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FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

OCEAN AND EARTH SCIENCES

The effect of environmental variation on species functional traits

by

Camilla Cassidy

Thesis for the degree of Doctor of Philosophy

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Abstract

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The traits of organisms – their physiological, behavioural or life-history characteristics – determine their ability to both mediate and respond to their environment. Quantification of traits offers a valuable utility through which to represent the functional roles and contributions of species, allowing incorporation of species performance into projections of environmental or ecological change. However, by the predominant use of single or mean trait values, a majority of current trait-based approaches implicitly assume that conspecific individuals are identical, and that species performance will be unaffected by environmental variation.

Environmental gradients across spatiotemporal scales and increasing impacts from anthropogenic activity mean that global ecosystems are not uniformly exposed to the same suite of biotic and abiotic factors. The trait expression of component organisms is known to shift in response to these factors, potentially altering species functional contributions, and complicating efforts to predict ecosystem functioning and service provision in the face of widespread change. Under conventional approaches, understanding of ecosystems and recommendations to ecosystem management may be in error. Quantification of intraspecific trait variation may contribute to alleviating these issues, yet this approach has so far received little attention.

Here, I explicitly incorporate the magnitude of intraspecific variation into trait-based study, using laboratory-based mesocosm experiments of benthic model systems. My results demonstrate that intraspecific trait variability arises in response to a number of differing biotic and abiotic factors. I show that this variability mechanistically underpins species-level trait responses, forming a fundamental component of biodiversity that determines species interactions and contributions to ecosystem functioning. By developing trait metrics that incorporate this intraspecific variability, I then demonstrate empirically that acknowledging the context-dependency of species' trait expression alters their assumed functional contributions. While species identity effects prevail across varying contexts, intraspecific trait expression underpins and identifies mechanisms of ecosystem change.

Collectively my findings comprise a novel and concise demonstration that quantifying intraspecific traits illuminates the sensitivity of organisms, highlighting the responsiveness of species to ecosystem change. In particular, I draw attention to the extent and importance of dissimilarity between what widely used methodologies would dictate to be identical trait identities. I show that integrating quantification of individual-level trait expression into trait-based ecosystem study adds value, offering mechanistic understanding as to the drivers of community- or ecosystem-level change. In doing so, I highlight the potential benefit these techniques may offer to improve predictive capacities. I conclude that, in order to understand and project the ecosystem consequences of environmental change, it will be necessary to acknowledge the full biodiversity in, and informative capacity offered by, natural systems and the intraspecific diversity they contain.

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Research Thesis: Declaration of Authorship

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Title of thesis: The effect of environmental variation on species functional traits

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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Cassidy, C., Grange, L. J., Garcia, C., Bolam, S. G., & Godbold, J. A. (2020). Species interactions and environmental context affect intraspecific behavioural trait variation and ecosystem function. *Proceedings of the Royal Society B*, *287*(1919), 20192143.

Signature: Date: 14/4/2020

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“The art of life lies in a constant readjustment to our surroundings.”

– Kakuzo Okakura, *The Book Of Tea* (1906)

Chapter 1 General introduction

1.1 Background

It is considered unequivocal that prevailing patterns of human action – from resource exploitation, land use and development – are exerting unprecedented pressures on ecological systems at a global scale (Allan et al., 2015; Pecl et al., 2017). Beyond sociocultural concerns inherent in the loss of pristine landscapes come direct consequences to ecosystem wellbeing, as the component species subject to these shifts fulfil and perform roles essential for the supply of valuable goods and services (de Groot et al., 2002; Diaz et al., 2006; Cardinale et al., 2012). The ability for species to mediate ecosystem processes (e.g. chemical accumulation, community biomass) and functions (e.g. chemical transport, primary and secondary production) is increasingly under threat from environmental changes including biodiversity loss, abiotic shifts, and complex feedback mechanisms between the two (Purcell et al., 2012; Pires et al., 2018). The size and composition of ecosystems are undergoing rapid alteration, and it is now regarded as unavoidable that continued anthropogenic climate change will occur even assuming swift behavioural change (Thébault et al., 2014; Haddad et al., 2015). Conservative estimates predict likely minimum global temperature increases of 0.8 - 1.2 °C above pre-industrial levels within the next thirty years (IPCC, 2018). These cumulative, detrimental impacts on biodiversity have prompted concern for the ecosystem function and associated service provision upon which human wellbeing depends (Millennium Ecosystem Assessment, 2005; Hooper et al., 2012; Cardinale et al., 2012; Mori et al., 2013; Mulder et al., 2015).

However, current research perspectives emphasize that it is the diversity and identity of biological traits expressed within a community rather than the number of species *per se* that fundamentally mediates ecosystem functioning (Balvanera et al., 2013; Gagic et al., 2015; Bannar-Martin et al., 2018). As a result, traits and trait-based approaches are increasingly adopted as predictive tools for ecosystem study and management (Rijnsdorp et al., 2015; Bolam et al., 2017), as they allow incorporation of species performance into projections of ecological (Ulrich et al., 2018; van der Sande et al., 2019) and environmental change (Lavorel & Garnier, 2002; Pakeman et al., 2009; Laughlin, 2014; Gámez-Virués et al., 2015), and offer understanding of the mechanisms underpinning the biotic control over ecosystem functioning or service delivery (Tyler et al., 2012; Adair et al., 2018).

1.2 Traits and their usage

A trait can be most simply defined as a morphological, physiological, reproductive or behavioural characteristic of an organism's phenotype. Functional traits can be split into effect traits, which are components of an organism's phenotype that influence ecosystem level properties, and response traits, that allow organisms to respond to and persist in their environment (Violle et al., 2007; Hébert et al., 2017). As such, unlike traditional approaches grounded in concepts of species richness, a trait-based approach describes species not by their taxonomic identity alone but by the biological characteristics governing fitness. Consequently, traits are able to contain a succinct and direct link between an organism, and its effects to ecosystem processes and functioning (Lavorel & Garnier, 2002; Hevia et al., 2017). The use of a trait-based approach quantifies the functional diversity in a system beyond an assumption of linearity with species richness by providing mechanistic insight into the characteristics which underpin functional potential (Schmidt et al., 2009). Taxonomically disparate species may have similar functional roles due to shared traits, or vice versa (Losos, 2008; Firn et al., 2010; Murray et al., 2013). Alternatively, trait differences among coexisting species can be limited by evolutionary constraints, such that phylogenetically closely related species are more similar than expected by chance due to genetic or physiological limitations restricting certain combinations of traits (Roscher et al., 2018b). Through a trait-based approach insight can be gained as to the functional contributions of specific species, which may be more or less distinct from the rest of their assemblage than would otherwise be assumed (Crisp & Cook, 2012). In this way, trait-based study offers a lens through which to re-contextualise ecological queries, and may contribute new perspective to longstanding debates (Mason & de Bello, 2013; Stuart-Smith et al., 2013; Funk et al., 2017). Indeed, throughout the last two decades, a sizeable effort has been dedicated to recasting longstanding ecological questions (Lamanna et al., 2014; Guittar et al., 2016; Gravel et al., 2016) or examining paleoecological phenomena (Blonder et al., 2014; Fournier et al., 2015) using trait-based metrics.

While the search for general patterns in traits within and between communities can be an end in of itself, traits provide an increasingly attractive tool by which to inform decision-making during ecological management (Garnier & Navas, 2012) and conservation (Frimpong & Angermeier, 2010). The utilisation of trait data within an abundance of potential frameworks or techniques (e.g. Bremner et al., 2006; Suding et al., 2008; Klumpp & Soussana, 2009; Pacifici et al., 2015) represents a promising aid for the widespread creation of problem-driven management strategies. Traits are widely employed to study the relationships of species characteristics, community structure and community assembly processes (Bannar-Martin et al., 2018) to functioning across gradients (Lepš et al., 2011; Schwoertzig et al., 2016) or at landscape scales (de Vries et al., 2012; Piano et al., 2016). In particular, traits related to complementary resource use

(Hooper et al., 2012) are prioritized when seeking to identify the role of functional identity or diversity for ecosystem-level resource use and productivity (Roscher et al., 2018b). These insights are key when seeking to predict and manage how changes in species and diversity will affect ecosystem or functional wellbeing. As a result, legislative bodies are increasingly turning to trait-based approaches as a method by which to understand the responses of individuals and communities to non-optimal conditions, the mechanisms by which these responses affect functions and services of interest, and strategies by which detrimental effects can be mitigated (Violle et al., 2007; Menezes et al., 2010; Bolam et al., 2017). By using trait-based approaches, specific taxa of interest can be identified as mechanistically underpinning ecosystem functions or goods and services of interest (Laughlin et al., 2014).

However, a majority of current trait-based approaches and proposed frameworks implicitly assume that trait expression remains constant between conspecifics, and that individuals and species make the same functional contributions irrespective of their biotic or abiotic context (e.g. Hulshof & Swenson, 2010; Koehler, Center & Cavender-Bares, 2012; Carmona et al., 2015). Thus, functional traits are assumed to be ‘robust’ and have negligible intraspecific variability when compared to interspecific variability (Albert et al., 2010a; Hevia et al., 2017). In reality, it is widely understood that conspecific individuals are not identical, and that organisms vary in their expression of traits (Bolnick et al., 2011; Griffiths et al., 2016; Zuo et al., 2017). Ecologists have long appreciated that age classes (Rudolf & Rasmussen, 2013), ontogenetic stages (Lusk & Warton, 2007; Spasojevic et al., 2014) or sexes (Bolnick et al., 2003) differ in ecologically significant ways. For example, despite being grouped irrespective of sex in a mean trait-based approach, the sexes found within dioecious species frequently exhibit distinct life strategies, with differing energetic and resource demands (e.g. Magurran & Garcia, 2000; Broekhuis et al., 2017; Li et al., 2019). Associated differences in body size can further influence the functional contributions of organisms (Reiss et al., 2009; Norkko et al., 2013; Pigot et al., 2016), by aggregating a number of correlated, functionally-relevant traits (Solan et al., 2004a; Woodward et al., 2005). Morphological differences within and between species can be used to determine both species responses to environmental conditions, and also to predict their ecological relationships and roles (Woodward et al., 2005; Séguin et al., 2014). Across many systems, metabolic theories have provided a mechanistic basis for establishing the scaling relationships between body size and ecosystem properties (Fritschie & Olden, 2016). However, phenotypic variation occurs beyond demographic influences of this kind (Ghalambor et al., 2015; Li et al., 2019).

1.3 Intraspecific trait variability

It is proposed that two primary processes drive context-dependent variation in trait expression: evolutionary adaptation to local conditions creating distinct genetic ecotypes, and phenotypic plasticity in response to prevailing environmental conditions (Mitchell & Bakker, 2014a). Most traits exhibit intermediate heritability, and hence may vary in part due to genetic recombination. Fine genotypic differences may contribute to the dissimilarity in traits between individuals of the same population (Nicotra et al., 2010; Valverde-Barrantes et al., 2013). However, the traits of individuals originating from spatially discrete locations are often those most clearly dissimilar, due to the influence of isolation on the genetic composition of individuals, and their origin in ecosystems with unique ecological and environmental histories (Messier et al., 2010; Bennett et al., 2016). The differing contexts experienced by disparate populations act as selection pressures to influence the permanent genetic identity of the individuals within (Weiher & Keddy, 1995; Calosi et al., 2013), though estimates of heritability vary widely between trait types (Geber & Griffen, 2003; Johnson et al., 2009). Such adaptation to specific conditions arises across broad geological timescales at the cost of local genetic diversity (Chevin et al., 2010).

Nonetheless, even individuals from highly constrained environments are able to vary in their phenotype (Calosi et al., 2013). There is evidence that morphologies, physiologies, and behaviours can be learned or develop flexibly in response to environmental factors, both abiotic and biotic. Trait values shift as species acclimate to new environmental contexts via phenotypic plasticity (Debouk et al., 2015; Wohlgemuth et al., 2017), that being the potential for modification of phenotypes in response to ecological and environmental conditions within genetically-determined constraints (Song et al., 2017; Oostra et al., 2018). This interaction of phenotypic and genetic adaptation is of particular interest to evolutionary biologists, as plasticity can be viewed as adaptive when the phenotype is altered in the same direction as favoured by natural selection in the environment. Non-adaptive phenotypic plasticity, by contrast, potentiates greater opportunity for evolutionary dynamics to act on species as organisms adopt novel and more numerous forms of trait expression (Ghalambor et al., 2015). Phenotypic plasticity underpins trait variation in response to environmental factors such as temperature (Baranov et al., 2016; Landeira-Dabarca et al., 2018), pCO_2 (Nilsson et al., 2012), pH (Ferrari et al., 2011; Calosi et al., 2013; Murray et al., 2013) and hypoxia (Calder-Potts et al., 2018). Indeed, the inherent plasticity of behaviour demonstrates it to be one of the most powerful ways by which organisms are able to adjust to rapid onset environmental change (Wong & Candolin, 2015). For example, some species have adjusted the timing of breeding and migration to match seasonal alterations in temperature (Charmantier & Gienapp, 2014; Merilä & Hendry, 2014), with evidence suggesting these changes have taken place via phenotypic rather than genetic adaptation (Santamaría et al., 2003;

Nagelkerken & Munday, 2016). However, it has been suggested that strong phenotypic plasticity may limit the potential for evolutionary responses to environmental stressors (Oostra et al., 2018). Where phenotypic plasticity is unrelated to genetic variation, for example in seasonally plastic species, populations are more likely to be vulnerable to environmental change (Reed et al., 2010). The acclimation of organisms to new conditions may also in part be maladaptive, either where environmentally induced phenotypes differ from the local optimum (Ghalambor et al., 2015), or where responses entail a physiological cost which energetically or metabolically burdens the organism and reduces fitness (Leroi et al., 1994; Woods & Harrison, 2001).

Acclimation and consequent variation in trait expression is also observed in response to biotic influences, primarily from density effects (Calder-Potts et al., 2018) and direct species interactions with neighbouring organisms (Hawlena et al., 2011; Violle et al., 2012; Valverde-Barrantes et al., 2013; Le Bagousse-Pinguet et al., 2015; Gruntman et al., 2017). Local density-dependent effects drive the expression of reproductive and life history traits, influencing space and resource use among conspecific individuals (Wilkin et al., 2006; Tinker et al., 2008; Bennett et al., 2016). Although it has been shown that high variation in these traits may decrease productivity in the short term, as some individuals within a population will express less productive or fit trait values, long-term productivity for communities may be higher where phenotypic variability is also highest (Norberg et al., 2001). Greater plasticity facilitates niche differentiation and divergent individuals compete less strongly (Gruntman et al., 2017), such that populations containing greater intraspecific variation and so more phenotypically or functionally diverse individuals often coincide with greater coexistence (File et al., 2012; Violle et al., 2012; Valverde-Barrantes et al., 2013) and resource use (Hughes et al., 2008), positively impacting multifunctional ecosystems (Stachowicz et al., 2008; Forrester et al., 2014). Organisms display distinct phenotypes as a method of maximising fitness in the presence of conspecifics by specialising physiologically or morphologically to exploit available niches (Kraft et al., 2015; Bennett et al., 2016). The extent of dissimilarity between traits determines interactions that influence trait expression, mechanisms of species coexistence (Turner et al., 2000; Bolnick et al., 2011; Pérez-Ramos et al., 2019) and net contributions to ecological processes and functioning (Aschehoug et al., 2016; Wohlgemuth et al., 2016). Studies involving the manipulation of intraspecific diversity have repeatedly found consequent changes in population productivity, stability and valuable ecosystem properties, including net productivity (Crutzinger et al., 2006; Fridley & Grime, 2010). However, recent evidence has suggested it is the hierarchical differences in the competitive advantage offered by trait values that more strongly determines competitive outcomes, rather than the extent of differences between those trait values themselves (Kraft et al., 2015; Bennett et al., 2016).

Traits that optimise fitness and performance in a given set of environmental conditions may allow certain individuals in a population to persist in the onset of adverse conditions, where a population of wholly homogenous conspecifics would not thrive (Cardinale et al., 2012; Jung et al., 2013; Laughlin, 2014; Mitchell & Bakker, 2014b). Within-species variability enhances the average species response to environmental variation as well as niche partitioning, and can enable species to establish in a wider portion of an environmental gradient (Valverde-Barrantes et al., 2013; Carlucci et al., 2014). In this way, quantifying trait variation becomes integral to anticipating the wellbeing of an assemblage subject to environmental change. When trait expression changes in response to context, shifts in the resultant assemblage structure can propagate throughout the ecosystem. There is growing evidence that understanding and incorporating intraspecific trait variation is essential to inferring ecological processes from trait patterns (Treseder & Vitousek, 2001; Bennett et al., 2016; Benavides et al., 2019). Intraspecific variation in traits influences the strength of ecological interactions, organism fitness, and mediates fluctuations in trait, species and population abundance (Clark, 2010; Lajoie & Vellend, 2015; Umaña et al., 2015). In particular, intraspecific trait variation underpins trophic relationships and predator-prey dynamics (Wimp et al., 2005; Post et al., 2008; Svanbäck et al., 2015). Further, applied forcing can alter species interactions by mediating the extent of intra- and interspecific differences, causing bottom-up change to established systems (Kerby et al., 2012). For example, Enquist et al. (2015) suggest that trait variance may decrease with strong abiotic forcing, due to filtering of organisms by competitive exclusion. Alternatively, it is possible that the trait variation may increase or otherwise change in response to increased immigration or competitive niche displacement (Weiher & Keddy, 1995). These dynamics, among others, result in quantifiable impacts to vital ecosystem functioning and processes (Bennett et al., 2016), as environmentally induced changes in intraspecific diversity have been shown to scale to affect functional diversity at a community level (Mao et al., 2017).

Across the abundant potential sources of trait variation, it is evident that some traits or trait types may respond differently to differing stimuli (Valverde-Barrantes et al., 2013), or vary to a greater extent than others (Jung et al., 2013; Griffiths et al., 2016). For example, Albert et al. (2010b) illustrated that differences between populations in one trait were nearly equal to differences between individuals within those populations, whereas for a different trait more variation was observed between individuals within a single population than was present between populations. Given the complex context-dependency of these responses, general patterns of potential drivers for this phenomenon are poorly quantified. A suggestion might be that greater plasticity can be found in traits which are not required to function within narrow windows to ensure the life of the organism and which are less strongly conserved, such as behavioural traits (Fisher et al., 2015).

The expression of different traits often also co-varies within individuals (Reich, 2014; Roscher et al., 2018a). The need to coordinate different functions to maximize performance and to respond to varying environmental conditions may constrain independent plastic responses of single traits, resulting in correlations among functionally related traits or processes (Maire et al., 2013). In summary, intraspecific variation stems from the dissimilarities between traits in individual organisms; but the potential for variation itself differs, as communities are exposed to differing conditions and the changes induced in individuals propagate through higher organisational levels. Ultimately, the shape and outcome of the trait distribution in an assemblage reflects the product of two dynamics – the introduction of traits, whether from new individuals or merely new trait expressions, and resultant variation in the functional contributions of the assemblage (Enquist et al., 2015).

Due to the high potential for differing trait identities, logistical constraints have largely dictated that intraspecific variation be overlooked during trait-based study (Reiss et al., 2009). Under most circumstances, it is likely not feasible to measure all individuals in a population (Carmona et al., 2015; Griffiths et al., 2016). Further, the inclusion of trait variation arguably complicates the premise of potential research questions; when intraspecific variation is recognised, individuals or taxa cannot be readily compared to one another as the traits forming the basis of these comparisons exhibit broad ranges of values (Chase & Knight et al., 2013). Consequently, many trait-based studies of species interactions implicitly assume that all conspecific individuals are effectively interchangeable (Bolnick et al., 2011) by the use of single or mean trait values. These are obtained either by measuring solely community-level average values during study, or by sourcing trait values from literature or databases (Kleyer et al., 2008; Kattge et al., 2011; Queriós et al., 2013; Degen et al., 2018; Vandepitte et al., 2018).

Despite a fast-growing literature on the ecology of trait variation, many of the parameters surrounding intraspecific traits remain largely unknown. There remains little consensus as to the necessity of, or methods for, explicitly incorporating intraspecific trait variation into trait-based study. There is some effort to adopt the use of ‘fuzzy coding’ techniques wherein species can be assigned multiple trait values at one time, denoting either uncertainty in the traits of species, the capacity for individuals to moderate expression, or for the presence of differing forms of expression within or between communities (Chevene et al., 1994; Degen et al., 2018). As may be apparent, the current best-practice for use of these techniques has not been well established, and results are difficult to compare across literature (Castella & Speight, 1996; Bremner et al., 2006; Tillin et al., 2006; Schmera et al., 2015; Howarth et al., 2018). Typically, those trait-based approaches that incorporate trait variation do so with a predominant focus on comparing the relative significance of intraspecific and interspecific variation (Garnier et al., 2001; Albert et al., 2010a; Siefert et al., 2015; Griffiths et al., 2016; Volf et al., 2016). A modest number of theoretical studies have investigated how intraspecific variation may affect population and community dynamics (Bolnick et al., 2011; Carlucci et al., 2014). The magnitude and reasons for this variation, and its implications for understanding the community and functioning of the ecosystem as a whole, are by contrast largely overlooked. To date, few studies have experimentally examined the effect of stressors on trait expression at the level of the individual (Wilkin et al., 2006; Jung et al., 2013; Charette & Derry, 2016; Guscelli et al., 2019). Further, little to no data exists which quantifies these effects under compositions that mirror the occurrence of these factors in natural communities (Heilpern et al., 2018). That is to say, little work exists featuring the inclusion of multiple biotic and abiotic factors (Mao et al., 2017; Vye et al., 2018), in multi-species interactions, or which considers intraspecific trait expression alongside the functional, ecosystem-level consequences it underpins (Reich et al., 2014; Guscelli et al., 2019). There thus exists substantial motivation to place intraspecific trait variation into a holistic, ecological context, wherein we may better understand its drivers and potential utility. Comparisons of biodiversity responses to ecological drivers are strongly confounded by the diversity and composition of the species pool (Chase & Knight, 2013), such that studies which employ more coarsely grained sampling methods are at risk of drawing erroneous conclusions as to the effects on ecosystem types or biogeographic regions (Cao et al., 2007). By comparison, where traits are in fact measured to the level of the individual, significant additional understanding and statistical explanatory power is gained within an ecosystem study and management context (Cerwenka et al., 2017). Existing diversity metrics are overly simplistic in that they fail to account for variability in the functional role of individuals within and between communities, and so may be inadequate for the widespread use of trait-based approaches to the study and projection of ecosystem functioning and service delivery (Youngsteadt et al., 2015; Spasojevic et al., 2016). Given that the practical constraints on the inclusion of intraspecific trait expression into study remain, it is thus necessary to demonstrate that intraspecific trait expression can be reconciled with existing methodologies. A priority, then, is to demonstrate that the potential variation of trait expression between ecological and environmental contexts aids in elucidating greater ecological and functional understanding.

The inclusion of intraspecific trait expression offers the opportunity to distinguish the underlying level of dissimilarity in supposedly identical or interchangeable systems; to understand how community-level net effects and ecosystem functioning are mechanistically underpinned by the trait expression and activities of component individuals (Crain et al., 2008; Möllmann et al., 2008; Evangelista et al., 2017); and to use the natural responses of individuals to their surroundings as potential predictive pathways (Funk et al., 2017; Cerwenka et al., 2017) or early warning tools

(Murray et al., 2013; Clements & Ozgul, 2016). Fundamentally, to derive the full potential benefits supposedly offered by trait-based study, especially in the context of changing ecosystems, we must consider explicitly incorporating intraspecific trait variability. By doing so, we afford awareness of the true diversity displayed by systems and seek to gain additional insight as to the sensitivities of species, and the vulnerabilities of associated ecosystem functions and services.

1.4 Thesis aims and objectives

My thesis seeks to address the lack of consideration given to intraspecific variation during trait-based studies, and seeks to demonstrate the importance and benefit of, and potential precedent for, quantifying this variation (Fig. 1.1). I aim to address the disconnect between the recognition that conspecific individuals are non-identical, and the lack of quantification of this aspect of diversity in trait-based approaches to ecosystem study. As such, my primary research aims are;

1) To illustrate the presence and persistence of intraspecific trait expression between measured contexts, conditions or treatments.
2) To demonstrate the poor suitability of a single or average trait value to adequately represent species trait expressions.
3) To illustrate the benefits, and indeed the necessity, of obtaining trait observations to the intraspecific level for the purposes of understanding biotic mediation of ecosystem functioning.

Using marine soft sediment invertebrate communities, I examine the intraspecific trait responses to a number of differing ecological and environmental factors. Key foci of my thesis within this scope are;

1) Intraspecific variation in trait expression arises in response to widespread ecological and environmental factors, however these responses are inferred to be of negligible importance to functioning, and are rarely explored. By quantifying intraspecific trait expression in two species from the same genus, originating from two populations with differing environmental histories and maintained in monoculture or in mixture, I test

Hypothesis (H1): Intraspecific variation is prevalent between individuals and communities of differing contexts, and contribute to differences in ecosystem function (Chapter 2).

2) Ecosystem responses to environmental stimuli are typically measured at the community or ecosystem scale. It is possible that the responses of individuals underpin the mechanisms of these broader scale changes, however the potential for these approaches has not been adequately demonstrated. I quantify intraspecific trait expression in communities of two species from the same genus exposed to one of two climate treatments, testing Hypothesis (H2): Quantifying trait expression of individuals and communities exposed to external abiotic factors identifies traits sensitive to environmental change, and context-dependency in the relationship of species and functioning (Chapter 3).

3) Changing species richness is understood to alter assemblage functional diversity, however trait-based approaches that assume that conspecifics are functionally identical do not acknowledge the effects of these changes on trait expression and so on the biodiversity-functioning relationship. Here, I will examine intraspecific variation in response to mixtures of variable species richness and species composition in a benthic community, testing Hypothesis (H3): Intraspecific variation in response to differing community biodiversity alters the functional contributions of individual species and their interactions (Chapter 4).

4) It is poorly understood in what contexts, if any, that the inclusion of intraspecific trait expression into trait-based study may benefit understanding of species traits and functional contributions. By parameterising a metric through which to explore the contributions of intraspecific trait variation to functional diversity and functional potential, I test Hypothesis (H4): Incorporating individual-level measurements into trait-based approaches alters understanding of trait expression and improves understanding of the trait-functioning relationship (Chapter 5).

Addressing the above hypotheses collectively improves understanding of the responses of individuals and communities of diverse species to a number of changing environmental conditions, increases our capacity for accurately anticipating or predicting the ecosystem consequences of natural and anthropogenic forcing, and provides quantifiable insights into the robustness of trait-based approaches in the face of this change.

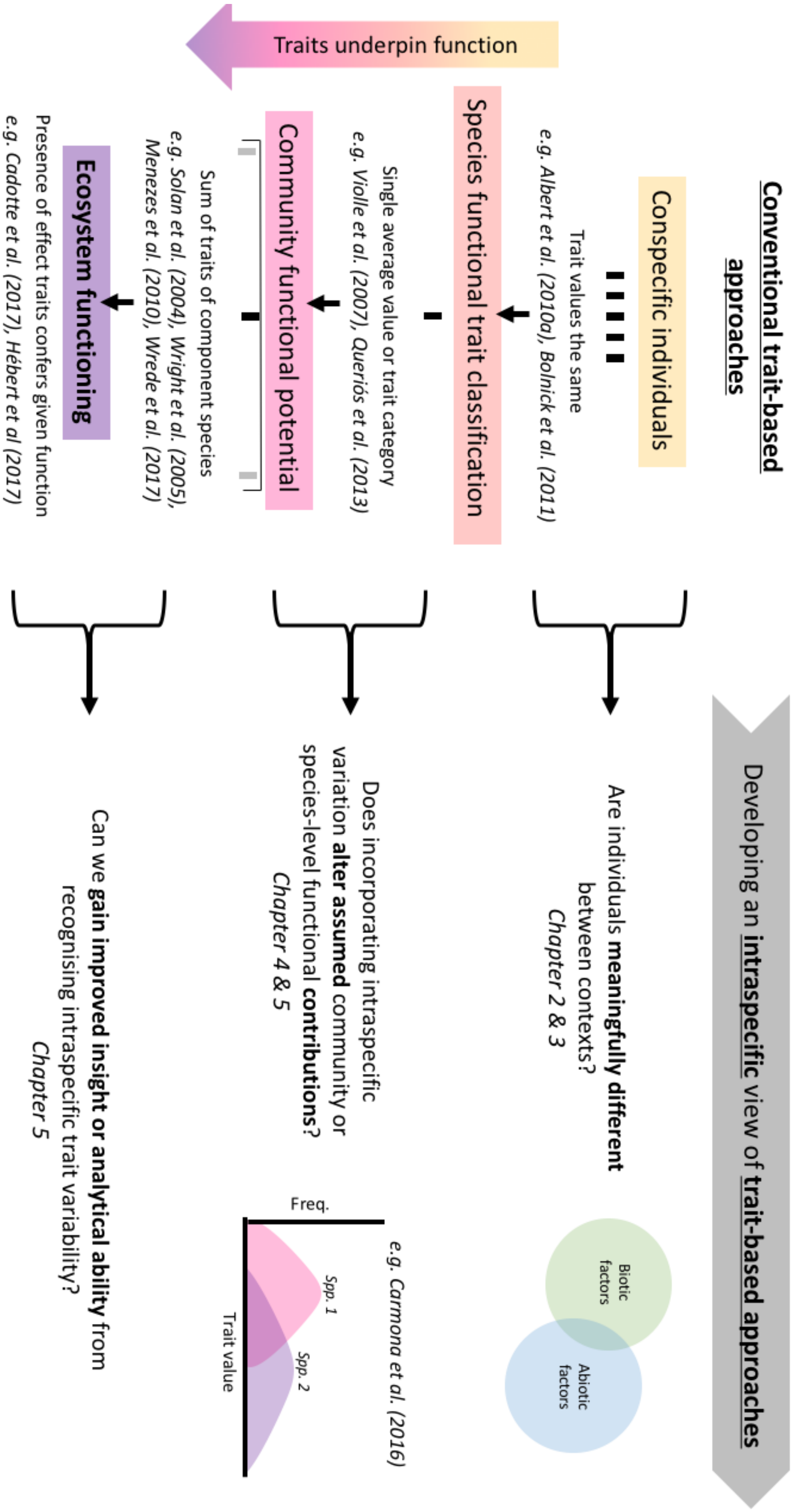
Conventional trait-based approaches
Conspecific individuals
Trait values the same
e.g. Albert et al. (2010a), Bolnick et al. (2011)
Species functional trait classification
Single average value or trait category
e.g. Violle et al. (2007), Queriós et al. (2013)
Community functional potential
Sum of traits of component species
e.g. Solan et al. (2004), Wright et al. (2005), Menezes et al. (2010), Wrede et al. (2017)
Ecosystem functioning
Presence of effect traits confers given function
e.g. Cadotte et al. (2017), Hébert et al (2017)
Traits underpin function
Developing an intraspecific view of trait-based approaches
Are individuals meaningfully different between contexts?
Chapter 2 & 3
Biotic factors
Abiotic factors
Does incorporating intraspecific variation alter assumed community or species-level functional contributions?
Chapter 4 & 5
e.g. Carmona et al. (2016)
Freq.
Spp. 1
Spp. 2
Trait value
Can we gain improved insight or analytical ability from recognising intraspecific trait variability?
Chapter 5

Fig. 1.1 Conceptual schematic representing current knowledge underpinning conventional single-value trait-based approaches, and the research questions at the core of this thesis necessary for development of intraspecific trait-based approaches. In the current and conventional view, seemingly identical individuals (Albert et al., 201a; Bolnick et al., 2011) of a species fall within trait categorisations (Violle et al., 2007; Queirós et al., 2013) that sum at the community level (Solan et al., 2004a; Wright et al., 2005; Menezes et al., 2010; Wrede et al., 2017) to underpin net functional potential (Cadotte et al., 2017; Hébert et al., 2017). To move beyond this framework, ecologists must look quantitatively rather than qualitiatively to identify if intraspecific variation is substantial or meaningful between contexts (Chapters 2 & 3, H1 & H2); if this variation alters assumed contributions of communities, species, or biodiversity to functional processes or targets (Chapters 4 & 5, H3 & H4); and as such whether incorporating these data will provide adequate or necessary benefit to the understanding ecosystems (Chapter 5, H4).

Chapter 2 Species interactions and environmental context affect intraspecific behavioural trait variation and ecosystem function

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2.1 Abstract

Functional trait-based approaches are increasingly adopted to understand and project ecological responses to environmental change, however most assume trait expression is constant between conspecifics irrespective of context. Using two species of benthic invertebrate (brittlestars *Amphiura filiformis* and *A.* c*hiajei*) I demonstrate that trait expression at individual and community levels differs with biotic and abiotic context. I use ANOVA and PERMANOVA to test the effect of species identity, density and local environmental history on individual (righting and burrowing) and community (particle reworking and burrow ventilation) trait expression, as well as associated effects on ecosystem functioning (sediment nutrient release). Trait expression differs with context, with repercussions for the faunal mediation of ecosystem processes; I find increased rates of righting and burial behaviour and greater particle reworking with increasing density that are reflected in nutrient generation. However, the magnitude of effects differed within and between species, arising from site-specific environmental and morphological differences. My results indicate that traits and processes influencing change in ecosystem functioning are products of both prevailing and historic conditions that cannot be constrained within typologies. Trait-based study must incorporate context-dependent variation, including intraspecific differences from individual to ecosystem scales, to avoid jeopardising projections of ecosystem functioning and service delivery.

2.2 Introduction

Decades of empirical study, motivated by unprecedented species loss and environmental change, have provided unequivocal evidence that altering biodiversity affects ecosystem functioning (e.g. primary production, nutrient cycling, sediment stability) and, ultimately, the provision of ecosystem services (Adair et al., 2018). Current research emphasizes that rather than the number of species, ecosystem functioning is instead mediated by the functional traits (e.g. behavioural, morphological or life history characteristics) expressed within a community (Gagic et al., 2015; Read et al., 2017). As a result, functional trait-based approaches are increasingly adopted as predictive tools by ecosystem managers (Rijnsdorp et al., 2015; Bolam et al., 2017) as they incorporate species performance into projections of environmental change. In doing so, they confer understanding of the biological mechanisms underpinning faunal mediation of ecosystem functioning (Laughlin, 2014; Funk et al., 2017; Thomsen et al., 2019).

Conventional trait-based approaches and proposed frameworks implicitly assume that the expression of traits remains constant between conspecifics, irrespective of biotic or environmental context (Albert et al., 2010a; Hevia et al., 2017). Studies may neglect intraspecific variability out of economic or logistical necessity, as measuring individual trait values *in situ* is not always possible. For management purposes, therefore, authors may rely on trait values from literature or databases to characterise the functional importance of species (Gogina et al., 2016; Bolam et al., 2017; Solan et al., 2019). In these approaches the quantification of trait values and allocation of species to functional groups is frequently based on single mean trait values per species, and does not account for the scope and importance of intraspecific trait variability (Finerty et al., 2016; Des Roches et al., 2018). If the type or value of traits expressed are understood to determine a species' role in the ecosystem (Wohlgemuth et al., 2017), any intraspecific variation potentially alters its contributions to ecosystem functioning and renders conventional typologies unsuitable.

Individual organisms are non-identical, with differing forms of trait expression distributed unevenly throughout communities (Carmona et al., 2016; Roscher et al., 2018a). It has long been appreciated that age classes, ontogenetic stages or sexes make differing contributions to ecosystem functioning. For example, the sex of individuals within a population is typically not quantified, despite knowledge that differing sexes can exhibit strongly distinct life strategies and energetic or resource demands (Rudolf & Rasmussen, 2013). Such physiological differences, including associated morphological differences in the mean and variance of body size, determine the scale of an individual's contribution to ecosystem functioning (Norkko et al., 2013; Fritschie & Olden, 2016). However, intraspecific variation occurs beyond demographic influences (Mitchell &

Bakker, 2014a). Some site-specific differences originate as a genetic component, stemming from long-term adaptation to historic conditions that creates distinct genetic ecotypes through multi-generational selection processes (Calosi et al., 2013; Robins et al., 2013). In addition, variation also arises over shorter temporal scales in the form of acclimation responses to prevailing biotic and abiotic conditions (Wohlgemuth et al., 2017).

Mechanisms of phenotypic plasticity result in widespread and often substantial trait variability over time and space (Roscher et al., 2018a). Transient trait expression in individuals alters their activities and potential contributions to ecosystem processes in response to habitat features (Törnroos et al. 2015; Read et al., 2017), climatic drivers (Baranov et al., 2016; Nagelkerken & Munday, 2016; Landeira-Dabarca et al., 2018; Peterson et al., 2019), and resource availability (Hawlena et al., 2011; Murray et al., 2017). Incorporating the context-dependency of trait expression is vital for accuracy in the increasingly urgent quantification of ecosystem functioning under changing abiotic conditions (Landeira-Dabarca et al., 2018). Trait expression, furthermore, also shifts dramatically in response to biotic influences, primarily from neighbouring individuals and/or species (Hawlena et al., 2011; Wohlgemuth et al., 2017; Calder-Potts et al., 2018; Thomsen et al., 2019). Competitive or complementary interactions determine species coexistence and exclusion (Turcotte & Levine, 2016; Pérez-Ramos et al., 2019), and so potentially facilitate enhanced productivity, ecosystem functioning and service delivery (Finerty et al., 2016). Within species, local density-dependent effects can influence the expression of movement and life history traits, influencing habitat use as conspecifics specialise behaviourally or physiologically to exploit available space and resources (Kraft et al., 2015) or escape predation (Rosenberg & Selander, 2000). It is increasingly recognised that intraspecific differences in trait expression are not only widespread but also form an important component of biodiversity (Des Roches et al., 2018). The representation of species using single or average trait values may fail to quantify responses to numerous aspects of ecological and environmental context (Read et al., 2017), jeopardising the reliability of approaches to ecosystem study and management (Reich et al., 2014; Bennett et al., 2016).

In this study, I investigate the importance of incorporating intraspecific and individual-level trait variation into trait-based study, illustrating that faunally-mediated community processes and ecosystem functioning with which these traits are associated are subject to context-dependent change. To achieve these aims, I interrogate the effect of biotic context and differing abiotic history on communities of two co-occurring species of infaunal marine invertebrate (brittlestars *Amphiura filiformis* and *A. chiajei*). I hypothesised that i) biotic and site-specific environmental context influence the expression of individual traits and community-level behaviour, and that ii) this variability would aid in understanding concurrent differences in biogeochemical proxies (nutrient concentration) for ecosystem function. To this effect, my results show that, contrary to the assumptions of prevailing trait-based modelling approaches, the trait expression and subsequent functional contributions of conspecific individuals cannot be assumed to be constant.

2.3 Materials and methods

2.3.1 Species collection and experimental design

Two species of ophiuroid brittlestars (*A. filiformis* and *A. chiajei*) were collected from two proximate sea lochs; Kilmaronag Shoal, Loch Etive (56°27'34.20"N, 5°20'29.28"W) and the Lynn of Lorne, Loch Linnhe (56°29'49.6"N, 5°29'56.2"W), Scotland, UK (Appendix A, Fig. A1). Taxa with pelagic larvae, such as these species, have substantial distribution potential and are exchanged across landscape-scale distances and hydrographical barriers only in these early ontogenetic stages (Robins et al., 2013; Ershova et al., 2019). Given the proximate distance (~12 km) and presence of substantial changes in seabed terrain and flow conditions between sites (Gage, 1972; Friedrich et al., 2014), I infer that individuals from each site are likely not genetically distinct but will have been exposed throughout their post-larval lifetimes to differing ecological and environmental conditions (Alp et al., 2012). Loch Etive is subject to greater stratification and more frequent episodic flushing relative to Loch Linnhe that affects nutrient and organic material dynamics (Friedrich et al., 2014). Sediment at Loch Etive is finer and contains a significantly higher total organic carbon (TOC) content in comparison to the Loch Linnhe site (ANOVA: $F_{2,10} = 30.78$, $P < 0.001$, Appendix A, Table A1 and Fig. A2 & A3).

Individuals were returned to the University of Southampton in isolated aerated water baths and acclimated to aquarium conditions (~ 12.6 ° C, 12 h light: 12 h dark cycle, continually aerated) for a 30-day period. Estuarine mud from Hamble-le-Rice, Hampshire (50°52'23.1"N 1°18'49.3"W), was sieved (500 µm mesh) in a seawater bath to retain the fine fraction and remove macrofauna and allowed to settle for 48 h before being homogenised and distributed to Perspex aquaria (internal dimensions, LWH 12 x 12 x 35 cm; settled depth ~ 10 cm overlaid with ~ 20 cm depth seawater, salinity 33). After 24 h and prior to the addition of the organisms, the seawater was replaced to remove excess dissolved nutrients associated with mesocosm assembly. Individuals were fed once a week with a flake-type aquarium food, after a partial water change (~50%) to avoid excessive accumulation of nutrients and metabolites.

My experiment required 102 aquaria arranged in a full factorial design (Appendix A, Table A2 & A3). Replicate faunal assemblages (hereafter referred to as ‘communities’) from each sampling site (2 levels: Loch Etive and Loch Linnhe, which represent historic exposures to discrete abiotic conditions hereafter referred to as ‘populations’) contained *A. filiformis* and *A. chiajei* in one of three species treatments (3 levels: monoculture of *A. filiformis*, monoculture of *A. chiajei*, or both species in mixture), across three naturally observed densities (3 levels: low, medium and high, between 250 - 1000 ind. m^{-2}, Appendix A, Table A3). These species were selected for use given their close taxonomic relation, their shared tolerance for variable biotic and abiotic contexts (Calder-Potts et al., 2018), and their widespread co-occurrence throughout European shelf waters (Gage, 1972) where they exert a dominant influence on local biochemical cycling (Murray et al., 2013). The three density levels manipulated span the range reported from across their European distribution *(*O’Connor et al., 1983; Duineveld et al., 1987; Munday & Keegan, 1992) and therefore are not location specific. For this study, I adjusted the densities of both species to reflect the approximate 3 *A. filiformis* : *2 A. chiajei* ratio observed at the sample sites only as to avoid introducing novel aspects of biotic context. Each combination of factors was replicated six times, with the exception of two treatments (n = 4 and n = 5) (total n = 102, Appendix A, Table A3).

2.3.2 Measures of individual trait expression

Individual-level behavioural trait expression was represented through movement and burial behaviours measured at the sediment surface following incubation and the quantification of community- and ecosystem-properties. Individuals were inverted and placed on the sediment surface in a temperature-controlled tray of sediment (3 cm depth overlaid with 5 cm depth seawater) under the same density and species treatment (monoculture or mixed) conditions in which they had been previously maintained. All individuals from each mesocosm were recorded simultaneously. A bench top video camera (uEYE USB camera, 1.3 MP, 25 FPS; IDS Imaging Development Systems, Obersulm, Germany) was used to record two righting and burial behaviours: i) the time taken for each individual to begin movement activity, a response trait, and ii) the time taken for each individual to right itself and bury fully into the sediment, an effect trait. Behaviour at the sediment surface reflects the strength and nature of organismal responses to their biological and physical surroundings (Rosenberg & Selander, 2000), and burial rate is indicative of functionally-relevant movement behaviours at the individual level (Nagelkerken & Munday, 2016).

As morphological traits can significantly influence an individual’s functional contribution (Norkko et al., 2013), I determined arm length (cm) and disc diameter (cm) using image analysis (ImageJ, version 1.46r; Schneider et al., 2012; Appendix A, Fig. A4), and biomass (g), for each individual.

Given the strong co-linearity between the metrics (Appendix A, Fig. A5), the mean arm length (mean length of all five arms for each individual, producing an individual-level morphological trait) was used to represent morphological trait expression due to its greater relevance in brittlestar motility and feeding behaviours (Rosenberg & Selander, 2000; Astley et al., 2012).

2.3.3 Measures of community behaviour

Burrow ventilation behaviour (bioirrigation) was estimated from the relative change in water column concentrations of the inert tracer sodium bromide (NaBr, dissolved in 20 mL = ~ 5 mM aquaria^{-1}), over an 8 h period (NaBr, dissolved in 20 mL = ~ 5 mM aquaria-1; Δ[Br−], mg L^{-1}; negative values indicate increased activity; Forster et al., 1999). Filtered water samples (5 mL, 0.45 µm cellulose acetate membrane filter) were taken on Day 29 of the experimental period and stored at 6 °C prior to colorimetric analysis (FIAstar 5000 flow injection analyser, FOSS Tecator).

Faunally mediated particle reworking (bioturbation) was estimated non-invasively using sediment profile imaging (f-SPI) (Solan et al., 2004b). To visualize particle movement 24 g dry weight aquaria^{-1} of dyed sediment that fluoresces in UV light (green colour; < 125 µm; Brianclegg Ltd., UK) was introduced to the sediment surface on Day 23 and imaged 8 days later (Day 31). This length of time is sufficient to allow visualisation of particle movement whilst avoiding vertical homogenization of the tracers. Images of all four sides of each mesocosm were taken within a UV illuminated imaging box. Following Solan et al. (2004b), images were saved in RGB colour mode with JPEG compression and analysed using a custom-made semi-automated macro that runs within ImageJ (version 1.46r), a Java-based public domain program (Schneider et al., 2012). From these data, the maximum depth of particle reworking ($^{f\text{-}SPI}L_{max}$) was calculated and surficial activity was estimated by quantifying surface boundary roughness (SBR), which is the maximum vertical deviation of the sediment-water interface (upper – lower limit; Hale et al., 2014).

2.3.4 Measures of ecosystem functioning

Ecosystem functioning was represented through the proxy of sediment nutrient release, which is mediated by the sediment movement behaviours of benthic fauna (Kristensen et al., 2014; Wohlgemuth et al., 2017). Nutrient concentrations (ammonium, NH_4- N; nitrate, NO_3-N; nitrite, NO_2-N; and phosphate, PO_4-P; µmol L^{1}) were determined from filtered water samples (20 mL, Fisherbrand, nylon 0.45 µm, ⌀ 25 mm) taken on the final day of the experiment (Day 30). Samples were frozen (−18 °C) and analysed using a segmented flow autoanalyser (QuAAtro39 AutoAnalyzer).

2.3.5 Statistical analysis

Permutational multivariate analysis of variance (PERMANOVA) and ANOVA were used to determine the independent and interacting effects of population (2 levels: Loch Etive, Loch Linnhe), density (3 levels: low, medium, high) and species identity (for intraspecific trait expression, 4 levels: *A. filiformis* in monoculture, *A. filiformis* in mixture, *A. chiajei* in monoculture, *A. chiajei* in mixture) or species mixture treatment (for community and ecosystem measures, 3 levels: *A. filiformis* monoculture, *A. chiajei* in monoculture, *A. filiformis - A. chiajei* mixed treatment) on individual and community behavioural trait expression, and associated ecosystem function. All statistical analyses were performed using the *R* statistical and programming environment (R Core Team, 2017) and the vegan package (Oksanen et al., 2017).

2.3.5.1 Individual trait expression

Multivariate analyses were used to represent overall differences in the behavioural ‘personalities’ of individuals between species identities and contexts (Moran et al., 2017), integrating response (time to begin movement) and effect (time to complete burial) traits. PERMANOVA (iterations = 999) was used, as it is robust to non-normality and differing correlation structures and so is particularly suited for the detection of differences in intraspecific trait expression (Mitchell & Bakker, 2014b). Patterns of intraspecific trait expression differ between the behavioural traits, and between context treatments (Appendix A, Fig. A6). Permutational analysis of multivariate dispersion (PERMDISP) was used to test for homogeneity of variance between populations ($F_{1,190} = 0.57$, $P = 0.45$), species identities ($F_{1,188} = 1.20$, $P = 0.31$) and densities ($F_{1,189} = 1.22$, $P = 0.30$). These results support that any significant differences in PERMANOVA between treatments are due to changes in the values of trait expression, not shifts in the overall extent of variation itself. Nevertheless, to negate any dispersion effects caused by unequal numbers of individuals between groups, I standardised abundance between species treatments and density levels (n = 192) (Appendix A, Table A3).

PERMANOVA models were developed to test the independent and interacting effects of; i) community-level effects (population, species identity, density), and ii) individual-level differences in morphological trait expression (mean arm length) between communities (population, species identity), on multivariate intraspecific behavioural trait expression. Data exploration showed there were differences in morphological trait expression between populations (ANOVA: $F_{1,188} = 4.03$, $P = 0.046$) and species (ANOVA: $F_{1,188} = 14.99$, $P < 0.001$) which may contribute to observed site-specific and interspecific effects.

To quantify the extent of intraspecific trait variation, the coefficient of variation (CV, the ratio of standard deviation to the mean) was determined for the expression of each individual-level trait (time to begin movement, time to complete burial, and mean arm length).

2.3.5.2 Community behaviour and ecosystem functioning

4-way ANOVA was used to test the independent and interactive effects of context (population, species treatment, density) and intraspecific variation in morphological trait expression (CV of mean arm length) on each community-level behaviour ($\Delta[Br^-]$, $^{f\text{-}SPI}L_{max}$, SBR), and a 3-way ANOVA was used to test the independent and interactive effects of context (population, species treatment, density) on nutrient concentration ($[NH_4\text{-}N]$, $[NO_3\text{-}N]$, $[NO_2\text{-}N]$, $[PO_4\text{-}P]$). Model assumptions were assessed visually for normality (Q-Q plot), heterogeneity of variance (plotted residuals vs. fitted values), and the presence of outliers or overly influential data points (Cook's Distance) and the minimal adequate effects structure was determined using backward selection informed by Akaike Information Criteria (AIC) (Zuur et al., 2009).

2.4 Results

2.4.1 Individual trait expression

With respect to all aspects of context (population, species identity, density), PERMANOVA revealed that behavioural trait expression was dependent on the independent effects of species identity ($F_{3,168} = 6.08$ $P < 0.001$), density ($F_{2,168} = 3.82$, $P < 0.001$), and population ($F_{1,168} = 4.24$, $P = 0.025$) (Fig. 2.1a – 2.1f).

When considered alongside only those aspects of context which define the identity (population, species identity) and morphological trait expression (mean arm length) of individuals, behavioural trait expression was dependent on the interactive effects of mean arm length x population of origin (PERMANOVA: $F_{1,176} = 3.71$, $P = 0.036$) (Fig. 2.1e – 2.1h), in addition to the independent effect of species identity (PERMANOVA: $F_{3,176} = 5.72$, $P < 0.001$) (Fig. 2.1a – 2.1b).

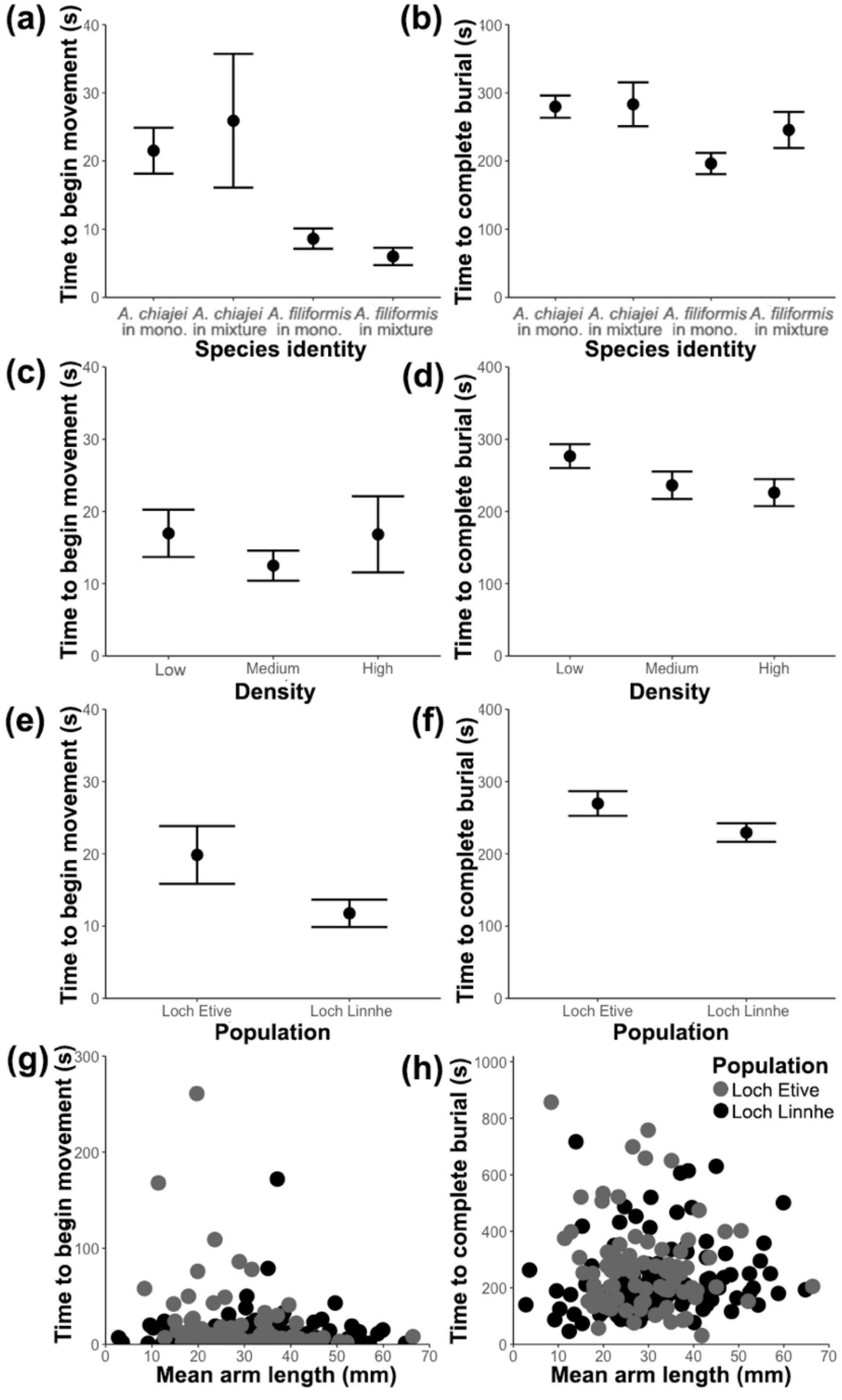


Fig. 2.1: The effect of biotic and abiotic context on time elapsed (mean ± SE) (s) for *Amphiura chiajei* and *Amphiura filiformis* to (**a, c, e, g**) begin movement and (**b, d, f, h**) complete burial into the sediment, where (**a**, **b**) show the independent effects of species identity, (**c**, **d**) show the independent effect of density, (**e**, **f**) show the independent effect of population of origin, and (**g**, **h**) show the interactive effect of population x mean arm length (mm).

Though analysed together in a multivariate manner, both movement behaviours (time to begin activity, and time to complete burial) were visualised independently to highlight differences in expression between each trait. Overall, *A. chiajei* took significantly longer before beginning or completing burial than *A. filiformis*, however intraspecific differences are present in both species and between individuals maintained in monoculture or in a mixed community. The extent of these context-dependent differences varied depending on the trait, and patterns between treatment conditions were consistently less prominent for the time taken to begin movement. For both *A. chiajei* and *A. filiformis,* the time taken to fully complete burial was increased in mixed species treatments in comparison to monoculture, with a similar if weaker pattern suggested for *A. chiajei* and the time taken to begin movement (Fig. 2.1a – 2.1b). For both species, the time taken to complete burial decreased with density (Fig. 2.1c – 2.1d). Individuals from Loch Linnhe had significantly (ANOVA: $F_{1,188} = 4.033$, $P = 0.046$) larger mean arm lengths (*A. filiformis* mean ± SE (n = 55) 27.88 ± 11.17, *A. chiajei* mean ± SE (n = 51) 36.54 ± 12.85, Appendix A, Fig. A7) than those originating from Loch Etive (*A. filiformis* mean ± SE (n = 40) 27.06 ± 7.57, *A. chiajei* mean ± SE (n = 46) 30.30 ± 11.68), and completed movement behaviours more rapidly (Fig. 2.1e – 2.1h). The coefficient of variation of both behavioural traits (time to begin activity and time to complete burial) within communities did not differ significantly between variables or their interactions (ANOVA: $P > 0.05$ for all, Appendix A, Table A4), though trends suggest comparatively greater extents of variation may occur for both behavioural traits for individuals maintained under elevated density or in a mixed species treatment, or those originating from Loch Etive (Appendix A, Fig. A8).

2.4.2 Community behaviour

Community-level bioturbation and bioirrigation behaviours were differentially affected by abiotic and biotic context (species mixture treatment, density, population) and morphological trait variation. The maximum depth of particle redistribution, ${}^{f\text{-}SPI}L_{max}$, was significantly affected by the independent effects of density (ANOVA: $F_{2,60} = 5.85$, $P < 0.001$) and population (ANOVA: $F_{1,60} = 8.68$, $P < 0.001$). ${}^{f\text{-}SPI}L_{max}$ increased with density (Fig. 2.2a), while remaining shallower in mesocosms with individuals from Loch Etive in comparison to Loch Linnhe (coefficient ± SE = 0.40 ± 0.51, t = 0.78, $P = 0.44$) (Fig. 2.2b). SBR differed significantly with the interactive effects of density x species treatment (ANOVA: $F_{4,74} = 3.16$, $P = 0.018$), and population of origin x morphological trait variation (ANOVA: $F_{1,74} = 4.81$, $P = 0.031$). The magnitude of differences in SBR between species treatments were increased at greater densities (Fig. 2.2c), with higher surface boundary roughness found in Loch Linnhe communities with greater morphological trait variation (CV mean arm length) (Fig. 2d). Though the extent of variation for average arm length did not differ significantly between densities (ANOVA: $F_{2,78}$ = 1.76, *P* = 0.18), species treatments (ANOVA: $F_{2,78}$ = 0.61, *P* = 0.55) or populations (ANOVA: $F_{1,78}$ = 0.02, *P* = 0.88), variation in the morphology of individuals was comparatively elevated for individuals originating from Loch Linnhe or maintained under medium density (Appendix A, Fig. A9). Bioirrigation activity ($\Delta[Br^-]$) did not vary with abiotic or biotic context as results showed that, although the density x population interaction was included in the minimal adequate mode, its effects were non-significant (ANOVA: $F_{2,90}$ = 1.11, *P* = 0.34, Appendix A, Fig. A10).

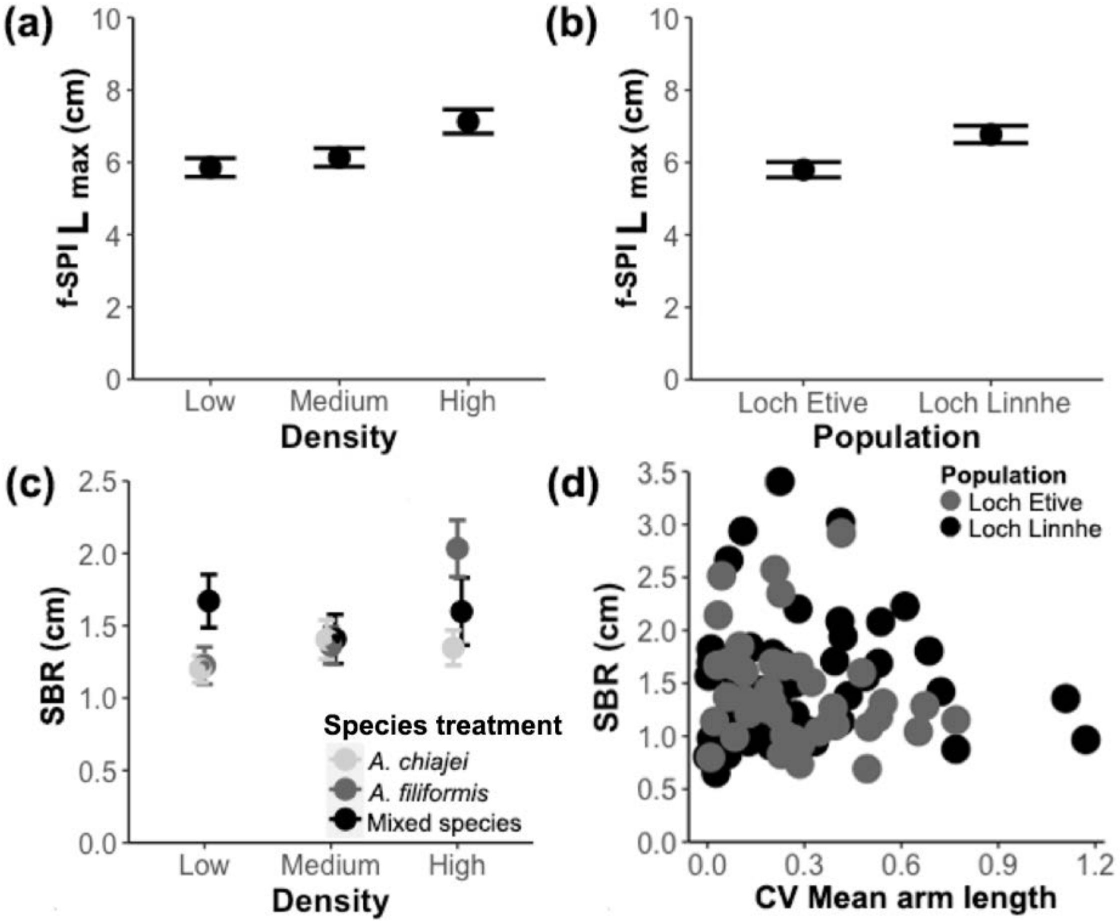


Fig. 2.2: The effects of biotic and abiotic context on (mean ± SE) (cm) (**a**, **b**) $^{f\text{-}SPI}L_{max}$ and (**c**, **d**) surface boundary roughness (SBR) in mesocosms containing *Amphiura chiajei* and *Amphiura filiformis* in monoculture or mixture, showing the (**a**) independent effect of density (n = 34), (**b**) the independent effect of population (n = 54), (**c**) the interactive effect of density x species treatment (n = 12), and (**d**) the interactive effect of morphological trait variation (CV of mean arm length) and population.

2.4.3 Ecosystem functioning

The effect of biotic and abiotic context on sediment nutrient release differed between nutrients (Fig. 2.3). [NH_4-N] was significantly influenced by the interactive effect of population x density (ANOVA: $F_{2,85} = 3.15$, $P = 0.048$). Overall, [NH_4-N] was increased in communities originating from Loch Linnhe in comparison to those from Loch Etive (coefficient ± SE = 2.31 ± 1.81, t = 1.27, $P = 0.21$), with clearer differences in [NH_4-N] between populations at lower densities (Fig. 2.3a). [NH_4-N] was also significantly affected by species treatment (ANOVA: $F_{2,85} = 3.22$, $P = 0.045$), being greatest in *A. chiajei* monoculture communities (Fig. 2.3b). [NO_3-N] was significantly affected by density (ANOVA: $F_{2,89} = 16.38$, $P < 0.001$) and population (ANOVA: $F_{1,89} = 6.95$, $P < 0.001$), decreasing with density, and with lower concentrations found in Loch Linnhe communities (coefficient ± SE = -3.95 ± 1.5, t = -2.64, $P < 0.001$) (Fig. 2.3c & 2.3d). [NO_2-N] was significantly affected by population (ANOVA: $F_{1,83} = 5.94$, $P = 0.017$), showing greater concentrations in communities originating from Loch Linnhe (coefficient ± SE = 17.83 ± 7.43, t = 2.4 $P = 0.019$) (Fig. 2.3e). [PO_4-P] was significantly affected by the interactive effect of species treatment x density (ANOVA: $F_{4,84} = 2.81$, $P = 0.030$), with overall PO_4-P concentration, and the magnitude of difference between species treatments, decreasing with density (Fig. 2.3f).

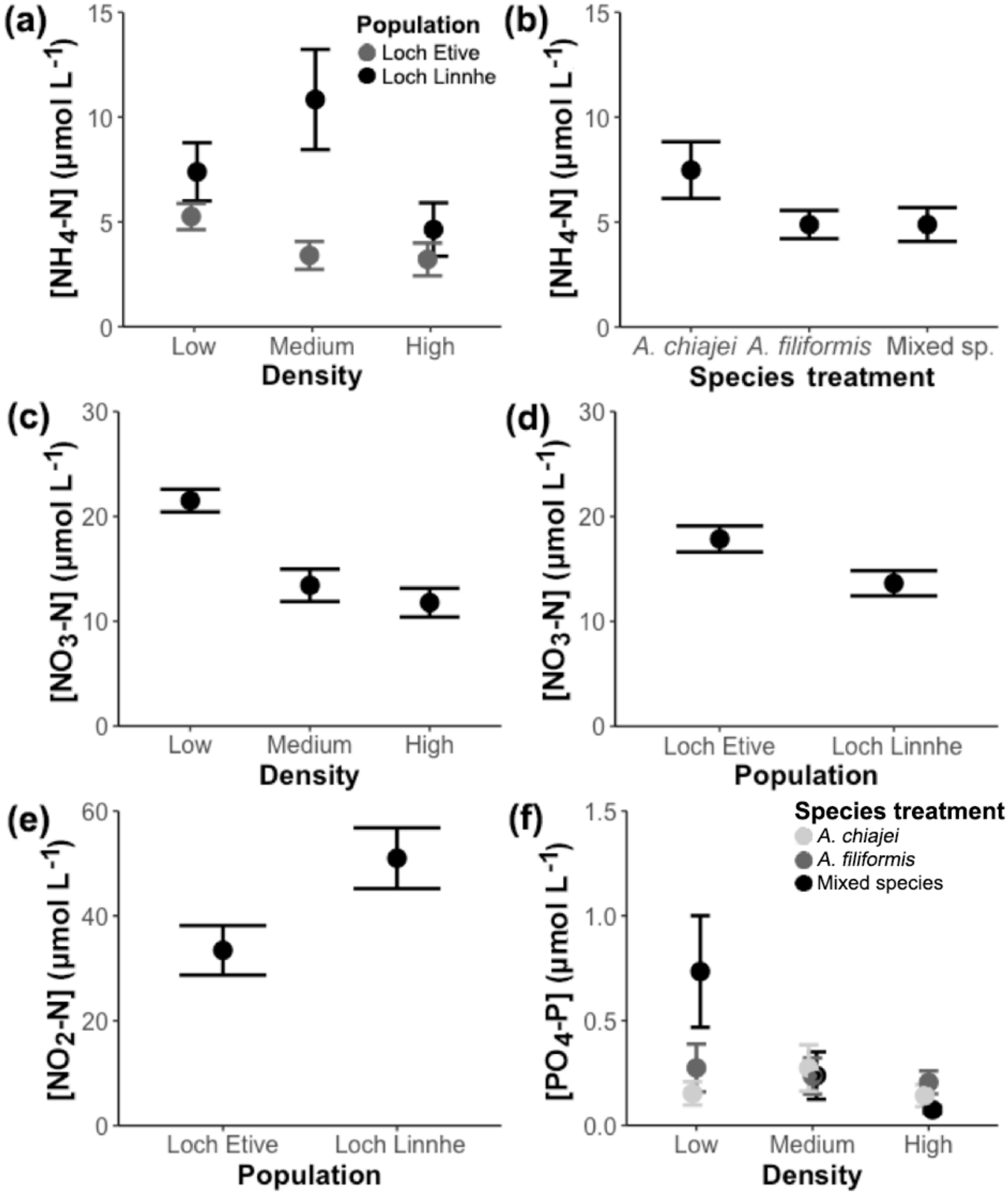


Fig. 2.3: The effects of differing biotic and abiotic context on (mean ± SE) (µmol L^{-1}) (**a**, **b**) [NH_4-N], (**c**, **d**) [NO_3-N], (**e**) [NO_2-N], and (**f**) [PO_4-P] in mesocosms containing *Amphiura chiajei* and *Amphiura filiformis* in monoculture or mixture where (**a**) shows the interactive effects of density x population (n = 18), (**b**) shows the independent effect of species treatment (n = 34), (**c**) shows the independent effects of density (n = 34), (**d, e**) shows the independent effect of population (n = 54), and (**f**) the interactive effect of density x species treatment (n = 12).

2.5 Discussion

Overall, my results demonstrate significant influence of context on the trait expression of individuals. I show that this context-dependency then affects the functional roles and contributions of species by mechanistically underpinning concurrent change in community behaviour and ecosystem functioning.

I found site-specific and interspecific differences in morphological trait expression. By consequence, it is difficult to interrogate the role of population or species *per se* in determining behavioural trait expression. Body size determines the scaling relationship between the traits expressed by a species and their ecosystem role, and larger individuals are often liable to have stronger effects on ecosystem functioning (Larsen et al., 2005). Given this relationship, intraspecific morphological variability has already been incorporated into some functional trait approaches via a community average (Solan et al., 2004a). Body size traits are a complex and potentially transient response to genetic influences, age, food and other resources (Liao et al., 2016). Even where two organisms are allegedly found within the same functional group, larger individuals are expected to have proportionally larger effects to ecosystem functioning (e.g. displace more sediment and pump more water (Norkko et al., 2013), and intraspecific morphological expression may be a significant influence on the functional roles of species. However, even beyond the contributions of morphological differences, individuals with shared local histories are likely to consistently express similar traits (Fisher et al., 2015; Moran et al., 2017; Peterson et al., 2019). Abiotic context influences the presence, plasticity and strength of traits expressed within a community (Calosi et al., 2013; Törnroos et al., 2015; Nagelkerken & Munday, 2016). Organic matter content and sediment grain size, which differ between Loch Etive and Loch Linnhe, notably affect organism behaviour in terms of sediment mixing and bioirrigation (Bulling et al., 2008; Godbold & Solan, 2009). Origin in the distinct conditions of either loch contributes to differences in trait expression at an individual-level, and in the community-level net effects which these traits in part underpin (Wohlgemuth et al., 2017).

Further, density and species identity influence intraspecific behavioural trait expression as community composition determines the neighbour-effects that dictate behaviours including space and resource use (De Backer et al., 2011; Kraft et al., 2015; Calder-Potts et al., 2018). These effects in turn underpin the role of shifting biodiversity in driving altered ecosystem functioning (Thomsen et al., 2019). Changes in the extent and structure of biodiversity alter not only functional diversity at the community-level, but form differing biotic contexts with influence on the trait expression and functional roles of component individuals (Wohlgemuth et al., 2017; Adair et al., 2018). Behavioural factors are among the more flexible aspects of an animal's phenotype as they are less likely to be constrained by strict physiological tolerances, and so their variation readily reflects short- and long-term responses of each species to local conditions (Fisher et al., 2015). The competitive advantage offered by this trait dissimilarity, and so its role in determining community structure, depends on whether individuals are involved in intra- and interspecific competition, as species may benefit from expressing novel (Finerty et al., 2016) or more acquisitive phenotypes (Bennett et al., 2016). My results show that, even where species are distinguished by interspecific differences in behavioural or morphological traits (Buchanan, 1964), each taxa may also display distinct intraspecific responses between communities of differing compositions (Zuo et al., 2017).

The potential for intraspecific variation should not be overlooked, given that it can strongly determine the functional identity and context-dependent contributions of each species (Des Roches et al., 2018). Context-dependent variation may have consequences for ecosystem functioning as it can change, expand, or narrow the distribution of relevant traits expressed and so alter the assumed functional contributions of organisms (Matesanz & Ramírez-Valiente, 2019). Differences in sediment reworking between treatments mechanistically underpin the differences in dissolved nutrient release observed between the same conditions, demonstrating that change in behavioural trait expression influences biogeochemical processes and so mediates the functioning of benthic habitats (Kristensen et al., 2014; Wohlgemuth et al., 2017). However, establishing the relative importance of intraspecific and interspecific variation has long been a focus of trait-based ecology (Albert et al., 2010a; Zuo et al., 2017). The necessity of considering intraspecific variation is likely to be determined by the extent of variability within a trait (Henn et al., 2018), the strength of its relationship with ecosystem function (Mensens et al., 2017), and indeed the research question at hand. I suggest that quantifying the extent of intraspecific variation should be a particular priority where taxa are compared across gradients, or where environmental conditions are changing. Mesocosm experimental studies or sub-sampling of trait expression *in situ* offers ability to establish the realised functional contributions or variability of species in complement to conventional trait-based study (Henn et al., 2018). It is probable that interspecific differences will exceed intraspecific differences in terms of magnitude (Derroire et al., 2018), and that quantification of intraspecific variability will be less likely to alter projections of functioning and service delivery at ecosystem-scales with high species richness (Wright et al., 2016). Nonetheless, to do so characterises the sources, pathways, and potential consequences of altered conditions (Albert et al., 2010a; Fisher et al., 2015). Intraspecific trait variation and its covariation with interspecific trait variation together determine community responses to ecological change (Zuo et al., 2017).

Given that natural systems are increasingly subject to drivers of ecological change, I highlight the need to determine the contexts in which intraspecific variability arises (Moran et al., 2017; Matesanz & Ramírez-Valiente, 2019). Within this framework, we must isolate the circumstances where it contributes to the functional integrity of ecosystems (Wright et al., 2016; Zuo et al., 2017). Failure to do so jeopardises understanding and prediction of ecosystem functioning due to inadequate characterisation of traits and, by result, biodiversity (Wohlgemuth et al., 2017; Adair et al., 2018; Des Roches et al., 2018). Trait-based models for predicting community structure across environmental gradients perform poorly when they fail to integrate the effects of intraspecific variation in functional traits, as existing typologies are insufficiently broad (Read et al., 2017). My findings demonstrate that trait-based approaches to ecosystem study require more detailed functional metrics than has previously been assumed. Future efforts should seek to report responses under multiple ecosystem conditions, to demonstrate the potential breadth of resulting intraspecific diversity, and consider how these effects will propagate up biological scales (Carmona et al., 2016; Finerty et al., 2016; Funk et al., 2017; Matesanz & Ramírez-Valiente, 2019).

2.6 Conclusions

My findings show that the expression of traits by individuals and so the net behaviour of their communities differs with biotic and abiotic context. Such changes in individual functional contributions have important implications for mediation of ecosystem functioning. My study highlights that trait-based approaches which do not consider the context-dependency of trait expression are at risk of misrepresenting the functional roles of taxa. Quantification of intraspecific variability will offer ecologists better insight into biological responses to environmental conditions, and aid ecosystem management approaches seeking to maintain good ecosystem function and service delivery in the face of environmental change.

Chapter 3 Long-term differences in climate drive intraspecific trait expression and ecosystem function

3.1 Abstract

Functional trait-based approaches are increasingly adopted to understand ecological responses to environmental change. However, most assume that trait expression is constant irrespective of context, potentially jeopardising projections of ecosystem functioning and service delivery. I challenge this assumption, using a benthic system to demonstrate differences in trait expression in two co-occurring species of invertebrate (the brittlestars *Amphiura filiformis* and *Ampihura* c*hiajei*) maintained under differing long-term (12 month) climatic (temperature and atmospheric [CO_2]) and species mixture conditions. I use ANOVA and PERMANOVA to quantify the effect of climate treatment (ambient temperature / 400 ppm atmospheric [CO_2] or ambient + 2 ° C / 550 ppm atmospheric [CO_2]) and species mixture on individual behavioural trait expression (righting and burrowing at the sediment surface) and net community behaviour (sediment reworking and burrow ventilation), and investigate associated effects on ecosystem functioning (sediment nutrient release). I find significant intraspecific variation in trait expression in response to altered climate condition and biotic context. Righting and burial rates are faster under near future conditions, but responses are further mediated depending on whether individuals are maintained in a monoculture or mixed species treatment. Context-dependent intraspecific variation in individual and community behaviour mechanistically underpins the functional role of species, and I observed these trait differences concomitantly to altered ecosystem functioning between climate and species treatments. My findings demonstrate that conspecific individuals express different traits depending on abiotic and biotic context and thereby make differing contributions to ecosystem functioning. Therefore, efforts to understand and manage the functional integrity and ultimately the provisioning of ecosystem services under altered environmental conditions requires substantially more detail than is conventionally assumed.

3.2 Introduction

Altered biodiversity, motivated on a global scale by unprecedented environmental and ecological change, can induce changes in ecosystem functioning and the reliable provision of ecosystem services (Pecl et al., 2017). Current research emphasises that biodiversity effects are underpinned by the diversity and composition of biological traits (i.e. behavioural, morphological or life-history characteristics) expressed within a community, rather than the number of species in of itself (Gagic et al., 2015). As a result, research has shifted to the use of species-level, non-phylogenetic trait values to provide mechanistic understanding of species-environment relationships (e.g. Baattrup-Pedersen et al., 2018; McLean et al., 2019) and the biotic control over ecosystem functioning (e.g. Bremner et al., 2006; Gogina et al., 2017; Hamilton et al., 2019). By doing so, the contributory roles of species are often assumed to show constancy irrespective of environmental or ecological context, and contemporary techniques may not accurately reflect the realised roles of species *in situ* (Moran et al., 2016; Jones & Cheung, 2018).

Intraspecific variation is a widespread feature of communities and arises from genetic variation (Mitchell & Bakker, 2014b), demographic differences including an individual's body size, age and sex (Rudolf & Rasmussen, 2013; Fritschie & Olden, 2016), and from phenotypic plasticity in response to prevailing environmental conditions (Jung et al., 2014; Törnroos et al., 2015; Moran et al., 2016). The nature and magnitude of intraspecific variation is itself highly variable (Nagelkerken & Munday, 2016; Spasojevic et al., 2016), and has been shown to arise in response to changes in temperature (Baranov et al., 2016; Landeira-Dabarca et al., 2018), pCO_2 (Nilsson et al., 2012), pH (Calosi et al., 2013; Murray et al., 2013) and hypoxia (Calder-Potts et al., 2018). Tolerances to environmental change vary throughout a species' range, and introduce further uncertainty into the ability to generalise and forecast ecosystem responses to climate change (Calosi et al., 2017; Peterson et al., 2018). In addition, given the high complexity of natural ecosystems, variation in trait expression is also driven by biotic conditions as interactions arise from species- and density-dependent effects (Bocedi et al., 2013; Wohlgemuth et al., 2016; Calder-Potts et al., 2018; Henn et al., 2018). Changes in trait expression at the individual- or community-level affect functional diversity (Bennett et al., 2016), with implications for the persistence of species (Edwards et al., 2018; Henn et al., 2018; Jara et al., 2019) and their contributions to ecosystem functioning (Bolnick et al., 2011; Chapter 1).

It is currently widely assumed that any intraspecific differences in trait expression induced by environmental condition will be insufficient to prompt measurable change in ecosystem functioning, however this is rarely quantified (Zuo et al., 2017). As such, trait-based approaches used to project ecosystem performance under changing environments (Laughlin et al., 2014;

Rijnsdorp et al., 2015; Bolam et al., 2017) - and any management recommendations which result from these predictions - may fail to accurately estimate the robustness of ecosystem functioning or service provision if they do not account for intraspecific variation. By contrast, quantifying intraspecific trait expression offers insight as to functional diversity within species, and how it may differ across ecological and environmental gradients (Jones & Cheung, 2018; Hamilton et al., 2019). Through this insight, we are better able to identify mechanisms through which context-dependent differences in organisms underpin changes in ecosystem functioning (Form & Riebesell, 2011; Godbold & Solan, 2013).

Responses to altered environmental conditions differ over time as short-term physiological changes can be maladaptive (Calosi et al., 2013; Jessop et al., 2018) and acclimation mechanisms may take months or years to develop (Langer et al., 2019; Sundin et al., 2019) such that short-term experiments risk misrepresenting species' actualised responses (Form & Riebesell, 2011; Godbold & Solan, 2013; Jung et al., 2014). By exposing individuals for a long-term, 12-month experimental duration we thus seek to illustrate established phenotypic variation under differing environmental regimes. In doing so, we are able to demonstrate that quantifying intraspecific expression offers uniquely valuable insight into the responses of species to environmental change (Volf et al., 2016; Henn et al., 2018), and concisely link the specific changes of species to that of their ecosystem.

Here, I quantify the intraspecific trait variability of two co-occurring species of infaunal marine invertebrates (brittlestars *Amphiura filiformis* and *Amphiura* c*hiajei*) following a 12-month exposure to one of two climate conditions; an ambient (ambient temperature/400 ppm atmospheric [CO_2]), and a near future scenario (ambient + 2°C/ 550ppm atmospheric [CO_2]) climate scenario (IPCC, 2018). I hypothesised that the variability and sensitivity of intraspecific behavioural trait expression, net community-level behaviours and associated effects on ecosystem function would differ between climate treatments and for species maintained in monoculture and a two-species mixture. To this effect, I examine the context-dependent responses to environmental conditions for both the expression of species traits and for associated ecosystem functioning in marine soft sediment systems. I then discuss the implications of these findings for trait-based management approaches in the coming decades.

3.3 Materials and methods

3.3.1 Species collection and experimental design

Two species of brittlestars (*A. filiformis* and *A. chiajei*, OF Müller) were collected from Loch Etive, Argyll and Bute, Scotland, UK (56°27'34.20"N, 5°20'29.28"W) (Appendix B, Table B1 and Fig. B1 & S2). Individuals were returned to the University of Southampton in aerated water baths and acclimated to aquarium conditions for a 60-day period.

To assemble mesocosms (Perspex aquaria, internal dimensions, LWH 12 x 12 x 35 cm), estuarine mud from Hamble-le-Rice, Hampshire (50°52'23.1"N 1°18'49.3"W), was sieved (500 µm mesh) in a seawater bath to retain the fine fraction and remove macrofauna, allowed to settle for 48 h before being homogenised, added to mesocosms (settled depth ~ 10 cm), and overlaid with seawater (depth ~ 20 cm). After 24 h and prior to the addition of the organisms, the seawater was replaced to remove excess dissolved nutrients associated with mesocosm assembly. Mesocosms contained *A. filiformis* and *A. chiajei* in one of three species treatments (*A. filiformis* in monoculture, *A. chiajei* in monoculture, or an *A. filiformis* – *A. chiajei* mixed species treatment). *A. filiformis* and *A. chiajei* were selected due to their shared tolerance for variable biotic and abiotic contexts (Calder-Potts et al., 2018; Cassidy et al., 2020), and their widespread co-occurrence throughout European shelf waters, where they exert dominant influence on local biochemical cycling (Murray et al., 2013). Both species exhibit a moderate maximum lifespan (Sköld et al., 1994), of which a 1 year incubation represents a substantive proportion of adult lifespan. Population densities of both species are highly variable, and the density used in this study (1000 ind. m^{-2} for *A. filiformis*, 700 ind. m^{-2} for *A. chiajei*) represents a moderate, non-location-specific value (O'Connor et al., 1983; Duineveld et al., 1987; Munday & Keegan, 1992) adjusted to the observed ratio of *A. filiformis* to *A. chiajei* at the sample site to avoid introduction of additional aspects of biotic context into the study (Appendix B, Table B2). After the experimental period, to negate any risk of dispersion effects, data were then standardised as n = 8 individuals per community (equally representing all component species) were randomly selected for analysis.

Adopting a full factorial design, replicate mesocosms of all three species treatments were maintained in a temperature-controlled room under one of two climate conditions; 'ambient' or 'ambient + 2 °C', hereafter referred to as 'future'. Mesocosms maintained under ambient conditions were held at the seasonal temperature at the sampling location (provided by Oban SeaLife Centre) and 404.08 ± 15.63 ppm atmospheric [CO_2]. Seawater temperature was adjusted fortnightly and ranged between 7.0 – 17.3 °C across the incubation period (Appendix B, Fig. B3). Mesocosms representing future conditions were maintained at ambient + 2 °C, and 561.56 ±

65.46 ppm atmospheric [CO_2], in line with conservative climate projections for the year 2100 (IPCC, 2018). Following Godbold & Solan (2013), levels of [CO_2] were controlled using a CO_2-air mixing system and monitored using infrared gas analysers (Licor LI-840A, 1 per climate condition). Mesocosms were covered (Perspex lid, thickness 2 mm) to minimise ambient air exchange. Each climate condition (n = 2) x species treatment (n = 3) was replicated five times (total n = 30) (Appendix B, Table B2). Mesocosms were continually aerated and fed twice weekly on a flake-type aquarium food, and maintained under these conditions for 12 months. To avoid excessive accumulation of nutrients, a partial (~ 50%) seawater change was performed once a week.

3.3.2 Seawater carbonate chemistry

Seawater pH (Mettler-Toledo InLab Expert Pro temperature–pH combination electrode), temperature and salinity (Mettler-Toledo InLab 737 IP67 temperature–conductivity combination electrode) were measured every 7 days (Appendix B, Fig. B3 & S4) and samples for determination of total alkalinity (A_T) and dissolved nutrient concentrations were taken every 28 days. A_T was analysed by titration (Apollo SciTech Alkalinity Titrator AS-ALK2) following standard protocols at the National Oceanography Centre, Southampton, UK Carbonate Facility. pCO_2 and concentrations of [HCO_3] and [CO_3] (µmol $KgSW^{-1}$) were calculated from A_T, measured pH, temperature and salinity using the *CO2SYS* program (version 2.1) (Pierrot et al., 2006) (Appendix B, Fig. B3 & S4).

3.3.3 Measures of intraspecific trait expression

Individual-level trait expression was represented through movement and burial behaviours measured at the sediment surface following incubation and the quantification of community- and ecosystem- properties. Individuals were inverted and placed on the sediment surface in a temperature-controlled tray of sediment (3 cm depth overlaid with 5 cm depth seawater) under the same climate and species mixture treatment (monoculture or mixed) conditions in which they had been maintained. A bench top video camera (uEYE USB camera, 1.3 MP,25 FPS, IDS Imaging Development Systems, Obersulm, Germany) was used to record two behavioural traits: i) the time taken (s) for each individual to begin movement activity, a response trait, and ii) the time taken (s) for each individual to complete burial into the sediment, an effect trait. For the former, behaviour at the sediment surface reflects the strength and nature of organismal responses to their surrounding stimuli (Rosenberg & Selander, 2000; Gutowsky et al., 2016), and for the latter, burial rate is indicative of functionally-relevant sediment movement behaviours at the individual level (Nagelkerken & Munday, 2016).

As morphological traits can influence an individual's functional contribution (Fritschie & Olden, 2016), arm length (cm), disc diameter (cm) and wet weight biomass (g) were determined for each individual. Arm length and disc diameter were quantified using image analysis (ImageJ, version 1.46r, Schneider et al., 2012; Appendix B, Fig. B5) on scaled images obtained with a bench top digital camera (1.3 megapixels). Given the strong co-linearity between the morphological metrics (Appendix B, Fig. B6), the mean length of an individual's five arms (cm) was chosen to represent intraspecific morphological trait expression due to its importance for motility and feeding behaviours (Astley et al., 2012).

3.3.4 Measures of community behaviour

Bioirrigation activity (burrow ventilation) was estimated by measuring relative change in water column concentrations of inert tracer sodium bromide on the final day of the incubation period (Forster et al., 1999). After addition and homogenisation of dissolved NaBr (5 mM aquaria^{-1}), water samples (25 ml) were taken immediately (0 h) and after 4 h and 8 h incubation. Water samples were filtered (0.45 µm cellulose acetate membrane filter) and stored at ambient temperature until colorimetric analysis (FIAstar 5000 flow injection analyser, FOSS Tecator at University of Aberdeen, Aberdeen). Bioirrigation activity was estimated from the change in the concentration of Br^{-} ($\Delta[Br^{-}]$, mg L^{-1}; negative values indicate increased bioirrigation activity) over 8 h.

Bioturbation (faunally mediated particle reworking) was estimated using sediment profile imaging (f-SPI) (Solan et al., 2004b). To visualize particle movement, 24 g dry weight of dyed sediment that fluoresces in UV light (green colour; Brianclegg Ltd., UK) was added to each mesocosm 8 days prior to the end of incubation period. This length of time is sufficient to visualise faunally-mediated particle movement, while avoiding vertical homogenization of the tracers. Images of all four sides of each mesocosm were taken in a UV illuminated imaging box (Teal et al., 2008). Images were saved in RGB colour mode with JPEG compression and analysed using a semi-automated macro that runs within ImageJ (version 1.46r), a Java-based public domain program (Schneider et al., 2012). From these data, the maximum ($^{f\text{-}SPI}L_{max}$), mean ($^{f\text{-}SPI}L_{mean}$) and median ($^{f\text{-}SPI}L_{median}$) depth of particle reworking was calculated, and surficial activity (surface boundary roughness, SBR) was estimated using the maximum vertical deviation of the sediment-water interface (upper – lower limit) (Hale et al., 2014).

3.3.5 Measures of ecosystem functioning

Ecosystem functioning was represented through the proxy of sediment nutrient release, which is mediated by the sediment movement behaviours of benthic fauna (Wohlgemuth et al., 2016). On the final day of the incubation period, nutrient concentrations (ammonium, [NH_4- N]; total nitrate, [NO_x-N]; and phosphate, [PO_4-P], µmol L^{-1}) were determined from seawater samples (20 mL, 0.45 µm pre-filtered, Agilent Captiva) taken and immediately frozen. [NH_4-N], [NO_x-N], and [PO_4-P] (µmol L^{-1}) were quantified using a segmented flow analyser (QuAAtro39 AutoAnalyzer).

3.3.6 Statistical analysis

PERMANOVA and ANOVA were used to determine the effect of climate (2 levels: ambient and future), and either species identity (for tests of individual trait expression, 4 levels: *A. filiformis* in monoculture, *A. filiformis* in mixture, *A. chiajei* in monoculture, *A. chiajei* in mixture) or species treatment (for tests of community behaviour and ecosystem functioning, 3 levels: *A. filiformis* monoculture, *A. chiajei* in monoculture, *A. filiformis - A. chiajei* mixed treatment) on individual and community trait expression, and associated ecosystem function. All statistical analyses were performed using the *R* statistical and programming environment (R Core Team, 2017) and the vegan package (version 2.4-5, Oksanen et al., 2017).

3.3.6.1 Intraspecific trait expression

Multivariate analyses were used to represent the cumulative differences in the trait changes of individuals between species identities and contexts (Pansch et al., 2014), integrating both a response (time to begin movement) and effect (time to complete burial) trait. Permutational multivariate ANOVA (PERMANOVA, iterations = 999) was used, as it is robust to non-normality and differing correlation structures and so is particularly suited for the detection of differences in intraspecific trait expression (Mitchell & Bakker, 2014b). Intraspecific variation differs between behavioural traits, and between climate and species treatments (Appendix B, Fig. B7). Permutational analysis of multivariate dispersion (PERMDISP) was used to test the homogeneity of variance between climate conditions ($F_{1,236} = 0.002$, $P = 0.98$) and species ($F_{1,236} = 2.528$, $P = 0.13$). These results support that any significant differences in PERMANOVA between treatments are due to changes in the values of trait expression, not shifts in the overall extent of trait variation. PERMANOVA models were used to test the independent and interacting effects of climate, species identity, and individual morphological trait expression (mean arm length) on multivariate behavioural trait expression, with the latter term as a continuous covariate.

Additionally, the extent of intraspecific trait variation (coefficient of variation, CV, the ratio of standard deviation to the mean) was determined for the expression of each individual-level trait (time to begin movement, time to complete burial, and mean arm length), and 2-way ANOVA was used to investigate the effects of climate and species treatment on the variability of trait expression (Roscher et al., 2018a).

3.3.6.2 Community behaviour and ecosystem functioning

3-way ANOVA was used to test the independent and interactive effects of context (climate, species treatment) and intraspecific morphological trait variation (CV of mean arm length of component individuals) on each community-level behaviour (${}^{\text{f-SPI}}L_{\text{mean}}$, ${}^{\text{f-SPI}}L_{\text{max}}$, ${}^{\text{f-SPI}}L_{\text{median}}$, SBR, $\Delta[Br^{-}]$), and 2-way ANOVA was used to test the independent and interactive effects of context (climate, species treatment) on nutrient concentration ($[NH_4\text{-}N]$, $[NOx\text{-}N]$, $[PO_4\text{-}P]$). Model assumptions were assessed visually for normality (Q-Q plot), homogeneity of variance (plotted residuals vs. fitted values), and the presence of outliers or overly influential data points (Cook's Distance). For ANOVA, the minimal adequate effects structure was determined using backward selection informed by Akaike Information Criteria (AIC) (Zuur et al., 2009).

3.4 Results

3.4.1 Intraspecific trait expression

PERMANOVA revealed that the overall behavioural trait expression of individuals at the sediment surface differed significantly between climate scenarios ($F_{1,237} = 6.30$, $P = 0.008$, Fig. 3.1a & 3.1c) and also depended on the species identity of the individual ($F_{3,237} = 11.29$, $P = 0.001$, Fig. 3.1b & 3.1d) (Appendix B, Fig. B8). Though analysed in a multivariate manner each behavioural trait is visualised independently to highlight differences in trait expression. The magnitude of differences between treatment conditions was less pronounced for the response trait of the time taken to begin movement (Fig. 3.1a & 3.1b) than for the effect that of the time taken to complete burial (Fig. 3.1c & 3.d). Individuals exposed to the future climate treatment took significantly less time to complete movement behaviours than individuals exposed to the ambient treatment, which can

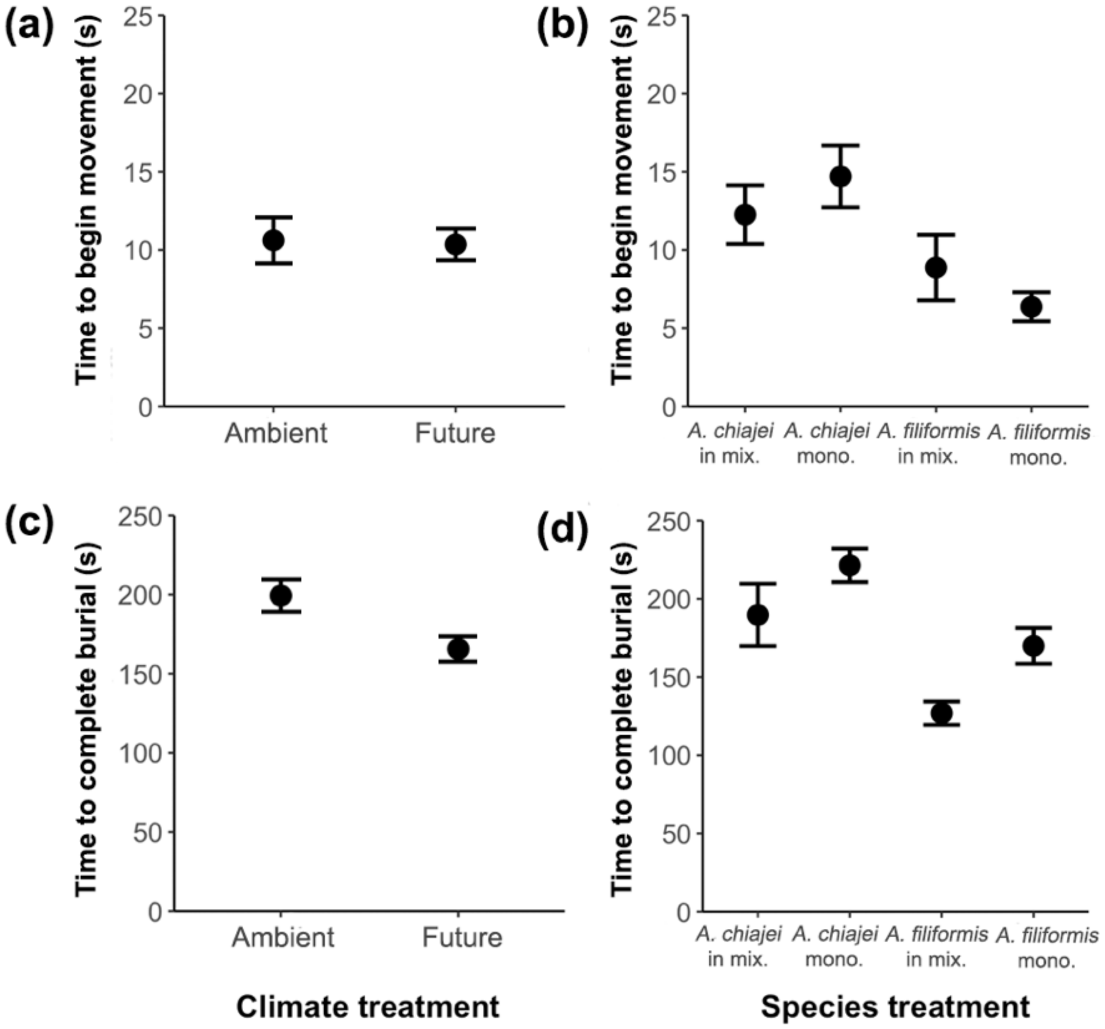


Fig. 3.1: The effect of climate and species identity on time elapsed (mean ± SE) (s) for individual *Amphiura chiajei* and *Amphiura filiformis* to (**a, b**) begin movement and (**c, d**) complete burial into the sediment, where (**a**, **c**) show the independent effects of climate treatment and (**b, d**) show the independent effect of species identity of individuals maintained in monoculture or in mixture containing both species.

be most clearly seen in the time taken to complete righting and burial (Fig. 3.1c). Although *A. chiajei* individuals generally took longer before beginning or completing movement than *A. filiformis* (Fig. 3.1b & 3.1c), I found intraspecific differences for both species depending on whether individuals were in monoculture or mixture. For *A. chiajei* the time taken to begin movement (Fig. 3.1b), and for both *A. chiajei* and *A. filiformis* the time taken to fully complete burial (Fig. 3.1d), was increased in mixed species treatments in comparison to the monocultures.

I found no significant effect of intraspecific morphological trait expression on behavioural trait expression ($F_{1,237} = 0.160$, $P = 0.85$). However, morphological trait expression differed significantly between species (ANOVA: $F_{1,224} = 31.15$, $P < 0.001$) irrespective of climate treatment, with *A. chiajei* individuals being slightly larger than *A. filiformis* (Appendix B, Fig. B9).

The extent of intraspecific variation (CV) of both behavioural traits (time to begin activity and time to complete burial) within communities did not differ significantly between climates or species mixture treatments (ANOVA: $P > 0.05$ for all explanatory variables, Appendix B, Table B4). However, trends do suggest that the extent of variation in the time taken to begin activity between individuals may be greater in communities maintained under ambient conditions, and for communities containing *A. chiajei* in either monoculture or in mixture (Appendix B, Fig. B10).

3.4.2 Community behaviour

Community-level bioturbation and bioirrigation behaviours were differentially affected by climate conditions, and their component species mixture treatment. Surface boundary roughness did not differ significantly with abiotic or biotic context (ANOVA intercept only model, Appendix B, Fig. B11). The median depth of particle redistribution, ${}^{f\text{-}SPI}L_{median}$, was significantly different between species treatments (ANOVA: $F_{2,26} = 5.87$, $P = 0.008$) and was shallowest when *A. filiformis* occurred in monoculture (Fig. 3.2a). The mean depth of particle redistribution, ${}^{f\text{-}SPI}L_{mean}$, was significantly affected by the interaction of climate condition x species treatment (ANOVA: $F_{2,22} = 5.07$, $P = 0.015$) and the interaction of climate condition x morphological trait variation (ANOVA: $F_{1,22} = 4.31$, $P = 0.015$). The results show mean burrowing depth was generally deeper under ambient conditions, and deepest overall when *A. chiajei* was maintained in monoculture under ambient conditions (Fig. 3.2b). Irrespective of species treatment, ${}^{f\text{-}SPI}L_{mean}$ decreased with increasing arm length and was shallower under future climate conditions (Fig. 3.2c). The maximum depth of particle redistribution, ${}^{f\text{-}SPI}L_{max}$, differed significantly between species treatments (ANOVA: $F_{2,22} = 4.56$, $P = 0.022$) and was deepest for *A. chiajei* in monoculture and the mixed species treatment (Fig. 2d). Bioirrigation activity ($\Delta[Br^{-}]$, mg l^{-1}) was significant affected by the interaction of climate x species treatment (ANOVA: $F_{2,23} = 33.26$, $P < 0.001$) (Fig. 3.2e). Bioirrigation activity was greatest under future conditions when *A. filiformis* and *A. chiajei* were maintained in monoculture, and lowest in the mixed community. By contrast, bioirrigation activity was greatest under ambient conditions in the mixed community, and lowest when *A. filiformis* and *A. chiajei* were maintained in monoculture. However, bioirrigation activity in *A. filiformis* monoculture communities appears higher under future conditions, with little activity under ambient conditions.

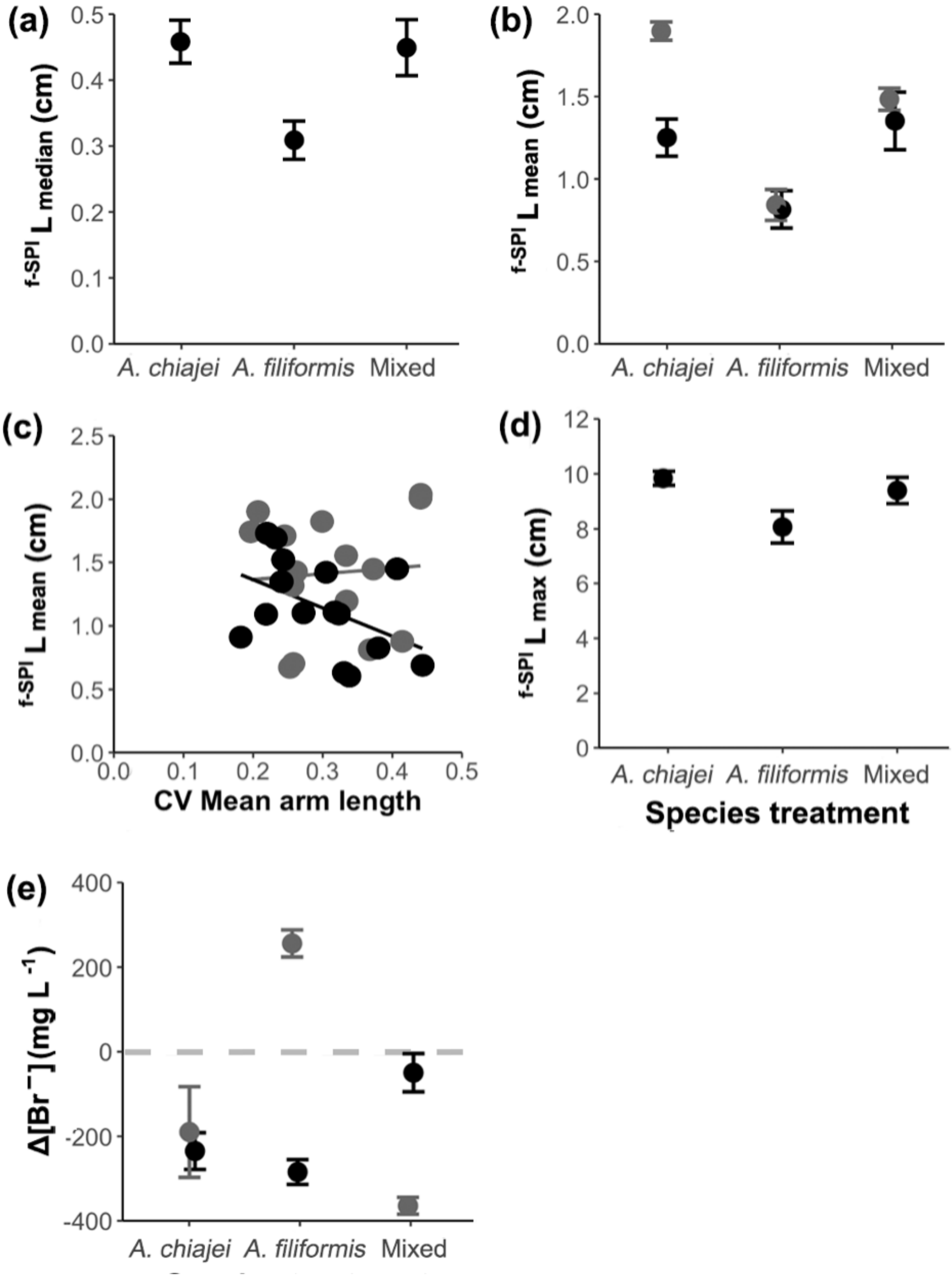


Fig. 3.2: The effects of climate and species treatment on (mean ± SE) (**a**) $^{\text{f-SPI}}\text{L}_{\text{median}}$ (cm), (**b, c**) $^{\text{f-SPI}}\text{L}_{\text{mean}}$ (cm), (**d**) $^{\text{f-SPI}}\text{L}_{\text{max}}$ (cm), and (**e**) bioirrigation activity ($\Delta[\text{Br}^-]$, mg L^{-1}) of *Amphiura filiformis* and *Amphiura chiajei*, showing (**a**) the independent effect of species mixture (n = 10), (**b**) the interactive effects of climate and species mixture treatment (n = 5), (**c**) the interactive effects of climate and intraspecific morphological trait variation (n = 5), (**d**) the independent effect of species mixture treatment, and (**e**) the interactive effects of climate and species mixture treatment. For (**b, c, e**) grey symbols represent ambient conditions and black symbols represent future conditions.

3.4.3 Ecosystem functioning

The effect of biotic and abiotic context on sediment nutrient release differed between nutrients (Fig. 3.3). [NH_4-N] was significantly affected by climate (ANOVA: $F_{1,24} = 21.80$, $P < 0.001$), where concentrations were greater under future conditions (Fig. 3.3a). [NO_x-N] was significantly affected by the independent effects of climate (ANOVA: $F_{1,26} = 9.89$, $P = 0.004$) (Fig. 3.3b) and species treatment (ANOVA: $F_{2,26} = 4.70$, $P = 0.018$) (Fig. 3.3c). [NO_x-N] was highest in the presence of *A. chiajei* in monoculture, and in communities maintained under ambient conditions. [PO_4-P] was not modified by abiotic or biotic context as results showed that, although climate, species treatment and their interaction were included in the minimal adequate model, all effects on [PO_4-P] were insignificant (Appendix B, Table B5 & Fig. B12).

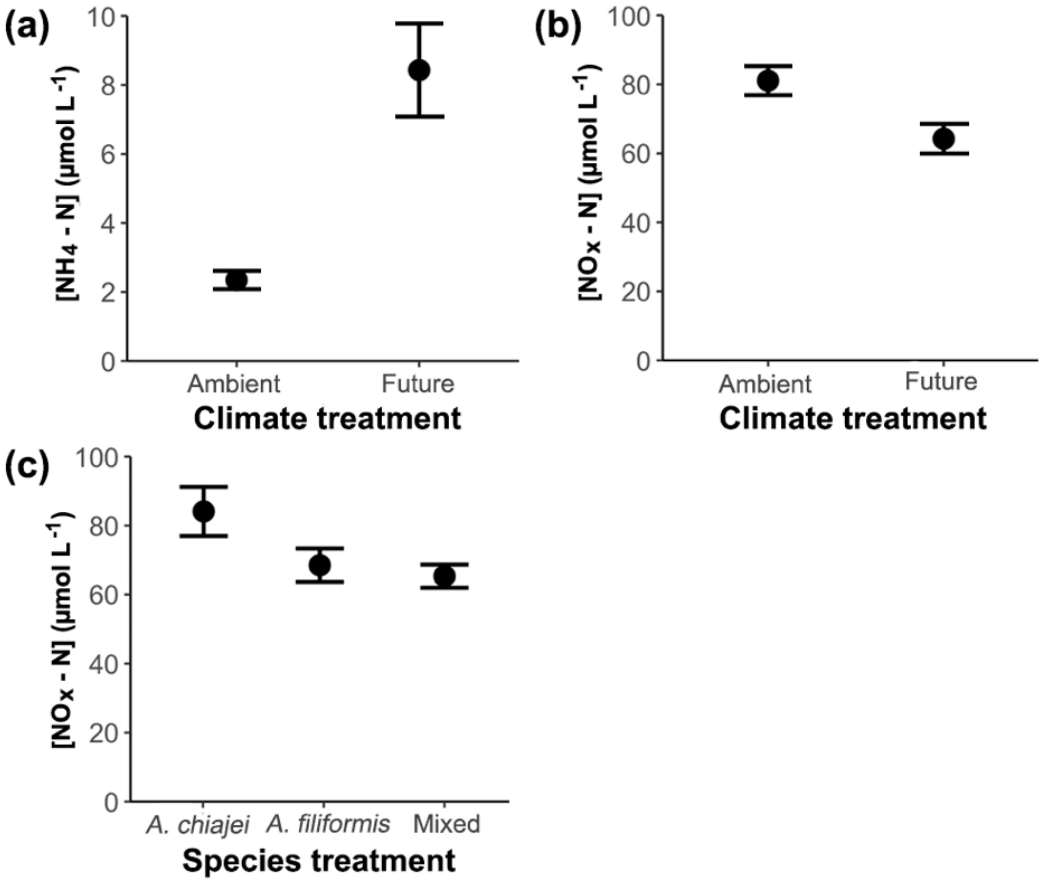


Fig. 3.3: The effects of climate and species treatment on communities of *Amphiura filiformis* and *Amphiura chiajei* maintained in monoculture or in mixture containing both species on (mean ± SE) (µmol L^{-1}) (**a**) [NH_4-N], and (**b**, **c**) [NO_x-N] from water samples taken in the final week of incubation where (**a, b**) shows the independent effect of climate (n = 15), and (**c**) shows the independent effect of species treatment (n= 10).

3.5 Discussion

Management approaches seeking to ensure the robust provision of ecosystem goods and services under changing conditions necessitate accurate representations of the characteristics that species express and the realised functional roles that they fulfil (Kimball et al., 2016). Conventional trait-based approaches - which incorporate species performance into ecosystem study by way of single mean or categorical trait classifications – carry the concomitant assumption that species contributions to ecosystem processes are not meaningfully affected by differences in environmental context across time or space (Guscelli et al., 2019). My findings demonstrate, however, that change in abiotic and biotic context influences individual trait expression and subsequently community and ecosystem performance.

Here, significant and consistent behavioural differences across species suggest trait expression is influenced by exposure to altered abiotic conditions as, irrespective of species, both *A. chiajei* and *A. filiformis* individuals performed righting and burial behaviours more rapidly under future climate scenarios. Changes in the expression of physiological traits, in particular those of energetics such as movement and behavioural performance, are biomarkers of environmental effects determining the integrity and so potential functional effects of organisms (McKensie et al., 2007; Gutowsky et al., 2016). Elevated temperatures increase the metabolic rate of species, altering the speed and overall scope of reactions and responses which organisms may express (Brockington & Clarke, 2001). Increased carbon dioxide concentrations influence organism biochemistry and, particularly in calcifying taxa, alter their resilience to pathogens, predation and competition (Mitchell et al., 2003; Watson et al., 2014; Barclay et al., 2019; Brown et al., 2019). Climatic change thus affects the energetic and metabolic resources which species can allocate to expressed life history, physiological or behavioural traits (Wood et al., 2010; Levy et al., 2017), impacting their contributions to community behaviour and functional potential. Given that behavioural traits are also indicators of species responsiveness to stimuli including disturbance or predation (Rosenberg & Selander, 2000; Watson et al., 2014), I infer that altered environmental conditions affect not solely species' functional roles but also the fitness and survivability of their populations (Wood et al., 2010; Godbold & Solan, 2013). While induced changes in effect traits are liable to have direct consequences for the functional contributions of species, impacts to response traits indicate sub-lethal effects which may then indirectly lead to a reduction in ecosystem functioning (Charette & Derry, 2016). Species that are negatively affected by environmental conditions are more likely to be at greater risk of extinction, where after their contributed traits and functional potential would be removed from the community (Thomsen et al., 2019).

The implications of such changes in biodiversity on the functioning of ecosystems are twofold, and particularly complex where environmental change co-occurs with (Spasojevic & Suding, 2012; Brown et al., 2019) and indeed drives (Eriksen et al., 2012; Bocedi et al., 2013) shifts in ecosystem structure. Overall change in biodiversity due to the removal or replacement of species determines the range of traits present at the species-level, and the magnitude of interspecific differences in traits may strongly influence the total functional potential of the community (Ricotta et al., 2016; Teixidó et al., 2018; Thomsen et al., 2019). Secondarily, however, even small changes in biodiversity can affect the functional performance of component individuals and their communities as they mediate behavioural responses to abiotic conditions. Assemblages of differing species mixture, richness, evenness and density determine an organism's biotic context and potential species interactions, and my findings show that these differences are a source of further intraspecific trait variation which can dynamically alter the assumed functional contributions of component taxa (Wohlgemuth et al., 2016; Calder-Potts et al., 2018; Thomsen et al., 2019). Irrespective of the climate condition under which they were maintained, both *A. filiformis* and *A. chiajei* individuals in a mixed community show a significantly more rapid behavioural response than that of their conspecifics in monoculture. These results carry implications for anticipating the functional potential of systems where local species richness has been altered, for example when comparing a recovering community to that of a baseline (Engst et al., 2016; Thomsen et al., 2019), or where restoration efforts conserve taxa to confer specific functional benefits (Laughlin et al., 2014). Under these circumstances, the assumed trait expression under one condition may fail to adequately characterise expression under another, and may lead to erroneous estimates of functional capacity and potentially improper management efforts to ensure continued ecosystem functioning (Kimball et al., 2016).

In quantifying intraspecific trait variation we are granted valuable insight as to the physiological sensitivities underpinning responses to abiotic change (Matesanz & Ramírez-Valiente, 2019; Guscelli et al., 2019), which may be contributory to community-level behaviours and ecosystem functioning. I show that intraspecific differences in individual-level movement and community-level sediment reworking and irrigation behaviour between species and climate treatments occur concurrently with ecosystem-level differences in dissolved nutrient release between climate treatments (Wohlgemuth et al., 2016; Godbold et al., 2017). As such, change in environmental factors affects the biotic control of ecosystem functioning by altering functional trait expression at the individual and community level (Roskosch et al., 2012; Guscelli et al., 2019; Cassidy et al., 2020). Incorporating intraspecific variation into trait-based approaches to ecosystem study thus offers improved understanding by both highlighting which traits are sensitive to change, and where this change occurs concomitantly to broader-scale community or ecosystem consequences

(Spasojevic & Suding, 2012; Llewelyn et al., 2016). There is yet scope that differences in intraspecific trait expression could be harnessed as early warning tools for faunally-mediated changes that will propagate to greater ecosystem scales (Murray et al., 2013). By consequence, practitioners quantifying intraspecific variation have greater ability to make evidence-based management decisions, ensuring that approaches are fit for purpose and acting to mitigate specific biological pathways affected by environmental change (Gornish & Prather, 2014).

More pressingly, ecologists and ecosystem managers must recognise that functional response and effect descriptors should not be used without consideration for the demonstrable influence of environmental condition (Guscelli et al., 2019; Matesanz & Ramírez-Valiente, 2019). Constraining the trait typologies of taxa into average values or functional groups is incompatible with the understanding that the physiology of species and the consequent performance of their communities and ecosystems is liable to change under altered environmental conditions. In particular, restoration approaches which seek to reach functional targets and achieve robust levels of ecosystem functioning and service delivery rely on the realised, *in situ* functional contributions of component species being appropriately characterised (Laughlin et al., 2014; Baattrup-Pedersen et al., 2018). If this requirement is not met, resulting techniques potentially misrepresent the traits and functional contributions of communities, and will therefore be unlikely to achieve management targets (Hamilton et al., 2019).

The urgency of considering intraspecific variability in a given system will likely be dependent on the relative extent of interspecific and intraspecific differences (Gagic et al., 2015; Zuo et al., 2017), the variability of a trait (Henn et al., 2018), and the strength of its mechanistic relationship with a function of interest (Moran et al., 2016; Mensens et al., 2017). Each measured trait will reflect only a small component of an organism's overall response to context (Kimball et al., 2016; Hamilton et al., 2019), and specific trait values or ranges may predispose organisms to greater climate vulnerability (Jones & Cheung, 2018). Therefore, selection both of traits and study methodologies must be made carefully. Future research efforts may seek to focus on such 'ground-truthing' work to provide *a priori* knowledge and ensure that detailed intraspecific attention will be allocated only where it will be of maximum utility. However, as global ecosystems are increasingly exposed to changing environmental and ecological conditions, from climate stressors (Jung et al., 2014; IPCC, 2018) to biodiversity (Gagic et al., 2015) and land-use change (Pecl et al., 2017), it will be ever more crucial for the maintenance of ecosystem function and service provision that we accurately quantify the breadth of causes and implications of intraspecific changes across flora and fauna. Given the potential logistical cost of these efforts, a key priority should be to establish which context-dependent changes in trait expression underpin functional consequences (Des Roches et al., 2018), and so under what circumstances quantifying phenotypic plasticity can inform (Jones & Cheung, 2018) and improve the confidence of predictive approaches (Kimball et al., 2016; Moran et al., 2016).

3.6 Conclusions

I find significant changes in an ecosystem function in response to altered climate condition and differing species compositions, with complementary changes in related intraspecific trait variation at individual- and community-levels. As such, I encourage explicit incorporation of intraspecific variation into trait-based study of changing ecosystems. My findings provide clear evidence that quantification of individual-level trait data offers coherent understanding of organism, community, and ecosystem responses to variable climate conditions which may be omitted by conventional techniques.

Chapter 4 Intraspecific trait variation as a result of species composition underpins the diversity-ecosystem functioning relationship

4.1 Abstract

The biodiversity-ecosystem functioning (BEF) relationship is underpinned by functional and trait diversity. Despite this, little consideration has been given to how species composition affects the variability of functional trait expression both within and between species. Here, I demonstrate that quantification and consideration of intraspecific trait expression is fundamental for interpreting species interactions and, therefore, the BEF relationship. GLS was used to identify effects of species richness and composition on the trait variation and ecosystem functioning of individuals and communities of four invertebrates (polychaetes *Hediste diversicolor* and *Nephtys hombergi*, bivalve *Macoma balthica* and gastropod *Peringia ulvae*) maintained in monoculture and all possible mixture combinations. Significant intraspecific variation between mixtures affects mechanisms of species coexistence, as the functional contributions of individuals, species and communities will be dependent on species composition and resulting trait differences. My findings highlight the inadequacy of relying on species-level typologies to characterise diversity effects, and demonstrate the need to harness mechanistic data for understanding and predicting functional consequences of changing biodiversity.

4.2 Introduction

A wealth of studies throughout the last three decades have established that diversity exerts a positive effect on both individual (Daam et al., 2019; van der Plas, 2019) and collective (Lefcheck et al., 2015; Gross et al., 2017; Meyer et al., 2018) ecosystem functions and services. This biodiversity-ecosystem functioning relationship is primarily underpinned by two additive processes; niche complementary, where diverse communities will comprise species with different resource use strategies, and selection, where competition favours species with optimal, high-yielding forms (Godbold et al., 2009; Turnbull et al., 2013; Hausch et al., 2018; Mahaut et al., 2020). How a given species is involved in these processes is dependent both on the taxa with which it co-occurs, and the functional traits that both parties express (Butterfield & Callaway, 2012; Fründ et al., 2013; He et al., 2013). Traits underpin a species' functional role by determining how it responds to and navigates in its environment to acquire and conserve preferred resources (Díaz & Cabido, 2001; Naeem & Wright, 2003; Cadotte et al., 2011). Trait differences between organisms are therefore directly linked to the complementarity and competitive ability of coexisting species, key components of biodiversity that influence how an ecosystem is structured (Jung et al., 2010; Start & Gilbert, 2019) and how it functions (Benavides et al., 2019).

Plasticity in trait expression at the individual-level alters the value of species traits and the extent of intraspecific and interspecific differences (Albert et al., 2010a; Zuo et al., 2017). Changes in the range of expressed trait values potentially affect the functional overlap, and similarity or redundancy, between taxa (de Bello et al., 2013; Roscher et al., 2015; Benavides et al., 2019). This will affect the nature of species interactions, and influence the strength and direction of the relationship between traits and functioning (Pruitt & Ferrari, 2011; Carlucci et al., 2014; Bulleri et al., 2016; Barry et al., 2019). By result, conventional approaches based on species mean or generalised trait values underestimate species interactions and struggle to distinguish the partitioning and utilisation of available resources (Violle et al., 2012; de Bello et al., 2013). The widespread omission of within-species variation mischaracterises species coexistence, and the true extent (De Laender et al., 2013) and effect of biodiversity on ecosystem functioning (Albert et al., 2010a; Bolnick et al., 2011; Zuo et al., 2017).

Quantification of intraspecific variation via measurement of individual-level traits is increasingly suggested as an approach through which to gain detailed insight into the functional contributions of species, and their concomitant effects to that of co-occurring taxa (Lichstein et al., 2007; Roscher et al., 2015; Raine et al., 2018; Benavides et al., 2019). Recent evidence in support of niche theory suggests that species adjust their trait expression in response to local richness or composition (Aschehoug & Callaway, 2014; Kumordzi et al., 2015; Chapter 2), and that this intraspecific variability may promote species complementarity (Jung et al., 2010; Le Bagousse-Pinguet et al., 2014). However, a deficit of sufficiently mechanistic data means that there is limited ability to understand how intraspecific variability relates to species interactions, and little precedent for how to reconcile this relationship with that between biodiversity-ecosystem functioning (Valverde-Barrantes et al., 2013; Benavides et al., 2019). Fundamentally, any plasticity in species traits that arises in response to the biodiversity of their community is a vital component of that biodiversity, and one which affects its contributions to ecosystem functioning (Valverde-Barrantes et al., 2013; Bennett et al., 2016). Biodiversity experiments or surveys which fail to incorporate these dynamics will result in an incomplete understanding of the biotic control of ecosystem functioning, as they are unable to identify how the interactions of species alter their trait expression, functional roles or contributions. To rely on recommendations or projections from these approaches is to potentially jeopardise the effectiveness of ecosystem management, by producing incorrect or insufficient targets for biodiversity to supply desired functioning and services. Management decisions will benefit from a more in-depth analysis of community and trait structure to reveal changes in functional diversity that will forewarn the loss of function and service delivery (Clements & Ozgul, 2016; Siwacka et al., 2020).

Here, I empirically investigated the importance of intraspecific trait expression for mediating the effects of changing biodiversity on ecosystem functioning in an intertidal soft-sediment ecosystem. Using four functionally contrasting sediment-dwelling invertebrate species, I quantified intraspecific trait expression alongside community-level behaviour (bioturbation and bioirrigation) and associated impacts on ecosystem functioning (dissolved nutrient concentrations). In demonstrating that the variability of species contributions to community behaviour and ecosystem functioning is underpinned by species-specific interactions and differences in individual trait expression, I show that understanding the BEF relationship necessitates appreciation for the variability of species' trait identities under differing community contexts.

4.3 Materials and methods

4.3.1 Species collection and experimental design

Four co-occurring sediment invertebrate species - the polychaetes *Hediste diversicolor* and *Nephtys hombergii*, the bivalve *Macoma balthica* and the gastropod *Peringia ulvae* - were collected from Bridgwater Bay National Nature Reserve, Somerset (51°12'27.41"N, 3°5'34.32"W) (Appendix C, Table C1 and Fig. C1 & C2), and transported to the University of Southampton in aerated water baths. These species were selected due both to their ubiquitous co-occurrence and numerical dominance in UK intertidal muddy sediments (Kay & Knights, 1975), as well as their contrasting morphologies, life histories and functional roles. Under categorical frameworks, *Hediste diversicolor* has been classified as a biodiffusor with free movement via burrow systems, *N. hombergii* a biodiffusive upward/downward conveyor with free movement through the sediment matrix, *M. balthica* a surficial modifier with limited movement, and *P. ulvae* a surficial modifier with slow, free movement through the sediment matrix (Queirós et al., 2013).

To assemble mesocosms, estuarine mud from Hamble-le-Rice, Hampshire (50°52'23.1"N 1°18'49.3"W), was sieved (500 µm mesh) in a seawater bath to remove macrofauna, allowed to settle for 48 h, homogenised, added to mesocosms (settled depth ~ 10 cm), and overlaid with seawater (depth ~ 20 cm, UV filtered, salinity 33). Mesocosms consisted of transparent Perspex aquaria (internal dimensions, LWH 12 x 12 x 35 cm). After 24 h and prior to the addition of the organisms, the seawater was replaced to remove excess dissolved nutrients associated with mesocosm assembly. Replicate (n = 4) macrofaunal communities were assembled in monoculture and mixtures of all possible two-, three- and four-species compositions (total n = 60) (Appendix C, Table C2). Total biomass was standardised across species richness treatments (1.5 g per mesocosm), rather than abundance, as body size integrates functional traits with influence on sediment reworking (Solan et al., 2004a; Wohlgemuth et al., 2016). All mesocosms were continually aerated and maintained at 14 ° C for 5 weeks. Mesocosms were fed twice a week with a 20 ml of dilute phytoplankton culture. To avoid excessive accumulation of nutrients and metabolites, a partial (~ 50%) seawater change was performed once a week.

4.3.2 Measures of intraspecific trait expression

At the end of the incubation period, individual-level trait expression was quantified by measuring movement and burial behaviours of individuals at the sediment surface using a bench top digital camera (1.3 megapixels, 30 frames per second). To measure the rate of movement (cm s^{-1}) of *P. ulvae*, the surface of each mesocosm was recorded for 10 min, and the movement of five randomly selected individuals across the sediment surface was quantified. All individuals of the other species were then removed from each mesocosm by sieving (500 µm mesh) in a seawater bath. *Hediste diversicolor, N. hombergii* and *M. balthica* were placed on the surface in a temperature-controlled tray of sediment (30 mm depth overlaid with 50 mm seawater) to record, i) the time taken to begin movement (s), and ii) the time taken to fully bury into the sediment (s).

All individuals were preserved in pH buffered formalin (10% formaldehyde), and individual biomass (g, wet weight biomass) and individual morphological traits were determined. Scale images (48-bit colour, 2400 dpi) of all individuals were taken using an Epson Perfection V88 Photo bench top scanner (Appendix C, Fig. C3). Morphological metrics for *H. diversicolor, N. hombergii* and *M. balthica* (animal width and length as viewed from the ventral surface (cm), and biovolume of the ventral surface (cm^2)) were measured using Image J (version 1.46r, Schneider et al., 2012). Due to the high collinearity between the four morphological trait metrics, individual biomass was used throughout analyses to represent morphological trait expression of *H. diversicolor, N. hombergii* and *M. balthica* (Appendix C, Fig. C4). The biomass (g, wet weight biomass) and size distributions of *P. ulvae* were consistent between mesocosms, and this variable was thus not included during analysis of individual-level behaviour (for details, see Appendix C, Fig. C5).

4.3.3 Measures of community behaviour

Burrow ventilation (bioirrigation activity) was estimated by measuring relative change in water column concentrations of the inert tracer sodium bromide (NaBr, 5 mM aquaria^{-1}) over an 8 h period (Forster et al., 1999; Godbold & Solan, 2013). Filtered water samples (25 ml, 0.45 µm cellulose acetate membrane filter) were taken on the final day of the incubation period and stored at ambient temperature until colorimetric analysis (FIAstar 5000 flow injection analyser, FOSS Tecator at University of Aberdeen, Aberdeenshire). Bioirrigation was estimated from the change in bromide concentration ($\Delta[Br^-]$, mg L $^{-1}$; negative values indicate increased bioirrigation activity).

Faunally-mediated particle reworking (bioturbation) was estimated using sediment profile imaging (f-SPI) (Solan et al., 2004b; Godbold & Solan, 2013) at the end of the incubation period. To visualise particle movement, 24 g dry weight of dyed sediment that fluoresces in UV light (green colour; < 125 µm; Brianclegg Ltd., UK) was added to each mesocosm and incubated for 8 d. This length of time allows faunally-mediated particle movement to be visualised while avoiding vertical homogenization of the tracers (Godbold & Solan, 2011). Images of all four sides of each mesocosm were taken in a UV illuminated imaging box. Following Solan et al. (2004b), images were saved in RGB colour mode with JPEG compression and analysed using a semi-automated macro that runs within ImageJ (version 1.46r), a Java-based public domain program (Schneider et al., 2012). From these data, the maximum ($^{f\text{-}SPI}L_{max}$), mean ($^{f\text{-}SPI}L_{mean}$) and median ($^{f\text{-}SPI}L_{median}$) depth of particle reworking was calculated, and surficial activity (surface boundary roughness, SBR) was estimated using the maximum vertical deviation of the sediment-water interface (upper – lower limit) (Hale et al., 2014).

4.3.4 Measures of ecosystem functioning

After an 8 d incubation period, nutrient concentrations (ammonium, NH_4- N; total nitrate, NO_x-N; and phosphate, PO_4-P, µ mol L^{-1}) were determined from seawater samples taken in the centre of each mesocosm at approximately 5 cm depth (20 mL, 0.45 µm pre-filtered, Agilent Captiva) using a segmented flow analyser (QuAAtro39 AutoAnalyzer).

4.3.5 Statistical analysis

All statistical analyses were performed using the *R* statistical and programming environment (R Core Team, 2017) and the nlme package (Pinheiro et al., 2014). For all analyses, the assumptions of initial Analysis of Variance (ANOVA) models were first assessed visually for normality (Q-Q plot), homogeneity of variance (residual vs. fitted values), and the presence of influential data points (Cook's distance > 1).

To determine the effect of species richness (4 levels, being the number of species in the community between 1 - 4) or species composition (15 levels overall and 8 levels per species, being the specific combination of species in a community) on individual trait expression (time taken to begin movement and complete burial) of *H. diversicolor, N. hombergii* and *M. balthica,* I used a 1-way ANOVA with a generalised least squares (GLS) approach (Zuur et al., 2009). Data exploration indicated small amounts of heterogeneity of variance in individual-level trait expression due to differences in the number of individuals per species and richness level. Therefore, GLS was used to incorporate the variance covariates *varFixed* or *varPower* for continuous explanatory variables (number of individuals per treatment level) and *varIdent* for categorical explanatory variables (species richness or species composition) to model the variance structure (Zuur et al., 2009). The optimal random effects structure was determined using restricted maximum likelihood (REML) estimation by comparing the initial model with and without a variance structure using AIC and visualisation of model residuals. The optimal fixed effects structure was then determined using maximum likelihood (ML) estimation.

One-way ANOVA models were developed to investigate the effect of species richness and species composition on the rate of surface movement of individual *P. ulvae* (cm s^{-1}), and also to test the effect of species richness and species composition on community-level behaviours (${}^{f\text{-}SPI}L_{mean}$, ${}^{f\text{-}SPI}L_{max}$, ${}^{f\text{-}SPI}L_{median}$, SBR, $\Delta[Br^{-}]$) and nutrient concentration ([NH_4-N], [NOx-N], [PO_4-P]). I used 4-way ANOVA to test whether the presence or absence of each species (*H. diversicolor, M. balthica, N. hombergii* and *P. ulvae*) within a community affected community-level behaviours (${}^{f\text{-}SPI}L_{mean}$, ${}^{f\text{-}SPI}L_{max}$, ${}^{f\text{-}SPI}L_{median}$, SBR, $\Delta[Br^{-}]$).

For *H. diversicolor*, *N. hombergii* and *M. balthica* communities, ANOVA was used to establish the relationship between the magnitude (mean) and variability (coefficient of variation, CV, the ratio of the standard deviation to the mean) of morphological trait expression (biomass), and the time taken for those individuals to begin movement or complete burial (Appendix C, Fig. C6 – C7 & Table C3 – C4). Where the presence of a species was shown to significantly affect community-level behaviour, I used variance partitioning to quantify the link between magnitude (mean) and variability (CV) of trait expression within a community, and sediment reworking behaviour ($^{f\text{-}SPI}L_{mean}$, $^{f\text{-}SPI}L_{max}$, $^{f\text{-}SPI}L_{median}$, SBR) of that same community (Appendix C, Table C5).

4.4 Results

4.4.1 Intraspecific trait expression

Overall, I found that species richness effects on individual-level trait expression (time taken to begin movement and time taken to complete burial) were species specific, and mediated by the presence or absence of individual species within a community. However, I found no significant relationship between the magnitude (mean) and variability (CV) of species' morphological trait expression within a community, and the intraspecific behavioural traits expressed by those same organisms (Appendix C, Fig. C6 – C7 & Table C3 – C4).

4.4.1.1 Effects of species richness on intraspecific behavioural trait expression

All species exhibited broad though largely non-significant trends with species richness in the expression of the two surface behaviours (Fig. 4.1). For *H. diversicolor or M. balthica* neither of the two surface behaviours were significantly affected by the species richness of their community (time taken to begin movement: *H. diversicolor*: F = 1.83, d.f. = 3, *P* = 0.15, Appendix C, Model C3, Fig. 4.1a, *M. balthica*: F = 2.12, d.f. = 3, *P* = 0.096, Appendix C, Model C5, Fig. 4.1e; time taken to complete burial: *H. diversicolor*: F = 0.18, d.f. = 3, *P* = 0.91, Supporting Model C4, Fig. 4.1b, *M. balthica*: F = 0.30, d.f. = 3, *P* = 0.83, Supporting Model C6, Fig. 4.1f). For *N. hombergii*, the time taken to complete burial did not differ between species richness levels (F = 1.21, d.f. = 3, *P* = 0.95, Appendix C, Model C2, Fig. 4.1d). Nevertheless, patterns in the results indicate that the time taken for individuals to begin movement in *M. balthica* and to complete burial in *N. hombergii* (Fig. 4.1e & 4.1d) increased in the highest richness treatments relative to that of individuals in monoculture, while the time to begin movement for *H. diversiolor* (coefficient ± SE = −0.41 ± 14.54, t = −0.03, *P* = 0.98) was greater and more variable in the monoculture treatment. However, for *N. hombergii* the time taken to begin movement was marginally significantly affected by species richness (F = 2.67, d.f. = 3, *P* = 0.048, Appendix C, Model C1), indicating that that towards higher levels of species richness, individuals may take longer to begin movement (Fig. 4.1c). The rate of surface movement of *P. ulvae* increased with species richness (ANOVA: $F_{7,152}$ = 2.27, *P* =

0.038, Fig. 4.3a), as individuals tended to move faster with elevated species richness from a mean (± SE) 0.29 ± 0.04 cm s^{-1} in monoculture up to 0.41 ± 0.03 cm s^{-1} in the three-species mixture.

4.4.1.2 Effects of species composition on intraspecific behavioural trait expression

My results suggest that the effects of biotic context on individual species behaviours were highly species-specific. The two surface behaviours of *H. diversicolor* (time taken to begin movement: F = 1.37, d.f. = 7, *P* = 0.23, Appendix C, Model C11, Fig. 4.2a, time taken to: complete burial (F = 0.59, d.f. = 7, *P* = 0.76, Appendix C, Model C12, Fig. 4.2b) did not differ between mixtures of differing species composition.

However, for all other taxa, differences were prevalent. *M. balthica* individuals expressed behaviours significantly differently between mixtures of differing species composition (time taken to begin movement: F = 3.65, d.f. = 7, *P* < 0.001, Appendix C, Model C9, Fig. 4.2e, time taken to complete burial: F = 4.97, d.f. = 7, *P* < 0.001, Appendix C, Model C10, Fig. 4.2f). Results show that the time taken for *M. balthica* to both begin movement (Fig. 4.2e) and complete burial (Fig. 2f) was shorter for individuals in the presence of *N. hombergii*, and longer in the presence of *H. diversicolor* in two- or three species mixtures. For *N. hombergii,* both behaviours varied significantly with species composition (time to begin movement: F = 3.92, d.f. = 7, *P* < 0.001, Appendix C, Model C7, Fig. 4.2c, time to complete burial: F = 3.30, d.f. = 7, *P* = 0.0021, Appendix C, Model C8, Fig. 4.2d). The time taken for *N. hombergii* to both begin movement (Fig. 4.2c) and complete burial (Fig. 4.2d) was fastest for individuals in communities with *H. diversicolor* or *P. ulvae* in two or three-species mixtures. In the presence of *M. balthica* however, the time taken for *N. hombergii* to begin movement and complete burial overall took longer. The rate of surface movement of *P. ulvae* also differed with species composition (ANOVA: $F_{3,156}$ = 2.87, *P* = 0.032, Fig. 4.3b), being lower when maintained with *H. diversicolor* and greater when maintained with *N. hombergii.*

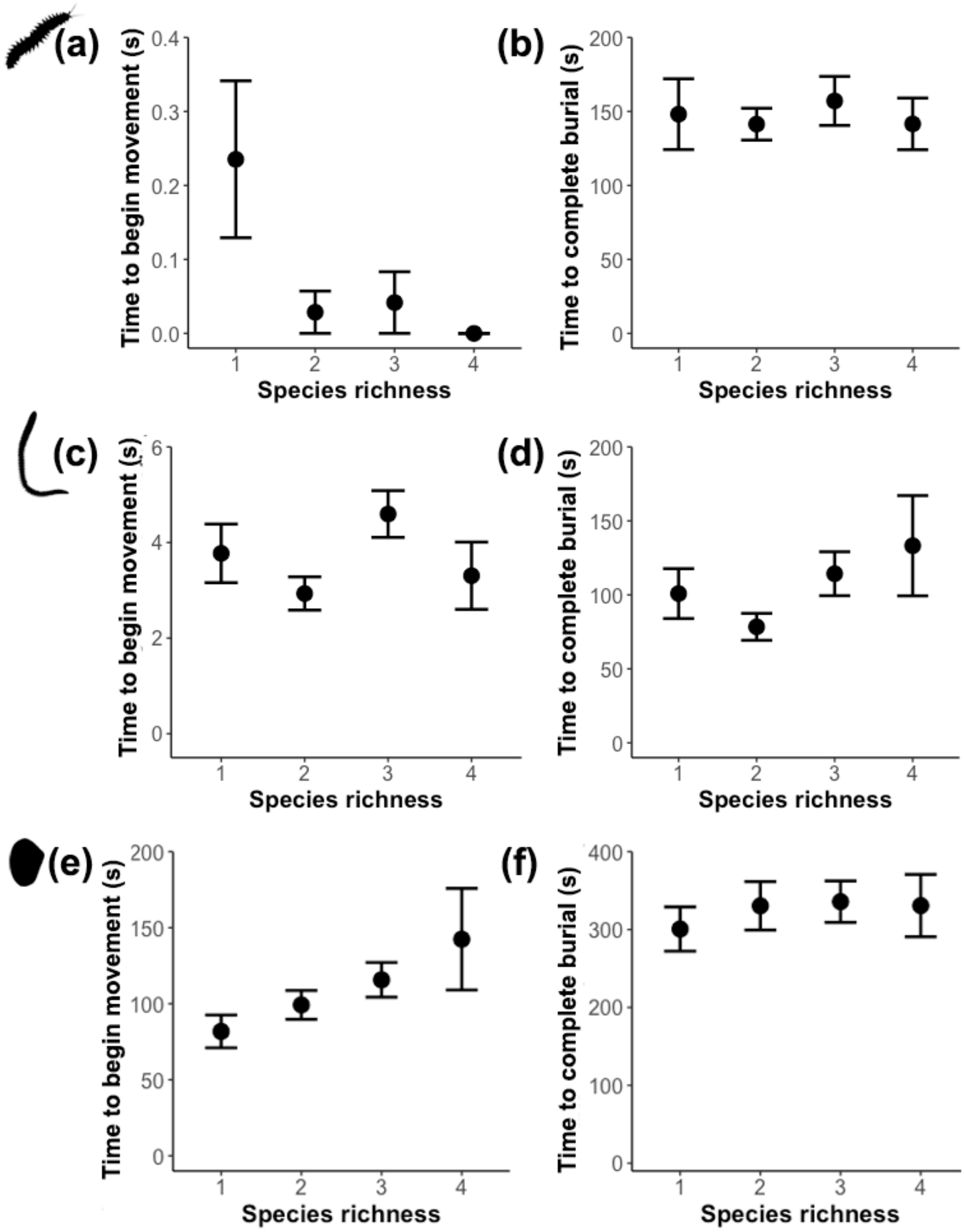


Fig. 4.1: The effect of species richness on the mean (± SE) (s) (**i**) time taken to begin behaviour and (**ii**) the time taken to complete burial for individuals of (**a, b**) *Hediste diversicolor*, (**c, d**) *Nephtys hombergii and* (**e, f**) *Macoma balthica*, showing significant differences between mixtures of differing species richness for *N. hombergii*.

In all figures,  represents *H. diversicolor*,  represents *N. hombergii*,  represents *M. balthica* and  represents *Peringia ulvae.*

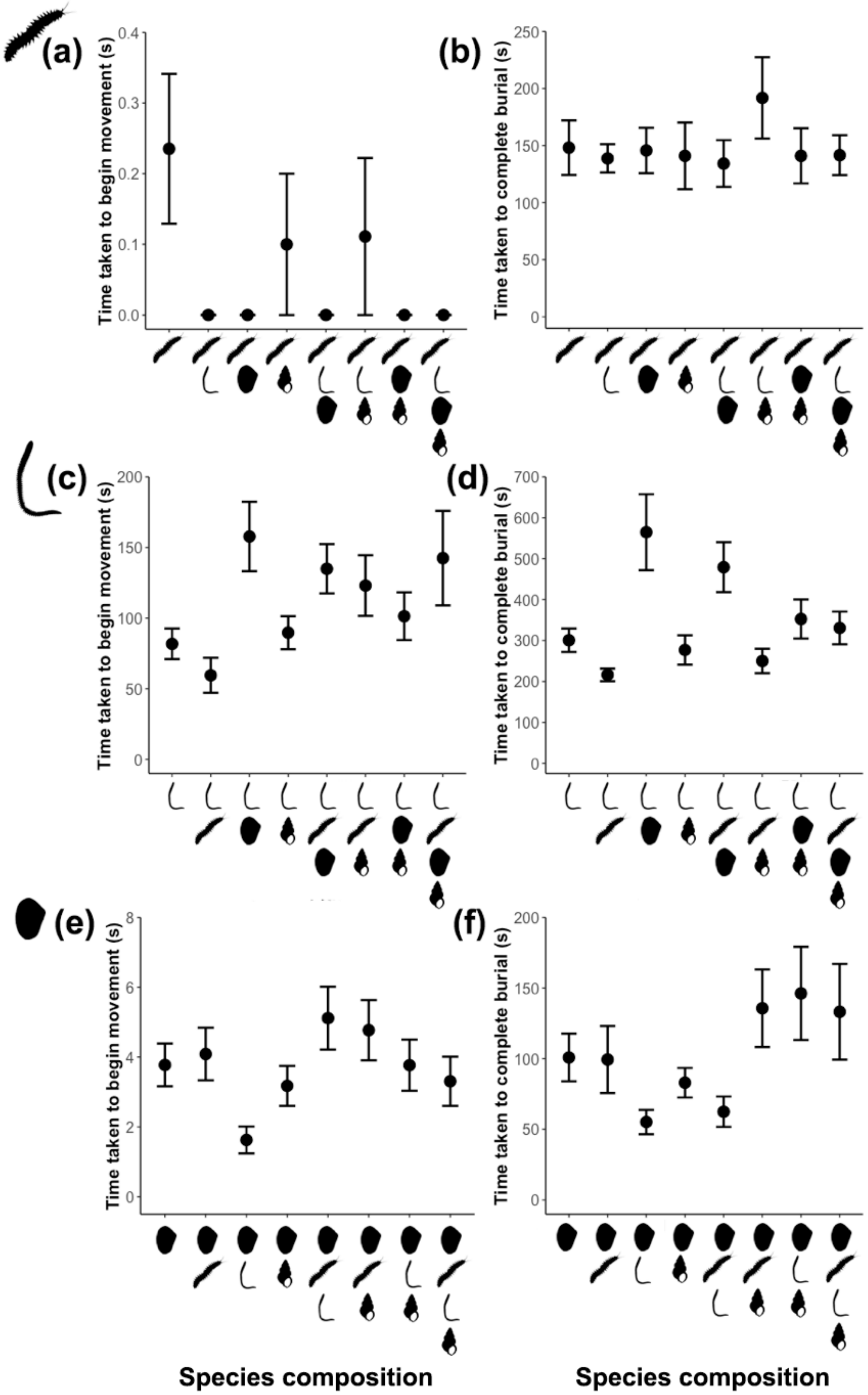


Fig. 4.2: The effect of species composition on the mean (± SE) (s) (**a, c, e**) time taken to begin behaviour and (**b, d, f**) the time taken to complete burial for (**a, b**) *Hediste diversicolor,* (**c, d**) *Nephtys hombergii* and (**e, f**) *Macoma balthica*, showing significant differences between differing species compositions for (**c, d**) *N. hombergii* and (**e, f**) *M. balthica*.

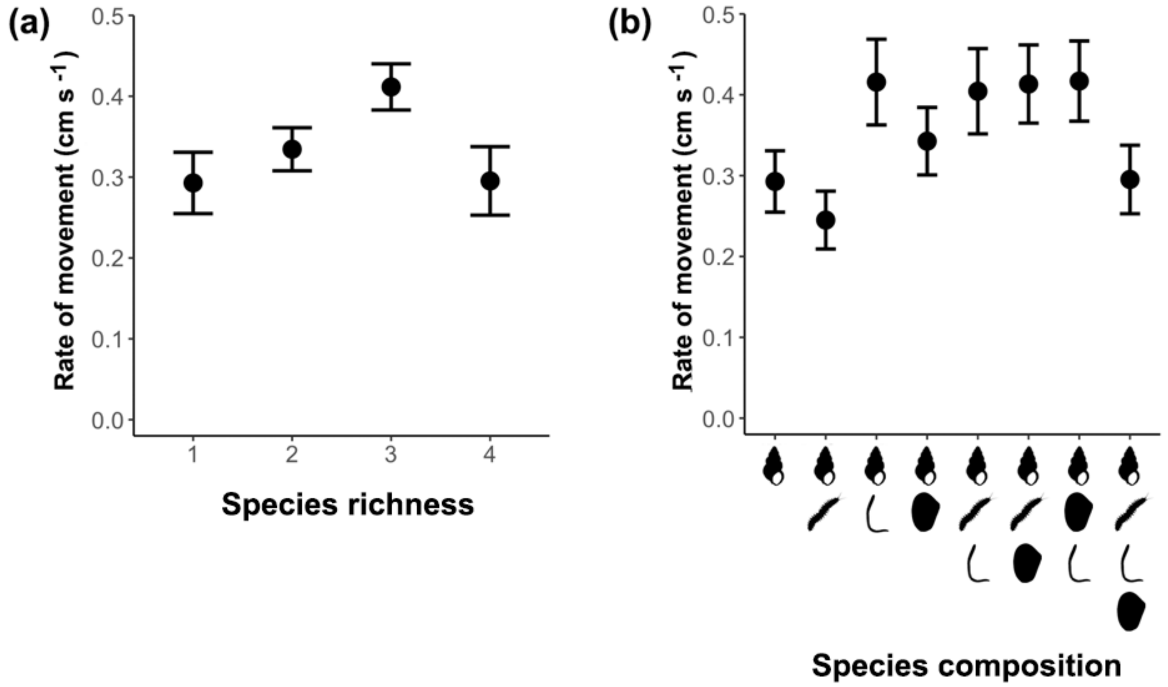


Fig. 4.3: The effect of (**a**) species richness and (**b**) species composition on the mean (± SE) rate of movement (cm s^{-1}) on the sediment surface of *Peringia ulvae*, showing significant differences between both species richness levels and species compositions.

4.4.2 Community behaviour

Overall, I found differences in community-level bioturbation behaviour between different levels of richness and between mixtures composed of differing species. Significant differences were highly dependent the presence or absence of specific species in mixture. Variance partitioning analysis showed that the inclusion of the mean and CV of individual-level behavioural and morphological traits reduced the variation in all community-level behaviours unexplained by species richness or composition (Appendix B, Table B5). Species composition consistently explained in excess of double the variation in community-level behaviour than was explained by species richness, when compared between models, in all tested combinations.

4.4.2.1 Effects of species richness on community-level behaviour

Bioirrigation ($\Delta[Br^-]$) did not differ with species richness (ANOVA: $F_{3,55} = 1.97$, $P = 0.13$, Appendix C, Table C8 & Fig. C8) or surface boundary roughness (ANOVA: $F_{3,56} = 1.05$, $P = 0.38$). However, patterns indicate that SBR increased was lowest in the four-species mixture in comparison to the other richness levels (Fig. 4.4a). Bioturbation depth became deeper with species richness (ANOVA: $^{f\text{-}SPI}L_{median}$: $F_{3,56} = 2.67$, $P = 0.0562$, Fig. 4.4b; $^{f\text{-}SPI}L_{mean}$: $F_{3,56} = 7.62$, $P < 0.001$, Fig. 4.4c; $^{f\text{-}SPI}L_{max}$: $F_{3,56} = 4.89$, $P < 0.001$, Fig. 4.4d). Mean bioturbation depth ($^{f\text{-}SPI}L_{mean,}$ mean ± SE) more than doubled from 0.74 ± 0.08 cm in monoculture to 1.71 ± 0.39 cm in the 4-species mixture (Fig. 4.4c), whilst maximum bioturbation depth ($^{f\text{-}SPI}L_{max}$, mean ± SE) increased from 5.99 ± 0.83 cm in monoculture to 10.33 ± 0.43 cm at the highest species richness level (Fig. 4.4d).

4.4.2.2 Effects of species composition on community-level behaviour

Bioirrigation ($\Delta[Br^-]$) did not differ significantly between mixtures composed of differing species (ANOVA: $F_{14,44} = 1.16$, $P = 0.34$, Appendix C, Table C8 & Fig. C8). However, all measures of sediment reworking were significantly affected by the species composition of the community. SBR differed with species composition (ANOVA: $F_{14,45} = 1.99$, $P = 0.04$), and was significantly influenced by the interactive effect of the presence of the species *M. balthica* x *P. ulvae* (ANOVA: $F_{1,51} = 6.75$, $P = 0.01$). SBR was consistently higher in mesocosms containing *M. balthica* (Fig. 4.5a). Overall, $^{f\text{-}SPI}L_{median}$ differed significantly between species mixtures (ANOVA: $F_{14,45} = 2.48$, $P = 0.01$), and was affected by the presence of *H. diversicolor* (ANOVA: $F_{1,56} = 9.57$, $P < 0.001$) and *P. ulvae* (ANOVA: $F_{1,56} = 18.54$, $P < 0.001$). $^{f\text{-}SPI}L_{median}$ was deeper in mesocosms containing *H. diversicolor* and *P. ulvae* than those in which they are absent, but which otherwise share the same species composition (Fig. 4.5b). $^{f\text{-}SPI}L_{mean}$ differed significantly with species composition (ANOVA: $F_{14,45} = 6.26$, $P < 0.001$), and was dependent on the interactive effect of the presence of *H. diversicolor* x *P. ulvae* (ANOVA: $F_{14,54} = 5.17$, $P = 0.03$) and *M. balthica* x *P. ulvae* (ANOVA: $F_{14,54} = 5.38$, $P = 0.02$). $^{f\text{-}SPI}L_{mean}$ was consistently deeper in mesocosms containing *H. diversicolor* and consistently shallower in mesocosms containing *P. ulvae*. In treatments containing both *P. ulvae* and *M. balthica,* $^{f\text{-}SPI}L_{mean}$ was found to be deeper in comparison to when these species are in monoculture (Fig. 4.5c). $^{f\text{-}SPI}L_{max}$ differed significantly with species composition (ANOVA: $F_{14,54} = 11.62$, $P < 0.001$), and species-specific effects were largely dominated by the presence of *H. diversicolor* and its interactions with other species. $^{f\text{-}SPI}L_{max}$ differed with interactive effect of the presence of *H. diversicolor* x *N. hombergii* (ANOVA: $F_{1,51} = 8.89$, $P < 0.001$), *H. diversicolor* x *M. balthica* (ANOVA: $F_{1,51} = 4.31$, $P = 0.04$), and *N. hombergii* x *P. ulvae* (ANOVA: $F_{1,51} = 6.24$, $P = 0.02$). I found that treatments containing *H. diversicolor* consistently reached the deepest depths and, where the species was absent, ${}^{f\text{-}SPI}L_{max}$ was instead driven by the interaction between other species (Fig. 4.5d).

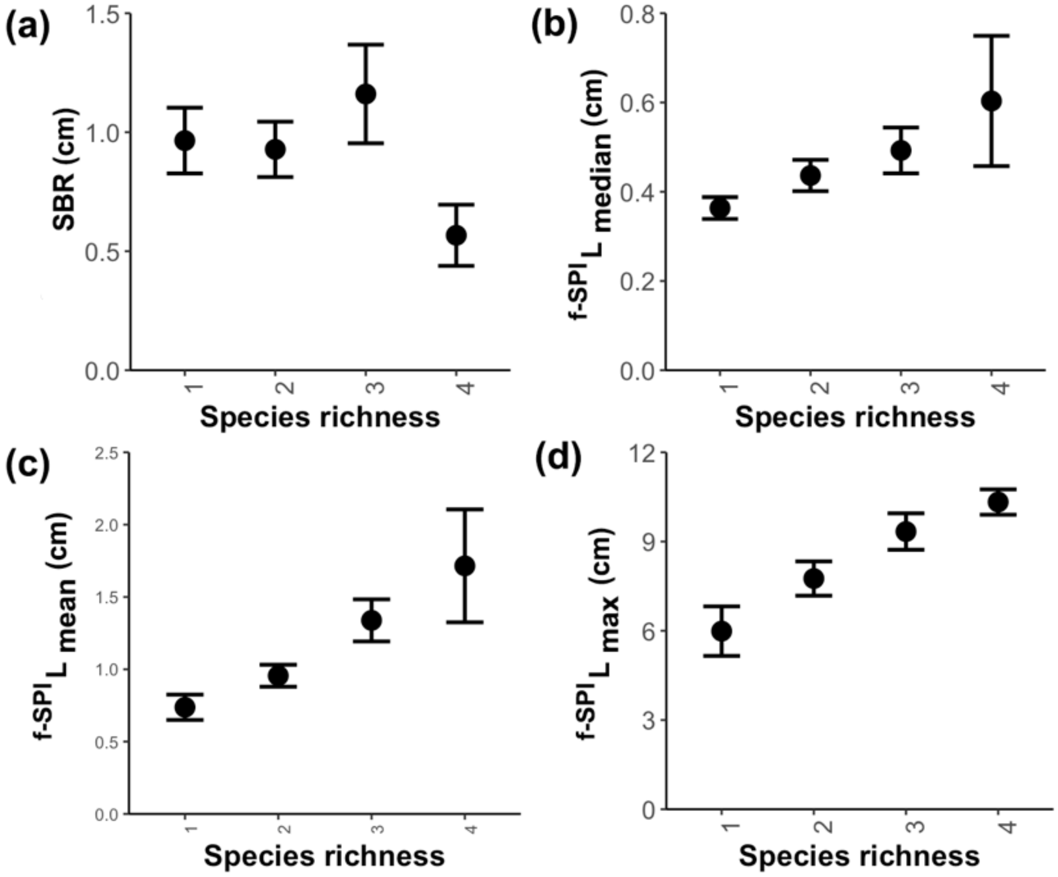


Fig. 4.4: The effect of community species richness on the mean (± SE) (cm) (**a**) surface boundary roughness (SBR), (**b**) median mixed depth, ${}^{f\text{-}SPI}L_{median}$, (**c**) mean mixed depth, ${}^{f\text{-}SPI}L_{mean}$, and (**d**) maximum mixed depth, ${}^{f\text{-}SPI}L_{max}$ of sediment reworking. Significant differences were prevalent between richness levels for (**c**) ${}^{f\text{-}SPI}L_{mean}$ and (**d**) ${}^{f\text{-}SPI}L_{max}$.

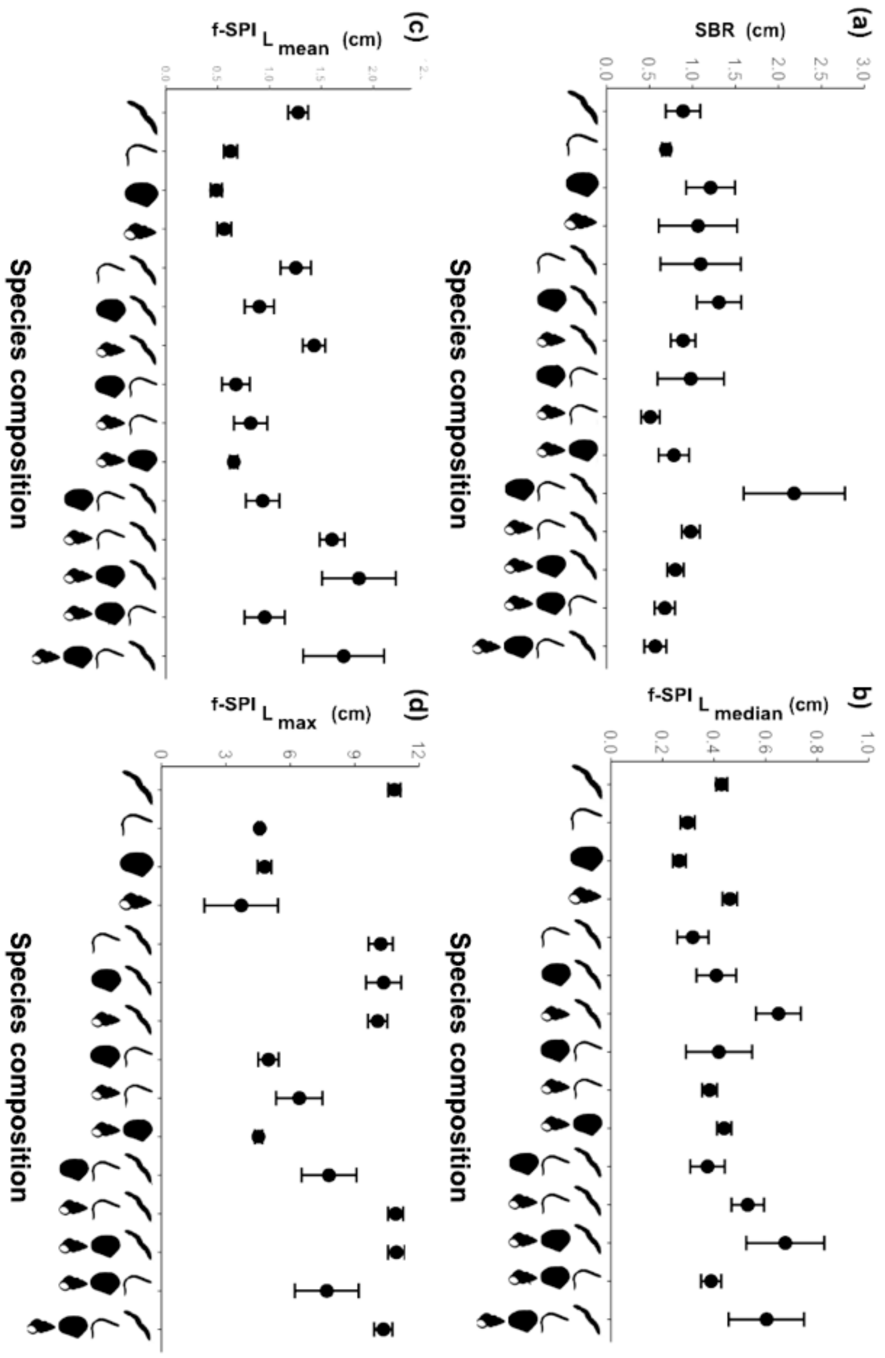


Fig. 4.5: The effect of species composition on the mean (± SE) (cm) (**a**) surface boundary roughness (SBR), (**b**) median mixed depth, $^{f\text{-}SPI}L_{median}$, (**c**) mean mixed depth, $^{f\text{-}SPI}L_{mean}$, and (**d**) maximum mixed depth, $^{f\text{-}SPI}L_{max}$, of sediment reworking, showing significant differences between species compositions for all net community behaviours. (**a**) SBR was dependent on the interactive presence of *Macoma balthica* x. *Peringia ulvae*. (**b**) $^{f\text{-}SPI}L_{median}$ was dependent on the independent effects of the presence of *Hediste diversicolor* and *P. ulvae*. (**c**) $^{f\text{-}SPI}L_{mean}$ was dependent on the interactive presence of the species *H. diversicolor* x *P. ulvae*, and *M. balthica* x *P. ulvae*. (**d**) $^{f\text{-}SPI}L_{max}$ was dependent on the interactive presences of *H. diversicolor x Nephtys hombergii*, *H. diversicolor* x *M. balthica*, and *N. hombergii* x *P. ulvae*.

4.4.3 Ecosystem functioning

Overall, I found no significant differences in nutrient concentration between communities of differing species richness. Instead, significant differences were dependent on species composition, and the presence or absence of specific species in mixture.

4.4.3.1 Effects of species richness on ecosystem functioning

No significant effects of species richness were found on [NH_4-N] (ANOVA: $F_{3,56} = 0.16$, $P = 0.92$), [NOx-N] (ANOVA: $F_{3,56} = 0.77$, $P = 0.52$) or [PO_4-P] (ANOVA: $F_{3,56} = 0.25$, $P = 0.86$) (Appendix C, Table C9 & Fig. C9).

4.4.3.2 Effects of species composition on ecosystem functioning

[NH_4-N] differed significantly between mixtures composed of differing species (ANOVA: $F_{14,45} = 2.75$, $P < 0.001$), and was significant affected by the presence of *H. diversicolor* x *N. hombergii* (ANOVA: $F_{1,47} = 6.20$, $P = 0.02$) and independently by the presence of *P. ulvae* (ANOVA: $F_{1,47} = 11.53$, $P < 0.001$). I found that [NH_4-N] was higher in communities containing *H. diversicolor* x *N. hombergii* and lower in species mixtures containing *P. ulvae* (Fig 4.6a). [NOx-N] differed significantly with species composition (ANOVA: $F_{14,45} = 5.23$, $P < 0.001$), and was affected independently by the presence of *H. diversicolor* (ANOVA: $F_{1,48} = 33.00$, $P < 0.001$), *N. hombergii* (ANOVA: $F_{1,48} = 11.71$, $P < 0.001$) and *P. ulvae* (ANOVA: $F_{1,48} = 16.53$, $P < 0.001$). [NOx-N] concentrations were higher in communities containing *N. hombergii* or *P. ulvae* and reduced in communities containing *H. diversicolor* (Fig. 4.6b). Finally, [PO_4-P] differed significantly with species composition (ANOVA: $F_{14,45} = 11.27$, $P < 0.001$). [PO_4-P] was mediated by the presence of *H. diversicolor* x *N. hombergii* (ANOVA: $F_{1,53} = 7.64$, $P < 0.001$), and independently by the presence of *P. ulvae* (ANOVA: $F_{1,53} = 4.29$, $P = 0.05$). Overall, [PO_4-P] concentrations were reduced in communities containing *H. diversicolor,* and elevated in communities containing *N. hombergii* or *P. ulvae* (Fig. 4.6c).

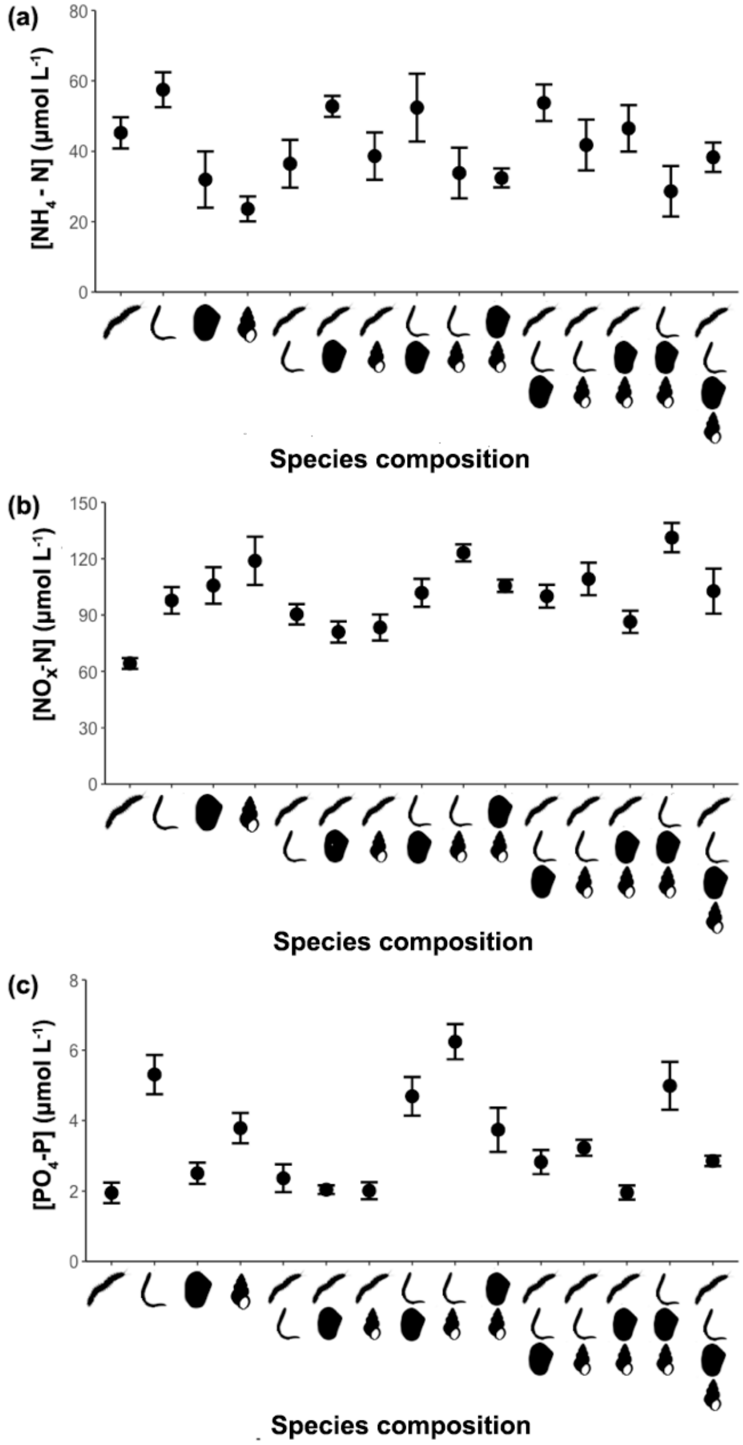


Fig. 4.6: The effect of species composition on the mean (± SE) concentration (µmol L^{-1}) of (**a**) [NH_4-N], (**b**) [NO_x-N], and (**c**) [PO_4-P], showing significant differences between species compositions for all nutrients. (**a**) [NH_4-N] was dependent on the interactive effect of the presence of *Hediste diversicolor* x *Nepthys hombergii*, and the independent effect of the presence of *Peringia ulvae*. (**b**) [NO_x-N] differed with the independent presence of *H. diversicolor*, *N. hombergii*, and *P. ulvae*. (**c**) [PO_4-P] differed significantly with the interactive effect of the presence of *H. diversicolor* x *N. hombergii*, and the independent presence of *P. ulvae*.

4.5 Discussion

My results show that individual-level quantification identifies significant intraspecific trait variation between species mixtures, and so demonstrate the necessity of incorporating this detail into study of biodiversity and the trait-ecosystem functioning relationship. Conventional trait-based approaches typically harness a single generalised value rather than measurement of individuals, which are frequently drawn from the literature or databases (e.g. Kleyer et al., 2008; Kattge et al., 2011; Queirós et al., 2013) that constrain species within broad trait typologies or functional groups. Within-species differences are assumed to be of negligible importance for ecosystem structure and functioning (Violle et al., 2012; Carlucci et al., 2014; Derroire et al., 2018). However, to interpret biodiversity effects as if traits are fixed at the species level may lead to mischaracterisation of biodiversity's effect on ecosystem functioning, as any species interactions are concluded on the basis that there is no context-dependency (Ashton et al., 2010; Pruitt & Ferrari, 2011; Butterfield & Callaway, 2012; Mondy & Usseglio-Polatera, 2014). Mechanisms of species interaction such as complementarity and competition are hypothesised or inferred based solely on interspecific trait differences (Godbold et al., 2009; Bulleri et al., 2013). For example, as complementarity relies on functional trait differences (Violle & Jiang, 2009; Valverde-Barrantes et al., 2013), I expected that the interspecific trait dissimilarity between the experimental species used would support a positive relationship between biodiversity and functioning (Bastias et al., 2017; Cadotte, 2017). Indeed, I found differences between species mixtures for both community-level behaviours, and an ecosystem function which these behaviours are known to mediate (Teal et al., 2010; Wohlgemuth et al., 2016; Murray et al., 2017). However, to draw such conclusions as to the biodiversity-functioning relationship based on solely species-level traits neglects to consider that species alter their trait expression within and in response to differing species mixtures (Start & Gilbert, 2019).

I found that intraspecific variation in trait expression is strongly mediated by biodiversity. The rate of individual-level movement behaviours changed with species richness particularly for *N. hombergii* and *P. ulvae*, and for all four species *H. diversicolor, N. hombergii, M. balthica* and *P. ulvae,* varied with species composition. Notably, the presence or absence of specific species had strong effects on the movement and burial behaviour of other taxa in their assemblage. For example, *N. hombergii* began movement behaviours and completed burial significantly faster when maintained in the presence of *M. balthica* across treatments of differing species composition, and vice versa. My results show that functional trait values of species are altered by biotic context at the level of the individual. Quantification of individual trait expression offers valuable mechanistic insight as to how the morphology, physiology and behaviour of species change with biodiversity (Song et al., 2017; Calder-Potts et al., 2018; Cassidy et al., 2020), and so allows pathways of influence between specific species to be identified. In particular, behavioural factors are among the more flexible aspects of an animal's phenotype given that they are less likely to be constrained by strict tolerances, and so readily and intuitively reflect responses to local species composition (Fisher et al., 2015; Raine et al., 2018; Start & Gilbert, 2019). Plasticity in response to composition is thus difficult to isolate from interactions inferred on the basis of species-level trait identities, as intraspecific variation in measurable traits alters the extent of interspecific differences. Any adjustments in the functional overlap between species influence trait-dependent mechanisms of coexistence such as facilitation and competition (de Bello et al., 2013; Bennett et al., 2016), meaning that intraspecific variation comprises a necessary consideration when seeking to understand the effects of trait and species diversity on ecosystem functioning (Jung et al., 2010; Siefert & Ritchie, 2016; Zwerschke et al., 2018). Inter- and intra-specific trait differences should not be viewed as dichotomous, but rather as inherently linked to one another and to biodiversity effects (Sih et al., 2012; Bastias et al., 2017).

To illustrate, I found substantial differences in sediment reworking and nutrient release between equally species rich communities comprised of *M. balthica*, *H. diversicolor* and *N. hombergii*, and those comprised of *M. balthica*, *H. diversicolor* and *P. ulvae.* All measures of mixed depth were comparatively deeper in the latter community. Distinguishing these communities is the presence of either *N. hombergii* and *P. ulvae.* These two species differ in their movement behaviours, habitat preference and feeding mode as per conventional species-level functional classifications (Huxham et al., 1995; Hedman et al., 2011), and so have discrete impacts on sediment reworking (Queirós et al., 2015). By living freely within the sediment matrix *N. hombergii* exhibits less connection with the sediment-water interface, while *P. ulvae's* surface behaviour is typified by shallow living to graze the sediment surface (Hale et al., 2014). Thus, the extent of sediment reworking within the community is likely to be affected by the way in which *P. ulvae* mixes surface sediment into the bed where it can then be distributed deeply throughout by deeper bioturbating species – here, *H. diversicolor.* This facilitating role is absent in communities where *N. hombergii* has replaced *P. ulvae.*

The broadly contrasting trait types and species-level activities of *N. hombergii* and *P. ulvae* have therefore uniquely contributed to the behaviour and functioning of the community through multiple mechanisms. The presence of any species in mixture will change the overall trait composition and thus the theoretical function potential of a community, with a positive but decelerating relationship between taxonomic and functional diversity (Godbold et al., 2009; Thompson et al., 2018; van der Plas et al., 2019). However, while experimental findings emphasise that ecosystem properties tend to be most strongly influenced by the traits of individual species (Langenheder et al., 2012; Gagic et al., 2015; De Groote et al., 2017), organisms are subject to species-specific interactions with others in their community (Bairey et al., 2019). The specific species composition of a community will alter its net contributions to functioning depending on whether specific trait combinations facilitate or compete with one another in terms of how species navigate space (Mermillod-Blondin et al., 2005; Godbold et al, 2011), use resources (Godbold et al., 2009; Bannar-Martin et al., 2018), or respond to physical or chemical cues (Maire et al., 2010). These interactions lead to strong identity effects that reduce the importance of diversity (Bulleri et al., 2013). Indeed, my results emphasise the importance of the presence or absence of specific species – and by extension, their traits – in mixture, rather than overall species richness in affecting community behaviour and ecosystem functioning. Further, the presence of each species in the community can also prompt cascades of intraspecific change in the individual-level trait expression of other co-occurring taxa (Werner & Peacor, 2003; Siefert & Ritchie, 2016), such as changes in the surface burial behaviour of *M. balthica,* which were faster in the presence of *N. hombergii* relative to the community containing *P. ulvae.* These changes are liable to broaden or narrow the trait differences between species from that assumed from typologies or values assigned at the species-level, so are necessary to consider when inferring species interactions or identity effects. Intraspecific variability promotes coexistence and maximises functioning by enabling species to pass through environmental filters (Jung et al., 2010). To disentangle the respective influence of species and functioning through trait-based approaches requires use of sufficiently detailed data for traits that are directly linked to species' resource use and competitive ability (Violle et al., 2007; Fründ et al., 2013; Mahaut et al., 2020).

My findings have implications for the forecasting and management of systems, particularly where biodiversity is changing, as my results show that the functional contributions of species are highly dependent on their biotic context in terms of richness and species composition. The removal of species from mixture sees the loss not solely of their specific trait values but also of their trait-based influences on other members of the community (Mouillot et al., 2014; Bannar-Martin et al., 2018), and the attainment or maintenance of a certain level of biodiversity *per se* may be insufficient to secure functional benefits (Wohlgemuth et al., 2016). Conservation and restoration approaches typically prioritise taxa which make key contributions to ecosystem functioning and service provision (Laughlin et al., 2014; Ostertag et al., 2015; Bolam et al., 2017). By collection of sufficiently mechanistic data, manipulative experiments and surveys alike will be better able to establish which species have strong influence on these functional deliverables, both directly and via impacts to other species (Start & Gilbert, 2019). Quantification at the individual-level will allow identification of taxa that adjust the trait expression of, and so potentially maximise net functioning of their mixture by interactions with, co-occurring species. Further, it will allow insight into complex pathways of cause-and-effect between species and context that dictate changes in the biodiversity-ecosystem functioning gradient under changing environmental conditions (Suttle et al., 2007; Butterfield & Callaway, 2013; Chamberlain et al., 2014; Zwerschke et al., 2018; Siwicka et al., 2020), for example where increased environmental stress leads to greater complementarity and a reduction in competition (He et al., 2019). Understanding these factors will aid our ability to generalise the biodiversity-ecosystem functioning relationship and identify the functional significance of community attributes (Godbold et al., 2009; Wohlgemuth et al., 2016; Thompson et al., 2018; Start & Gilbert, 2019). To quantify intraspecific variation provides additive benefit beyond the use of species-level trait values by granting more profound insight into the roles of traits in the mediation of ecosystem functioning, between communities as well as between species, and adoption of these approaches will improve the clarity and effectiveness of ecosystem management.

4.6 Conclusions

Overall, I show that species express behavioural traits differently between mixtures of differing composition, as facilitated by discrete species-specific interactions, and intraspecific differences in individual and community trait expression mechanistically contribute to patterns of ecosystem functioning. My results suggest that species cannot be assumed to offer consistent functional contributions irrespective of local ecological context, and that the effectiveness of approaches seeking to forecast ecosystem functioning based on species or trait diversity may be jeopardised should they fail to consider the potential effects of intraspecific variation on this relationship. I highlight that interspecific differences are dependent on intraspecific expression and vice versa, and suggest that both must receive consideration to understand mechanisms of species coexistence and the biodiversity-ecosystem functioning relationship.

Chapter 5 Incorporating intraspecific variation alters functional trait metrics and their utility for understanding and predicting ecosystem functioning

5.1 Abstract

It has been shown that the expression of functional traits by conspecific organisms is highly variable between individuals and communities, and is altered in response to biotic and abiotic conditions. However, many of the trait-metrics that are widely used rely on categorical typologies to represent species morphological, behavioural or physiological traits that largely omit these differences, and in doing so fail to accurately resolve species contributions to ecosystem functioning. Here, I demonstrate that incorporating quantitative measurements of trait expression at the individual-level into trait metrics strongly alters the perceived functional role of species and improves the explanatory power of traits for understanding biological mediation of ecosystem functioning. For empirical data from two model benthic invertebrate systems, multivariate analysis and a variance partitioning approach were applied to metrics that characterise increasingly greater levels of intraspecific measurement, derived from a marine benthic trait metric (bioturbation potential) commonly used to predict ecosystem functioning. My results show that individual-level data describe different information from and better explain changes in ecosystem functioning than a conventional metric which classifies traits into discrete typologies. Quantitatively measuring trait expression better identifies context-dependent changes in species performance, and aids in mechanistically and empirically understanding resultant variability in the trait-functioning relationship. I highlight that trait-based study must carefully consider the perceived trade-offs of information and effort entailed by conventional approaches.

5.2 Introduction

It is clear that conspecific individuals are non-identical, and trait variation is prevalent throughout species in response to a complex and dynamic array of abiotic (Törnroos et al., 2015; Baranov et al., 2016; Calder-Potts et al., 2018; Chapter 2 - 3) and biotic (Chamberlain et al., 2014; Wohlgemuth et al., 2016; Murray et al., 2017; Chapter 2 - 4) factors. Over the past decade the ecological importance of intraspecific variation has been increasingly emphasised (Albert et al., 2010a; Bolnick, 2011; de Bello et al., 2013; Roscher et al., 2015), and variation in the traits expressed by species has been shown to underpin niche differentiation and resource use (Canham et al., 1999; Hart et al., 2016; Hausch et al., 2018; Mahaut et al., 2020), species interactions (Hanksi & Singer, 2001; Pruitt & Ferrari, 2011; Chamberlain et al., 2014; Chapter 4), and population or ecosystem productivity (Fridley & Grime, 2010; Caliman et al., 2012; Start & Gilbert, 2019). By result, quantification of individual-level trait expression can provide detailed mechanistic insight into the functional roles and identities of species.

The determination of trait expression at the scale of the individual can reveal information about species performance under differing environmental or ecological conditions and identify acclimation or adaptation responses (Debouk et al., 2015; Bresta et al., 2018). To do so is necessary to highlight resulting pathways of cause and effect whereby induced changes in species expression alter functional contributions across communities (Calder-Potts et al., 2018; Silva et al., 2019), and so identify traits and trait values key to the provision of ecosystem functions and the delivery of ecosystem goods and services (Bresta et al., 2018; DuBois et al., 2019). Empirical measurement across the range of trait values present in a population allows the confidence and uncertainty of any trait-based analyses and projections to be adjusted (Roscher et al., 2018a), and is a valuable component of Bayesian statistical techniques (Clark, 2005; Norros et al., 2017). As such, it is increasingly suggested that this intraspecific variation be incorporated into trait-based approaches to provide valuable insight into the biotic mediation of ecosystem functioning and, at the same time, improve predictive approaches used to forecast the ecosystem consequences of changing biodiversity (Start & Gilbert, 2019; Benavides et al., 2019).

However, there is little precedent for how intraspecific trait variation can be reconciled with existing trait-based approaches. Conventional trait metrics use minimal quantitative data from measured organisms. These approaches generally constrain the traits representing species' functional potential within categorical typologies, or represent traits using a generalised 'average' value sourced from the literature (e.g. Kleyer et al., 2008; Kattge et al., 2011; Queirós et al., 2013). These techniques are favoured for study that advises ecosystem management (Ostertag et al., 2015; Bolam et al., 2017; Klimkowska et al., 2019), which typically concerns substantial spatial scales where expert knowledge would be needed for many taxa, or empirical efforts would be prohibitively extensive. The accessibility and low logistical intensity of conventional metrics affords the ability to readily make predictions and high-level estimations of functional diversity and functional potential (Messier et al., 2010; Guittar et al., 2016; Gravel et al., 2016), including changes across spatiotemporal gradients (Lammana et al., 2014; van der Sande et al., 2019) or those induced by species loss or turnover (de Vries et al., 2012; Schwoertzig et al., 2016; Howarth et al., 2018). To rely on such metrics, however, introduces inaccuracies as they fail to incorporate the context-dependency of species responses to environmental factors or stressors (Lepš et al., 2011; Pescador et al., 2015; Volf et al., 2016; Salo et al., 2020). Fuzzy-coding (Chevene et al., 1994; Castella & Speight, 1996) may be used to incorporate trait variability, however practices vary widely between practitioners (Mondy & Usseglio-Polatera, 2014; Schmera et al., 2015; Howarth et al., 2018). Notably, the use of categorical approaches still fails to resolve the roles and functional contributions of taxa that share typologies or exist within the same functional group - such as those which are taxonomically close or morphologically similar - yet express the traits which define these typologies in different ways or to differing extents. Incorporating intraspecific differences into trait metrics will relieve potential sources of procedural error carried by current practices and offers valuable opportunity to improve the understanding of how species both respond to, and contribute to the functioning of, their ecosystem.

The grounding of trait measurement in an individual or individuals, and the completeness of this sampling relative to the population density, will have a serious impact on the value of any functional trait computed and on any conclusions or projections drawn from such data. Thus, studies seeking to represent the contributions of taxa to functional diversity must consider biases entailed by their sampling scheme or lack thereof (Pakeman, 2014). Here, I demonstrate this within populations of benthic invertebrate species, by generating trait metrics using increasingly complete individual-level data. I highlight the ability of these metrics to discriminate differing functional trait expression and explain variation in ecosystem functioning beyond that of a widely accepted metric based on trait categorisations (bioturbation potential, Solan et al., 2004a). I then assess under which circumstances the measurement of intraspecific variation to identify their context-dependency is likely to be a worthwhile expenditure of sampling time and effort.

5.3 Methodology

5.3.1 Case study selection and background

I use data from two experimental manipulations of model benthic systems (hereafter Case Study 1 & 2) to demonstrate potential applications where individual-based trait metrics could be used to represent species performance. Case Study 1 uses data from Chapter 4, an experiment in which three species of sediment-dwelling invertebrates (the polychaetes *Hediste diversicolor* and *Nephtys homergii*, and the bivalve mollusc *Macoma balthica*) were maintained in monoculture and all possible combinations of 2- and 3-species mixtures. Case Study 2 uses data from Chapter 3, an experiment in which replicate communities of two ophiuroid echinoderm species (*Amphiura* *filiformis* and *Amphiura chiajei*) in either monoculture or in mixture were maintained under contrasting climate conditions (ambient: temperature ° C / 400 ppm atmospheric [CO_2], or anticipated future: ambient temperature + 2 ° C / 550 ppm atmospheric [CO_2]). These case studies were chosen as both quantified individual and community trait expression under differing biotic and abiotic contexts in combination with measurements of ecosystem functioning in the form of dissolved sediment nutrient release (ammonium, [NH_4- N]; nitrate, [NO_3-N]; nitrite, [NO_2-N]; and phosphate, [PO_4-P], µmol L^{-1}).

Table 5.1 The three traits defining biomass (B_i), motility (M_i), and sediment reworking (R_i) used to calculate the per capita bioturbation potential of individuals from a single-species population (BP_i), and their individual-level counterparts (B_q, M_q and R_q) used to calculate the new quantitative metrics ^{Subsampled}Arithmetic, ^{Total}Arithmetic, and Distribution mean.

BP_i (Solan et al., 2004a)		**^{Subsampled}Arithmetic, ^{Total}Arithmetic, and Distribution mean**		
B_i	Total biomass/total abundance, of a species within a community (g)	**B_q**	Individual measures of biomass (g)	
M_i	Classification of motility (1 = live within fixed tube, 2 = limited movement, 3 = slow free movement through the sediment matrix, 4 = free movement through a burrow system)	**M_q**	Time taken for individuals to fully burrow once having begun movement, following placement on the sediment surface (s)	
R_i	Classification of reworking mode (1 = epifauna, 2 = surficial modifier, 3 = upwards/downwards conveyor, 4 = biodiffusor, 5 = regenerator)	**R_q**	(Maximum mixed depth + Median mixed depth) / 2 (g)	*Integrates both the total spatial extent of biogenic mixing, and the depth of highest reworking intensity within the mixed region.*

For benthic systems, population (BP_p) or community (BP_c) bioturbation potential (Solan et al., 2004a) is a commonly adopted and adapted (e.g. Van Colen et al., 2012; Gogina et al., 2017; Wrede et al., 2018; Meyer et al., 2019) index used to summarise species contributions to sediment reworking processes and to project associated ecosystem function. To represent the per capita bioturbation potential of individuals (BP_i), average biomass data (total species biomass/ abundance) (B_i) is combined with broad trait classifications of the motility (M_i) and sediment reworking (R_i) activities of individual species (Fig. 5.1a), in the form of categorical integers of increasing magnitude or extent (Table 5.1). Over 1000 European bioturbating taxa have had trait values assigned in line with these classifications (Queirós et al., 2013; Zhang et al., 2019) based on either expert knowledge or empirical measurements. BP_i has been used by practitioners of ecosystem management seeking to represent the comparative roles of species and their relationships with benthic processes, which are known to be necessary for good ecosystem health and service delivery in shelf sea ecosystems (Birchenough et al., 2012; Sciberras et al., 2016).

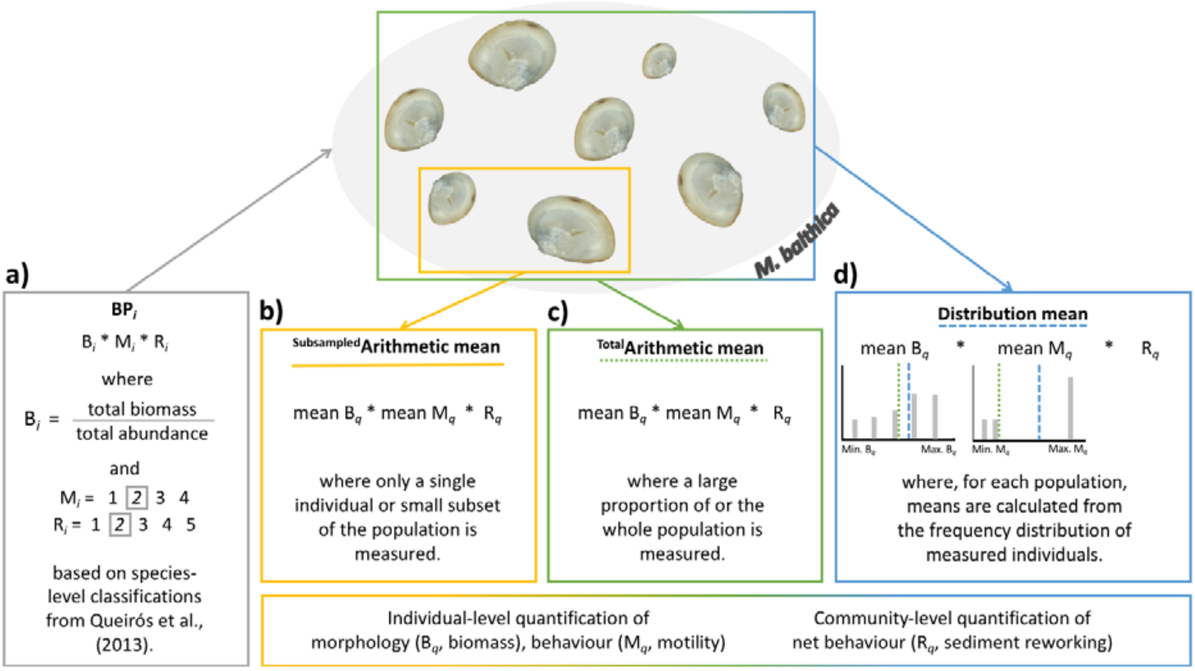


Fig. 5.1 Schematic representation of how (**a**) categorical trait metric BP_i, and, quantitative metrics (**b**) the $^{\text{Subsampled}}$Arithmetic mean, (**c**) the $^{\text{Total}}$Arithmetic mean and (**d**) the Distribution mean can be calculated to represent individuals from a sampled community. For BP_i the trait values are based on an average biomass (B_i) taken from a population and, illustrative purposes, categorical classifications of species behaviour (M_i, R_i) for bivalve *Macoma balthica* from Queirós et al. (2013). For the mean-based metrics, traits representative of the morphological and behavioural characteristics of interest were measured at the individual-level (B_q, M_q), and the net community-level (R_q).

BP_i was used to derive three additional metrics to represent the trait expression of the individuals comprising each single species (hereafter referred to as a 'population') within each replicate community in Case Study 1 & 2. Mesocosms containing mixed species communities contained multiple populations, and therefore the trait metrics were calculated independently for each species. First, the a) BP_i was calculated based on a population-level average for B_i and the categorical trait types for M_i and R_i outlined in Queirós et al. (2013). I then use measurements at the individual-level to produce quantitative trait values for the biomass (B_q) and motility (M_q) of every individual, while a measure of sediment reworking (R_q) is derived from the measured maximum and median mixed depth at the community level (Table 5.1). From these values, three mean trait metrics were calculated to represent the trait expression of individuals, taking the mean B_q * mean M_q * R_q, to determine b) the ^{Subsampled}Arithmetic mean, where trait expression is based on a random subsample of individuals the population (one individual in Case Study 1, three individuals in Case Study 2), c) the ^{Total}Arithmetic mean, where trait expression is based on the all individuals within the population, or d) the Distribution mean, where trait expression is based on the probability distribution of all individuals within the population (Fig. 5.1).

5.3.2 Distribution mean and probability distribution approach

The distribution of traits can be viewed as probabilistic when one considers that the magnitude of trait expression by an individual will be within the minimum and maximum for that population or species (Carmona et al., 2016). At any given time this individual is expressing multiple traits, for each of which a discrete value falls somewhere within its own range. Combined, these trait ranges recall the concept of the niche as a hypervolume proposed by Hutchinson (1957), where an individual in a realised role could theoretically persist at any point within the boundaries of the volume (Villéger et al., 2008). Fitness is not uniform across this volume as certain combinations of traits result in individuals being less suited to their environment (and so reflect adaptive differences or phenotypic plasticity) or are biologically improbable, and are therefore less likely to be found. As a result, not all trait values within a species, community, or region (Díaz et al., 2004; Valverde-Barrantes et al., 2013; Laughlin et al., 2015) are equally represented along the range of potential values (Carmona et al., 2016), and the hypervolume forms a distribution curve. Incorporating the distribution of traits into a trait metric reduces the influence of rare, outlying forms of trait expression. In addition, it may highlight differences between two communities that previously shared similar average trait values, given that two distributions within the same bounds approximate the same mean even if one has a unimodal and the other a bimodal distribution of trait expression (Laughlin et al., 2015; Zuo et al., 2017). In order to calculate the Distribution mean, I produced a probability distribution for each individual-level trait (B_q, M_q)

using a histogram of bin number *n,* where *n* is the number of individuals measured, and the resulting probability for each bin represents the likelihood of an individual within that population expressing a trait value within a given range. The mean from each probability distribution was calculated for each trait, which was then multiplied by the measured R_q in that community.

5.3.3 Statistical analysis

In order to identify if individual-level quantification can differentiate trait expression across communities and treatment conditions, principal component analysis (PCA) was used to visualise the relative direction and extent of variation of BP_i, the ^{Subsampled}Arithmetic mean, the ^{Total}Arithmetic mean and the Distribution mean between populations of the same species. This demonstrates whether quantitative data incorporates novel differences in trait expression absent in categorical metrics. Broadly positive relationships between metrics were expected given that they characterise the same traits; as such, strongly positive associations suggest the metrics representing trait expression follow consistent patterns, while weaker or negative correlations suggest they confer differing or indeed opposing information about individuals. Data were standardised (each value taken relative to the upper limit of the metric's range) to ensure metrics were of a comparable scale.

A variance partitioning approach was then adopted to examine the extent to which the quantification of individual-level trait expression can improve the explanatory power of traits for dissolved nutrient concentrations ([NH_4- N], [NO_3-N], [NO_2-N], [PO_4-P]). For each population, the value of the trait metrics BP_i, the ^{Subsampled}Arithmetic mean, ^{Total}Arithmetic mean and the Distribution mean were multiplied by the numerical abundance of the population to represent population-level bioturbation potential. 4-way ANOVA models were developed to test the proportion of variation in each nutrient explained BP_p, the ^{Subsampled}Arithmetic mean, ^{Total}Arithmetic mean and the Distribution mean, in that order. These tests demonstrate how much, if any, explanatory power of the biotic mediation of ecosystem functioning can be gained through more detailed characterisation of a population's trait expression, as the addition of each metric potentially reduces the amount unexplained variation in nutrient release by representing more intraspecific variation between communities. The proportion of the total variability in the dependent variable (nutrient concentration) that is accounted for by the variability in each independent variable (trait metric) is determined by the ratio of the sum of squares to the total sum of squares (Legendre & Legendre, 1998; Godbold & Solan, 2009) and expressed as a percentage. This procedure assumes that effects are additive and so interaction terms were not included in analysis. Due to the complexity of the biogeochemical drivers which govern sediment nutrient release, for which macrofaunal mediation through burrowing is only one component (Wrede et al., 2018), I do not seek to imply a direct relationship of the resulting percentage magnitude between a population's traits and functioning. However, it is well understood that there exists some degree of causal relationship between the traits of organisms, the behaviour of their communities, and the consequences of this behaviour at the ecosystem level (Birchenough et al., 2012; Carmona et al., 2016; Cadotte, 2017). Additionally, existing metrics such as BP_p/BP_c are already used as proxies through which the trait information of species can be compared to ecosystem-level properties (Murray et al., 2017; Wrede et al., 2018; Zhang et al., 2019). As such, I present the outcomes of the variance partitioning only as a relative comparison of the extent to which increasingly detailed information carried within each trait metric can alter the strength of the apparent relationship between a species and ecosystem functioning to which it is understood to contribute to some degree.

All work was completed in the *R* statistical and programming environment, and visualisations were produced with the gggenes package (R Core Team, 2017). Prior to analyses, data were assessed for normality (Q-Q plot), heterogeneity of variance (plotted residuals vs. fitted values) the presence of overly influential data points (Cook's Distance).

5.4 Results

5.4.1 Case Study 1

5.4.1.1 Principal component analysis (PCA)

For all populations irrespective of component species (Fig. 5.2a, Appendix D, Table D1), the first two axes accounted for 93.05% of the total variation (PC1: 76:02%, and PC2: 17.03%). BP_i made the strongest contributions to representing the variability of individuals between populations. All metrics were positively correlated with one another along PC1, while the $^{\text{Subsampled}}$Arithmetic and $^{\text{Total}}$Arithmetic means were independent from the Distribution mean along PC2. The resulting loadings illustrate contrasts in the trait information conveyed; the $^{\text{Subsampled}}$Arithmetic and $^{\text{Total}}$Arithmetic means convey similar information to one other, but little similarity with the Distribution mean.

The similarity or dissimilarity in the information conveyed by the trait metrics, and resulting differences in their contributions to the total variability across the principal components, is apparent when the populations of each species were subset and analysed separately (Fig. 2b – 2d). BP_i was consistently a poorer overall contributor to the total variance than was the case when all populations were analysed together. Instead, the Distribution mean was the single greatest contributor to the total variability, and so represented the greatest amount of variation between populations. For PCA of *H. diversicolor* populations contained in monoculture, two and three species treatments (Fig. 2b, Appendix B, Table B1), the first two axes accounted for 91.5% of the total variation among populations (PC1: 64.7%, and PC2: 26.8%). The $^{\text{Subsampled}}$Arithmetic mean, $^{\text{Total}}$Arithmetic mean and BP_i were positively correlatved to one another along PC1. PC2 had a strong positive loading for the Distribution mean, which was weakly correlated with the $^{\text{Subsampled}}$Arithmetic and $^{\text{Total}}$Arithmetic means. Overall there was a strong positive association in the trait information conveyed by the $^{\text{Subsampled}}$Arithmetic mean, $^{\text{Total}}$Arithmetic mean and BP_i, while the Distribution mean characterised differing variation.

For PCA of only *N. hombergii* populations (Fig. 5.2c, Appendix B, Table B1), the first two axes accounted for 98.82% of the total variation (PC1: 63.2%, and PC2: 35.6%). BP_i was opposed to the Distribution mean and, to some extent, to the $^{\text{Subsampled}}$Arithmetic and $^{\text{Total}}$Arithmetic means. All metrics were positively correlated along PC2, but BP_i and the Distribution mean were the main explanatory variables. As such, there was an overall positive association between all metrics, but a far weaker association in the trait information conveyed with BP_i than the three individual-based metrics had with one another.

Lastly, for PCA of only *M. balthica* populations (Fig. 5.2d, Appendix B, Table B1), the first two axes accounted for 96.1% of the total variation (PC1: 72.4%, and PC2: 23.7%). PC1 was mostly explained by the Distribution mean, and PC2 by the $^{\text{Subsampled}}$Arithmetic mean, while BP_i represented little variation between populations. The $^{\text{Subsampled}}$Arithmetic was independent from the other three metrics, which all showed positive correlation with one another.

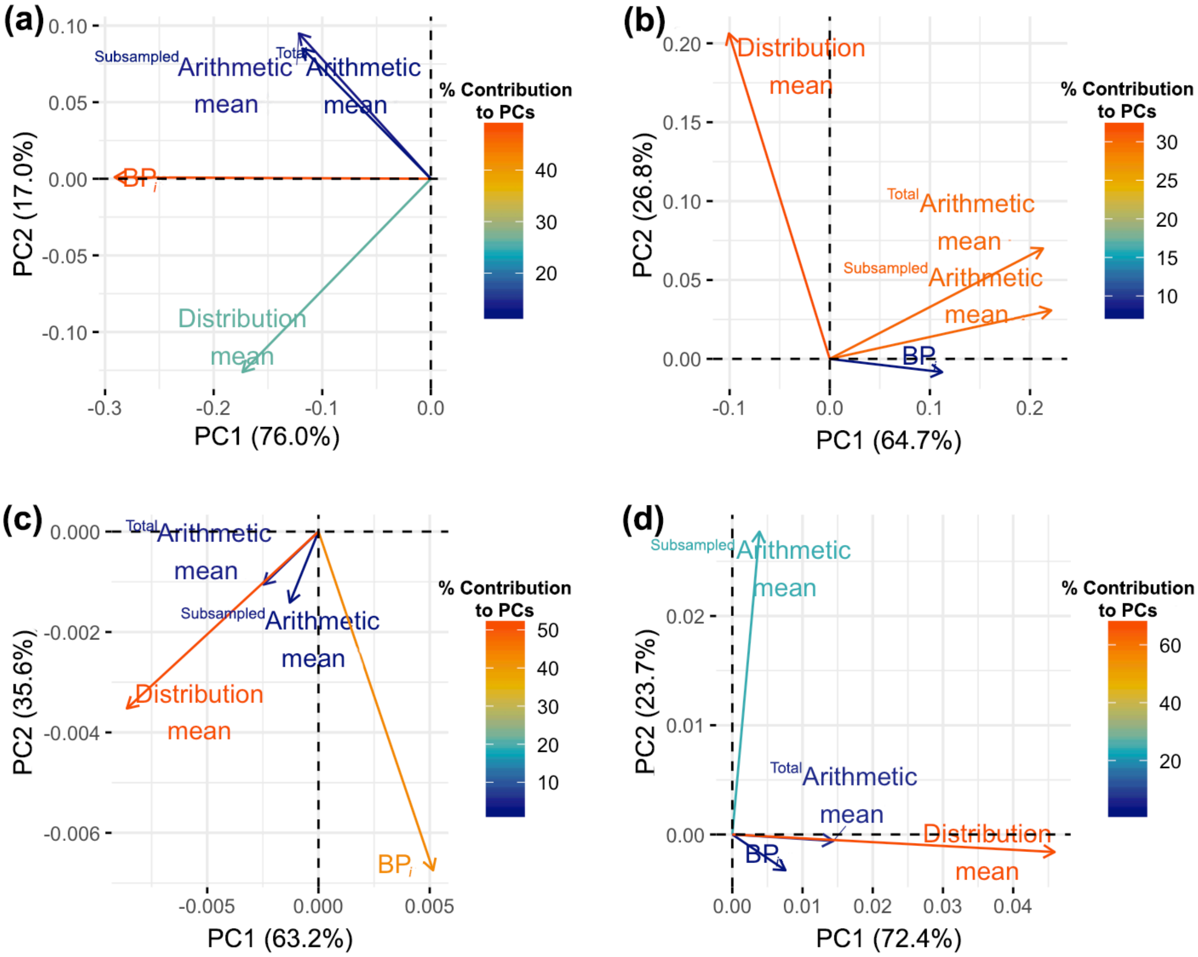


Fig. 5.2 Principal component analysis (PCA) for metrics (BP_i, ^{Subsampled}Arithmetic mean, ^{Total}Arithmetic mean, and Distribution mean) representing trait expression all populations of (**a**) *Hediste diversicolor, Nepthys hombergii* or *Macoma balthica*, (**b**) only *H. diversicolor*, (**c**) only *N. hombergii* and (**d**) only *M. balthica*, showing loadings of variables across the two main principal components (PC1 and PC2), where arrow colour indicates the percentage contribution of each variable to the principal components. Populations are single-species communities of individuals originating from communities of variable species composition.

5.4.1.2 Variance partitioning

Variance partitioning results are shown for all populations irrespective of species, and then for populations of each species in turn. The trait metric that best explained variation in nutrient concentration was variable between species and differed with the nutrient in question (Appendix D, Table D2).

Across all populations, BP_p makes up only a small proportion of the total variance explained in ecosystem function (Fig. 5.3a). Instead, much of the explained variation is gained through the incorporation of the metrics based on individual-level measurement. In particular, a high proportion of explanatory power for [NO$_3$-N] and [PO$_4$-P] was gained through quantitative measurement of only a single individual to characterise the population via the ^{Subsampled}Arithmetic mean. For *H. diversicolor* populations (Fig. 5.3b), [NO$_3$-N] and [NO$_2$-N] gain comparatively large explanatory power (12.11% and 13.16% respectively) from the measurement of single individuals. However, the greatest contributors to the explained variance for [NH$_4$- N] and [NO$_3$-N] is the measurement of all individuals in the community as per the ^{Total}Arithmetic mean. [NO$_2$-N] gains substantial explanatory power through incorporating the distribution of trait values through the measured populations as from the Distribution mean. In *N. hombergii* populations (Fig. 5.3c), much of the variance for all nutrients is explained by the value of BP$_p$, particularly for [NO$_2$-N] (31.30%), and the other metrics had comparatively little additive effect to reduce unexplained variation. By contrast, while for *M. balthica* populations BP$_p$ accounted for much of the explained variation in [NH$_4$-N] and [NO$_2$-N] (47.85% and 16.66% respectively), the additive effects of the quantitative metrics were variable between nutrients (Fig. 5.3d). The incorporation of the Distribution mean more than doubled the explanatory power of traits for [NO$_3$-N], while the additive effect of metrics gained reduced unexplained variation evenly for [PO$_4$-P].

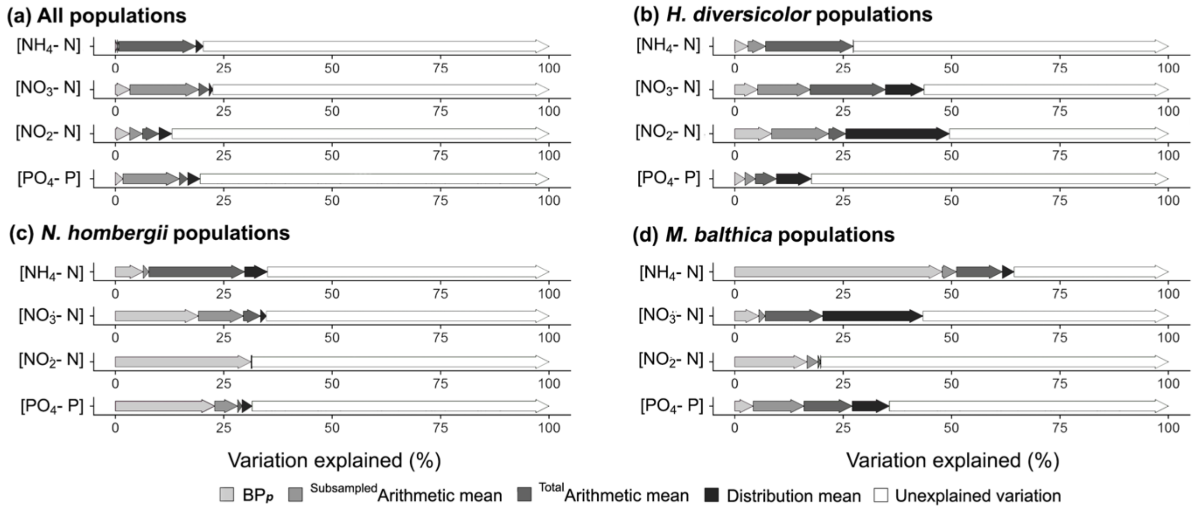


Fig. 5.3 Visual summary of the variance partitioning approach for Case Study 1, showing the percentage of variation explained in [NH$_4$- N], [NO$_3$-N], [NO$_2$-N], [PO$_4$-P] by four trait metrics in populations of (**a**) *Hediste diversicolor, Nepthys hombergii* or *Macoma balthica*, (**b**) only *H. diversicolor*, (**c**) only *N. hombergii* and (**d**) only *M. balthica*. Percentages were calculated as the ratio of the sum of squares for each group level to the total sum of squares. Populations are single-species communities of individuals originating from communities of variable species composition.

5.4.2 Case Study 2

5.4.2.1 Principal component analysis (PCA)

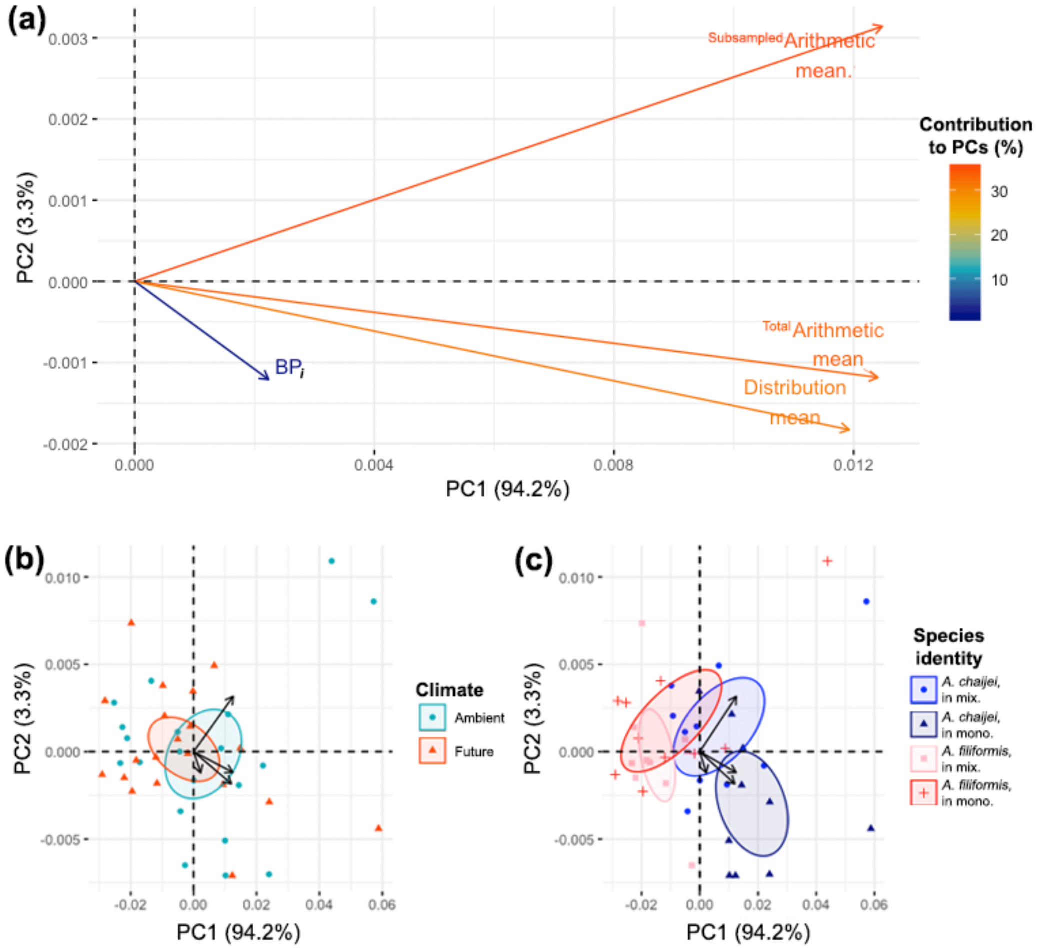


Fig. 5.4 Principal component analysis (PCA) for metrics (BP$_i$, $^{\text{Subsampled}}$Arithmetic mean, $^{\text{Total}}$Arithmetic mean, and Distribution mean) representing trait expression of populations containing either *Amphiura chiajei* or *Amphiura filiformis* in monoculture or mixed communities. (**a**) shows loadings of variables across the two main principal components (PC1 and PC2), where arrow colour indicates the percentage contribution of each variable to the principal components. Biplots (**b**, **c**) show the directions of the loadings of the variables in addition to the locations of populations maintained in different (**b**) climate (ambient or future) or (**c**) species identity (monoculture or mixture) treatments within the space. Populations with similar trait expression are closer together, showing their relationship with the directionality of the variables (consistent from (**a**)). Ellipses show the 95% confidence interval around the group mean. Populations are single-species communities of individuals originating from communities of variable species composition.

The first two axes accounted for 97.49% of the total variation (PC1: 94.17%, and PC2: 3.31%) (Fig. 5.4, Appendix D, Table D3). All mean-based metrics (^{Subsampled}Arithmetic, ^{Total}Artithmetic, and Distribution mean) were positively correlated along PC1. Overall, the positive correlation for BP_i was weaker and it contributed less to variation between *A. chiajei* and *A. filiformis* populations.

Populations maintained under ambient conditions had greater variability in their trait expression than those maintained under future climate conditions (Fig. 5.4b). With regards to species identity (Fig. 5.4c), the species *A. chiajei* and *A. filiformis* can be distinguished along the directionality of BP_i and of the ^{Subsampled}Arithmetic and ^{Total}Artithmetic mean, due primarily to differences in morphology (B_i and B_q) between species because *A. chiajei* individuals are larger (Appendix B, Fig. B6 & B9). However, only the quantitative individual-based means are able to distinguish between *A. chiajei* and *A. filiformis* maintained in under differing species treatments, as they incorporate additional differences in the expression of movement (M_q) and reworking (R_q) behaviour between populations. Both *A. chiajei* and *A. filiformis* maintained in either monoculture or mixed species communities separate out along the direction of variation of the ^{Total}Artithmetic mean and Distribution mean, but have no clear relationship with BP_i.

5.4.2.2 Variance partitioning

Variance partitioning results are shown for populations of both *A. chiajei* (Fig. 5.5.a - d, Appendix D, Table D4) and *A. filiformis* (Fig. 5.5e - h, Appendix D, Table D5) from communities differing in climate condition and species mixture, indicating that the best explanatory metric for any nutrient was highly context-dependent.

For *A. chiajei* populations under ambient conditions (Fig. 5.5a), BP_p explains the vast majority (53.49%) of variance explained in [PO_4-P]. The incorporation of trait measurements from a single individual via the ^{Subsampled}Arithmetic mean strongly reduces unexplained variance in [NH_4- N], [NO_3-N]and [NO_2-N]. However, for [NO_2-N] the strongest contributor to the explained variation was the Distribution mean.

For populations maintained under future conditions (Fig. 5.5b), BP_p explains a moderate proportion of total explained variation in [NH_4- N], [NO_3-N] and [NO_2-N]. However, the addition of the ^{Subsampled}Arithmetic mean makes the greatest reductions in unexplained variance for [NH_4- N] and [NO_2-N], while the addition of the ^{Total}Arithmetic mean halves the remaining variance left unexplained in [NO_3-N]. For [PO_4-P], BP_p, the ^{Subsampled}Arithmetic and ^{Total}Arithmetic mean make very little contribution to explaining variance, which is instead best explained by the Distribution mean.

A similar pattern is found in *A. chiajei* populations drawn from monoculture communities (Fig. 5.5c), where the additive effect of the $^{\text{Subsampled}}$Arithmetic mean for [NH_4- N], [NO_3-N] and [NO_2-N], and the further additive effect of the $^{\text{Total}}$Arithmetic mean for [NO_3-N], improves the proportion of variation explained by trait metrics. In [PO_4-P], variance is bested explained by the Distribution mean.

For *A. chiajei* populations from mixed communities (Fig. 5.5d), across all nutrients, the addition of each metric in turn reduced unexplained variation. For [NH_4- N], [NO_2-N] and [PO_4-P] the greatest contributions came from the addition of the $^{\text{Total}}$Arithmetic mean, but for [NO_3-N], the additive effects were even across all metrics.

For *A. filiformis* populations maintained under ambient conditions (Fig. 5.5e), the incorporation of the $^{\text{Subsampled}}$Arithmetic made the greatest contributions to explaining variance in [NH_4- N], [NO_2-N] and [PO_4-P]. For [NO_3-N], the greatest explanatory power came from the addition of the Distribution mean.

For *A. filiformis* populations under future conditions (Fig. 5.5f), the $^{\text{Total}}$Arithmetic mean made the strongest contributions to explaining variation in [NH_4- N] and [NO_2-N]. For [PO_4-P], the additive effects of each successively more explained metric explained a greater proportion of trait variation than that before it, with the Distribution mean offering the greatest contributions to the explanatory power of traits.

In *A. filiformis* populations originating from monoculture communities (Fig. 5.5g), the overall proportion of variance explained in all nutrients was low (between 8.07% for [NH_4- N] and 44.08% for [NO_3-N]). BP_p made the strongest contributions to explanatory power for [NO_3-N], while in [PO_4-P] the incorporation of the Distribution mean most greatly reduced unexplained variation.

Finally, in *A. filiformis* populations originating from mixed communities (Fig. 5.5h), BP_p explained only a small proportion of total variation in [NH_4- N] and [NO_2-N], while the additive effect of the $^{\text{Subsampled}}$Arithmetic makes the greatest contributions to reducing unexplained variation, followed by the $^{\text{Total}}$Arithmetic mean. For [NO_3-N], the greatest proportion of variation is explained by the additive effect of the Distribution mean.

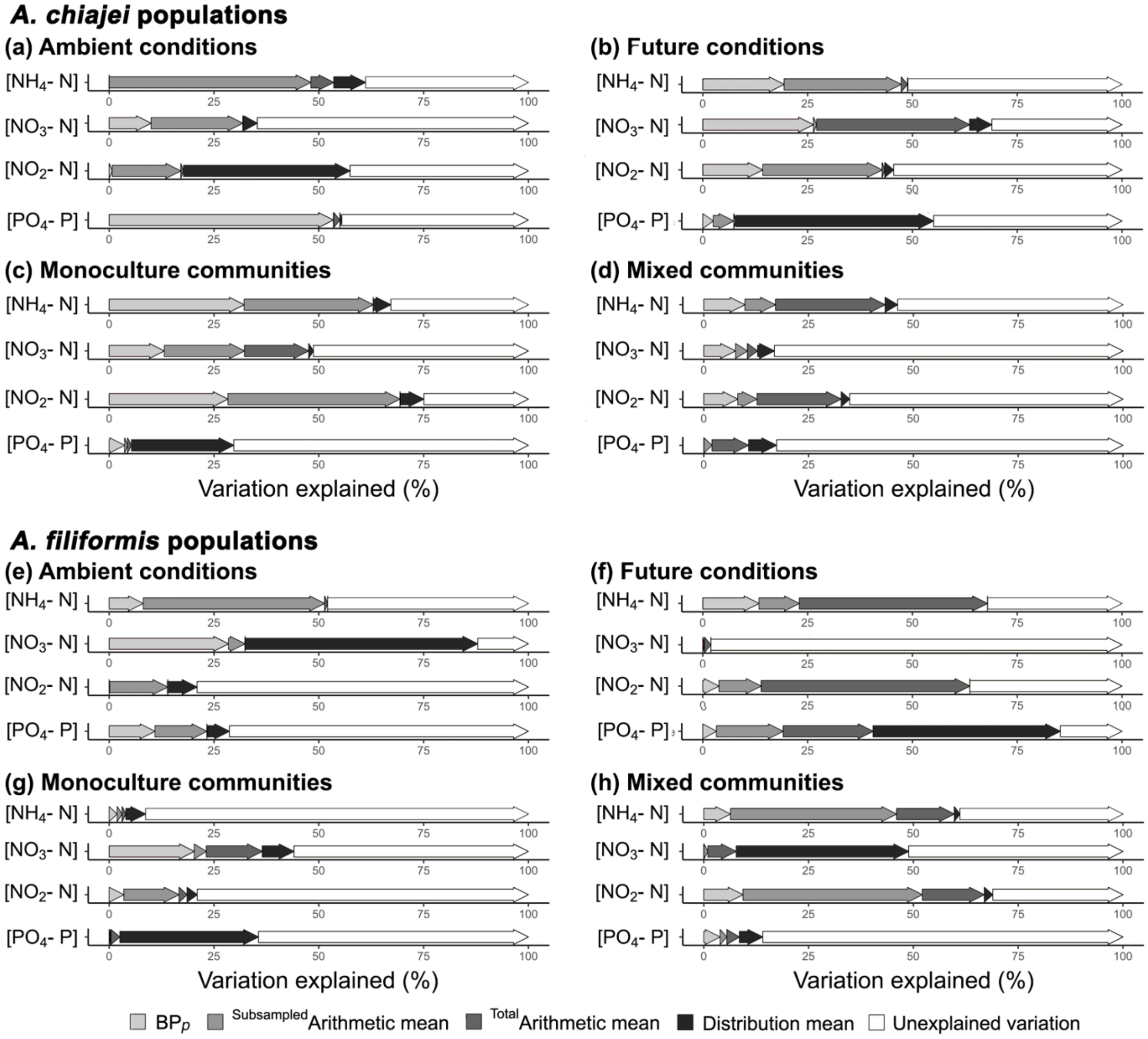


Fig. 5.5 Visual summary of the variance partitioning approach for Case Study 2, showing the percentage of variation explained in [NH_4- N], [NO_3-N], [NO_2-N], [PO_4-P] by four trait metrics for populations of *Amphiura chiajei* (**a, d**) or *Amphiura filiformis* (**e, h**) maintained under (**a, e**) ambient conditions or (**b, f**) future conditions, and in (**c, g**) monoculture or (**d, h**) mixed communities. Percentages were calculated as the ratio of the sum of squares for each group level to the total sum of squares. Populations are single-species communities of individuals originating from communities of variable species composition.

5.5 Discussion

I find that, while categorical trait types represent broad interspecific differences in functional role (Murray et al., 2017), the incorporation of quantitative data characterises dynamic and context-dependent intraspecific differences in the strength or range of potential functional contributions. This is apparent in my results, as the categorical BP_i was found to be a strong contributor to the total variation in trait expression between individuals of differing species. However, BP_i offers little ability to distinguish the functional potential of individuals which share a functional classification but express their traits differently. In categorical metrics, intraspecific variation may be represented only by a single quantitative component. For BP_i, this is a value for biomass from a population average (total biomass/numerical abundance) (Hodgson et al., 1999). Biomass aggregates numerous aspects of physiology known to underpin processes associated with ecosystem functioning (Norkko et al., 2013; Wohlgemuth et al., 2016), and the use of biomass or other 'soft' but multifaceted traits (e.g. morphological characteristics such as size, chemical composition or density) offers a useful source of trait information with minimal sampling effort (Hodgson et al., 1999; Funk et al., 2017; Raine et al., 2018). This approach allows some integration of context-dependent differences, where morphology can be used as a proxy effect and response trait. However, greater incorporation of intraspecific measurements of morphology and/or behaviour conveys different information about trait expression from those based primarily on generalised species-level classifications. By incorporating individual-level measurements, quantitative trait metrics characterise disparate trait information between individuals and communities, and substantial context-dependency in traits and functional roles becomes apparent within species.

Notably, context-dependent trait expression that arises in response to differing biotic or abiotic conditions cannot be resolved by single trait values. These concerns are particularly relevant for ecosystem management scenarios which need to take into account variation in environmental conditions between communities or assess the altered functional potential of an ecosystem exposed to rapid climatic change (Wrede et al., 2018; Chapter 3). Under these circumstances changes in species morphology are unlikely to be quantifiable over short-term or rapid changes in context, as morphological changes occur over longer or multi-generational timescales in response to selection pressures (Solan et al., 2004a; Tredennick et al., 2018). Functionally-relevant aspects of behaviour, however, may rapidly diverge from their expected magnitudes (Miller et al., 2019). Categorical representations of species traits are unable to resolve these intraspecific differences, and instead characterise populations with differing context-dependent behavioural trait expression as having unaltered functional capacity. Quantitative measurement at the individual level is necessary to identify this substantial potential variation.

An assumption inherent to conventional trait-based approaches is that broad interspecific differences conveyed by trait typologies will adequately represent differences in functional potential (Violle et al., 2007; Griffiths et al., 2016; Raffard et al., 2017; Klimkowska et al., 2019), and that the magnitude of intraspecific variation between populations is insufficient to render their usage inappropriate (Griffiths et al., 2016; Murray et al., 2017). I show in Case Study 2, however, that such categorisations do not necessarily allow the traits of species to be strongly linked to measured proxies of ecosystem functioning. Variation in the categorical BP_p between populations explained only a small proportion of variation in dissolved nutrient concentrations. By contrast, the incorporation of intraspecific variation in response to biotic and abiotic factors via quantitative substantially improved the capacity to link the traits of species to ecosystem functioning. Notably, the $^{\text{Subsampled}}$Arithmetic mean alone improved the explanatory power of traits, particularly for [NH_4- N] and [NO_2-N], and so here demonstrate that measurement of even a single individual's expression can greatly improve the ability of metrics to represent bioturbation and functional potential beyond that offered by conventional approaches. Trait-based approaches grounded in categorical trait types decouple the link between organism behaviour and function by assuming that trait occurrence is a linear function of, or is otherwise directly linked to, functional potential. In doing so, the prominent roles of particularly dominant taxa are potentially obscured (Valdemarsen et al., 2018), as is the altered performance of species responding to their environment (Murray et al., 2017) and the distribution of these values within the community (Carmona et al., 2016). Further, categorical metrics assume that the functions to which species contribute are fixed, and so are unable both to represent context-dependency in the strength of the trait-function relationship but also shifts in the functions which traits underpin, or potential multifunctionality (Gross et al., 2017). By contrast, individual-based measurements integrate quantitative characterisation of the species as a whole (de Bello et al., 2011; Hale et al., 2014), while also allowing comparison of dynamic site-, context- or community-specific effects on ecosystem functioning (Enquist et al., 2015; Murray et al., 2017; Cassidy et al., 2020). Through PCA, I show that metrics grounded in individual-level measurement reveal differences in trait expression between populations maintained under differing biotic and abiotic conditions. Through variance partitioning, I show that these differences reveal context-dependency in the strength or shape of the trait-ecosystem relationship.

My results thus demonstrate that intraspecific differences are not negligible, and that formally incorporating their quantification into trait-based approaches is necessary for representing the strength and range of species' functional contributions (Baraloto et al., 2010; Carmona et al., 2015; Ali et al., 2017). Differences in the values and variability of traits underpin differences in ecosystem functioning (Giffith et al., 2016). By grounding trait metrics in quantitative measurements able to incorporate this intraspecific variation, I gain improved understanding of how biota mediate ecosystem functioning (Chapter 2 & 3). My findings show that these metrics more effectively represent species trait expression, including where expression differs between populations, and are better able to relate that expression to functioning. Individual-level sampling provides sufficiently mechanistic data as to identify trait-functioning relationships that would be overlooked by conventional metrics (Guscelli et al., 2019). For example, here the Distribution mean explains the greatest proportion of variance under only a small number of tested conditions (in Case Study 1 solely for *H. diversicolor* populations, and in Case Study 2 chiefly for [PO_4-P] for *A. chiajei* or *A. filiformis* populations). Biogeochemical mechanisms mediating nutrient release can be strongly influenced by the trait values throughout the sampled populations (Cornwell & Ackerly, 2009), the distributions of which are transient as age classes undergo predictable changes over time (Norkko et al., 2013; Fontana et al., 2019) or where external selection pressures drive expression (Solan et al., 2004a; Thygesen et al., 2005; Morrongiello et al., 2019). The shape of trait distributions in terms of their skewness and kurtosis creates strong empirical relationships with the ability of ecosystems to provide multiple simultaneous functions and services, and is required to predict the functional consequences of biodiversity change (Gross et al., 2017). My results emphasise that, to meaningfully interrogate the presumed links between the species traits, their performance, and their effects on ecosystem processes and functioning (Funk et al., 2017; Murray et al., 2017; Wrede et al. 2018), metrics applied to represent traits should seek to incorporate quantitative measurements from the individuals in communities of interest.

While trait-based approaches should theoretically maximise the accuracy of metrics used to represent functional identity (Gagic et al., 2015) and so include as extensive sampling as is possible, these choices will likely be informed by logistical constraints. In practice, sampling decisions are made to reduce target variance, representing broad trends in expression while also minimising demands of cost or time (Lavorel et al., 2007; Baraloto et al., 2010; Enquist et al., 2015). Though measurement of only single or few individuals is liable to skew from the random selection of rare or outlying trait values, my results for the $^{\text{Subsampled}}$Arithmetic and $^{\text{Total}}$Arithmetic mean suggest that even minimal sampling can offer an advantageous trade-off for a small expenditure of effort that results in metrics adept at characterising trait expression. Further, by using individuals as the sampling unit, individual-level dynamics influencing community or ecosystem processes can be estimated *post hoc*. These dynamics include the total extent of phenotypic variability (Song et al., 2017), and the relative contribution of inter- and intra-specific variability (Pérez-Harguindeguy et al., 2016; Ali et al., 2017; Zuo et al., 2017). The distribution of trait values across communities as per a Distribution-type mean can also be calculated, and used to identify optimal functional strategies, trait values that arise in response to certain aspects of context, or trait values with specific implications for functioning (Muscarella & Uriarte, 2016). These efforts will also increase the availability of detailed, quantitative information as to a trait's potential extent of variability and the strength of its mechanistic link with functioning (Violle et al., 2007). By result, future work will be optimised as the decision of which metric to adopt can be based on sufficiently mechanistic data (Benavides et al., 2019).

Categorical trait typologies are versatile abstractions that simplify trait-based study of ecosystems (Guscelli et al., 2019), and should persist to represent species' relative functional potential in large-scale studies or modelling approaches (Solan et al., 2004a). However, by their use we risk obscuring context-specific differences and intraspecific effects which can strongly influence understanding of this relationship (Birchenough et al., 2012; Carmona et al., 2015; Gogina et al., 2017). My results provide empirical support to the recommendation to utilise increasingly detailed trait metrics (Baraloto et al., 2010; Chase & Knight, 2013) which move beyond species-based typologies and instead recognise the role of population- or site-level differences (Murray et al., 2017; Miller et al., 2019). I recommend that individual-level trait measurement be considered a priority for adoption where i) work includes *in situ*, manipulative or experimental components, ii) traits are related directly to measured proxies for ecosystem functioning, or where iii) study species or iv) environmental parameters are data poor or exposed to changing conditions. Though dependent on the size and nature of the work, it is under i) that the premise of individual-level measurement is mostly likely to complement the existing remit without necessitating additional effort to the point of impracticality, and under ii) that these efforts are most likely to return insight into the trait-functioning relationship. Quantification of intraspecific data under iii) and iv) allows identification of novel differences in trait expression which affect species functional potential, that may be obscured by conventional approaches, and which are valuable in informing further study (Chapter 3). Given that natural systems are increasingly subject to drivers of environmental and ecological change, quantifying realised trait expression will be ever more important to ensuring that ecosystem management approaches successfully conserve and restore species whose traits underpin functioning and service delivery (Laughlin, 2014; Ostertag et al., 2015).

5.6 Conclusions

I show that incorporating the variability of individual expression into metrics in trait-based analysis alters our understanding of organism's functional potential. As such, analytical approaches should avoid the assumption that intraspecific trait variation is inherently unimportant or uninformative, as categorical metrics have limited capacity to discern context-dependent trends in species expression, or their effects to ecosystem functioning. However, while extensive measurement of individuals offers an improved mechanistic insight, it is likely only an appropriate expenditure of time and effort within the context of specific scientific queries. Trait metrics must be selected not by reliance on convention or assumption but with consideration of the research task and its logistical demands, the extent of differences between relevant species and treatment groups, and their role in mediating ecosystem functions of interest.

Chapter 6 General discussion

Under the environmental and ecological challenges presented by the Anthropocene, managing the ecosystem-level consequences of changing environmental conditions, including altered biodiversity (Hooper et al., 2012), will require ever more detailed understanding of the roles species play in providing ecosystem goods and services for human wellbeing (Mimura et al., 2017). It is anticipated that the coming decades will see unprecedented change in the context (IPCC, 2018), composition (Mulder et al., 2015), and functional contributions (Thébault et al., 2014; Douglas et al., 2019) of natural systems. Indeed, even predictions based on species richness and extinction rate indicate that the continuing loss of species will have profound consequences for the functional capacity of ecosystems (Mace et al., 2014). Research suggests that changes in biodiversity will alter the magnitude and variability of functioning within and between ecosystems (Heilpern et al. 2018), but outcomes may vary from functional deterioration (Solan et al. 2004) to resistance or even the enhancement of ecosystem functioning (Oliver et al., 2015) depending on the species and ecosystem investigated.

Thus, it is increasingly important that we understand the mechanistic underpinning of how ecosystems function, while also appreciating the full scope of their functional diversity, should either of these aspects be subject to change. Over the past two decades, development of trait-based approaches has grown out of the understanding that functional diversity is paramount in underpinning the performance and wellbeing of ecosystems, rather than taxonomic richness *per se* (Bremner et al., 2006; Gagic et al., 2015; Bannar-Martin et al., 2018). Incorporating the impacts of the trait loss that accompanies species change into predictions of ecosystem function is seen as imperative for development of effective conservation and management strategies (Allgeier et al., 2016). However, despite a longstanding and indeed growing acknowledgment of the presence and relevance of intraspecific variability (Albert et al., 2010a; Bolnick et al., 2011), the within-species component of diversity has been repeatedly overlooked under these frameworks. Such an assumption of robustness is demonstrably flawed; species express a substantial range of intraspecific trait variation in response to both intrinsic structuring components of their communities such as their composition in terms of density and the presence of co-occurring species (Chapter 2 & 4), and also in response to external environmental factors (Chapter 3, and references therein).

It can be inferred that the decision to overlook intraspecific diversity during trait-based study, while owed in a practical sense to logistical constraints, is justified under the assumption that the functional diversity of communities is primarily driven by species-level differences (Ali et al., 2017;

Zuo et al., 2017). Authors which quantify intraspecific trait variation often do so with a view to establishing under what conditions it is necessary to include (Kichenin et al., 2013; Siefert et al., 2014; Des Roches et al., 2018). By result they imply that, if deemed irrelevant, trait variation can be omitted without substantial impacts to the accuracy of approaches representing or predicting ecosystem functioning (Jung et al., 2014; Spasojevic et al., 2016). While such an assumption of robustness may be accurate under certain circumstances (Violle et al., 2007; Shipley et al., 2016), my findings demonstrate that this does not preclude our understanding of these species or systems from benefitting from more detailed quantification. Quantification of context-dependent trait expression at multiple organisational levels represents a largely untapped component of functional diversity (Bennett et al., 2016; Guscelli et al., 2019), moving beyond broad species-level classifications to ground representations of traits in realised measures of *in situ* performance. An intraspecific approach potentially provides fundamental accuracy for those seeking to understand the biotic control of ecosystem functioning.

Trait-based approaches to functional ecology relate species richness to ecosystem functioning (Thompson et al., 2018), though the exact shape of this relationship is often highly debated (Oliver et al., 2015). Broadly, the biodiversity-ecosystem functioning (BEF) relationship is underpinned by the assumption that the presence of additional species confers greater likelihood of species with novel, previously unrepresented trait values that elevate community functional diversity (O’Connor et al., 2017) or provide functional redundancy (Delgado-Baquerizo et al., 2016). However, the performance and associated functional activity of equally rich communities is strongly affected by structural changes in species evenness and dominance (Mouillot et al., 2014; Wohlgemuth et al., 2016). Further, the trait values relied upon to characterise functional contributions are unlikely to robustly represent the realised expressions of species. Functional trait classifications in terms of life history, physiological or behavioural typologies are poor representations of species functional potential as they cannot resolve species of similar functional types that perform their respective behaviours to differing magnitudes (Wright et al., 2006; Murray et al., 2014), and fail to constrain the potentially diverse phenotypic plasticity of single taxa. Between two communities of identical species richness, differences in ecosystem functioning are determined not solely by changes in the species composition driven by interspecific trait differences, but also by the cumulative intraspecific variation of all taxa (Chapter 4).

Conspecific individuals vary substantially in their trait expression as do, concomitantly, the community net behaviours and ecosystem functioning they underpin (Bolnick et al., 2011). Variation across these organisational and indeed spatio-temporal scales is attributable to a number of sources, including to genetic components (Alberto et al., 2013). Though outside the experimental scope of this thesis, it is apparent that selection pressures and evolutionary processes form a necessary consideration when comparing populations given that they facilitate the emergence of differences in morphological, behavioural and physiological traits associated with functioning over several generations (Réale et al., 2003; Calosi et al., 2013; Valverde-Barrantes et al., 2013). An aspect of particular interest is that, by result, different populations may have unique genetically-determined constraints on their capacity to plastically adjust their trait expression (Song et al., 2017; Oostra et al., 2018; Start & Gilbert, 2019). Indeed, even genetically isolated populations whose trait signals strongly reflect long-term selection and adaptation to local conditions are able to acclimate to an altered environmental context (Calosi et al., 2013); this resilience potentially leads to the new population being functionally distinct from that of the original due to the possession of new forms of trait expression. Comparisons that substitute trait information from taxonomically close species from differing environments may be in error (Degen et al., 2018; Wrede et al., 2018). Intraspecific trait variation can emerge even over short temporal scales, with implications for how ecologists have conventionally viewed members of the same species from different assemblages, histories or conditions as functionally interchangeable (Moran et al., 2016). Both biotic (Chapter 2 & 4) and abiotic components (Chapter 2 & 3) dynamically alter the presumed functional role of species, and provide evidence to the ever-more widely accepted supposition that conspecifics cannot be assumed to make equal contributions to functional processes across communities or ecosystems. As such, the conventional approaches undertaken to represent organismal traits and so functional potential during ecological study must either be used with significant caveats, or improved.

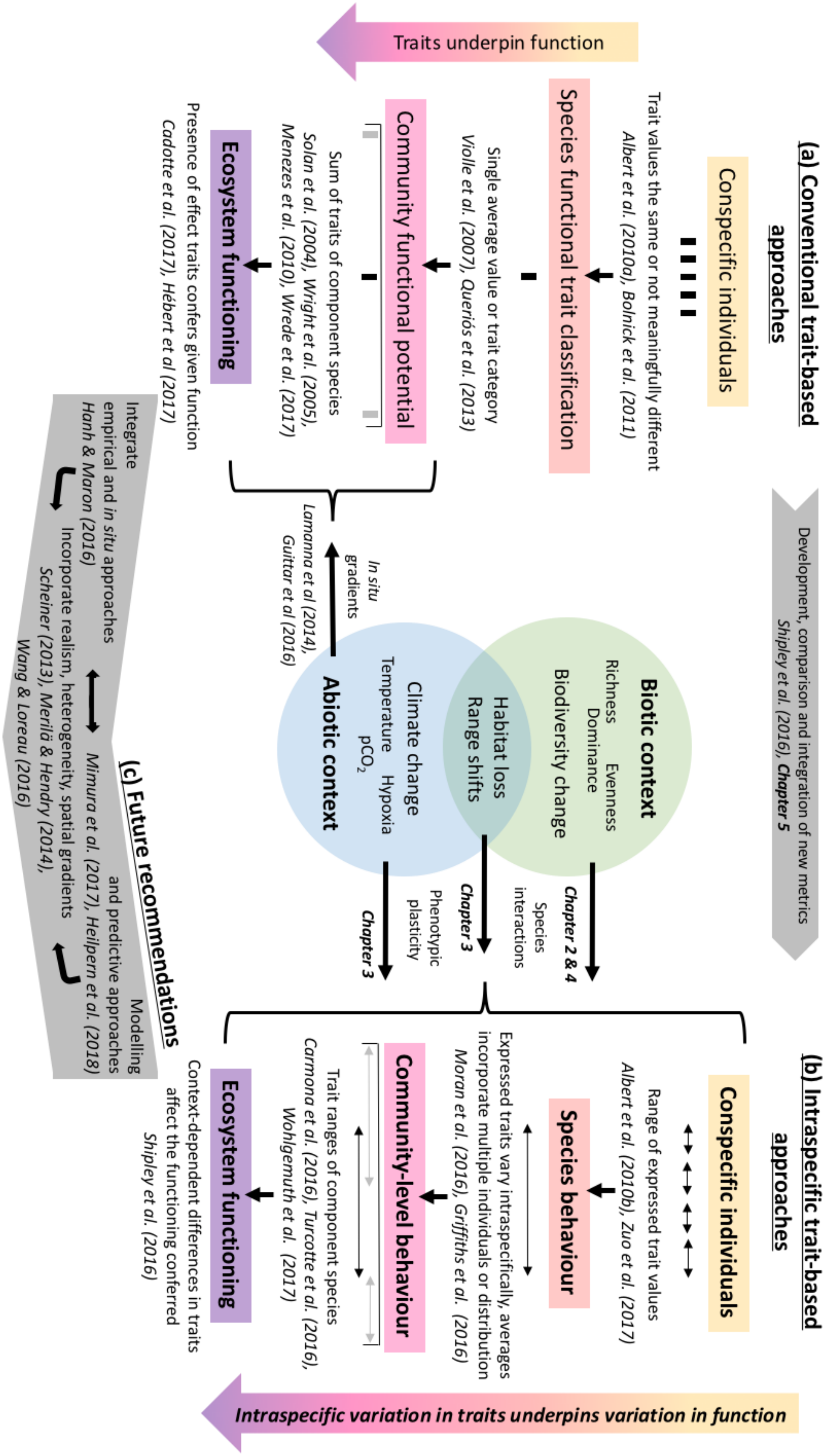

(a) Conventional trait-based approaches
Conspecific individuals
Trait values the same or not meaningfully different
Albert et al. (2010a), Bolnick et al. (2011)
Species functional trait classification
Single average value or trait category
Violle et al. (2007), Querios et al. (2013)
Community functional potential
Sum of traits of component species
Solan et al. (2004), Wright et al. (2005), Menezes et al. (2010), Wrede et al. (2017)
Ecosystem functioning
Presence of effect traits confers given function
Cadotte et al. (2017), Hébert et al (2017)
Traits underpin function
Development, comparison and integration of new metrics
Shipley et al. (2016), Chapter 5
Biotic context
Richness Evenness
Dominance
Biodiversity change
Habitat loss
Range shifts
Climate change
Temperature Hypoxia
pCO_2
Abiotic context
In situ gradients
Lamanna et al (2014), Guittar et al (2016)
Chapter 2 & 4
Species interactions
Chapter 3
Phenotypic plasticity
Chapter 3
(b) Intraspecific trait-based approaches
Conspecific individuals
Range of expressed trait values
Albert et al. (2010b), Zuo et al. (2017)
Species behaviour
Expressed traits vary intraspecifically, averages incorporate multiple individuals or distribution
Moran et al. (2016), Griffiths et al. (2016)
Community-level behaviour
Trait ranges of component species
Carmona et al. (2016), Turcotte et al. (2016), Wohlgemuth et al. (2017)
Ecosystem functioning
Context-dependent differences in traits affect the functioning conferred
Shipley et al. (2016)
Intraspecific variation in traits underpins variation in function
(c) Future recommendations
Integrate empirical and in situ approaches
Hanh & Maron (2016)
Incorporate realism, heterogeneity, spatial gradients
Scheiner (2013), Merilä & Hendry (2014), Wang & Loreau (2016)
Modelling and predictive approaches
Mimura et al. (2017), Heilpern et al. (2018)

Fig. 6.1 Conceptual schematic representing current knowledge underpinning conventional single-value trait-based approaches, and the complementary knowledge base supporting trait-based approaches which incorporate intraspecific variation, expanded from Fig. 1.1 in line with the findings of this thesis. In a (**a**) conventional view, identical individuals (Albert et al., 201a; Bolnick et al., 2011) of a species fall within trait categorisations (Violle et al., 2007; Queirós et al., 2013) that sum at the community level (Solan et al., 2004a; Wright et al., 2005; Menezes et al., 2010; Wrede et al., 2017) to underpin net functional potential (Cadotte et al., 2017; Hébert et al., 2017). When (**b**) intraspecific variation is recognised, however, the dynamic range of trait values expressed by conspecifics (Albert et al., 2010b; Zuo et al., 2017) exposed to biotic and/or abiotic stimuli (Chapters 2 - 4) potentially alters the behaviour of species (Moran et al., 2016; Griffiths et al., 2016) and so the net functional behaviour of their communities and associated effects to ecosystem functioning (Carmona et al., 2016; Turcotte et al., 2016; Wohlgemuth et al., 2017). Bolded text indicates where this information is quantitative; an intraspecific perspective incorporates substantially more measurement of realised values. As such, developing these approaches to most effectively gain their benefits (**c**) in future necessitates the creation and integration of new metrics into existing frameworks (Hanh & Maron, 2016; Shipley, 2016; Chapter 5), while better isolating what aspects of context perpetuate relevant intraspecific variation (Scheiner, 2013; Merilä & Hendry, 2014; Wang & Loreau, 2014) with a view to improving their predicative capability (Mimura et al., 2017; Heipern et al., 2018).

The increasing environmental and ecological changes to which organisms are exposed merits consideration of how species' responses can be incorporated most seamlessly into current practices, ways of thinking, and prevailing methodologies (Fig. 6.1). There exists a need to reconcile the accepted understanding that individuals are non-identical, and that this is an important determinant of ecosystem functioning and provisioning, with the prevailing practices of ecosystem study (Mimura et al., 2017). Before suggesting methods by which intraspecific trait variation can be utilised within trait-based study, it must first be identified what these approaches aim to achieve. Conventional categorical trait classifications typically seek to relate physiological or behavioural typologies of species to ecosystem properties and processes (Wrede et al., 2018). It is however possible to measure traits reflective of these typologies and so of their impacts directly within individuals, automatically encompassing context-dependency in a quantitative measurement, with remarkable accuracy even when single or few individuals are measured (Chapter 5). Existing theory can then be augmented with these observations. Providing twofold benefits, these observations both provide mechanistic insight and explanatory power when attempting to understand the pathways underpinning interactions or broad-scale trends (Snelgrove et al., 2014), while also facilitating adjustment of predictions from coarser, conventional methods in line with new insights as to their variability, error or confidence (Carmona et al., 2016).

Avenues through which trait-based study could seek to gain these benefits include micro-scale experimental approaches measuring individuals to accompany larger *in situ* sampling schemes which instead focus on community means, with the aim of providing ground-truthing and validation of the functioning inferred, or predicted, by use of these single values (Carmona et al., 2015). The use of single value measures across landscape or basin scales (e.g. Bolan et al., 2017; Wrede et al., 2017) would gain additional confidence if empirical work on subsamples of differing contexts provided no evidence of substantial intraspecific difference (Start & Gilbert, 2019). By contrast, should differences be prevalent, these insights would allow adjustment of the inferred community functional potential across the scope of the study system (Chase & Knight, 2013). Alternatively, just as current trait-based approaches refer to published databases of categorical trait types (e.g. Kleyer et al., 2008; Kattge et al., 2011; Queirós et al., 2013), research effort could be dedicated to generating complementary datasets that facilitate monitoring of the ongoing changes in intraspecific variation and thus provide valuable baseline data for assessing the consequences for populations, communities, ecosystems, and the delivery of goods or services. Practitioners of ecosystem study will then be better able to identify when substantial intraspecific trait differences are emerging relative to other known values for a species of interest, and can better anticipate when these differences will become so large as to be of consequence for human wellbeing. For maximum efficiency, such efforts should likely combine the modelling of variation for larger sets of species, and explicit empirical monitoring of variation for selected taxa (Umaña et al., 2015; Mimura et al., 2017).

For the former, modelling approaches may be uniquely able to simulate the extent of variation in taxa which are difficult to measure, for example by relating changes in proxies such as population size or habitat area to differences in variability, based on the longstanding observation that species with larger population sizes or ranges have greater trait differentiation (Frankham, 2012). However, the strength of these links is difficult to predict as they are context-dependent (Wood et al., 2015) and grounded primarily in adaptive genetic rather than plastic trait change (Fraser et al., 2014), so should be employed with care lest they misestimate trait variation.

With regards to empirical study, intensive experimental work such as that underpinning the findings of Chapters 2 – 4 could be pooled to create datasets comprising direct measurements of functional activities under a range of environmental parameters, which authors may then use and scale or otherwise adjust appropriately to their sampled population. For extensively studied species, new experiments are needed outside of current environmental ranges to better anticipate responses to changing conditions (Luck et al., 2012; Alberto et al., 2013). For rare or data-poor species, empirical measurements will be vital to ensure functional contributions are not overlooked by conflating taxonomic identity with functional potential (Wrede et al., 2017; Violle et al., 2017), and that highly functional traits can be identified (Hébert et al., 2016). The strategic collection of biological information will allow us to generalize insights and determine our broader ability to anticipate species' responses to anthropogenic disturbances, and their implications (Urban et al., 2016). Traits to be quantified in this manner must be selected with care, as each will differ in the strength of their response to context factors (Minden & Olde Venterink, 2019) and effect on ecosystem functioning (Hale et al., 2014; Luck et al., 2012). Notably, traits or certain trait types may be more relevant for measurement in certain types of species than others. For example, the cascading effects of variation in predator traits through trophic systems can alter community composition and ecosystem function (Start & Gilbert et al., 2019). By increasing accuracy and making uncertainties explicit, scientists will be better able to deliver projections of biodiversity, and concomitant functional potential, to support more informed decisions by policymakers and land managers. Empirical techniques still present some degree of potential error arising from the simplified nature of mesocosm studies which do not exhaustively represent complex, natural ecosystems (Stewart et al., 2013). In particular, biotic context may play a role, as a species whose trait expression is measured in isolation for the purpose of establishing its functional role may in reality adjust these contributions when in mixture (Chapter 4). Further, 'space for time' substitution is prevalent in a majority of experimental approaches, which may fail to capture reactions or interactions that develop over longer temporal scales (Stachowicz et al., 2008; Scheiner, 2013; Merilä & Hendry, 2014; Chapter 3). Nonetheless, use of resulting quantitative data within predictive approaches would strongly increase the likelihood of any estimated functional capacity being of an appropriate magnitude (Chapter 5), and ensure that projected ecosystem functioning is of a unit-based value that can be compared directly to measured data. A theoretical end use combines the accuracy of intensive intraspecific sampling with the low-cost benefits of modelling, providing measures of variation (Clark, 2005; Norros et al., 2017) and adjusting error around predictions made from species-level classifications (Bolnick et al., 2011; Hahn & Maron, 2016). Trait frameworks which span organisational scales, such as that discussed by Carmona et al. (2016), suggest avenues through which both approaches can be incorporated. If one must work exclusively at the level of the individual, then functional ecology grounded in trait-based approaches is at risk of forfeiting the generalized predictive ability which motivates it (Shipley et al., 2016).

It remains probable that a majority of authors, ecosystem managers, and legislative bodies will continue to harness single trait metrics within ecosystem study in the coming years. Through a lens of practicality, the reasons for this have been well established; single-trait approaches are logistically efficient, and in many contexts interspecific variability is sufficiently greater in magnitude than intraspecific variability so as to justify the sole use of the former (Zuo et al., 2017). In this context, techniques based in single values or categorical trait classifications – such as the use of BP_c/BP_i (Solan et al., 2004a), IP_c (Wrede et al., 2018), community-weighed means (CWM) (Muscarella & Uriarte, 2016), and Ecosystem Demography (ED) models (Longo et al., 2019) - are valuable tools through which to compare the functional potential of differently species rich assemblages. In essence, single value and in particular categorical trait-based approaches provide context for a projected BEF gradient. Possession of a trait is assumed to relate to functioning through a linear or other direct relationship (Murray et al., 2017; Heilpern et al., 2018). However, as ecologists increasingly rely upon the characteristics of species as predictors of ecosystem responses to environmental change, we must seek to provide the most accurate information, not solely that which is convenient. This aspiration necessitates recognising that, just as a BEF gradient overly simplifies the relationship of species richness to functioning, so does the reliance of trait types or single trait values to characterise individuals' contributions to that functioning (Snelgrove et al., 2014; Luck et al., 2012). To achieve this, trait-based approaches should seek to recognise that individuals are non-identical, and the acknowledgement that individuals vary in response to widespread biotic and abiotic conditions with direct and indirect consequences for BEF should take an increasing role in ecosystem study. As outlined, this could be achieved through the use of intraspecific study to augment or adjust the predictions gained through current, conventional single mean or categorical value techniques (Carmona et al., 2015).

Should ecologists fail to recognise intraspecific variation, what currently presents as an untapped opportunity to identify mechanisms influencing the biotic control of functioning may instead risk becoming a source of error. Particularly where the delivery of ecosystem goods or services is imperilled by environmental or ecological change, the trait expression and consequent functional contributions of species should not be assumed (Henn et al., 2018). If an erroneous assumption is made, any ecosystem management approaches in place may be rendered inefficient at best or ineffective at worst, failing to meet targets for ecosystem and human wellbeing. Evidence suggests that the extent of encountering these risks will be dependent on the traits and taxa in question, as the variability and values of each trait has a unique relationship with, and implications for, functioning (Hébert et al., 2016; Mensens et al., 2017; Henn et al., 2018). Between ecosystems, intraspecific variation will be more or less consequential for understanding the functional contributions of species – however, it is evident that the extent of these consequences cannot be assumed (Minden & Olde Venterink, 2019; Start & Gilbert, 2019).

The findings presented within this thesis demonstrate the viability and value of quantifying intraspecific trait variation and encourage movement towards its explicit consideration during study of ecosystem functioning and, more broadly, ecosystems as a whole. Intraspecific variability should be viewed not as an obstacle to research which must be overlooked or overcome, but rather a substantial source of insight as to the responses of organisms to their prevailing context. Where possible, ecologists should seek to utilise this additional source of functional diversity to better understand, and so better protect, species and ecosystems. Where not possible, it is imperative that practitioners of ecosystem study and management instead appreciate the substantial assumptions inherent in the use of approaches which do not consider intraspecific variation and adjust the error of or confidence in their conclusions appropriately. Much work will likely be needed for the appreciation of intraspecific variation to develop into adoption of techniques grounded in individual-level quantification, and species-based trait values are likely to persist, offering substantial utility in certain contexts. Crucially however, my results provide a clear reminder that the unit of biology is the species only by convention and convenience, and that variation prevails across ecological scales to that of the organism.

6.1 Summary of conclusions and recommendations

Revisiting the key foci and research priorities established at the beginning of this thesis (Chapter 1.3, Fig. 1.1), my findings suggest that:

- Intraspecific variation in trait expression is widespread and inherent in natural systems, and may develop in response to biotic context (here, species composition and density), and exposure to abiotic change (here, change in climate conditions as represented through temperature and pH) (Chapters 2, 3 & 4, Hypotheses H1, H2 & H3).
- Crucially, this intraspecific trait variation occurs concomitantly to differences in community-level effect behaviour and ecosystem functioning which traits are known to mechanistically underpin; thus, contrary to the assumptions which support use of single-value trait approaches, intraspecific variation may have consequences for ecosystem functioning (Chapters 2 & 3, Hypotheses 1 & 2).
- The functional contributions of species and their communities can be best understood when the potential for this variation is acknowledged (Chapter 4), and by explicitly

incorporating intraspecific variation into quantitative trait-based study ecologists may gain greater ability to understand the biotic control of ecosystem function (Chapter 5, Hypothesis H4).

- The direction and extent of intraspecific variation differs between traits, and across species traits will be of differing utility in understanding the contributions of organisms to functioning. As such, a crucial step in the development of intraspecific trait-based approaches will be establishing the circumstances under which trait variation arises and under which it is sufficiently relevant for inclusion. Suggestions for such efforts include modelling or mesocosm-style experiments to establish databases of trait information, similar to that which already exists for categorical metrics, or small-scale intraspecific studies to accompany larger sampling schemes and validate the generalisability of conventional, single-value approaches.

Appendix A

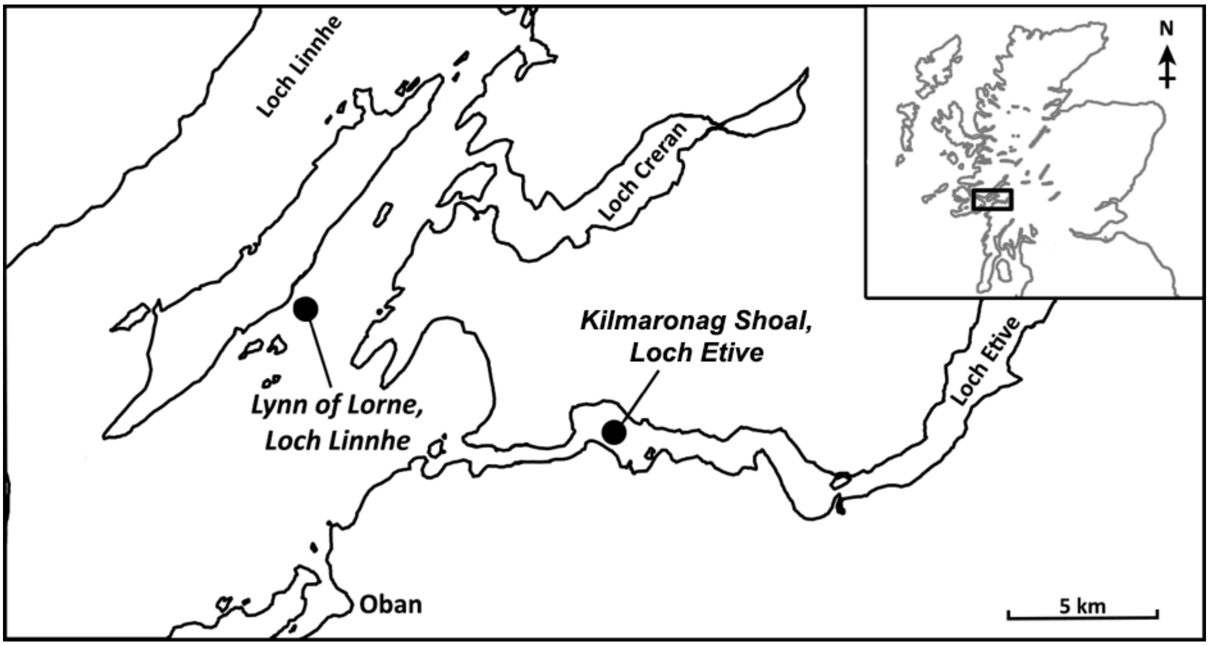


Fig. A1 Sampling locations at Kilmaronag Shoal, Loch Etive (56°27'34.20"N, 5°20'29.28"W), and the Lynn of Lorne, Loch Linnhe (56°29'49.6"N, 5°29'56.2"W), Scotland, UK.

Appendix A

Sediment parameters

Sediment parameters were measured by laser diffraction (Malvern Mastersizer 2000) at the Department of Geography, University of Cambridge following standard protocols (http://www.geog.cam.ac.uk/facilities/laboratories/techniques/). Particle size parameters were calculated using logarithmic graphical measures (Blott & Pye, 2001).

Table A1: Sediment parameters (mean ± SD, n = 5) for sampling sites (n = 5).

	Kilmaronag Shoal, Loch Etive	**Lynn of Lorne, Loch Linnhe**	**Hamble Estuary**
Mz (µm)	233.4 ± 44.9	253.5 ± 35.5	26.3 ± 1.6
Mz (Phi)	3.6 ± 1.1	2.9 ± 0.4	6.7 ± 0.1
Sorting (µm)	298.0 ± 66.7	209.6 ± 63.6	31.9 ± 2.2
Sorting (Phi)	2.4 ± 0.2	2.1 ± 0.4	1.7 ± 0.02
Kurtosis (µm)	14.4 ± 8.9	6.0 ± 2.7	8.8 ± 1.0
Kurtosis (Phi)	3.3 ± 1.1	4.5 ± 1.6	2.3 ± 0.03
Skewness (µm)	3.7 ± 0.7	1.3 ± 0.6	2.3 ± 0.2
Skewness (Phi)	0.6 ± 0.7	1.4 ± 0.5	0.01 ± 0.07
Results below 63 µm (%)	44.7 ± 22.8	23.8 ± 9.4	94.4 ± 1.0
TOC (%)	9.9 ± 5.4	2.9 ± 0.8	7.6 ± 0.6

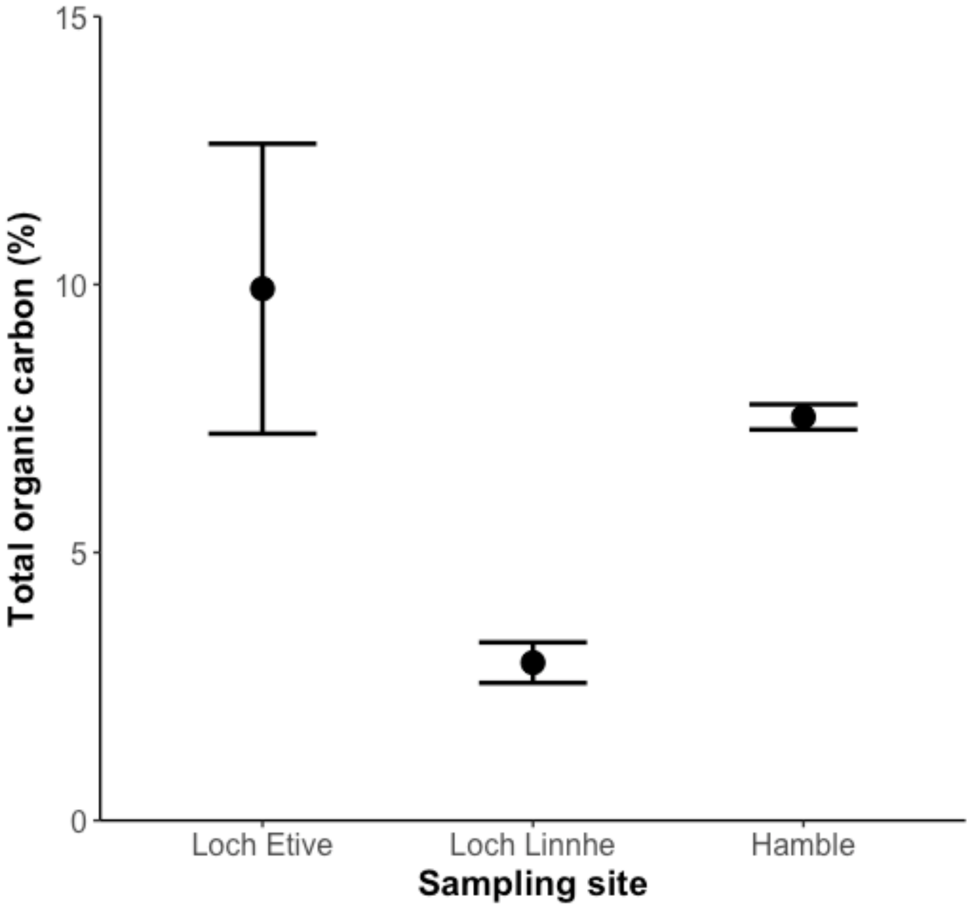


Fig. A2: Total organic carbon (TOC) content (mean ± SE) (%) at Loch Etive (56°27'34.20"N, 5°20'29.28"W, n = 4), Loch Linnhe (56°29'49.6"N, 5°29'56.2"W, n = 5), and Hamble (50°52'23.1"N 1°18'49.3"W, n = 5), showing a significant difference between sites (ANOVA: $F_{2,10}$= 30.78, *P* < 0.001).

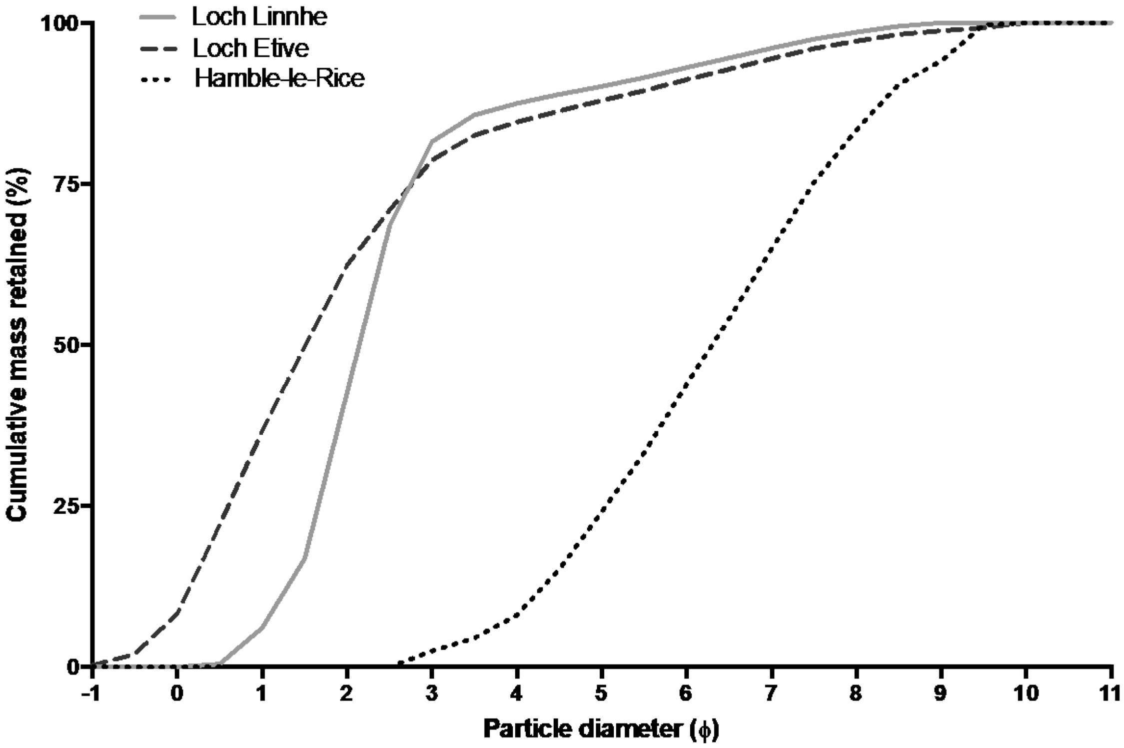


Fig. A3: Cumulative sediment particle size distributions for sampling sites at Lynn of Lorne, Loch Linnhe and Kilmaronag Shoal, Loch Etive, and for sediment used during mesocosm incubations from Hamble-le-Rice, Hampshire.

Table A2: Aspects of ecological context manipulated in fully cross-factored design, showing the number and nature of treatment levels, and identity of individuals in the respective mesocosms.

	Population (Sampling site)	**Species treatment**	**Density**
Number of treatment levels	2	3	3
Treatment levels	1) Kilmaronag Shoal, **Loch Etive** 2) Lynn of Lorne, **Loch Linnhe**	1) ***Amphiura filiformis* monoculture** *(Species identity of component individuals: A. filiformis* in monoculture) 2) ***Ampihura chiajei* monoculture** *(Species identity of component individuals: A. chiajei* in monoculture) 3) ***A. filiformis-A. chiajei* mixed community** *(Species identity of component individuals: A. filiformis* in mixed community, or *A. chiajei* in mixed community)	1) **Low** (250 ind. m-2 *A. filiformis*, 175 ind. m-2 *A. chiajei*) 2) **Medium** (500 ind. m-2 *A. filiformis*, 350 ind. m-2 *A. chiajei*) 3) **High** (1000 ind. m-2 *A. filiformis*, 700 ind. m-2 *A. chiajei*)

Table A3: Number of replicate mesocosms (n = 102), and *A. filiformis* (n = 370) and *A. chiajei* (n = 242), for all combinations of context. Replicates were constrained by abundance of *A. chiajei* from the Loch Etive site. Six cores were lost to mortality. Two individuals representing the species mixture were randomly selected from each core (n = 192).

		Ampihura filiformis **monoculture**	***Amphiura chiajei*** **monoculture**	**Mixed species treatment**
Loch Linnhe	Low density	n = 6 250 ind. m^{-2} *A. filiformis* 3 ind. core $^{-1}$	n = 6 175 ind. m^{-2} *A. chiajei* 2 ind. core $^{-1}$	n = 6 250 ind. m^{-2} *A. filiformis* 2 ind. core $^{-1}$ *A. chiajei* 1 ind. core $^{-1}$
	Medium density	n = 6 500 ind. m^{-2} *A. filiformis* 6 ind. core $^{-1}$	n = 6 350 ind. m^{-2} *A. chiajei* 4 ind. core $^{-1}$	n = 6 500 ind. m^{-2} *A. filiformis* 4 ind. core $^{-1}$ *A. chiajei* 2 ind. core $^{-1}$
	High density	n = 6 1000 ind. m^{-2} *A. filiformis* 12 ind. core $^{-1}$	n = 6 700 ind. m^{-2} *A. chiajei* 8 ind. core $^{-1}$	n = 6 1000 ind. m^{-2} *A. filiformis* 8 ind. core $^{-1}$ *A. chiajei* 4 ind. core $^{-1}$
Loch Etive	Low density	n = 6 250 ind. m^{-2} *A. filiformis* 3 ind. core $^{-1}$	n = 6 175 ind. m^{-2} *A. chiajei* 2 ind. core $^{-1}$	n = 6 250 ind. m^{-2} *A. filiformis* 2 ind. core $^{-1}$ *A. chiajei* 1 ind. core $^{-1}$
	Medium density	n = 5 500 ind. m^{-2} *A. filiformis* 6 ind. core $^{-1}$	n = 6 350 ind. m^{-2} *A. chiajei* 4 ind. core $^{-1}$	n = 5 500 ind. m^{-2} *A. filiformis* 4 ind. core $^{-1}$ *A. chiajei* 2 ind. core $^{-1}$
	High density	n = 4 1000 ind. m^{-2} *A. filiformis* 12 ind. core $^{-1}$	n = 6 700 ind. m^{-2} *A. chiajei* 8 ind. core $^{-1}$	n = 4 1000 ind. m^{-2} *A. filiformis* 8 ind. core $^{-1}$ *A. chiajei* 4 ind. core $^{-1}$

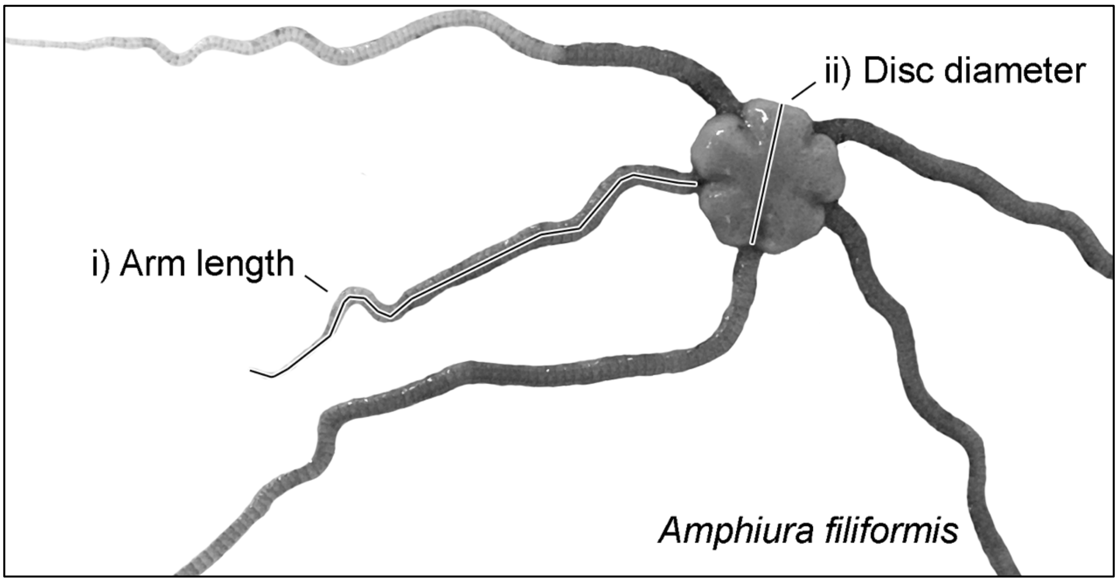


Fig. A4: Morphological measurements made on *Amphiura chiajei* and *Amphiura filiformis* individuals during image analysis (ImageJ, version 1.46r, Schneider et al., 2012); i) Arm length, measured as a line directly through the centre of the limb, where the total length of all five limbs was averaged for analysis. ii) Disc diameter, measured as the largest of the five distances across the lines of symmetry, from the disc as its widest point to the base of the opposite arm.

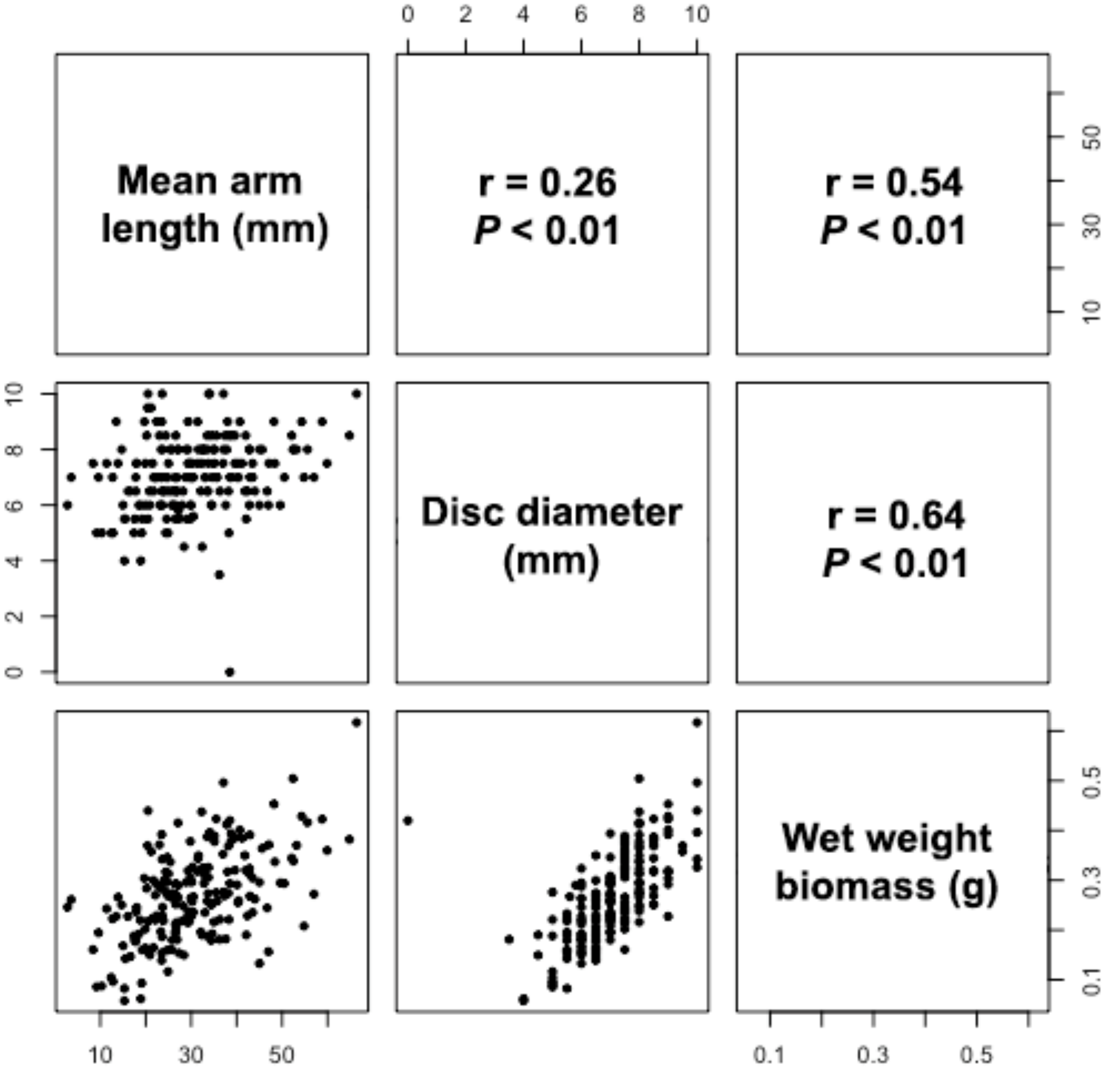


Fig. A5: Pairs plot of morphological variables of mean arm length (mm), disc diameter (mm) and wet weight biomass (g) of *Amphiura chiajei* and *Amphiura filiformis,* shown against the Pearson correlation coefficient on the inverse panel.

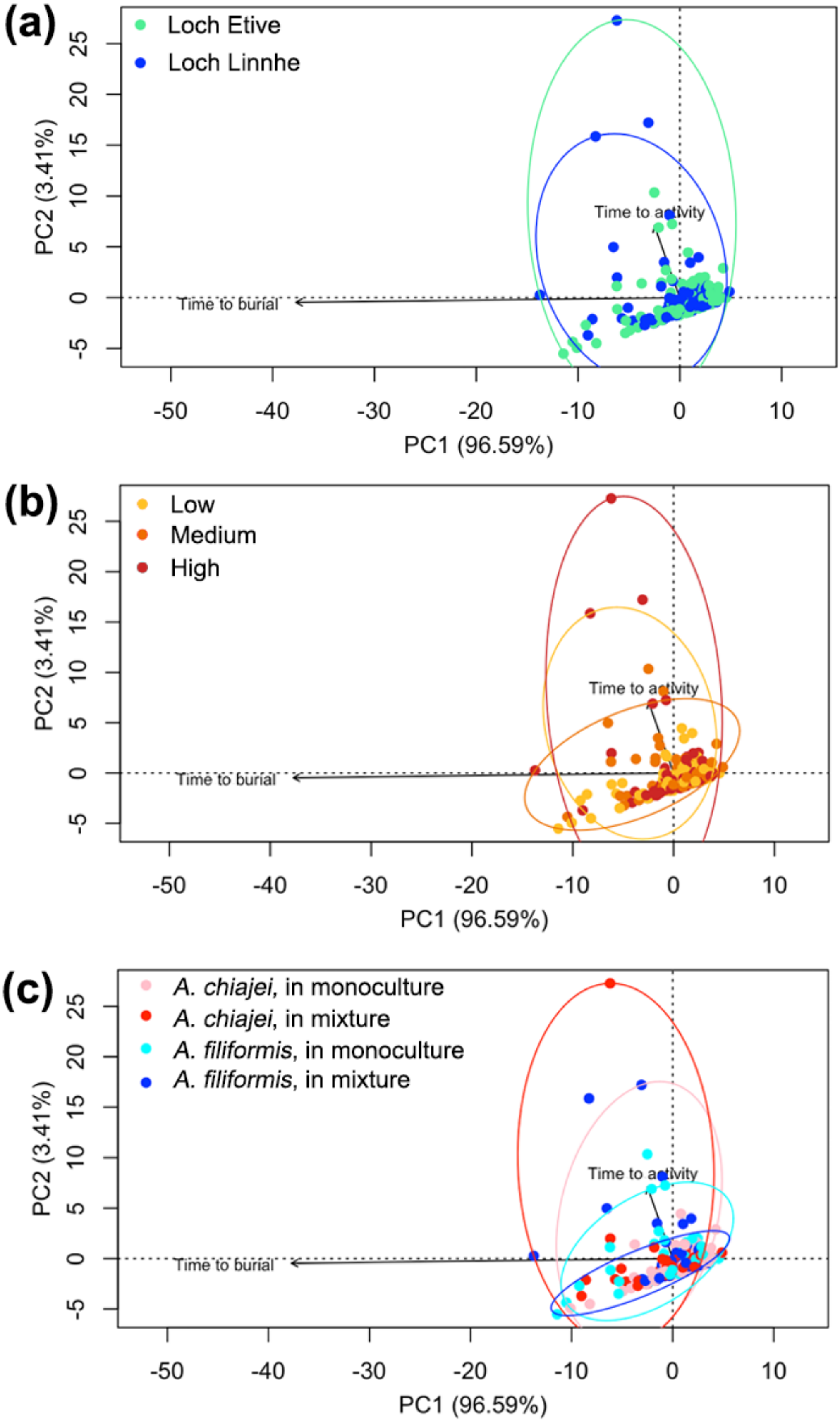


Fig. A6: Biplots of constrained ordination with Principle Component Analysis (PCA) in the *vegan* package in *R* (Oksanen et al., 2017; URL: https://CRAN.R-project.org/package=vegan). Plots show the multivariate behavioural traits ‘Time to (begin) activity’ and ‘Time to (complete) burial’ of individuals and the (**a**) Population (**b**) Density and (**c**) Species identity treatments under which these individuals were maintained. Arrows indicate the variation of the traits across all individuals, while coloured ellipses encircle the individuals belonging to each treatment group.

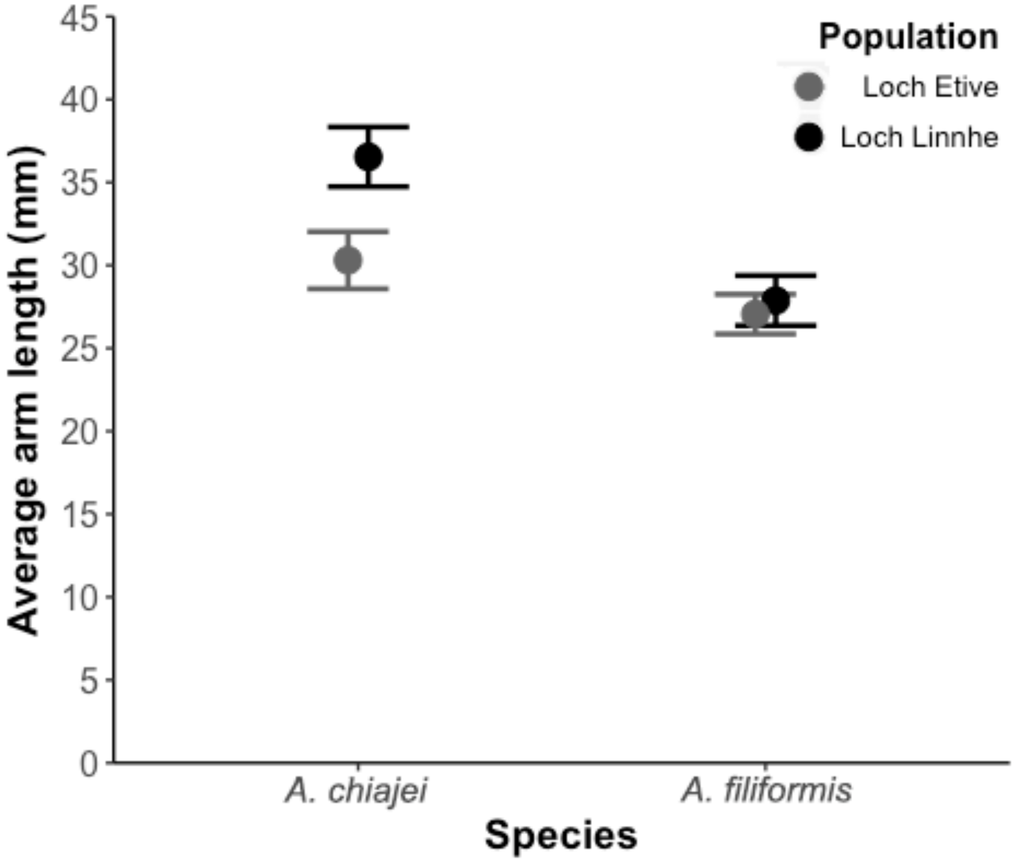


Fig. A7: Mean arm length (mean ± SE) (cm) of *Amphiura chiajei* and *Amphiura filiformis* originating from two populations in Loch Etive (56°27'34.20"N, 5°20'29.28"W) and Loch Linnhe (56°29'49.6"N, 5°29'56.2"W), Scotland, UK. Analysis showed a significant difference in average arm length between species (ANOVA: $F_{1,188}$ = 14.996, $P < 0.001$) and populations (ANOVA: $F_{1,188}$ = 4.033, $P = 0.046$).

Table A4: Results table for ANOVA of coefficient of variance (CV) of behavioural traits i) time taken to begin behaviour and ii) time taken to complete burial, showing results for all terms in the minimum adequate model following model selection based on Akaike Information Criteria (AIC) from the context factors Density, Species Mixture Treatment, Population, and their interactions.

i) CV Time taken to begin behaviour

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Density	2	0.1672739	0.08363693	0.5775962	0.56340796
Population	1	0.3368041	0.33680407	2.3259671	0.13090038
Species Mixture Treatment	2	0.6637300	0.33186498	2.2918578	0.10722049
Density * Species Mixture Treatment	4	1.3859010	0.34647524	2.3927562	0.05677979
Residuals	86	12.4529489	0.14480173		

i) CV Time taken to complete burial

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Density	2	0.04847546	0.02423773	0.37345964	0.6895729
Population	1	0.00237216	0.00237216	0.03655071	0.8488795
Species Mixture Treatment	2	0.20612455	0.10306228	1.58800361	0.2108675
Density * Population	2	0.01378756	0.00689378	0.10622071	0.8993560
Density * Species Mixture Treatment	4	0.38815904	0.09703976	1.49520753	0.2117686
Population * Species Mixture Treatment	2	0.16478266	0.08239133	1.26950162	0.2867119

Density * Population * Species Mixture Treatment	4	0.44212026	0.11053006	1.70306876	0.1577676
Residuals	78	5.06224132	0.06490053		

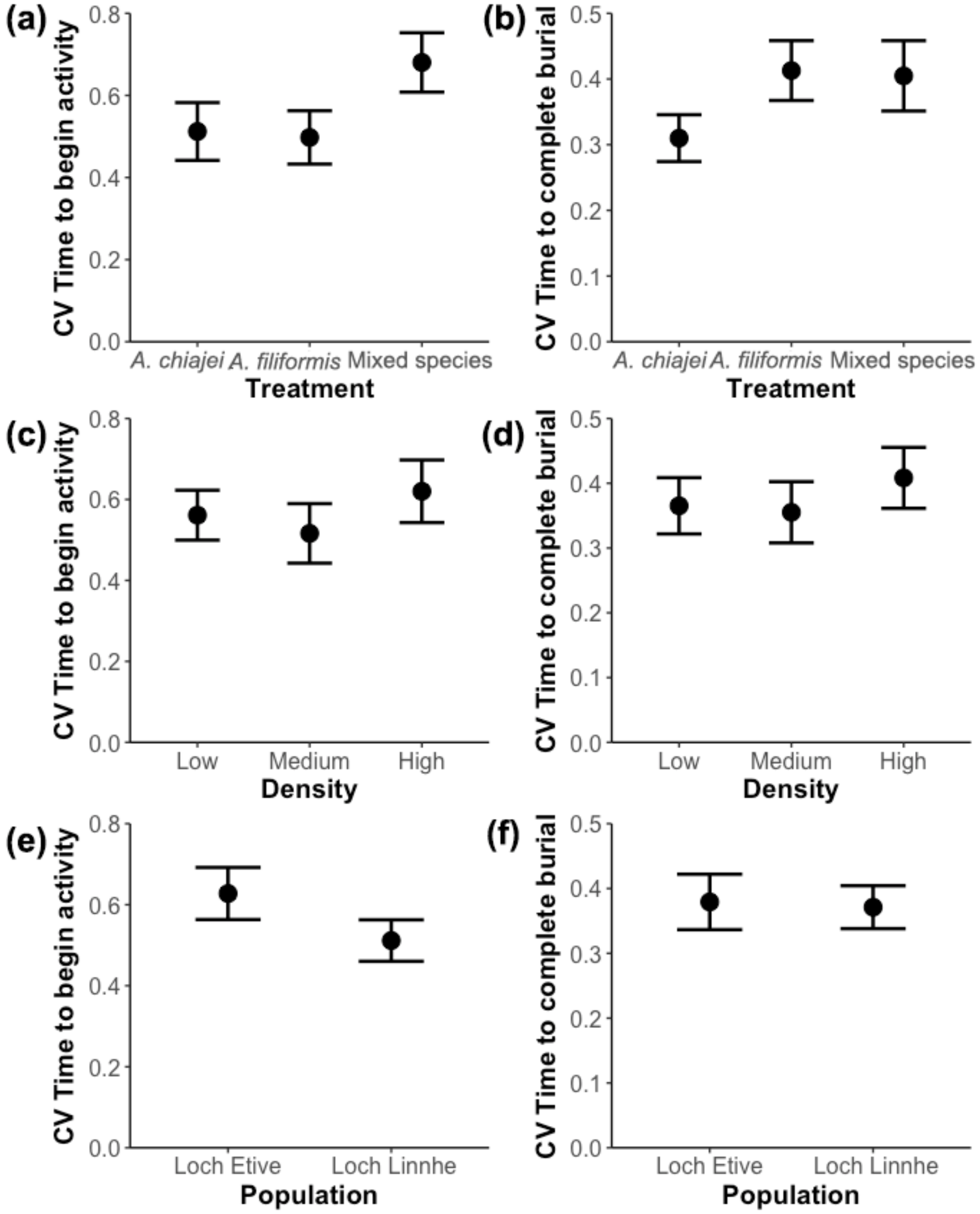


Fig. A8: Coefficient of variation (CV, the ratio of standard deviation to the mean) (mean ± SE, n = 6) of the time (**a, c, e**) taken to begin activity and (**b, d, f**) complete burial for individuals of the species *Amphiura chiajei* and *Amphiura filiformis* maintained under differing (**a – b**) species mixture treatments and (**c – d**) densities, and (**e – f**) originating from different populations.

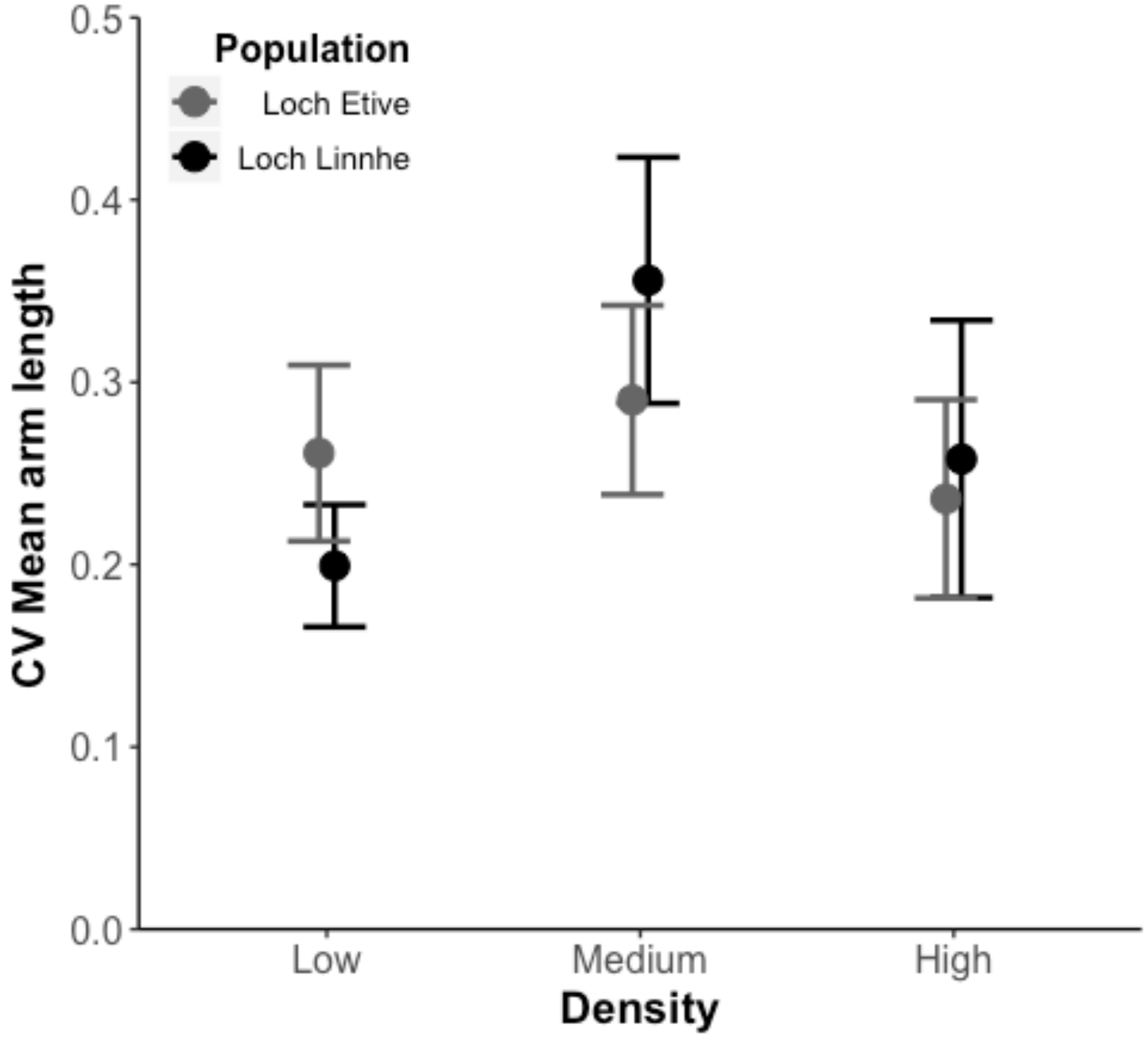


Fig. A9: Coefficient of variation (CV, the ratio of standard deviation to the mean) for the mean arm length of individuals of species *Amphiura chiajei and Amphiura filiformis,* showing a non-significant difference between densities and populations (ANOVA: $F_{1,94}$ = 0.02, *P* = 0.8836).

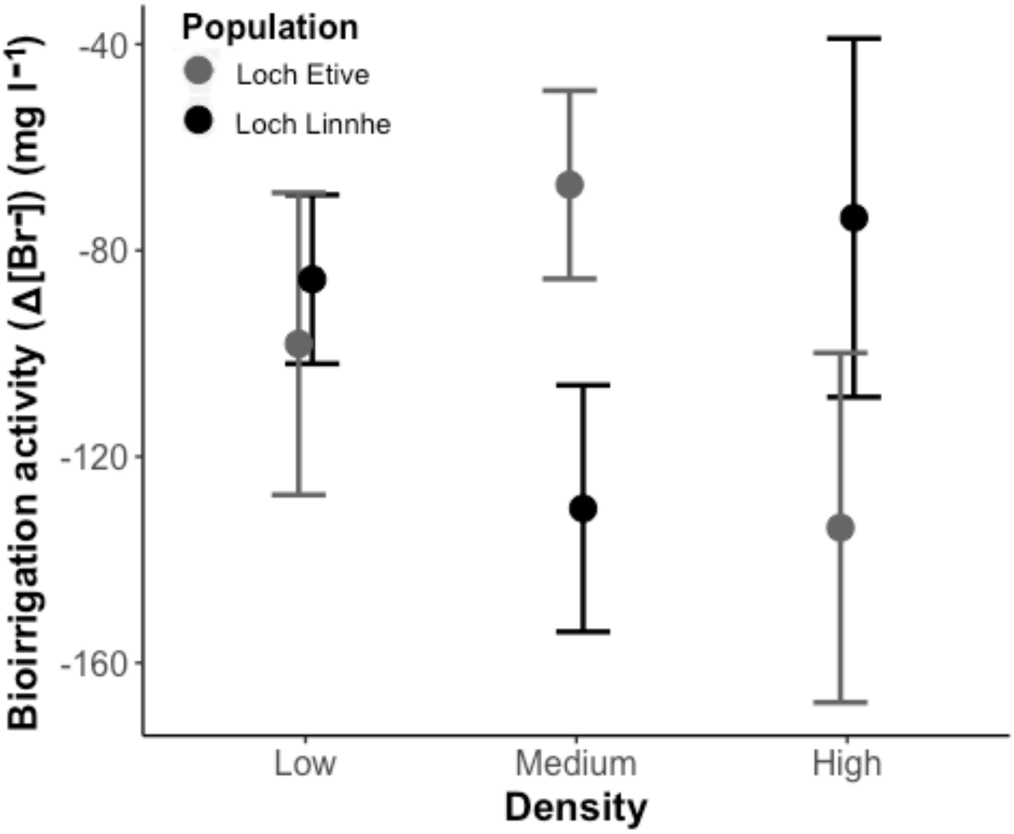


Fig. A10: Bioirrigation activity (mean ± SE) (Δ[Br−], mg L^{-1}) for *Amphiura chiajei* and *Amphiura filiformis* maintained under differing densities and originating from populations in either Loch Etive or Loch Linnhe, showing a non-siginificant interaction of density x population (ANOVA: $F_{2,89}$ = 2.24, *P* = 0.1120).

Appendix B

Sediment parameters

Sediment parameters were measured by laser diffraction (Malvern Mastersizer 2000) at the Department of Geography, University of Cambridge following standard protocols (http://www.geog.cam.ac.uk/facilities/laboratories/techniques/). Particle size parameters were calculated using logarithmic graphical measures (Blott & Pye, 2001).

Table B1: Sediment parameters (mean ± SD, n = 5) for sampling sites (n = 5).

	Kilmaronag Shoal, Loch Etive	Lynn of Lorne, Loch Linnhe	Hamble Estuary
Mz (µm)	233.4 ± 44.9	253.5 ± 35.5	26.3 ± 1.6
Mz (Phi)	3.6 ± 1.1	2.9 ± 0.4	6.7 ± 0.1
Sorting (µm)	298.0 ± 66.7	209.6 ± 63.6	31.9 ± 2.2
Sorting (Phi)	2.4 ± 0.2	2.1 ± 0.4	1.7 ± 0.02
Kurtosis (µm)	14.4 ± 8.9	6.0 ± 2.7	8.8 ± 1.0
Kurtosis (Phi)	3.3 ± 1.1	4.5 ± 1.6	2.3 ± 0.03
Skewness (µm)	3.7 ± 0.7	1.3 ± 0.6	2.3 ± 0.2
Skewness (Phi)	0.6 ± 0.7	1.4 ± 0.5	0.01 ± 0.07
Results below 63 µm (%)	44.7 ± 22.8	23.8 ± 9.4	94.4 ± 1.0
TOC (%)	9.9 ± 5.4	2.9 ± 0.8	7.6 ± 0.6

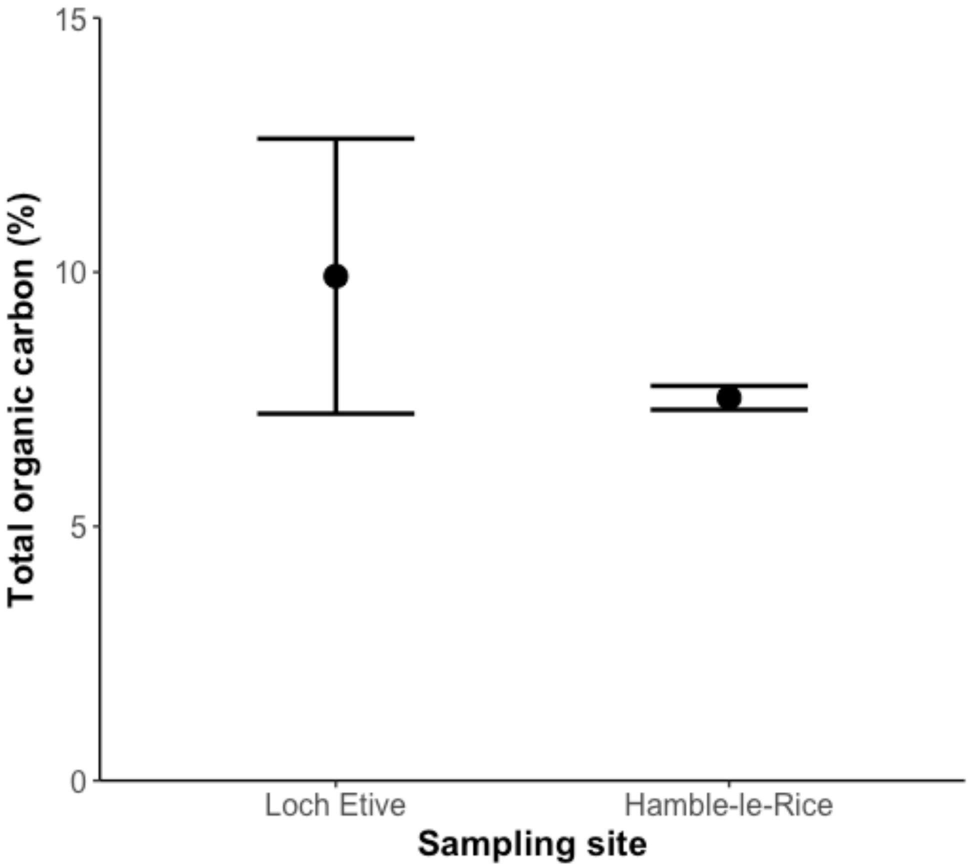


Fig. B1: Total organic carbon (TOC) content (mean ± SE) (%) at Loch Etive (56°27'34.20"N, 5°20'29.28"W, n = 4) and Hamble-le-Rice (50°52'23.1"N 1°18'49.3"W, n = 5), showing no significant difference between sites (ANOVA: $F_{1,7} = 1.002$, $P = 0.35$).

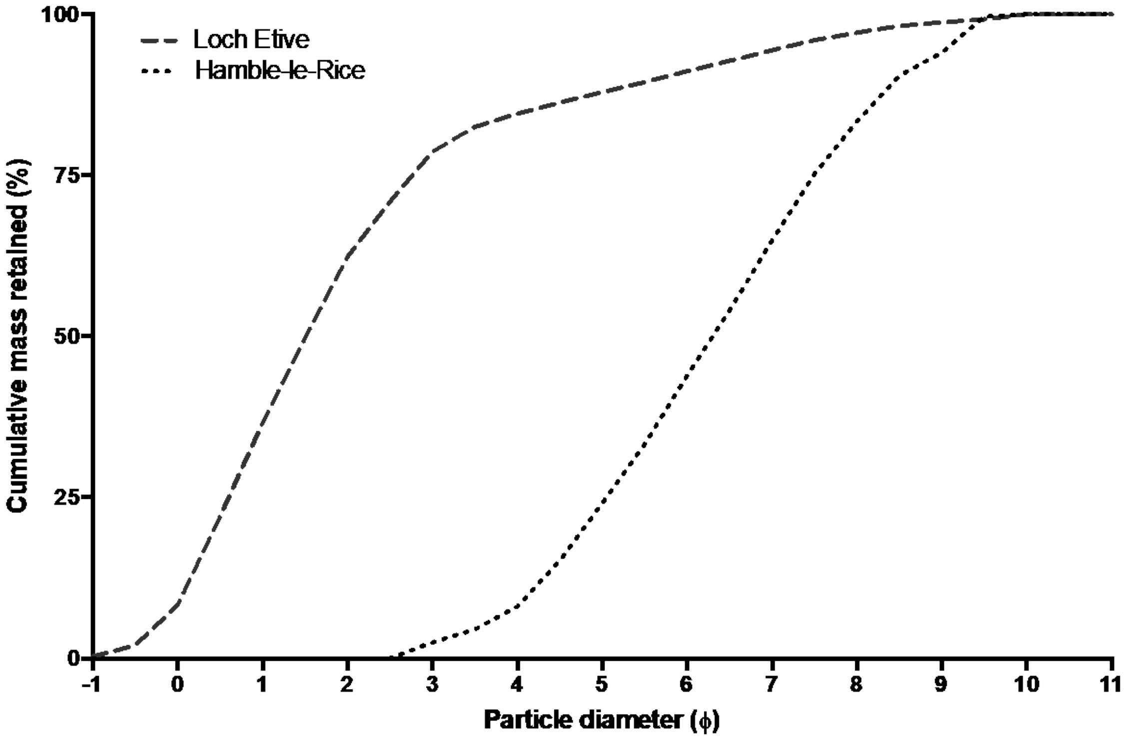


Fig. B2: Cumulative sediment particle size distributions for Kilmaronag Shoal, Loch Etive (dashed line) and for sediment used during mesocosm incubations from Hamble-le-Rice, Hampshire (dotted line).

Table B2: Number of replicate mesocosms (n = 30), and *Amphiura filiformis* (n = 200) and *Amphiura chiajei* (n = 120) within mesocosms, for all combinations of climate and species mixture treatment. For analysis, eight individuals were randomly selected from each core (n = 240) to standardise abundance between treatment groups.

	***A. filiformis* monoculture**	***A. chiajei* monoculture**	**Mixed species treatment**
Ambient climate condition	n = 5 1000 ind. m^{-2} *A. filiformis* 12 ind. $core^{-1}$	n = 5 700 ind. m^{-2} *A. chiajei* 8 ind. $core^{-1}$	n = 5 1000 ind. m^{-2} *A. filiformis* 8 ind. $core^{-1}$ *A. chiajei* 4 ind. $core^{-1}$
Future climate condition	n = 5 1000 ind. m^{-2} *A. filiformis* 12 ind. $core^{-1}$	n = 5 700 ind. m^{-2} *A. chiajei* 8 ind. $core^{-1}$	n = 5 1000 ind. m^{-2} *A. filiformis* 8 ind. $core^{-1}$ *A. chiajei* 4 ind. $core^{-1}$

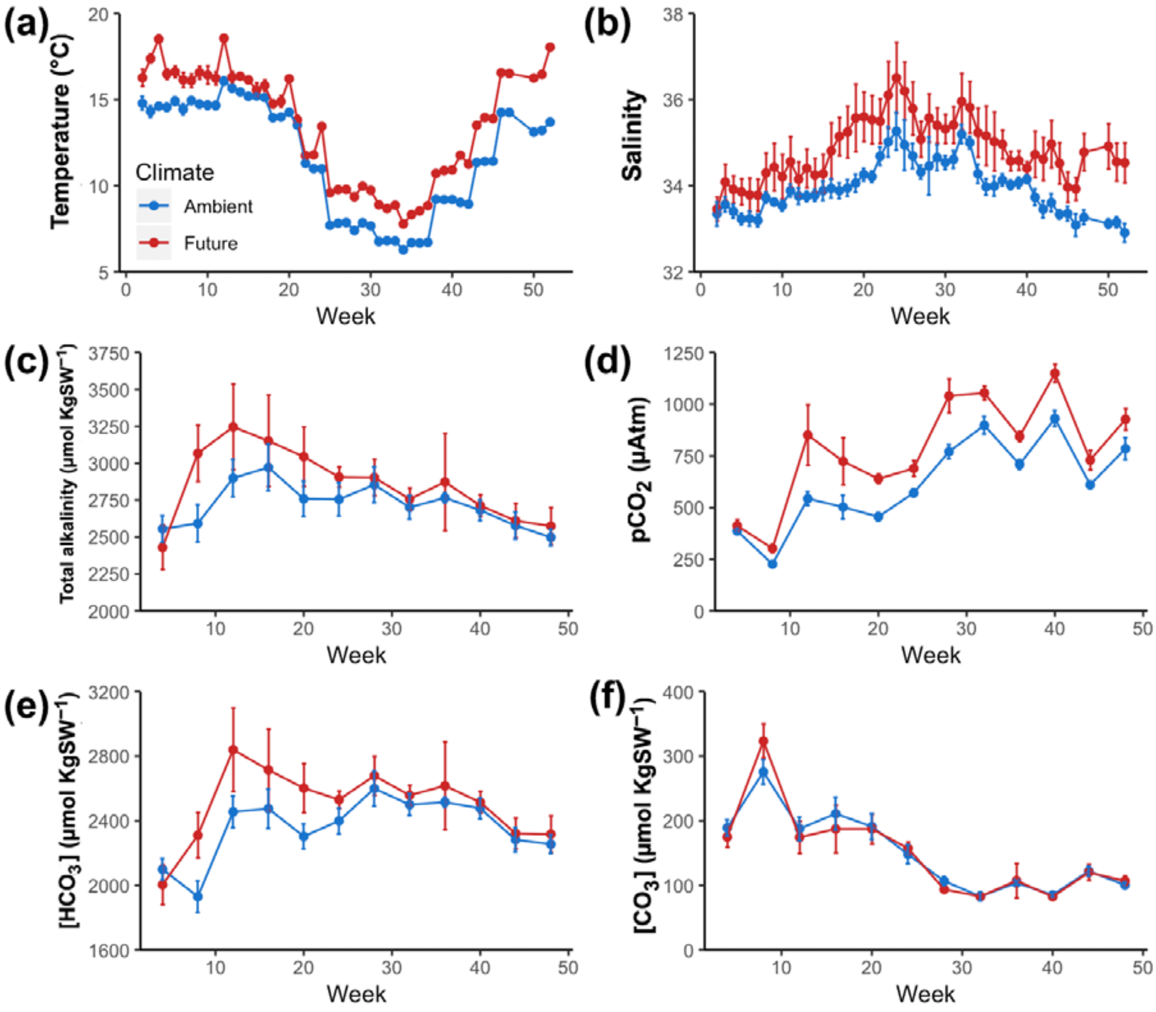


Fig B3: Weekly seawater (a) temperature (°C) and (b) salinity (Mettler-Toledo InLab 737 IP67 temperature–conductivity combination electrode) and monthly (c) total alkalinity (A_T) (µmol KgSW^{-1}), (d) pCO_2 (µAtm), (e) [HCO_3] (µmol KgSW^{-1}) and (f) [CO_3] (µmol KgSW^{-1}) for mesocosms of either ambient (ambient temperature/400 ppm [CO_2]) or future (ambient temperature + 2/550 ppm [CO_2]) climate condition, taken between Week 2 (7/08/17) – Week 52 (16/07/18). Error bars indicate standard deviation of (**a – b**) all cores or (**c – f**) *n* = 9 replicates, 3 from each species treatment (*Amphiura filiformis*, *Amphiura chiajei* or both species in mixture). pCO_2, [HCO_3], [CO_3] were calculated using *CO2Sys* (Pierrot et al., 2006).

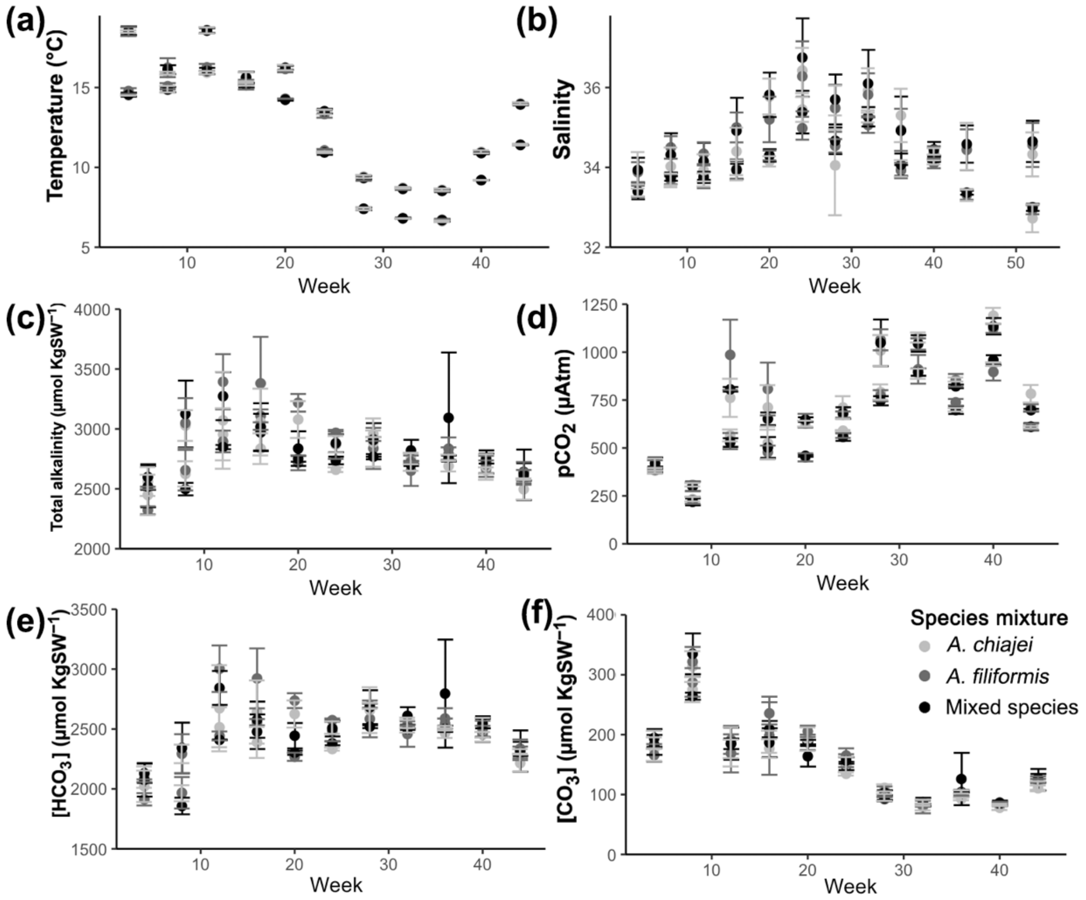


Fig B4: Weekly seawater (a) temperature (°C) and (b) salinity (Mettler-Toledo InLab 737 IP67 temperature–conductivity combination electrode) and monthly (c) total alkalinity (A_T) (µmol KgSW^{-1}), (d) pCO$_2$ (µAtm), (e) [HCO$_3$] (µmol KgSW^{-1}) and (f) [CO$_3$] (µmol KgSW^{-1}) across mesocosms of both climate treatments composed of either *Amphiura chiajei, Amphiura filiformis,* or both species in a mixed treatment, taken between Week 2 (7/08/17) – Week 52 (16/07/18). Error bars indicate standard deviation of (**a – b**) all cores or (**c – f**) n = 3 per each species treatment. pCO$_2$, [HCO$_3$], [CO$_3$] were calculated using *CO2Sys* (Pierrot et al., 2006).

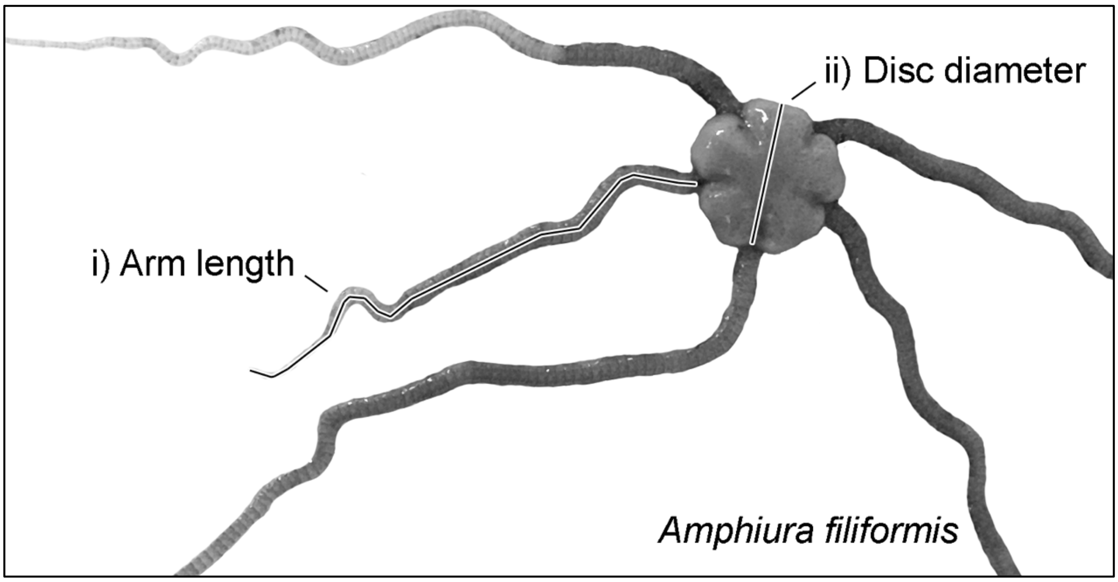


Fig. B5: Morphological measurements made on *Amphiura chiajei and Amphiura filiformis* individuals during image analysis (ImageJ, version 1.46r, Schneider et al., 2012); i) Arm length, measured as a line directly through the centre of the limb, where the total length of all five limbs was averaged for analysis. ii) Disc diameter, measured as the largest of the five distances across the lines of symmetry, from the disc as its widest point to the base of the opposite arm.

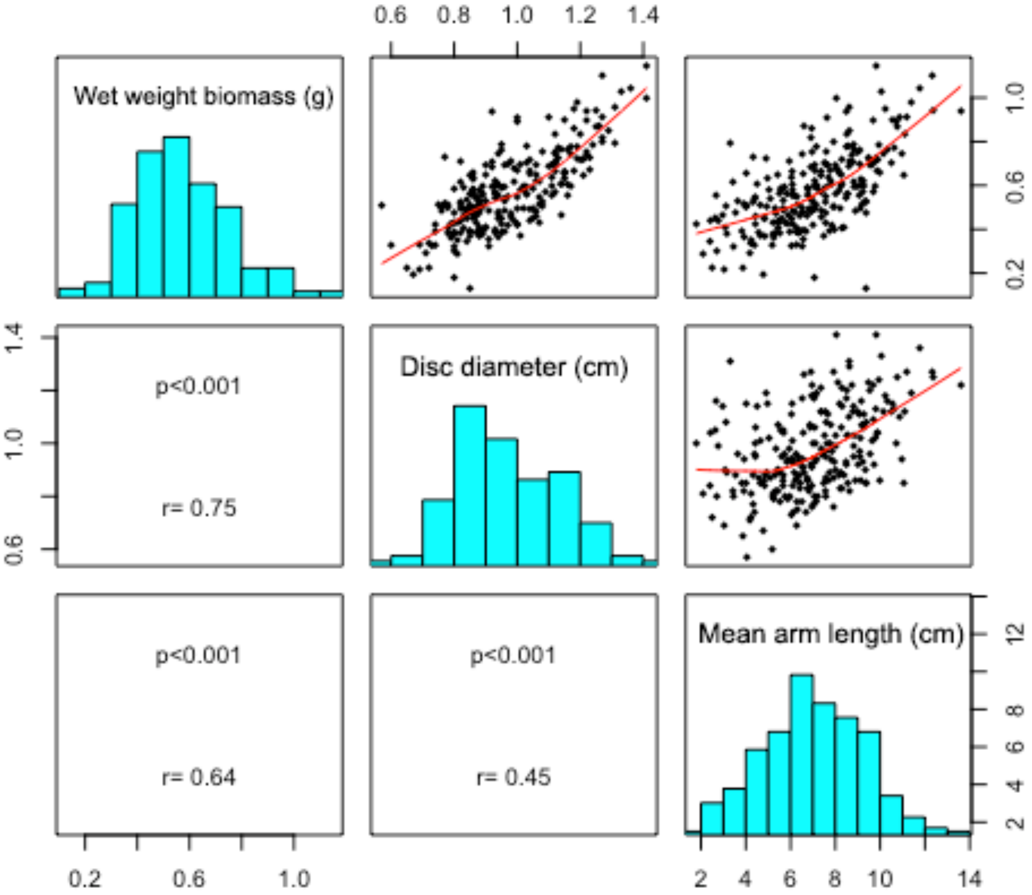


Fig. B6: Pairs plot of morphological variables of wet weight biomass (g), disc diameter (cm) and mean arm length (cm) of *Amphiura chiajei* and *Amphiura filiformis,* shown against the Pearson correlation coefficient on the inverse panel, demonstrating significant co-linearity between measured morphological traits.

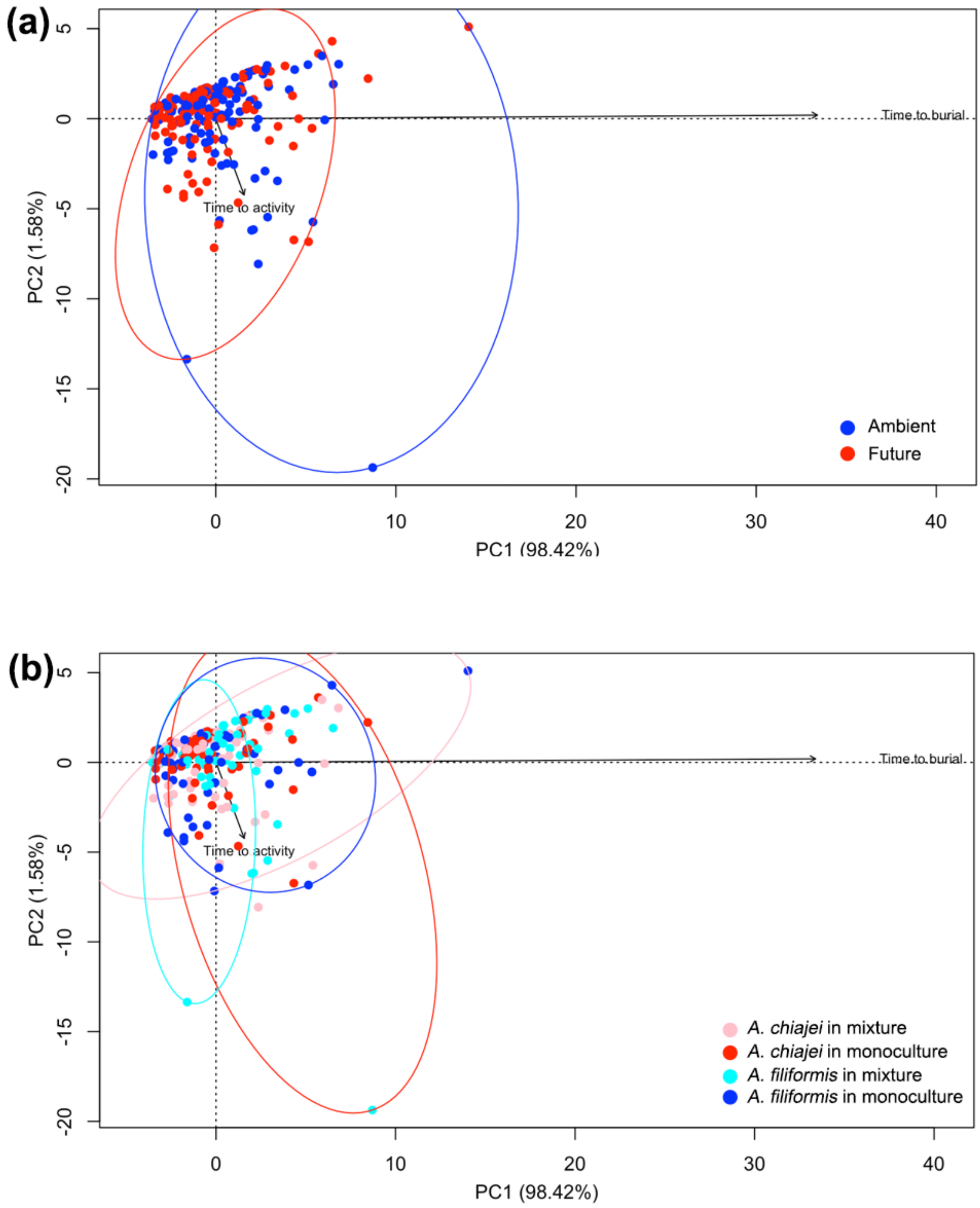


Fig. B7: Biplots of ordination with Principle Component Analysis (PCA) in the *vegan* package in *R* (Oksanen et al., 2017). Plots show the multivariate behavioural traits ‘Time to (begin) activity’ and ‘Time to (complete) burial’ of individuals and the (a) Climate and (b) Species mixture treatments under which these individuals were maintained. Arrows indicate the variation of the traits across all individuals, while coloured ellipses encircle the individuals belonging to each treatment group.

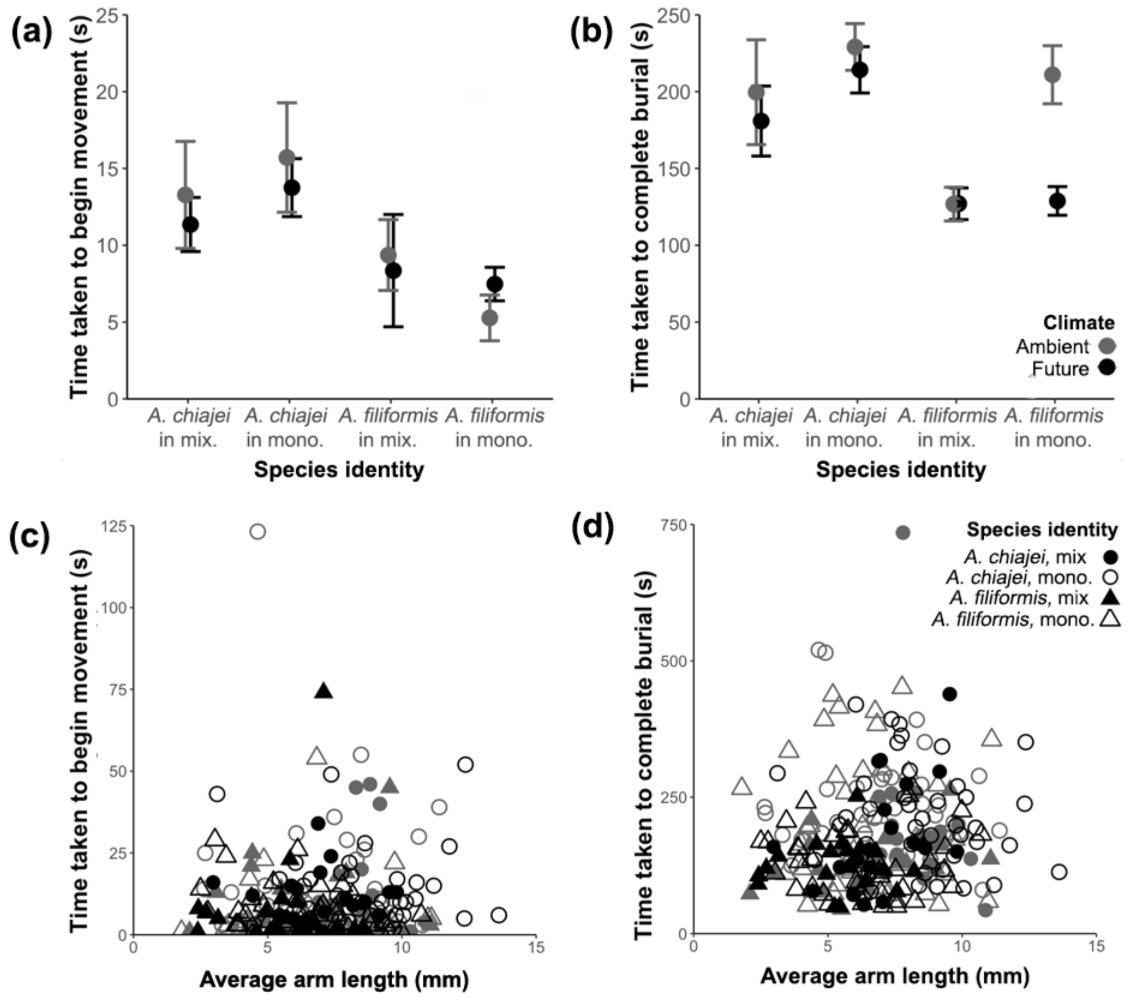


Fig. B8 The effect of climate (ambient: ambient temperature/400 ppm [CO_2]; future: ambient temperature + 2 °C/550 ppm [CO_2]) and species identity (maintained in mixture, or in monoculture) on time elapsed (mean ± SE) (s) for *Amphiura chiajei* and *Amphiura filiformis* to (**a, c**) begin movement and (**b, d**) complete burial into the sediment. (**a**) and (**b**) show a non-significant interaction of climate x species identity (PERMANOVA: $F_{3,237}$ = 2.15 *P* = 0.062). (**c**) and (**d**) show a non-significant interaction between climate x species identity x average arm length (mm) (PERMANOVA: $F_{3,237}$ = 1.99 *P* = 0.096). For all panels, grey symbols represent ambient climate conditions and black symbols represent future climate conditions. For (**c**) and (**d**), circular symbols represent *A. chiajei* while triangular symbols represent *A. filiformis*, and solid circles represent species when in mixture while unfilled symbols represent species in monoculture.

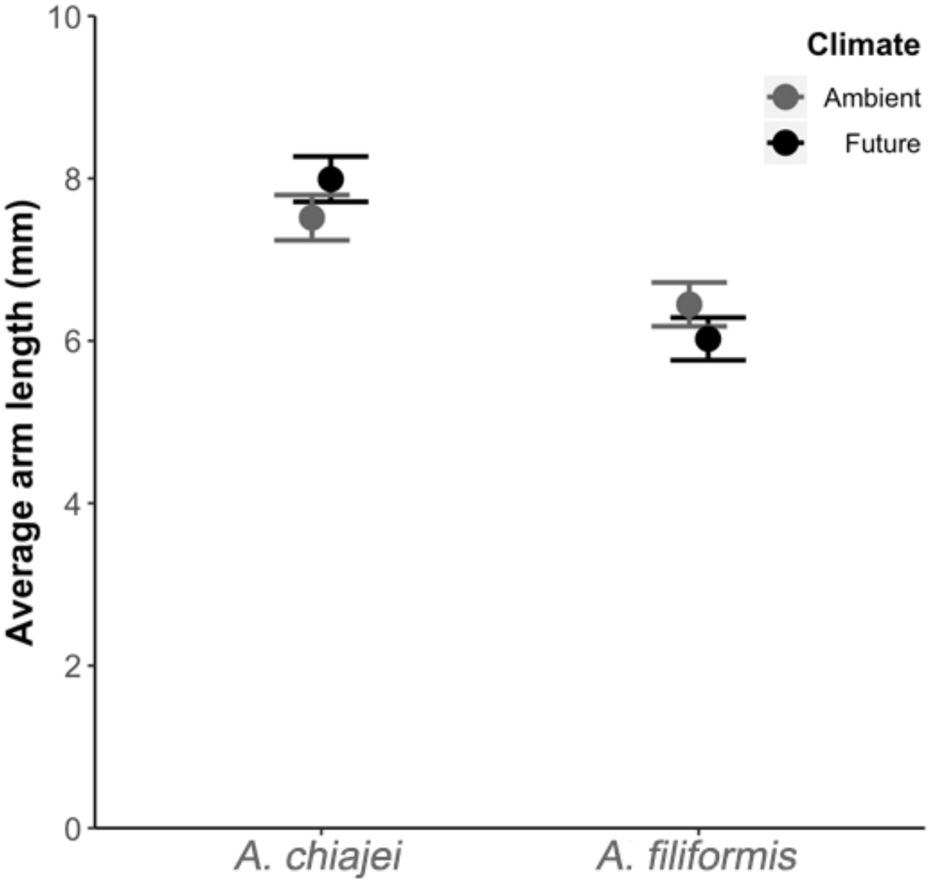


Fig. B9: Morphological trait expression (mean arm length) (mm) of individuals of species *Amphiura chiajei* and *Amphiura filiformis* showing a significant difference between species (ANOVA: $F_{1,224}$ = 31.15, *P* < 0.001), but a non-significant difference between applied climate treatments (ANOVA: $F_{1,234}$ = 0.16, *P* = 0.849).

Table B4: Results table for analysis of variance of the effect of climate (ambient: ambient temperature/400ppm [CO_2]; future: ambient temperature + 2 °C/550 ppm [CO_2]) on the coefficient of variance (CV, the ratio of the standard deviation of the mean)) of intraspecific behavioural traits i) time taken to begin behaviour and ii) time taken to complete burial, showing results for all terms in the minimum adequate model following model selection based on Akaike Information Criteria (AIC) from the context factors Climate and Species Mixture Treatment, and their interactions.

i) Time taken to begin behaviour

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Climate	1	0.4608	0.4608	3.2945	0.0802
Residuals	28	3.9163	0.1399		

ii) Time taken to complete burial

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Climate	1	0.0023	0.0023	0.0744	0.7871
Residuals	28	0.8508	0.0304		

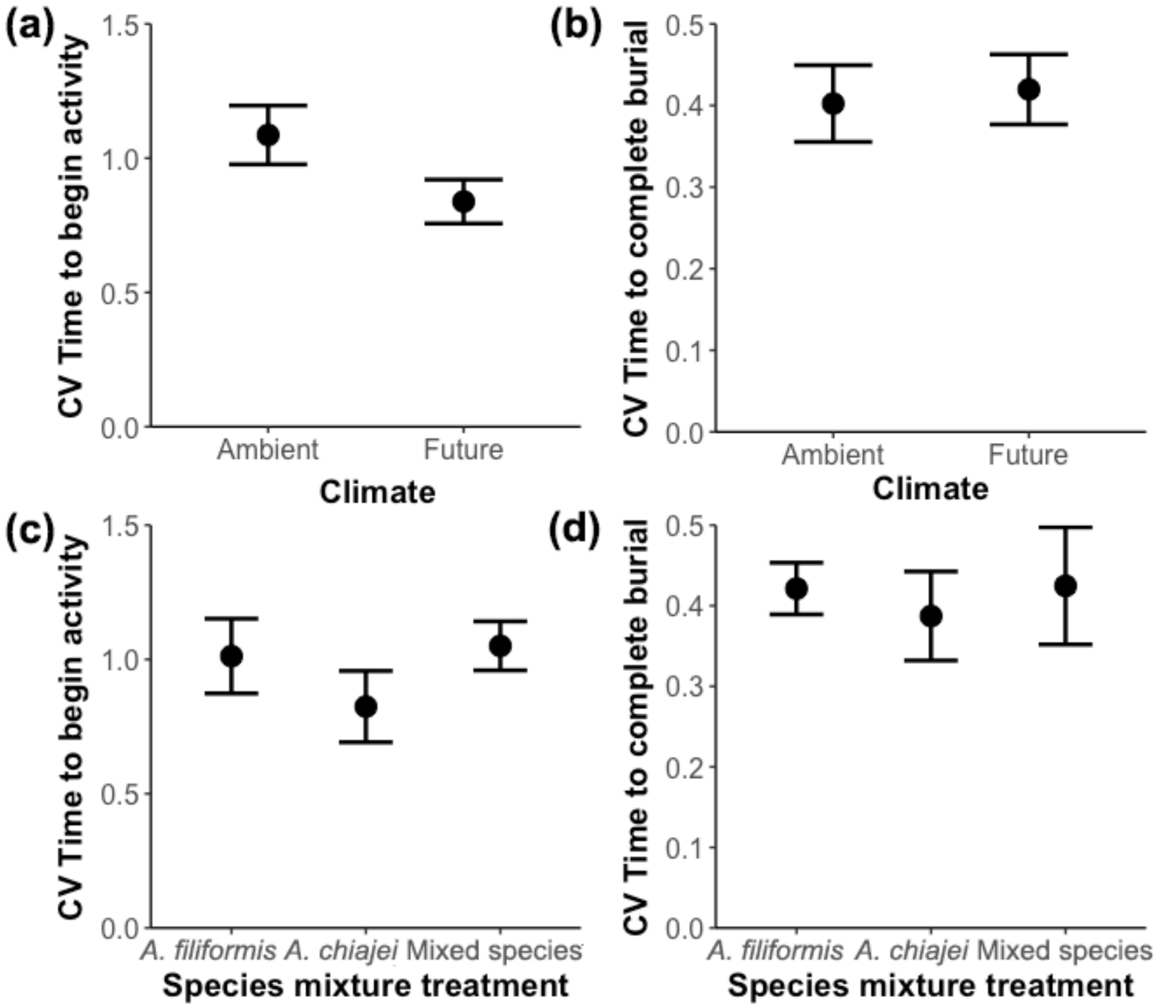


Fig. B10: Coefficient of variation (CV, the ratio of standard deviation to the mean) (mean ± SE, n = 5) of the time (**a, c**) taken to begin activity and (**b, d**) complete burial for individuals of the species *Amphiura filiformis and Amphiura chiajei* (**a – b**) originating from different populations and (**c – d**) maintained under differing species mixture treatments.

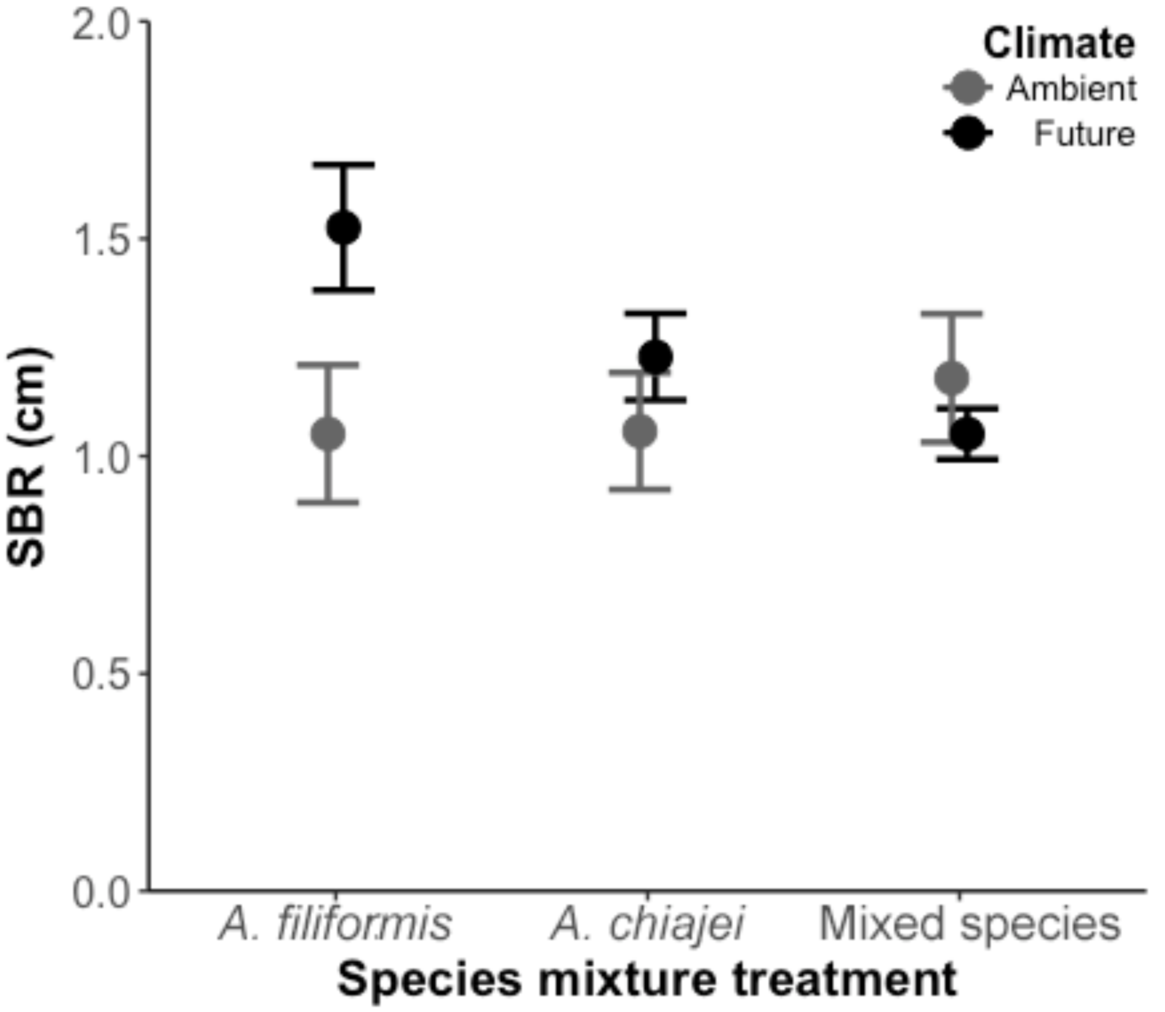


Fig. B11: The effects of biotic and abiotic context on surface boundary roughness (SBR) (cm) (mean ± SE, n = 5) in mesocosms containing *Amphiura filiformis* and *Amphiura chiajei* in monoculture or mixture, showing only a marginally significant ($P < 0.1$) interaction between climate and species mixture treatment (ANOVA: $F_{2,24} = 2.75$, $P = 0.084$).

Table B5: Results table for analysis of variance of the effect of climate (ambient: ambient temperature/400ppm [CO_2]; future: ambient temperature + 2 °C/550 ppm [CO_2]) and species treatment (*Amphiura filiformis* in monoculture, *Amphiura chiajei* in monoculture, or a mixed treatment) on [PO_4-P] (µmol L^{-1}), showing results for all terms in the minimum adequate model following model selection based on Akaike Information Criteria (AIC) from the context factors Climate and Species Mixture Treatment, and their interactions.

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Climate	1	0.0001	0.00012	0.0002	0.9877
Species treatment	2	0.7801	0.39004	0.7930	0.4640
Climate x species treatment	2	1.8842	0.94212	1.9155	0.1691
Residuals	24	11.8044	0.49185		

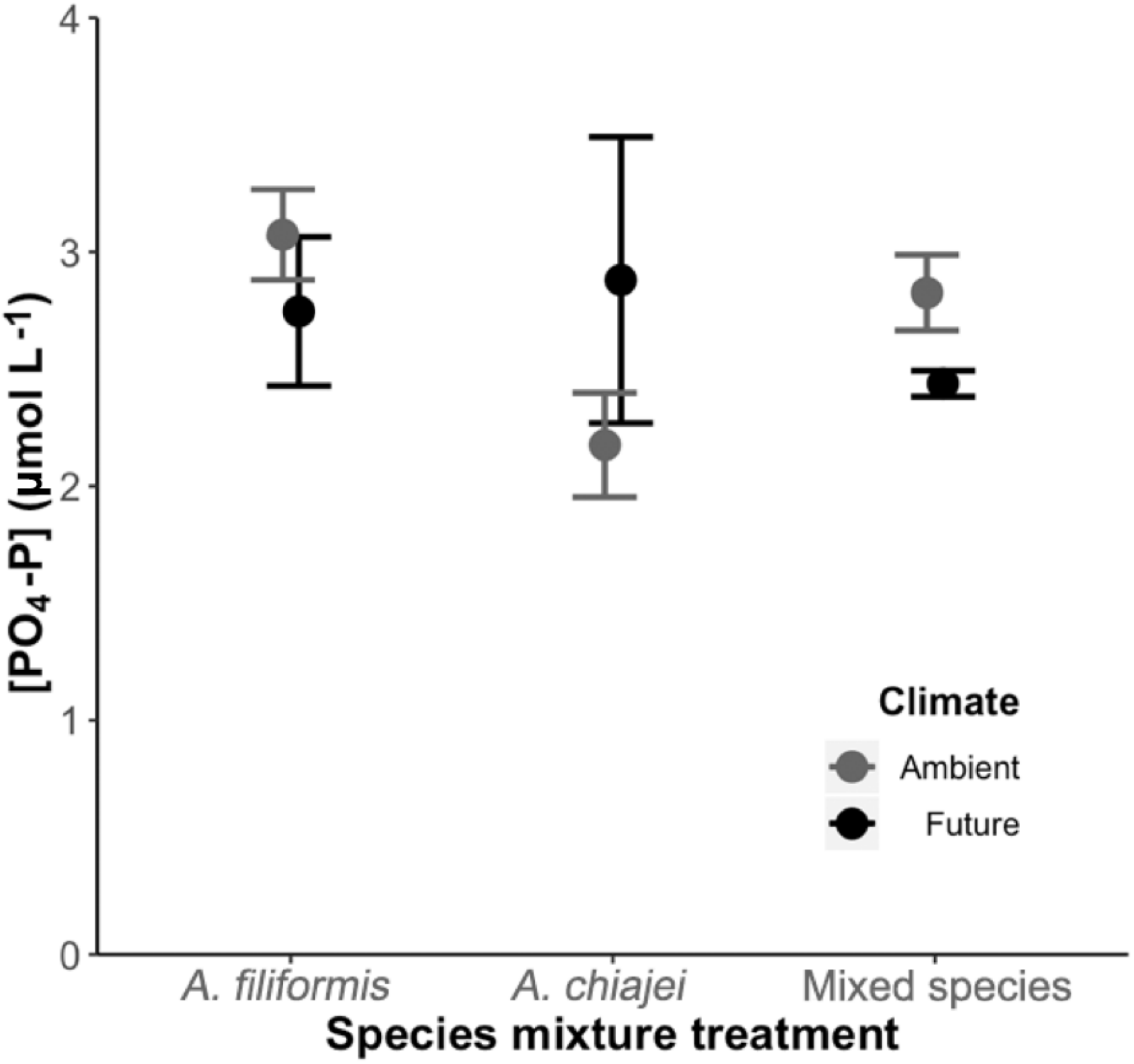


Fig. B12: The effects of biotic and abiotic context on [PO_4-P] (μmol L^{-1}) (mean ± SE, n = 5) in mesocosms containing *Amphiura filiformis* and *Amphiura ch iajei* in monoculture or mixture, showing no significant independent or interacting effects (Table S5).

Appendix C

Sediment parameters

Sediment parameters were measured by laser diffraction (Malvern Mastersizer 2000) at the Department of Geography, University of Cambridge following standard protocols (http://www.geog.cam.ac.uk/facilities/laboratories/techniques/). Particle size parameters were calculated using logarithmic graphical measures (Blott & Pye, 2001).

Table C1: Sediment parameters (mean ± SD, n = 5) for sampling sites (n = 5).

	Bridgwater Bay National Nature Reserve	**Hamble Estuary**
Mz (µm)	21.3 ± 3.9	26.3 ± 1.6
Mz (Phi)	6.3 ± 0.2	6.7 ± 0.1
Sorting (µm)	24.9 ± 9.0	31.9 ± 2.2
Sorting (Phi)	1.4 ± 0.1	1.7 ± 0.02
Kurtosis (µm)	22.6 ± 13.5	8.8 ± 1.0
Kurtosis (Phi)	3.5 ± 0.1	2.3 ± 0.03
Skewness (µm)	3.4 ± 1.4	2.3 ± 0.2
Skewness (Phi)	0.3 ± 0.2	0.01 ± 0.07
Results below 63 µm (%)	97.8 ± 2.1	94.4 ± 1.0
TOC (%)	7.2 ± 0.4	7.6 ± 0.6

Fig. C1: Cumulative sediment particle size distributions for Bridgwater Bay National Nature Reserve, Somerset (dashed line) and for sediment used during mesocosm incubations from Hamble-le-Rice, Hampshire (dotted line).

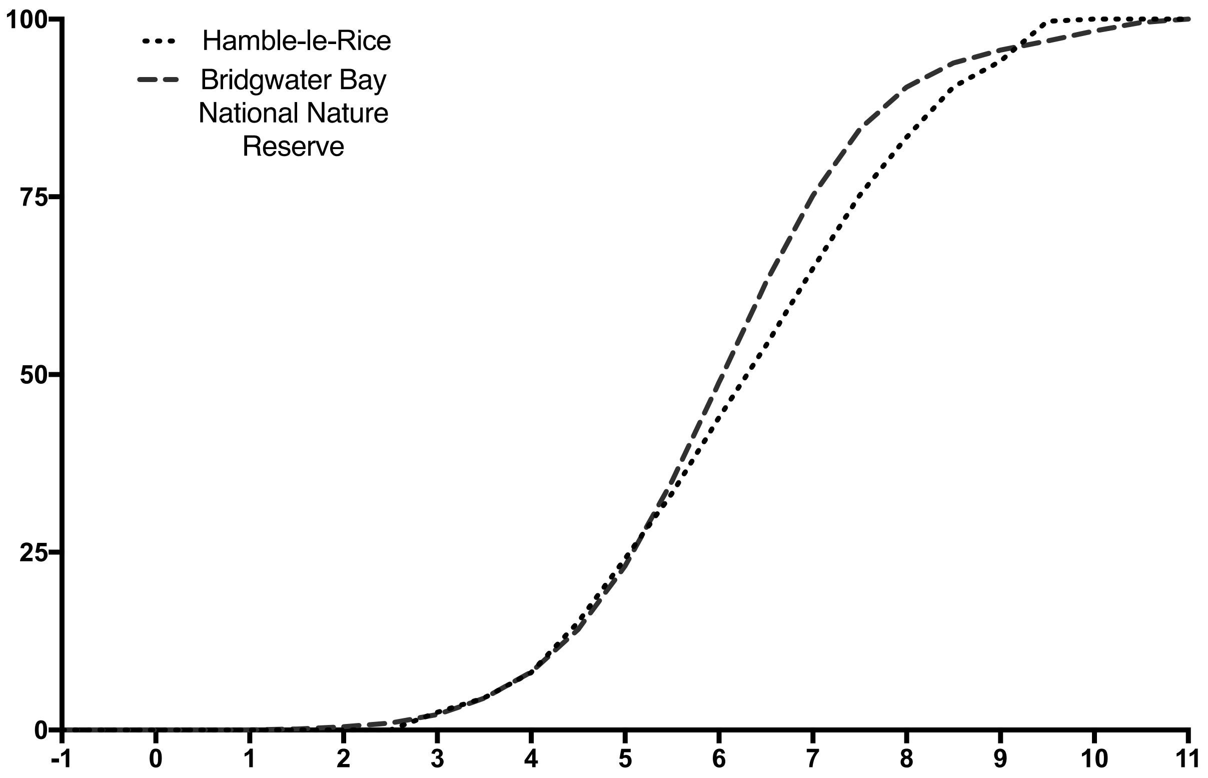


Fig. C2: Sampling site at Bridgwater Bay National Nature Reserve, Somerset, UK (51°12’27.41"N, 3°5'34.32"W), where (**a**) shows location relative to local geography and (**b**) shows location relative to the British Isles.

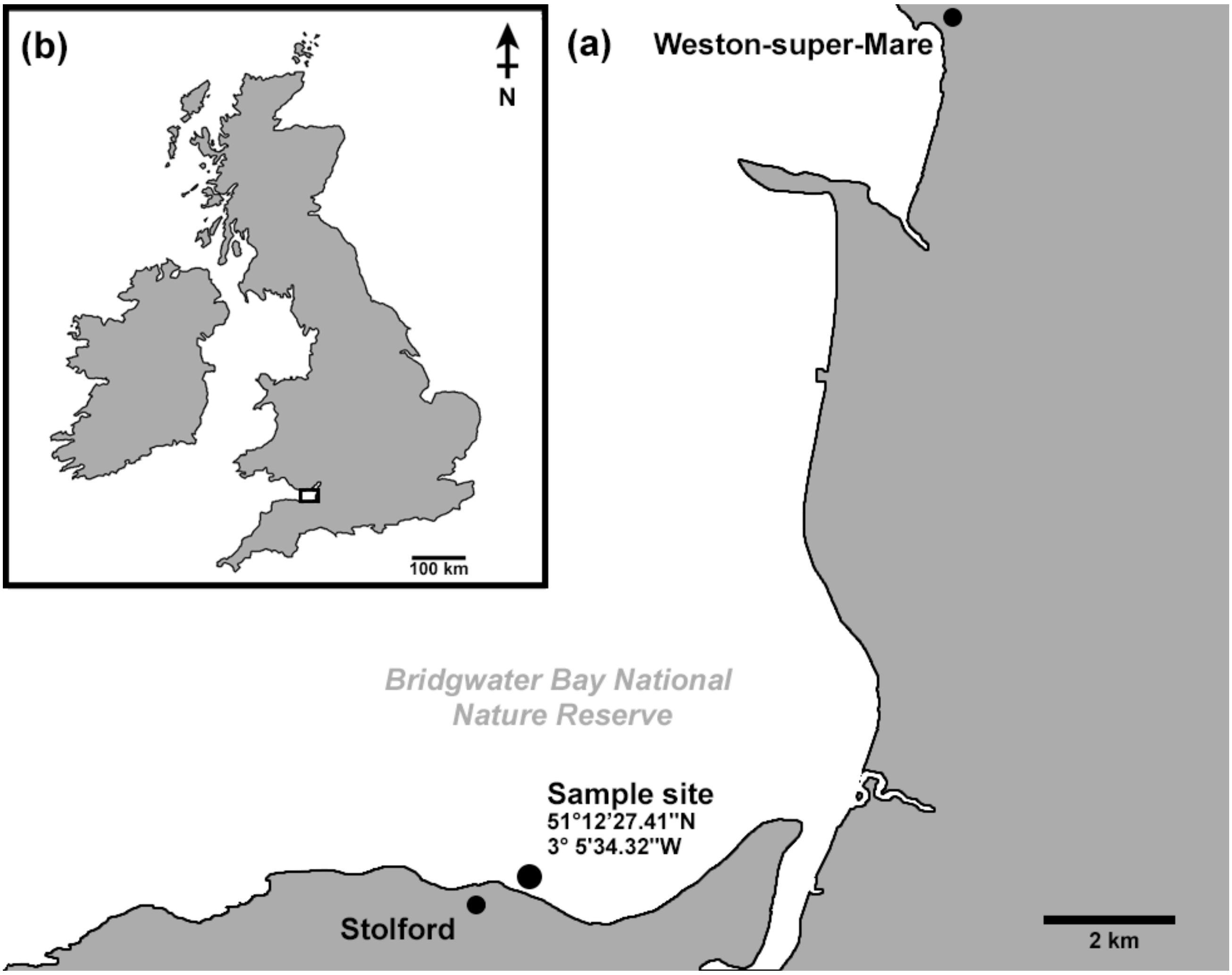


Table C2: Number of replicate cores (n = 60), and species biomass within cores, for all combinations of *Hediste diversicolor, Nephtys hombergii, Macoma balthica* and *Periginia ulvae*.

Species richness	**Species composition**	**Biomass *H. diversicolor* (g)**	**Biomass *N. hombergii* (g)**	**Biomass *M. balthica* (g)**	**Biomass *P. ulvae* (g)**	**n**
1	*H. diversicolor*	1.5 g	*0 g*	*0 g*	*0 g*	4
1	*N. hombergii*	*0 g*	1.5 g	*0 g*	*0 g*	4
1	*M. balthica*	*0 g*	*0 g*	1.5 g	*0 g*	4
1	*P. ulvae*	*0 g*	*0 g*	*0 g*	1.5 g	4
2	*H. diversicolor,* *N. hombergii*	0.75 g	0.75 g	*0 g*	*0 g*	4
2	*H. diversicolor,* *M. balthica*	0.75 g	*0 g*	0.75 g	*0 g*	4
2	*H. diversicolor,* *P. ulvae*	0.75 g	*0 g*	*0 g*	0.75 g	4
2	*N. hombergii,* *M. balthica*	*0 g*	0.75 g	0.75 g	*0 g*	4
2	*N. hombergii,* *P. ulvae*	*0 g*	0.75 g	*0 g*	0.75 g	4
2	*M. balthica,* *P. ulvae*	*0 g*	*0 g*	0.75 g	0.75 g	4
3	*H. diversicolor,* *N. hombergii,* *M. balthica*	0.5 g	0.5 g	0.5 g	*0 g*	4
3	*H. diversicolor,* *N. hombergii,* *P. ulvae*	0.5 g	0.5 g	*0 g*	0.5 g	4
3	*H. diversicolor,* *M. balthica,* *P. ulvae*	0.5 g	*0 g*	0.5 g	0.5 g	4

3	*N. hombergii,* *M. balthica,* *P. ulvae*	*0 g*	0.5 g	0.5 g	0.5 g	4
4	*H. diversicolor,* *N. hombergii,* *M. balthica,* *P. ulvae*	0.375 g	0.375 g	0.375 g	0.375 g	4

Fig. C3: Examples of the dimensions quantified during morphological analysis of *Hediste diversicolor, Nephtys hombergii* and *Macoma balthica*, using Image J (version 1.46r) on scale images (48-bit colour, 2400 dpi) obtained by scanning individuals using an Epson Perfection V88 Photo bench top scanner; (**i**) length (cm), (**ii**) width at the midpoint (cm), and (iii) biovolume (cm^2), on the ventral surface, shown for (**a**) *N. hombergii* and (**b**) *M. balthica. Hediste diversicolor* was measured as for *N. hombergii.*

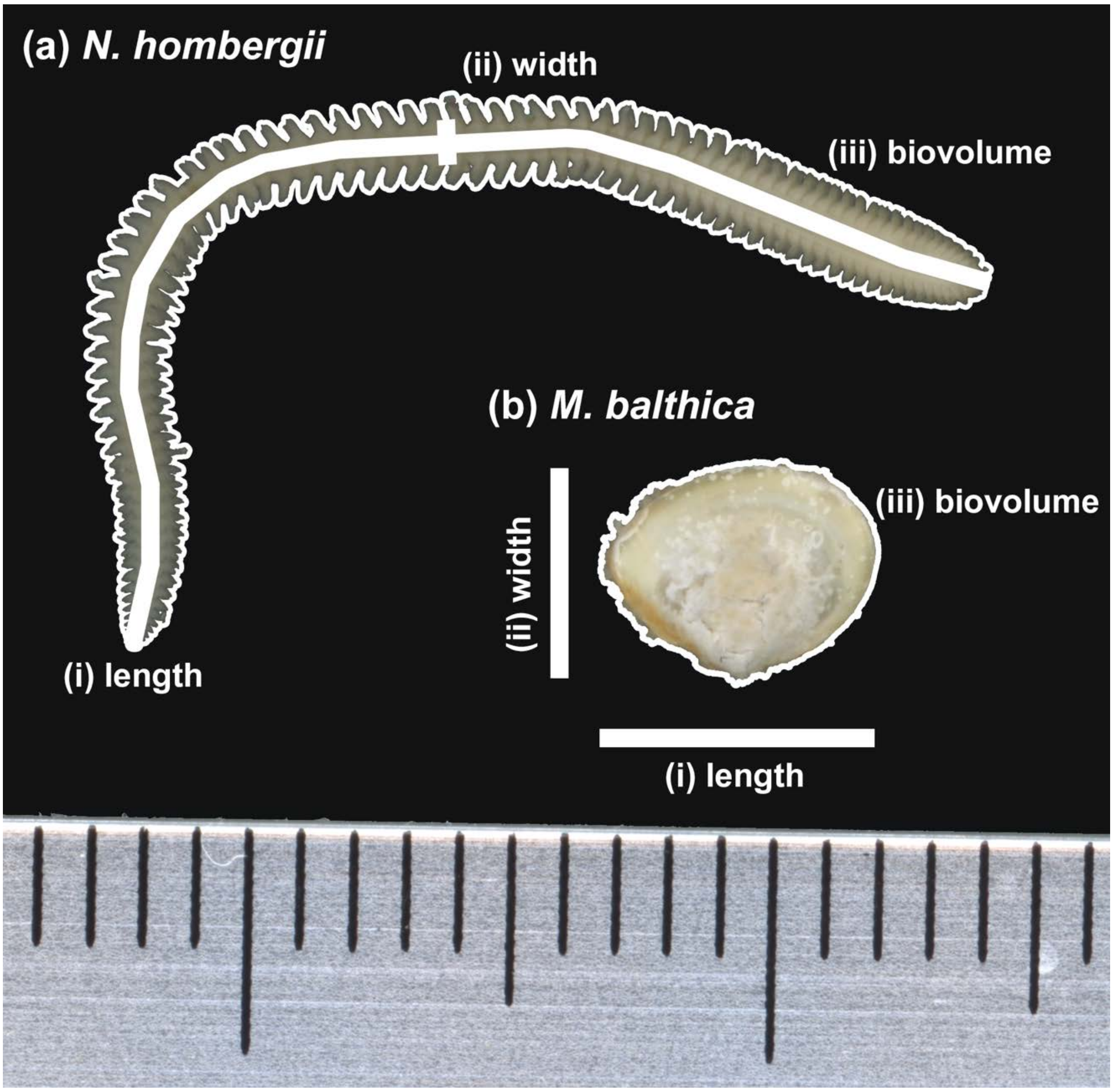


Fig. C4: Pairs plot of morphological variables of wet weight biomass (g), length (cm), width (cm) and biovolume (cm^2) of *H. diversicolor* (black), *M. balthica* (medium grey) and *N. hombergii* (light grey), shown against the Pearson correlation coefficient on the inverse panel.

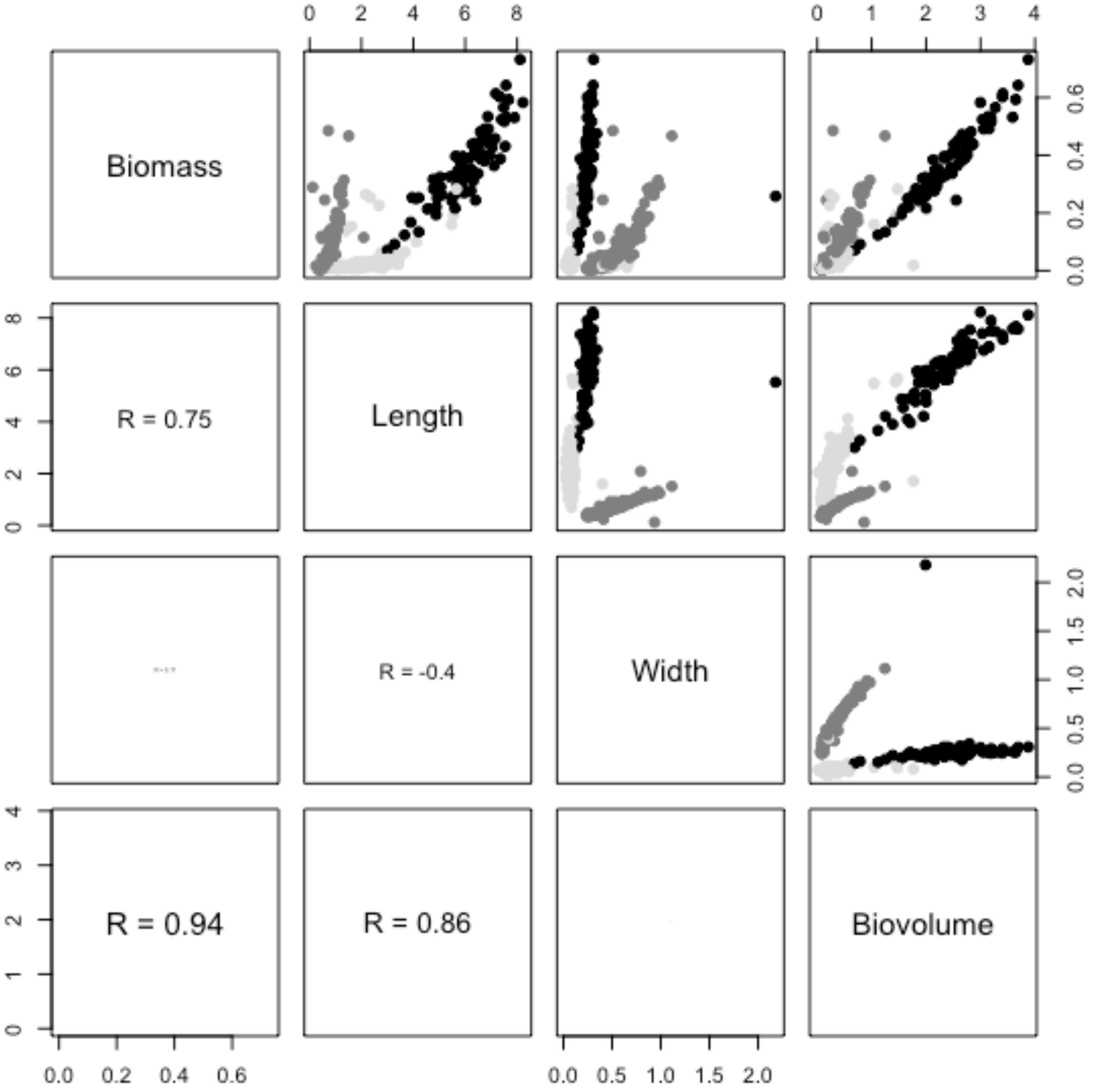


Fig. C5: Percentage (%) of total *Peringia ulvae* biomass within mesocosms belonging to size classes (1-5) (mean ± SE, n = 16). Individuals were preserved in formalin (10% formaldehyde), blotted dry, and allocated visually into one of five size classes based on their body size. The biomass within a given size class was then represented as a percentage of the total biomass of the community. Size distribution was determined in this manner for half of all mesocosms containing *P. ulvae* (16/32, two full sets of replicate species composition treatments). The consistency of the proportion of individuals belonging to each size class between cores led to the decision to remove this morphological aspect from analysis, given especially that total *P. ulvae* biomass was standardised between replicates.

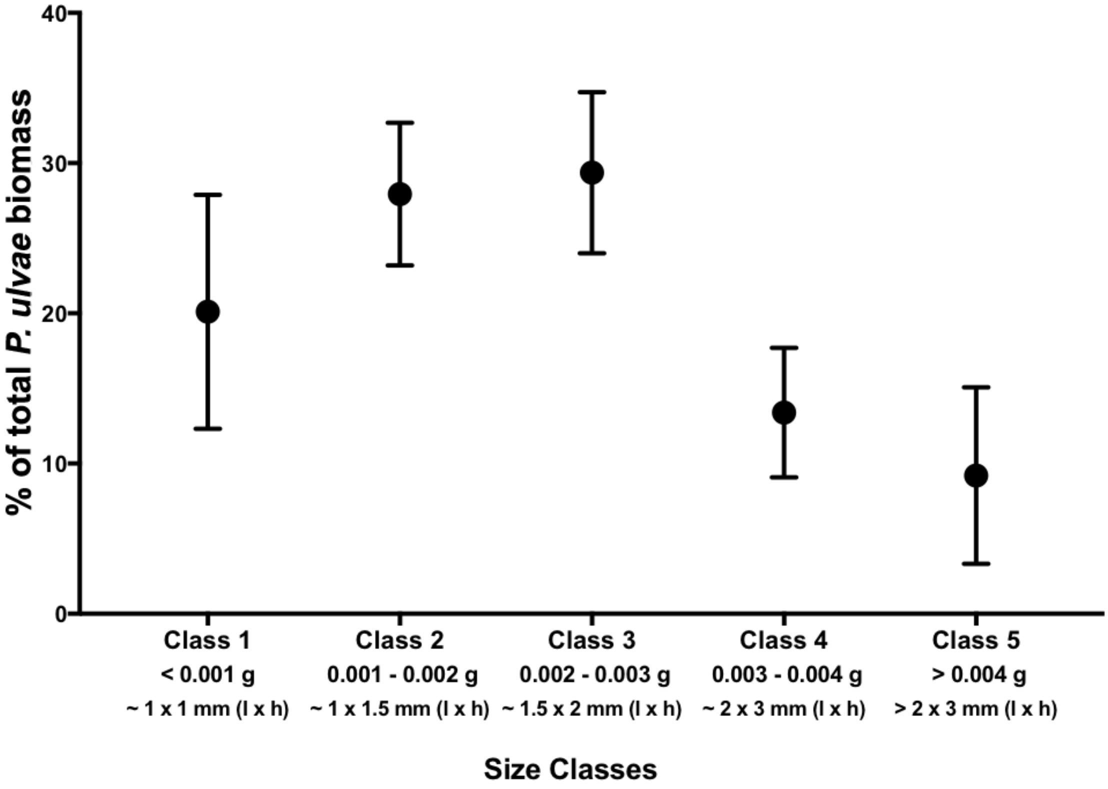
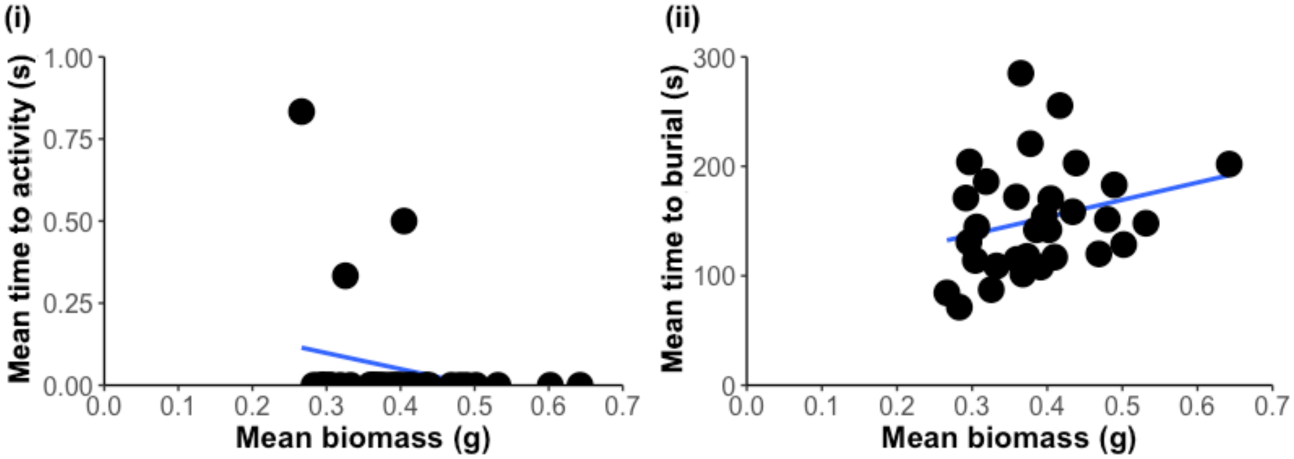
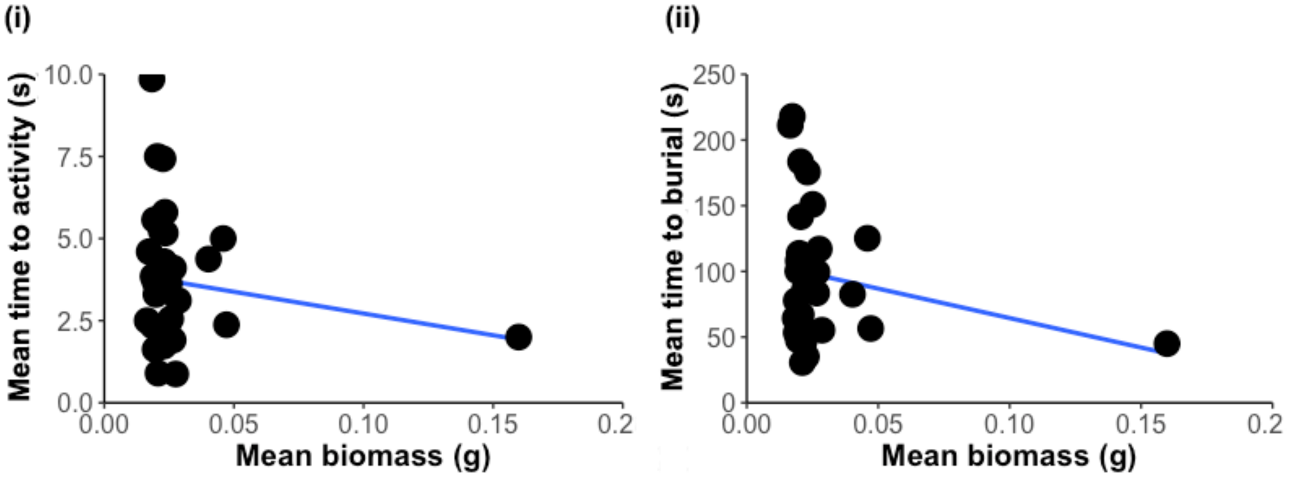


Fig. C6: Mean (**i**) time to begin activity and (**ii**) complete burial (s) for (**a**) *Hediste diversicolor,* (**b**) *Nephtys hombergii,* and (**c**) *Macoma balthica* communities shown against their mean individual biomass (g). Blue line represents a simple linear regression line.

(a) ***H. diversicolor***



(b) ***N. hombergii***



(c) ***M. balthica***

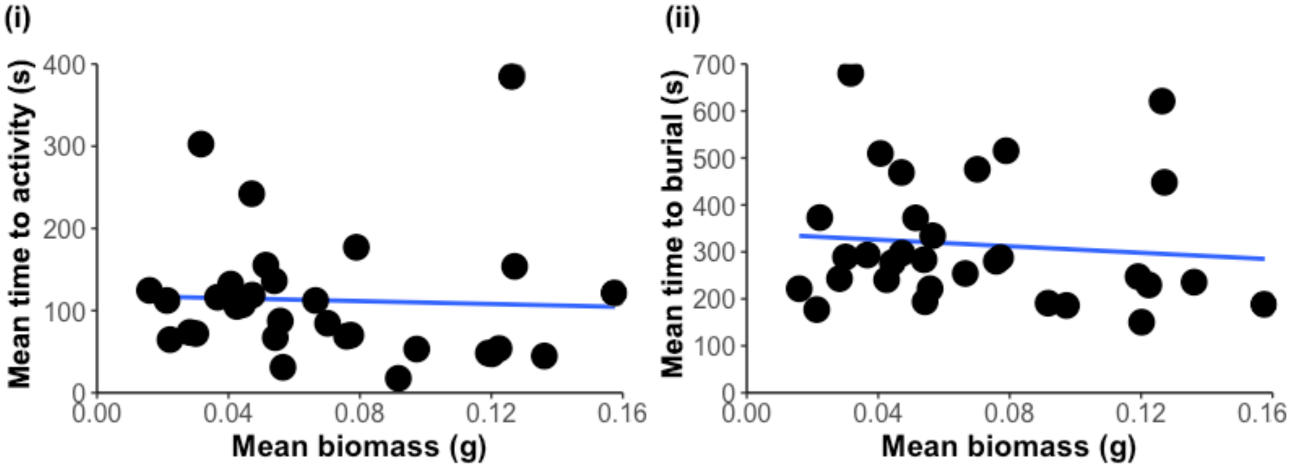
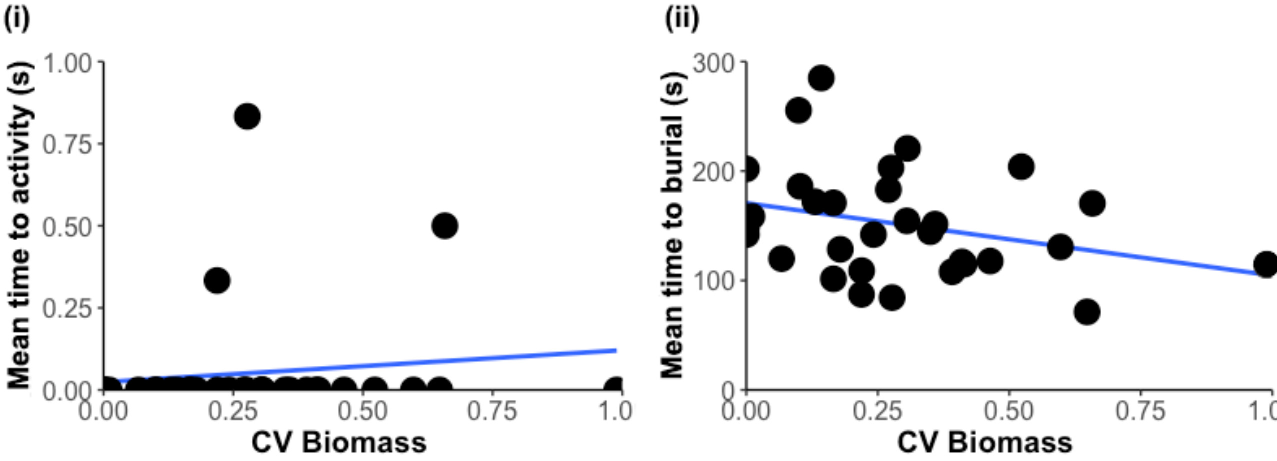
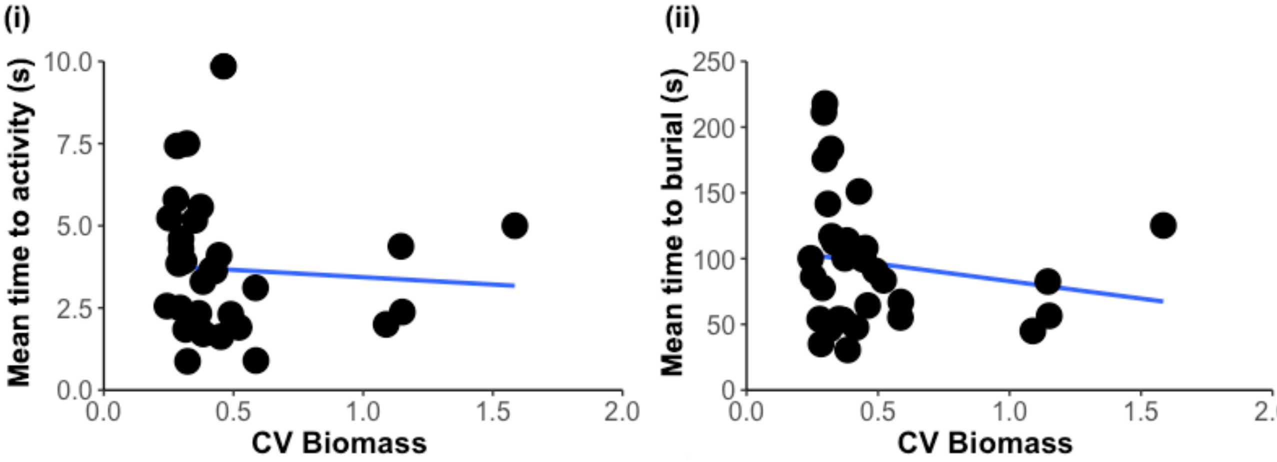


Fig. C7: Mean (**i**) time to begin activity and (**ii**) complete burial (s) for (**a**) *Hediste diversicolor,* (**b**) *Nepthys hombergii,* and (**c**) *Macoma balthica* communities shown against the coefficient of variance (CV) of their individual biomass. Blue line represents a simple linear regression line.

(a) ***H. diversicolor***



(b) ***N. hombergii***



(c) ***M. balthica***

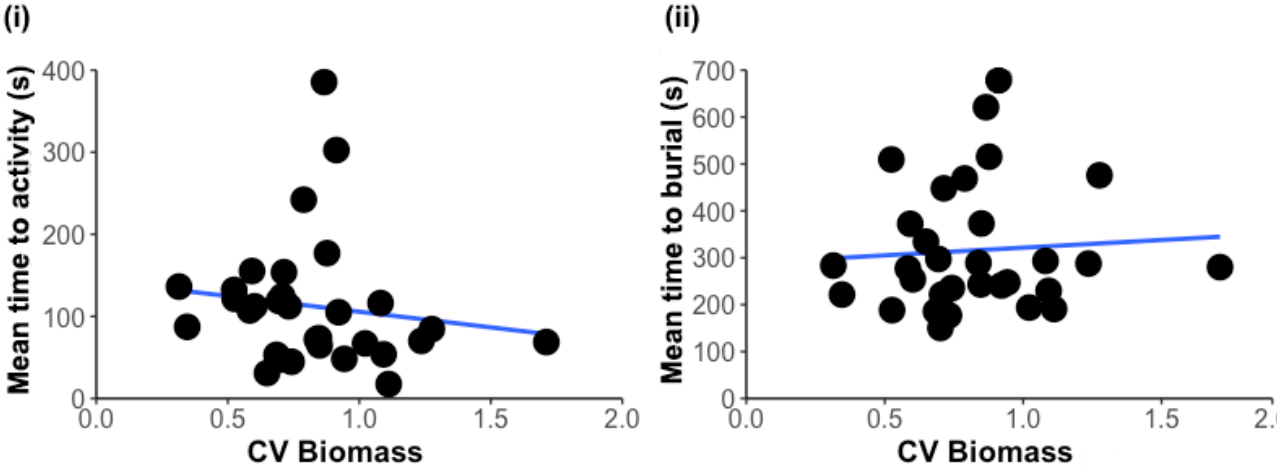


Table C3: Results of one-way ANOVAs testing the effect of mean individual biomass (g) of (**a**) *Hediste. diversicolor, (***b***) Nepthys hombergii,* and (**c**) *Macoma balthica* communities on their mean (**i**) time to begin activity and (**ii**) complete burial (s).

(a) H. diversicolor

(i) Mean time to begin activity (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
Mean biomass	1	0.015944	0.015944	2.0012	0.1675
Residuals	30	0.239010	0.007967		

(ii) Mean time to complete burial (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
Mean biomass	1	0.015119	0.0151193	2.2455	0.1448
Residuals	29	0.195260	0.0067331		

(b) *N. hombergii*

(i) Mean time to begin activity (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
Mean biomass	1	0.0005098	0.00050978	0.8056	0.3766
Residuals	30	0.0189838	0.00063279		

(ii) Mean time to complete burial (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
Mean biomass	1	0.0010063	0.00100631	1.633	0.2111
Residuals	30	0.0184872	0.00061624		

(c) *M. balthica*

(i) Mean time to begin activity (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
Mean biomass	1	0.000087	0.00008705	0.0555	0.8154
Residuals	29	0.045497	0.00156887		

(ii) Mean time to complete burial (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
Mean biomass	1	0.000459	0.00045917	0.2951	0.5911
Residuals	29	0.045125	0.00155604		

Table C4: Results of one-way ANOVAs testing the effect of the variability (coefficient of variation, CV) of individual biomass (g) of (**a**) *Hediste diversicolor, (***b***) Nephtys hombergii,* and (**c**) *Macoma balthica* communities on their mean (**i**) time to begin activity and (**ii**) complete burial (s).

(a) H. diversicolor

(i) Mean time to begin activity (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
CV biomass	1	0.02303	0.023032	0.4568	0.5043
Residuals	30	1.51271	0.050424		

(ii) Mean time to complete burial (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
CV biomass	1	0.14056	0.140561	2.9222	0.09805
Residuals	29	1.39495	0.048102		

(b) *N. hombergii*

(i) Mean time to begin activity (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
CV biomass	1	0.01398	0.01398	0.1386	0.7123
Residuals	30	3.02534	0.10085		

(ii) Mean time to complete burial (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
CV biomass	1	0.08523	0.085233	0.8656	0.3596
Residuals	30	2.95408	0.098469		

(c) *M. balthica*

(i) Mean time to begin activity (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
CV biomass	1	0.04565	0.045651	0.5597	0.4604
Residuals	29	2.36534	0.081564		

(ii) Mean time to complete burial (s)

	d.f.	**Sum Squares**	**Mean Sum Squares**	**F-value**	***p***
CV biomass	1	0.01146	0.011457	0.1385	0.7125
Residuals	29	2.39954	0.082743		

Appendix C

Table C5: Results of the variance partitioning approach taken where community-level behaviours ($^{f\text{-}\ f\text{-}SPI}L_{max}$, $^{SPI}L_{mean}$, $^{f\text{-}SPI}L_{median}$) showed significant differences depending on the presence or absence of *Hediste diversicolor*. The magnitude (mean) and variability (coefficient of variance, CV) of individual *H. diversicolor* behavioural and morphological traits was tested against the relevant community-level behaviours in, and compared between, three ANCOVA models containing (**i**) the species richness, (**ii**) the species richness and the average value of the traits of each species, and (**iii**) the species richness and the CV of the traits, and then the (**iv**) the species composition, (**v**) the species composition and the mean value of the traits, and (**vi**) the species composition and the CV of the traits.

$^{f\text{-}SPI}L_{max}$

(i) ~ Species richness (%)		**(iv) ~ Species composition (%)**	
Species richness	Unexplained variation	Species composition	Unexplained variation
4.238	95.762	41.827	58.173

(ii) ~ Species richness + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)					**(v) ~ Species composition + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)**				
Species richness	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation	Species comp.	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
5.121	6.490	0.0220	0.758	87.609	48.286	3.820	0.075	1.136	46.680

(iii) ~ Species richness + CV time to begin + CV time to complete burial + CV biomass (%)					**(vi) ~ Species composition + CV time to begin + CV time to complete burial + CV biomass (%)**				
Species richness	CV time to begin	CV time to burial	CV biomass	Unexplained variation	Species comp.	CV time to begin	CV time to burial	CV biomass	Unexplained variation

5.121	2.231	1.606	0.746	90.295	48.286	0.103	0.369	0.003	51.238

$^{\text{f-SPI}}L_{\text{mean}}$

(i) ~ Species richness (%)					**(iv) ~ Species composition (%)**				
Species richness				Unexplained variation	Species composition				Unexplained variation
12.395				87.605	42.647				57.353
(ii) ~ Species richness + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)					**(v) ~ Species composition + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)**				
Species richness	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation	Species comp.	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
10.841	21.465	0.833	0.002	66.858	40.500	22.992	0.201	0.197	36.110
(iii) ~ Species richness + CV time to begin + CV time to complete burial + CV biomass (%)					**(vi) ~ Species composition + CV time to begin + CV time to complete burial + CV biomass (%)**				
Species richness	CV time to begin	CV time to burial	CV biomass	Unexplained variation	Species comp.	CV time to begin	CV time to burial	CV biomass	Unexplained variation
10.841	1.538	3.271	0.737	83.613	40.500	4.728	0.712	2.750	51.310

$^{\text{f-SPI}}L_{\text{median}}$

(i) ~ Species richness (%)					**(iv) ~ Species composition (%)**				
Species richness				Unexplained variation	Species composition				Unexplained variation

6.795	93.205	37.712	62.288

(ii) ~ Species richness + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)

(v) ~ Species composition + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)

Species richness	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation	Species comp.	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
6.606	7.150	0.080	6.903	79.260	37.707	10.397	0.142	7.111	4.644

(iii) ~ Species richness + CV time to begin + CV time to complete burial + CV biomass (%)

(vi) ~ Species composition + CV time to begin + CV time to complete burial + CV biomass (%)

Species richness	CV time to begin	CV time to burial	CV biomass	Unexplained variation	Species comp.	CV time to begin	CV time to burial	CV biomass	Unexplained variation
6.606	0.250	2.901	1.179	89.063	37.707	0.785	0.122	12.961	48.425

Table C6: Results of the variance partitioning approach taken where the community-level behaviour ($^{f\text{-}\ f\text{-}SPI}L_{max}$) showed significant differences depending on the presence or absence of *Nepthys hombergii*. The magnitude (mean) and variability (coefficient of variance, CV) of individual *N. hombergii* behavioural and morphological traits was tested against the relevant community-level behaviours in, and compared between, three ANCOVA models containing i) the species richness, ii) the species richness and the average value of the traits of each species, and iii) the species richness and the CV of the traits, and then the iv) the species mixture, v) the species mixture and the mean value of the traits, and vi) the species mixture and the CV of the traits.

$^{f\text{-}SPI}L_{max}$

(i) ~ Species richness (%)					**(iv) ~ Species composition (%)**				
Species richness				Unexplained var.	Species composition				Unexplained var.
34.955				65.045	70.529				29.471
(ii) ~ Species richness + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)					**(v) ~ Species composition + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)**				
Species richness	Mean time to begin	Mean time to burial	Mean biomass	Unexplained var.	Species comp.	Mean time to begin	Mean time to burial	Mean biomass	Unexplained var.
34.955	0.0455	6.937	6.701	51.361	70.529	0.887	0.627	2.001	25.957
(iii) ~ Species richness + CV time to begin + CV time to complete burial + CV biomass (%)					**(vi) ~ Species composition + CV time to begin + CV time to complete burial + CV biomass (%)**				
Species richness	CV time to begin	CV time to burial	CV biomass	Unexplained var.	Species comp.	CV time to begin	CV time to burial	CV biomass	Unexplained var.
34.955	7.416	2.919	2.002	52.708	70.529	1.785	0.018	0.241	27.427

Table C7: Results of the variance partitioning approach taken where community-level behaviours ($^{f\text{-}\ f\text{-}SPI}L_{max}$, $^{SPI}L_{mean}$, SBR) showed significant differences depending on the presence or absence of *Macoma balthica*. The magnitude (mean) and variability (coefficient of variance, CV) of individual *M. balthica* behavioural and morphological traits was tested against the relevant community-level behaviours in, and compared between, three ANCOVA models containing i) the species richness, ii) the species richness and the average value of the traits of each species, and iii) the species richness and the CV of the traits, and then the iv) the species mixture, v) the species mixture and the mean value of the traits, and vi) the species mixture and the CV of the traits.

$^{f\text{-}SPI}L_{max}$

(i) ~ Species richness (%)					**(iv) ~ Species composition (%)**				
Species richness				Unexplained variation	Species composition				Unexplained variation
33.329				66.671	81.606				18.394
(ii) ~ Species richness + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)					**(v) ~ Species composition + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)**				
Species richness	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation	Species comp.	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
33.329	3.372	5.837	2.921	54.540	81.606	0.450	1.098	0.445	16.401
(iii) ~ Species richness + CV time to begin + CV time to complete burial + CV biomass (%)					**(vi) ~ Species composition + CV time to begin + CV time to complete burial + CV biomass (%)**				
Species richness	CV time to begin	CV time to burial	CV biomass	Unexplained variation	Species comp.	CV time to begin	CV time to burial	CV biomass	Unexplained variation
33.329	2.648	0.072	3.417	60.534	81.606	0.025	0.0003	2.747	15.621

$^{f\text{-}SPI}L_{mean}$

(i) ~ Species richness (%)

Species richness	Unexplained variation
39.711	60.288

(iv) ~ Species composition (%)

Species composition	Unexplained variation
60.365	39.635

(ii) ~ Species richness + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)

Species richness	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
39.160	0.040	0.015	4.467	56.318

(v) ~ Species composition + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)

Species comp.	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
62.345	0.550	0.059	1.578	35.469

(iii) ~ Species richness + CV time to begin + CV time to complete burial + CV biomass (%)

Species richness	CV time to begin	CV time to burial	CV biomass	Unexplained variation
39.160	7.187	0.012	0.972	52.670

(vi) ~ Species composition + CV time to begin + CV time to complete burial + CV biomass (%)

Species comp.	CV time to begin	CV time to burial	CV biomass	Unexplained variation
62.345	4.519	1.065	0.030	32.041

SBR

(i) ~ Species richness (%)

Species richness	Unexplained variation
8.628	91.37

(iv) ~ Species composition (%)

Species composition	Unexplained variation
46.769	53.231

(ii) ~ Species richness + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)

Species richness	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
9.852	0.0002	0.874	4.683	84.592

(iii) ~ Species richness + CV time to begin + CV time to complete burial + CV biomass (%)

Species richness	CV time to begin	CV time to burial	CV biomass	Unexplained variation
9.852	0.005	16.845	1.155	72.144

(v) ~ Species composition + Mean time to begin movement + Mean time to complete burial + Mean biomass (%)

Species comp.	Mean time to begin	Mean time to burial	Mean biomass	Unexplained variation
65.893	0.208	1.098	1.470	31.330

(vi) ~ Species composition + CV time to begin + CV time to complete burial + CV biomass (%)

Species comp.	CV time to begin	CV time to burial	CV biomass	Unexplained variation
65.893	0.580	1.189	2.306	30.031

Statistical models for intraspecific trait variation

Coefficient tables are presented without correction for the alpha-error, as Bonferroni correction increases the beta error and tends to obscure multiple significant results if p-values are moderate and the statistical power is low (Moran, 2003).

i) Species richness

Model C1: Time to begin movement (s) for *N. hombergii*

Initial linear regression model:

Lm(Time to begin movement ~ as.factor(Richness))

Minimal adequate model:

gls(Time to begin movement ~ as.factor(Richness), weights= varComb(varIdent(form=~1|as.factor(Richness)),varPower(form=~Number of individuals)))

Coefficient table:

	d.f.	**F-value**	**p**
Intercept	1	221.94684	<.0001
Species richness	3	2.66624	0.0477

Model C2: Time to complete burial (s) for *N. hombergii*

Initial linear regression model:

Lm(Time to complete burial ~ as.factor(Richness))

Minimal adequate model:

No minimal adequate model, intercept only (F = 1.21, d.f. = 3, p = 0.9479).

Model C3: Time to begin movement (s) for *H. diversicolor*

Initial linear regression model:

Lm(Time to begin movement ~ as.factor(Richness))

Minimal adequate model:

No minimal adequate model, intercept only (F = 1.83, d.f. = 3, p = 0.1482).

Model C4: Time to complete burial (s) for *H. diversicolor*

Initial linear regression model:

Lm(Time to complete burial ~ as.factor(Richness))

Minimal adequate model:

No minimal adequate model, intercept only (F = 0.18, d.f. = 3, p = 0.9097).

Model C5: Time to begin movement (s) for *M. balthica*

Initial linear regression model:

Lm(Time to begin movement ~ as.factor(Richness))

Minimal adequate model:

No minimal adequate model, intercept only (F = 2.12, d.f. = 3, p = 0.0965).

Model C6: Time to complete burial (s) for *M. balthica*

Initial linear regression model:

Lm(Time to complete burial ~ as.factor(Richness))

Minimal adequate model:

No minimal adequate model, intercept only (F = 0.30, d.f. = 3, p = 0.8256).

ii) Species composition

Model C7: Time to begin movement (s) for *N. hombergii*

Initial linear regression model:

Lm(Time to begin movement ~ as.factor(Species composition))

Minimal adequate model:

gls(Time to begin movement ~ as.factor(Species composition), weights= varComb(varIdent(form=~1|as.factor(Species composition)),varPower(form=~Number of individuals)))

Coefficient table:

	d.f.	F-value	p
Intercept	1	200.04358	<.0001
Species composition	7	3.91847	0.0004

Model C8: Time to complete burial (s) for *N. hombergii*

Initial linear regression model:

Lm(Time to complete burial ~ as.factor(Species composition))

Minimal adequate model:

gls(Time to complete burial ~ as.factor(Species composition), weights= varComb(varIdent(form=~1|as.factor(Species composition)),varPower(form=~Number of individuals)))

Coefficient table:

	d.f.	F-value	p
Intercept	1	227.57052	<.0001
Species composition	7	3.30013	0.0021

Model C9: Time to begin movement (s) for *M. balthica*

Initial linear regression model:

Lm(Time to begin movement ~ as.factor(Species composition))

Minimal adequate model:

gls(Time to begin movement ~ as.factor(Species composition), weights= varComb(varIdent(form=~1|as.factor(Species composition)),varPower(form=~Number of individuals)))

Coefficient table:

	d.f.	F-value	p
Intercept	1	302.34432	<.0001
Species composition	7	3.64941	<.0001

Model C10: Time to complete burial (s) for *M. balthica*

Initial linear regression model:

Lm(Time to complete burial ~ as.factor(Species composition))

Minimal adequate model:

gls(Time to complete burial ~ as.factor(Species composition), weights= varComb(varIdent(form=~1|as.factor(Species composition)),varPower(form=~Number of individuals)))

Coefficient table:

	d.f.	**F-value**	**p**
Intercept	1	784.3307	<.0001
Species richness	7	4.9708	<.0001

Model C11: Time to begin movement (s) for *H. diversicolor*

Initial linear regression model:

Lm(Time to begin movement ~ as.factor(Species composition))

Minimal adequate model:

No minimal adequate model, intercept only (F = 1.37, d.f. = 7, p = 0.2326).

Model C12: Time to complete burial (s) for *H. diversicolor*

Initial linear regression model:

Lm(Time to complete burial ~ as.factor(Species composition))

Minimal adequate model:

No minimal adequate model, intercept only (F = 0.59, d.f. = 7, p = 0.7586).

Table C8: Results table for ANOVA of bioirrigation ($\Delta[Br^-]$) (mg L $^{-1}$) from communities differing in i) species richness and ii) species composition.

i) $\Delta[Br^-]$ ~ Species richness

	Df	Sum of Squares	Mean Sum of Squares	F	*P*
Species richness	3	31417.76	10473	1.966	0.13
Residuals	55	292979.04	5327		

i) $\Delta[Br^-]$ ~ Species composition

	Df	Sum of Squares	Mean Sum of Squares	F	*P*
Species composition	14	87409.0	6243	1.159	0.339
Residuals	44	236987.8	5386		

Fig. C8: Bioirrigation, as indicated by Δ[Br⁻] (mg L $^{-1}$), from communities of varying (**a**) species richness level (1 – 4 component species) and (**b**) species composition. Across all levels, differences were statistically insignificant between (**a**) species richness (ANOVA: $F_{3,55}$ = 1.97, *P* = 0.13) and (**b**) species composition (ANOVA: $F_{14,44}$ = 1.16, *P* = 0.34) levels. However, trends suggest a reduction in bioirrigation (increase in Δ[Br⁻]) with species richness and the incorporation of more species together in mixture. Δ[Br⁻] was (mean ± SE) -643.08 ± 16.19 mg L $^{-1}$ in monoculture, and elevated in the four-species mixture to -591.83 ± 38.77 mg L $^{-1}$.

 represents *Hediste diversicolor*,  represents *Nephtys hombergii*,  represents *Macoma balthica* and  represents *Peringia ulvae*.

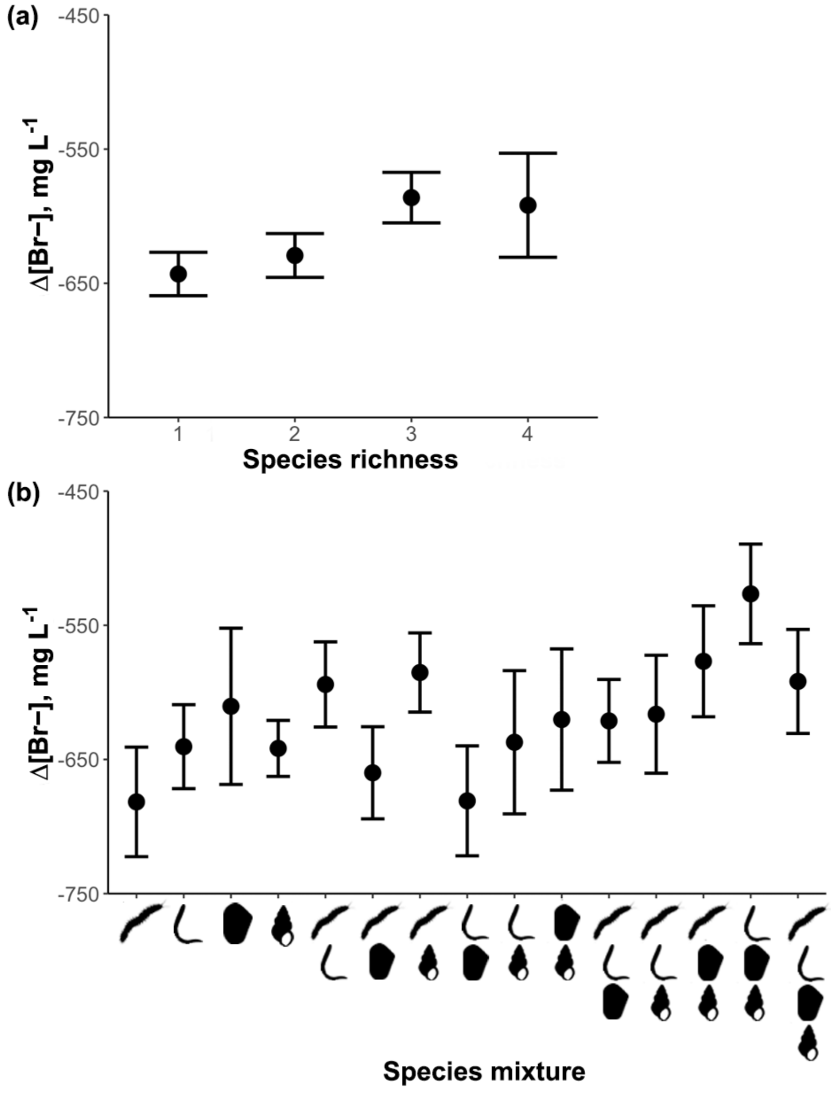


Table C9: Results table for ANOVA of nutrient concentrations (µmol L^{-1}) for i) [NH_4-N], ii) [NOx-N] and iii) [PO_4-P] from communities of variable species richness.

i) [NH_4-N]

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Species richness	3	105.879	35.29	0.159	0.924
Residuals	56	12456.671	222.44		

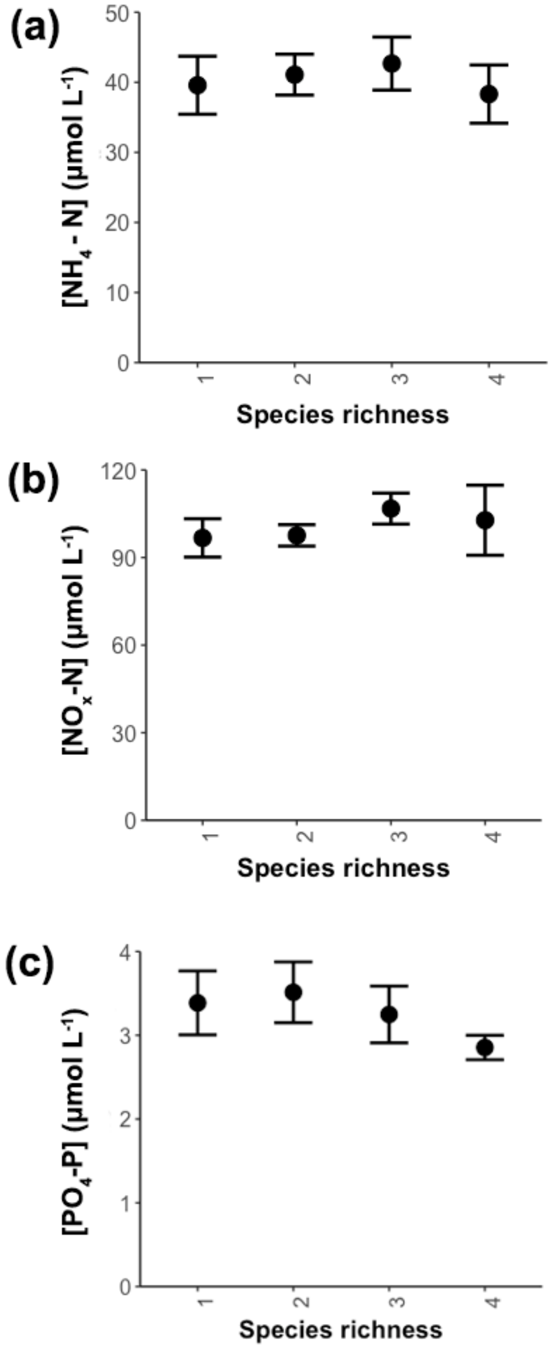
ii) [NOx-N]

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Species richness	3	1077.511	359.2	0.767	0.517
Residuals	56	26221.278	468.2		

iii) [PO_4-P]

	Df	**Sum of Squares**	**Mean Sum of Squares**	**F**	***P***
Species richness	3	1.79643	0.5988	0.248	0.863
Residuals	56	135.30817	2.4162		

Fig. C9: The effect of community species richness on the concentration (µmol L^{-1}) of dissolved nutrients (**a**) [NH_4-N], (**b**) [NO_x-N], and (**c**) [PO_4-P], showing no significant differences between richness levels for any nutrient.



Appendix D

Table D1: Principal component analysis (PCA) of data for four trait metrics (BP$_i$, $^{\text{Subsampled}}$Arithmetic mean, $^{\text{Total}}$Arithmetic mean, and Distribution mean) representing trait expression of communities containing (**a**) *Hediste diversicolor, Nepthys hombergii* and *Macoma balthica*, (**b**) only *H. diversicolor* communities, (**c**) only *N. hombergii* communities and (**d**) only *M. balthica* for Case Study 1. Linear coefficients (eigenvector) of each PC are given for each metric.

	(a) All communities				**(b) *H. diversicolor* communities**			
	PC1	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**
Eigenvalue	0.144	0.032	0.012	0.001	0.117	0.048	0.011	0.004
% variation	76.02	17.02	6.22	0.73	64.73	26.81	6.43	2.04
% variation, cumulative	76.02	93.05	99.27	100.00	64.76	91.53	97.96	100.00
Eigenvector								
BPc	-0.768	-0.006	-0.631	-0.105	0.328	-0.381	-0.925	0.188
$^{\text{Subsampled}}$Arithmetic	-0.321	0.529	0.272	0.737	0.647	0.140	0.072	-0.747
$^{\text{Total}}$Arithmetic	-0.312	0.474	0.494	-0.659	0.623	0.318	0.336	0.621
Distribution	-0.458	-0.704	0.532	0.110	-0.294	0.937	-0.162	-0.095

	(c) *N. hombergii* communities				**(d) *M. balthica* communities**			
	PC1	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**
Eigenvalue	1.084e^{-04}	6.103e^{-05}	2.031e^{-06}	2.914e^{-08}	2.386e^{-03}	7.824e^{-04}	1.228e^{-04}	4.538e^{-06}
% variation	63.21	35.58	1.18	0.02	72.40	23.74	3.73	0.14
% variation, cumulative	63.21	98.80	99.98	100.00	72.40	96.14	99.86	100.00

Eigenvector								
BP_i	0.495	-0.864	0.097	0.013	0.328	-0.381	-0.925	0.188
^{Subsampled}Arithmetic	-0.124	-0.181	-0.972	-0.085	0.647	0.140	0.072	-0.747
^{Total}Arithmetic	-0.237	-0.135	0.138	-0.953	0.623	0.318	0.336	0.621
Distribution	-0.827	-0.450	0.163	0.294	-0.294	0.937	-0.162	-0.095

Table C2: Results of the variance partitioning approach for Case Study 1, showing the percentage of variation explained in the nutrient concentrations [NH$_4$- N], [NO$_3$-N], [NO$_2$-N], [PO$_4$-P] by four increasingly detailed trait metrics (BP$_i$, calculated as per the trait categorisations of Queirós et al., 2013); the ^{Subsampled}Arithmetic mean, coded as ^{S}A mean; the and ^{Total}Arithmetic mean, coded as ^{T}A mean; and the Distribution mean, coded as DM) for (**a**) all communities, (**b**) *Hediste diversicolor* communities, (**c**) *Nepthys hombergii* communities and (**d**) *Macoma balthica* communities. The remaining unexplained variation is also shown. Percentages are calculated as calculated as the ratio of the sum of squares for each group level to the total sum of squares.

	(a) All communities (%)					**(b) *H. diversicolor* communities (%)**				
	BP$_i$	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**	**BPc**	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**
[NH$_4$- N]	0.50	0.01	6.66	0.05	92.79	1.68	10.29	1.91	1.80	84.33
[NO$_3$-N]	3.22	14.97	3.59	0.50	77.7	4.81	0.03	8.08	0.87	86.21
[NO$_2$-N]	3.11	0.39	4.84	1.10	90.57	8.09	4.28	8.59	4.99	74.04
[PO$_4$-P]	1.68	10.29	1.91	1.80	84.33	2.11	1.88	1.16	0.11	94.74

	(c) *N. hombergii* communities (%)					**(d) *M. balthica* communities (%)**				
	BP$_i$	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var**	**BPc**	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**
[NH$_4$- N]	8.14	5.25	13.28	8.15	65.18	3.18^{-}	29.86	2.98	2.61	61.37
[NO$_3$-N]	8.26	13.92	13.41	3.97	60.43	11.15	11.79	4.87	31.31	40.88
[NO$_2$-N]	0.91	3.15	0.57	6.83	88.53	0.36	3.95	0.46	0.25	94.98
[PO$_4$-P]	10.64	9.39	7.50	2.32	70.16	5.75	4.35	8.29	30.08	51.53

Table C3: Principal component analysis (PCA) of data for four trait metrics (BP$_i$, ^{Subsampled}Arithmetic mean, ^{Total}Arithmetic mean, and Distribution mean) representing trait expression of communities containing *Amphiura chiajei* and *Ampihura filiformis* for Case Study 2. Linear coefficients (eigenvector) of each PC are given for each metric.

	PC1	**PC2**	**PC3**	**PC4**
Eigenvalue	0.0214	0.0040	0.0033	0.0013
% variation	94.16	3.32	2.18	0.03
% variation, cumulative	94.16	97.49	99.67	100.00
Eigenvector				
BP$_i$	0.1045871	- 0.3018075	- 0.9414436	0.10797093
^{Subsampled}Arithmetic mean	0.5838125	0.7834505	- 0.1958925	-0.08363187
^{Total}Arithmetic mean	0.5804100	- 0.2952948	0.2416496	0.71939609
Distribution mean	0.5579863	- 0.4559808	0.1300598	- 0.68104131

Table C4: Results of the variance partitioning approach for Case Study 2, showing the percentage of variation explained in the nutrient concentrations [NH$_4$- N], [NO$_3$-N], [NO$_2$-N], [PO$_4$-P] by four increasingly detailed trait metrics (BP$_i$, calculated as per the trait categorisations of Queirós et al., 2013); the $^{\text{Subsampled}}$Arithmetic mean, coded as ^{S}A mean; the and $^{\text{Total}}$Arithmetic mean, coded as ^{T}A mean; and the Distribution ('D') mean) for communities of *Ampihura chiajei* maintained under (**a**) ambient conditions in monoculture, (**b**) ambient conditions in mixture, (**c**) future conditions in monoculture, and (**d**) future conditions in mixture. Percentages are calculated as calculated as the ratio of the sum of squares for each group level to the total sum of squares.

	(a) Ambient conditions					**(b) Future conditions**				
	BP$_i$	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**	**BP$_i$**	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**
[NH$_4$- N]	0.003	48.12	5.45	7.60	38.82	19.41	27.92	1.50	0.13	51.04
[NO$_3$-N]	10.02	21.85	0.23	3.23	64.67	26.40	0.77	36.48	5.31	31.04
[NO$_2$-N]	0.73	16.35	0.65	39.71	42.55	14.32	28.46	0.62	2.12	54.47
[PO$_4$-P]	53.49	0.09	1.43	0.47	44.52	2.50	4.90	0.41	47.26	44.93

	(c) Monoculture communities					**(d) Mixed communities**				
	BP$_i$	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var**	**BP$_i$**	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**
[NH$_4$- N]	32.20	30.78	0.01	4.21	32.80	9.81	7.29	26.26	2.99	53.75
[NO$_3$-N]	13.16	19.12	15.32	1.12	51.28	7.58	2.83	2.43	4.01	83.15
[NO$_2$-N]	28.34	41.03	0.18	5.52	24.93	8.12	4.59	20.08	2.02	65.19
[PO$_4$-P]	3.68	0.69	0.94	24.42	70.30	0.08	1.90	8.71	6.69	82.62

Table C5: Results of the variance partitioning approach for Case Study 2, showing the percentage of variation explained in the nutrient concentrations [NH$_4$- N], [NO$_3$-N], [NO$_2$-N], [PO$_4$-P] by four increasingly detailed trait metrics (BP$_i$, calculated as per the trait categorisations of Queirós et al., 2013); the ^{Subsampled}Arithmetic mean, coded as ^{S}A mean; the and ^{Total}Arithmetic mean, coded as ^{T}A mean; and the Distribution ('D') mean) for communities of *Amphiura filiformis* maintained under (**a**) ambient conditions in monoculture, (**b**) ambient conditions in mixture, (**c**) future conditions in monoculture, and (**d**) future conditions in mixture. Percentages are calculated as calculated as the ratio of the sum of squares for each group level to the total sum of squares.

	(a) Ambient conditions					**(b) Future conditions**				
	BP$_i$	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**	**BP$_i$**	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**
[NH$_4$- N]	8.13	43.26	0.73	0.003	47.88	13.41	9.62	44.87	0.09	32.01
[NO$_3$-N]	28.47	3.94	0.02	55.48	12.09	0.38	0.07	1.49	0.003	98.06
[NO$_2$-N]	0.17	13.80	0.01	6.99	79.03	3.86	10.06	49.78	0.01	36.29
[PO$_4$-P]	10.93	12.36	0.22	5.18	71.31	3.25	15.93	21.43	44.69	14.69

	(c) Monoculture communities					**(d) Mixed communities**				
	BP$_i$	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var**	**BP$_i$**	**^{S}A mean**	**^{T}A mean**	**D mean**	**Unexp. var.**
[NH$_4$- N]	1.90	1.18	0.92	4.71	91.30	6.39	39.61	13.77	1.33	38.90
[NO$_3$-N]	20.32	2.85	13.35	7.56	55.92	0.04	0.96	6.75	41.13	51.12
[NO$_2$-N]	3.50	13.17	1.92	2.42	78.99	9.36	42.78	14.77	2.02	31.06
[PO$_4$-P]	0.29	0.16	2.10	33.06	64.39	3.91	1.60	2.97	5.6-	85.91

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