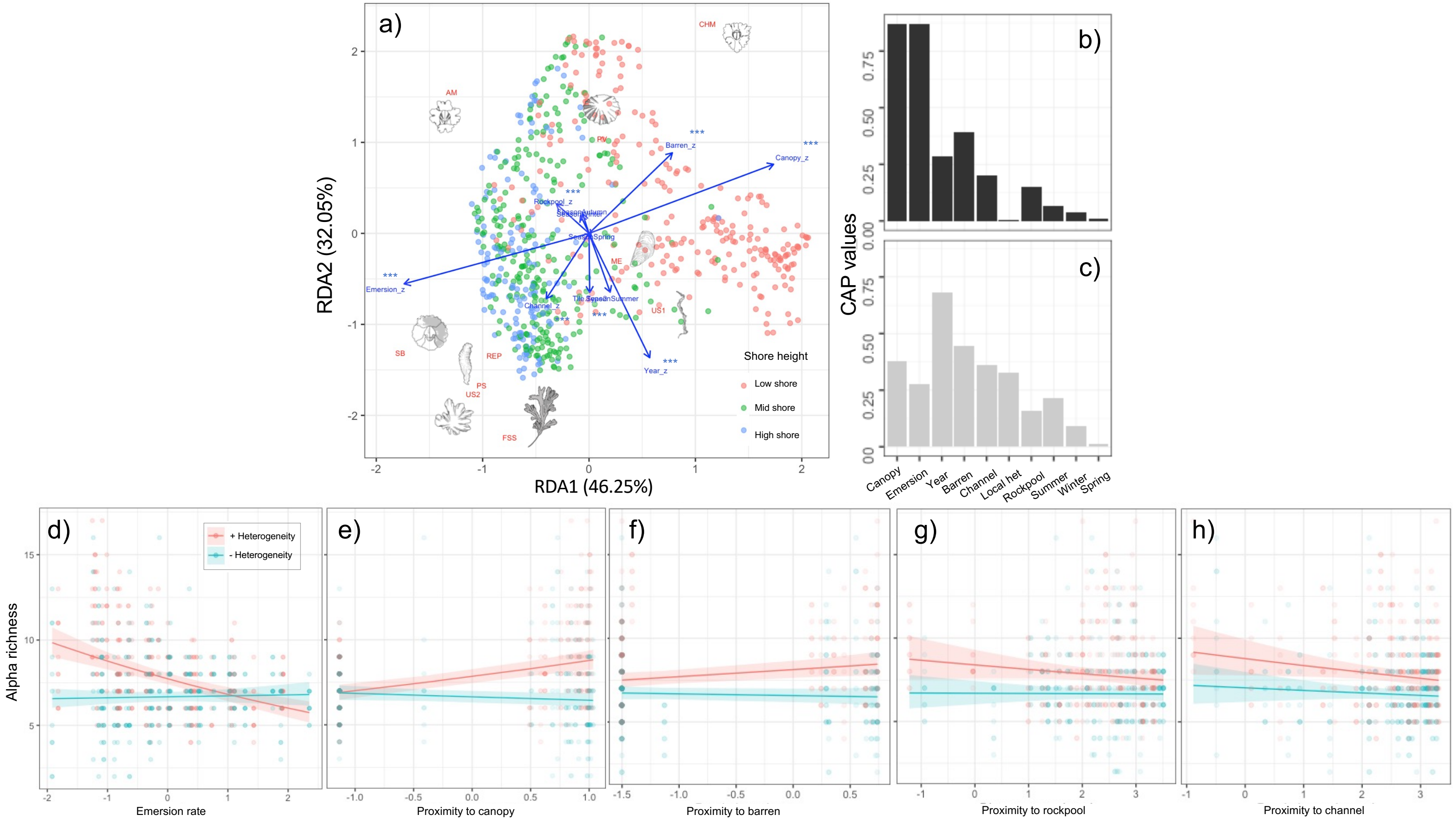

Figure 3. Heterogeneity and landscape feature ffects on community composition and alpha richness. Results from a) db-RDA on untransformed cover data per date and plot, the contribution of individual factors to the b) first and c) second db-RDA axes. At the bottom, mixed-effects linear models showing alpha richness response to d) emersion rate, e) proximity to canopy, f) proximity to barren, g) proximity to rockpool and h) proximity to channel.

4.4.2. Hypothesis 2: The interaction between local heterogeneity effects and landscape heterogeneity

Landscape heterogeneity had a positive effect on gamma richness, mean alpha richness and species turnover, although these effects changed across local heterogeneity treatments and seasons (Figure 4). Heterogeneous communities showed overall higher gamma richness ($t_{local} = -29.24$, $P<0.001$; $t_{landscape} = 11.17$, $P<0.001$; $t_{local\ x\ landscape} = 4.80$, $P<0.001$; Figure 4a) and mean alpha richness ($t_{local} = -28.42$, $P<0.001$; $t_{landscape} = -2.36$, $P<0.05$; $t_{local\ x\ landscape} = -2.16$, $P<0.05$; Figure 4b). In contrast, while heterogeneous communities presented higher mean species turnover at low landscape heterogeneity, non-heterogeneous communities showed higher turnover at high landscape heterogeneity ($t_{local} = -11.91$, $P<0.001$; $t_{landscape} = 18.50$, $P<0.001$; $t_{local\ x\ landscape} = 9.79$, $P<0.001$; Figure 4c). These differences in turnover could help explain the reduction in gamma richness, especially in locally heterogeneous communities, at high landscape heterogeneity (Figure 4a). This, in turn, resulted in antagonistic effects explaining the overall interaction between local and landscape heterogeneity.

Across seasons, autumn presented the highest gamma richness ($t_{local\ x\ landscape\ x\ season} = 6.07$, $P<0.001$; Figures 4d-e) and mean alpha richness ($t_{local\ x\ landscape\ x\ season} = 2.69$, $P<0.05$; Figures 4f-g) and mean species turnover ($t_{local\ x\ landscape\ x\ season} = 21.80$, $P<0.001$; Figures 4h-i), while spring and winter presented the lowest levels across variables (Figures 4d-i). An interaction existed between winter and the other seasons for heterogeneous communities, by which gamma richness decreased at high landscape heterogeneity (Figures 4d,f,h). This coincided with the reduction in differences in gamma richness across local heterogeneity treatments, and the presence of higher turnover on non-heterogeneous tiles at high landscape heterogeneity (Figures 4a,c).

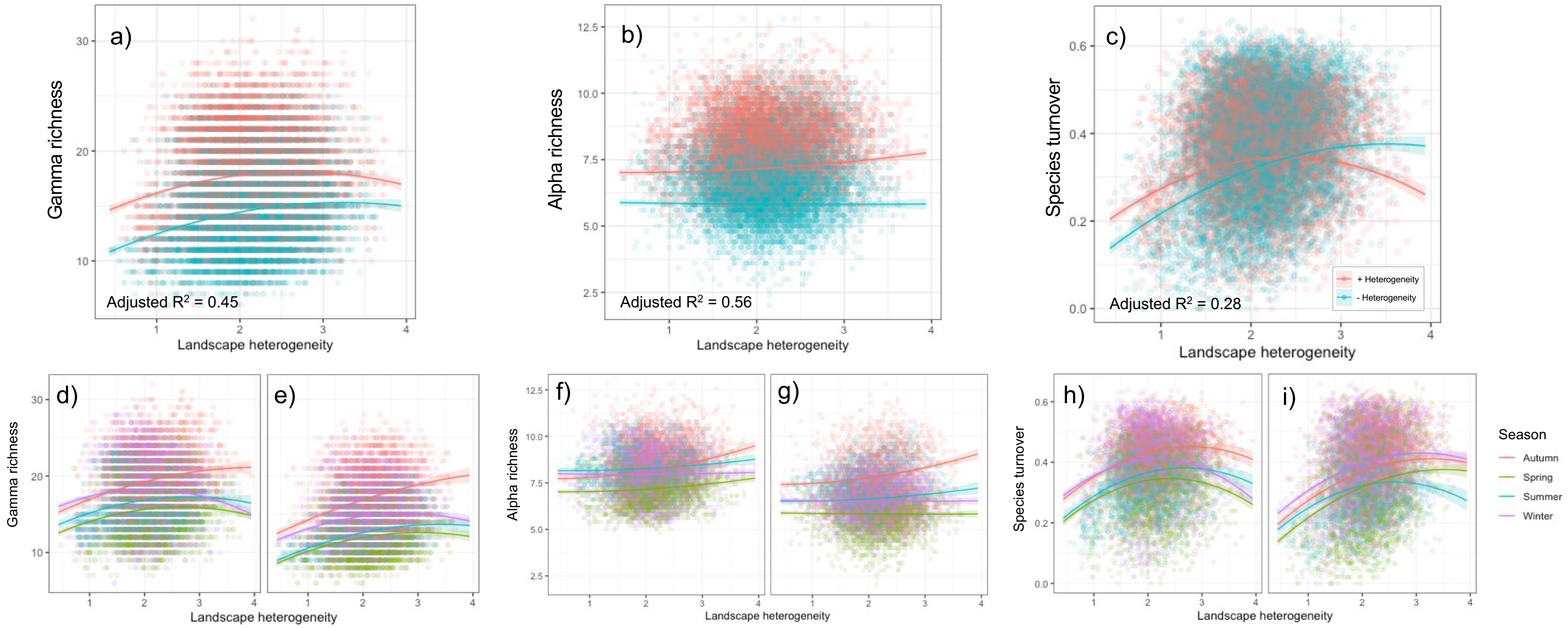

Figure 4. Landscape heterogeneity effects across local heterogeneity treatments on gamma richness, mean alpha richness and turnover. Results from mixed-effects linear models showing landscape heterogeneity effects across local heterogeneity treatments on a) gamma richness, b) mean alpha richness among included tiles, c) mean species turnover across included tiles. At the bottom, landscape heterogeneity effects across seasons on d) gamma richness on heterogeneous tiles, e) gamma richness on non-heterogeneous tiles, f) mean richness on heterogeneous tiles, g) mean richness on non-heterogeneous tiles, h) mean species turnover on heterogeneous tiles and i) mean species turnover on non-heterogeneous tiles.

4.4.3. Hypothesis 3: Combined local and landscape heterogeneity effects across seasons

Across cold and warm months, both local and landscape heterogeneity promoted gamma richness following a pattern of positive additive effects but showed contrasting variation over the year (Figures 5a-b). While local heterogeneity effects were larger in cold months, landscape heterogeneity effects were larger in warm months (Figure 5c). In addition, local heterogeneity had larger effects on alpha richness (Figure 5d), but landscape heterogeneity explained differences in species turnover, particularly in the warm months (Figure 5e). Finally, local heterogeneity promoted cover and richness in species groups to a greater extent than did landscape heterogeneity during the cold months, but these roles shifted in the warm months with landscape heterogeneity having a dominant effect on species group cover and richness and local heterogeneity effects being almost negligible (Figure 5f).

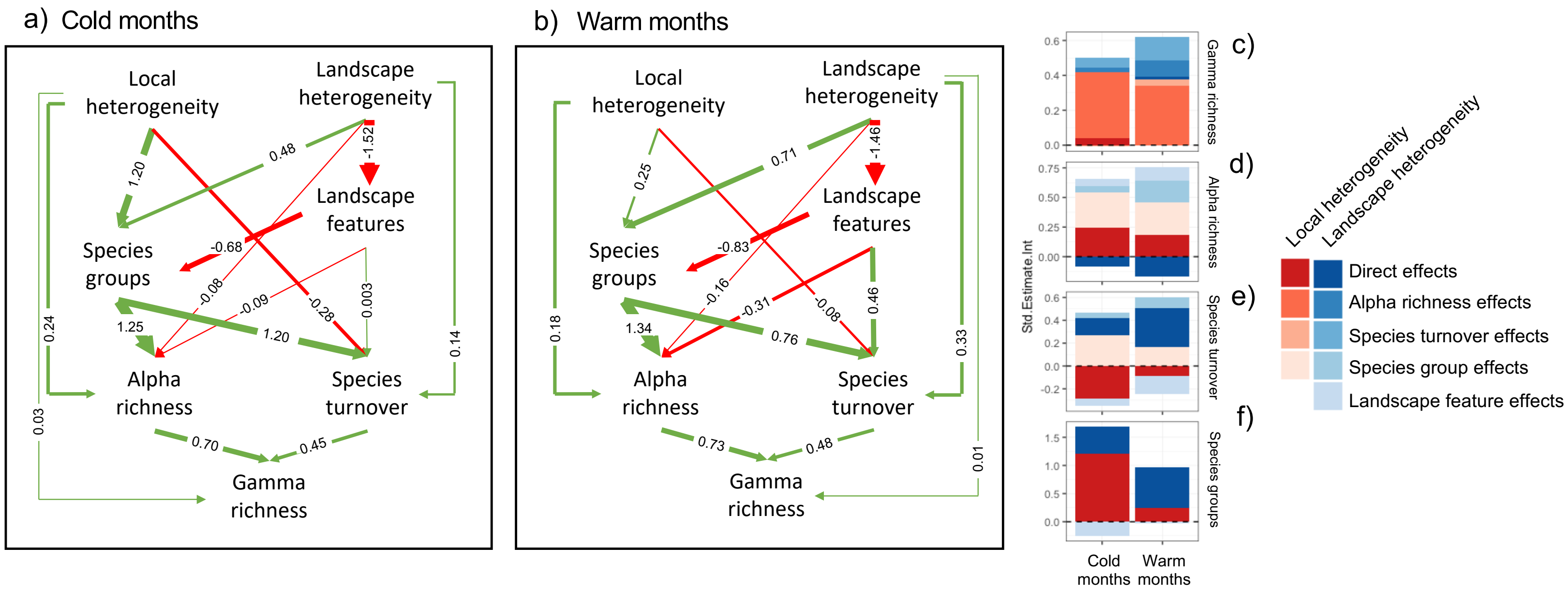

Figure 5. Mechanisms connecting local and landscape heterogeneity with gamma richness across seasons. Piecewise SEM (pSEM) results for local and landscape heterogeneity effects on gamma richness, through direct pathways on mean alpha richness and turnover, and indirect pathways through species group cover and richness. On the left, multigroup pSEMs showing local and landscape heterogeneity effects on gamma richness, and indirect effects through species groups (cumulative effects on and from cover and richness across all species groups considered) on a) cold-months and b) warm-months communities. Green and red lines indicate positive and negative significant ($P<0.05$) effects, respectively. Numbers on lines indicate the standardised path coefficients (SPC). All SPC were significantly different across multigroups. At the right, the sum of SPCs representing local and landscape heterogeneity effects on c) gamma richness, d) mean alpha richness, e) mean species turnover and f) species groups. Colour coding indicates the source of SPCs across response variables. Numbers inside parenthesis in a-b indicate the effects on cover (left) and richness (right) summed across all species groups. Arrows from landscape heterogeneity result from the sum of SPCs across all landscape components. Arrows going into landscape features and species groups are the sum of all effects on each individual landscape feature or species group, respectively. Likewise, arrows from landscape feature and species group result from the sum across all individual effects of each landscape feature or species group, respectively. SEM results obtained from analysis based on metamodel shown in Supplementary Materials 13.

4.4.4. Hypothesis 4: Combined local and landscape heterogeneity effects across species groups

To allow an overview of seasonal effects, the previous analysis summarised effects of heterogeneity on species groups *overall*, combining effects on richness and cover of the various groups. Next, as heterogeneity effects differed across species groups and the species groups themselves were expected to interact (e.g., through competition), I will now present results from the pSEM to elucidate heterogeneity effects on individual species groups, the associations across species groups and possible interactions in cold and warm seasons. Heterogeneity effects on consumers, barnacles and ephemeral algae depended mostly on direct heterogeneity effects (Figure 6 a-b), while effects other suspension feeders, other macroalgae and other invertebrates largely depended on associations across species groups. Barnacles, consumers, and other suspension feeders benefited from heterogeneity across seasons. Other invertebrates, other macroalgae and other encrusting organisms were largely benefited in the warm months, while ephemeral macroalgae were most benefited from heterogeneity in the cold months. Overall, local heterogeneity effects across species groups tended to be larger in the cold months, while landscape heterogeneity effects in the warm months.

Associations played an important role in determining heterogeneity effects across species groups (Figure 6 a-b). The major associations changes between seasons. In cold months included facilitative associations between barnacles and ephemeral macroalgae, other suspension feeders and other invertebrates, and between ephemeral macroalgae and other encrusting organisms. Barnacles also facilitated the cover and richness of other macroalgae, other invertebrates and other encrusting organisms by reducing the presence of dead barnacles. In the warm months, competitive and consumer associations were common, with barnacles (competition), dead barnacles (competition), other suspension feeders (competition) and consumers (grazing) presenting negative associations with ephemeral macroalgae. Facilitative interactions still existed, with other suspension feeders and barnacles promoting cover and richness of other macroalgae, other invertebrates and other encrusting organisms. All these associations resulted in important cascading effects of heterogeneity within the community, with groups such as other macroalgae, other invertebrates and other encrusting organisms benefiting the most.

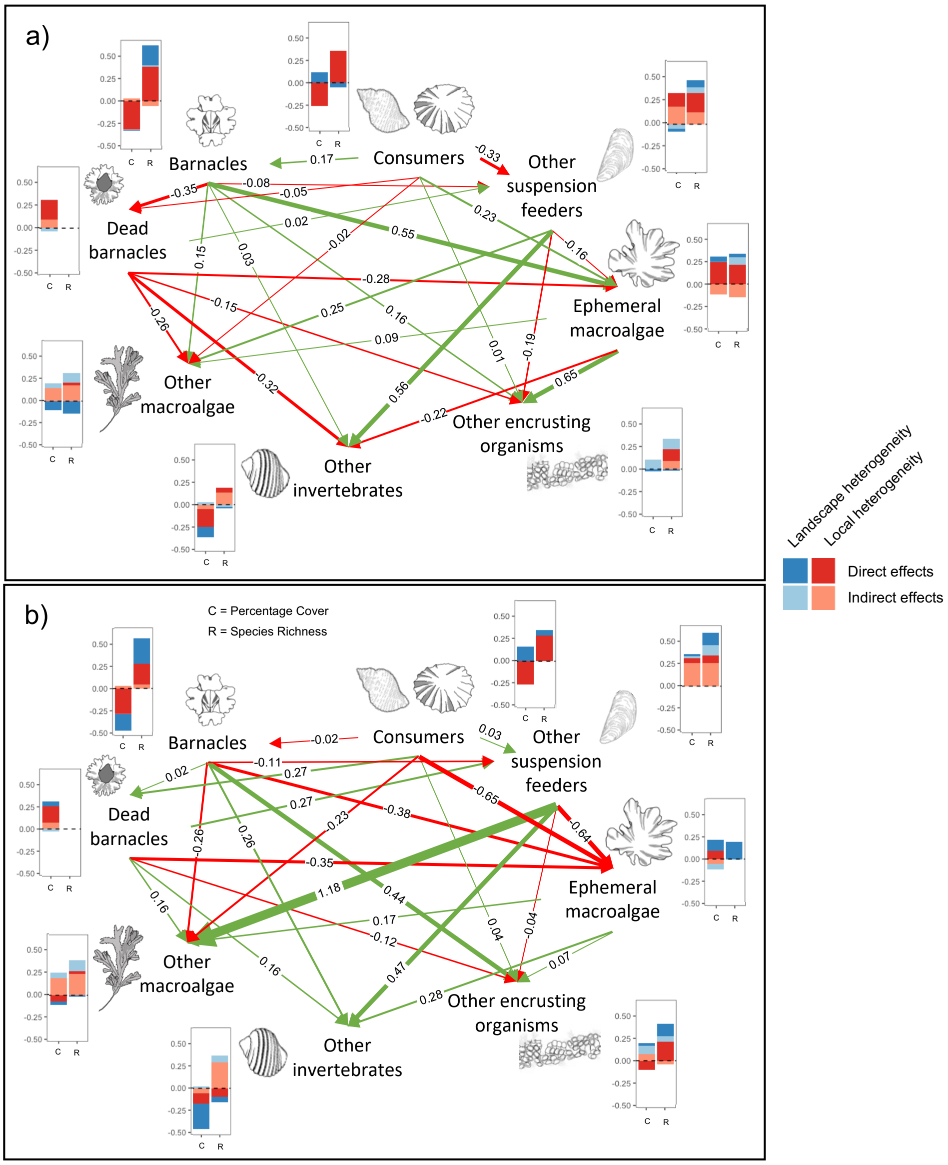

Figure 6. Combined local and landscape heterogeneity effects on percentage cover and species richness per species group. Local and landscape heterogeneity effects on the cover and richness of each species group, and associations between cover and richness across species groups for a) cold months and b) warm months. Within each barplot, direct effects (solid colors) indicate direct heterogeneity effects on each group, and indirect effects (light colors) result from cascading heterogeneity effects across species groups through the associations shown in each pSEM. Although not shown in the plot, direct landscape and local heterogeneity effects originate from landscape and local heterogeneity variables directly linked with each one of the species group considered. SEM results presented here are a subset of the main SEM model results (Supplementary Materials 13) that only considers the species groups observed in the experiment.

Green and red lines indicate positive and negative significant ($P<0.05$) effects, respectively. Numbers on lines indicate the sum of standardised path coefficients (SPC) across cover and richness for each species group. All SPC were significantly different across multigroups. Coefficients in a-b are the sum of SPCs for cover and richness effects for each link between species groups.

The direct and indirect (cascading) heterogeneity effects on species groups resulted in mostly positive heterogeneity effects on alpha richness (Figure 7 a-b) and species turnover (Figure 7 c-d). Barnacles and consumers presented the largest heterogeneity effects on alpha richness, while consumers, other suspension feeders, ephemeral macroalgae and other suspension feeders contributing the most to species turnover (although heterogeneity effects from the latter three presented large seasonal fluctuations). Cascading effects (indirect effects) presented an important role, since indirect effects originating from barnacles (alpha richness), other suspension feeders (species turnover) and consumers (alpha richness and species turnover) showed important contributions to both alpha richness and species turnover (probably due to their cascading effects on other macroalgae, other invertebrates and other encrusting organisms). Both direct and indirect (cascading) effects fluctuated seasonally, with local heterogeneity effects being stronger in the cold months, and cascading effects being stronger in the warm months (only for alpha richness). Overall, local heterogeneity played a larger role shaping both the associations across species groups and the resulting effects on alpha richness and species turnover among seasons.

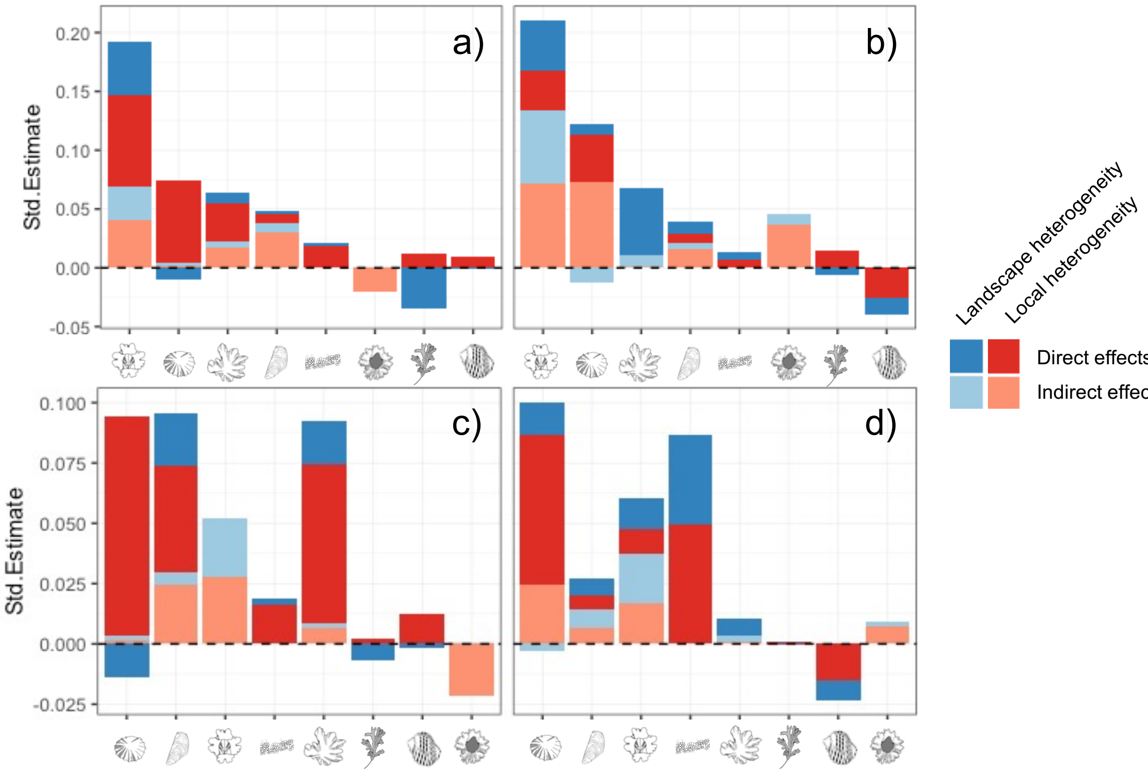

Figure 7. Combined local and landscape heterogeneity effects on alpha richness and species turnover mediated by species groups. Local and landscape heterogeneity effects resulting from the contribution of each species group to alpha richness in cold (a) and warm (b) months; and species turnover in cold (c) and warm (d) months. Direct heterogeneity effects (solid colors) originate from the direct effects that each species group had on alpha richness and species turnover, while indirect heterogeneity effects (light colors) originate from the effects that each species group had on the direct effects of other species groups on alpha richness and species turnover.

4.5. Discussion

Results from my simulation of experimental landscapes show that local and landscape heterogeneity can interactively drive gamma richness. Following an antagonistic interaction, local heterogeneity effects on mean alpha richness decreased as landscape heterogeneity effects on mean species turnover increased. In other words, locally heterogeneous tiles resisted compositional turnover across heterogeneous landscapes and therefore dampened the accumulation of new species and overall gamma diversity. This response was further explained by differences across seasons, with local heterogeneity increasing mean alpha richness and landscape heterogeneity increasing mean species turnover more strongly in cold and warm months, respectively. Approximately half of local heterogeneity effects and a quarter of landscape heterogeneity effects on alpha richness and turnover occurred through effects on species richness across species groups, which were mostly additive across species groups. These results reveal the link between local and landscape heterogeneity and show promising avenues of research suggesting that interactive and combined local and landscape heterogeneity effects are important for biodiversity and to sustain it across seasons and within species groups.

Landscape context, in the form of emersion rate, proximity to canopy and proximity to limpet barrens, was key to shape community composition and revealed important interactions between landscape features and local heterogeneity effects. Low emersion rate allowed for reduced stress, more diversity (e.g., Scrosati et al. 2011), and stronger local heterogeneity effects potentially due to more species being present in the vicinity (e.g., Navarro-Barranco et al. 2022). Similarly, close to macroalgae canopy, local heterogeneity was benefited also because of putative increases in diversity (Eriksson et al. 2006), while increases in local heterogeneity effects around limpet barren patches would have been caused by local heterogeneity refugia allowing species to escape grazing (e.g., Ling 2008). Despite the effect rockpools and channels have driving species composition and diversity (e.g., Griffin et al. 2010), neither proximity to channel nor proximity to rockpool were found to have large effects on community composition or modify local heterogeneity effects. It is possible that their effects were masked, since both rockpools and channels can modify the occurrence of canopy and barrens (e.g., Underwood et al. 1987; Martins et al. 2007). Alternatively, the topography of the shore could have correlated rockpools and channels occurrence with emersion rate (e.g., more rockpools and channels in the high shore). As a result, landscape context shaped community composition and showed individual mechanisms (in the form of interactions between landscape features and local heterogeneity effects) that would help explain landscape-local heterogeneity effects.

The local and landscape heterogeneity interaction was explained by changes in species turnover. Species turnover increased with landscape heterogeneity for non-heterogeneous tiles, while it showed a humped relationship for heterogeneous tiles – thus turning into an antagonistic interaction. This response resulted from heterogeneous tiles resistance to variability across heterogeneous landscapes. Spatial invariability would have occurred either due to heterogeneous tiles buffering environmental conditions and thus being more robust to environmental variation, or due to landscape heterogeneity allowing species to occur in non-heterogeneous tiles that would have been already present in heterogeneous tiles. In intertidal rocky shores, local heterogeneity may allow species usually found in the low-stress lower shore (e.g., *Mytilus edulis*) to colonise areas in the high-stress higher shore by reducing desiccation stress (Hand & Menze 2007). Some of these low-shore species may also be found in proximity to rockpools or macroalgae or away from limpet barrens, but still occur on heterogeneous tiles as these reduce desiccation stress, grazing effects and increase recruitment (e.g., Sebens 1991; Grabowski et al. 2008; McAfee et al. 2022). Despite these results, other types of interactions among local and landscape heterogeneity may still exist in other cases, such as synergistic interactions by which more species can capitalise on local heterogeneity in heterogeneous landscapes due to the wider range of niches provided. Considering additional effects such as environmental gradient strength and heterogeneity facets at the local and landscape scales, the magnitude of seasonal effects or the species pool size may shed more light on the mechanisms behind this interaction.

Seasonality was key to understand the link between heterogeneity and gamma richness, which was marked by increased local heterogeneity effects in cold months and larger landscape heterogeneity effects in warm months. The largest gamma richness differences across local heterogeneity treatments occurred during the cold months, as the differences in species turnover indicated antagonistic effects at high landscape heterogeneity. Local heterogeneity may have allowed more species to survive harsher conditions (e.g., McAfee et al. 2022) and reduced species turnover, while some of these species would have not survived more extreme conditions at high landscape heterogeneity and created humped relationships in gamma richness. In warm months, the interaction between heterogeneities disappeared potentially due to the lack of need of local refugia, the lower harshness of environmental conditions at higher landscape heterogeneity, and the provision of new niches at high landscape heterogeneity. SEM results further suggested additive effects across local and landscape heterogeneity, with local heterogeneity dominating in the cold months, while landscape heterogeneity increasing its effects during the warm months. It is thus possible that rather than competing against one another, local and landscape heterogeneity hold partially complementary roles across seasons, helping maintain diversity over the year.

Heterogeneity effects on gamma richness also targeted species group cover and richness across seasons, with cascading effects magnifying heterogeneity effects in the warm months. Heterogeneity presented mostly positive additive effects on cover and richness of almost all species groups. Over the year, landscape heterogeneity increased cover and richness across species groups in the warm months, while local heterogeneity played a larger role in the cold months. This would have been the case of barnacles and other suspension feeders, which spawn during the spring and autumn blooms and benefit from specialised niches at high landscape heterogeneity (warm months) and survive the cold months in local heterogeneity refugia (e.g., Starr et al. 1991). In addition, dominant species group effects (e.g., barnacles, consumers, ephemeral macroalgae and other suspension feeders) on alpha richness and species turnover were magnified by cascading effects. The observed putative facilitation associations (e.g., Yakovis & Artemieva 2017) and competitive release by consumers (e.g., Steneck et al. 1991) resulted in positive cascading effects, which were larger in the warm months and on alpha richness potentially due to environmental constraints being more important in the cold months and for species turnover. These cascading effects were also mostly driven by local heterogeneity, as it has been seen to modulate species associations and interactions (e.g., Stephen Gosnell et al. 2012), but for barnacles it was also dictated by landscape heterogeneity possibly due to increases in barnacle recruitment leading to density-dependent effects (e.g., Menge 2000). Overall, heterogeneity helped sustain cover and richness across species groups, which in turn were important mediators of heterogeneity effects on gamma richness both directly and, to a lesser extent, through cascading effects.

In summary, my results provide novel evidence on the combined and interactive effects of local and landscape heterogeneity on gamma richness. An antagonistic interaction between local and landscape heterogeneity occurred due to the reduction in species turnover during the cold months only found in heterogeneous tiles. Both heterogeneity effects combined across seasons, with landscape heterogeneity effects increasing in warm months to compensate for a decrease in local heterogeneity effects. Heterogeneity effects also promoted richness within and across species groups. Species groups were important mediators of heterogeneity effects on gamma richness, with cascading effects playing an important role in the warm months while environmental constraints being more important in the cold months. Results provided here reflect the importance of combining local and landscape heterogeneity to promote biodiversity and sustain it across seasons and species groups.

5. General discussion. Towards a mechanistic understanding linking local heterogeneity with ecological communities

5.1. The need for a mechanistic framework

Throughout this thesis, I have showed evidence of heterogeneity's multifaceted nature, and the variety of ways in which it can modify local environmental conditions or local ecosystem to affect diversity, abundance, biomass, and the overall ecosystem functioning (Chapter 2). Heterogeneity effects structuring communities and ecosystem functioning can vary depending on the considered heterogeneity facet, substrate type, the targeted trophic and organismal group and the background geographical location and environmental settings like changes in environmental stress or species pool size (Chapter 2; Figure 1a,b,c,d). However, heterogeneity effects may crucially depend on the specific community mechanisms developing across temporal and spatial scales (Chapter 3 & 4; Figure 1e,f). Despite decades of research, the mechanisms behind heterogeneity effects on species communities have not been unequivocally supported by existing hypotheses (MacArthur & MacArthur 1961; Connel & Orias 1964; Allouche et al. 2012), with unexpected community responses to heterogeneity still common (e.g., Tamme et al. 2010) and new mechanisms being unravelled (e.g., Laanisto et al. 2013). This may indicate that the deductive and hypothesis-based approach so far pursued has important limitations, and that an inductive and mechanism-based perspective may help shade light on these unexpected outcomes.

Along the development of hypotheses about heterogeneity effects on diversity, other experimental efforts have focused on investigating system-specific mechanisms explaining heterogeneity effects on species communities (e.g., Bell et al. 1991). These studies frequently included disparate terms and a wide range of methodologies and metrics, with goals ranging from quantifying effects on rocky shore limpet diversity to heterogeneity effects on the ability of gibbons to move among trees in the rainforest (e.g., Cannon & Leighton 1994; Worden 2015). Such differences made comparisons across studies cumbersome, needing the input of a broad range of experts to collate information across fields (Bell et al. 1991). To this end, the identification of individual mechanisms can help better integrate heterogeneity effects into other ecological frameworks. From ecological stability (Chapter 3), and spatial scales (Chapter 4) to species-area effects (Henneron et al. 2019), trophic theory (e.g., Murdoch 1977) and metacommunity theory (e.g., Hamm & Drossel 2017), an improved understanding of heterogeneity mechanisms can help better predict ecological outcomes across ecosystems.

Ultimately, moving from a hypothesis-based to a mechanism-centred framework may facilitate the application of heterogeneity measures to conservation and restoration by focusing on those mechanisms that improve the structure and functioning of ecosystems (e.g., Frainer et al. 2018).

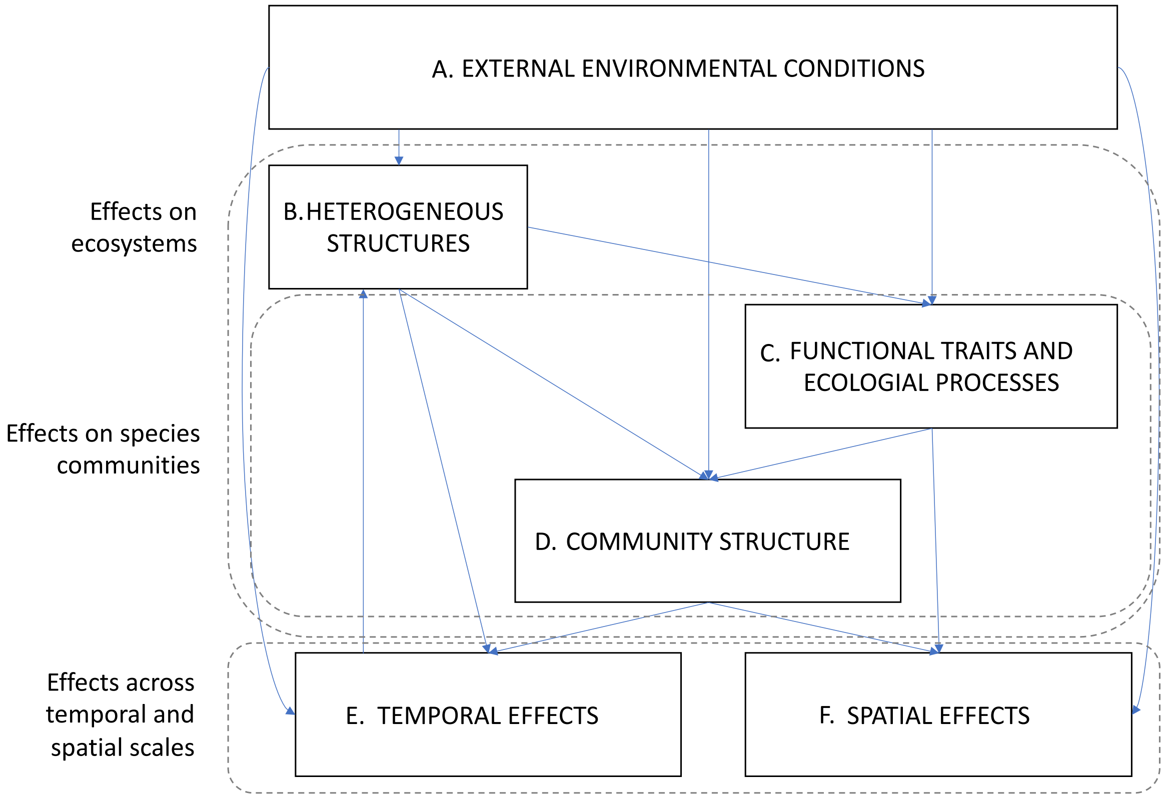

Figure 1. Contributions of this thesis towards the understanding of heterogeneity effects on species communities. From the top, a) how external environmental conditions may affect ecosystems and the subsequent response of pecies communities to heterogeneity, b) how heterogeneous communities may affect species communities through d) community structure (i.e., species diversity, species richness, abundance, biomass), and c) how may it influence functional traits and ecological processes. Finally, how all these effects may expand over temporal scales comprising more than one time point (e) and spatial scales beyond the plot scale (f).

In this section, I put my thesis results in a wider context and discuss mechanisms that may help explain the expectations from heterogeneity hypotheses and expand to other scenarios not considered by current hypotheses. I then explore current evidence on how a heterogeneous structures – species trait framework can help move beyond these mechanisms and the framework established by the current hypotheses. Next, I identify some external factors that can determine the local effect of heterogeneity and how scaling up both in space and time can change these effects through additional mechanisms. Finally, I discuss how this knowledge can be applied to current biodiversity issues.

5.2. Resource, refugia and exclusion effects underpin heterogeneity effects on species communities

The increase in the range of environmental conditions provided by heterogeneity can quickly turn into a myriad of different effects when examined closely. Under the umbrella of ‘environmental conditions’, there can be large effects on species communities, such as competition release (e.g., Cramer & Willig 2005) or predatory and grazing escape (Kuntze et al. 2023), as well as more intricate effects, such as trait trade-offs (e.g., Denno & Roderick 1991), density-dependent effects (e.g., Johnson 2007) and cascading effects (e.g., Grabowski 2004). All these effects can have a direct positive effect on species (resource effects; e.g., Diehl 1993), mitigate or negate negative effects (refugia effects; e.g., O’Neill & Thorp 2011) or present a negative effect (exclusion effects; Fahrig 2003) for the community. Specific hypotheses may be linked to individual mechanisms or to the interactions across multiple mechanisms, as all mechanisms may co-occur within the same community as they can affect different species.

Resource effects provide or increase previously non-existent, unavailable, or limiting resources for the establishment, survival, and reproduction of organisms at the local site. The provision of resources can be linked to food availability (e.g., nutrients, prey items or organic matter; e.g., Niemi & Hanowski 1984; Douglas & Lake 1994; Schmid 2000; Hurlbert 2004; Corkum & Cronin 2004; Eriksson et al. 2006; Alsterberg et al. 2017), roosting and breeding sites (e.g., Niemi & Hanowski 1984; Ruiz-Olmo & Jimenez 2009; Biagolini-Jr et al. 2017) and, more generally, can consider physical space as a limiting factor (e.g., Johnson et al. 2003). Heterogeneity can modify the availability of suspended organic matter by, for example, altering the water flow (e.g., Taniguchi & Tokeshi 2004; Whalen & Stachowicz 2017), can provide predatory ambush sites (e.g., James & Heck 1994), nesting opportunities (e.g., Niemi & Hanowski 1984) or simply provide physical space for larvae settlement (e.g., Smith et al. 2014). Typically, increasing resource availability is linked to higher species diversity by reducing species competition, as it is more likely to find different environmental conditions that allow for niche partitioning (e.g., Whalen & Stachowicz 2017). However, the presence of resources itself could also allow new species to colonise that were previously excluded due to resource scarcity (i.e., niche availability). Thus, resource effects lead to higher diversity by increasing the availability of a limiting factor within the ecosystem, and thus promoting niche availability and niche partitioning.

Refugia effects reduce or mitigate the influence of abiotic stressors such as extreme temperatures, disturbance effects like storms or waves, and negative species interactions such as competition and predation (e.g., Reeves et al. 2020). Refugia effects usually refer to heterogeneity's capacity to reduce abiotic stressors (e.g., Burnaford 2004) and predation (Krause et al. 1998), whereby physical 'safe' spaces allow species to escape negative effects, increase their survival, and thus lead to higher diversity. The removal and reduction of these negative effects allows for the establishment, survival, and reproduction of organisms at the local site. In intertidal rocky shores, species with low tolerance to temperature and desiccation may only be able to survive in the high shore in presence of local refugia that can provide water to allow them to cool down and keep moist during the low tides (e.g., Turner 1983; Sara et al. 2021). Alternatively, organisms in the intertidal may be able to coexist by finding spaces where they can escape the presence of dominant species, as is the case for suspension feeders (Whalen & Stankovicz 2017). Thus, refugia effects can contribute to niche availability, by providing environments for new species, and to niche partitioning, by allowing subdominant species to avoid competition by colonising different spaces.

Exclusion effects may occur when increasing heterogeneity reduces resource availability, increases environmental stress, or generates harsher disturbance regimes (e.g., Rogers et al. 2018). Structures like boulders in a rocky shore may serve as a refuge for predatory snails and seastars, leading to a decline in the overall cover of organisms around (Stephen Gosnell et al. 2012). The increase in heterogeneous structures may also lead to more fragile formations, which in highly disturbed environments may lead to the continued removal of organisms and thus impoverished communities (e.g., Wernberg & Connell 2008). Other highly heterogeneous structures may present spaces too small for organisms to colonise (Allouche et al. 2012), to navigate (Laanisto et al. 2013) and thus lead to small populations subject to stochasticity. All these effects would contribute to explain the observed negative heterogeneity effects on species communities (e.g., Tamme et al. 2010).

Effects do not necessarily occur in isolation, as each can affect different species within a community, and may interact with one another to result in the overall heterogeneity effects on the species community. Generally, the increase in both resources and refugia is linked to niche theory and the promotion of species richness (hypothesis 1 in Introduction; MacArthur & MacArthur 1961). However, as communities develop, the presence of more refugia or resources can result in communities with more biomass and lead to higher local productivity (hypothesis 2 in Introduction; Connell & Orias 1964). In this sense, the increase in heterogeneity begets more resources and potentially more heterogeneity (e.g., facilitation cascades by promoting the recruitment of foundation species that increase surface area available for organisms; Thomsen et al. 2010; Gribben et al. 2019), thus leading to an increase in species diversity. The opposite can also be true, since increasing heterogeneity may limit the physical space available for species, and such resource limitation can result in smaller populations and lower diversity (hypothesis 3 in Introduction; Allouche et al. 2012; Laanisto et al. 2013). Interactions can also be more nuanced, as predatory refugia may be limiting in the amount of physical space available, and lead to reduced body size and productivity in the prey species – and the consequent trade-off between increasing predation risk or reducing productivity (Heck Jr & Crowder 1991). Ultimately, responses to resource and refugia effects may interact with one another, resulting in synergistic, additive or antagonistic effects that then define the overall heterogeneity effects on species communities.

5.3. Linking heterogeneous structures to species traits to move beyond resource, refugia and exclusion effects

Even when accounting for resource and refugia effects within a community, there is still variability in heterogeneity effects across communities that is not explained. Heterogeneous structures (e.g., trees or macroalgae) benefit some organisms (e.g., fish and microalgae) more than others (e.g., macroinvertebrates), which can be linked to specific traits (Chapter 2). For example, large 3D structures such as trees, algae or reefs benefit more organisms with high mobility (e.g., fish or birds), while structures with lots of intricate patterns and small spaces will benefit generally smaller organisms (e.g., microinvertebrates or insects; Flores-Abreu et al. 2014). These two effects can already have important consequences for communities and ecosystems, since e.g., only highly mobile predators will be able to reach species on large 3D structures, and ecosystem functions within intricate structures will not be carried out by large organisms but rather by lots of small ones. Understanding which species will benefit from heterogeneity is crucial to predict not only heterogeneity effects on community structure, but also to reveal how heterogeneity may affect ecosystem functioning.

Not all structures will be relevant for all species, as some structures will present larger effects on the community (i.e., keystone structures; Tews et al. 2004) and some species will benefit more than others, resulting in disparate ecological dynamics depending on the type of heterogeneous structures present (e.g., St. Pierre & Kovalenko 2014). Certain species traits have been more strongly linked to heterogeneity features (e.g., locomotion type, body size), indicating the ways in which heterogeneity can modify community structure and functioning. Heterogeneous structures with small feature sizes and high feature variation may tend to select for small body sizes and allocate species with high mobility for which finding small less accessible spaces does not suppose a large energy expenditure. Heterogeneous environments providing only small areas for each species will result in smaller populations, which will survive through high mobility and ephemeral strategies. In contrast, structures providing refuge against harsh environmental conditions will present more vulnerable species and traits, and thus potentially less ephemeral strategies. The linking of heterogeneity features and species traits may allow to predict what communities inhabit a particular area by assessing the heterogeneity structures found within and assess the overall functioning of the ecosystem.

The interaction between heterogeneous structures and species traits interactions may further shed light on more intricate processes involved in diversity responses to heterogeneity (Vernham et al. 2023). Heterogeneous structures may impose trait trade-offs, by which species are, for example, forced to either invest in wintering strategies or predatory strategies (e.g., Dobel 1987; Stephen Gosnell et al. 2012). In other cases, the presence of heterogeneity will allow prey to escape predation at the expense of inhabiting less productive environments that reduce individual growth (i.e., body size) and population size, thus leading to a trade-off in which to choose between escaping predation or limiting body size (e.g., Taylor and Taylor 1977; Taylor 1984 in Downing 1991). Thus, much work remains to be done to fully understand all the ways in which heterogeneity can shape species communities and determine ecosystem functioning.

5.4. Heterogeneity and the wider environment – the relative effects of heterogeneity

Heterogeneity effects can be further modulated by the conditions found outside the local ecosystem. External environmental conditions can increase the need for heterogeneity and amplify heterogeneity effects on the community or decrease the community response to heterogeneity. A first hypothesis suggests that heterogeneity can help ameliorate the effects of stressful conditions in the environment, with heterogeneity effects increasing with the external environmental stress (Chapter 2; e.g., De Frenne et al. 2019). Under more environmental stressful conditions, heterogeneity refugia would be more needed, leading to larger differences between heterogeneous and environments than in less stressful conditions.

For example, ameliorating effects of heterogeneity on desiccation may only be important if the external temperature is high enough to place a physiological constraint in the form of excessive dehydration or heating. If milder conditions are presented, the effects of heterogeneity on the local environment may be negligible. Alternatively, in resource-depleted areas, the provision of resources in heterogeneous environments can present an important advantage for the community and become a refuge from resources depletion stress (e.g., Hall et al. 2018). The 'amelioration hypothesis' has received mixed support in this thesis (e.g., Chapter 2 and 3), and there is a few counterarguments to be posed and evidence so far is not conclusive (Yang et al. 2015). It is possible that within stressful landscapes, less-resistant species that can use the refugia are rarer and may not be able to capitalise on heterogeneity. Heterogeneity may also provide larger gradients under more stressful conditions, since e.g., providing humidity in a humid landscape creates smaller gradients than providing humidity in a dry landscape. Then, the larger gradients would further increase the range of environmental conditions available and thus increase species diversity. Lastly, the increasing effects of heterogeneity with environmental stress may depend on the nature of stress, since organisms may respond differently to resource depletion than to the presence of grazers, for example. More evidence and hypothesis testing needs to be conducted to define the mechanisms under which heterogeneity effects change along with multiple environmental stress gradients and consider potentially confounding effects with other co-occurring environmental factors and differences across focal species communities.

Disturbance regime, and particularly how large disturbance effects are, can also determine the importance of heterogeneity effects. When little disturbance is found, species do not need refugia to escape such effects and thus heterogeneity refugia effects may be lower. This can be the case of sheltered rocky shores, where wave action and storm surges hardly ever lead to the removal of organisms (e.g., Wernberg & Connell 2008). In contrast, when too much disturbance is encountered, refugia offered by heterogeneity may not protect organisms, and even heterogeneous structures may disappear due to physical damage. Under these circumstances, like in the case of hurricanes or extreme grazing, heterogeneity effects may be rendered null since no refugia will be available to escape such disturbance events. Importantly, while some heterogeneous structures may protect in front of certain disturbance, other disturbance may still cause an impact on the community or even be enhanced in presence of heterogeneity. This could be the case of sediment accumulation or chemical deposition around urban areas, where heterogeneous structures may contribute to sediment accumulation and increase toxicity effects for the community (e.g., Gibbons 1988; Aguilera et al. 2016). Thus, not only disturbance magnitude, but also the pairing of different heterogeneous structures with specific disturbance types is important to understand how heterogeneity effects will change in the presence of multiple disturbance.

Lastly, the arrival of species from the wider environment has another role determining heterogeneity effects. The number of species in the regional or species pool will determine how many species are available to benefit from heterogeneity effects (e.g., Ron et al. 2018). Previous studies have confirmed the positive effect of species pool on heterogeneity effects (e.g., Duflot et al. 2014) and others have suggested that this positive effect only exists up to a saturating point, after which all the species that can benefit from heterogeneity would already be present locally (McCoy & Bell 1991). Another important effect from species pool is the presence of specific species or functional groups in the species pool. For example, the presence of predators at a wider scale will drive the importance of structure as the provider of predator refuges – if there are no predators, this structural refuge effect is negligible (e.g. Dobel 1987; Stephen Gosnell et al. 2012). In contrast, if predator abundance is high at a wider scale, then the presence of predator refuges can be essential for the presence of prey groups. Overall, the size and composition of the species pool may further add complexity to heterogeneity effects under specific stress and disturbance settings.

5.5. Finding the relevant temporal and spatial scales at which heterogeneity shapes communities

Both heterogeneity and its effects on communities are not impermanent, as they change over time and space along with their effects on diversity (e.g., Thompson et al. 2021). Changes in the role of heterogeneity over space may depend on successional and stability dynamics, propagating heterogeneity effects from a single time point over longer periods of time (Chapter 3). As we also consider plots of different sizes, and since different systems will present relevant heterogeneous structures at different spatial scales (Chapter 2; Chytry et al. 2023; Aguilera et al. 2014), the spatial scaling of local heterogeneity effects and ultimate integration into landscape heterogeneity effects will help understand at which spatial scales local heterogeneity may be more relevant (Chapter 4).

In Chapter 3, I have showed evidence that communities in heterogeneous environments develop earlier into mature successional stages and tend to vary less over time and ultimately reach different community states. According to literature, abiotic heterogeneity is fundamental for early communities and becomes less relevant as secondary biotic structures develop (e.g., Dean & Connell 1987; Swanson et al. 2011). For example, intertidal rocky shore communities in early succession present barnacles, mussels and macroalgae using substrate rugosity, while in more mature successional stages it is the macroalgae and sessile invertebrate structures that provide with most heterogeneous structures (Dean & Connell 1987). These secondary biotic structures, however, may not be able to withstand disturbance as well as abiotic substrate rugosity does and lead to less stable communities (e.g., Turner et al. 1998). For example, the presence of large macroalgae in the intertidal rocky shore provides environments suitable for many epibiotic species, but they tend to be removed by storm surges more often than the basal substrate on which they are does (e.g., Castorani et al. 2018). Indeed, several study cases show the intricate dynamics in which more mature successional systems provide more environments for more species but lead to more variable disturbance-recovery dynamics than abiotic substrates (e,g,, Luzuriaga & Escudero 2008).

Heterogeneity has another more central role in determining how communities respond to disturbance, by increasing or reducing resistance and recovery during disturbance events (Chapter 3). Heterogeneity does not only increase resistance to disturbance by providing refugia that increases mean temporal population stability, but it can also promote recovery by increasing mechanisms such as temporal species asynchrony and temporal statistical averaging that allow for more swift species replacements after extinctions occur (Chapter 3). However, it cannot be stated that heterogeneity promotes resilience and community stability overall, since there are several negative effects that also originate from heterogeneity. The reduction in competition caused by heterogeneity leads to a decrease in temporal species asynchrony, and the reduction in consumer abundance allows more ephemeral species to proliferate and prevents the creation of free space for new species to arrive (Chapter 3). All these mechanisms lead to suggest that heterogeneity effects on resilience and stability are variable and may depend on these and other mechanisms, plus respond to several related compositional and environmental factors (Chapter 3).

Added to the temporal dynamics, local heterogeneity effects may weaken across spatial scales and be linked to landscape heterogeneity. Evidence has suggested that heterogeneity effects are only present within small habitat patches, and that heterogeneity effects diminish as the patch size increases. This hypothesis has been showcased as the ‘habitat diversity’ hypothesis, and it is supported by the increased variability in diversity at low patch area levels (e.g., Chen et al. 2020). Possible mechanisms behind this would be that as patch size increases, potential sampling effects increase as well, which will eventually bring into the patch all the species that would otherwise benefit from heterogeneity. Alternatively, I have looked at the role of local heterogeneity within a landscape presenting varying degrees of landscape heterogeneity to elucidate the role of local heterogeneity at larger spatial scales (Chapter 4). While local heterogeneity tended to promote species richness at the local site, landscape heterogeneity increased species turnover, and thus both led to higher gamma species richness. However, there are still several relevant questions remaining, like uncovering the mechanisms behind local heterogeneity effects decreasing across spatial scales, and what are the implications for community stability and resilience across spatial scales.

5.6. A mechanistic understanding to apply heterogeneity to conservation

As a result of all these mechanisms, heterogeneity promotes a wide array of community responses, from cascading effects to feedback effects, and thus modulate the diversity and functioning of communities (Soukup et al. 2022). Understanding such effects may allow to harness the management of local heterogeneity to promote diversity, ecosystem processes and restore ecosystems. For example, local heterogeneity can trigger or reduce trophic cascading effects within communities, which contribute to increasing the diversity and functioning of the community. Heterogeneity can also promote processes such as trophic cascades or connect environments and allow for the successful dispersal of species. Given the widespread effects of local heterogeneity within communities, there is great potential in using heterogeneity as a tool for the conservation of natural communities.

Successful case studies of applying heterogeneity to promote diversity and functioning include from the straightforward increase of diversity at a given time, to the reestablishment or alteration of natural processes such as cascading effects. The modification of simplified substrate, such as the one found in harbours, allows for the colonisation of more species that may not thrive due to desiccation, grazing or predation, and find refuge in the holes and crevices provided by heterogeneity (e.g., Ushiama et al. 2019). Such effects are also found for terrestrial urban areas, where the presence of parks and gardens allows for birds and arthropods to thrive in an otherwise unhospitable environment (Ossola et al. 2019). Increasing heterogeneity within an environment may also allow to interrupt trophic cascades by reducing the chance of predators and grazers to encounter their prey and hampering the movement of predators and grazers within the environment. For example, the deployment of structures such as sunk wood in a lake can completely shift the ecosystem dynamics, since grazers must spend less energy escaping predation and can have larger effects on algae populations. Also, changes in heterogeneity can also hamper grazers such as limpets (*Patella* spp.), which tend to move and survive less in rough substrates with no smooth surfaces (e.g., Griffin et al. 2009). Applying appropriate heterogeneous structures may also promote the presence of foundation species (e.g., Hall et al. 2019). As these species colonise the local environment, they create more structures that allow for further species to colonise and develop into facilitation cascades (Gribben et al. 2019).

Finally, caution must be taken when modifying heterogeneity in the environment, since focusing on local heterogeneity within the wrong context may misplace resources and be ultimately detrimental for biodiversity. To maximise heterogeneity effects, we may want to focus on small habitat patches where local heterogeneity places a more important role. However, large area patches may provide larger benefits for the overall environment, and thus prioritising local heterogeneity effects may ultimately be detrimental (e.g., Chen et al. 2020). In addition, the focus solely on heterogeneity effects on diversity, excluding considerations of heterogeneity effects on ecosystem functioning, can result in unstable systems that do not fully develop into mature and diverse communities. That would be the case for communities where heterogeneity promotes destabilising mechanisms (Chapter 3). Rather, heterogeneity can be used for many other purposes, such as the enhancement of connectivity, modulating species interactions or increasing local productivity (Chapter 2). Placing a focus on the functional consequences of heterogeneity, thus, opens the door to biodiversity benefits that are not constrained to direct effects of heterogeneity on species diversity.

5.7. Conclusions

Heterogeneity provides multiple benefits to species communities that expand beyond the expectations set by the initial hypotheses discussed in this thesis. Focusing on resource, refugia and exclusion effects, we can better understand the specific and more general effects of heterogeneity on species communities. By linking heterogeneous structures to functional traits, we can assess more nuanced mechanisms and explain heterogeneity effects across species and communities. Heterogeneity mechanisms also help inform how the variation in wider environmental conditions may influence local heterogeneity effects, as well as understand how these will vary across temporal and spatial scales. Lessons learned from these mechanistic effects on ecosystem functioning are manyfold and highlight the potential role of heterogeneity in conservation and restoration. To this end, we need to further our understanding of heterogeneity role driving ecosystem functioning across spatial and temporal scales.

6. References

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7. Supplementary Materials

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Supplementary Materials 1:

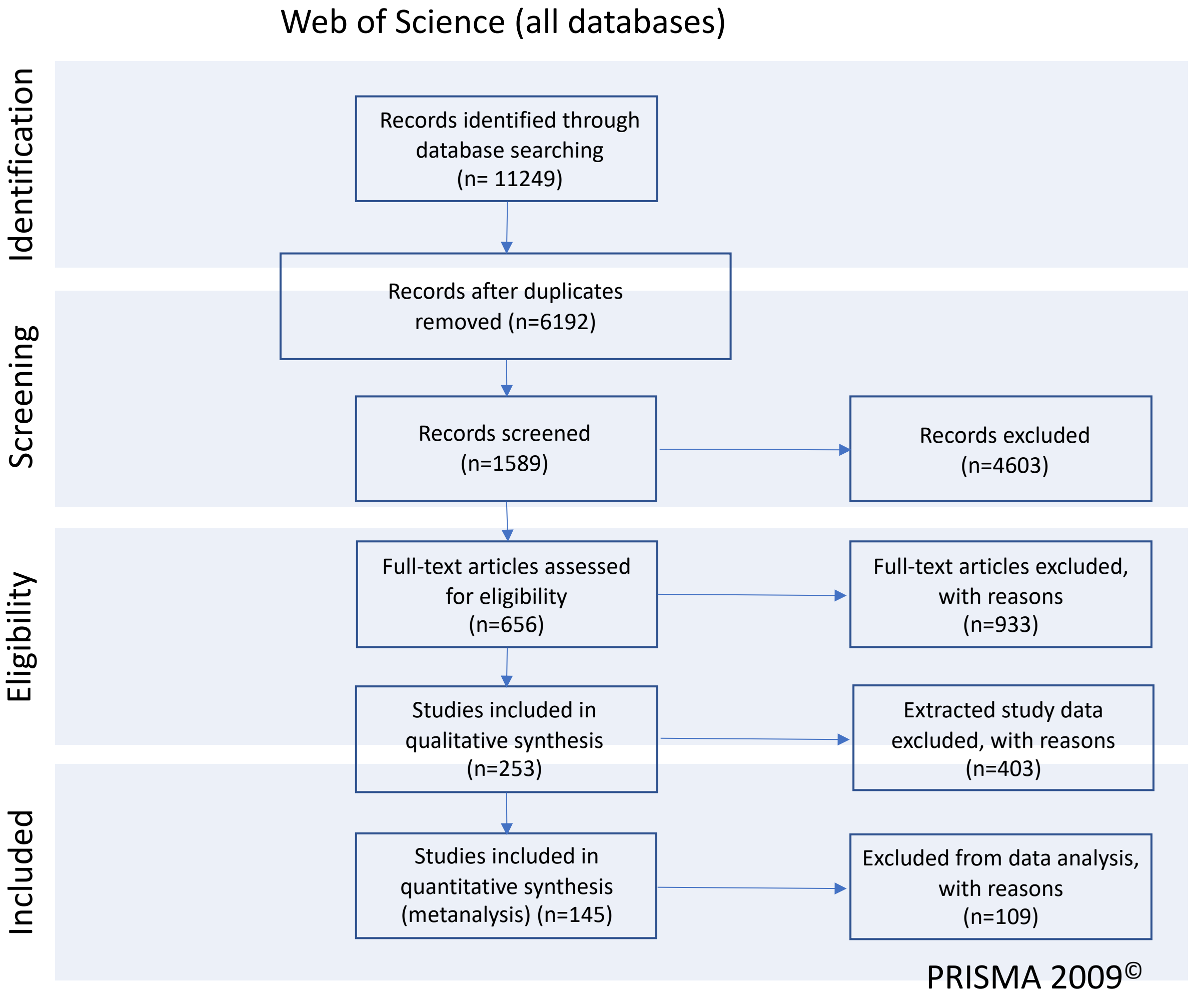


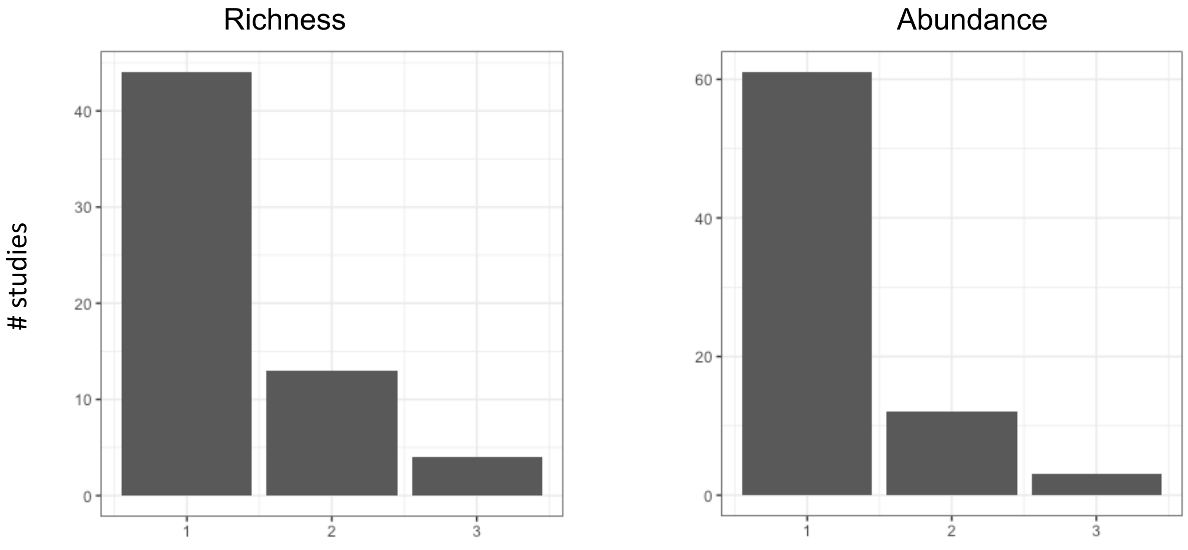
Figure S1. PRISMA flow diagram. Summary of the literature search and selection process following the PRISMA guidelines. Note that many studies had to be removed from the main analysis in the last step due to potentially confounded variables and experimental designs.

Supplementary Materials 2:

Table S1. Summary of how many studies were found within each facet for the models run for macroinvertebrate + microinvertebrate data comparing heterogeneity effects across facets. Table showing how many studies were found for each facet, and how many studies for each combination of facets. Total per row will be larger than the actual number of studies shown in results. That is because, when there is an interaction with >1 other facet, there is double counting since this is a pairwise matrix. E.g. a study accounting for complexity-3d amount-feature size will count for complexity as: complexity-3d amount and complexity-size, so instead of putting one counter, we put two.

Richness	complexity	feature 2D amount	feature 3D amount	feature id	feature size	feature variation
complexity	13	1	3	0	2	2
feature 2D amount	-	18	4	0	6	3
feature 3D amount	-	-	30	0	7	1
feature id	-	-	-	2	0	0
feature size	-	-	-	-	8	1
feature variation	-	-	-	-	-	4

Abundance	complexity	feature 2D amount	feature 3D amount	feature id	feature size	feature variation
complexity	13	0	2	0	3	1
feature 2D amount	-	21	5	0	4	3
feature 3D amount	-	-	34	0	2	2
feature id	-	-	-	3	0	0
feature size	-	-	-	-	9	1
feature variation	-	-	-	-	-	4



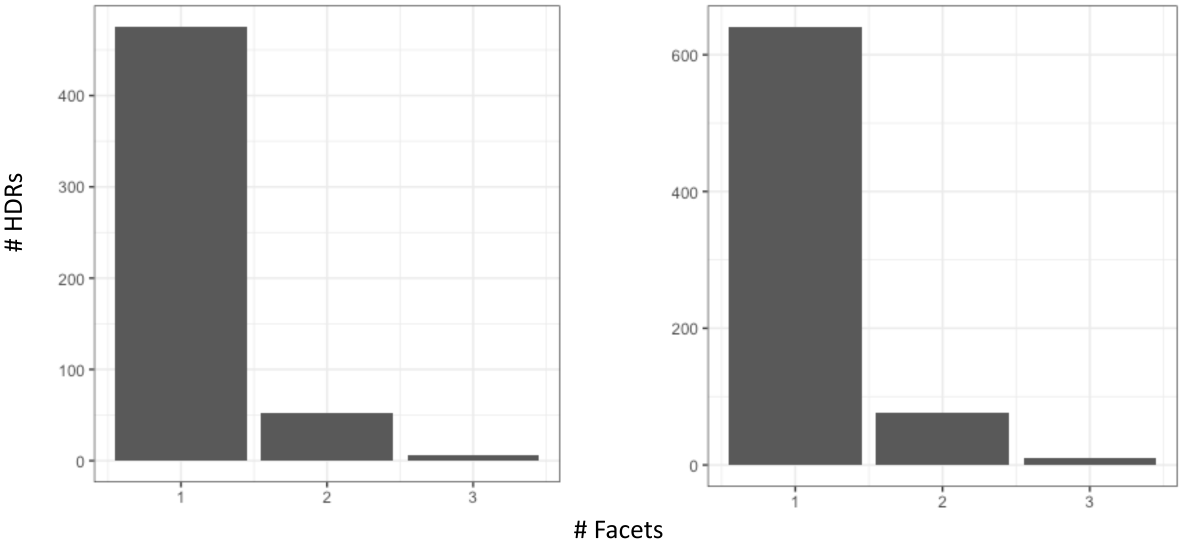


Figure S2. How many studies presented only one facet, or more than one facet. At the top, how many studies presented one, two or three heterogeneity facets for species richness (left) and abundance (right). At the bottom, how many HDRs presented one, two or three heterogeneity facets for species richness (left) and abundance (right). For studies presenting >1 facet, it does not mean that all HDRs share more than one facet. It means that for those studies, at least one HDR is shared across X facets – e.g. across 20 HDRs, one is shared across e.g. 2 facets.

Supplementary Materials 3:

Table S2. Response metrics used in the metanalysis.

Metric category	**Metrics used**
Species richness	Number of species
Species diversity	Shannon diversity
Species evenness	Pielou diversity
Abundance	Number of individuas sqm^{-1}
Biomass	Grams sqm^{-1}
Grazing	% cover of microalgae removed, distance travelled by grazer (m).
Recruitment	Number of individuas sqm^{-1}, Number of individuas g^{-1}
Predation	Reduction in prey abundance (Number of individuas sqm^{-1}), reduction in prey biomass (Grams sqm^{-1}), % of prey removed.
Body size	Shell diameter, shell size, mean individual body mass, mean individual body size.

Supplementary Materials 4:

Model description for metanalysis data models

All linear mixed-effects models presented the form specified in Fox (2002; based on Laird & Ware 1982). While in this section I will focus on describing model specification, please refer to Fox (2002) for a detailed explanation on the model form and coefficients.

For the models testing the effects of heterogeneity across heterogeneity facets on benthic invertebrate species richness and abundance, I used the following model specification:

$$\begin{aligned} y_{ij} = {} & \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{3ij} + \beta_4 x_{4ij} + \beta_5 x_{5ij} + \beta_6 x_{6ij} + \beta_7 x_{7ij} + \beta_8 x_{8ij} \\ & + \beta_9 x_1 x_{3ij} + \beta_{10} x_1 x_{4ij} + \beta_{11} x_1 x_{5ij} + \beta_{12} x_1 x_{6ij} + \beta_{13} x_1 x_{7ij} + \beta_{14} x_1 x_{8ij} \\ & + b_{i1} z_{1ij} + b_{i2} z_{2ij} + \varepsilon_{ij} \end{aligned}$$

$$b_{ik} \sim N(0, \psi_k^2), \mathrm{Cov}(b_k, b_{k'}) = \psi_{kk'}$$

$$\varepsilon_{ij} \sim N(0, \sigma^2 \lambda_{ijj}), \mathrm{Cov}(\varepsilon_{ij}, \varepsilon_{ij'}) = \sigma^2 \lambda_{ijj'}$$

where

- y_{ij} is the response variable, for all *j* observations in *i* groups.
- $\beta_1, \dots, \beta_{14}$ are the fixed-effect coefficients, corresponding to heterogeneity (β_1 and β_2; variables standardised to 0-1 corresponding to a linear [x] and quadratic [x^2] terms, respectively), heterogeneity coefficient of variation (β_3; continuous variable with no units), substrate type (β_4; categorical variable with two levels: abiotic substrate and biogenic substrate), season (β_5; categorical variable with four levels: winter, spring, summer and autumn), depth (β_6; metres), biogeographical region (β_7; categorical variable with seven levels: Temperate Australasia, Temperate North Atlantic, Mediterranean, Temperate South America, Temperate South Africa, Temperate North Pacific, Tropical regions), taxonomic group (β_8; categorical variable with two levels: microinvertebrates and macroinvertebrates). Fixed effects corresponding to coefficients β_3, β_4, β_5, β_6, β_7, β_8 were only included if data was found across more than one level, and if they helped explain patterns in the data (i.e., at least one level had a significant effects). Coefficients β_9, β_{10}, β_{11}, β_{12}, β_{13}, β_{14} correspond to the interaction across coefficients, which were excluded if not significant.
- x_{1ij},x_{2ij} are the fixed-effect regressors for observation j in group i.
- $b_{1k}, \dots, b_{2k}$ is the random-effect coefficients for group i, assumed to be multivariately normally distributed. Here, study ID and plot ID were included as random effects to account for variability between and within study (Thompson & Sharp 1999).
- z_{1ij} is the random-effect regressors.

- ε_{ij} is the error for observation j in group i. The errors for group I are assumed to be multivariately normally distributed.
- ψ_k are the variances and $\psi_{kk'}$ the covariances among the random effects, assumed to be constant across groups.
- $\sigma^2 \lambda_{ijj'}$ are the covariances between errors in group i.

For the models testing the effects of heterogeneity across organismal groups, I used the following model specification:

$$
\begin{aligned}
y_{ij} = \; & \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{3ij} + \beta_4 x_{4ij} + \beta_5 x_{5ij} + \beta_6 x_{6ij} + \beta_7 x_{7ij} + \beta_8 x_{8ij} + \beta_9 x_{9ij} \\
& + \beta_{10} x_1 x_{3ij} + \beta_{11} x_1 x_{4ij} + \beta_{12} x_1 x_{5ij} + \beta_{13} x_1 x_{6ij} + \beta_{14} x_1 x_{7ij} + \beta_{15} x_1 x_{8ij} \\
& + \beta_{16} x_1 x_{9ij} + \beta_{17} x_5 x_{7ij} \\
& + b_{i1} z_{1ij} + b_{i2} z_{2ij} + \varepsilon_{ij} \\
b_{ik} \sim \; & N(0, \psi_k^2), \mathrm{Cov}(b_k, b_{k'}) = \psi_{kk'} \\
\varepsilon_{ij} \sim \; & N(0, \sigma^2 \lambda_{ijj}), \mathrm{Cov}(\varepsilon_{ij}, \varepsilon_{ij'}) = \sigma^2 \lambda_{ijj'}
\end{aligned}
$$

where

- y_{ij} is the response variable, for all *j* observations in *i* groups.
- $\beta_1, \dots, \beta_{17}$ are the fixed-effect coefficients, corresponding to heterogeneity (β_1 and β_2; variables standardised to 0-1 corresponding to a linear [x] and quadratic [x^2] terms, respectively), heterogeneity coefficient of variation (β_3; continuous variable with no units), substrate type (β_4; categorical variable with two levels: abiotic substrate and biogenic substrate), season (β_5; categorical variable with four levels: winter, spring, summer and autumn), depth (β_6; metres), latitude (β_7; decimal degrees), response metric (β_8; categorical variable with five levels: abundance, biomass, Shannon diversity, species richness, species evenness), heterogeneity facet (β_9; categorical variable with six levels: substrate 3D amount, substrate 2D amount, substrate complexity, feature size, feature variation, feature richness). Fixed effects corresponding to coefficients β_3, β_4, β_5, β_6, β_7, β_8, β_9 were only included if data was found across more than one level, and if they helped explain patterns in the data (i.e., at least one level had a significant effects). Coefficients β_{10}, β_{11}, β_{12}, β_{13}, β_{14}, β_{15}, β_{16}, β_{17} correspond to the interaction across coefficients, which were excluded if not significant.
- x_{1ij}, x_{2ij} are the fixed-effect regressors for observation j in group i.

- $b_{1k}, \dots, b_{2k}$ is the random-effect coefficients for group i, assumed to be multivariately normally distributed. Here, study ID and plot ID were included as random effects to account for variability between and within study (Thompson & Sharp 1999).
- z_{1ij} is the random-effect regressors.
- ε_{ij} is the error for observation j in group i. The errors for group I are assumed to be multivariately normally distributed.
- ψ_k are the variances and $\psi_{kk'}$ the covariances among the random effects, assumed to be constant across groups.
- $\sigma^2 \lambda_{ijj'}$ are the covariances between errors in group i.

For the models testing the effects of heterogeneity across ecological processes and related proxies, I used the following model specification:

$$
\begin{aligned}
y_{ij} = {} & \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{3ij} + \beta_4 x_{4ij} + \beta_5 x_{5ij} \\
& + \beta_6 x_1 x_{3ij} + \beta_7 x_1 x_{4ij} + \beta_8 x_1 x_{5ij} \\
& + b_{i1} z_{1ij} + b_{i2} z_{2ij} + \varepsilon_{ij} \\
b_{ik} \sim {} & N(0, \psi_k^2), \mathrm{Cov}(b_k, b_{k'}) = \psi_{kk'} \\
\varepsilon_{ij} \sim {} & N(0, \sigma^2 \lambda_{ijj}), \mathrm{Cov}(\varepsilon_{ij}, \varepsilon_{ij'}) = \sigma^2 \lambda_{ijj'}
\end{aligned}
$$

where

- y_{ij} is the response variable, for all *j* observations in *i* groups.
- $\beta_1, \dots, \beta_8$ are the fixed-effect coefficients, corresponding to heterogeneity (β_1 and β_2; variables standardised to 0-1 corresponding to a linear [x] and quadratic [x^2] terms, respectively), heterogeneity coefficient of variation (β_3; continuous variable with no units), depth (β_4; metres), heterogeneity facet (β_5; categorical variable with six levels: substrate 3D amount, substrate 2D amount, substrate complexity, feature size, feature variation, feature richness). Fixed effects corresponding to coefficients β_3, β_4, β_5 were only included if data was found across more than one level, and if they helped explain patterns in the data (i.e., at least one level had a significant effects). Coefficients β_6, β_7, β_8 correspond to the interaction across coefficients, which were excluded if not significant.
- x_{1ij}, x_{2ij} are the fixed-effect regressors for observation j in group i.
- $b_{1k}, \dots, b_{2k}$ is the random-effect coefficients for group i, assumed to be multivariately normally distributed. Here, study ID and plot ID were included as random effects to account for variability between and within study (Thompson & Sharp 1999).
- z_{1ij} is the random-effect regressors.

- ε_{ij} is the error for observation j in group i. The errors for group I are assumed to be multivariately normally distributed.
- ψ_k are the variances and $\psi_{kk'}$ the covariances among the random effects, assumed to be constant across groups.
- $\sigma^2\lambda_{ijj'}$ are the covariances between errors in group i.

Supplementary Materials 5:

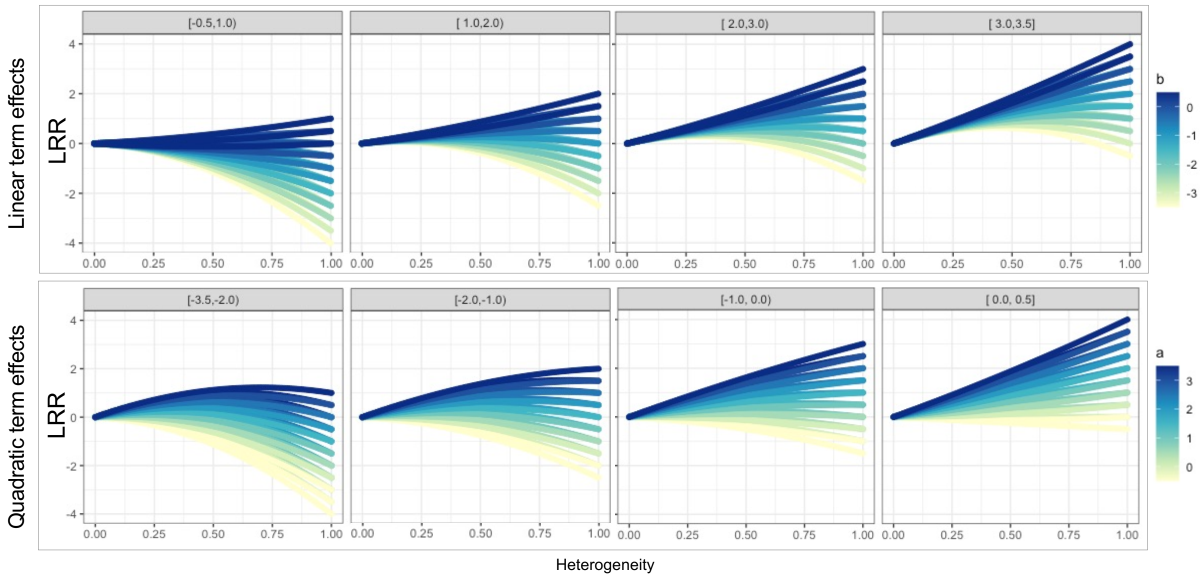


Figure S3. Interpretation of metanalysis model coefficients. Data showing the simulations run with the formula y = x + x^2 to aid in the interpretation of the linear (a; x) and quadratic (b; x^2) terms from the quadratic function within the range of values found in the study.

Supplementary Materials 6:

Table S3. Data structure for data used in models looking into ecological processes and related proxies. Summary of how many studies (numbers outside brackets, at the left of the slash), HDRs (numbers outside brackets, at the right of the slash) and observations (numbers inside brackets) were included for each comparison within moderators for the models comparing heterogeneity effects across ecological processes.

Factor	Levels	Grazing	Recruitment	Predation	Body size
Substrate	Biogenic	0	5-35 (247)	3-13 (41)	3-44 (259)
	Rock	5-29 (167)	9-32 (446)	5-7 (87)	3-3 (161)
Study System	Intertidal	5-29 (167)	8-26 (398)	5-15 (49)	4-44 (215)
	Subtidal	0	6-41 (295)	3-5 (79)	1-3 (205)
Organismal group	Microinvertebrates	0	2-26 (131)	2-4 (14)	0
	Fish	0	4-14 (196)	3-5 (79)	2-4 (209)
	Macroalgae	0	1-4 (36)	0	0
	Microalgae	0	1-9 (18)	0	0
	Macroinverebrates	5-29 (167)	4-11 (282)	3-9 (23)	3-43 (211)
	Large macroinverebrates	0	2-3 (30)	1-2 (12)	0
Heterogeneity facet	Substrate 3D amount	1-2 (18)	6-45 (306)	5-9 (101)	1-1 (155)
	Substrate 2D amount	2-7 (30)	7-13 (290)	2-8 (16)	3-19 (110)
	Feature size	2-20 (119)	2 -7(63)	1-3 (11)	1-24 (84)
	Feature variation	0	0	0	0
	Feature richness	0	0	0	0
	Substrate complexity	0	2-2 (34)	0	2-3 (71)

Supplementary Materials 7:

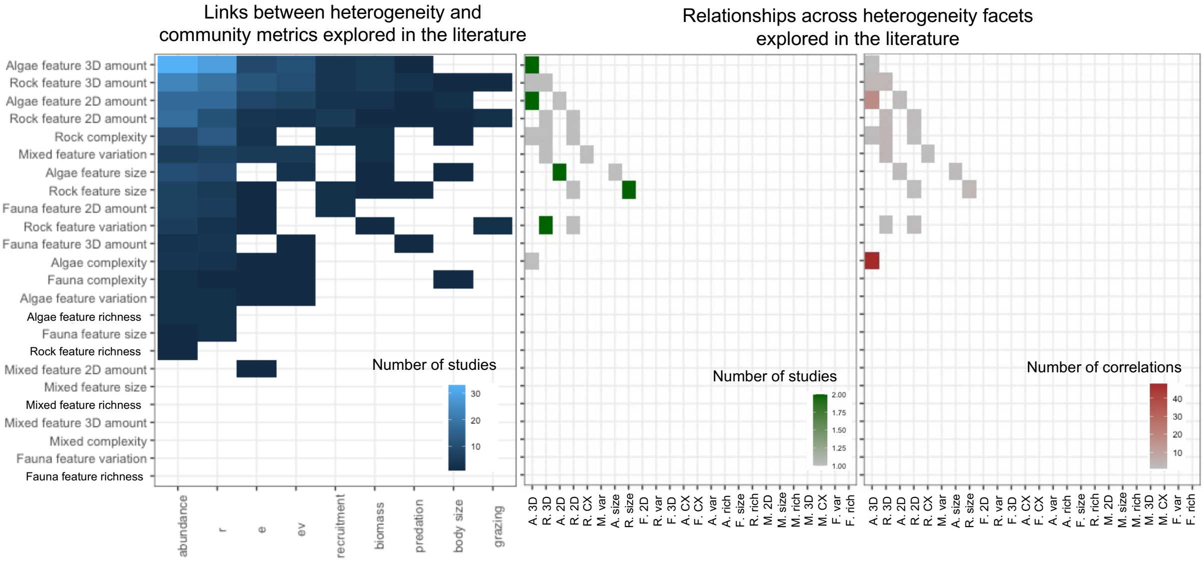


Figure S4. Summary of correlations among heterogeneity metrics. Summary of correlations found across heterogeneity metrics within the same study that targeted the same response variable. On the left, how many studies were found quantifying the same relationship between a specific heterogeneity facet, substrate, and response metric. On the center, how many studies were found assessing the effects of multiple heterogeneity facets simultaneously. On the right, how many correlations (HDRs) were found assessing the effects of multiple heterogeneity facets simultaneously.

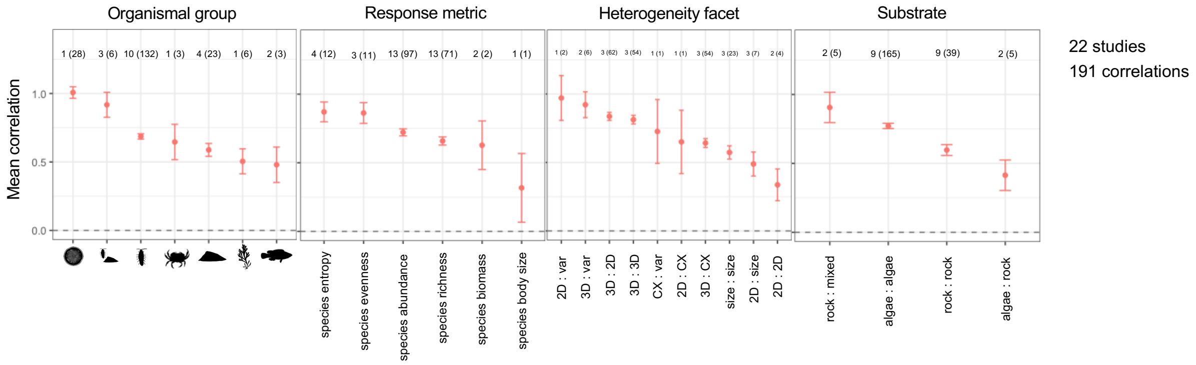


Figure S5. Summary of mean correlation (in absolute values, and 95% C.I.) found across heterogeneity metrics within the same study that targeted a response variable for a given organismal group (left), response metrics (center-left), or across heterogeneity predictors belonging to different heterogeneity facets (center-right) or substrates (right). Numbers on top of each dot correspond to the number of studies (no brackets), the number of effect size groups (in brackets).

Supplementary Materials 8:

All linear mixed-effects models presented the form specified in Fox (2002; based on Laird & Ware 1982). While in this section I will focus on describing model specification, please refer to Fox (2002) for a detailed explanation on the model form and coefficients.

For the models testing the effects of heterogeneity on percentage (%) water cover (model A) and surface temperature (model B), I used the following model specification:

$$
\begin{aligned}
y_{ij} = {} & \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_1 x_{2ij} \\
& + b_{i1} z_{1ij} + \varepsilon_{ij}
\end{aligned}
$$

$$b_{ik} \sim N(0, \psi_k^2), \mathrm{Cov}(b_k, b_{k'}) = \psi_{kk'}$$

$$\varepsilon_{ij} \sim N(0, \sigma^2 \lambda_{ijj}), \mathrm{Cov}(\varepsilon_{ij}, \varepsilon_{ij'}) = \sigma^2 \lambda_{ijj'}$$

where

- y_{ij} is the response variable, corresponding to % water cover (model A) and surface temperature (model B), for all *j* observations in *i* groups.
- $\beta_1, \ldots, \beta_3$ are the fixed-effect coefficients, corresponding to time (seconds) and heterogeneity (categorical variable with two levels: heterogeneous, non-heterogeneous). Note that
- x_{1ij}, x_{2ij} are the fixed-effect regressors for observation j in group i.
- b_{ik} is the random-effect coefficients for group I, assumed to be multivariately normally distributed. Here, tile was included as a random effect to account for the effect of repeated measures (e.g., Schielzeth & Nakagawa 2013).
- z_{1ij} is the random-effect regressors.
- ε_{ij} is the error for observation j in group i. The errors for group I are assumed to be multivariately normally distributed.
- ψ_k are the variances and $\psi_{kk'}$ the covariances among the random effects, assumed to be constant across groups.
- $\sigma^2 \lambda_{ijj'}$ are the covariances between errors in group i.

For the models testing the effects of heterogeneity on species richness, species evenness, percentage (%) cover of Other suspension feeders, % cover of *Astrominius modestus*, % cover of consumers, % cover of native barnacles, % cover of ephemeral macroalgae, temporal cover stability, mean population temporal stability, temporal species asynchrony, temporal statistical averaging and temporal compositional stability, I used the following model specification:

$$y_{ij} = \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_1 x_{2ij}$$

$$+ b_{i1}z_{1ij} + \varepsilon_{ij}$$

$$b_{ik} \sim N(0, \psi_k^2), \mathrm{Cov}(b_k, b_{k'}) = \psi_{kk'}$$

$$\varepsilon_{ij} \sim N(0, \sigma^2 \lambda_{ijj}), \mathrm{Cov}(\varepsilon_{ij}, \varepsilon_{ij'}) = \sigma^2 \lambda_{ijj'}$$

where

- y_{ij} is the response variable, for all *j* observations in *I* groups.
- $\beta_1, \ldots, \beta_3$ are the fixed-effect coefficients, corresponding to emersion rate (no units) and heterogeneity (categorical variable with two levels: heterogeneous, non-heterogeneous).
- x_{1ij}, x_{2ij} are the fixed-effect regressors for observation j in group i.
- b_{ik} is the random-effect coefficients for group I, assumed to be multivariately normally distributed. Here, transect was included as a random effect to account for variability across transects due to e.g., differences in wave exposure.
- z_{1ij} is the random-effect regressors.
- ε_{ij} is the error for observation j in group i. The errors for group I are assumed to be multivariately normally distributed.
- ψ_k are the variances and $\psi_{kk'}$ the covariances among the random effects, assumed to be constant across groups.
- $\sigma^2 \lambda_{ijj'}$ are the covariances between errors in group i.

Supplementary Materials 9:

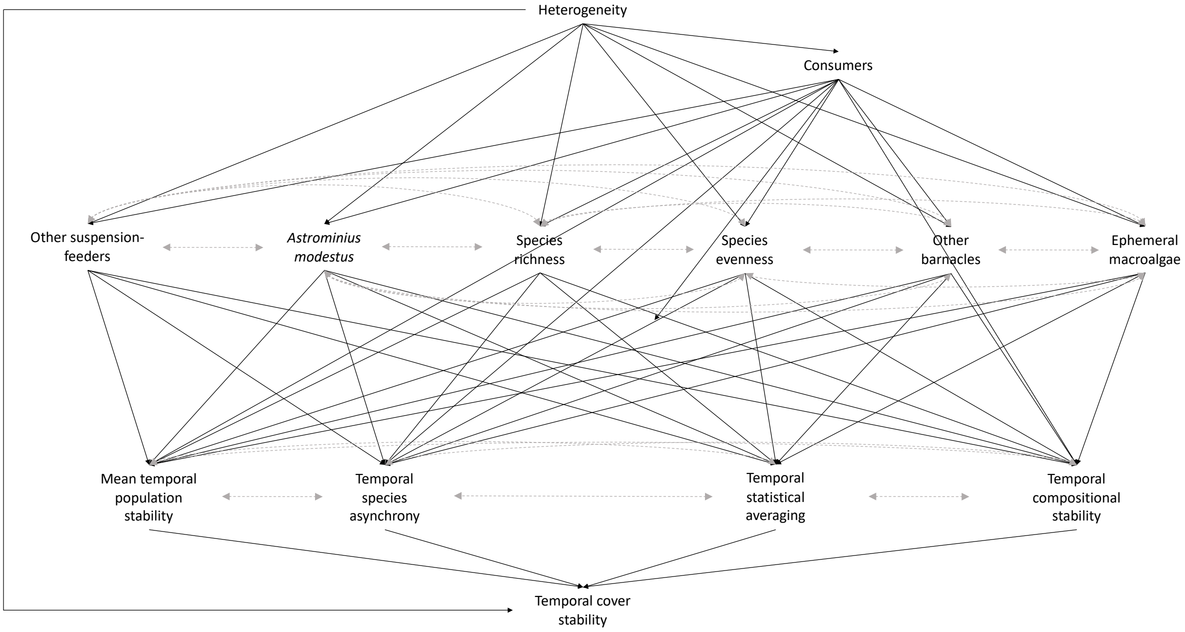


Figure S6. Hypothesised links used in the SEM analysis to test hetereogeneity effects on temporal cover stability. Metamodel indicating the hypothesised links between heterogeneity and community components, heterogeneity and stability facets or dimensions, and the links between community components and stability facets or dimensions. Solid black lines indicate the hypothesised links among variables, with the pointed arrow indicating the causal direction in each link. Grey dashed lines indicate links among variables that were not causally related but could be correlated due to exogenous variables not accounted for in the metanalysis.

Supplementary Materials 10:

Table S4. Model output4492 for PERMANOVA analysis.

	Df	Sum Sq	R^2	Pseudo-F	P	
a) Differences in location (PERMANOVA)						
Emersion gradient	2	26.388	0.17217	89.4401	0.001	***
Heterogeneity	1	4.042	0.02637	27.3986	0.001	***
Date	1	14.019	0.09146	95.029	0.001	***
Heterogeneity x Emersion gradient	2	1.923	0.01255	6.5195	0.001	***
Emersion gradient x date	2	3.694	0.0241	12.5202	0.001	***
Heterogeneity x Date	1	1.332	0.00869	9.0295	0.001	***
Heterogeneity x Emersion gradient x Date	2	0.527	0.00344	1.7869	0.044	*
Residual	687	101.345	0.66122			
Total	698	153.27	1			
b) Differences in dispersion (PERMADISP)						
b.1)						
Heterogeneity x Emersion gradient x Date	65	11.2686		12.245	1.00E-03	***
Residuals	633	8.9622				
b.2)						
Heterogeneity x Emersion gradient	5	12.5745		187.12	0.001	***
Residuals	693	9.3141				

Supplementary Materials 11:

Table S5. Summary of studies looking at heterogeneity-stability relationships in the literature.

Title	Authors & Year	Year	System	Focus organisms	Question	Type of study	Predictor	Response variable	Effect	Type of stability	Direction
Experimental Studies on Predation: Dispersion Factors and Predator–Prey Oscillations	Huffaker	1958	Grassland	Herbivorous and predatory mites	Does refugia provide stability in predator-prey interactions?	Lab experiment	Number of rubber balls	Species survival	Refugia	Interaction stability	+
Habitat heterogeneity and disturbance influence patterns of community temporal variability in a small temperate stream	Brown	2007	Streams	Stream macroinvertebrate communities	Does habitat heterogeneity decrease temporal variability? Is this relationship more important during floods (disturbance events)?	Field experiment	Particle size	Euclidean distances in a correspondence analysis comprising all communities, but following the same type of communities over time	Resources and refugia	Compositional stability	+
The stability–diversity relationship in stream macroinvertebrates: influences of sampling effects and habitat complexity	HEIKKI MYKRÄ, JANI HEINO, JARI OKSANEN, TIMO MUOTKA	2011	Streams	Strean invertebrate commuities	Is the relationship betweel richness and stability modified by key environmental variables? Including habitat complexity (measured as canopy cover)	Survey	Canopy cover	Mean Bray-Curtis similarity across years (not only consecutive years) for each site	Refugia	Compositional stability	+
Habitat complexity, dispersal and metapopulations: Macroscopic study of a predator-prey system	Jana, D and Bairagi, N	2014				Theoretical				Interaction stability	+
Habitat complexity: approaches and future directions	Kovalenko, KE ; Thomaz, SM ; Warfe, DM	2012	Rocky shores and coral reefs			Review				Interaction stability	+
Habitat heterogeneity and activity of an omnivorous ecosystem engineer control stream community dynamics	Brown and Lawson	2010	Streams	Stream macroinvertebrate communities	Does habitat heterogeneity control community dynamics alongside the presence of a keyston species?	Field experiment	Simpson using substrate type relative abundance	Temporal variability (CV) of total abundance and Compositional variability (ED-MDS)	Refugia	Compositonal and aggregate stability	+
Temperature-buffering by oyster habitat provides temporal stability for rocky shore communities	McAfee, D; Bishop, MJ and Williams, GA	2022	Oyster beds	Invertebrate communities	structure provided by oysters would increase community stability during a tropical hot season	Field experiment	Oyster presence	LRR for abundance and diversity	Refugia	Disturbance effects	+
Habitat attributes mediate herbivory and influence community development in algal metacommunities	Griffin Srednick, Alyssa Cohen, Olivia Diehl, Kaela Tyler, Stephen E. Swearer	2023	Coral reefs	Herbivorous fish and algal communities	habitat attributes (e.g., structural complexity and spatial heterogeneity) mediate the effects of herbivory on tropical marine macroalgal communities by reducing accessibility and detectability, respectively, leading to variable trajectories among algal species at community (within patch) and metacommunity (i.e., among patch) scales	Field experiment	Herbivory (cage presence)	Algae cover	Refugia	Interaction stability	+
Could spatial heterogeneity in flow disturbance drive temporal stability of native-invasive species co-occurrence in riverscapes?	Boddy, NC and McIntosh, AR	2021	Streams	Fish community	Heterogeneity in flow disturbance can increase co-occurrence stability?	Field surveys	River disturbance index	Fish abundance and variability (CV) of proportional abundance of native fish	Refugia	Interaction stability and compositional stability	+
Interacting effects of landscape and management on plant–solitary bee networks in olive orchards	Carlos Martínez-Núñez, Antonio J. Manzaneda, Sandra Lendínez, Antonio J. Pérez, Luis Ruiz-Valenzuela, Pedro J. Rey	2019	Agricultural landscapes	Bees	Intermediate landscape heterogeneity increases network stability?	Field experiment	Landscape complexity	Network robustness	Resources and refugia	Interaction stability	~
Habitat Heterogeneity and Fish Community Structure: Inferences from North Temperate Lakes						Review					
Spatial heterogeneity reduces temporal variability in stream insect communities	Brown	2003	Streams	stream invertebrate communities	Both an increased number of microhabitat refugia and the effects of statistical averaging via increased species richness should lead to an inverse relationship between spatial heterogeneity and variability in community composition.	Field survey	Simpson, evenness and contagion based on the relative abundance of each substratum type	Temporal variability (Euclidean distance in a Correspondence Analysis)	Refugia and statistical averaging	Compositional stability	+
Heterogeneous landscapes promote population stability	Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. and Thomas, C.D.	2010	terrestrial landscapes	Butterfly populations	What are the effects of landscape heterogeneity on population stability at a range of spatial scales?	Field survey	Shannon on habitat types used by species	CV and SD per population	Resources and refugia	Population stability	+
High assemblage persistence in heterogeneous habitats: an experimental test with stream benthic algae.	SCHNECK, F. and MELO, A.S.	2013	Streams	Benthic algae	Greater habitat heterogeneity (substrate roughness) increases persistence of assemblages	Field experiment	acrylic substrate with different forms	Euclidean distances in CA, and distance to centroid	Refugia	Compositional stability	+
Managing Aquatic Habitat Structure for Resilient Trophic Interactions	Ward, Charlotte A., Tunney, Tyler D., and McCann, Kevin S..	2023	Streams and lakes	Fish predator and fish prey	Does increasing habitat structure stabilise the consumer-resource relationship?	Theoretical	Prey refugia availability	Stability (consumer and prey populations at equilibrium density)	Refugia	Interaction stability	~
Age-structured predator–prey model with habitat complexity: oscillations and control											

Supplementary Materials 12:

All linear mixed-effects models presented the form specified in Fox (2002; based on Laird & Ware 1982). While in this section I will focus on describing model specification, please refer to Fox (2002) for a detailed explanation on the model form and coefficients.

For the models testing the effects of proximity to landscape feature and local heterogeneity on species richness, I used the following model specification:

$$
\begin{aligned}
y_{ij} = {} & \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{3ij} + \beta_4 x_{4ij} + \beta_5 x_{5ij} + \beta_6 x_{6ij} + \beta_7 x_{7ij} + \beta_8 x_{8ij} \\
& + \beta_9 \, x_1 x_{2ij} + \beta_{10} \, x_1 x_{3ij} + \beta_{11} \, x_1 x_{4ij} + \beta_{12} \, x_1 x_{5ij} + \beta_{13} \, x_1 x_{6ij} \\
& + b_{i1} z_{1ij} + \varepsilon_{ij}
\end{aligned}
$$

$$b_{ik} \sim N(0, \psi_k^2), \mathrm{Cov}(b_k, b_{k'}) = \psi_{kk'}$$

$$\varepsilon_{ij} \sim N(0, \sigma^2 \lambda_{ijj}), \mathrm{Cov}(\varepsilon_{ij}, \varepsilon_{ij'}) = \sigma^2 \lambda_{ijj'}$$

where

- y_{ij} is the response variable, for all *j* observations in *I* groups.
- $\beta_1, \dots, \beta_{13}$ are the fixed-effect coefficients, corresponding to heterogeneity (β_1; categorical variable with two levels: heterogeneous, non-heterogeneous), emersion rate (β_2; no units), proximity to canopy (β_3; metres), proximity to rockpool (β_4; metres), proximity to channel (β_5; metres), proximity to limpet barren (β_6; metres), season (β_7; categorical variable) and year (β_8).
- x_{1ij}, x_{2ij} are the fixed-effect regressors for observation j in group i.
- b_{ik} is the random-effect coefficients for group I, assumed to be multivariately normally distributed. Here, tile was included as a random effect to account for the effect of repeated measures (e.g., Schielzeth & Nakagawa 2013).
- z_{1ij} is the random-effect regressors.
- ε_{ij} is the error for observation j in group i. The errors for group I are assumed to be multivariately normally distributed.
- ψ_k are the variances and $\psi_{kk'}$ the covariances among the random effects, assumed to be constant across groups.
- $\sigma^2 \lambda_{ijj'}$ are the covariances between errors in group i.

For the models testing the effects of landscape and local heterogeneity on gamma richness, mean alpha richness and spatial turnover, I used the following model specification:

$$y_{ij} = \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_1 x_{2ij} + \beta_4 x_{4ij} + \beta_5 x_{5ij}$$

$$\varepsilon_{ij} \sim N(0, \sigma^2 \lambda_{ijj}), \mathrm{Cov}(\varepsilon_{ij}, \varepsilon_{ij'}) = \sigma^2 \lambda_{ijj'}$$

where

- y_{ij} is the response variable, for all *j* observations in *I* groups.
- $\beta_1, \dots, \beta_5$ are the fixed-effect coefficients, corresponding to landscape heterogeneity (β_1; no units) and local heterogeneity (β_2; categorical variable with two levels: heterogeneous, non-heterogeneous), season (β_4; categorical variable) and year (β_5).
- x_{1ij}, x_{2ij} are the fixed-effect regressors for observation j in group i.
- ε_{ij} is the error for observation j in group i. The errors for group I are assumed to be multivariately normally distributed.
- $\sigma^2 \lambda_{ijj'}$ are the covariances between errors in group i.

Supplementary Materials 13:

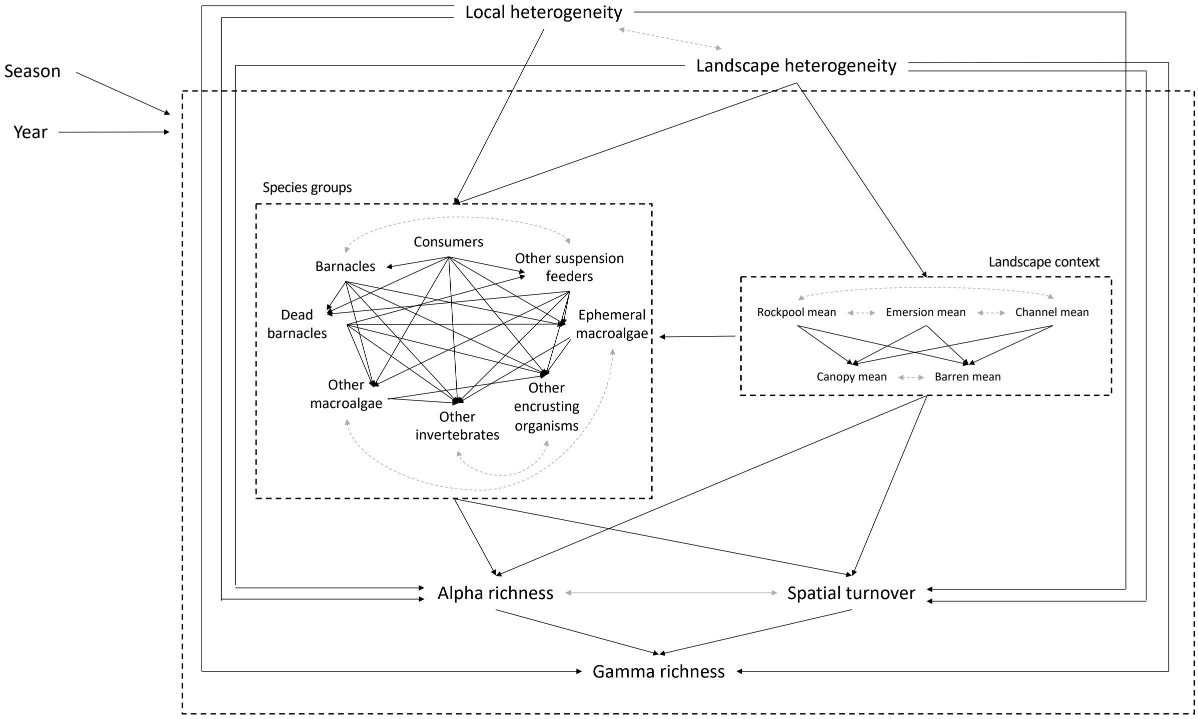


Figure S7. Hypothesised links used in the SEM to test the effects of landscape and local heterogeneity on gamma richness. Metamodel indicating the hypothesised links between local and landscape heterogeneity with species groups, landscape context and species diversity (alpha richness, spatial turnover and gamma richness). Solid black lines indicate the hypothesised links among variables, with the pointed arrow indicating the causal direction in each link. Grey dashed lines indicate links among variables that were not causally related but could be correlated due to exogenous variables not accounted for in the metanalysis. Arrows pointing into dashed boxes indicate that there is a black arrow going from the predictor into each one of the response variables within the dashed box. For example, the dashed arrow between the dashed box for ‘Landscape context’ into the dashed box for ‘Species groups’ indicate that each variable within Landscape context links with an arrow to each variable within the Species groups box. Another example is the arrow between landscape heterogeneity into the landscape context box, indicating that there is an arrow going from landscape heterogeneity into each variable within the landscape context box.

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