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Investigating the role of traits in species invasiveness in marine and terrestrial ecosystems

by

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Abstract

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Invasive species have been identified as one of the leading causes of global biodiversity loss. Understanding why some introduced non-native species become invasive whilst others do not, is a major focus of invasion ecology. Addressing this key knowledge gap is required to effectively manage current biological invasions and to predict and therefore prevent the introduction of future invaders. Measurable characteristics of an organism, or species traits, provide a common metric that can be used across different taxa and ecosystems to better understand ecological processes underpinning biological invasions. To investigate how traits can be used to understand the processes of invasive species in their novel environment, I focused on two broad taxonomic groups, terrestrial plants and seaweeds (i.e. marine macroalgae).

First, I investigated whether different forms of invasiveness, specifically a binary classification of invasive and non-invasive, and continuous dimensions of invasiveness (local abundance, geographic range size, environmental range size, and spread rate), were correlated with different traits. To do this I made use of a published dataset of invasive and non-invasive terrestrial plants from Czechia. Different traits were associated with dimensions of invasiveness than were found using the binary classification alone. However, traits consistently explained the binary classification better than the continuous dimensions, showing that both approaches are valuable to identify traits associated with species invasiveness.

Second, I undertook a systematic review that aimed to quantitatively summarise research that has investigated traits of invasive seaweeds. I found that there were a growing number of papers investigating this research area, spanning a range of methodologies and aims, with morphological traits being the most commonly measured trait group. Research gaps included a lack of papers investigating more than one species, and studies of biomechanical traits.

Third, I tested the importance of enemy release for the success of two invasive seaweed species in the UK, through herbivory experiments and by comparing defence traits with six functionally similar native seaweed species. I found no evidence to support the enemy release hypothesis as an important mechanism in the invasiveness of two UK seaweeds, and that the traits related to defence against herbivory did not explain patterns in herbivore choice.

Finally, I investigated how traits of native species can influence the dispersal and introduction of invasive species, through sequencing seaweed pathogens. I found the first record of the *Maullinia* pathogen in New Zealand, which was closely related to pathogen populations previously found in Chile. From this I inferred that the pathogen was likely dispersed through buoyant seaweed species, which had rafted for tens of thousands of kilometres. Ultimately, this thesis adopted a multi-faceted approach to better understand how traits can be used to investigate invasive species in their novel environment, in both terrestrial and marine ecosystems.

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1. Chapter_3_Data_Mabey.xlsx (DOI: https://doi.org/10.5258/SOTON/D2408)

Research Thesis: Declaration of Authorship

Print name: Abigail Lisa Mabey

Title of thesis: Investigating the role of traits in species invasiveness in marine and terrestrial ecosystems

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;
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5. I have acknowledged all main sources of help;
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    2. Mabey, A. L., Catford, J. A., Rius, M., Foggo, A., & Smale, D. A. (2022) Herbivory and functional traits suggest that enemy release is not an important mechanism driving invasion success of brown seaweeds. Biological Invasions. https://doi.org/10.1007/s10530-022-02894-4

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Definitions and Abbreviations

AIC	Akaike information criteria
ANOVA	Analysis of variance
BIC	Bayesian information criteria
C:N	Carbon to nitrogen ratio
CNS	Carbon, nitrogen, and sulphur
ERH	Enemy release hypothesis
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IUCN	International Union for Conservation of Nature
MA	*Maullinia* detected in Australia
MC	*Maullinia* detected in Chile
ML	Maximum-likelihood
PCA	Principal component analysis
PCR	Polymerase chain reaction
RGR	Relative growth rate
UK	United Kingdom
USA	United States of America
UV	Ultraviolet

Chapter 1 Introduction

1.1 Background to invasive species

A by-product of globalisation has been the redistribution of species around the globe (Meyerson and Mooney 2007). Through both accidental and intentional means, humans have transported and introduced species to areas beyond their natural biogeographic ranges, where they have subsequently established, reproduced, and dispersed into areas where they could not otherwise have reached (Blackburn *et al*. 2011). Acting like an uncontrolled and unplanned experiment, the introduction of these species provides an opportunity to investigate and understand the rules of community assembly in relation to biological invasions (Pearson *et al*. 2018).

1.1.1 Causes and drivers of invasions

Determining the processes behind successful biological invasions is essential to understand the causes and drivers of invasive species, and to identify actions that may limit future invasions. Whilst there is ambiguity in the definition of invasiveness, species are generally considered invasive once they are dispersing, reproducing and surviving at multiple sites beyond the native range (Blackburn *et al*. 2011). To achieve this, invasive species must be able to survive novel environmental and ecological conditions, successfully reproduce, form self-sustaining populations, and increase their distribution (Catford *et al*. 2009, Gurevitch *et al*. 2011).

This continuous process of invasion has been conceptualised as a stage-based framework, where invasive species must pass through a series of barriers (Richardson *et al*. 2000, Blackburn *et al*. 2011) (Figure 1.1). Perceiving the process of invasion as stage-based suggests that there are series of filters through which a species must pass through, selecting for different characteristics at each stage depending upon the abiotic and biotic conditions (Pearson *et al*. 2018). Environmental conditions tend to select for species with similar characteristics (Keddy 1992, Diaz *et al*. 1998), whereas biotic interactions (such as competition) can select for species with different characteristics (MacArthur and Levins 1967, Hess *et al*. 2020).

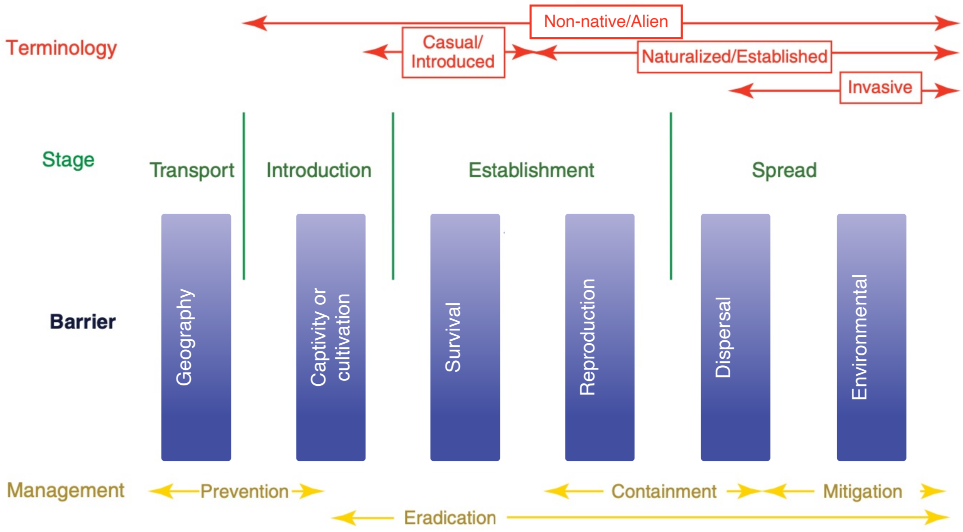

Figure 1.1 The framework which proposes that the invasion process can be divided into a series of stages (green text) with barriers in each stage which the invasive species must overcome (shown in the purple boxes) to pass to the next stage. Species are referred to using different terms depending on where in the invasive process they have reached (red text), and that different management interventions apply at different stages (yellow text). Figure adapted from Blackburn *et al*. (2011).

Although a stage-based approach provides a clear and apparently linear framework, in reality invasions are continuous, non-linear, and context-dependent, and as such different causes and drivers of invasiveness will interact with each other to produce different outcomes (Catford *et al*. 2009, 2022, Pyšek *et al*. 2020). In particular, direct and indirect drivers of invasiveness will influence the magnitude and rate of species invasions (Pyšek *et al*. 2020). Even the presence of previous invasive species may facilitate the invasion of others (known as invasional meltdown (Simberloff and Von Holle 1999, Braga *et al*. 2018, Redding *et al*. 2019)), which could also be exacerbated by other direct drivers such as climate change, pollution, and land use change (Chytrý *et al*. 2008, Walther *et al*. 2009, Crooks *et al*. 2011). Indirect effects such as economic activity are known to increase the probability of species being introduced, in part due to the increased movement of goods (Hanspach *et al*. 2008, Maurel *et al*. 2016, Pyšek *et al*. 2020), which may include the intentional movement of invasive species or goods to which invasive species are accidentally attached (Humair *et al*. 2015, Fowler *et al*. 2016).

The number of introduced propagules, and the frequency of introduction events, are referred to as propagule pressure, which has been shown to positively correlate with the probability of a species becoming invasive (Lockwood *et al*. 2005, Pyšek *et al*. 2015). A greater influx of propagules provides more protection from demographic and environmental stochasticity (Lockwood *et al*. 2005, 2009, Blackburn *et al*. 2015), and should provide a greater reserve of genetic diversity (Hovick and Whitney 2019). The number of propagules produced will also be affected by the length of time the species has been present in the non-native range, which has also been found to positively correlate with invasiveness (Pyšek and Jarošík 2005).

The success of introduced propagules will be influenced by a range of other factors, including the traits and quality of the propagules (Uyà *et al*. 2018), whether the abiotic conditions are suitable for the introduced species, and the biotic interactions of the recipient native community. The introduced species must be able to successfully pass-through environmental filters to survive, and this will be partially determined by resource availability (Catford *et al*. 2009). There are several lines of evidence to suggest that disturbance increases the likelihood of a species becoming invasive through reducing competition from native species and increasing resource availability (Crawley *et al*. 1999, De Leij *et al*. 2017), although this is more likely where the invasive species has traits that promote colonisation, such as high fecundity and fast growth (Rejmánek and Richardson 1996). Human activity such as pollution can also increase resource availability, and facilitate invasive species success (Walsh *et al*. 2016).

Interactions between invasive and native species will influence the ability of the invader to spread. The ability of a community to hinder invasive species is known as biotic resistance (Levine *et al*. 2004, Kimbro *et al*. 2013), and can include interspecific competition between the invader and native species (Leger and Espeland 2010, Gioria and Osborne 2014), and the presence of natural enemies such as pathogens, parasites and herbivores or predators (Levine *et al*. 2004), which can interact to produce synergistic effects (Santamaría *et al*. 2021). However, biotic interactions can also facilitate invasive species. This could include the invaders experiencing a release from consumption or infection from natural enemies (Keane and Crawley 2002), potentially resulting in the invasive species being able to re-allocate resources from defence traits to ones which confer a competitive advantage (Blossey and Nötzold 1995). Invasive species can also facilitate the establishment and success of other invaders through invasional meltdown (Green *et al*. 2011, Braga *et al*. 2018). Biotic interactions will vary spatially and temporally (Britton-Simmons 2004, Kurr and Davies 2018), transcend trophic levels, and will interact and be mediated by abiotic conditions (Catford *et al*. 2009).

Whilst the drivers and causes of invasions are varied and complex, understanding how they contribute to non-native species success and failures provides a chance to test and further understand the rules of community assembly, both in general and in regards to biological invasions (Pearson *et al*. 2018). Through comprehending these drivers and associated processes, insights can be gained into developing effective methods to prevent and manage future and ongoing invasions.

1.1.2 Impacts of invasions

Both the volume and global dispersal of invasive species provides cause for concern, especially when considered alongside other environmental problems such as habitat loss and climate change (Pyšek *et al*. 2020). Invasive species have been identified as one of the top five leading causes of global biodiversity loss (IPBES 2019), cause severe economic damage (including expensive eradication programmes) (Walsh *et al*. 2016, Hoffmann and Broadhurst 2016, Zenni *et al*. 2021), affect the provision of ecosystem services (Pejchar and Mooney 2009), and negatively affect human wellbeing (Bacher *et al*. 2018). Whilst these impacts are not universal, with some species having negligible or even positive impacts (White and Shurin 2011, South *et al*. 2016), the overall picture of invasive species is one of increased taxonomic and functional similarity across the globe, and resultant biodiversity loss (IPBES 2019, Muthukrishnan and Larkin 2020, Pyšek *et al*. 2020). Managing, predicting, and preventing further species introductions requires a greater understanding of the mechanisms and commonalities of biological invasions.

1.2 Trait-based approaches in ecology

Functional traits are defined as a measurable feature of an organism that potentially affects performance or fitness, and that can be measured at the individual level (Cadotte *et al*., 2011; Dawson *et al*., 2021). Species traits can influence the environmental tolerances and habitat requirements of a species, how species interact, and the contributions of species to ecosystem functions (Cadotte *et al*. 2011). Ultimately, traits underpin distributions, community structure, and evolutionary dynamics (McGill *et al*. 2006), which means that they have great potential to yield insights into ecological processes (Cadotte *et al*. 2011) (Figure 1.2). Using traits to understand the mechanisms and processes of community assembly can be an extremely useful approach to explain and predict complex systems, including biological invasions (Funk *et al*. 2017, Pearson *et al*. 2018).

a)

Example traits	**Organismal processes**	**Community processes**	**Ecosystem processes**
Leaf chemistry and longevity	Carbon balance Disease resistance	Competition Herbivory Succession	Decomposition Nutrient cycling Productivity
Leaf and stem hydraulic traits	Drought resistance	Competition and facilitation	Hydrology Precipitation patterns
Fine root traits	Soil resource uptake	Competition and facilitation	Decomposition Soil development

b)

Example traits	**Organismal processes**	**Community processes**	**Ecosystem processes**
Frond chemistry	Carbon balance	Competition Herbivory	Decomposition Nutrient cycling
Morphological traits	Resource acquisition	Competition and facilitation	Productivity

Figure 1.2 Functional traits have been used to understand ecological processes occurring at several scales, including organismal, community, and ecosystem scales. Examples are given here of how a) terrestrial plants traits and b) marine seaweed traits influence a variety of ecological processes. Figure adapted from Funk *et al*. (2017).

Understanding and predicting community processes from species traits, rather than the more general categorisations of taxonomic identities, has been described as a holy grail in ecology (Lavorel and Garnier 2002, Funk *et al*. 2017). Previous studies have found that traits within communities and regional species pools have explained large proportions of variance in ecological structure and function (Sutton-Grier and Megonigal 2011, de Bello *et al*. 2012, Edwards *et al*. 2013, Funk *et al*. 2017), suggesting that they are important determinants of community assembly. The wider ecosystem will affect the traits present in a community, as severe environmental conditions will filter traits to ones suitable for the environment (Cornwell and Ackerly 2009, Kooyman *et al*. 2010, Jung *et al*. 2010, Swenson *et al*. 2012), but competition between species may result in divergent traits to facilitate different approaches to resource limitation (Ludlow 1989).

Traits provide a common metric, with which we can draw generalisations without needing to know taxonomic identities or exact species compositions. Combined with information on environmental gradients and biotic interactions, traits can provide a general and flexible framework with which to identify patterns, therefore predicting how communities will vary with environmental change, including through the introduction of invasive species (McGill *et al*. 2006, Cadotte *et al*. 2015, Laughlin *et al*. 2017).

1.3 Using a trait-based approach to increase understanding of biological invasions

Traits have become an especially valuable tool in invasion science and biosecurity (Palma *et al*. 2021a). They have been used to predict invasiveness (Pheloung *et al*. 1999), identify which traits correlate with invasiveness (Rejmánek and Richardson 1996, Pyšek and Richardson 2007, van Kleunen *et al*. 2010a) and with different forms of invasiveness (Fristoe *et al*. 2021, Palma *et al*. 2021b), to comprehend biotic interactions between invasive and native species (Schwartz *et al*. 2016), and to understand their dispersal (Fraser & Waters, 2013), as explained below.

1.3.1 Predicting invasiveness and impacts

One of the most promising aspects of using a trait-based approach to understanding invasive species is the potential to predict which species may become invasive (Fournier *et al*. 2019). As an introduced species moves through the stages of invasion, it will effectively pass through a series of filters (Figure 1.3), and whether or not it passes through these filters will partially depend upon its traits (Pearson *et al*. 2018). Therefore, it may be possible to predict which species have the highest potential to become invasive based upon their traits according to the rules of community assembly (Pearson *et al*. 2018). Over the past few decades, trait-based invasion science has been a productive area of scientific research, and has identified some correlations between traits and invasiveness (Palma *et al*. 2021a). For example, for terrestrial plants, height has been found to advance plant invasiveness (Pyšek and Richardson 2007, van Kleunen *et al*. 2010b, Moravcová *et al*. 2015), potentially acting as a proxy for competitive ability (Palma *et al*. 2021a).

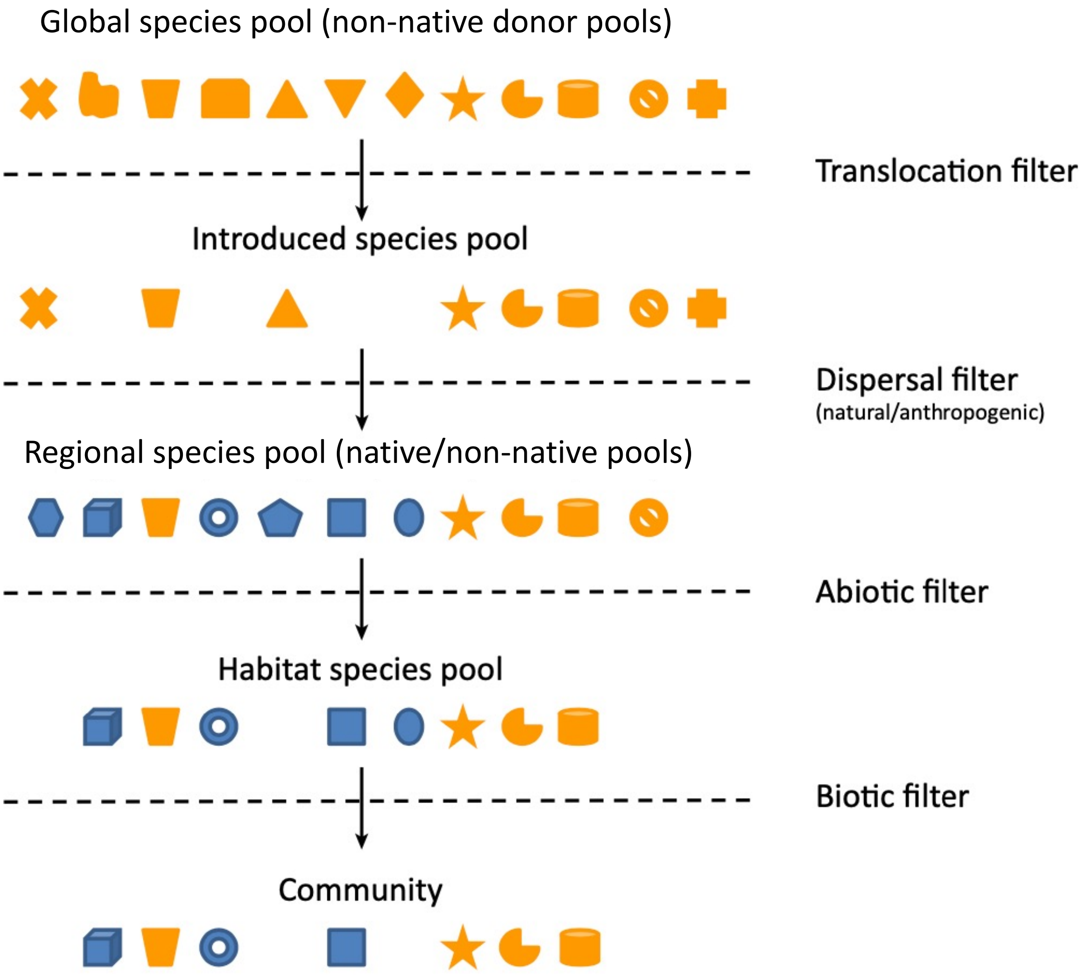

Figure 1.3 Diagram representing community assembly of native (blue) and introduced (orange) species. Whether each species passes through the hierarchal filters of translocation, dispersal, abiotic and biotic conditions is determined by its species traits (each shape represents a species with unique traits). Figure adapted from Pearson *et al*. (2018).

Although species traits have been used in biosecurity policies and approaches (Williamson and Fitter 1996, Pheloung *et al*. 1999, Gordon *et al*. 2012), universal rules for the relationship between traits and species invasiveness remain elusive (Palma *et al*. 2021b). Further research is required to provide a more detailed understanding of how traits influence the invasion process, how trait-invasion relationships may vary predictably with context (Catford *et al*. 2022), and to apply this knowledge to prioritise the monitoring and management of invasive species.

1.3.2 Definitions of invasiveness

Given the variety of invasive species, and the ecosystems in which they invade, it is not practical, or even possible, for a single universal definition of invasiveness to be used across all taxa and realms. However, this can lead to differences amongst papers in how species are defined as invasive. A traditional approach amongst invasion ecologists has been to use binary classifications. These can include comparisons between groups of invasive and native species (Monteiro *et al*. 2009), invasive and non-invasive species (van Kleunen *et al*. 2010b), or comparisons between invasive and native populations of the same species (Schwartz *et al*. 2016), to name a few (see van Kleunen *et al*. (2010a)). These varying comparisons provide different insights into the species characteristics associated with invasiveness. Provided the appropriate inferences are drawn for each type of comparison and that the traits selected are “fit for purpose” (Violle *et al*. 2007), group-based comparisons can help increase understanding and prediction of invasions (van Kleunen *et al*. 2010a).

The binary approach often relies upon classifying non-native species within the appropriate stage of invasion, and therefore making assumptions about the species current behaviour and population dynamics within the invaded range (Blackburn *et al*. 2011, Palma *et al*. 2021a). Whilst this approach has the benefit of being broadly applicable to a wide range of species to provide a basis for comparison, accurately categorising a species or population within the stages of invasion can be challenging, and result in the loss of biological information. Specifically, the stages of invasion are a simplification of a continuous, nonlinear process, and binary classifications are unlikely to account for interactions between stages, temporal changes, or differences between populations (Palma *et al*. 2021a). Additionally, classifying a species as invasive does not always account for the specific way in which the species invades, and the traits associated with that particular process (Catford *et al*. 2016). Ultimately, binary classifications can conflate different types of invasiveness, loosing ecological information and obscuring traits which vary depending on the definition of invasiveness used.

Given the limitations of binary approaches to classifying species as invasive, researchers are increasingly using continuous metrics to examine species invasiveness. Using continuous metrics avoids the invasive and non-invasive binary grouping, allowing for graduations on the spectrum, therefore acting as a more representative measure of species invasiveness (Palma *et al*. 2021a). This flexible approach considers the variety of ways in which species invade ecological communities, and provides a methodology for transparent hypothesis testing (Palma *et al*. 2021b). By focusing on demographic processes this approach can benefit invasive species management, as different types of invasiveness are likely to have varying impacts, and subsequently require different management actions (Yokomizo *et al*. 2009, Palma *et al*. 2021b).

Invasiveness has been quantified using measures of local abundance, geographic range size, environmental range size, and spread rate (Speek *et al*. 2011, Moravcová *et al*. 2015, Catford *et al*. 2016, Fristoe *et al*. 2021, Palma *et al*. 2021b). These metrics reflect the continuous and multidimensional nature of species invasions, and allows for an in depth understanding of how different traits correlate with different mechanisms used to invade native communities (Dawson *et al*., 2012; Fristoe *et al*., 2021; Palma *et al*., 2021b; van Kleunen *et al*., 2018). This approach is particularly important when the well-established life-history trade-offs of plant strategies are considered. Traits that correlate positively with one form of invasiveness may correlate negatively with another. For example, smaller seed mass may contribute to increased spread rate and geographic range size (Moles and Westoby 2006, Palma *et al*. 2021b), but the same trait would have a limited effect on environmental range size, as small seeds are less tolerant of abiotic stress (Moles and Westoby 2006). Analyses by (Palma *et al*. 2021b) confirm that these relationships will be variable, given that seed mass correlated differently depending on which dimension of invasiveness was used (Figure 1.4). By considering invasiveness as a continuous and multidimensional process, this approach preserves ecological information and allows for a more detailed approach to understanding the mechanisms of invasiveness.

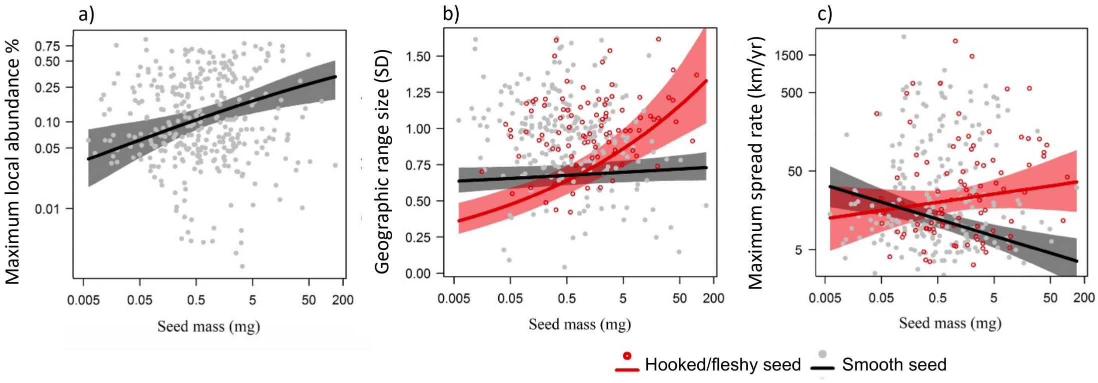

Figure 1.4 Predicted a) maximum local abundance, b) geographic range size and c) maximum spread rate of non-native plants with seed mass. Lines represent the average response and shade represents the estimated 95% credible intervals. The dots represent the mean trait values of the species included. Figure adapted from Palma *et al*. (2021b).

1.3.3 Enemy release hypothesis

Given the complexity of biological invasions, it is perhaps to be expected that a number of hypotheses have been developed to explain the different aspects of invasiveness (Catford *et al*. 2009, Jeschke 2014, Enders *et al*. 2020). These hypotheses collectively seek to explain the entirety of the invasion process, from explaining patterns in introduction due to propagule pressure (Lockwood *et al*. 2005), to the response of introduced species to abiotic environments such as disturbance (Catford *et al*. 2012), and interactions with the native community (Kimbro *et al*. 2013). One commonly used hypothesis that seeks to explain interactions between the invasive species and the native community is the enemy release hypothesis.

The enemy release hypothesis is based upon invasive species being released from coevolved natural enemies in their introduced range, and that the invasive species can benefit through a direct reduction in attack from herbivores, pathogens, and parasites (Keane and Crawley 2002, Mitchell and Power 2003, Liu *et al*. 2007). This hypothesis is closely linked to other hypotheses, including the evolution of increased competitive ability, where the invasive species could potentially change the allocation of resources from defence mechanisms to competitive traits (Herms and Mattson 1992, Blossey and Nötzold 1995, Schwartz *et al*. 2016). Therefore, species traits can be used to provide greater insights into understanding the mechanisms of enemy release, and how it may provide an advantage to invasive species.

Support for the enemy release hypothesis is variable, as results differ depending upon the recipient native community, the invader investigated and the experimental approach (Colautti *et al*. 2004, Heger and Jeschke 2014). Studies testing this hypothesis have generally focussed on terrestrial ecosystems (Heger and Jeschke 2014), but where enemy release has been tested in marine systems, differences in herbivore preference varied amongst seaweeds by taxonomic or functional groups (Enge *et al*. 2017). Further research is required to understand the importance of the enemy release hypothesis in marine systems and investigating the traits which potentially affect herbivore preference will help to yield insights into this.

1.3.4 Traits of native species can affect invasion success

Native species can influence the introduction, establishment, and dispersal of non-native species (Fraser & Waters, 2013; Gross *et al*., 2013). The role of biotic resistance, where native species inhibit establishment of non-native populations, is well known and understood (Levine *et al*. 2004, Kimbro *et al*. 2013). However, the role and ways in which native species can facilitate the initial invasion of non-native species and secondary, post-introduction dispersal has gained far less attention. To help address this knowledge gap, and based on the premise that traits of native species can be used to predict native-non-native interactions (Byun and Lee 2017), I examine how traits of native seaweeds may affect dispersal of non-native species. I focus on the trait of buoyancy in seaweed species because it facilitates long distance dispersal and because floating seaweed rafts have been found to carry pathogens and invertebrates across several hundred kilometres (Fraser *et al*., 2011; Fraser & Waters, 2013).

As a research field, invasion ecology generally focuses on species introduced by humans (Richardson *et al*. 2000, Pyšek *et al*. 2020), typically excluding species that can disperse long distance and across biogeographic boundaries without human involvement. However, human-induced global environmental change is altering natural environmental conditions, including dispersal pathways, such that humans may indirectly be responsible for introductions of additional species (Diez *et al*. 2012, Ricciardi *et al*. 2021), even if they are transported by ocean rafting. Climate change is expected to increase the frequency and intensity of storm events (Sobel *et al*. 2016, Baldini *et al*. 2016), and alter ocean currents (Thornalley *et al*. 2018), which is likely to increase the frequency and patterns of ocean rafting. Additionally, more regions will become susceptible to invasions as the climate shifts (Bellard *et al*. 2013). Climate change has already resulted in the melting of the Artic ice sheets, facilitating further spread between oceans and continents (Ricciardi *et al*. 2017), and changing temperatures have made Antarctica more vulnerable to introductions (Duffy *et al*. 2017), which may be caused by rafting seaweed (Fraser *et al*., 2018). Determining the role of buoyant seaweed in transporting species across long distances will be essential to identify areas vulnerable to these introductions, which can be used to direct monitoring schemes. It is thus important for invasion ecology to consider events and processes of introductions which are a result of indirect human activity.

1.4 Comparisons across terrestrial plants and seaweeds

Applying a trait-based approach provides great potential to predict ecological processes in complex systems, and has been applied to a wide range of taxa, including but not limited to terrestrial and aquatic plants (Pyšek *et al*. 2009, Catford and Jansson 2014, Dalla Vecchia *et al*. 2020), fungi (Dawson *et al*. 2019), macroalgae (Nyberg and Wallentinus 2005), birds (Blackburn *et al*. 2009) and invertebrates (Blight *et al*. 2017). In this thesis I focus on two broad taxonomic groups, terrestrial plants and seaweeds (i.e. marine macroalgae), to investigate how traits can be used to investigate invasive primary producers across these realms.

The concept of invasive species possessing a suite of characteristics which enabled their invasiveness was first developed by Baker (1965) with the ideal weed hypothesis. This predicted that invasive plants would have traits related to competitive strategies, such as fast growth rates and high fecundity. Since the seminal work by Baker (1965), traits of terrestrial plants have been used to formulate hypotheses and investigate a broad range of questions related to invasion biology, resulting in the creation of several large, open access trait databases (Moravcová *et al*. 2010, 2015, Wang *et al*. 2018, Fraser 2020). This considerable volume of data has allowed increasingly complex statistical techniques to be applied on broad spatial scales (Fristoe *et al*. 2021). This provides great potential for yielding insights into relationships between traits and terrestrial invasive plants.

In contrast to terrestrial plants, invasive seaweeds are understudied (Lowry *et al*. 2013), despite their ecological, economic, and cultural importance in marine systems (Smit 2004, Delaney *et al*. 2016, Nurjanah *et al*. 2016, Mouritsen *et al*. 2018). Invasive seaweeds have been transported around the globe through human activity (Naylor *et al*. 2001), resulting in the continued homogenisation of marine ecosystems. Further research into the mechanisms of invasiveness in marine systems is needed to predict, prevent, and manage future invasions.

1.5 Thesis structure and objectives

The overarching aim of my thesis was to investigate how traits can be used to understand and generalise processes related to species invasiveness. To achieve this, I focused on primary producers from both terrestrial and marine ecosystems. Terrestrial plants have been well studied, resulting in large volumes of data which can be used to provide in depth explanations, such as how traits correlate with different types of invasiveness. In contrast, seaweeds have been investigated far less, providing an opportunity to explore how traits are used to understand invasions in marine systems, often building from hypotheses developed using terrestrial plant data. To achieve my aim, I focus on four key objectives which I detail below, before providing an outline of each chapter.

My four key objectives are:

Objective 1: assess how traits of terrestrial plants correlate with different ways of defining species invasiveness.

Using a trait database measured from terrestrial plants in Czechia (Kubát *et al*. 2002, Kubešová *et al*. 2010, Moravcová *et al*. 2010), I used mixed models to investigate which traits correlated with a binary classification and four continuous dimensions of invasiveness [Chapter 2].

Objective 2: identify trends and gaps in research that investigates the traits of invasive seaweeds.

I systematically searched the peer-reviewed literature to identify papers that investigated traits of invasive marine seaweeds, and summarised the information to identify commonalities and gaps in the research [Chapter 3].

Objective 3: determine whether enemy release is likely to be an important mechanism in the success of two invasive seaweed species, and whether any observed enemy release is due to traits associated with defence against herbivory.

I used herbivory experiments and traits related to defence against herbivory (carbon to nitrogen ratio, polyphenolic concentration, tensile strength, and compensatory growth) to investigate whether two invasive seaweeds experienced enemy release compared to six native ones [Chapter 4].

Objective 4: determine how traits of native seaweeds can facilitate the transportation and introduction of invasive species.

I sampled buoyant, habitat-forming seaweed populations to determine whether the non-native protist pathogen *Maullinia* was present in New Zealand and used genetic analysis to determine whether this pathogen was closely related to other populations found across the Southern Ocean, and thus likely to have been transported across biogeographic boundaries via ocean-rafting [Chapter 5].

In Chapter 2, I used trait data previously collected from 87 invasive and non-invasive plant species in Czechia (Kubát *et al*. 2002, Kubešová *et al*. 2010, Moravcová *et al*. 2010) to investigate which traits correlated with different ways of characterising invasiveness. These were either binary classifications (invasive or non-invasive), or dimensions of invasiveness (local abundance, geographic range size, environmental range size, or spread rate). I also investigated the relationships between the binary classifications and the dimensions of invasiveness, to see if this could provide an explanation for differences in correlated traits. Investigating how relationships amongst traits and invasiveness vary depending on the definition used is needed to provide clarity into how traits relate to invasiveness.

Chapter 3 used a systematic approach to search peer-reviewed literature to find papers which investigated the traits of invasive species. Through quantifying the data across the papers found, I was able to identify key trends and knowledge gaps for three specific objectives. First, through identifying the rate of publications and characteristics of the studies examining traits of invasive seaweeds. Second, clarifying which and how many species were investigated, and finally assessing which traits have been measured and how the traits have been used. Whilst seaweeds are relatively understudied when compared to terrestrial plants, the increased use of seaweed traits to answer ecological questions suggests that this is an important area of research. Therefore this detailed review is well timed to identify trends and gaps in research, which could be used to prioritise future research efforts.

In Chapter 4, I investigated the importance of the enemy release hypothesis in marine systems through using herbivore choice and no-choice experiments, and measuring the traits of invasive and native seaweeds that could confer defence against herbivory (specifically carbon to nitrogen ratio, polyphenolic concentrations, tensile strength and compensatory growth). Although the enemy release hypothesis is well researched in terrestrial systems, there is ambiguity around whether invasive seaweeds experience this phenomenon. Both of the invasive seaweeds used in this chapter are notorious invaders and clarifying whether enemy release contributes to their spread and abundance in novel areas will be important for their management.

Chapter 5 aimed to determine whether native buoyant seaweed species could be responsible for the dispersal of pathogens to previously uninfected areas. This was done through sampling populations of *Durvillaea* (a genus of habitat-forming seaweed) in New Zealand and using genetic analysis to identify whether the protist pathogen *Maullinia* was present in the infection. *Maullinia* was previously unrecorded in New Zealand, so its presence would suggest it had been transported through the dispersal of buoyant seaweed species. Understanding the processes of pathogen dispersal and distributions is needed to monitor and manage future disease outbreaks. Whilst *Durvillaea* is taxonomically a fucoid, I refer to it as a kelp throughout Chapter 5. Although some phycologists use the word kelp to solely refer to the order Laminariales, kelp is often used to refer to large brown seaweeds, and is included in the common name of *Durvillaea* (bull kelp), so this is a justified use of the term (see Fraser (2012) for further justification).

1.6 Publications and author contributions

This section details the publication status and author contributions for each chapter in this thesis.

Chapter 2 has been prepared for submission as:

Mabey, A.L., Moravcová, L., Palma, E., Pyšek, P., Rius, M., Smale, D.A., & Catford, J.A., Identifying traits associated with dimensions of plant invasion success.

Author contributions: A.L.M. and J.A.C. contributed to the study conception and design, with input from M.R. and D.A.S. Data collection was performed by P.P. and L.M. or was found by A.L.M. from an accredited source. Data analysis was performed by A.L.M. with guidance from J.A.C., E.P., P.P. and L.M. The first draft of the manuscript was written by A.L.M., and all authors commented on and contributed to previous versions of the manuscript.

Chapter 3 has been prepared for submission as:

Mabey, A.L., Rius, M., Smale, D.A. & Catford, J.A., The use of traits in invasive seaweed research: A systematic review.

Author contributions: A.L.M., J.A.C., M.R. and D.A.S. contributed to the study conception and design. Data collection and analysis was performed by A.L.M. The first draft of the manuscript was written by A.L.M., and all the authors commented on and contributed to previous versions of the manuscript.

Chapter 4 has been published in the journal *Biological Invasions* as:

Mabey, A.L., Catford, J.A., Rius, M., Foggo, A. & Smale, D.A. (2022) Herbivory and functional traits suggest that enemy release is not an important mechanism driving invasion success of brown seaweeds. *Biological Invasions,* https://doi.org/10.1007/s10530-022-02894-4.

Author contributions: A.L.M., J.A.C., M.R. and D.A.S. contributed to the study conception and design. Data collection was performed by A.L.M. and A.F. Data analysis was performed by A.L.M. The first draft of the manuscript was written by A.L.M., and all authors commented on and contributed to previous versions of the manuscript.

Chapter 5 has been published in the journal *Marine Biology* as:

Mabey, A.L., Parvizi, E., & Fraser, C.I. (2021). Pathogen inferred to have dispersed thousands of kilometres at sea, infecting multiple keystone kelp species. *Marine Biology*, 168(4), 47. https://doi.org/10.1007/s00227-021-03853-8.

Author contributions: C.I.F developed the study conception and design. Data collection was performed by A.L.M, C.I.F. and E.P. Phylogenetic analysis was performed by C.I.F. The first draft of the manuscript was written by A.L.M., with comments and contributions from C.I.F and E.P.

Chapter 2 Identifying traits associated with dimensions of plant invasion success

2.1 Abstract

Trait-based approaches for understanding species invasions have primarily relied on binary comparisons between invasive and non-invasive species. However, species' invasiveness can manifest differently, and the typical binary approach may obscure traits associated with different definitions of invasiveness. We use both demographic dimensions of invasiveness (geographic range size, environmental range size, local abundance, and maximum spread rate) and a traditional binary classification (invasive and non-invasive) to assess the correlation between traits and invasiveness if different measures of species' invasion success are applied. To achieve this, we used 10 traits for both invasive and non-invasive species in Czechia to ask two questions: (1) *how do different characteristics of invasiveness relate to each other?* and (2) *what traits are linked with different ways to characterise invasiveness?* Species classified as invasive were more likely to be abundant, had large environmental range sizes, and faster spread rates. However, we found that height was the only trait strongly correlated with both the probability of being classified as invasive and a dimension of invasiveness (geographic range size). Seedling relative growth rate and species residence time correlated positively with environmental and geographic range size respectively, and both traits also showed a weak positive correlation with the probability of being invasive. Using the four demographic dimensions of invasiveness, we identified traits and covariates associated with different forms of invasiveness that were not apparent using the binary classification (residence time, seedling relative growth rate, and anemochory). However, in all cases, traits explained the binary classification better than the continuous demographic dimensions, as in previous studies that showed that binary classifications are a useful tool to investigate traits associated with species invasiveness. As such, our work shows that both the binary classification and the demographic dimensions of invasiveness are valuable approaches to assessing the mechanisms of biological invasions, being most beneficial when the interactions between them are understood.

2.2 Introduction

Predicting which species are most likely to become invasive is a principal goal of invasion ecology, with a range of approaches and techniques being applied to the problem (Rejmánek and Richardson 1996, Crawley *et al*. 1996, Rejmánek 1996, Colautti *et al*. 2004, Felker-Quinn *et al*. 2013, Moravcová *et al*. 2015). The ability to anticipate which species have a high probability of becoming invasive prior to their establishment would allow greater biosecurity controls to be implemented for high-risk species, inhibiting their establishment and subsequent impacts (Weber *et al*. 2009, Wilson *et al*. 2011). Prevention is the most effective and efficient management strategy for invasive species (Leung *et al*. 2002, Venette *et al*. 2021). In this study, we focused on the use of traits to predict species invasiveness. Traits can be defined as measurable characteristics of an organism that affect its fitness (Cadotte *et al*. 2011). One of the benefits of using a trait-based approach to understand species invasions, and also community assembly more generally, is that it allows general assumptions and patterns to be applied across species, communities, and systems without needing to know the exact species composition in question (McGill *et al*. 2006).

Previous approaches for identifying traits related to invasiveness have used binary classifications to compare invasive species to a baseline, whether that is native species (Leffler *et al*. 2014), non-native non-invasive species (van Kleunen *et al*. 2010b), or native populations (Pyšek and Richardson 2007, van Kleunen *et al*. 2010a, Helsen *et al*. 2021). These binary classifications have yielded insights into traits associated with invasiveness, but building knowledge across studies is hampered by the lack of a singular definition of invasiveness. The invasion process is multifaceted, continuous, and context-dependent, meaning that it is almost impossible to singularly define a species as invasive in a way that could be applied across ecosystems and taxa. How species are defined as invasive depends upon the context in which species are being considered. Invasive species listed as noxious may be defined by impact on natural vegetation (IUCN 2000) whereas species listed as invasive for purposes of management focus on ecological attributes which affect species demography (Palma *et al*. 2021b). The definition based on ecological attributes rather than impact also applies to approaches that study invasions primarily for scientific purposes, to understand mechanisms of invasion (Richardson *et al*. 2000, Blackburn *et al*. 2011). These methodological differences would lead to differences in the relationships between traits and invasiveness, which can make it difficult to compare across studies, and may influence which traits are identified as important for invasive species (Palma *et al*. 2021b, Catford *et al*. 2022).

Previous studies have classified plant invasiveness through both combined population performance measures (Colautti *et al*. 2014), and through individual metrics (Moravcová *et al*. 2015, Catford *et al*. 2016, McGeoch and Latombe 2016, Carboni *et al*. 2016, Klinerová *et al*. 2018, Fristoe *et al*. 2021, Palma *et al*. 2021b). A review of invasive species definitions revealed that geographic range size, environmental range size, local abundance, and spread rate were often used to define invasiveness (Catford *et al*. 2016). These four dimensions provided demographic information about the way in which species become invasive, and have the potential to be used to identify traits that are most likely to correlate with different demographic dimensions of invasiveness (Catford *et al*. 2016). Studies in south-eastern Australia and Europe focusing on hundreds of terrestrial plant species have found that these four dimensions were largely independent of each other (Catford *et al*. 2016, Fristoe *et al*. 2021) and therefore represent different ways in which species can be considered invasive. Binary classifications of invasive and non-invasive species may not consider all these different ways in which species can be invasive. For example, the definition of invasiveness provided by Richardson *et al*. (2000) has been used widely in the past 20 years, and is based upon one demographic form of invasiveness, the rate of spread. This could mean that traits which relate to other forms of invasiveness are conflated within this definition.

Plant strategies are constrained by well-established life-history trade-offs. A well-defined example of this is the seed mass-fecundity trade-off (Muller-Landau 2010). Larger seeds have higher tolerance during establishment but exhibit reduced fecundity as a trade-off (Moles and Westoby 2004). When applied to the dimensions of invasiveness, previous research shows that smaller seed mass (which is positively related to fecundity) can contribute to increased spread rate and geographic range size (Moles and Westoby 2006, Palma *et al*. 2021b). However, this will have a limited effect on environmental range size as smaller seeds are less tolerant to environmental stress (Moles and Westoby 2006). The relation between abundance and seed size is variable, as it can depend upon both the strategy of the plant, and the environmental conditions the plant is in, although there is some evidence that species with large seeds may have a positive correlation with abundance (Leishman and Murray 2001). By considering different forms of invasiveness, this approach can provide fresh insights into factors that contribute to invasiveness that may be obscured through traditional binary classifications (Carboni *et al*. 2016, Fristoe *et al*. 2021, Palma *et al*. 2021b).

Here, we use both demographic dimensions of invasiveness (geographic range size, environmental range size, local abundance, and maximum spread rate) and a traditional binary classification (invasive and non-invasive) to assess the correlation between traits and invasiveness if various measures of species' invasion success are applied. We investigated two main questions: (1) *how do different characteristics of invasiveness relate to each other?* and (2) *what traits are linked with different ways to characterise invasiveness?* This approach will assess whether continuous dimensions of invasiveness provide greater or less clarity than binary classifications to understand the role of species' traits in the demographic processes that drive their invasion ability.

2.3 Methodology

2.3.1 Species data

This study used trait data collected by Moravcová *et al*. (2010), Kubešová *et al*. (2010), and Kubát *et al*. (2002) of 87 herbaceous plant species that represent a high proportion of the introduced flora of Czechia, accounting for 38% of the 229 naturalised neophytes in Czechia as reported in Pyšek *et al*. (2012b) (also see Moravcová *et al*., (2015)).

Continuous metrics of invasiveness were calculated for geographic range size, environmental range size, local abundance and maximum spread rate using species distributions in Czechia. Species distributions were based on presence data in 2,716 grid cells (measuring ~5.5 km × ~6 km) covering the country (Slavík 1998).

2.3.2 Binary classification

Species were either classified as invasive (32% of the 87 species), naturalised (62%) or casual (6%) (Pyšek *et al*., 2012a). These criteria were based upon definitions set out by Richardson *et al*. (2000), where invasive plants with self-sustainable populations produce reproductive offspring that disperse at a considerable distance from the parent taxa, thus having the potential to spread over a large area. For the purposes of this study, naturalised (non-native plants with self-sustainable populations which recruit offspring close to the adult plant) and casual (non-native plants which have not formed self-sustainable populations, therefore relying on repeated introductions) species are combined into the same category of non-invasive, to facilitate a binary comparison.

2.3.3 Dimensions of invasiveness

Geographic range size is a measure of the spatial extent of species distribution within Czechia. For each grid where a species was recorded, the central coordinates of the grid cell were used. From this list of coordinates, the standard deviation was calculated for longitude and latitude, and the geometric mean of these values was used to give a continuous metric for species geographic range size.

Environmental range size is a measure of the range of abiotic conditions in which a species occurs. We preselected 43 environmental variables deemed important for the survival of the species that represent three main groups: soil properties, land use, and temperature and precipitation (Table 7.1). For each environmental variable, the average value was calculated for each of the 2,716 grid cells used to measure species distributions (except for population data, which was calculated based on the central coordinates of each grid cell due to the format of the data) using software QGIS (v. 3.10.8). Before estimating species' environmental range size, we reduced the number of environmental variables whilst minimising data loss with a principal component analysis (PCA). In order to run the PCA, missing values for each grid cell were imputed using the R package 'missMDA' (Josse and Husson 2016). The PCA was run using the R package 'FactoMineR' (Lê *et al*. 2008), and was interpreted using the R package 'factoextra' (Kassambara and Mundt 2020). Based on the results of the PCA, we retained nine variables, which collectively explained 81.6% of variation in environmental conditions (Figure 7.1). For each species, the geometric mean of the standard deviation for each variable, based on the cells where the species was present, was calculated to give the environmental range size.

Local abundance was represented by the maximum recorded percentage cover measured across phytosociological plots sampled in Czechia (plot sizes were up to 10 m^2) taken from Pladias database of the Czech flora (www.pladias.cz, Chytrý *et al*. 2021). Maximum percentage cover represents the potential of the species to dominate locally.

The maximum spread rate was recorded as the estimated maximum spatial distance travelled per year between presence records in consecutive years (Williamson *et al*. 2005). The central coordinates of each grid square were used to calculate a distance matrix between all of the grid cells using the R package geodist using the vincenty method of geodesic distance calculation (Padgham and Summer 2021). Using the year of first record in a grid cell, the maximum recorded distance travelled was estimated across consecutive years for each species. This maximum recorded cumulative distance travelled and the corresponding year was used to fit a self-starting logistic model (Catford *et al*. 2016) (using the nls() function in the R package 'stats' (R Core Team 2021)) using the equation:

$$D_{it} = \frac{asym_i}{\left(1 + exp\left(\frac{(mid_i - t)}{scal_i}\right)\right)}$$

Where D_{it} is the predicted distance spread by taxon i after time t has passed, $asym_i$ is asymptotic spread distance for each taxon, mid_i time at which taxon i has spread to half its asymptotic spread, and $scal_i$ time elapsed between reaching half and approximately ¾ of each taxon asymptotic spread. The maximum spread rate was calculated from the steepest gradient of the curve, between $t = mid$ and $t = mid + scal$. This approach aimed to estimate the maximum potential spread rate of species within Czechia, with the assumption that all occurrence data but the first record results from within-country spread, not from new introductions. However, it is likely that there were multiple introduction events to Czechia and thus our approach is not intended to be a measure of spread from population to population across Czechia, but rather an indication of how quickly species could continuously disperse over space and time. Previous studies have found evidence of long-distance dispersal, the rates of which are comparable to the values generated in this study (Pyšek and Hulme 2005, Nathan 2006, Martín-Vélez *et al*. 2021).

2.3.4 Database of functional traits and covariates

Traits used in this study were from the dataset created by Moravcová *et al*. (2010) and Kubešová *et al*. (2010) through species sampling and seed collections between 2005 and 2007 in Czechia (see Moravcová *et al*., (2010) and Kubešová *et al*. (2010) for the list of localities and detailed methods used to measure the traits). Plant height was from the dataset in Kubát *et al*. (2002). These traits were selected with the aim of incorporating the whole reproductive cycle from seed production to dispersal potential to establishment, thereby increasing the probability that the traits would be related to the demography and distribution of the species.

Reproduction was represented by two traits: fecundity, which was measured as the average number of propagules per plant or single shoot of a clonal species, and capacity for vegetative reproduction (yes or no).

Traits related to dispersal referred to the potential for propagules to be dispersed by a range of vectors. This included measuring propagule weight and anemochory. Anemochory was measured through terminal velocity (Moravcová *et al*. 2010), whereby resultant low values indicate greater capacity for wind dispersal. Anemochory was therefore inverted to make the scale more intuitive and represented by 1/Anemochory. Propagule weight was also included, as it has been shown to influence dispersal and be correlated to species' establishment and growth (Weis 1982, Houssard and Escarré 1991).

Establishment traits included total maximal germination (which represents the maximal germination achieved under the best regime from all tested germination regimes), seedling establishment, and seedling relative growth rate. Finally, height, genome size and life history (defined as annual or perennial) were also included as previous studies have found them to be important predictors of invasiveness (Moravcová *et al*. 2015, Pyšek *et al*. 2018, Mathakutha *et al*. 2019). The plant height represents the mean of the minimum and maximum value given in (Kubát *et al*. 2002).

The species residence time was included as a covariate in all models except for maximum spread rate (to prevent overfitting due to small sample size) as residence time has consistently been found to positively relate to invasiveness (Pyšek *et al*. 2009, 2015, Williamson *et al*. 2009, Fristoe *et al*. 2021). Species residence time also implicitly accounts for some variation in propagule pressure, as more propagules will enter the environment the longer the species is present (Moravcová *et al*. 2015). Propagule pressure could not be included explicitly as it was not possible to measure or estimate it over this scale (Moravcová *et al*. 2015). Whether the species was introduced accidentally or deliberately, here referred to as the introduction pathway, was also included as a covariate for geographic range size and environmental range size models, because the way of introduction has been shown to influence traits and success of invasive species (Pyšek *et al*. 2011, Donaldson *et al*. 2014). The introduction pathway for each species was collected from the Pladias database of the Czech flora (Chytrý *et al*. 2021).

Species traits and covariates are presented in Table 2.1, along with their expected correlations with the dimensions of invasiveness. Given the high number of covariates that could be included in each model, a hypothesis-based approach was used to select those that were most appropriate.

Table 2.1 Variables used in the Bayesian linear mixed models, their units or categories, and the expected effect on the relevant dimensions of invasiveness (+, positive correlation; –, negative correlation; v, context dependent correlation). If continuous variables required transforming to a normal distribution, the type of transformation is shown in brackets (L = log, T = Tukey's ladder of powers, Lg = logit, and I = inverted).

		Dimensions of invasiveness			
Explanatory variable	**Units / categories**	**Geographic range size (T)**	**Environmental range size**	**Local abundance (Lg)**	**Maximum spread rate (T)**
Traits					
Height (L)	m	+	v	v	+
Fecundity (L)	n per plant	+	-	-	+
Genome size (T)	1C-value (Pg DNA)		-		
Vegetative reproduction	Yes / no	+ (yes)		+ (yes)	
Life history	Annual / perennial	- (perennial)	+ (perennial)		
Propagule weight (L)	$g_{(n=25)}$	v	-	v	
Anemochory (I, T)	m/s				+
Total maximal germination (Lg)	TG_{max}, %	+	+	+	
Seedling relative growth rate	RGR, g·g·day^{-1}	+	+	v	
Total seedling establishment	%		+		
Other					
Species residence time	Years	+	+	+	
Introduction pathway	Deliberate / accidental	N/A	N/A		

2.3.5 Statistical analysis

To investigate whether a species was more or less likely to be classified as invasive (opposed to non-invasive) depending on each of the four demographic dimensions of invasiveness, we used logistic regression with the glm() function (R Core Team 2021). The probability that the taxon i was classified as invasive was (Catford *et al*. 2016):

$$logit(p_i) \sim t_i + \beta_1 g_i + \beta_2 e_i + \beta_3 a_i + \beta_4 s_i$$

Where t is the intercept term for taxon i, β are the estimated regression coefficients, and g_i, e_i, a_i, and s_i are the geographic range size, environmental range size, local abundance, and maximum spread rate for taxon i, respectively. To examine how the dimensions of invasiveness related to the binary classification in multidimensional space, a PCA was fitted to the transformed dimensions (see Table 2.1) using the R package ‘FactoMineR’ (Lê *et al*. 2008), and was interpreted using the R package ‘factoextra’ (Kassambara and Mundt 2020). We used observations that were complete for all four dimensions (n=33).

Bayesian linear mixed models were used to identify traits that correlated with the dimensions of invasiveness, with a separate model fitted for each dimension. Bayesian inference was used for these models since it averages over the uncertainty in all model parameters to achieve the most reasonable inferences, which was required given the complexity of these models and the small number of groups (Gelman and Hill 2007). The traits included in mixed models for each dimension are shown in Table 2.1, along with the expected correlations and the relevant transformations of each continuous variable. Variables were removed to find the best fitting model, which was determined through selecting the lowest AIC score, and where models were indistinguishable (where the AIC scores differed by two or less (Burnham and Anderson 2004)) the model with the highest R^2 was chosen (which was calculated using the R package ‘MuMIn’ (Bartoń 2020)). Each model was fitted using the blmer() function with R package ‘blme’ (Chung *et al*. 2013). A gamma covariance prior was fitted for each model as recommended by Chung *et al*. (2013), and a bobyqa optimiser was included in the models for environmental range size and maximum spread rate to achieve model convergence. To partially account for phylogeny, the genus was included in each model as a random effect and allowed to vary by the intercept. This calculation is known to be a good proxy for phylogeny, as genera have previously been found to explain between 40-80% of trait variance in this dataset (Moravcová *et al*. 2010). The equation for the linear mixed models was as follows (Barr *et al*. 2013):

$$Y \sim t_i + P_{0p} + \beta_1 V_1 + \ldots + \beta_n V_n + e_p$$

Where Y is the dimension of invasiveness, t is the intercept term for taxon i, P_{0p} is the random effect (representing genus) allowed to vary by intercept, V are the explanatory variables of the model (Table 2.1), and e_p is the observation-level error. P-values were calculated using the R package 'parameters' (Lüdecke *et al*. 2020).

To investigate the probability of taxon i being classified as invasive (opposed to non-invasive) depending upon the set of traits used in the dimension-specific models (Table 2.1), Bayesian mixed models were used with the family set as binomial, using the bglmer() function with the R package 'blme' (Chung *et al*. 2013). Four models were fitted, with each including the same independent variables as the previous models for geographic range size, environmental range size, local abundance, or maximum spread rate, respectively (Table 2.1) to facilitate comparisons across models. As with the previous set of models, a gamma covariance prior was fitted for each model as recommended by Chung *et al*. (2013), a bobyqa optimiser was included for all models, and genus was included in each model as a random effect and allowed to vary by the intercept to partially account for phylogeny. The probability that taxon i was classified as invasive was:

$$logit(p_i) \sim t_i + P_{0p} + \beta_1 g V_1 + \cdots + \beta_n V_n + e_p$$

Where t is the intercept term for taxon i, P_{0p} is the random effect (representing genus) allowed to vary by intercept, V are the explanatory variables of the model, and e_p is the observation-level error. R-squared values were calculated using the R package 'MuMIn' (Bartoń 2020).

All analyses were carried out in R version 4.1.2 (R Core Team 2021). Missing trait data was calculated through multiple imputations using the R package 'MissForest' (Stekhoven and Bühlmann 2012) for eight traits that were missing between 2-18% of data (Figure 7.2). Missing data was not imputed for the dimensions of invasiveness, so species were excluded from the relevant model if there was no data available for the relevant dimension of invasiveness. As a result, 87 species were included in the geographic and environmental range size models, 71 species in the abundance model, and 35 species for the spread rate model. Due to the differing sample sizes, transformations and correlations were carried out separately on each data set to ensure the most suitable transformations were used. All variables were centred by subtracting the mean and standardised by dividing by two standard deviations. Variables were either log-transformed (using log() function (R Core Team 2021)) , logit-transformed (using R package 'car'

(Fox and Weisberg 2019)) or transformed through Tukey's ladder of powers (using R package 'rcompanion' (Mangiafico 2021)) to achieve a near-normal distribution (Table 2.1). Pearson's correlation coefficient was used to calculate the correlations between each dimension of invasiveness. Pearson's correlation coefficient was also calculated for the continuous traits included in each model, and variables with r-squared values over 0.6 were excluded (Figure 7.3). Variance inflation factors were calculated for each model, and variables were retained if the values were less than five (James *et al*. 2013). Effect plots were made using the R packages 'ggeffects' (Lüdecke 2018) and 'ggplot2' (Wickham 2016), and forest plots were made using the R package 'sjPlot' (Lüdecke 2021).

2.4 Results

(1) How do different characterisations of invasiveness relate to each other?

There was strong evidence that local abundance and maximum spread rate were significantly positively correlated ($r^2=0.61$, $p<0.001$). The correlations amongst the remaining dimensions were weaker, with all r-squared values being less than 0.50 (Figure 2.1).

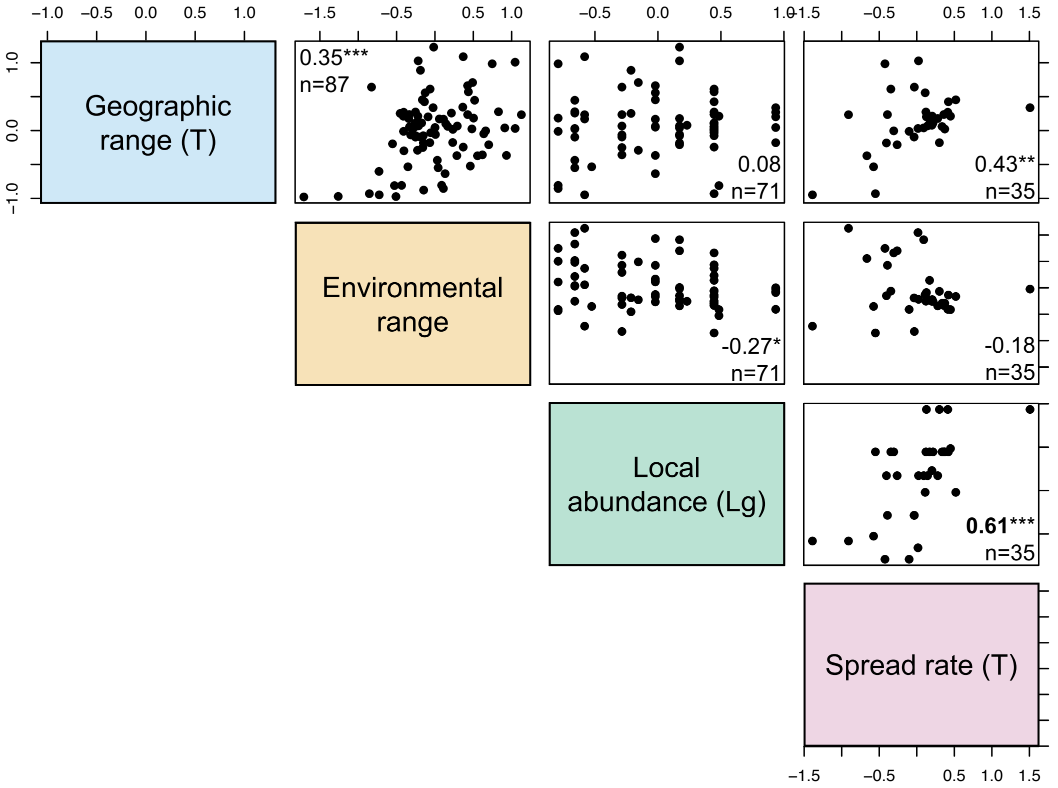

Figure 2.1 Correlation matrix of the four dimensions of invasiveness. Sample size (n) and Pearson's correlation coefficient are shown in each panel, with correlations over 0.6 highlighted in bold. Significance is shown by asterisk, where * p<0.05, **p<0.01, and ***p<0.001. Transformations are shown in brackets (T = Tukey's ladder of powers transformation, and Lg = logit transformation), and all dimensions were centred and standardised.

Subtle correlations between the probability of a species being classified as invasive and the dimensions of invasiveness revealed that invasive species in Czechia tended to have faster spread rates (β=2.275, p=0.109), higher abundance (β=0.476, p=0.642), and broader environmental ranges (β=0.213, p=0.805), but narrower geographic ranges (β=-0.857, p=0.476) than species classified as non-invasive. Whilst none of the slope coefficients were statistically significant and the trends are generally very weak and should thus be interpreted with caution (Table 7.2), these indistinct relationships still provide some evidence of the expected relationships between the probability of being classified as invasive and the four dimensions of invasiveness, particularly for maximum spread rate (Muff *et al*. 2021).

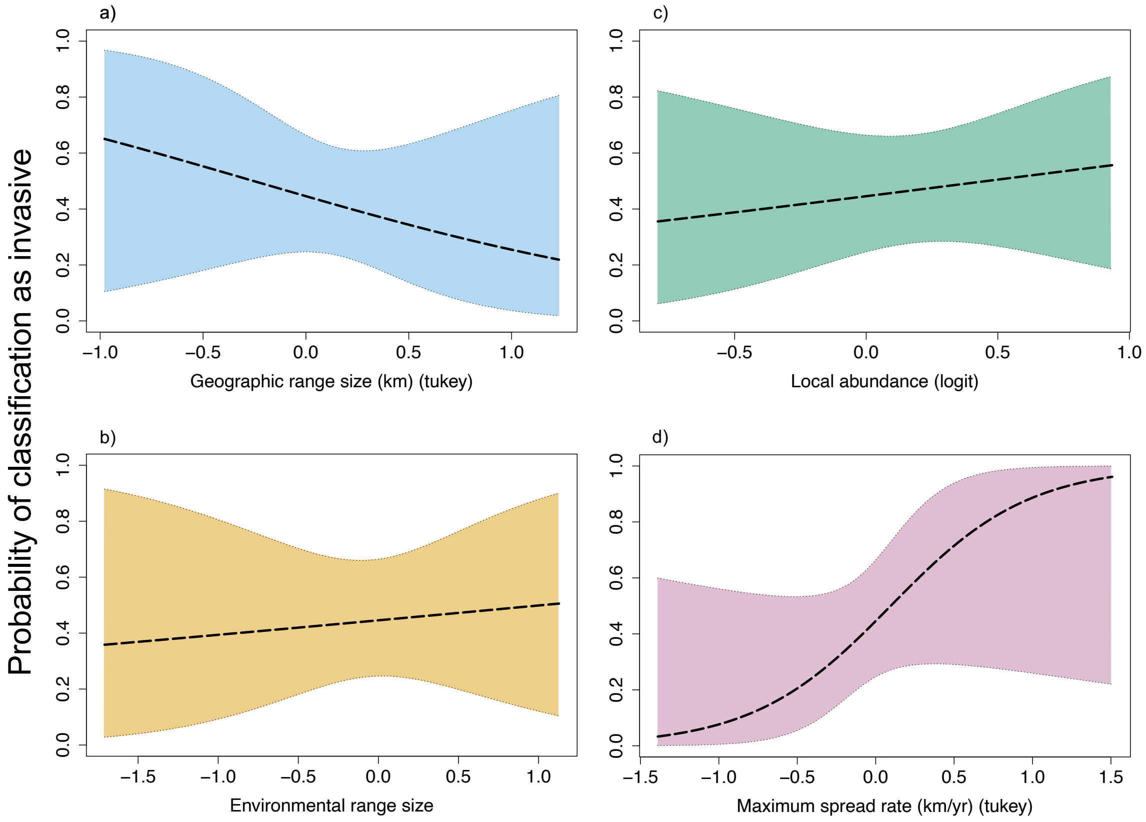

Figure 2.2 Predicted probabilities of non-native herbaceous plant species being classified as invasive (opposed to non-invasive) based on a) geographic range size, b) environmental range size, c) local abundance or d) maximum spread rate. The transformations are shown in brackets. The 95% confidence intervals are shown in different colours. None of the slope coefficients were significant and so were represented by dotted lines.

These relationships among the dimensions of invasiveness and the binary classification of invasive and non-invasive are supported in a PCA analysis. Invasive species are more likely to have higher maximum spread rates and greater local abundances, and higher environmental range sizes (although support for this is weaker) (Figure 2.3, Table 7.3). However, there is a large amount of overlap between invasive and non-invasive species, suggesting that the dimensions of invasiveness do not clearly drive differences amongst the two groups.

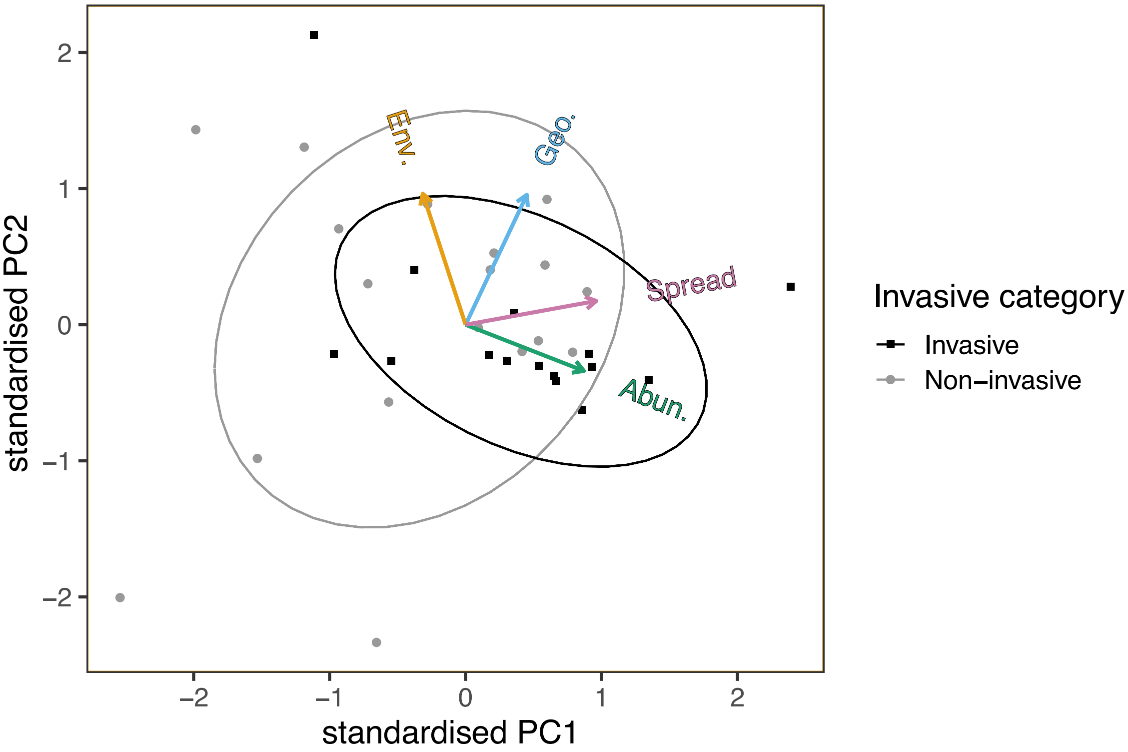

Figure 2.3 Biplot of the four dimensions of invasiveness (Geo. = geographic range size (Tukey's ladder of powers transformed), Env. = environmental range size, Abun. = local abundance (logit transformed) and Spread = maximum spread rate (Tukey's ladder of powers transformed)) for 33 herbaceous plant species. Invasive species are shown in black squares, and non-invasive species are shown in grey circles.

(2) What traits are linked with different ways to characterise invasiveness, and how strong are these relationships?

Using the full models with all variables revealed that species residence time had a positive effect on geographic range size (β=0.368, p=0.001), seedling relative growth rate had a positive effect on environmental range size (β=0.280, p=0.073), height had a positive effect on local abundance (β=0.379, p=0.026), and anemochory had a positive effect on maximum spread rate (β=0.383, p=0.096) (Figure 2.4a-d; Tables 7.4-7.7). There was little to no evidence that the remaining traits had any effect on the dimensions of invasiveness. Of the logistic models used to predict the probability of a species being classified as invasive, there was moderate evidence that height had a positive effect on a species being classified as invasive (β=3.215, p=0.028) and weak evidence that perennial species were less likely to be classified as invasive (β=-2.318, p=0.056) (Figure 2.4e-h; Table 7.8, also see Tables 7.9-7.11). In every case, traits explained the probability of a species being classified as invasive (opposed to non-invasive) (marginal r^2 = 0.25-0.37) better than they explained the species' dimensions of invasiveness (marginal r^2 = 0.10-0.17) (Figure 2.4).

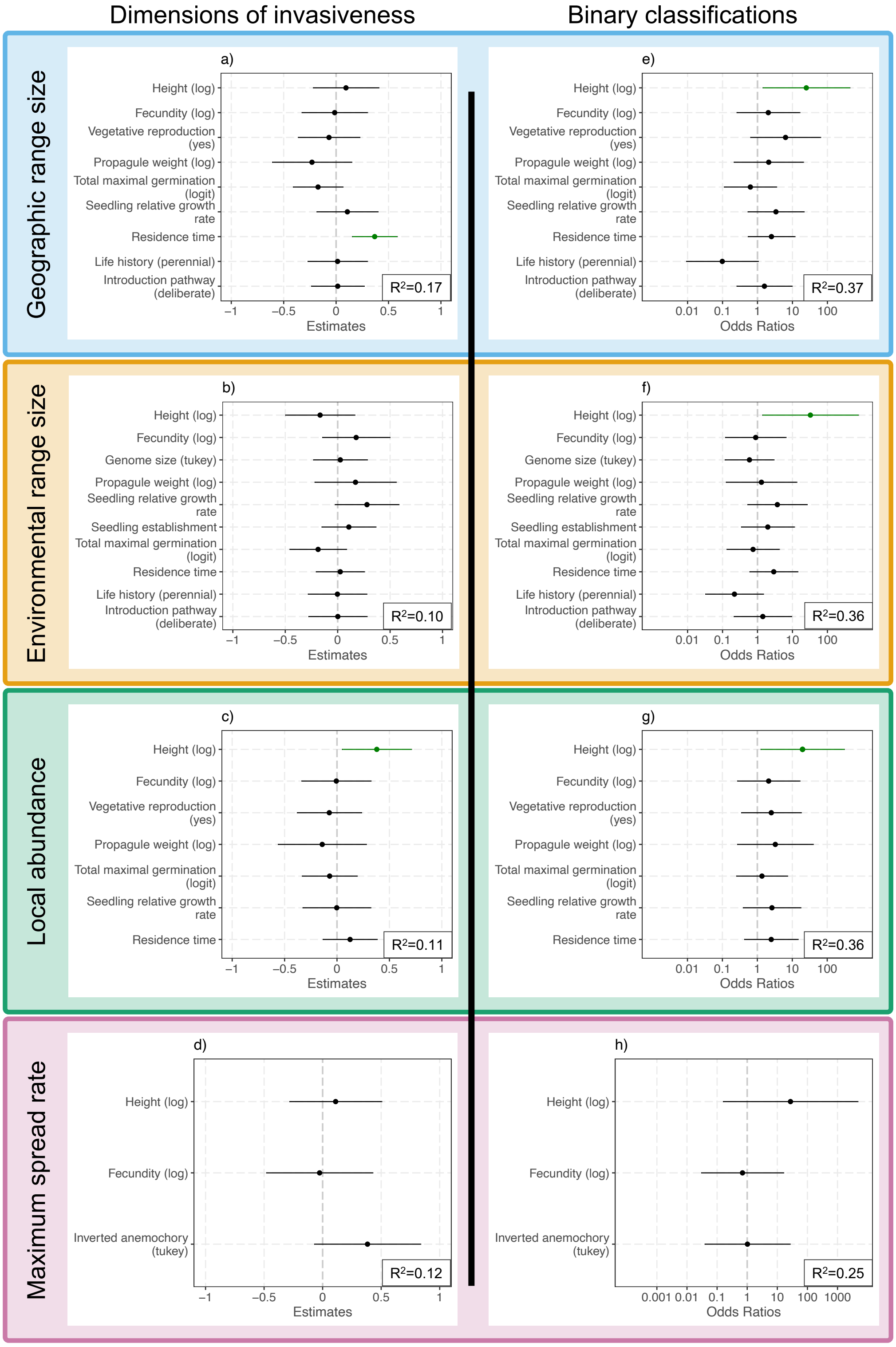

Figure 2.4 Predicted effects of traits and other covariates on a) geographic range size (n=87), b) environmental range size (n=87), c) local abundance (n=71), d) maximum spread rate (n=35), and e-h) probability of being classified as invasive (opposed to non-invasive) (n=87, 87, 71 and 35 respectively). Marginal r^2 is shown for each model. Positive significant effects are shown in green, and nonsignificant effects are shown in black. Plots show the effects of traits predicted to be important for each dimension (a-d) (Table 2.1), with the same set of traits used to predict the probability of invasiveness in corresponding logistic models (e-h) to facilitate comparison between models before model selection.

After model selection, the data showed strong evidence that species residence time had a positive effect on geographic range size (β=0.355, p=0.001) (Figure 2.5, Table 7.4). There was moderate evidence that seedling relative growth rate had a positive effect on environmental range size (β=0.273, p=0.019), and little evidence that total maximal germination had a negative effect on environmental range size (β=-0.181, p=0.105) (Table 7.5). There was moderate evidence that height had a positive effect on local abundance (β=0.302, p=0.017) (Table 7.6), and weak evidence that 1/anemochory had a positive effect on maximum spread rate (β=0.385, p=0.049) (Table 7.7). For the binary classification, there was moderate evidence that height had a positive effect on the probability of being classified as invasive (β=3.657, p=0.009), and weak evidence that annual species were more likely to be classified as invasive (β=-2.061, p=0.059). There was little evidence that vegetative reproduction (β=1.323, p=0.177), seedling relative growth rate (β=0.880, p=0.237), and residence time (β=0.894, p=0.246) influenced the probability of being classified as invasive (Table 7.8). There was also little evidence that fecundity had a negative effect on the probability of a species being classified as invasive when traits selected for maximum spread rate (see Table 2.1) were included in the logistic model (β=-0.349, p=0.798) (Table 7.11). Height was the only trait for which there was moderate evidence for both continuous demographic dimensions of invasiveness and the binary classification.

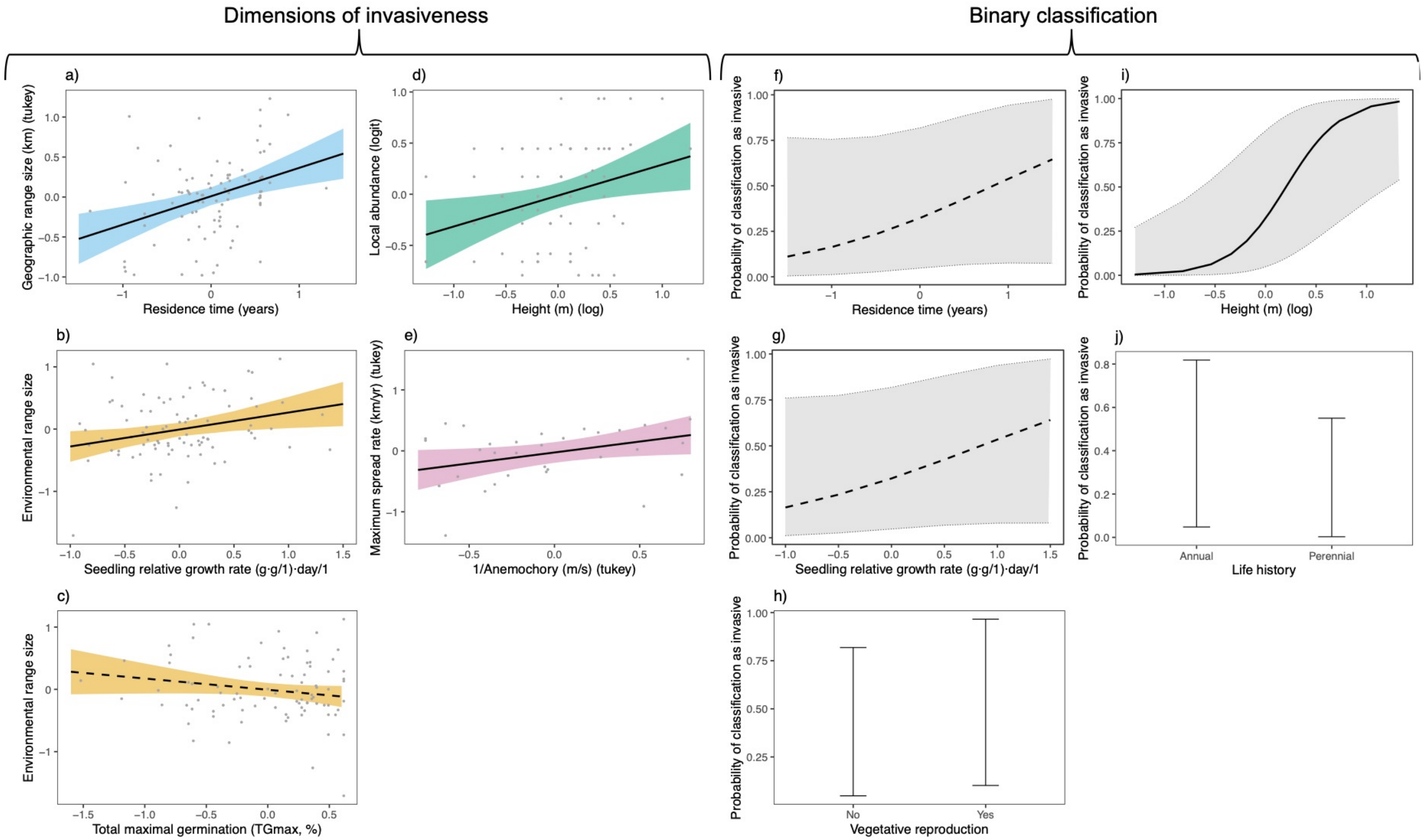

Figure 2.5 Predicted a) geographic range size, b-c) environmental range size, d) local abundance, e) maximum spread rate, and f-j) probability of being classified as invasive (opposed to non-invasive) of herbaceous plants (selecting from the same set of traits as used for geographic range size (Table 2.1)) across values of traits or covariates. Black lines represent the estimated average response, and the shaded areas show 95% confidence intervals. Mean trait values included in the analysis are shown by grey dots in a-e). Figures show the variables retained after model selection (chosen by lowest AIC values). Significant relationships ($p<0.05$) are shown with a solid line. In panel e), high values of 1/Anemochory have a better capacity for wind dispersal.

2.5 Discussion

Using a dataset of herbaceous plants which have been introduced to Czechia, we investigated which traits were related to invasiveness defined either using a binary classification (invasive or non-invasive) or four continuous demographic dimensions of invasiveness (geographic range size, environmental range size, local abundance, and maximum spread rate). Whilst there was weak evidence that species classified as invasive tended to be more abundant, have large environmental range sizes, and faster spread rates, the only trait found to explain both the binary classification of invasiveness and a dimension of invasiveness was height, which positively related to abundance and the probability of being classified as invasive. Whilst seedling relative growth rate also correlated positively with environmental range size and the probability of being invasive, the latter relationship was subtle. In all cases, traits explained the binary classification better than the continuous demographic dimensions, which provides further support that showed that binary classifications were a useful tool to investigate species invasiveness (Pyšek *et al*. 2009, Moravcová *et al*. 2010, van Kleunen *et al*. 2010b).

(1) How do different characterisations of invasiveness relate to each other?

Continuous dimensions of invasiveness have shown independence in previous studies (Catford *et al*. 2016, Fristoe *et al*. 2021). However, we found that species that have high spread rates are also likely to be abundant (Figure 2.1). Spread rate is often difficult to measure, especially for a large number of species (Fristoe *et al*. 2021), so if abundance could be used as a proxy, this would be valuable for studies investigating multiple dimensions as abundance is easier to quantify. However, given this pattern was not observed in (Catford *et al*. 2016), it may be unique to this dataset.

We found that invasive species in Czechia tend to have broad environmental ranges, be more abundant, and spread rapidly. Invasive species also tended to have smaller geographic range sizes, a phenomenon also observed in Catford *et al*. (2016). Species with broad environmental tolerances may have smaller geographic ranges if the suitable conditions are constrained in geographic space, which could explain the trend observed here. This result also reflects that some species are classified as locally invasive in the Czech Republic (Pyšek *et al*. 2012a).

The maximum spread rate had the largest effect on the probability of being classified as invasive (opposed to non-invasive) (Figure 2.2), which can be explained given the criteria for the binary classification used in this study. Species were classified as invasive when they produced offspring at a certain distance from the parent taxa (>100 m / <50 years for taxa spread by seeds, and >6 m / 3 years for taxa spread by roots, stolons, rhizomes or creeping stems) (Richardson *et al*. 2000). Through this classification, species with higher spread rates are more likely to be classified as invasive. The high correlation between local abundance and maximum spread rate observed in this paper would likely explain the importance of height in the binary model, suggesting that height may be important for abundance, which could itself drive spread rates (Thompson *et al*. 1999), in addition to traits such as anemochory.

(2) What traits are linked with different ways to characterise invasiveness?

Height was repeatedly found to relate positively to the probability of being classified as invasive (Figure 2.4), which is consistent with previous findings (Speek *et al*. 2011, Gallagher *et al*. 2015, Moravcová *et al*. 2015, Divíšek *et al*. 2018) and with the relationships between height and abundance (Figure 2.5). The previous study has shown that height was the most important trait determining whether a species becomes invasive in plant communities representing a range of habitats in Czechia, and that the invaders were taller than native plant species in the invaded community (Divíšek *et al*. 2018). Several other traits and covariates were found to have weak correlations with the probability of being classified as invasive, two of which, seedling relative growth rate and species residence time, were also found to correlate positively with environmental range size and geographic range size, respectively (Figure 2.5). However, both relationships were subtle and so were deemed less important than height as an explanatory variable.

Geographic range size was found to correlate positively with species residence time. This pattern was expected as species residence time has consistently been found to explain invasiveness in plant species (Pyšek and Jarošík 2005, Pyšek *et al*. 2009, Catford *et al*. 2016, Fristoe *et al*. 2021), providing further evidence that the longer a species is present, the further it is able to establish across the landscape. In this study, the species residence time was found to better explain geographic range size than any of the traits included in the analysis. This could be because geographic range size may have been driven by multiple anthropogenic introductions to distinct geographic areas, which could have facilitated spatial range expansion for a myriad of plant types, with little dependence on their specific traits (Pyšek *et al*. 2015).

Environmental range size was found to correlate with two traits, positively with seedling relative growth rate, and negatively (to a lesser extent) with total maximal germination. Seedling relative growth rate is likely to confer an advantage when competition amongst seedlings is minimal, such as in open or recently disturbed habitats (Turnbull *et al*. 2012), so increased habitat heterogeneity could facilitate a wider environmental range size for these species (Questad and Foster 2008). The negative correlation with maximal germination was unexpected, as greater germination in differing conditions should correlate to greater environmental range size (Fernández-Pascual *et al*. 2017). The fact that it does not (Figure 2.5) may be because germination is not the deciding factor in determining environmental range, as traits which relate to survival after germination may be more important.

Local abundance was predicted to have a context-dependent relationship with height, as the influence of height on abundance will vary with the surrounding environment, factors driving competition, and habitats (Divíšek *et al*. 2018). For example, the importance of height will depend on whether light is a limiting factor in becoming abundant and may be less important where other factors are limiting (Grubb 1998). We found that taller species were more likely to be abundant, suggesting that light is a limiting factor in forming abundant populations in Czechia.

Species with propagules more suited for wind dispersal (anemochory) were found to have higher maximum spread rates. This was expected, as the ability of species to spread across the landscape will be partly dependent on the ability of propagules to disperse (Pyšek and Hulme 2005).

The binary classification of invasive and non-invasive species was consistently better explained by traits and covariates than any of the four continuous dimensions of invasiveness (Figure 2.4). This pattern was observed regardless of the set of traits hypothesised for each dimension. Therefore, even though the binary classification may obscure invasive definitions and categorisations (McGeoch *et al*. 2012), it appears as a useful tool to identify traits that are important for invasiveness. Binary classifications have the added benefit of requiring substantially less information than the dimensions of invasiveness, which usually require detailed records only available for a smaller number of species.

The process of invasion is being increasingly recognised as multidimensional, with varying traits being linked to different forms of invasiveness (Speek *et al*. 2011, Lai *et al*. 2015, Carboni *et al*. 2016, Catford *et al*. 2019, Fristoe *et al*. 2021, Palma *et al*. 2021b). An investigation into the native and non-native flora of Europe found that different types of invasiveness (formed through combinations of geographic range size, abundance and environmental range size) had differing combinations of traits, and that invasive species followed similar rules of assembly as native species (Fristoe *et al*. 2021). This suggests that the finding of different traits relating to different forms of invasiveness holds true at large macroecological scales and at the national scale examined in this study. Where species distribution data is available to calculate the dimensions of invasiveness, using continuous variables can be advantageous at a range of scales, although binary classifications are still a useful alternative where this data is not available.

2.5.1 Conclusion

In previous studies, binary classifications have been successfully used to provide insights into how traits relate to invasiveness. Binary classifications of invasiveness are advantageous in that they require less information than would be required to calculate or measure the continuous dimensions of invasiveness. However, we found that hypothesising that species traits were most important for each dimension allowed the identification of traits that would not have been apparent in the binary classification alone. Therefore, where data is available, using the dimensions of invasiveness can provide a more nuanced approach to understanding the relationships between traits that confer invasiveness by promoting a particular demographic process than binary classifications. The dimensions can also be used to specify how binary classifications relate to demographic dimensions, which may be especially useful where the ecological criteria behind a binary classification have not been clearly reported. Understanding which dimensions drive binary classifications of invasiveness would help to explain how traits relate to ecological patterns, and this could be used to facilitate comparisons between studies that use different definitions of invasiveness.

2.6 Acknowledgements

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Chapter 3 The use of traits in invasive seaweed research: A systematic review

3.1 Abstract

Traits have been used extensively in invasion ecology, providing a common metric across taxa and ecosystems that allow comparisons based on the functional responses and effects of biota. However, most work on traits has focused on terrestrial plants, despite the vulnerability of marine systems to invasive species, and in particular invasive seaweeds. Research that focuses on individual invasive seaweed species has intensified in recent years, yet few studies have synthesised the evidence to identify commonalities or knowledge gaps. Here we present a systematic review of 322 papers that investigate the traits of seaweed species from across the globe, to answer the question '*what are the trends and gaps in research that investigates traits of invasive seaweeds?'* To answer this question, we had three main aims: (1) *to identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds*, (2) *to clarify which and how many species have been investigated*, and (3) *to assess which traits have been measured, and how they have been used*. Our review revealed that publication rates for this area of research are increasing, that study regions were concentrated in Europe and North America, that 158 species were studied in total but 35% of studies investigated *Sargassum muticum* and *Undaria pinnatifida*, and that the most researched traits were morphological, which were used to address a wide range of research objectives. Key research gaps included relatively few studies from South America, Asia, and Africa, a lack of papers researching more than one species, and measurements of biomechanical traits. Altogether, this review provides an overview of this important area of research, and highlights the varied ways in which traits of invasive seaweeds can be utilised to answer important ecological questions.

3.2 Introduction

Traits can be defined as measurable features of an organism that potentially affects its' performance or fitness, and that can be measured at the individual level (Cadotte *et al*. 2011, Dawson *et al*. 2021). They provide a common metric across taxa and systems, allowing ecologists to move from taxonomic assessments and comparisons to ones based on functional responses and effects (Funk *et al*. 2017). Traits have been widely used across community ecology, ecosystem functioning, and biogeography (Díaz and Cabido 2001, McGill *et al*. 2006, Suding and Goldstein 2008, Violle *et al*. 2014, Cadotte *et al*. 2015) within the context of (amongst other objectives) predicting responses to environmental change, understanding ecological processes, and predicting species interactions (Matteodo *et al*. 2013, Funk *et al*. 2017, Schleuning *et al*. 2020, Birks 2020). They have become an especially valuable tool in invasion science and biosecurity (Palma *et al*. 2021a).

Non-native species are those which are transported to areas beyond their native range through accidental or intentional human transport (Pimentel *et al*. 2005, Hewitt *et al*. 2007, Aguiar and Ferreira 2013). Some of these non-native species may become invasive through increasing their population and range sizes (Blackburn *et al*. 2011). Some species displaying similar behaviour may also be considered invasive even within their own native range (Valéry *et al*. 2009). Invasive species have been recognised as one of the leading causes of biodiversity loss and can have significant economic impacts (IPBES 2019, Zenni *et al*. 2021). Identifying traits common to invasive species has proven to be a useful tool to prevent the intentional introduction of species that may become problematic, for example via the Weed Risk assessment in Australia (Pheloung *et al*. 1999), or to predict which non-native species should be prioritised for monitoring and management (Grewell *et al*. 2016). Whilst the use of traits to predict invasive species began with terrestrial plants (Baker 1965), it has been increasingly applied to other taxa and ecosystems (Nyberg and Wallentinus 2005, Jarošík *et al*. 2015, McKnight *et al*. 2017, Dalla Vecchia *et al*. 2020, Tobias *et al*. 2022).

Seaweeds (i.e. marine macroalgae) are important primary producers broadly distributed across the ocean biome, and have significant ecological, economic, and cultural value (Smit 2004, Delaney *et al*. 2016, Nurjanah *et al*. 2016, Mouritsen *et al*. 2018). Often through human activity, such as aquaculture (Naylor *et al*. 2001), seaweeds have been transported outside of their native range, and have subsequently become established in recipient ecosystems across the globe (Langar *et al*. 2002, Chandrasekaran *et al*. 2008, Nejrup and Pedersen 2010, Primo *et al*. 2010, Lapointe and Bedford 2011, Vasconcelos *et al*. 2011). The rate of marine introductions is expected to rise in future, due to expanding global shipping (Seebens *et al*. 2016, Sardain *et al*. 2019), increases in invasive species rafting on plastics and anthropogenic debris (Carlton *et al*. 2017) and global warming making more areas suitable for invasive species (Bellard *et al*. 2013). Despite this, seaweeds are generally under-researched relative to terrestrial plants (Lowry *et al*.

2013). More information on the processes and mechanisms underpinning seaweed invasiveness is needed to prevent and monitor current and future seaweed invasions.

The largest investigation of traits of invasive seaweeds was carried out by Nyberg and Wallentinus (2005), who investigated 13 categorical traits of 113 invasive and non-native seaweed species in Europe. Nyberg and Wallentinus (2005) successfully used these traits to predict which species were most likely to become invasive, finding commonalities amongst them such as tolerance to pollutants and a high likelihood of transportation. The continued increase of research investigating traits of invasive seaweeds, combined with the growing availability of seaweed trait data shared via databases (Mauffrey *et al*. 2020), suggests that there is great potential for the use of seaweed traits to answer ecological questions. Therefore, it is timely to undertake a detailed review of the ways in which traits have been used to investigate invasive seaweeds, to identify trends and gaps, and to help prioritise future research efforts.

Here we present a global review of papers that investigate traits of invasive seaweeds. Using a systematic and reproducible methodology, we screened the scientific literature to find relevant papers to answer the research question ‘what are the trends and gaps in research that investigates traits of invasive seaweeds?’ To answer this question, we had three main aims: (1) *to identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds*, (2) *to clarify which and how many species have been investigated*, and (3) *to assess which traits have been measured, and how they have been used*. We expected there to be an increasing publication rate innkeeping with the wider scientific literature (McCallen *et al*. 2019), that Rhodophyta would be the most investigated seaweed taxonomic group (Schaffelke *et al*. 2006), and that the majority of traits studied would be morphological (Dalla Vecchia *et al*. 2020). Finally, we highlight research gaps and make recommendations for further work.

3.3 Methodology

The databases Web of Science (Core Collection and BIOSIS Citation Index), Scopus and EBSCO*host* Greenfile were searched for records on 21 January 2021 using the following search string:

(trait* OR character* OR growth* OR life* OR phenotyp* OR morpholo* OR attribute*)

AND

(invas* OR nonnative* OR native* OR nonindigenous* OR indigenous* OR alien* OR casual* OR exotic* OR foreign* OR naturali* OR introduc* OR allochthonous*)

AND

(seaweed* OR macroalga* OR alga* OR chlorophyta* OR rhodophyta* OR phaeophyceae* OR hydrophyt* OR macrophyt*)

Search results were selected to include articles only, and to include results from the maximum number of years possible for each database (Web of Science: 1950-2021, Scopus: All years to present, and EBSCO*host* Greenfile: 1973-2021). Irrelevant categories were removed from the Web of Science search (Table 7.12), and in total 19,954 records were downloaded from all three databases (Figure 7.4). Duplicates were removed using the duplicated() function (R Core Team 2021), leaving 15,001 original records.

All of these records were screened by title using the R package ‘metagear’ (Lajeunesse 2016). Titles were accepted if they mentioned a seaweed, an unspecified invasive or non-native species (or a synonym of), or an unspecified aquatic macrophyte or hydrophyte. 3,067 records were accepted and were screened by abstract (also using the R package ‘metagear’) and were included where the abstract referenced an invasive or non-native (or a synonym of) seaweed, or an unspecified invasive or non-native species. Records which did not include abstracts were automatically accepted to be screened by full paper. 1,272 records were accepted and searched by full paper and were included in the final review if they measured traits of an invasive or non-native seaweed. Papers which recorded morphological measurements purely for taxonomic classifications or as first records of species in a new area were not included, as characteristics were chosen for taxonomic reasons, not ecological ones. Review papers were only included if they described how the papers were selected, to ensure that the traits included were representative and chosen systematically. Whilst this will have resulted in some apparent duplicates, we are interested in how traits are used to answer questions, so where the same traits may be used to answer different questions is within the scope of this systematic review. This resulted in 322 papers being included in the analysis (Figure 7.4).

For each paper included in this review, fifteen categories were used to collect data, similar to those in Dalla Vecchia *et al*. (2020)’s systematic review of the use of functional traits in macrophyte studies. Each category contributed to understanding the three main aims of the systematic review. The first aim (1) *to identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds,* was investigated through collecting the year and journal of publication, the geographic area of first author, the geographic area of study, the method of data collection, the type of study, and the habitat the invasive species were collected from. To answer the second aim, (2) *to clarify which and how many species have been investigated*, we collected data on the taxonomic classification of the invasive species, the name of the invasive species, whether a criteria for invasiveness was included, the number of invasive species in the study, and whether the study included a comparison to a baseline (a native species or native population of the invasive species – see (van Kleunen *et al*. 2010a)) . Finally, to investigate the third aim (3) *to assess which traits have been measured, and how they have been used*, we recorded the trait category, the environmental variables measured, and the main aim of the study.

The *geographic area of first author* was recorded as the country of the associated institution of the first author. Each country was sorted by continent for ease of comparison and analysis. The *geographic area of study* was recorded as the continent where the population of the invasive species was collected from. When the geographic area of study was greater than a single continent, the reported larger geographic area was recorded instead (e.g., global, or northern hemisphere). Multiple geographic areas were recorded for both first author location and the geographic area of study, but this was more common for the latter group.

The *method of data collection* recorded whether traits were measured from individuals grown under natural conditions (*observational*), or from individuals grown under manipulated conditions (*experimental*). The *type of study* recorded whether the data was collected from species grown in the *field* or the *laboratory*, or whether the study was a *review* or *modelling* paper. The *habitat type* was recorded as the environment from which the invasive species was collected. *Artificial* included anthropogenic habitats such as harbours or breakwaters. *Rocky habitats* included any natural rocky substrata, including reefs and rocky shores. *Sandy / sedimentary habitats* included beaches, estuaries, and lagoons. *Vegetated habitats* included seagrass meadows, marshes, and algal mats. Any habitats not included in the previous categories were recorded as *other*, and studies which did not record any habitat were included as *unknown*.

The *taxonomic classification of the invasive species* was recorded, either as *Phaeophyceae*, *Chlorophyta*, or *Rhodophyta*. The *name of the invasive species* in the study was recorded, and to ensure that the current taxonomic name was included in this review, all species names were checked on AlgaeBase (Guiry and Guiry 2022) and the currently accepted name was used. The way in which a species is classified as invasive has been proven to affect which traits are determined as important. To investigate whether studies accounted for this, we recorded whether a criteria for invasiveness was included. We found that the criteria matched four demographic dimensions of invasiveness which were previously identified in (Catford *et al*. 2016). These were local abundance, geographic range size, environmental range size, and spread rate, which can be combined to give 15 classifications of invasiveness. Given that many papers used the terms invasive and non-native interchangeably, in this review these dimensions are used to justify the research into the invasive (or non-native species) rather than as an explicit definition of invasiveness. The *number of invasive species in the study* was recorded, and for ease of analysis were grouped into three categories, either one species, between two and five species, or more than six species. Whether *the study included a baseline* was recorded as *yes* if the study also measured traits from either native species or native populations of the invasive species.

For ease of analysis and comparisons, *trait categories* were used to group measured traits into seven comparable groups. *Morphology* included measures of size or branching diameter. *Biochemical* included the elemental composition of tissues. *Productivity* included fresh and dry weight, and measures of growth rate. *Physiology* included physiological processes such as photosynthesis, nutrient uptake rates, respiration, and pigment content. *Biomechanics* measured mechanical strength and related features. *Fitness* included traits related to reproduction and dispersal. *Other* included any traits not covered by the previous categories.

The *environmental variables* measured alongside traits were grouped into ten categories. *Water* included physical or chemical measures of the water column, including temperature, salinity, or nutrient content. *Sediment / substrate* included differences or characteristics of the sediments or substrate. *Climate* included meteorological variables, such as air temperature. *Anthropogenic* included environmental conditions caused by human activities, such as nutrient pollution, climate change, or control methods. *Depth / light* included measures of the depth in the water column, and variations in light. *Hydrology / topology* included information on the hydrological regime, often through differences amongst sites. *Biotic* included interactions or changes of the natural community, including measures of natural enemies, biotic resistance, or microbial communities.

Time / season included studies which measured how traits changed over time, including both short time-periods (days) or long time-periods (months or years). *None* is where no environmental variables were measured, and *other* included any environmental variables not included in the categories above.

Finally, the *main aim* of the paper was recorded to characterise the purpose of the research, and therefore the reason for measuring the traits. *Environmental gradients* measured how traits varied along environmental gradients, often to investigate the invasive potential of species in different environmental conditions. *Competition* included papers which measured how traits related to competition, which may have been inter- or intra-specific. *Natural enemies* measured how traits related to herbivores or pathogens. *Anthropogenic* investigated the effects of human-induced pressures such as pollution, climate change, or management. *Impact* investigated the effects of invasive species on the surrounding community. *Invasive process* included papers which investigated how traits changed with the invasive process, such as propagule pressure or differences between native and invasive populations. *Other* included any main aims which were not included in the previous categories. Several papers had more than one main aim, but no paper had more than two. The bar charts and chord diagrams were created in Rstudio using R 4.1.2, using packages ‘ggplot2’ and ‘Rcolorbrewer’ for the bar charts (Neuwirth 2014, Wickham 2016), and ‘circlize’ for the chord diagrams (Gu *et al*. 2014).

Given our focus on trends in the literature, we re-ran the search on 27 February 2022 in Web of Science and EBSCO*host* Greenfile to estimate how many new papers may have been excluded from our systematic review. In the 13 months that had elapsed since our initial search date of 21 January 2021, we estimate that approximately 19 additional papers could be included if we had used a February 2022 search date. This accounts for <6% of the 322 papers used in our review and is thus not expected to significantly change the results presented here (See 7.2.1. Updated search methods and results).

3.4 Results

(1) *To identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds*.

The first paper investigating traits of invasive seaweeds found in this review was published in 1975 in the journal *Botanica Marina*. Since then, the number of papers investigating this research area has increased, as 39% of the 322 papers included in this review were published between 2014-2021. This reflects trends in the wider literature, as the number of publications which mention ecology, invasive species and traits in the title, abstract or keywords has also increased since the 1980's (see 7.2.2. Rate of publications for invasive ecology trait papers) (Figure 3.1). The papers included in this review were published in a wide range of journals (Table 7.13), with the journal *Botanica Marina* being the most common (35% of papers in this review) (Figure 3.1).

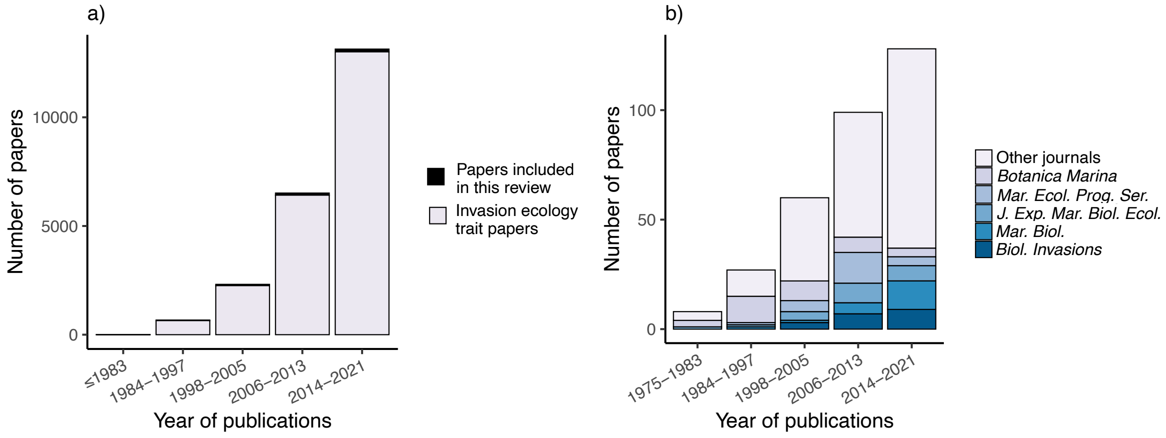

Figure 3.1 The a) number of papers published on the research area of invasive ecology and traits (see 7.2.2. Rate of publications for invasive ecology trait papers) over time, alongside the number of papers in this review, and b) the number of papers included in this review published over time, with the five most common journals they were published in shown by stacked bars.

First authors were mostly based in Europe (54% of papers), followed by North America (23%). Africa (2%) and Asia (2%) had the lowest number of first author affiliations. The geographic study area followed a similar trend, with the majority of studies sampling European and North American populations (57% and 25% respectively), with Africa and Asia being the least studied (2% and 2%). Of the study type, many studies investigated seaweeds grown in the field (56% of all papers). Most field studies were observational (grown in unmanipulated conditions) (80% of field studies, 45% of all papers), whereas experimental studies largely took place in laboratory conditions (94% of laboratory studies, 26% of all papers), and fewer papers combined lab and field studies (12% of all papers). Whilst many papers did not record the habitat type where seaweed samples were collected (n=111, 34%), for those which did the majority were taken from rocky habitats (31%) (Figure 3.2).

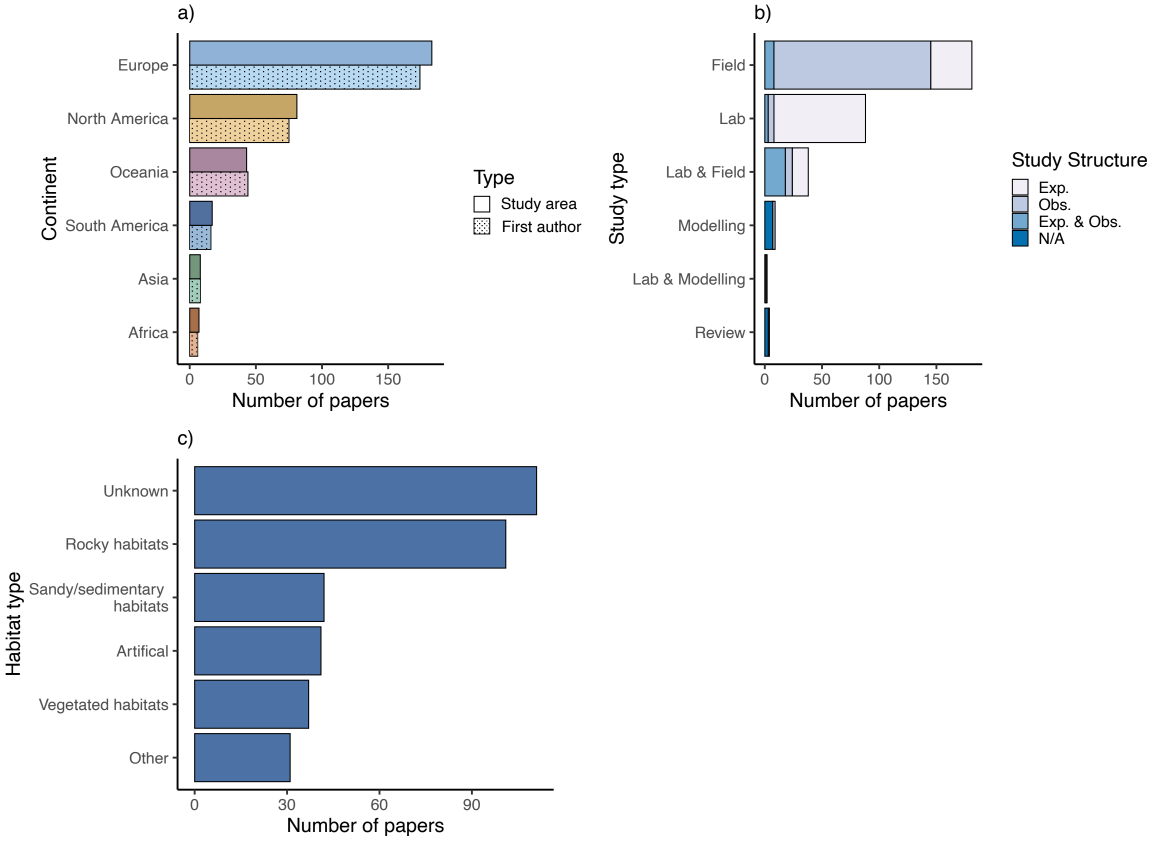

Figure 3.2 The a) geographic area of first author affiliation and the study area (where the invasive species were sampled from) (two papers had a global study area, and two had a study area of the Northern Hemisphere which are not shown). Multiple geographic areas were recorded for both first author and study locations, but more so for the latter (Table 7.14). The number of papers which b) used field, lab, review or modelling to collect data or draw conclusions, with the structure of the study shown in stacked bars (Exp. = experimental, Obs. = Observational, N/A = study did not include experiments or observational data), and c) the habitat type where the invasive species populations were collected from.

(2) *To clarify which, and how many, species have been investigated.*

The papers included in this review have measured the traits of 158 seaweed species (Table 7.15). Of these, the most investigated taxonomic classification was Rhodophyta (65% of all species), and Chlorophyta was the least studied (11%), following broader trends in both the number of orders and the proportion of orders which include a non-native species (Schaffelke *et al*. 2006) (Figure 3.3). However, the most investigated seaweed species (*Sargassum muticum* and *Undaria pinnatifida*) both belong to the Phaeophyceae (Figure 3.3). Eight papers (2%) included invasive native species.

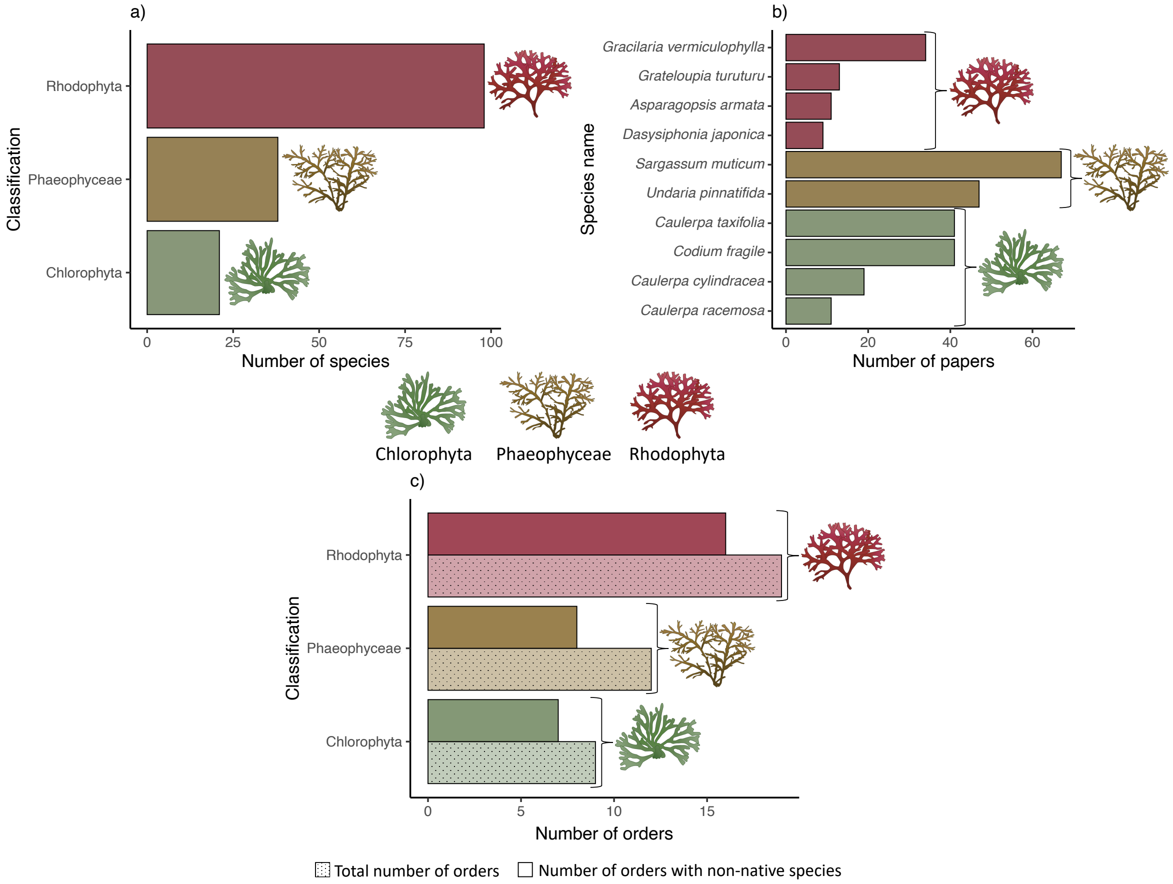

Figure 3.3 The number of a) invasive species in each taxonomic group investigated across all papers in this review (two papers each investigated one charophyte species, see (Nyberg and Wallentinus 2005; Sahlin *et al*. 2011) which are not shown), b) the number of papers which investigated the ten most studied invasive species found in this review, and c) the total number of orders for each taxonomic group, and the number of orders which contain non-native species with data taken from Schaffelke *et al*. (2006). Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/).

Most papers did not describe the criteria used for classifying species as invasive (20% of all papers), but of those that did, geographic range size (15%) and spread rate (10%) were the most frequently used criteria (Figure 3.4).

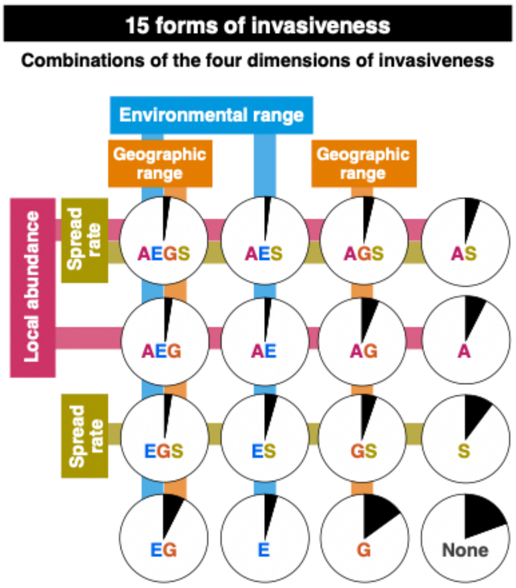

Figure 3.4 Proportion of 322 trait-based studies that classify invasive seaweed species into 15 forms of invasiveness, based on the dimensions of invasiveness (local abundance, geographic range size, environmental range size and spread rate) and their combinations, as described in Catford *et al*. (2016). The black portion of each pie chart indicates the proportion of the 322 studies that explicitly used the corresponding criteria to classify the species as invasive, as represented by the letters (Where *G* = geographic range size, *E* = environmental range size, *A* = local abundance, and *S* = maximum spread rate). For example, *EGS* indicates that the dimensions environmental range size, geographic range size, and maximum spread rate were explicitly used as criteria for invasiveness. *None* represents studies in which none of the four dimensions of invasiveness were explicitly used as criteria for invasiveness. Figure modified from Catford *et al*. (2016).

Previous investigations have used comparisons between invasive species and native or non-invasive species (here referred to as baseline) to investigate whether invasive species have different characteristics (van Kleunen *et al*. 2010a). We found that the majority of papers did not include comparisons to a baseline (61% of all papers), suggesting that they are not investigating differences between invasive species and native species or native populations of the invasive species (Figure 3.5). Most papers investigated one invasive species (91%), and 1% investigated more than six (Figure 3.5).

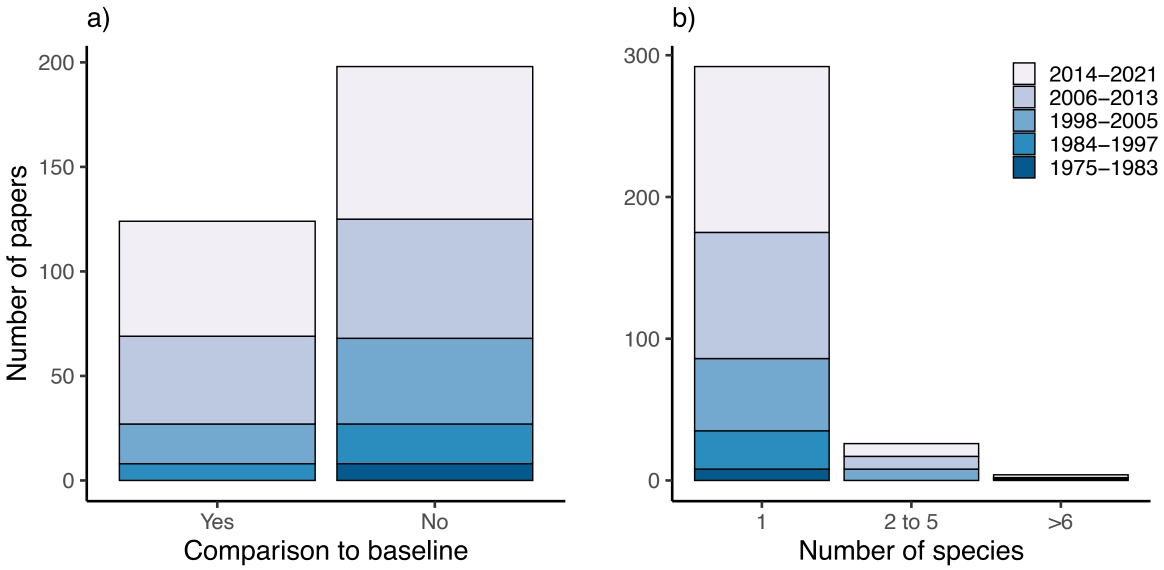

Figure 3.5 The number of papers which a) compared the invasive species to a baseline (either a native species or a native population of the invasive species) and the number of papers which b) studied one, two-five, or more than six invasive species within the same paper. Stacked bars show the years of publication.

(3) *To assess which traits have been measured, and how they have been used.*

Morphological traits were the most investigated (49% of all papers), followed by productivity (42%), reproduction (30%) and biochemical (29%) traits. Biomechanical traits were the least investigated (3%) (Figure 3.6). The most measured environmental variables related to season / time (39%), and physical and chemical parameters of the water column (33%). Depth / light, hydrology / topology, and biotic environmental variables were also regularly investigated (24%, 19%, and 22% respectively). Environmental gradients were the primary main aim investigated by a large margin (31%). Commercial application was the least investigated (8%), however most of these studies were published between 2014 and 2021 (Figure 3.6).

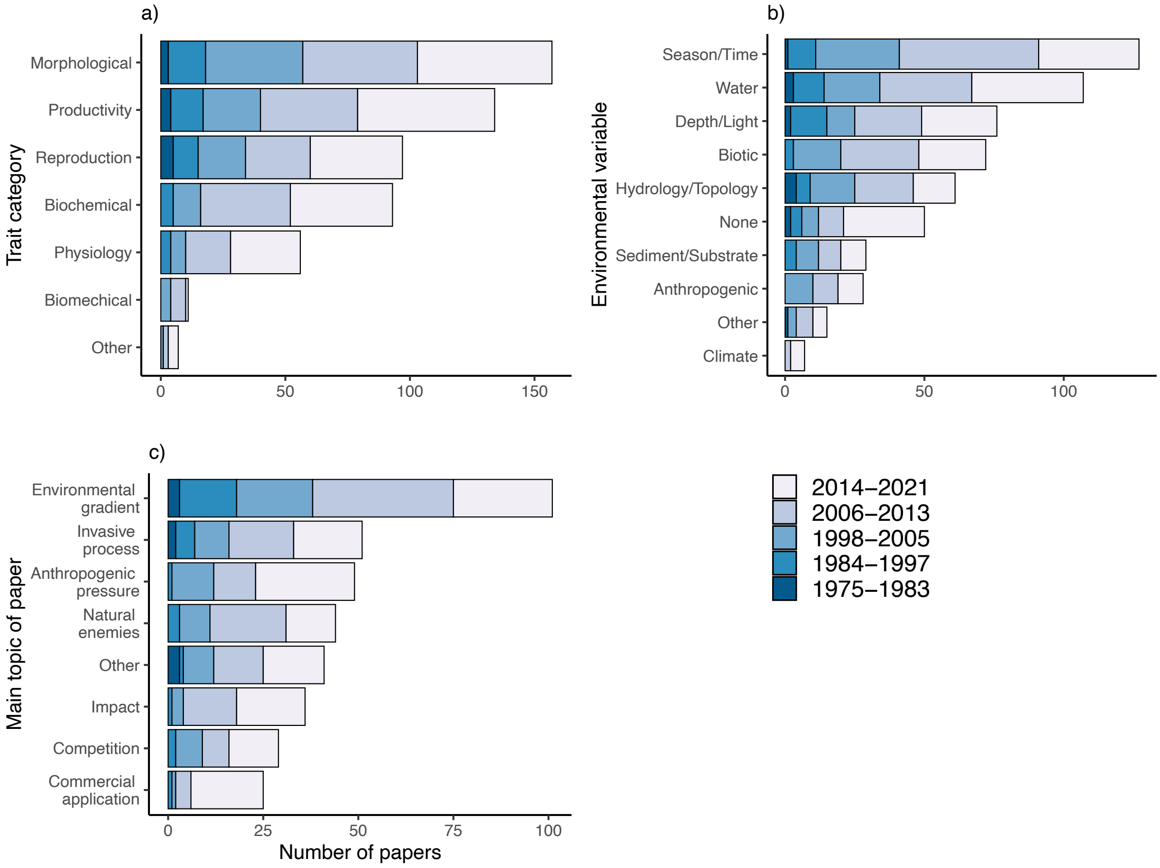

Figure 3.6 Number of papers which measured a) categories of traits, and b) environmental variables to reach the c) main aims of the paper.

There were no clear trends in which traits were used to investigate certain environmental variables, or certain main aims (Figure 3.7). In general, nearly all trait categories were used to investigate all other aims except for commercial application, which was exclusively investigated using biochemical traits.

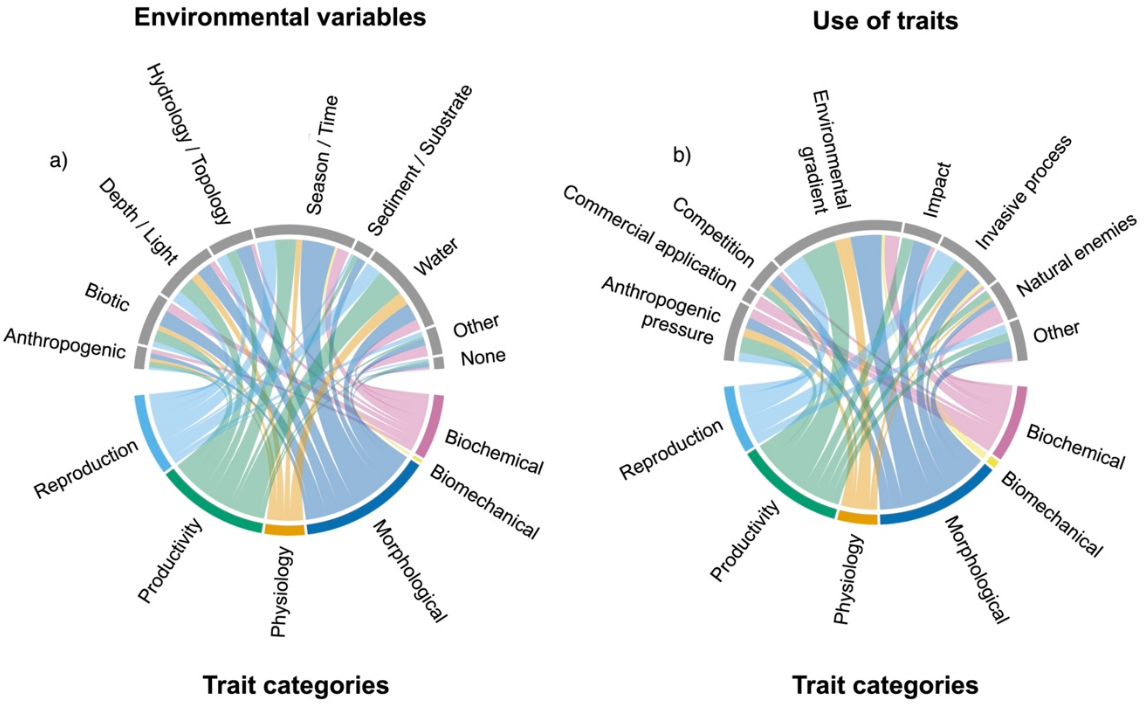

Figure 3.7 The proportion of papers in which trait categories were investigated a) alongside environmental variables, or b) how the traits have been used to investigate main aims. For clarity, links with less than 5 connections are not shown in this figure.

3.5 Discussion

In this systematic review we identified several key trends in how studies have investigated traits of invasive seaweeds. These included an increase in publications over time, a higher research effort in Europe and North America, a research focus on *Sargassum muticum* and *Undaria pinnatifida*, and morphological and productivity traits being the most investigated, and biomechanical traits the least. These results have addressed the three aims of this review, as explained below.

(1) To identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds.

The increase of publications over time is in keeping with wider trends in the literature, where more papers are being published in ecology generally, and for the specific subjects of both traits and invasive species (including when they are considered separately) (McCallen *et al*. 2019, Anderson *et al*. 2021). The increasing number of papers suggests that this is an important area of research, and traits of invasive seaweeds will continue to be used to answer ecological questions in marine ecosystems.

The most studied geographic areas were in Europe, North America, and Oceania, with Asia and Africa being extremely under-represented in the papers included in this review. Greater research output in Europe, North America, and Oceania has also been found in several reviews of the conservation and invasion science literature (Pyšek *et al*. 2006, Lowry *et al*. 2013, Di Marco *et al*. 2017, Watkins *et al*. 2021). This consistent trend is likely to reflect the greater amount of funding available in these areas. Papers in this review were only included if they were in English, which may have influenced the geographic distribution observed, particularly for underrepresented regions. However, only 3% of the records screened by full paper were excluded for this reason, so we do not expect the results to be substantially affected.

(2) To clarify which, and how many, species have been investigated.

Species belonging to the Rhodophyta were the most researched, which was to be expected given that this group contains both the highest number of species and the highest proportion of non-native orders (compared to Phaeophyceae and Chlorophyta) (Schaffelke *et al*. 2006, Guiry 2012) (Figure 3.3). Despite this, the most investigated species were not Rhodophyta, but were Phaeophyceae, specifically the fucoid *Sargassum muticum* and the kelp *Undaria pinnatifida.* These species may have been investigated more because they are widespread invaders (Engelen *et al*. 2015, Epstein and Smale 2017), and can become abundant and drive ecological change in native communities (Harries *et al*. 2007, Salvaterra *et al*. 2013, Heiser *et al*. 2014, McLaughlan *et al*. 2014, Epstein *et al*. 2019). Therefore, these species could be more likely to be noticed, and therefore be prioritised for research. In contrast, invasive species that are undetected due to misidentification as a native or another invasive species, known as cryptic invaders (Morais and Reichard 2018), may be under researched. Some of the least investigated species in this review included known cryptic invaders such as *Polysiphonia morrowii* (Geoffroy *et al*. 2012) and *Ulva ohnoi* (Flagella *et al*. 2010). Advances in technology have made genetic analysis more frequent in ecological studies (Diepeveen and Salzburger 2012, Anderson *et al*. 2021) which can be used to identify cryptic species, potentially making it easier to identify and study them.

Most papers investigated only one invasive species (Figure 3.5), likely due to limitations in collecting trait data from many species, especially where experimental conditions need to be maintained. The increasing availability of trait databases may facilitate trait-based studies across more species, and between invasive species and native species, and invasive species and their native populations. Trait databases are currently dominated by terrestrial plants (Kleyer *et al*. 2008, Paula *et al*. 2009, Fraser 2020), but databases for seaweed species are increasing, including the recently published dataset of 12 traits across 85 UK species (Mauffrey *et al*. 2020), and a dataset of European seaweed traits which is currently in development (Robuchon *et al*. 2015). Whilst these datasets are not specific to invasive seaweeds, the availability of seaweed trait data may facilitate studies across a wider number of species, including invasive species, and their native populations.

Many papers did not explicitly provide a criteria for why species were considered invasive, and often used non-native and invasive as interchangeable terms. Given the wide remit of invasion research, it is not practical that a single universal definition of invasiveness could be used across all papers, and indeed would be impractical and inappropriate to do so across different taxa. Therefore, it is vital that going forwards papers explicitly state the criteria for their terminology, and to be consistent with it, to allow for the flexibility required by this varied research area and to facilitate comparisons across papers and species (Catford *et al*. 2016, Fristoe *et al*. 2021, Palma *et al*. 2021b). We therefore recommend that papers investigating invasive species provide clear definitions of why a species is considered invasive (such as high abundance, or its impact on native communities). If the species is not considered invasive, then authors should clarify that the species is at an earlier stage of the invasive process and refer to it as non-native (or a synonym of).

(3) To assess which traits have been measured, and how they have been used.

The most measured traits were those relating to morphology and productivity. These are often referred to as ‘soft traits’, as they are relatively easy to measure, can be measured *in situ*, and are generally inexpensive as they do not require specialist equipment and are useful for measuring traits from a large number of species, or over a long period of time (Hodgson *et al*. 1999, Cornelissen *et al*. 2003). However, soft traits do not generally provide a direct mechanistic link with a species’ ecology or ecophysiology, but are usually correlated with, and thus broadly indicative of, hard traits (traits which capture a precise function (Belluau and Shipley 2018)).

Consequently, soft traits are often correlated with multiple aspects of a species’ life history (Lavorel and Garnier 2002, Westoby *et al*. 2002), and can provide less predictive power than more expensive to measure hard traits (Belluau and Shipley 2018).

Both morphological and productivity trait categories were measured in papers which also recorded changes over seasons and years. These temporal studies addressed a range of aims, including how changes in traits over time affected the impact of an invasive seaweed on the native community (Veiga *et al*. 2014, Najdek *et al*. 2020), whether the season affected the invasive potential of a seaweed under climate change scenarios (Atkinson *et al*. 2020), and reproductive phenology to predict future range shifts (Chefaoui *et al*. 2019). Dalla Vecchia *et al*. (2020) also found that both morphological and productivity trait categories were the most studied for aquatic plants, suggesting that these trait categories are easily applicable across taxa.

Despite the importance of biomechanical traits in determining the hydrodynamic conditions in which seaweeds can survive (Demes *et al*. 2013), very few papers examined these traits. Of those that did, biomechanical traits were linked to differences in ploidy (Lees *et al*. 2018), dispersal potential (Watanabe *et al*. 2009, Oróstica *et al*. 2012), and recruitment to different sediments (Scheibling and Melady 2008). This represents a clear knowledge gap, and further research examining these traits is needed.

The most researched main aim was related to environmental gradients, where the study investigated environmental variables (such as light, nutrient availability, and temperature), and measured how traits changed along these gradients. All trait categories were used in papers which investigated environmental gradients, and were used for a variety of purposes, including investigating the realised niches of species (Koerich *et al*. 2020) and how this changes throughout the invasion process (Sotka *et al*. 2018), potential ranges of invasive species (Desmond *et al*. 2019), and conditions required for bloom formation (Bermejo *et al*. 2020). Measuring how traits vary along environmental gradients may investigate how invasive species adapt to novel environmental conditions (Weinberger *et al*. 2008), or phenotypic plasticity (Zanolla *et al*. 2015). Understanding relationships between species traits and environmental gradients is clearly a key research objective.

Overall, each trait group was used to measure all the main aim categories and were measured alongside all the environmental variables. The only exception was the main aim of commercial application, which was exclusively investigated using biochemical traits, such as identifying bioactive compounds for use in biofouling materials (Pinteus *et al*. 2020, 2021). The broad application to different aims reflects the benefit of a trait-based approach, and how these measurements can be applied to a wide range of questions.

In recent years (2014-2021), most papers focused on examining seaweed traits related to anthropogenic pressures and commercial applications. This suggests that there is increasing interest in researching how invasive species respond to human-induced stressors such as climate change and pollution, for which previous studies have shown a link (Lapointe and Bedford 2011, Dijkstra *et al*. 2019). As pressures such as climate change, pollution, and habitat degradation increase, this research area may become more important to understand the relationships between anthropogenic pressures and invasive seaweeds.

3.5.1 Concluding remarks and future directions

The use of traits to investigate invasive seaweeds is a growing research area, and this trend is likely to continue. Through quantifying the methods, species, and aims used in investigations of traits of invasive seaweeds, we provided an overview of the main trends in this review. Through this we have identified several research gaps, and so propose these recommendations for future research:

i) More research is required in under-studied regions, especially Asia, Africa, and South America. It will be impossible to understand how global scale stressors (i.e. increased shipping, climate change) will mediate seaweed invasions without information from these areas.

ii) The terms non-native and invasive should not be used interchangeably, and where species are considered invasive an explicit criteria should be included in the paper. This will be more challenging for species where there is less research available, but providing a criteria for invasiveness will still help maintain consistency across papers, and therefore facilitate comparisons.

iii) One of the benefits of a trait-based approach is that comparisons can be made across species and functional groups, however most papers investigated one invasive species, and did not compare it to a native species or population. Whilst it can be more time intensive and expensive to measure traits from multiple species, doing so will facilitate the general conclusions that can be drawn from trait studies. Additionally, investigating a broader range of species will also help to draw these comparisons, as there is currently a strong research bias towards only a few species (e.g., *S. muticum* and *U. pinnatifida*).

iv) Morphological and productivity trait categories are clearly important and are used to investigate a range of aims. In contrast, biomechanical traits are understudied, even though the ability of seaweeds to physically withstand hydrodynamic forces is an important driver of survival and distribution. The reason for this research gap is unclear, but we recommend that these traits are prioritised for future research.

This systematic review provided an overview of the ways in which traits are used to investigate invasive seaweeds. As pressures on the environment continue to increase, using a functional approach to understand invasiveness of seaweeds will allow for generalisations across taxa and ecosystems, which will be useful for conservation and policy decisions. Through providing a concise summary of the research so far, this review has identified knowledge gaps and future research directions for invasive seaweed research.

3.6 Acknowledgements

We thank Rebecca Spake for assistance with designing the search string and for recommendations on software to use for screening results. A.L.M. was supported by the Natural Environmental Research Council (Grant number NE/L002531/1) and a School of Biological Sciences Studentship at the University of Southampton. D.A.S. was supported by a UKRI Future Leaders Fellowship (MR/S032827/1).

Chapter 4 Herbivory and functional traits suggest that enemy release is not an important mechanism driving invasion success of brown seaweeds

This chapter has been accepted for publication in *Biological Invasions*. The text provided is reproduced from the published version and is written in the style of the journal.

4.1 Abstract

Invasive species are a global threat to biodiversity and there is a pressing need to better understand why some species become invasive outside of their native range, and others do not. One explanation for invasive species success is their release from concurrent natural enemies upon introduction to the non-native range. The so-called enemy release hypothesis (ERH) has conflicting support, depending upon the ecosystem and species investigated. To date, most studies testing the generality of the ERH have focused on terrestrial ecosystems. Here, we tested whether enemy release might contribute to the success of the invasive non-native brown seaweeds *Undaria pinnatifida* and *Sargassum muticum* in the United Kingdom. We conducted choice and no choice experiments to determine herbivore preference on these invaders relative to six functionally-similar native species. We also measured and compared species traits associated with defence against herbivory (carbon to nitrogen ratio, polyphenolic concentration, tensile strength and compensatory growth). There were no differences in the biomass consumed between invasive and native species for either choice or no choice tests. The carbon to nitrogen ratio (a measure of nutritional quality) was significantly lower for *S. muticum* compared to the three native fucoid species, but measures of the other three defence traits were similar or even greater for invasive species compared with native species. Taken together, it is unlikely that the ERH applies to invasive seaweeds in the northeast Atlantic, suggesting that other factors may contribute to the success of invasive species in this system.

4.2 Introduction

A major challenge for ecologists is to understand why some species are successful and can become invasive outside their native range, and why some do not. There have been many proposed explanations for why some species become invasive (Catford *et al*. 2009), which ultimately stem from the characteristics of the recipient ecosystems and communities, characteristics of the invaders themselves, and the amount and type of propagule pressure (MacArthur and Levins 1967, Eschtruth and Battles 2011, Ricciardi *et al*. 2013, Kimbro *et al*. 2013, McKnight *et al*. 2017, Vedder *et al*. 2021). One leading explanation is the release from coevolved natural enemies in their introduced range, known as the enemy release hypothesis (ERH) (Keane and Crawley 2002). The enemy release hypothesis is based upon the premise that invasive species can benefit through a direct reduction in consumption from native herbivores and attack from pathogens and parasites (Mitchell and Power 2003, Liu *et al*. 2007), partially through changing the allocation of resources from defence mechanisms to growth and reproduction, thereby increasing competitiveness as well as direct benefits such as increased lifespan (Herms and Mattson 1992, Blossey and Nötzold 1995, Schwartz *et al*. 2016).

In the marine realm, herbivory by benthic invertebrates can strongly influence intertidal and shallow subtidal ecosystems, affecting recruitment, growth, diversity and abundance of seaweed species in particular (Aguilera 2011, Poore *et al*. 2012, Williams *et al*. 2013, Aguilera *et al*. 2015). Reducing herbivory can be achieved through traits that reduce attractiveness of the seaweed to herbivores, such as chemical and mechanical defences, and lowering of nutritional quality (Duffy and Hay 1990). For example, chemical defences in brown algae include phlorotannins which have multiple transient secondary roles, including herbivore defence, before transitioning to unreactive components of the cell wall, allowing brown seaweeds to invest in both growth and defence (Arnold and Targett 2003). Seaweeds can also limit the effect of herbivory on their fitness by increasing growth to offset biomass lost to consumers (Duffy and Hay 1990). These traits can be costly, reducing overall fitness of an individual or species relative to its competitors (Dworjanyn *et al*. 2006, Haavisto *et al*. 2017). If invasive species experience release from herbivory, redirecting resources to growth and reproduction instead of costly defence traits could confer an advantage relative to native competitors (Blossey and Nötzold 1995, Schwartz *et al*. 2016).

Numerous studies have tested the ERH, but support for this hypothesis is inconsistent, with results varying by the type of invader, the experimental approach, and the recipient native community (Colautti *et al*. 2004, Heger and Jeschke 2014). The majority of investigations into the ERH, however, have focused on plants in terrestrial ecosystems. Heger and Jeschke (2014) reviewed 176 empirical tests of the ERH, of which 147 (83.5%) focussed on terrestrial systems, and just 15 (8.5%) on marine systems, with only five papers focussed on algae. Interestingly, studies that tested the ERH in marine ecosystems and those that focussed on algae had higher levels of empirical support than other habitat types and taxonomic groups, suggesting that research in both terrestrial and marine ecosystems is needed to more fully understand the generality of the ERH.

Even amongst seaweed species, differences in herbivore preference between invasive and native species may vary between taxonomic or functional groups. Enge *et al*. (2017) conducted a meta-analysis of 35 papers that examined feeding preference of native herbivores for non-native compared to native seaweeds. Whilst non-native species were preferred less than native species, suggesting non-native species escaped herbivory, when grouped taxonomically this trend was only observed in filamentous species. Palatability of native and non-native brown seaweeds was similar (Enge *et al*. 2017). There has been a clear research bias towards only a few invasive seaweeds (e.g. *Caulerpa* spp., *Codium fragile* spp., *Sargassum muticum*), which have provided both strong support (Gollan and Wright 2006, Bulleri and Malquori 2015) and limited evidence for the ERH (Pedersen *et al.* 2016). Given that release from herbivory may vary temporally and spatially (Britton-Simmons *et al*. 2011), further investigations are required to determine whether the ERH describes an important mechanism influencing the spread of invasive seaweeds in marine ecosystems. In particular, understanding the specific mechanisms and traits that may influence herbivore preference will help to clarify the importance of ERH in these ecosystems.

The kelp *Undaria pinnatifida* and the fucoid *Sargassum muticum* are invasive non-native seaweeds which are both native to Asia (Epstein and Smale 2017, Le Cam *et al*. 2020), and were first recorded in the United Kingdom (UK) in 1991 (Farrell and Fletcher 2000) and 1973 (Jones and Farnham 1973) respectively. These species were accidentally introduced into the UK attached to oysters used in aquaculture or attached to vessel hulls (MacLeod *et al*. 2016). Since introduction to the UK, these global invaders have proliferated and have spread rapidly along the UK coastline (Harries *et al*. 2007, Epstein and Smale 2017), often becoming abundant (Harries *et al*. 2007, Heiser *et al*. 2014), and in some cases causing detectable ecological change in native ecosystems (Salvaterra *et al*. 2013, McLaughlan *et al*. 2014, Epstein *et al*. 2019). These factors of spread rate, abundance, and impact all contribute to their classification as invasive species. Despite their relative success in occupying new habitats in their invaded ranges, the importance of enemy release as a mechanism facilitating the invasion of *U. pinnatifida* and *S. muticum* remains unclear. Previous investigations have found conflicting results, concluding that *S. muticum* is both readily consumed by native herbivores (Kurr and Davies, 2018; Strong *et al*., 2009) and grazed less than native species (Monteiro *et al*. 2009, Pedersen *et al*. 2016). Fewer investigations have examined the role of the ERH in mediating the spread of *U. pinnatifida*, but where it has been investigated *U. pinnatifida* was consumed at equal rates to native species (Thornber *et al*. 2004, Jiménez *et al*. 2015, Cardoso *et al*. 2020).

This study aims to contribute to our understanding of the importance of the ERH in marine ecosystems by examining herbivore choice alongside the role of traits that may offer defence against herbivory in native and invasive brown seaweeds. We addressed two specific questions: (1) Are these invasive species more readily consumed by native generalist herbivores than native seaweed species of similar functional groups? (2) Do invasive and native seaweed species differ in their traits related to defence against herbivory? We predicted that the ERH would be an important mechanism in explaining the success of both *U. pinnatifida* and *S. muticum*, and therefore these species would be consumed less readily than native species. The traits investigated (carbon to nitrogen ratio, polyphenolic concentration, tensile strength and compensatory growth) are expected to explain the patterns shown in the herbivore experiments, to determine whether any observed enemy release is due to characteristics of the invasive seaweeds, or whether they are not differentiated among by herbivores.

4.3 Methodology

4.3.1 Study species

Four kelp species and four fucoid species were used for this study. Kelp species included the invasive non-native *Undaria pinnatifida* and the natives *Saccharina latissima*, *Laminaria digitata*, and *Saccorhiza polyschides* (n.b. although *S. polyschides* is taxonomically-speaking not a true kelp belonging to the order Laminariales, it is included here due to its functional similarity with kelps (Norton 1977, Teagle *et al*. 2017)). The fucoid species were the invasive non-native *Sargassum muticum* and the natives *Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum*. The native species were chosen due to their general ecological similarity to the two invasive species, to reduce the variability regarding herbivore choice and allow for meaningful comparisons (Cacabelos *et al*. 2010). All species were sampled in June 2019 from the rocky shores in and around Plymouth Sound on the southwest coast of the UK (Figure 7.5; Table 7.16). All species were sampled by collecting the whole individual (excluding the holdfast) from one population for each species. Following collection, samples were immediately returned to the laboratory in cool boxes where they were stored in an aerated seawater tank for no more than a week before the experiments began.

The seaweed species used in these experiments are consumed by a range of herbivores, including sea urchins (Cacabelos et al. 2010, Cardoso et al. 2020), gastropods (Hagerman 1966, Cacabelos et al. 2010, Jiménez et al. 2015), amphipods, and isopods (Hagerman 1966, Jiménez et al. 2015). In this study, the native generalist herbivores *Steromphala cineraria* and *Littorina littorea* (Bakker 1960, Norton *et al*. 1988) were selected to graze on kelp and fucoid species respectively. A significant part of the diet of *Steromphala* species can come from kelp, as they can consume both the kelp tissue directly, and the associated biofilm and epiphytes (Leclerc et al. 2013, Pessarrodona et al. 2019). *Littorina littorea* consumes a wide range of both micro and macroalgae (Menge 1975, Watson and Norton 1985). These generalist herbivores are used in this study because they have been found to exert top-down pressure and influence algal assemblage diversity and composition in intertidal ecosystems (Lubchenco 1978, Turner and Todd 1991), and are therefore an important part of the trophic structure. Given that specialist herbivores are rare in marine ecosystems (Lubchenco and Gaines 1981, Poore and Hill 2006, Cacabelos et al. 2010), and that generalist herbivores have shown stronger impacts on seaweed community structure (Hay and Steinberg 1992), our focus on generalist herbivores to investigate the enemy release hypothesis is both valid and representative of herbivore-seaweed interactions in this ecosystem. Sixty individuals of each species were collected from the Plymouth sound area during June 2019; herbivores were immediately returned to the laboratory where they were kept in a 34 L tank of aerated seawater for four days without food to acclimatise to experimental conditions and standardise time since feeding.

4.3.2 Experimental design and set up

The midsection of the thallus of each seaweed sample was blotted dry and cut to a standardised wet weight (2 ± (0.5) g for kelp species, and 3 ± (0.5) g for fucoid species) and epiphytes were removed. Choice and no choice experiments were carried out in a temperature-controlled room held at 15-17°C on a light: dark cycle of 8: 16 hours. During the experiments, 800 ml tanks were filled with 450 ml of untreated seawater, which was changed every other day. Choice and no choice experiments consisted of paired tanks (Figure 4.1): the treatment tank contained one herbivore, and the control tank did not contain a herbivore. One herbivore was used per treatment tank because this stocking density was proportional to the size of the seaweed sample.

It also facilitated the measurement of individual grazing rates and standardisation by herbivore wet weight. For choice experiments, ten replicates were included for each combination of invasive and native species, and for the no-choice experiments five replicates were used for each seaweed species. Fewer replicates were used during the no choice tests as less variability was expected given the herbivores only had one choice available. During the choice tests, native seaweed species were compared against the invasive species of the corresponding coarse taxonomic group (i.e., kelp or fucoid). The experiments ran for seven days to ensure sufficient time for the herbivores to consume the seaweed samples. The seaweed samples were blotted dry and weighed at the beginning and end of the experiment.

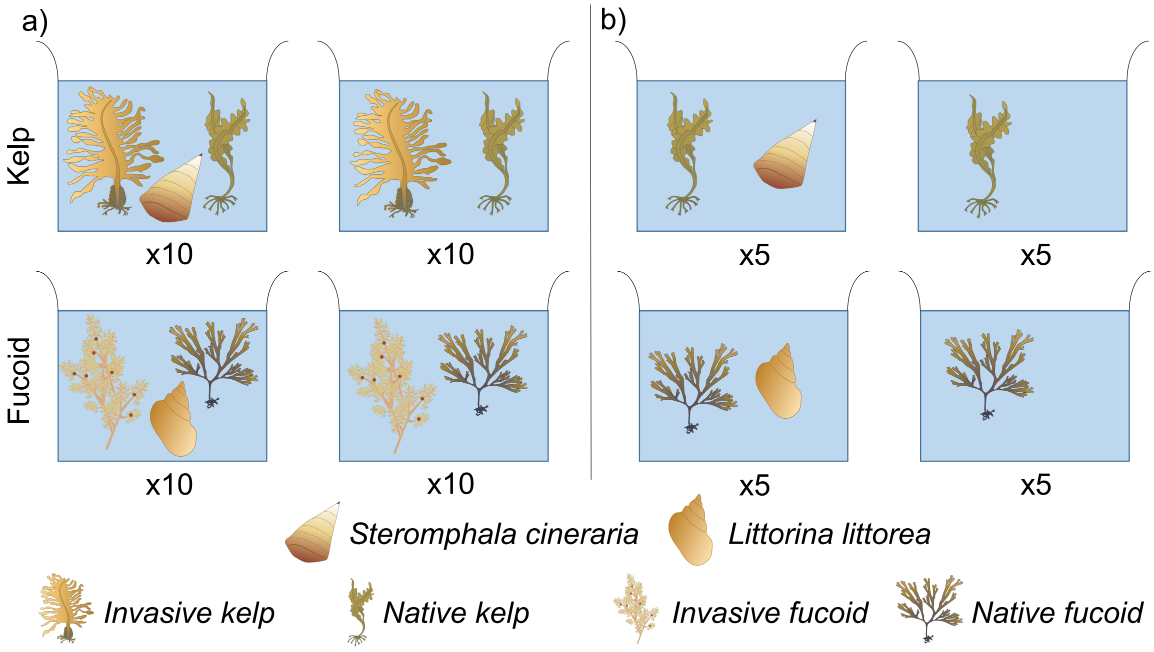

Figure 4.1 Experimental design of a) choice tests between invasive and native species and b) no choice tests of invasive and native species with native herbivores present in the treatment tanks and absent in the control tanks. Kelp species included were *Undaria pinnatifida* (invasive), *Saccharina latissima*, *Laminaria digitata*, and *Saccorhiza polyschides* (native). The fucoid species included were *Sargassum muticum* (invasive), *Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum* (native). The number of replicates is shown under each tank type. Drawings are courtesy of Tracey Saxby, Diana Kleine, and the Integration and Application Network (ian.umces.edu/symbols/).

The amount of biomass consumed was scaled to account for autogenic mass changes in the control samples using the formula $[(T_B * C_E/C_B)-T_E]$, where T and C are the treatment and control wet weights respectively at the beginning (B) and end (E) of the experiments (Sotka *et al*. 2002), which corrects for autogenic growth. The amount of biomass consumed was then divided by the wet weight of the herbivore (including the shell) in grams at the start of the experiment to control for herbivore weight.

4.3.3 Tissue carbon to nitrogen ratio

Tissue carbon to nitrogen ratio (hereafter C:N) of the midsection of the thallus was measured to determine food quality (Ebeling *et al*. 2014, Krumins *et al*. 2015). Additional samples not used in herbivory experiments were frozen then freeze-dried. The freeze-dried samples were ground to a powder using a pestle and mortar. Approximately 1 mg of the samples were weighed into tin capsules and were analysed using an Elemental PYRO Cube Elemental Analyser running in CNS mode and equipped with a thermal conductivity detector. C:N was calculated for each sample. C:N of ten samples were measured and calculated for each species, except for *A. nodosum* where only nine samples could be measured and therefore C:N calculated.

4.3.4 Total polyphenolic concentration

Total polyphenolic concentration is a measure of chemical defence, which deters herbivores from consuming plant and algal tissue (Steinberg 1988, Van Alstyne 1988). Polyphenolic concentration was measured from six of the same samples which were also measured for C:N (which were selected at random), and was also measured from three of the no choice replicates to see whether polyphenolic concentrations varied in the presence or absence of herbivory in fucoid species (there was not enough sample remaining to perform these analyses on kelp samples from no choice analysis). All samples came from the mid-section of the thallus. Polyphenolic concentration was determined by applying an adapted version of the Hargrave *et al*., (2017) method. 100 mg of powdered freeze-dried material the midsection of the thallus was weighed and added to 1 ml of methanol (50 %, diluted with distilled water) in a 1.5 ml Eppendorf tube. The samples were vortexed and refrigerated for 24 hours. The samples were vortexed again and centrifuged for 5 minutes at 17,000 x ***g***. 100 µl of the supernatant was decanted into another 1.5 ml Eppendorf tube, and was diluted with 900 µl of distilled water. The samples were vortexed, and 160 µl was pipetted into a 96-well plate with 20 µl Folin-Ciocalteu reagent (50%, diluted with water). After 5 minutes incubation at room temperature, 10 µl 1.5 M Na_2CO_3 was added. Absorbance was read at 765 nm (FLUOstar OPTIMA microplate reader, BMG Labtech) with a solvent blank. Absorbance was converted to percentage total of dry mass using a phloroglucinol standard curve.

4.3.5 Tensile strength

Tensile strength was measured to examine how physical characteristics (i.e., robustness) influence susceptibility to herbivory. For kelp species, samples from the mid-section of the blade were cut to approximately 20 mm by 70 mm. For fucoid species, a mid-section of the thallus was cut to an approximate length of 85 mm. *Fucus* samples were also cut to an approximate width 10 – 25 mm, depending on the width of the thallus. For *S. muticum* samples, an approximately 90 mm section of the primary axis was used, and the width of the axis was measured twice to allow the cross-sectional area to be calculated. None of the samples used to measure tensile strength had been exposed to herbivory. For each sample, the width and length of the samples were measured to 1 mm, and the thickness of the samples were measured to 0.1 mm. Where the thickness was not uniform across the sample (such as for *Fucus* species) the average thickness was calculated from the maximum and minimum thickness. Each sample was secured in place with clamps (Figure 7.6), leaving a 30 mm (±2 mm) gap in the centre. The clamps were pulled apart at a constant speed, and the distance between the clamps was measured every 0.05 kg for fragile seaweeds, and every 0.1 kg for stronger seaweeds. This continued until the seaweed sample ruptured. The number of samples measured for each species varied depending upon the amount of thallus available: seven samples were measured for *U. pinnatifida*, eight samples for *F. serratus*, nine samples each for *S. latissima*, *L. digitata*, and *F. vesiculosus*, ten samples each for *S. muticum* and *A. nodosum*, and 12 samples were measured for *S. polyschides*. Force to tear (F_t) was calculated using the methods in Pérez-Harguindeguy *et al*. (2013). The force at breaking (N) was divided by the cross-sectional area (mm^2) (which was calculated by multiplying the width by the thickness).

4.3.6 Compensatory growth

Compensatory growth was measured as a potential mechanism to mitigate damage from herbivory (Cerda *et al*. 2009). The experiment to test for compensatory growth consisted of three replicates per species, which included a treatment and a control in separate tanks (two tanks per replicate). For the treatment samples, an emery board was used to mimic the rasping motion of the snail radula (Borell *et al*. 2004). The emery board was used to make 20 scrapes on the same point of the sample. The seaweed was blotted dry and weighed before and after the treatment to quantify how much mass had been lost. This was done daily for seven days, except on day 3 and day 6, when no treatment was applied to allow the samples to grow without artificial herbivory. The samples were still blotted dry and weighed on these days. The control plants were not treated but still weighed daily after being blotted dry. For each species, three samples were included as a control, and three underwent treatment, resulting in six samples per species. Where sample weight could not be accurately determined at the end of the experiment, samples were excluded from analysis. This experiment ran for seven days, in the same room and conditions as the choice and no choice tests.

Percentage change in mass was calculated for the control samples using the equation $[((M_n – M_{n-1}) / M_n) \times 100]$ where M_n is the mass on day *n*, and M_{n-1} is the mass on the previous day. The same equation was used to calculate percentage change in mass for treated samples, but to account for the loss in mass from the treatment, M_n was the weight before the treatment, and M_{n-1} was the weight after the treatment was applied. The percentage change in mass was calculated for each sample on each day of the experiment, and then this was used to calculate the average percentage change in mass of each sample over seven days (the length of the experiment) for ease of statistical analysis.

4.3.7 Statistical analysis

All analysis was completed in Rstudio using R 4.1.2. One-way ANOVA tests were used to test for differences among species for no choice tests, C:N, polyphenolic concentration, and tensile strength with kelp and fucoid species being analysed separately using the R package ‘stats’ (R Core Team 2021). Assumptions of equal variance and normality were tested using Levene’s test and Shapiro-Wilks test respectively, using the R packages ‘car’ (Fox and Weisberg 2019) and ‘stats’ (R Core Team 2021). Where these assumptions were not met, the dependent variable was log transformed (which was required for all of the C:N data, the polyphenolic concentration data for kelp species, and the tensile strength data for kelp species). Where the assumptions were met, Tukey posthoc pair-wise tests were implemented using the R package ‘stats’ (R Core Team 2021). Even after log transformation, the assumption of normality was not met for the tensile strength kelp data, so a Kruskal Walis test was applied using R package ‘stats’ (R Core Team 2021), with a Dunn test for post hoc analysis using R package ‘FSA’ (Ogle *et al*. 2021). Some replicates degraded to the point where the wet weight could not be determined accurately before the end of the experiment, and so were not included in analyses (Table 7.23).

Paired Wilcoxon tests were used to analyse the difference of biomass consumed between invasive and native species in the choice tests, and unpaired Wilcoxon tests were used to analyse the difference between the percentage change in mass (averaged over seven days) for treatment and control groups for the polyphenolic concentration in the no choice tests for fucoid species, and to analyse the difference between treatment and control groups for compensatory growth. Wilcoxon tests were used as they are non-parametric, and all tests were two-sided. All Wilcoxon tests used the R package 'stats' (R Core Team 2021).

4.4 Results

4.4.1 Choice experiments

There was no evidence that either herbivore consumed invasive seaweeds more or less than native species for either kelp or fucoid species (Figure 4.2; Table 7.17).

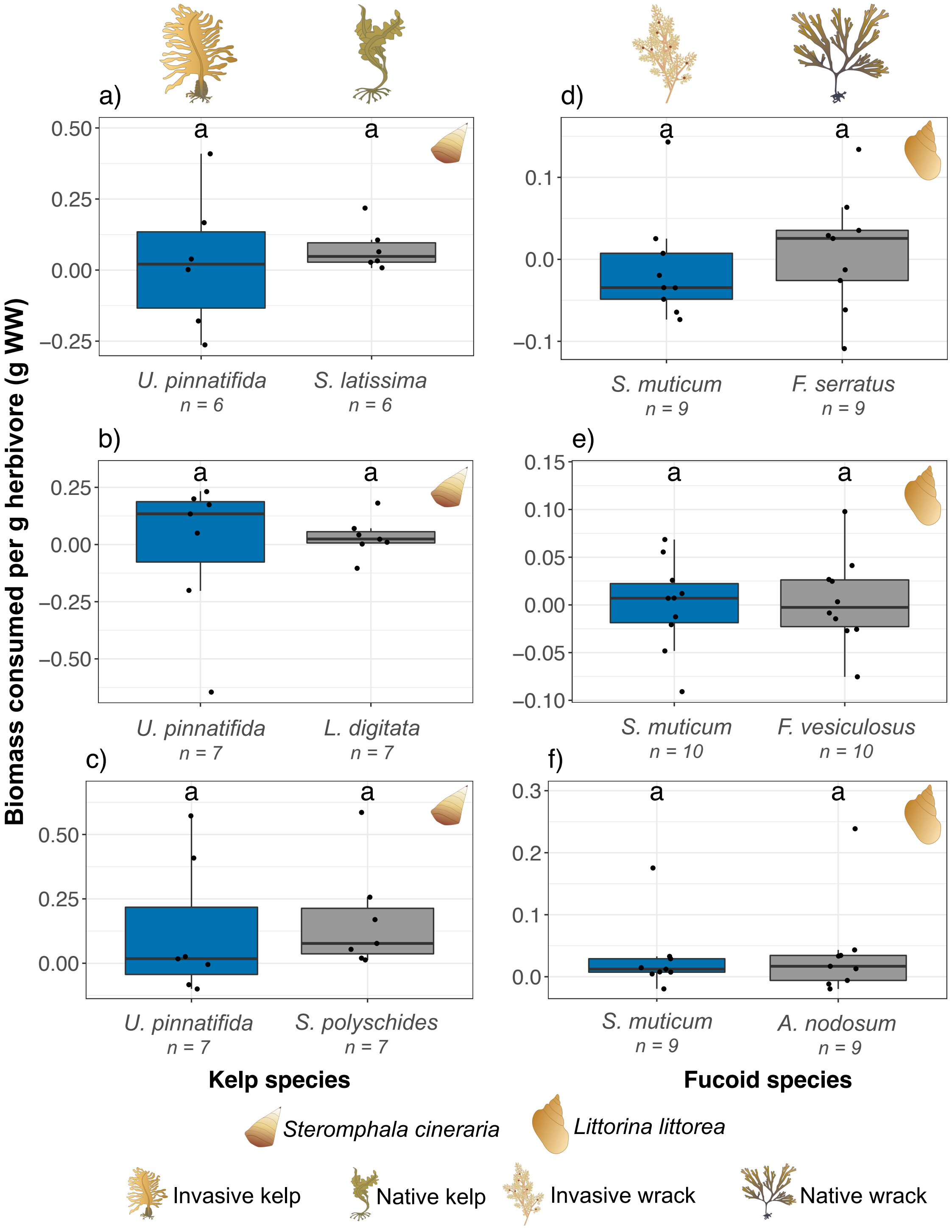

Figure 4.2 Proportion of biomass consumed per g herbivore during choice tests between an invasive species (blue) and a native species (grey). Each graph represents a different comparison between an invasive seaweed and a functionally similar native species. Kelp species are shown in the left column, and fucoids are shown in the right column. Different herbivores were used for comparisons between kelp species (a-c) and fucoid species (d-f). Sample sizes are show under species names. Different letters indicate significant differences (paired Wilcoxon test, $p < 0.05$). Drawings are courtesy of Tracey Saxby, Diana Kleine, and the Integration and Application Network (ian.umces.edu/symbols/).

4.4.2 No choice experiments

There was moderate evidence to suggest that there were differences in the amount of biomass consumed per unit herbivore amongst kelp species [$F_{3,12} = 5.297$, $p = 0.015$] (Figure 4.3). These differences were driven by *S. polyschides* for which there was moderate evidence that this species was consumed more than *U. pinnatifida* ($p=0.048$), *S. latissima* ($p=0.036$), or *L. digitata* ($p=0.033$) (Table 7.18). Amongst fucoid species, there was strong evidence to suggest there were differences in the amount of biomass consumed per unit herbivore [$F_{3,16} = 6.4$, $p = 0.005$] (Figure 4.3). This was explained by moderate evidence that *F. serratus* was consumed more than *S. muticum* ($p=0.011$), and strong evidence that *F. serratus* was consumed more than *A. nodosum* ($p=0.006$) (Table 7.18). For both kelp and fucoid species, there was no evidence that the invasive species *U. pinnatifida* and *S. muticum* were consumed differently to the majority of native species used in this comparison.

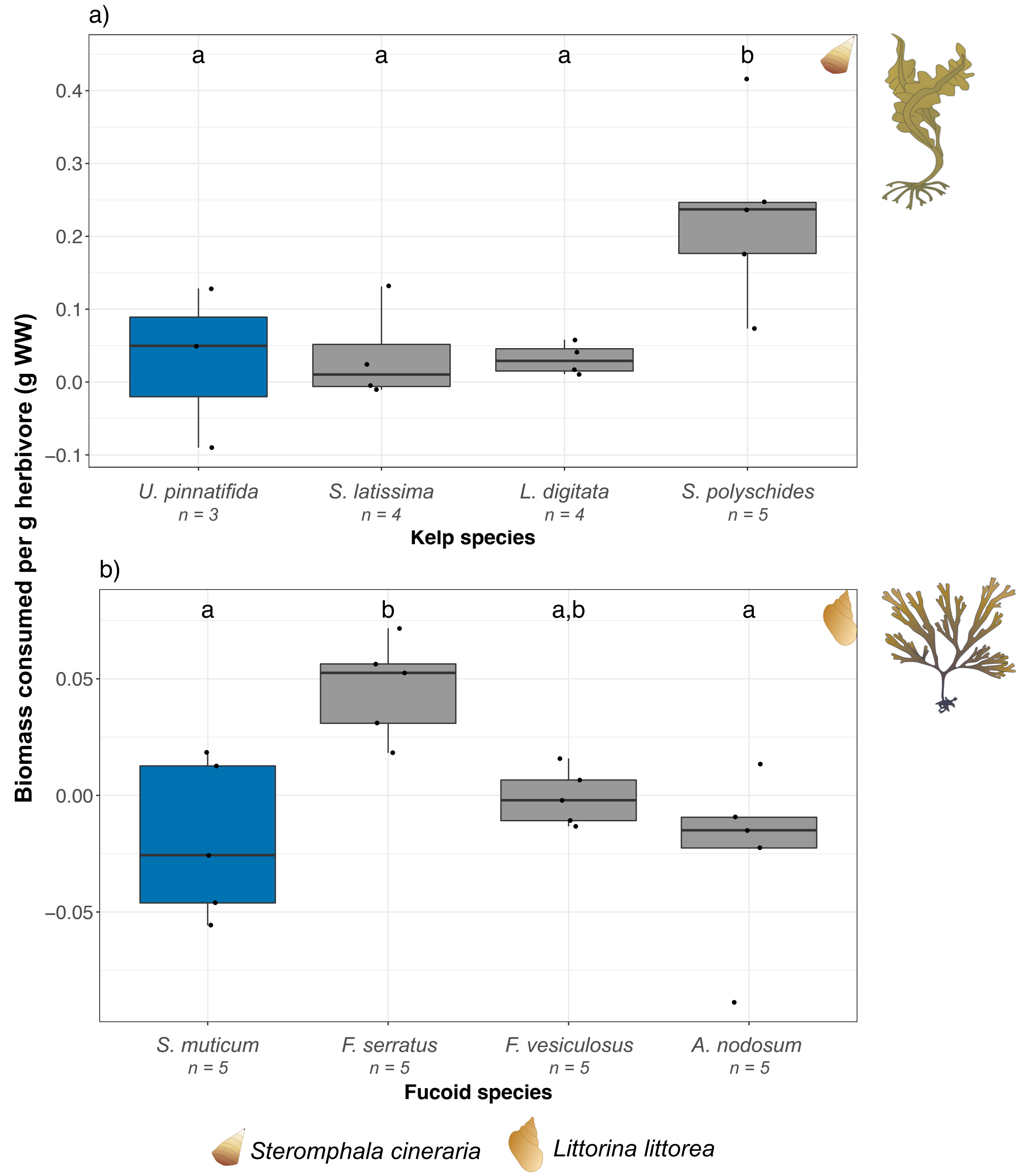

Figure 4.3 Biomass consumed per unit herbivore during no choice tests of invasive (blue) and native (grey) species. Different herbivores were used for a) kelp and b) fucoid species. Different letters indicate significant differences (Tukey post hoc, $p < 0.05$). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby, Diana Kleine, and the Integration and Application Network (ian.umces.edu/symbols/).

4.4.3 Tissue carbon to nitrogen ratio

There was very strong evidence that carbon to nitrogen ratio of the midsection of the thallus differed amongst species for both kelp [$F_{3,36} = 32$, $p < 0.001$] and fucoid species [$F_{3,35} = 15.12$, $p < 0.001$] (Figure 4.4). There was very strong evidence that the invasive *U. pinnatifida* had lower C:N than *S. latissima* ($p<0.001$) and *L. digitata* ($p<0.001$), but no evidence that C:N differed between *U. pinnatifida* and *S. polyschides* ($p=0.656$) (Table 7.19). There was moderate evidence that *U. pinnatifida* had lower C:N than *F. serratus* ($p=0.019$) and *F. vesiculosus* ($p=0.019$), and very strong evidence that *U. pinnatifida* had lower C:N than *A. nodosum* ($p<0.001$) (Table 7.19).

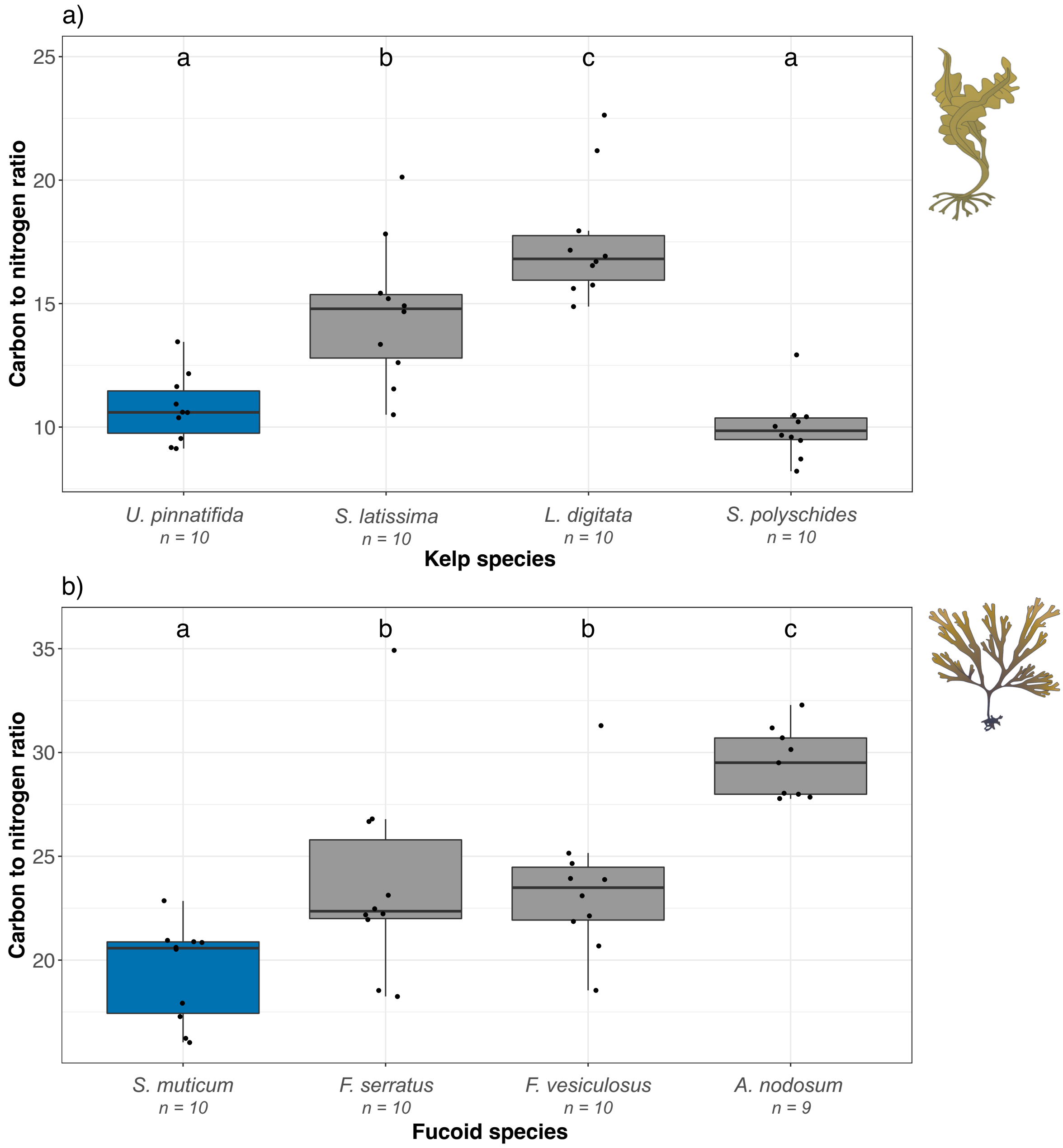

Figure 4.4 Carbon to nitrogen ratio of invasive (blue) and native (grey) seaweed samples of a) kelp and b) fucoid species. Different letters indicate significant differences (Tukey post hoc, $p < 0.05$). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/).

4.4.4 Total polyphenolic concentration

There was very strong evidence that polyphenolic concentrations differed amongst species for both kelp [$F_{3,18}$ = 48.42, p < 0.001] and fucoid species [$F_{3, 20}$ = 9.373, p < 0.001] from samples which were not exposed to herbivory (Figure 4.5). There was very strong evidence that the invasive *U. pinnatifida* had higher percentage dry weight of polyphenolic concentrations than the three native species (p<0.001 for all comparisons) (Table 7.20). Polyphenolic concentrations of *S. muticum* was similar to *F. vesiculosus* (p=0.877) and *A. nodosum* (p=0.484), although there was strong evidence that polyphenolic concentrations of *S. muticum* were higher than *F. serratus* (p=0.003) (Table 7.20). There was no discernible difference between polyphenolic concentrations in the control and treatment samples taken from no-choice experiments for all species (Figure 7.7, Table 7.22).

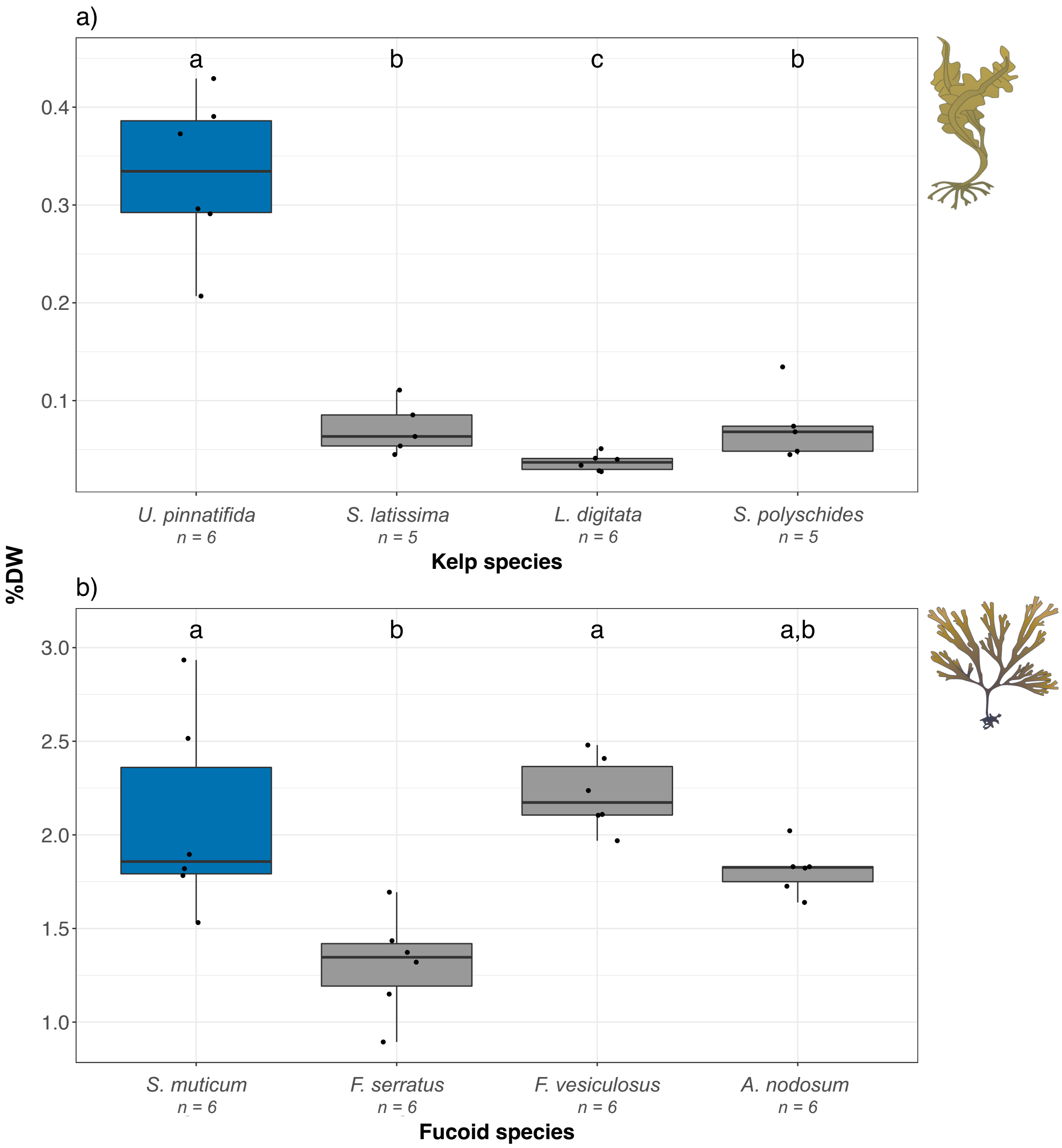

Figure 4.5 Percentage dry weight of polyphenolic of invasive (blue) and native (grey) seaweed samples of a) kelp and b) fucoid species. Different letters indicate significant differences (Tukey post hoc, p < 0.05). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/).

4.4.5 Tensile strength

There was very strong evidence that tensile strength of the midsection of the thallus differed amongst species for both kelp [$H_3 = 25.58$, $P < 0.001$] and fucoid species [$F_{3,33} = 8.556$, $p < 0.001$] (Figure 4.6). Amongst kelp species, there was strong evidence that *U. pinnatifida* was weaker than *S. latissima* (p=0.003) and *L. digitata* (p<0.001), but there was no discernible difference in tensile strength between *U. pinnatifida* and *S. polyschides* (p=0.135) (Table 7.21). There was very strong evidence that *S. muticum* was weaker than *F. vesiculosus* (p<0.001), and weak evidence that *S.* muticum was weaker than *A. nodosum* (p=0.075) (Table 7.21). There was no discernible difference in tensile strength between *S. muticum* and *F. serratus* (p=0.969) (Table 7.21).

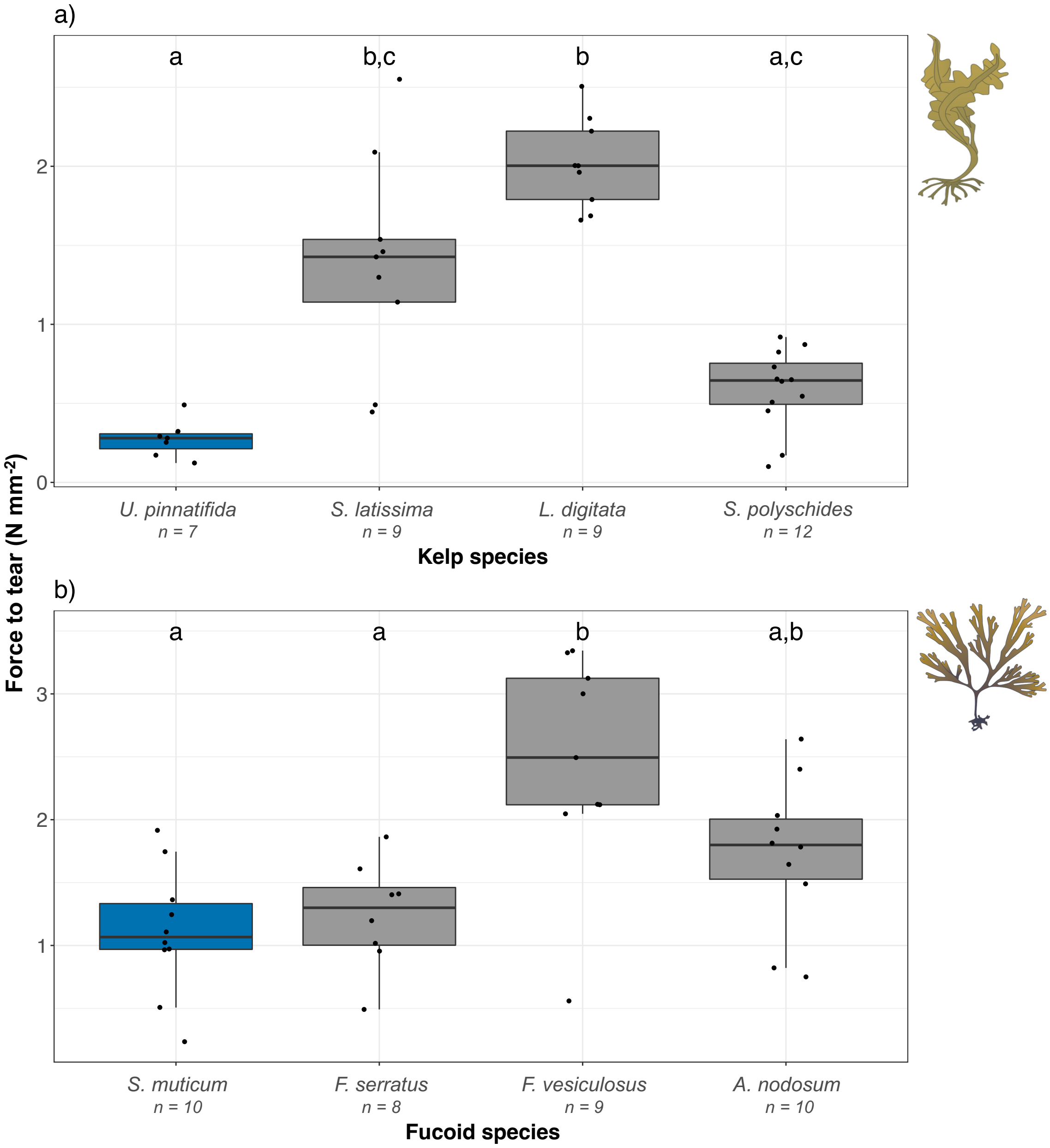

Figure 4.6 Force required to tear invasive (blue) and native (grey) seaweed samples of a) kelp and b) fucoid species. Different letters indicate significant differences (Dunn post hoc (kelp species), Tukey post hoc (fucoid species), $p < 0.05$). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/).

4.4.6 Compensatory growth

There was no evidence that any of the species showed compensatory growth, as in all cases there was no evidence that the percentage change in biomass increased for samples which underwent artificial herbivory, relative to those samples that did not (Figure 7.8-7.9, Table 7.24). In most cases, samples exposed to artificial herbivory decreased in mass more than control samples.

4.5 Discussion

In this study, we found no evidence that these invasive seaweeds experienced a release from consumption by generalist gastropods, and limited evidence that either of these species exhibited different herbivore defence traits relative to native species. Therefore, it is unlikely that the ERH is an important mechanism in facilitating the success of the invasive *U. pinnatifida* and *S. muticum* in this system.

We initially predicted that the invasive species would experience less consumption by native generalist herbivores than comparable seaweeds species from the same coarse functional group (i.e., kelps or fucoids). We found no evidence to support this hypothesis, as there was no discernible difference in the amount of biomass consumed between invasive and the native species of similar functional groups. Therefore, it is unlikely that these invasive species are escaping herbivory from the two generalist gastropod herbivores used in this study. Previous investigations have found that other herbivores, such as amphipods (Jiménez *et al*., 2015), sea urchins (Pedersen *et al*. 2016, Cardoso *et al*. 2020) and other gastropod species (Jiménez *et al*. 2015) also showed no difference in consumption of either *S. muticum* or *U. pinnatifida* compared to native species.

Our second prediction was that traits related to defence against herbivory, specifically tissue C:N, polyphenolic concentration, tensile strength and compensatory growth, would reflect and explain the patterns in consumption observed in the herbivory experiments. Given that in both choice and no choice experiments there was no evidence that invasive species were consumed more or less than native species, it is expected that there would also be no discernible difference amongst invasive and at least one native species for the majority of traits measured. This was true for all traits except for C:N of *S. muticum* for which there was strong evidence it was lower than native species, and polyphenolic concentration of *U. pinnatifida* for which there was strong evidence that it was higher than native species. Overall, these patterns suggest that herbivore consumption is not primarily driven by traits against herbivory, but caveats are noted below.

C:N was measured to investigate the nutritional quality of the seaweeds, where species with lower C:N would have more nitrogen available per unit of food, therefore being more attractive to herbivores (Coviella *et al*. 2002). Given that herbivores are nitrogen limited, it is expected that they would have a preference for seaweeds with low C:N relative to similar species (Mattson 1980, Van Alstyne *et al*. 2001). Despite *S. muticum* having lower C:N relative to the three native fucoid species included in this study, the invasive fucoid was not consumed more, suggesting that C:N does not drive herbivore choice in this system. This is supported by Schwartz *et al*. (2016), who found that herbivores preferred the native species *F. vesiculosus* with high C:N, rather than the invasive *S. muticum* with low C:N in Germany. Amongst the kelp species, there was no discernible difference amongst the invasive *U. pinnatifida* and the native *S. polyschides*, indicating that the invasive species does not have more nitrogen per gram of food than the native species, and thus should not be more palatable.

The second trait investigated in this study was polyphenolic concentration, where high concentrations have been shown to deter herbivory in seaweeds (Steinberg 1984, 1988), and which can also be produced in response to other stressors, such as increased temperatures (Hargrave *et al*. 2017, Mannino and Micheli 2020). *U. pinnatifida* had relatively higher concentrations of polyphenolics compared to the native kelp species. This relative difference was not reported in a study by Cardoso *et al*. (2020), who found *U. pinnatifida* to have similar levels of polyphenolics as *S. polyschides* in a Portuguese population. Given the relatively high levels of polyphenolics detected in *U. pinnatifida* we could expect lower rates of herbivory on the invasive species, but this was not observed. The increased polyphenolic concentration may offset against the other traits that make *U. pinnatifida* more susceptible to herbivory, such as low C:N and low tensile strength which would be predicted to increase the likelihood of consumption (Duffy and Hay 1990, Van Alstyne *et al*. 2001). Higher polyphenolic concentrations could also be a result of increased growth as phlorotannins are incorporated into the cell wall (Arnold and Targett 2003), although this was not observed for *U. pinnatifida* in the compensatory growth tests. Amongst the fucoid species, there was no difference between the invasive *S. muticum* and the majority of the native species. The concentrations of polyphenolics reported in this study are lower than expected and lower than have been reported for the same species elsewhere (Cacabelos *et al*. 2010, Schwartz *et al*. 2016, Cardoso *et al*. 2020). The reasons for this are unclear, but could be due to the inherent variability in polyphenolic concentrations, attributable to seasonality (Ragan and Jensen 1978, Steinberg 1995, Mannino and Micheli 2020), or environmental stressors such as UV radiation (Swanson and Druehl 2002).

The physical properties of seaweeds can also affect their attractiveness to herbivores (Duffy and Hay 1990). Here we used tensile strength to act as proxy for the toughness of seaweeds, with the expectation that seaweeds with lower tensile strength would be consumed more as they would be mechanically easier to consume. Both *U. pinnatifida* and *S. muticum* were in the lower range of tensile strength, but there was little to no evidence that tensile strength was associated with whether the species was invasive or native. The morphological structure of the whole seaweed has also been found to influence herbivory (Steneck and Watling 1982, Duffy and Hay 1990). However, given that the invasive and native species compared in this study were of the same functional groups (kelp or fucoid), it is unlikely that the gross morphological differences would have affected the patterns in consumption found for these herbivores (Enge *et al*. 2017).

Whilst the native seaweed species used in this study were selected due to functional similarities to the invasive seaweeds, some of these native species were a closer match than others. Specifically, *U. pinnatifida* and *S. polyschides* are both short-lived annual species (Teagle et al. 2017) and *S. muticum* and *F. serratus* are abundant canopy forming species (Critchley et al. 1990, Ingólfsson 2008). Whilst there was still no difference in the amount of biomass consumed in the choice tests, both invasive species were consumed significantly less in the no-choice tests than either *S. polyschides* or *F. serratus* respectively. This could be explained by higher polyphenolic concentrations conferring defence to both invasive species, relative to these two native species. However, *S. muticum* was still consumed less in the no-choice tests despite being more palatable than *F. serratus* with a lower C:N ratio. Whilst this does not provide evidence to support the ERH, the difference in trait values between invasive species and functionally similar native species demonstrates the importance of selecting appropriate species for invasive and native comparisons.

A potential explanation for the lack of evidence for the ERH observed in this study is that time-since-invasion was not accounted for. Kurr and Davies (2018) found that grazing rates on *S. muticum* increased with time-since-invasion, suggesting that native marine herbivores may acquire an ability to feed on novel foods over time. The populations of *U. pinnatifida* and *S. muticum* sampled in this study were approximately 16 and 33 years old respectively (based upon the year each species was first recorded in the Plymouth area, which was 2003 (Heiser et al. 2014) and 1976 (Boalch and Potts 1977) respectively). Given that the introduced *U. pinnatifida* population is relatively young, we would expect to find evidence of enemy release even if there was a temporal effect, which we did not observe. It is possible that *S. muticum* experienced reduced herbivory when it was first introduced to the Plymouth area, but either way, we found no evidence that either invasive species is currently benefiting from enemy release, suggesting that any potential benefit of enemy release is relatively temporary.

In conclusion, we did not find evidence to support the ERH as an explanation for the invasion success and proliferation of either *U. pinnatifida* or *S. muticum* in the northeast Atlantic. We believe that the effect sizes and variabilities demonstrated in our data provide strong evidence that our robust experimental approaches provide genuine 'evidence of absence' of effects, and thus these are not merely experimental artefacts or 'absence of evidence'. Whilst there were some exceptions, the traits of the invasive species were generally similar to or greater than those of native species, suggesting that there is no prolonged selection against these traits as we would expect to see if the invasive species were escaping herbivory. Combined with the lack of evidence for escape from herbivory from our choice and no choice experiments, as well as those from similar studies (Jiménez *et al*. 2015, Pedersen *et al*. 2016, Cardoso *et al*. 2020), this makes it unlikely that these invasive species are experiencing enemy release from herbivores. It is more likely that other traits such as fast growth (Norton 1977, Choi *et al*. 2007), thermotolerance (Henkel and Hofmann 2008) and high reproductive output (Casas *et al*. 2008) can better explain the spread of *U. pinnatifida* and *S. muticum* outside of their native ranges.

4.6 Acknowledgements

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Chapter 5 Pathogen inferred to have dispersed thousands of kilometres at sea, infecting multiple keystone kelp species.

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5.1 Abstract

Protistan pathogens have been found to infect populations of some large brown macroalgae. Infection could reduce the ability of macroalgae to withstand hydrodynamic pressures through weakening tissues and reducing flexibility. Widespread mortality of macroalgae if disease outbreaks were to occur could have important flow-on consequences for biodiversity and ecosystem function. Recent discoveries of the protistan pathogen *Maullinia* infecting the ecologically keystone southern bull kelp *Durvillaea* in Chile, Australia, and on Marion Island, raise the possibility that this pathogen is dispersing across ocean basins with buoyant hosts. To determine whether *Maullinia* also infects southern bull kelp in New Zealand, samples of gall-like tissue from *Durvillaea antarctica*, *D. poha*, and *D. willana* were collected from intertidal sites, and genetic analyses (sequencing of partial 18S rRNA) carried out. *Maullinia* infections were detected in all three species of *Durvillaea*. Phylogenetic analyses show a close relationship of New Zealand *Maullinia* to *M. braseltonii* previously detected in Chile and on Marion Island. Based on its genetic similarity to distant lineages and its presence on buoyant hosts that have been shown to drift long distances at seas, we infer that *Maullinia* has dispersed across the Southern Ocean through rafting of infected bull kelp. Understanding the capacity of pathogens to disperse across oceans is critical part of forecasting and managing ecosystem responses to environmental change.

5.2 Introduction

Pathogens can have a major effect on ecosystem processes, and can exercise controls on populations through reducing the biomass and abundance of species, influencing the phenotypes of hosts, and altering species interactions (Price *et al*. 1986, Harvell *et al*. 2002, Groner *et al*. 2016, Fischhoff *et al*. 2020). Despite this, implications of disease have been understudied by ecologists relative to other biotic interactions (Campbell *et al*. 2014).

Parasites and pathogens are common in macroalgae, and whilst not all diseases will go on to disrupt ecosystem processes (Harley *et al*. 2012, Groner *et al*. 2016), when foundational species such as macroalgae are disrupted, it can have disproportionate impacts which cascade through trophic levels and alter habitat functioning (Harvell *et al*. 1999, Schiel 2006, Cohen *et al*. 2018). Such impacts are of particular concern in marine ecosystems where high levels of connectedness can facilitate rapid spread of pathogens over large distances (McCallum *et al*. 2003). Dispersal to new areas is likely to result in novel contact between the pathogen and the host, which could have serious consequences if the hosts have little or no resistance to the unfamiliar pathogen (Harvell *et al*. 2002, Cohen *et al*. 2018). Climate change is predicted to exacerbate the problem, through expanding pathogen ranges and making hosts more susceptible to infection through increased stress (Campbell *et al*. 2011, Kumar *et al*. 2016, Cohen *et al*. 2018). Early monitoring in combination with long term data collection, including assessing disease prevalence, is essential to enable us to effectively respond to and manage disease outbreaks through understanding how host-pathogen interactions vary with climate change and extreme events (Harvell *et al*. 2002, Burge *et al*. 2014, Groner *et al*. 2016).

Maullinia is an intracellular, protistan pathogen genus first described just 20 years ago when it was found on filamentous brown algae in Chile (Maier *et al*. 2000). Thus far, relatively little research has been carried out to understand the ecology of this pathogen, and the potential impact it could have on macroalgal communities. *Maullinia* has been found across the Southern Hemisphere, in Chile, the Falkland Islands, sub-Antarctic islands, and Australia on both filamentous brown algae and on southern bull kelp species (Maier *et al*. 2000, Goecke *et al*. 2012, Blake *et al*. 2017, Murúa *et al*. 2017). *Maullinia* can cause yellowish galls, between 0.5 – 4.0 cm in size (Goecke *et al*. 2012, Blake *et al*. 2017, Murúa *et al*. 2017) to form on southern bull kelp blades. Additionally, *M. ectocarpii* has been found to infect gametophytes of kelp species *Macrocystis* and *Desmarestia*, which could disrupt the life cycle of these keystone kelp species, particularly in a commercial context (Maier *et al*. 2000). Southern bull kelp (*Durvillaea*) are large and ecologically important keystone species occupying intertidal and shallow subtidal zones (Fraser *et al*. 2020). To withstand the wave forces in these dynamic environments, *Durvillaea* species are highly flexible and strong (Kelly and Brown 2000). The formation of galls on the blades of *Durvillaea* could reduce the kelps' elasticity and flexibility, which could affect their health and survival (Goecke *et al*. 2012). *Durvillaea* species provide refuge for understory species, and act as a substratum for diverse epiphyte taxa (Taylor and Schiel 2005). Some species host diverse invertebrate fauna in their holdfasts, many of which depend on the macroalgae for food and habitat. Additionally, stranded *Durvillaea* detritus is an important food source for marine and terrestrial fauna (Jaramillo *et al*. 2006, Dufour *et al*. 2012). These foundational species are essential for the healthy functioning of intertidal ecosystems in the cool-temperate Southern Hemisphere, as well as having important economic and social roles in aquaculture (Murúa *et al*. 2017).

The *Durvillaea* genus includes three buoyant species, whose thalli contain a gas-filled honeycomb structure (Fraser *et al*. 2020). This trait has promoted long-distance dispersal of *Durvillaea* species such as *D. antarctica*, which has been found washed up as drift on coasts thousands – and even tens of thousands – of kilometres away from known source populations (Moore and Cribb 1952, Fraser *et al*. 2011, 2018, Waters *et al*. 2018). These buoyant species are an important mechanism for the dispersal of coastal taxa, as they can transport other organisms with them, such as invertebrates, other algal species, and marine parasites (Thiel and Gutow 2005a, 2005b, Fraser and Waters 2013). Emerging data showing a wide distribution of *Maullinia* across the Southern Hemisphere suggest that *Maullinia* might also disperse with these buoyant hosts. Research into the dispersal of *Maullinia* without host organisms is limited. The life cycle of *Maullinia* does include resting spores (Maier *et al*. 2000, Parodi *et al*. 2010, Goecke *et al*. 2012, Murúa *et al*. 2017), which may be able to survive for periods without the host (Neuhauser *et al*. 2011), but the extent of this is currently unknown, as is its ability to disperse on artificial substrate. Additionally, *M. ectocarpii* has been found to form cysts on sporangia of filamentous seaweeds (Maier *et al*. 2000), but there are no records of *M. ectocarpii* forming cysts on artificial substrate and dispersing in this way. Blake *et al*. (2017) found evidence that a *Maullinia* lineage on buoyant *Durvillaea* in Chile was indistinguishable from a lineage on buoyant *Durvillaea* on the distant sub-Antarctic Marion Island in the Indian Ocean, and that a lineage found on the filamentous alga *Ectocarpus* in Chile was closely related to lineages detected on non-buoyant *Durvillaea* in Australia, suggesting long-distance dispersal had recently occurred. Additionally, *Maullinia* prevalence differed with latitude, suggesting that environmental parameters affect the susceptibility of *Durvillaea* to infection (Blake *et al*. 2017).

New Zealand is a centre of diversity for southern bull kelp species, with several buoyant and non-buoyant species found in the region (Fraser *et al*. 2020). To date, however, *Maullinia* infections have not been recorded from New Zealand bull kelp populations. Given the evidence for long distance dispersal of these marine pathogens around the Southern Hemisphere, we hypothesised that *Maullinia* would also be present in New Zealand. We tested this hypothesis using targeted sampling of tissue from three sympatric but ecologically and morphologically distinct *Durvillaea* species in New Zealand (the buoyant species *D. antarctica* and *D. poha*, and the non-buoyant species *D. willana*), followed by genetic sequencing to test for presence of the pathogen.

5.3 Methodology

5.3.1 Sampling

Sampling was conducted at eight sites on the south-east coast of the South Island, New Zealand, and one site on the North Island near Wellington (Figure 5.1). The majority of the sampling occurred between February and March 2020 with the exception of Taieri Beach and Island Bay which were sampled in March and December 2019, respectively in the intertidal zone of rock platforms (Table 7.25). *Durvillaea poha*, *D. antarctica* and *D. willana* were visually examined for signs of any pathogenic infection such as lesions or galls. 123 tissue samples from individual *Durvillaea* species were collected from infected kelp to test the presence of *Maullinia* via genetic analysis. Samples were either air-dried on a clean paper towel after initial desiccation in high-concentration ethanol, or air dried in an oven at 50°C for several hours, and then stored over silica gel beads.

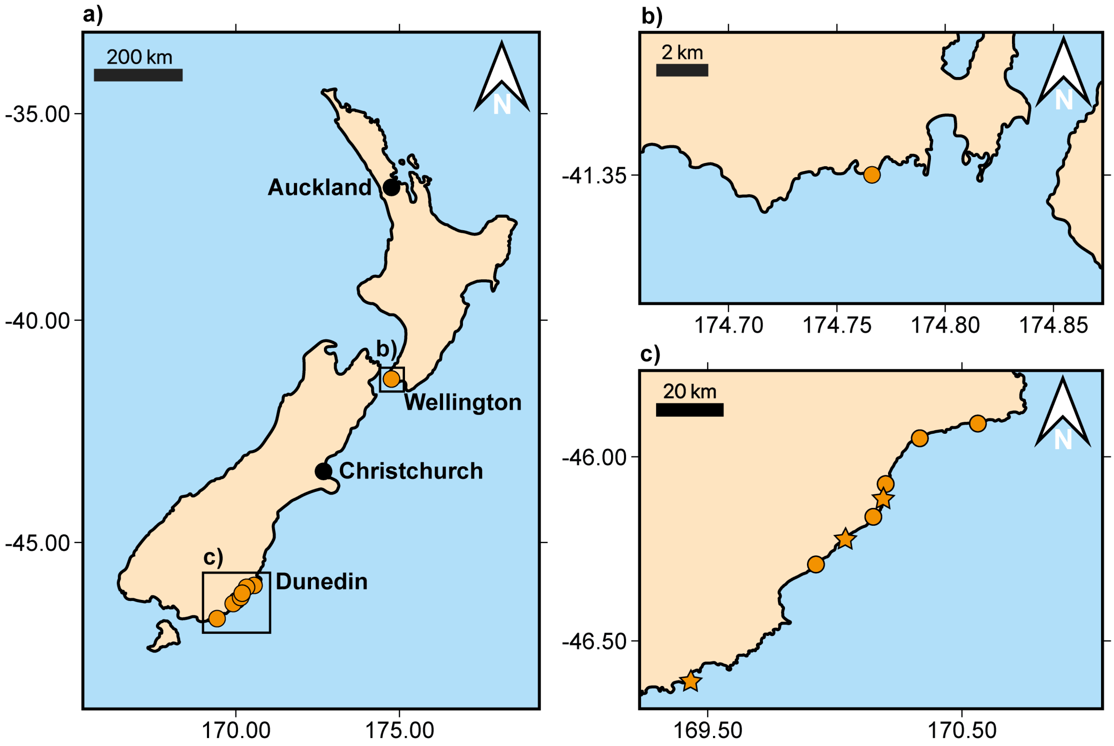

Figure 5.1 Sites in New Zealand where field sampling was conducted in b) one site in the North Island and c) eight sites in the South Island. Stars in panel c) represent sites where *Maullinia* was confirmed from *Durvillaea* hosts.

5.3.2 Genetic analysis

All 123 samples had DNA extracted and underwent PCR. DNA extraction and PCR followed methods described in Blake *et al*. (2017). Small (<2 mm) pieces of infected, dried kelp tissue were excised using a scalpel sterilized with bleach and ethanol, and DNA was extracted using the standard Chelex® protocol (Walsh *et al*. 1991). Extractions were diluted 1:100 in MilliQ water to reduce the likelihood of alginates inhibiting PCR. PCR amplification was conducted in a 20 µl solution, comprising 12.9 µl of MilliQ water, 0.5 µM each of forward and reverse primer (Mau2F and Mau9R: Goecke *et al*. 2012), 4 µl of MyTaq Red Reaction buffer, 0.1 µl of MyTaq Red DNA Polymerase (Bioline), and 1 µl of the diluted DNA extraction. The primers amplified part of the 18S nuclear ribosomal gene. PCRs were run in an Eppendorf Mastercycler using a touchdown PCR protocol: 96°C for 4 min initial denaturation, followed by two cycles of 96°C for 25 s, 65 °C for 25 s and 72°C for 1.5 min followed by two cycles each with a primer annealing temperature of 60°C and 58°C and finally 30 cycles with a primer annealing temperature of 54°C and a final slope of 72°C for 10 min (Goecke *et al*. 2012). PCR products (~1200 bp in size) were purified using gel purification via a MEGAquick-spin™ plus fragment DNA purification kit (iNtRON). Some samples also showed amplification of a smaller fragment (~300 bp); sequencing revealed that these amplicons were from the host (BLAST results showed close match to a part of the 18S marker amplified from *Durvillaea*), suggesting that the primers can sometimes anneal to New Zealand bull kelp DNA. By gel purifying amplicons, we were able to target the pathogen rather than the host. For samples where *Maullinia* sequences were confirmed, COI sequences of the host were subsequently obtained following methods in Fraser *et al*. (2009) to verify host identification, as *D. poha* and *D. antarctica* can sometimes be misidentified in the field. Sequencing was carried out using the forward primer by the University of Otago's Genetic Analysis Services (Otago, New Zealand), using an Applied Biosystems 3730xl capillary sequencer (Thermo Fisher Scientific).

5.3.3 Phylogenetic analysis

Sequences were aligned, and ambiguities assessed by eye using Geneious Prime version 2020.1.1 (Kearse *et al*. 2012). Sequences were trimmed to 764 bases to remove poor-quality sequence tails. Original sequences from Blake *et al*. 2017, and published sequences from known *Maullinia* species (*M. braseltonii*: GenBank accession JX163857, and *M. ectocarpii*, accession AF405547) were aligned with new sequences from this study. A mid-point rooted ML tree was built using PhyML (Guindon *et al*. 2010) via a TRN + I model (best model as assessed by the AICc of jModeltest2: Darriba *et al*. 2012), with the proportion of invariable sites set at 0.809.

5.4 Results and Discussion

The protistan pathogen *Maullinia* was confirmed from three bull kelp species in New Zealand: the buoyant *D. antarctica* (one individual) and *D. poha* (three individuals), and the solid bladed *D. willana* (one individual) (Table 5.1). *Maullinia* was detected at three intertidal sites on the South Island across a coastal distance of >70 km (Figure 5.2) suggesting the pathogen might be widespread, albeit probably at low prevalence, in southern New Zealand. Two sequences of *Maullinia* were detected. The first was detected from one individual of *D. willana*, a non-buoyant bull kelp species, and was identical to the most common sequence of *M. braseltonii* detected from buoyant bull kelp in Chile by Blake *et al*. (2017), lineage MC1 (GenBank accession MF872446) (Figure 5.2). The second sequence was detected from one individual of *D. antarctica* and three individuals of *D. poha* – the two buoyant hosts – and were identical across all sites and samples to each other, but the sequence had not been previously detected elsewhere (GenBank accession MW131091). This lineage is most likely also *M. braseltonii*, as it differed from the other *D. willana*-

associated sequence at only five out of 764 nucleotide sites (<1%; four transitions and two transversions). Both sequences found in this study were highly similar to sequences of *M. braseltonii* detected from buoyant species *D. incurvata* (recently split from *D. antarctica* (Fraser *et al*. 2020)) in Chile, and *D. antarctica* in the sub-Antarctic (Blake *et al*. 2017). That two lineages were detected could indicate multiple past introductions, or perhaps evolution of the pathogen driven by different host tissue types (buoyant, inflated blades versus non-buoyant, solid blades); a larger-scale study could, in future, aim to test such hypotheses.

Table 5.1 *Maullinia* sequences and host *Durvillaea* species with associated GenBank accession numbers and site locations.

***Maullinia* sp.**	**Host *Durvillaea* sp.**	**GenBank accession number**	**Number of samples found**	**Sample site**
M. braseltonii	*D. willana*	MF872446	1	Akatore
M. braseltonii	*D. antarctica* *D. poha*	MW131091	4	Toko Mouth and Tautuku Peninsula

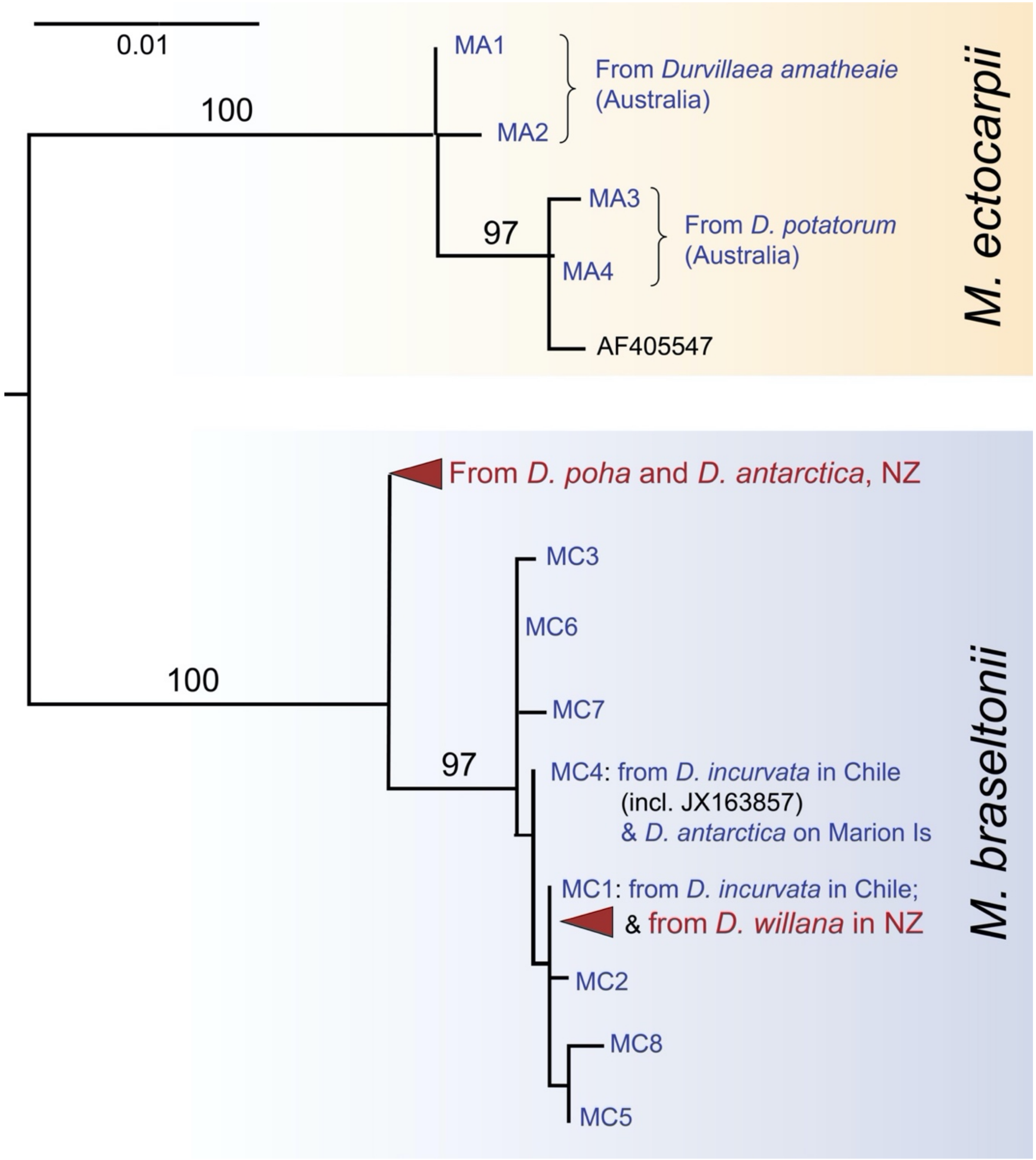

Figure 5.2 Maximum likelihood phylogeny of published and new *Maullinia* partial 18S data. The samples from New Zealand (this study) group with previously detected sequences from southern bull kelp from Chile and the sub-Antarctic. Blue text indicates data from Blake *et al*. (2017) (code MA refers to *Maullinia* detected in Australia, and code MC refers to strains collected from Chile, in that study), and red text indicates sequences from this study. The phylogeny is midpoint-rooted, with bootstrap values >90% shown.

The discovery of *M. braseltonii* on bull kelp in New Zealand and its genetic similarity to geographically distant lineages suggests that *M. braseltonii* could have arrived through long-distance rafting of infected, buoyant kelp, either dispersing from Chile or sub-Antarctic islands to

New Zealand, or vice versa. Further sampling could help to clarify the direction of travel. Our finding supports previous inferences of long-distance dispersal of marine pathogens via rafting with buoyant macroalgae (Fraser and Waters 2013, Blake *et al*. 2017). Blake *et al*. (2017) found *M. ectocarpii* in Australia on bull kelp taxa *D. potatorum* and *D. amatheiae*, so we might have expected to find *M. ectocarpii* in New Zealand (geographically relatively close to Australia), but these solid-bladed *Durvillaea* species are non-buoyant and thus have limited dispersal opportunities (Fraser *et al*. 2020, Hay 2020). In contrast, *M. braseltonii* – which as we show here can infect both buoyant and non-buoyant *Durvillaea* – has now been shown to have a wide geographic range, infecting bull kelp in Chile, Marion Island (sub-Antarctic Indian Ocean) and New Zealand – locations separated by thousands of kilometres of ocean. *Maullinia braseltonii* might also be a more generalist pathogen than *M. ectocarpii*, as the same strain of *M. braseltonii* was found to infect both *D. antarctica* and *D. poha.* In contrast, strains of *M. ectocarpii* appear to be host specific in Australia (Blake *et al*. 2017). The capacity of the pathogen to infect several host species, including both buoyant and non-buoyant taxa in addition to filamentous alga previously found to be infected by *M. ectocarpii* (Maier *et al*. 2000), shows that *Maullinia* is a versatile and generalist pathogen.

From previous reports of *Maullinia* infection of bull kelp, we expected to find yellowish galls to indicate the pathogen’s presence (Goecke *et al*. 2012, Blake *et al*. 2017). None of the bull kelp populations surveyed, however, showed these distinctive galls – instead showing only minor blemishes on host tissue – suggesting that galls are not always indicative of *Maullinia* infections. There might, however, be some seasonality in gall development, or environmental factors that influence the prevalence and manifestation of infections (Schade *et al*. 2016, Ford *et al*. 2018, Honjo *et al*. 2020). With the potential of disease outbreaks to have major impacts on population health and viability, further research is urgently needed to better understand the characteristics of this relatively newly discovered (Goecke *et al*. 2012), but apparently highly dispersive (Blake *et al*. 2017; this study) kelp pathogen.

Maullinia prevalence on bull kelp hosts has been found to vary with latitude and the associated environmental parameters (Blake *et al*. 2017). Infection prevalence increased towards higher latitudes in both Chile and Australia, which could be due to increased population density in southern parts of *Durvillaea*’s range, or it could be that the *Maullinia* pathogen is more prevalent in colder waters (Blake *et al*. 2017), which may mean that increased temperatures could counteract the virulence of this pathogen (Blake *et al*. 2017). However this could be offset by physiological stresses caused by increased temperatures increasing organisms' susceptibility to disease (Case *et al*. 2011, Campbell *et al*. 2011, Beattie *et al*. 2018, Thomsen *et al*. 2019). Predicting how environmental change will affect the prevalence and impacts of *Maullinia* on *Durvillaea* is therefore currently difficult. *Durvillaea* species comprise a large proportion of the macroalgae biomass in coastal ecosystems in New Zealand (Thomsen *et al*. 2019, Hay 2020) and it would be devastating for nearshore marine communities if a disease outbreak were to significantly reduce the biomass of these species (Taylor and Schiel 2005, Jaramillo *et al*. 2006, Dufour *et al*. 2012, Murúa *et al*. 2017). Previous mortality events of *Durvillaea* have led to the increased spread of the highly invasive kelp *Undaria pinnatifida* (Thomsen *et al*. 2019), and the replacement of *Durvillaea* with this species would change the character and functioning of the ecosystem (Stuart 2004, Russell *et al*. 2008).

Understanding the controls of pathogen distributions is essential for monitoring and managing future disease outbreaks. Further assessment of macroalgal populations in New Zealand and elsewhere will be important to determine the virulence and potential risks this pathogen poses for coastal communities.

5.5 Acknowledgements

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Chapter 6 Overview and future research directions

Invasive species are one of the leading causes of global biodiversity loss. Understanding why some species become invasive is essential to control their spread and to mitigate their impacts. Predicting and understanding drivers of biological invasions is a key goal of invasion ecology and functional traits provide a valuable approach for addressing this goal. This thesis provides multiple examples of how traits can be used to investigate invasive species. In this final chapter, I discuss the main findings in relation to the four research objectives of my thesis and put these findings into the context of the wider literature. I then explore the implications of this thesis for future research.

6.1 Main findings and implications

The overarching aim of my thesis was to investigate how traits can be used to understand and generalise processes related to invasiveness, which I achieved through focusing on primary producers from both terrestrial and marine ecosystems. To achieve this aim I focused on four key objectives. Below, I provide brief summaries of how the objectives were met, before detailing the implications of the results and setting them within the context of the wider literature.

6.1.1 Summaries of main findings

Objective 1: assess how traits of terrestrial plants correlate with different ways of defining species invasiveness.

Using a trait database measured from terrestrial plants in Czechia (Kubát *et al*. 2002, Kubešová *et al*. 2010, Moravcová *et al*. 2010), I found that height was the only trait strongly correlated with both a demographic dimension of invasiveness (geographic range size) and the probability of being classified as invasive. Whilst traits were more strongly related to the binary classification than the dimensions of invasiveness, using the four demographic dimensions allowed me to identify several traits and covariates that were not apparent using the binary classification alone (residence time, seedling relative growth rate, and anemochory). Overall, both the demographic dimensions and the binary classification of invasiveness were useful approaches to identify traits associated with invasiveness, and were most useful when the interactions between them were explored.

Objective 2: identify trends and gaps in research that investigates the traits of invasive seaweeds.

A systematic review of the peer-reviewed literature investigating traits of invasive seaweeds showed that there were an increasing number of papers being published in this research area. Overall, 158 species were included in this review, but most studies measured traits from a single invasive species. The most researched traits were morphological and were used to address a wide range of research objectives. The review highlighted that there were relatively few studies from South America, Asia, and Africa, and that biomechanical traits were the least investigated type of trait out of the six categories that I recorded. This review provided an overview of this growing research area and showed how traits of invasive seaweeds were being used to address ecological questions.

Objective 3: determine whether enemy release is likely to be an important mechanism in the success of two invasive seaweed species, and whether any observed enemy release is due to traits associated with defence against herbivory.

Through herbivory experiments and measuring traits related to defence against herbivory for invasive and native seaweed species, I found no evidence that the two focal invasive seaweeds experienced enemy release. There was no difference in the biomass consumed between two invasive and six native seaweeds for either the choice or no-choice tests, and herbivore consumption did not reflect patterns in the traits related to defence against herbivory. Taken together, these findings suggest that other traits such as a high reproductive output (Casas *et al*. 2008), fast growth (Norton 1977, Choi *et al*. 2007), or thermotolerance (Henkel and Hofmann 2008) may contribute to the success of these two invasive seaweeds.

Objective 4: determine how traits of native seaweeds can facilitate the transportation and introduction of invasive species.

Phylogenetic analyses showed a high level of relatedness between pathogen infections in habitat-forming seaweed populations in New Zealand and similar infections found in Chilean seaweed populations. The genetic similarity observed between these distant lineages of pathogens, combined with the pathogens presence on buoyant hosts that have been shown to drift long distances, I inferred that the buoyant seaweed species rafted across the Southern Ocean, transporting pathogens at the same time. Understanding the ability of seaweeds to disperse pathogens across oceans is critical to forecast and manage ecosystem responses to environmental change.

6.1.2 Implications of main findings

The definition of invasiveness used will affect which traits are found to be correlated with invasiveness. As demonstrated in Chapter 2, continuous demographic dimensions can be used to identify traits associated with specific mechanisms of invasiveness, and can also be used to yield insights into how demographic dimensions (abundance, environmental range size, geographic range size, and spread rate) relate to existing binary characteristics. These are not the only continuous metrics which have been used to investigate traits related to invasive species, as previous investigations have used combined population performance measures (Colautti *et al*. 2014), or frequency of occurrence (McGeoch and Latombe 2016, Klinerová *et al*. 2018). However, the dimensions of invasiveness used in Chapter 2 have the advantage of representing demographic processes, and reflect different ways in which invasive species can invade native communities (Fristoe *et al*. 2021, Palma *et al*. 2021b). This approach has so far been focused on terrestrial plants, but could be used to investigate other taxa. Chapter 3 shows that the four dimensions are used as criteria for invasiveness amongst seaweed species. In particular, percentage cover (a measure of abundance) is frequently used as an indication of invasive success, or estimated impact on the native environment (Incera *et al*. 2011, Gennaro *et al*. 2015, Uyà *et al*. 2017, Eggertsen *et al*. 2021). If this information was available for a large number of invasive seaweed species, it could be used to identify common traits associated with this form of invasiveness.

As well as identifying traits associated with different forms of invasiveness, traits can be used to predict and understand biotic interactions between invasive and native species. In Chapter 4, I focus on interactions between two invasive seaweeds and common herbivores by measuring traits related to defence against consumers (carbon to nitrogen ratio, polyphenolic concentration, tensile strength, and compensatory growth). Ultimately, I found no evidence of herbivore escape in this system. This suggests that traits such as thermotolerance (Henkel and Hofmann 2008), fast growth (Norton 1977, Choi *et al*. 2007) or high reproductive output (Casas *et al*. 2008), among other factors, may be more important in explaining invasion success. However, some trait differences were observed amongst native and invasive species, such as higher polyphenolic concentrations in *Undaria pinnatifida*. This could have been caused by physiological processes of the alga (Arnold and Targett 2003), or abiotic conditions (Swanson and Druehl 2002).

Although the enemy release hypothesis is frequently used to explain the success of invasive species, several investigations also found no support for this hypothesis amongst marine seaweeds (Jiménez *et al*. 2015, Pedersen *et al*. 2016, Cardoso *et al*. 2020). Additionally, Cardoso *et al*. (2020) also found that the traits they measured (carbon, nitrogen and phenolic content) did not affect herbivore choice, suggesting that other determinants of herbivore choice may be more important in the systems studied, such as responses to predation (Duffy and Hay 1991). Given the many factors that influence invasion success, using traits to test specific hypotheses, such as enemy release, is an extremely useful approach to understanding biological invasions.

Investigating the traits of native species can yield insights into the interactions and effects that native species have on invasive species, including invasive species dispersal and introduction. By determining the relatedness of seaweed pathogens across the Southern Ocean, I showed that it is highly likely that the trait of buoyancy in the keystone, habitat-forming seaweed genus *Durvillaea* facilitates the dispersal and introduction of the *Maullinia* pathogen across tens of thousands of kilometres. Whilst this is a passive method of dispersal and the *Maullinia* pathogen is not yet invasive in New Zealand, understanding the controls and potential of long-distance dispersal via ocean rafting is essential to predict future species introductions. Fraser *et al*. (2011) found that as well as pathogens, invertebrates were also successfully transported via rafts of buoyant seaweeds. The variety of species transported in this manner increases the potential for species to be introduced, but also for it to facilitate secondary (post-introduction) spread of invasive species. Although not through seaweed rafting, secondary spread of the invasive jellyfish species '*Mnemiopsis leiydi'* has occurred across western Eurasia due to rafting on ocean currents (Jaspers *et al*. 2018). Climate change is also expected to exacerbate the potential effects of dispersal via ocean rafting (Pyšek *et al*. 2020), highlighting how human activities can indirectly affect this method of dispersal. This exacerbation could occur due to changing ocean currents (Thornalley *et al*. 2018), more areas being vulnerable to invasions due to increasing temperatures (Bellard *et al*. 2013, Fraser *et al*. 2018), and increased intensity and frequency of storm events (Sobel *et al*. 2016, Baldini *et al*. 2016). Understanding how traits such as buoyancy facilitate long distance dispersal and subsequent redistribution of species highlights the open system of the marine realm. Integrating the connectivity of ocean systems, and how human activities may affect and change that connectivity, into risk assessments for invasive marine species will be required to mitigate the impact and spread of invasive species (Jaspers *et al*. 2018).

6.2 Directions for future research

One of the benefits of a trait-based approach is that it can be applied across a range of species to explore commonalities without needing to know the exact species or taxonomic composition. Despite this, in Chapter 3 I found that many studies investigating traits of invasive seaweeds measured traits from one invasive species. This is likely due to the lack of available, open access trait data for marine seaweeds. In contrast, terrestrial plants are well studied, which has resulted in a large number of open access trait databases (Kleyer *et al*. 2008, Moravcová *et al*. 2010, Wang *et al*. 2018, Fraser 2020, Chytrý *et al*. 2021). This facilitates large, complex studies, which can use multiple species to draw conclusions, often over large geographic scales (Fristoe *et al*. 2021). Researchers are beginning to collate trait databases for native and invasive seaweed species (see Mauffrey *et al*. (2020)), and as databases increase in size and number, their potential for use in invasive seaweeds research will increase considerably. To accompany this, a standardised guide for the measurement of seaweed traits would be beneficial, as it would facilitate comparisons across species and studies, similar to guides already developed for terrestrial plants (Pérez-Harguindeguy *et al*. 2013) and macrofungi (Dawson *et al*. 2019). Therefore, I recommend that the development of open access trait databases, and guides for trait measurements, are made a priority for invasive seaweed research.

Dimensions of invasiveness are being increasingly used as transparent approaches for hypothesis testing (Palma *et al*. 2021b), and are providing important insights into how traits are associated with different forms of invasiveness (Catford *et al*. 2016, Fristoe *et al*. 2021, Palma *et al*. 2021b). Given the proven potential of this approach, applying it to other taxa, particularly other primary producers, would be a promising area of research, and could be used to test whether generalisations hold across ecosystems and taxa.

Finally, this thesis highlights some of the varied causes and drivers of invasions which can be investigated using species traits, but biological invasions are highly context dependent. Reliably predicting how trait-invasion relationships, and indeed invasions more generally, vary predictably with context (de Moura Queirós *et al*. 2011, Latombe *et al*. 2019, Sapsford *et al*. 2020, Catford *et al*. 2022), will likely require a holistic approach. An interesting area of work in this regard are invasion syndromes (Kueffer *et al*. 2013). This concept aims to combine introduction pathways, non-native species traits, and characteristics of the recipient ecosystem, collectively resulting in predictable impacts and dynamics that can be managed with management and policy actions (Novoa *et al*. 2020). This approach can be applied across taxa and ecosystems and provides a dynamic and systematic method to integrate species traits within the wider context of biological invasions, providing a promising direction of future research.

6.3 Concluding remarks

This thesis highlights the many ways in which traits can be used to understand and generalise processes related to invasiveness across multiple ecosystems. This included investigating how traits are associated with different forms of invasiveness, how traits can yield insights into biotic interactions between invasive and native species, and summarising the varied research studying traits of invasive seaweeds. Using species traits to explain and predict biological invasions will be an increasingly important approach to mitigate and prevent the impacts of invasive species across the globe.

Chapter 7 Appendices

7.1 Appendices for Chapter 2

Table 7.1 List of variables used to calculate environmental range size, and their sources.

Variable group	Variable	Source
Soil properties	Soil calcium carbonate ($g \cdot kg^{-1}$)	(Ballabio *et al*. 2019)
	Soil cation exchange capacity ($cmol \cdot kg^{-1}$)	(Ballabio *et al*. 2019)
	Soil carbon to nitrogen ratio	(Ballabio *et al*. 2019)
	Soil nitrogen ($g \cdot kg^{-1}$)	(Ballabio *et al*. 2019)
	Soil phosphorus ($mg \cdot kg^{-1}$)	(Ballabio *et al*. 2019)
	Soil pH in $CaCl_2$	(Ballabio *et al*. 2019)
	Soil pH in H_2O to $CaCl_2$ ratio	(Ballabio *et al*. 2019)
	Soil pH in H_2O	(Ballabio *et al*. 2019)
Temperature and precipitation	Annual Mean Temperature	(Fick & Hijmans, 2017) - WorldClim
	Mean Diurnal Range (Mean of monthly (max temp - min temp))	(Fick & Hijmans, 2017) - WorldClim
	Isothermality (Mean Diurnal Range / Temperature Annual Range) (×100)	(Fick & Hijmans, 2017) - WorldClim
	Temperature Seasonality (standard deviation ×100)	(Fick & Hijmans, 2017) - WorldClim
	Max Temperature of Warmest Month	(Fick & Hijmans, 2017) - WorldClim
	Min Temperature of Coldest Month	(Fick & Hijmans, 2017) - WorldClim
	Temperature Annual Range (Max Temperature of Warmest Month - Min Temperature of Coldest Month)	(Fick & Hijmans, 2017) - WorldClim
	Mean Temperature of Wettest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Mean Temperature of Driest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Mean Temperature of Warmest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Mean Temperature of Coldest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Annual Precipitation	(Fick & Hijmans, 2017) - WorldClim
	Precipitation of Wettest Month	(Fick & Hijmans, 2017) - WorldClim
	Precipitation of Driest Month	(Fick & Hijmans, 2017) - WorldClim
	Precipitation Seasonality (Coefficient of Variation)	(Fick & Hijmans, 2017) - WorldClim
	Precipitation of Wettest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Precipitation of Driest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Precipitation of Warmest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Precipitation of Coldest Quarter	(Fick & Hijmans, 2017) - WorldClim
	Average rainfall (1986 – 2000)	Czech Hydrometeorological Institute (https://www.chmi.cz/)
	Average temperature (1986 – 2000)	Czech Hydrometeorological Institute (https://www.chmi.cz/)
	Vegetation growing season length 2000- 2016	European Environment Agency (https://www.eea.europa.eu/data-and-maps/data/annual-above-ground-vegetation-season)

Variable group	Variable	Source
Land use	Richness of forest-related species and habitats indicator (2012 dataset)	European Environment Agency (https://www.eea.europa.eu/data-and-maps/data/richness-of-forest-related-species)
	Evergreen/Deciduous Needleleaf Trees	(Tuanmu and Jetz 2014) EarthEnv
	Deciduous Broadleaf Trees	(Tuanmu and Jetz 2014) EarthEnv
	Mixed/Other Trees	(Tuanmu and Jetz 2014) EarthEnv
	Shrubs	(Tuanmu and Jetz 2014) EarthEnv
	Herbaceous Vegetation	(Tuanmu and Jetz 2014) EarthEnv
	Cultivated and Managed Vegetation	(Tuanmu and Jetz 2014) EarthEnv
	Regularly Flooded Vegetation	(Tuanmu and Jetz 2014) EarthEnv
	Urban/Built-up	(Tuanmu and Jetz 2014) EarthEnv
	Snow/Ice	(Tuanmu and Jetz 2014) EarthEnv
	Barren	(Tuanmu and Jetz 2014) EarthEnv
	Open water	(Tuanmu and Jetz 2014) EarthEnv
	Population (km^2)	Czech Statistical Office (https://vdb.czso.cz)

Table 7.2 Results of a logistic regression to test the probability of a species being classified as invasive dependent on their estimated values for the four dimensions of invasiveness.

Variables	β	Std. error	p
(Intercept)	-0.218	0.458	0.635
Geographic range	-0.857	1.201	0.476
Environmental range	0.213	0.862	0.805
Local abundance	0.476	1.025	0.642
Spread rate	2.275	1.421	0.109
Model fit	**R^2**		
Theoretical	0.302		
Delta	0.237		

Table 7.3 Eigen value, factor scores and contribution of the principal component axes to variation in different dimensions of invasiveness. Transformations of each dimension are shown in brackets. The first two axes are shown in Figure 2.3.

Components	PC1	PC2	PC3	PC4
Eigen value	1.78	1.28	0.65	0.29
Variance (%)	44.56	31.91	16.34	7.18
Cumulative variance (%)	44.56	76.48	92.82	100.00
Geographic range size (Tukey)	10.24	45.94	28.71	15.12
Environmental range size	4.99	46.72	48.02	0.28

Local abundance (Logit)	38.17	5.81	23.09	32.93
Maximum spread rate (Tukey)	46.61	1.54	0.18	51.67

Table 7.4 Results of Bayesian linear mixed models used to explore the relationship between geographic range size and the traits and covariates (as shown in Table 2.1) of non-native herbaceous plants, with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) **Full model** (n=87)				b) **Model selection** (n=87)			
Fixed effects	β	**Std. error**	**t value**	**p**	β	**Std. error**	**t value**	**p**
(Intercept)	0.021	0.094	0.218	0.828	0.010	0.056	0.169	0.866
Residence time	0.368	0.108	3.398	0.001	0.355	0.100	3.562	0.001
Propagule weight	-0.230	0.191	-1.204	0.232	NA	NA	NA	NA
Height	0.094	0.158	0.597	0.552	NA	NA	NA	NA
Fecundity	-0.014	0.158	-0.087	0.931	NA	NA	NA	NA
Vegetative reproduction (yes)	-0.068	0.148	-0.458	0.649	NA	NA	NA	NA
Maximal germination	-0.172	0.120	-1.436	0.155	NA	NA	NA	NA
Seedling relative growth rate	0.107	0.147	0.729	0.468	NA	NA	NA	NA
Life history (perennial)	0.014	0.144	0.099	0.921	NA	NA	NA	NA
Introduction (deliberate)	0.015	0.127	0.121	0.904	NA	NA	NA	NA
Random effects	**Variance**	**Std. dev.**			**Variance**	**Std. dev.**		
Genus	0.101	0.318			0.093	0.305		
Residual	0.141	0.376			0.142	0.377		
Model fit	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**
	157.951	187.542	0.172	0.517	129.634	139.497	0.118	0.466

Table 7.5 Results of Bayesian linear mixed models used to explore the relationship between environmental range size and the traits and covariates (as shown in Table 2.1) of non-native herbaceous plants, with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) **Full model** (n=87)				b) **Model selection** (n=87)			
Fixed effects	$\boldsymbol{\beta}$	**Std. error**	**t value**	**p**	$\boldsymbol{\beta}$	**Std. error**	**t value**	**p**
(Intercept)	-0.003	0.096	-0.034	0.973	-0.006	0.056	-0.114	0.910
Seedling relative growth rate	0.280	0.154	1.818	0.073	0.273	0.114	2.396	0.019
Maximal germination	-0.187	0.137	-1.367	0.176	-0.181	0.110	-1.637	0.105
Height	-0.168	0.167	-1.005	0.318	NA	NA	NA	NA
Fecundity	0.176	0.162	1.086	0.281	NA	NA	NA	NA
Genome size	0.025	0.130	0.195	0.846	NA	NA	NA	NA
Propagule weight	0.170	0.196	0.868	0.388	NA	NA	NA	NA
Seedling establishment	0.106	0.130	0.817	0.417	NA	NA	NA	NA
Residence time	0.025	0.117	0.211	0.833	NA	NA	NA	NA
Life history (perennial)	-0.002	0.142	-0.018	0.986	NA	NA	NA	NA
Introduction (deliberate)	0.001	0.141	0.010	0.992	NA	NA	NA	NA
Random effects	**Variance**	**Std. dev.**			**Variance**	**Std. dev.**		
Genus	0.053	0.230			0.046	0.215		
Residual	0.208	0.456			0.197	0.444		
Model fit	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**
	170.530	202.586	0.100	0.283	139.096	151.426	0.076	0.252

Table 7.6 Results of Bayesian linear mixed models used to explore the relationship between local abundance and the traits and covariates (as shown in Table 2.1) of non-native herbaceous plants, with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) Full model (n=71)				**b) Model selection** (n=71)			
Fixed effects	β	**Std. error**	**t value**	**p**	β	**Std. error**	**t value**	**p**
(Intercept)	0.008	0.079	0.103	0.918	-0.013	0.064	-0.202	0.841
Height	0.379	0.166	2.284	0.026	0.302	0.123	2.450	0.017
Fecundity	-0.007	0.166	-0.040	0.968	NA	NA	NA	NA
Vegetative reproduction (yes)	-0.074	0.155	-0.476	0.636	NA	NA	NA	NA
Propagule weight	-0.141	0.211	-0.667	0.507	NA	NA	NA	NA
Maximal germination	-0.070	0.132	-0.532	0.597	NA	NA	NA	NA
Seedling relative growth rate	-0.002	0.163	-0.015	0.988	NA	NA	NA	NA
Residence time	0.125	0.130	0.957	0.342	NA	NA	NA	NA
Random effects	**Variance**	**Std. dev.**			**Variance**	**Std. dev.**		
Genus	0.115	0.339			0.098	0.314		
Residual	0.145	0.381			0.143	0.379		
Model fit	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**
	131.625	154.252	0.109	0.503	109.078	118.129	0.086	0.458

Table 7.7 Results of Bayesian linear mixed models used to explore the relationship between maximum spread rate and the traits and covariates (as shown in Table 2.1) of non-native herbaceous plants, with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) **Full model** (n=35)				b) **Model selection** (n=35)			
Fixed effects	**β**	**Std. error**	**t value**	**p**	**β**	**Std. error**	**t value**	**p**
(Intercept)	-0.025	0.088	-0.279	0.782	-0.027	0.086	-0.308	0.760
1/Anemochory	0.383	0.223	1.721	0.096	0.358	0.174	2.053	0.049
Height	0.111	0.193	0.575	0.570	NA	NA	NA	NA
Fecundity	-0.026	0.223	-0.117	0.908	NA	NA	NA	NA
Random effects	**Variance**	**Std. dev.**			**Variance**	**Std. dev.**		
Genus	0.118	0.343			0.119	0.344		
Residual	0.127	0.357			0.116	0.341		
Model fit	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**	**R^2 marginal**	**R^2 conditional**
	64.142	73.474	0.125	0.545	57.710	63.932	0.120	0.565

Table 7.8 Results of Bayesian logistic mixed models used to explore the relationship between a binary classification of invasiveness (invasive or non-invasive) and the traits and covariates of non-native herbaceous plants selected to explain geographic range size (as shown in Table 2.1), with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) **Full model** (n=87)					b) **Model selection** (n=87)				
Fixed effects	**β**	**Std. error**	**z value**	**p**		**β**	**Std. error**	**z value**	**p**	
(Intercept)	-0.980	0.630	-1.555	0.120		-0.742	0.561	-1.322	0.186	
Height	3.215	1.467	2.192	0.028		3.657	1.394	2.624	0.009	
Vegetative reproduction (yes)	1.847	1.184	1.561	0.119		1.323	0.980	1.350	0.177	
Seedling relative growth rate	1.215	0.949	1.279	0.201		0.880	0.745	1.182	0.237	
Residence time	0.919	0.794	1.158	0.247		0.894	0.770	1.160	0.246	
Life history (perennial)	-2.318	1.213	-1.911	0.056		-2.061	1.089	-1.892	0.059	
Fecundity	0.711	1.064	0.668	0.504		NA	NA	NA	NA	
Propagule weight	0.738	1.172	0.630	0.529		NA	NA	NA	NA	
Maximal germination	-0.469	0.885	-0.530	0.596		NA	NA	NA	NA	
Introduction (deliberate)	0.456	0.935	0.487	0.626		NA	NA	NA	NA	
Random effects	**Variance**	**Std. dev.**				**Variance**	**Std. dev.**			
Genus	1.564	1.250				1.735	1.317			
Model fit	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**
	109.006	136.131	**Theoretical**	0.428	0.612	102.174	119.435	**Theoretical**	0.406	0.611
			Delta	0.368	0.527			**Delta**	0.349	0.525

Table 7.9 Results of Bayesian logistic mixed models used to explore the relationship between a binary classification of invasiveness (invasive or non-invasive) and the traits and covariates of non-native herbaceous plants selected to explain environmental range size (as shown in Table 2.1), with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) **Full model** (n=87)				b) **Model selection** (n=87)			
Fixed effects	***β***	**Std. error**	**z value**	**p**	***β***	**Std. error**	**z value**	**p**
(Intercept)	-0.788	0.617	-1.276	0.202	-0.638	0.515	-1.239	0.215
Height	3.484	1.617	2.155	0.031	3.314	1.184	2.799	0.005
Seedling relative growth rate	1.308	1.005	1.302	0.193	0.924	0.707	1.307	0.191
Residence time	1.071	0.815	1.314	0.189	1.007	0.730	1.379	0.168
Life history (perennial)	-1.518	0.982	-1.546	0.122	-1.334	0.794	-1.680	0.093
Fecundity	-0.120	1.025	-0.117	0.907	NA	NA	NA	NA
Genome size	-0.529	0.831	-0.637	0.524	NA	NA	NA	NA
Propagule weight	0.260	1.193	0.218	0.828	NA	NA	NA	NA
Seedling establishment	0.678	0.897	0.756	0.450	NA	NA	NA	NA
Maximal germination	-0.292	0.887	-0.329	0.742	NA	NA	NA	NA
Introduction (deliberate)	0.349	0.973	0.359	0.720	NA	NA	NA	NA
Random effects	**Variance**	**Std. dev.**			**Variance**	**Std. dev.**		
Genus	1.704	1.305			1.403	1.184		

	a) Full model (n=87)					**b) Model selection** (n=87)				
Model fit	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**
	112.951	142.542	**Theoretical**	0.413	0.614	102.089	116.884	**Theoretical**	0.379	0.565
			Delta	0.356	0.528			**Delta**	0.321	0.477

Table 7.10 Results of Bayesian logistic mixed models used to explore the relationship between a binary classification of invasiveness (invasive or non-invasive) and the traits and covariates of non-native herbaceous plants selected to explain local abundance (as shown in Table 2.1), with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) **Full model** (n=71)					b) **Model selection** (n=71)				
Fixed effects	***β***	**Std. error**	**z value**	**p**		***β***	**Std. error**	**z value**	**p**	
(Intercept)	-1.457	0.676	-2.156	0.031		-1.046	0.422	-2.482	0.013	
Height	2.978	1.410	2.113	0.035		3.198	1.078	2.967	0.003	
Seedling relative growth rate	0.962	0.975	0.987	0.324		0.650	0.682	0.953	0.340	
Fecundity	0.745	1.055	0.706	0.480		NA	NA	NA	NA	
Vegetative reproduction (yes)	0.918	1.013	0.907	0.365		NA	NA	NA	NA	
Propagule weight	1.185	1.279	0.926	0.355		NA	NA	NA	NA	
Maximal germination	0.304	0.865	0.351	0.726		NA	NA	NA	NA	
Residence time	0.916	0.909	1.008	0.314		NA	NA	NA	NA	
Random effects	**Variance**	**Std. dev.**				**Variance**	**Std. dev.**			
Genus	1.544	1.243				0.905	0.951			
Model fit	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**
	93.229	113.593	**Theoretical**	0.409	0.598	85.292	94.343	**Theoretical**	0.372	0.508
			Delta	0.359	0.524			**Delta**	0.318	0.433

Table 7.11 Results of Bayesian logistic mixed models used to explore the relationship between a binary classification of invasiveness (invasive or non-invasive) and the traits and covariates of non-native herbaceous plants selected to explain maximum spread rate (as shown in Table 2.1), with genus fitted as a random effect. The results from a) the full model and b) the best fitting model after model selection using AIC are shown.

	a) **Full model** (n=35)					b) **Model selection** (n=35)				
Fixed effects	**β**	**Std. error**	**z value**	**p**		**β**	**Std. error**	**z value**	**p**	
(Intercept)	-0.425	0.727	-0.584	0.559		-0.426	0.719	-0.593	0.553	
Height	3.311	2.635	1.257	0.209		3.317	2.646	1.254	0.210	
Fecundity	-0.360	1.610	-0.223	0.823		-0.349	1.302	-0.268	0.789	
1/Anemochory	0.019	1.670	0.011	0.991		NA	NA	NA	NA	
Random effects	**Variance**	**Std. dev.**				**Variance**	**Std. dev.**			
Genus	3.623	1.903				3.67	1.916			
Model fit	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**	**AIC**	**BIC**		**R^2 marginal**	**R^2 conditional**
	53.672	61.449	**Theoretical**	0.271	0.653	51.691	57.913	**Theoretical**	0.271	0.656
			Delta	0.251	0.605			**Delta**	0.251	0.607

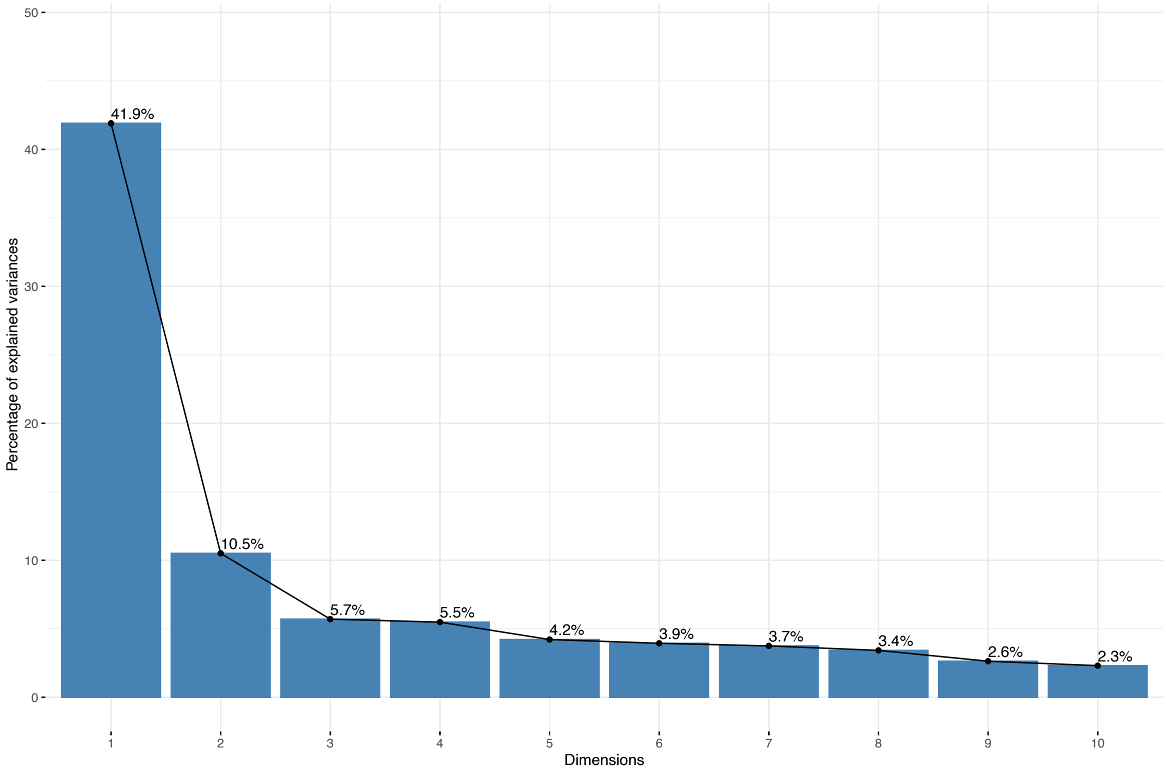

Figure 7.1 Scree plot of a PCA analysis using 43 variables of environmental conditions from Czechia (Table 7.1) to characterise environmental range size. The first nine variables of the PCA analysis explain 81.55% of the variation in environmental range size.

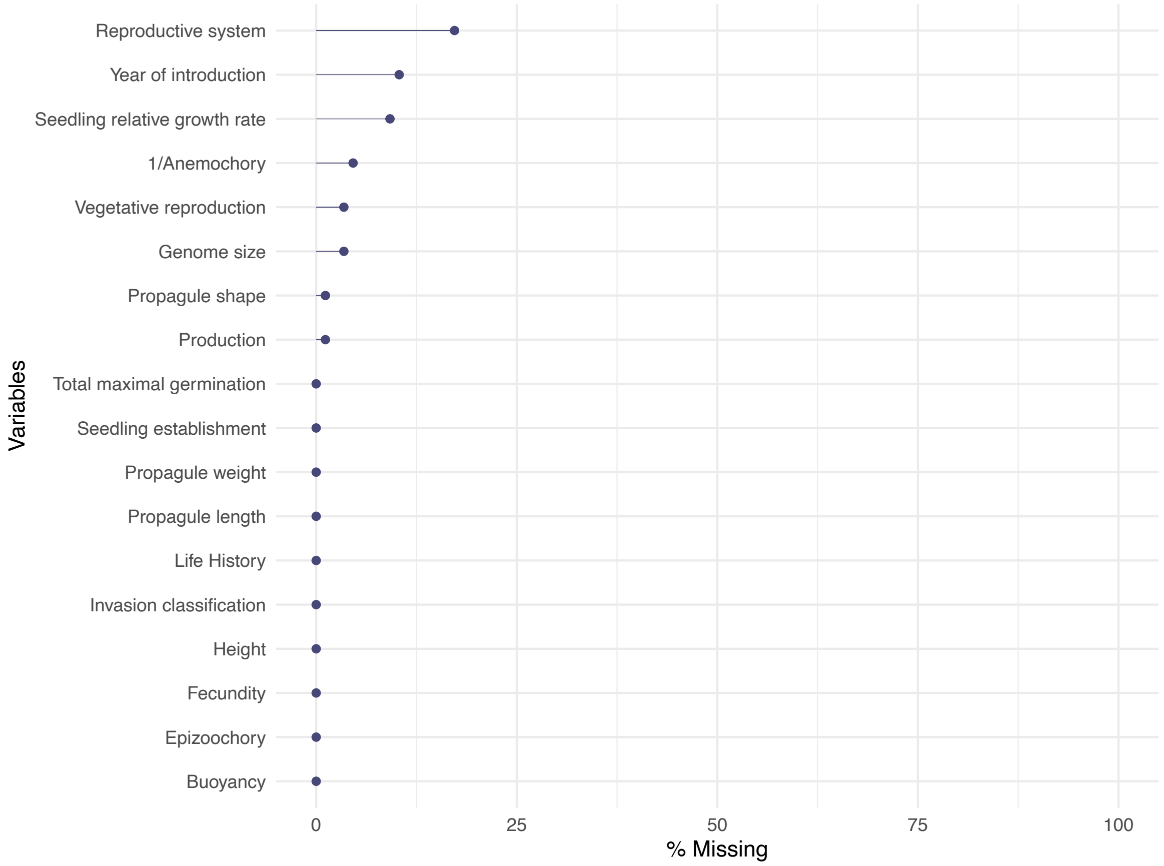

Figure 7.2 Percentage of missing data that was imputed for the traits included in this study.

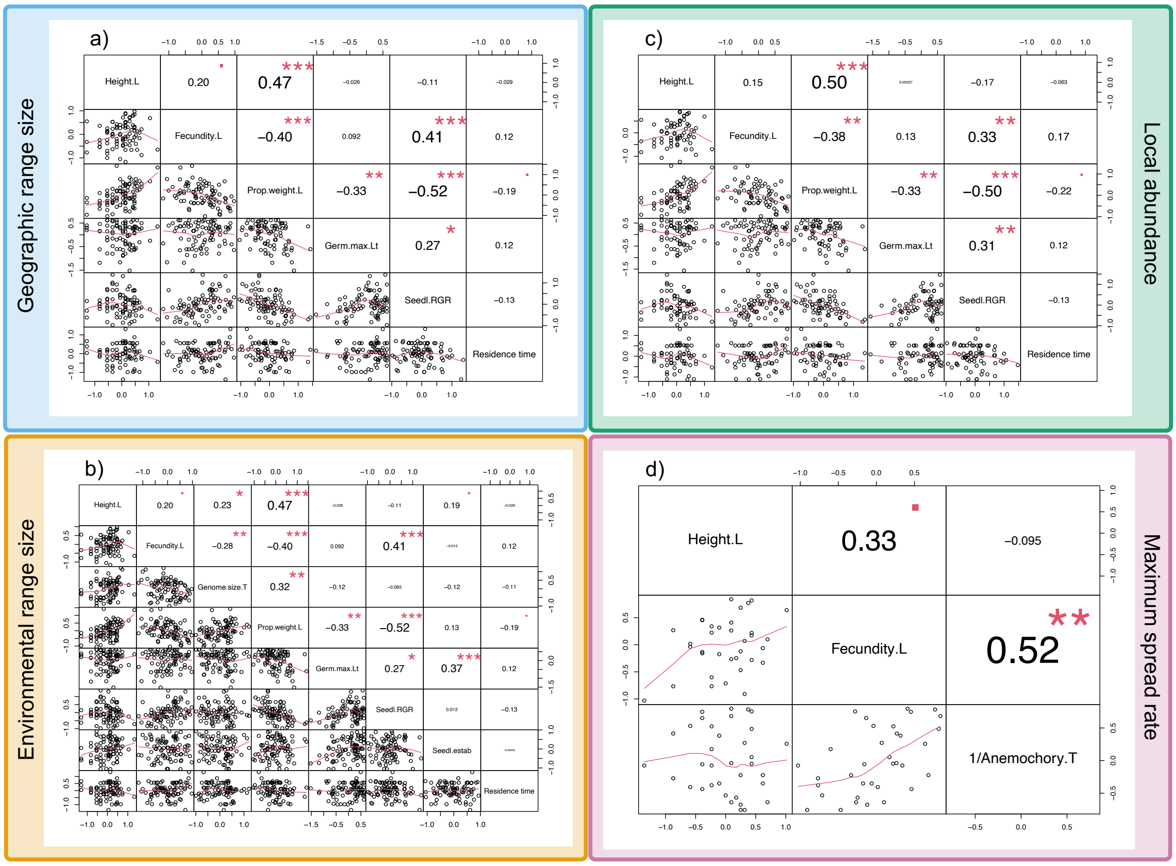

Figure 7.3 Pearson's correlation coefficients among continuous traits and covariates included in Bayesian mixed models with either a) geographic range size, b) environmental range size, c) local abundance, or d) maximum spread rate as the dependent variable. All variables have been centred and standardised, and transformations are shown (T = Tukey's ladder of powers, L = log, and Lt = logit). Significance is shown by asterisk, where ***p<0.0001, **p<0.001, *p<0.05, ·p<0.1.

7.2 Appendices for Chapter 3

Table 7.12 Web of Science categories included and excluded from 21st January 2021 search.

Included	#	Excluded	#
Virology	50	Social work	1
Acoustics	68	Religion	1
Physical geography	112	Rehabilitation	1
Mechanics	114	Otorhinolaryngology	1
Polymer science	143	Literature	1
Geography	207	Ethnic studies	1
Computer science	158	Emergency medicine	1
Mycology	156	Biomedical social sciences	1
Microscopy	175	Art	1
Entomology	291	Architecture	1

Included	#	Excluded	#
Parasitology	304	Women’s studies	2
Physical sciences other topics	369	Psychiatry	2
Pathology	323	Operations research management science	2
Immunology	320	Nursing	2
Palaeontology	527	Film radio television	2
Business economics	484	Family studies	2
Geology	609	Cultural studies	2
Biophysics	450	Criminology penology	2
Food science technology	503	Transplantation	3
Reproductive biology	612	Mineralogy	3
Spectroscopy	505	Linguistics	3
Mathematics	624	Arts humanities other topics	3
Behavioural sciences	663	Transportation	4
Instruments instrumentation	563	Rheumatology	4
Mathematical computational biology	648	Philosophy	4
Crystallography	550	Anaesthesiology	5
Infectious disease	596	Robotics	7
Energy fuels	628	Allergy	6
Optics	646	Construction building technology	10
Anatomy morphology	926	Urban studies	9
Pharmacology pharmacy	827	Orthopedics	9
Evolutionary biology	889	Legal medicine	11
Oceanography	1082	Obstetrics gynecology	10
Fisheries	1074	International relations	13
Meteorology atmospheric sciences	1332	History philosophy of science	11
Toxicology	1273	Sport science	15
Cell biology	1125	Ophthalmology	13
Developmental biology	1575	Pediatrics	14
Microbiology	1504	Surgery	16
Biotechnology applied microbiology	1471	Metallurgy metallurgical engineering	16
Public environmental occupational health	1697	Integrative complementary medicine	17
Water resources	2148	Mining mineral processing	20
Chemistry	1653	Tropical medicine	20
Agriculture	1964	Social issues	20
Physiology	1959	Public administration	21
Material science	1680	Dentistry oral surgery medicine	22
Physics	1833	Astronomy astrophysics	20
Genetics heredity	1927	Urology nephrology	21
Nutrition dietetics	2433	Medical informatics	23
Science technology other topics	2177	Geriatrics gerontology	28
Engineering	2257	Automation control systems	34
Biodiversity conservation	3391	Imaging science photographic technology	36

Included	#	Excluded	#
Life sciences biomedicine other topics	3604	Thermodynamics	35
Biochemistry molecular biology	3957	Demography	38
Plant sciences	4811	Sociology	42
Zoology	5321	Communication	43
Marine freshwater biology	8500	Nuclear science technology	44
Environmental sciences ecology	9782	Archaeology	53
Remote sensing	22	General internal medicine	44
Forestry	324	Dermatology	47
		Education educational research	46
		Telecommunications	47
		Research experimental medicine	51
		Psychology	59
		Respiratory system	57
		Health care sciences research	60
		Electrochemistry	60
		Social sciences other topics	78
		Government law	72
		Hematology	66
		History	74
		Information science library science	94
		Cardiovascular system cardiology	75
		Anthropology	109
		Geochemistry geophysics	139
		Neuroscience neurology	98
		Radiology nuclear medicine medical imaging	112
		Medical laboratory technology	116
		Oncology	122
		Gastroenterology hepatology	186
		Veterinary sciences	196
		Endocrinology metabolism	691

Table 7.13 The journals included in this review, and the number of papers published in each journal.

Journal	Number of papers
Algae	1
Algal Research	1
Algal Research-Biomass Biofuels and Bioproducts	1
Antioxidants	1
Applied Sciences-Basel	1
Aquatic Biology	2
Aquatic Botany	12
Aquatic Conservation-Marine and Freshwater Ecosystems	1
Aquatic Invasions	3

Journal	Number of papers
Aquatic Living Resources	2
Aquatic Toxicology	1
Archives of Environmental Contamination and Toxicology	1
Biochemical Systematics and Ecology	1
BioInvasions Records	3
Biological Conservation	1
Biological Invasions	19
Biology and Environment-Proceedings of the Royal Irish Academy	2
Biosystems	1
BMC Ecology	1
Botanic Marina	35
Botanical Journal of Scotland	1
Brazilian Journal of Oceanography	1
British Phycological Journal	1
Chemical Engineering Journal	1
Chemosphere	1
Ciencias Marinas	1
Comptes Rendus de L’Academie des Sciences Serie III-Sciences de la Vie-Life Sciences	1
Continental Shelf Research	2
Coral Reefs	4
Cryptogamie Algologie	4
Current Science	1
Diversity and Distributions	2
Ecological Indicators	1
Ecological Modelling	1
Ecology	2
Ecoscience	1
Ecosystems	1
Environmental Science and Pollution Research	1
Estuarine Coastal and Shelf Science	3
European Journal of Phycology	6
Evolutionary Applications	1
Frontiers in Marine Science	1
Fuel	1
Harmful Algae	5
Helgoland Marine Research	2
Helvetica Chimica Acta	1
Hydrobiologia	12
Hydrology	1
Industrial Crops and Products	1
Journal of Applied Ecology	1
Journal of Applied Microbiology	1
Journal of Applied Phycology	9

Journal	Number of papers
Journal of Aquatic Plant Management	1
Journal of Ecology	6
Journal of Experimental Marine Biology and Ecology	22
Journal of Phycology	7
Journal of the Marine Biological Association of the United Kingdom	8
Journal of the Royal Society Interface	1
Journal of Theoretical Biology	1
Limnology and Oceanography	1
Marine and Freshwater Research	2
Marine Biology	20
Marine Biology Research	1
Marine Biotechnology	1
Marine Drugs	3
Marine Ecology Progress Series	24
Marine Ecology-An Evolutionary Perspective	3
Marine Ecology-Pubblicazioni Della Stazione Zoologica di Napoli I	1
Marine Environmental Research	8
Marine Pollution Bulletin	4
Mediterranean Marine Science	2
Metabolomics	1
Methods in Ecology and Evolution	1
Molecular Ecology	1
Oecologia	3
Oikos	1
Pacific Science	3
Phycologia	7
Phycological Research	3
Physiologia Plantarum	1
PLOS One	6
Revista de Biologia Marina y Oceanografia	2
Revista del Museo Argentino de Ciencias Naturales, Nueva Serie	1
Rhodora	3
Royal Society Open Science	1
Russian Journal of Marine Biology	1
Sarsia	1
Science of the Total Environment	3
Scientia Marina	1
Scientific Reports	2
Simulation	1
Tetrahedron	1

Table 7.14 The number of papers with first author locations in each country, and the number of papers in which invasive seaweed populations were studied in each country.

First author location	Number of papers	Study area	Number of papers
		Algeria	1
Argentina	8	Argentina	7
Australia	22	Australia	20
		Azores	1
		Bahamas	1
		Barbados	1
Brazil	5	Brazil	6
Canada	19	Canada	21
Chile	3	Chile	3
China	2	China	2
Croatia	5	Croatia	4
Denmark	8	Denmark	14
Egypt	1	Egypt	1
France	18	France	34
French Polynesia	2	French Polynesia	3
Germany	10	Germany	11
		Guadeloupe	1
		Iceland	2
India	1	India	1
Ireland	4	Ireland	3
Italy	32	Italy	32
		Jamaica	1
Japan	1	Japan	1
Malta	1	Malta	1
		Martinique	1
		Mediterranean	2
Mexico	3	Mexico	7
Morocco	3	Morocco	3
		New Caledonia	1
New Zealand	20	New Zealand	22
Norway	10	Norway	7
Portugal	19	Portugal	19
		Réunion	1
South Africa	2		
South Korea	3	South Korea	2
Spain	34	Spain	35
		St Vincent	1
Sweden	10	Sweden	8
Taiwan	1	Taiwan	1
		Tanzania	1
The Netherlands	3	The Netherlands	4

First author location	Number of papers	Study area	Number of papers
Turkey	1	Turkey	1
UK	19	UK	21
USA	53	USA	55
		UNK	1
		NA	7

Table 7.15 Number of papers investigating traits of the below invasive species and the associated taxonomic groups. All species names have been confirmed in Algaebase (Guiry and Guiry 2022).

Taxa	Species name	Number of papers
Rhodophyta	*Acanthophora nayadiformis*	2
Rhodophyta	*Acanthophora spicifera*	7
Rhodophyta	*Acrochaetium balticum*	2
Rhodophyta	*Acrothamnion preissii*	3
Phaeophyceae	*Acrothrix gracilis*	2
Rhodophyta	*Agardhiella subulata*	2
Rhodophyta	*Aglaothamnion cordatum*	1
Rhodophyta	*Aglaothamnion feldmanniae*	2
Rhodophyta	*Aglaothamnion halliae*	2
Rhodophyta	*Ahnfeltiopsis flabelliformis*	2
Phaeophyceae	*Alaria esculenta*	2
Rhodophyta	*Anotrichium furcellatum*	2
Rhodophyta	*Antithamnion amphigeneum*	2
Rhodophyta	*Antithamnion densum*	3
Rhodophyta	*Antithamnion diminuatum*	3
Rhodophyta	*Antithamnion nipponicum*	1
Rhodophyta	*Antithamnion pectinatum*	4
Rhodophyta	*Antithamnionella elegans*	2
Rhodophyta	*Antithamnionella spirographidis*	2
Rhodophyta	*Antithamnionella sublittoralis*	2
Rhodophyta	*Antithamnionella ternifolia*	3
Rhodophyta	*Asparagopsis armata*	11
Rhodophyta	*Asparagopsis taxiformis*	6
Phaeophyceae	*Asperococcus scaber*	2
Chlorophyta	*Avrainvillea amadelpha*	1
Rhodophyta	*Bonnemaisonia hamifera*	6
Rhodophyta	*Bostrychia radicans*	1
Rhodophyta	*Botryocladia madagascariensis*	2
Rhodophyta	*Botryocladia wrightii*	2
Rhodophyta	*Caulacanthus ustulatus*	4
Chlorophyta	*Caulerpa cylindracea*	19
Chlorophyta	*Caulerpa filiformis*	1
Chlorophyta	*Caulerpa parvifolia*	1

Taxa	Species name	Number of papers
Chlorophyta	*Caulerpa prolifera*	1
Chlorophyta	*Caulerpa racemosa*	11
Chlorophyta	*Caulerpa scalpelliformis*	3
Chlorophyta	*Caulerpa taxifolia*	41
Chlorophyta	*Caulerpa taxifolia var. distichophylla*	2
Chlorophyta	*Caulerpa webbiana*	1
Rhodophyta	*Ceramium bisporum*	2
Rhodophyta	*Ceramium cingulatum*	1
Rhodophyta	*Ceramium strobiliforme*	2
Charophyta	*Chara connivens*	2
Rhodophyta	*Chondria coerulescens*	2
Rhodophyta	*Chondria curvilineata*	2
Rhodophyta	*Chondria polyrhiza*	2
Rhodophyta	*Chondria pygmaea*	2
Rhodophyta	*Chondrus giganteus*	2
Phaeophyceae	*Chorda filum*	2
Phaeophyceae	*Cladosiphon zosterae*	2
Chlorophyta	*Codium fragile*	41
Chlorophyta	*Codium fragile subsp. atlanticum*	2
Chlorophyta	*Codium fragile subsp. scandinavicum*	2
Chlorophyta	*Codium isthmocladum*	1
Rhodophyta	*Colaconema codicola*	2
Phaeophyceae	*Colpomenia peregrina*	4
Rhodophyta	*Corynomorpha prismatica*	1
Phaeophyceae	*Corynophlaea umbellata*	2
Phaeophyceae	*Corynophlaea verruculiformis*	2
Rhodophyta	*Dasya baillouviana*	2
Rhodophyta	*Dasya sessilis*	2
Rhodophyta	*Dasysiphonia japonica*	9
Chlorophyta	*Derbesia rhizophora*	2
Phaeophyceae	*Desmarestia viridis*	2
Phaeophyceae	*Desmotrichum tenuissimum*	2
Chlorophyta	*Dictyosphaeria cavernosa*	2
Phaeophyceae	*Dictyota cyanoloma*	1
Phaeophyceae	*Ectocarpus siliculosus*	2
Rhodophyta	*Eucheuma denticulatum*	2
Rhodophyta	*Eutrichosiphonia paniculata*	2
Phaeophyceae	*Fucus distichus*	1
Phaeophyceae	*Fucus distichus subsp. evanescens*	6
Phaeophyceae	*Fucus serratus*	1
Phaeophyceae	*Fucus spiralis*	2
Rhodophyta	*Ganonema farinosum*	2
Rhodophyta	*Goniotrichiopsis sublittoralis*	2
Rhodophyta	*Gracilaria multipartita*	2

Taxa	**Species name**	**Number of papers**
Rhodophyta	*Gracilaria parvispora*	1
Rhodophyta	*Gracilaria salicornia*	6
Rhodophyta	*Gracilaria sp.*	1
Rhodophyta	*Gracilaria vermiculophylla*	34
Rhodophyta	*Grallatoria reptans*	3
Rhodophyta	*Grateloupia doryphora*	6
Rhodophyta	*Grateloupia imbricata*	1
Rhodophyta	*Grateloupia patens*	2
Rhodophyta	*Grateloupia subpectinata*	2
Rhodophyta	*Grateloupia turuturu*	13
Rhodophyta	*Griffithsia corallinoides*	2
Rhodophyta	*Gymnophycus hapsiphorus*	2
Phaeophyceae	*Halothrix lumbricalis*	2
Rhodophyta	*Herposiphonia parca*	2
Rhodophyta	*Hypnea cornuta*	2
Rhodophyta	*Hypnea esperi*	2
Rhodophyta	*Hypnea flagelliformi*	1
Rhodophyta	*Hypnea musciformis*	2
Rhodophyta	*Hypnea spinella*	2
Rhodophyta	*Hypnea valentiae*	2
Rhodophyta	*Kappaphycus alvarezii*	2
Rhodophyta	*Laurencia brongniartii*	3
Rhodophyta	*Laurencia caduciramulosa*	1
Rhodophyta	*Laurencia chondrioides*	2
Rhodophyta	*Laurencia dendroidea*	1
Rhodophyta	*Laurencia okamurae*	2
Phaeophyceae	*Leathesia marina*	2
Rhodophyta	*Lithophyllum yessoense*	2
Rhodophyta	*Lomentaria hakodatensis*	2
Rhodophyta	*Lophocladia lallemandii*	6
Phaeophyceae	*Macrocystis pyrifera*	2
Rhodophyta	*Mastocarpus sp.*	1
Rhodophyta	*Mastocarpus stellatus*	2
Rhodophyta	*Mazzaella japonica*	1
Rhodophyta	*Melanothamnus harveyi*	4
Rhodophyta	*Melanothamnus sphaerocarpus*	1
Rhodophyta	*Melanothamnus spp.*	1
Rhodophyta	*Neopyropia yezoensis*	2
Rhodophyta	*Pachymeniopsis lanceolata*	2
Phaeophyceae	*Padina boergesenii*	2
Phaeophyceae	*Papenfussiella kuromo*	1
Phaeophyceae	*Petalonia binghamiae*	3
Rhodophyta	*Phrix spatulata*	2
Rhodophyta	*Pikea californica*	2

Taxa	Species name	Number of papers
Rhodophyta	*Platysiphonia caribaea*	2
Rhodophyta	*Plocamium secundatum*	2
Rhodophyta	*Polysiphonia morrowii*	3
Rhodophyta	*Polysiphonia senticulosa*	2
Rhodophyta	*Predaea huismanii*	2
Phaeophyceae	*Pylaiella littoralis*	2
Rhodophyta	*Rhodophysema georgei*	2
Phaeophyceae	*Saccharina japonica*	2
Phaeophyceae	*Saccharina japonica var. ochotensis*	2
Rhodophyta	*Sarconema filiforme*	2
Rhodophyta	*Sarconema scinaioides*	2
Phaeophyceae	*Sargassum assimile*	1
Phaeophyceae	*Sargassum carpophyllum*	1
Phaeophyceae	*Sargassum fluitans*	1
Phaeophyceae	*Sargassum horneri*	2
Phaeophyceae	*Sargassum muticum*	67
Phaeophyceae	*Sargassum natans*	1
Phaeophyceae	*Sargassum pacificum*	1
Phaeophyceae	*Sargassum siliquosum*	1
Rhodophyta	*Scageliopsis patens*	3
Phaeophyceae	*Scytosiphon dotyi*	2
Rhodophyta	*Solieria chordalis*	4
Phaeophyceae	*Sphaerotrichia divaricata*	2
Rhodophyta	*Spongoclonium caribaeum*	3
Phaeophyceae	*Stypopodium schimperi*	2
Rhodophyta	*Symphyocladia marchantioides*	3
Rhodophyta	*Symphyocladiella dendroidea*	2
Phaeophyceae	*Turbinaria ornata*	2
Chlorophyta	*Ulva armoricana*	1
Chlorophyta	*Ulva australis*	2
Chlorophyta	*Ulva ohnoi*	1
Chlorophyta	*Ulva prolifera*	2
Chlorophyta	*Ulvaria obscura*	2
Phaeophyceae	*Undaria pinnatifida*	47
Rhodophyta	*Vertebrata fucoides*	2
Rhodophyta	*Womersleyella setacea*	3
Rhodophyta	*Xiphosiphonia pinnulata*	3

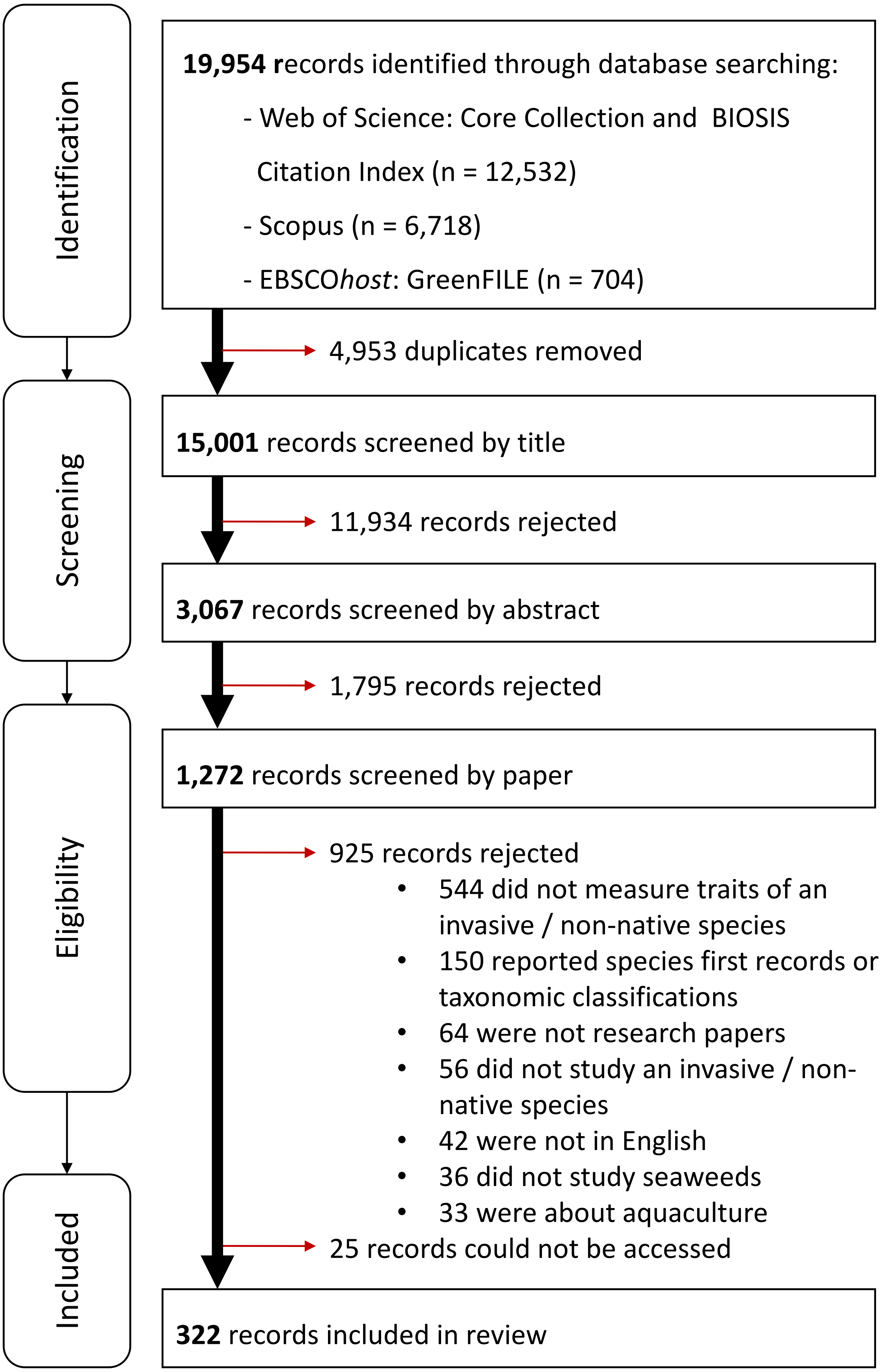

Figure 7.4 Flow chart depicting process by which records were selected.

7.2.1 Updated search methods and results

The search was re-run in Web of Science and EBSCO*host* Greenfile (Scopus could not be accessed) with the same conditions to estimate how many new publications would be included in this review. There were 1,198 new papers published between 21.01.2021 and 27.02.2022. In the original search, 1.6% of papers were included in the review, so to estimate the number of new papers that may be included, 1,198 was multiplied by 0.016. This estimated that approximately 19 extra papers would be included in this review if it was run on the 27.02.2022. If these papers were included, they would account for 6% of the total papers included in this review. Therefore, we do not believe that these papers would significantly change the results presented.

7.2.2 Rate of publications for invasive ecology trait papers

To quantify the rate of publications for invasive ecology trait papers, we ran a search on the 10.03.22 in Web of Science using the search string:

(ecology OR bio* AND conservation OR ecological OR biodiversity)

AND

(alien OR non-native OR introduced OR non-indigenous OR invasive OR invader OR exotic OR invasion OR nonnative OR nonindigenous)

AND

(trait OR characteristic OR growth OR life OR phenotype OR morphology OR attribute)

This resulted in 22,592 results. The publication years were downloaded, and 2,022 excluded, resulting in 22,330 results.

7.3 Appendices for Chapter 4

Table 7.16 Details of sampling sites.

Name	Coordinates	Substrate	Habitat	Exposure
West Hoe	50.36, -4.14	Rocky shore	Intertidal	Moderately exposed
Mount Batten	50.35, -4.13	Rocky shore	Subtidal	Moderately exposed
Wembury Point	50.32, -4.08	Rocky shore	Intertidal	Moderately exposed

Table 7.17 V-values and p-values from paired Wilcoxon tests to compare amount of biomass consumed during the choice tests.

Species comparison	V-value	p-value
U. pinnatifida and *S. latissima*	13	0.6875
U. pinnatifida and *L. digitata*	15	0.9375
U. pinnatifida and *S. polyschides*	17	0.6875
S. muticum and *F. serratus*	28	0.5703
S. muticum and *F. vesiculosus*	29	0.9219
S. muticum and *A. nodosum*	23	1.0000

Table 7.18 Results of two one-way ANOVA's and associated post hoc tests to investigate the difference in the amount of biomass consumed per unit herbivore during no-choice tests for kelp and fucoid species respectively. Where p<0.05 is shown in bold.

	Kelp species						**Fucoid species**				
	Df	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**		**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**
Species	3	0.134	0.045	5.297	**0.015**	Species	3	0.015	0.005	6.4	**0.005**
Residuals	12	0.101	0.008			Residuals	16	0.013	0.001		
Tukey post hoc test						**Tukey post hoc test**					
Species comparisons	**Diff**	**Lwr**	**Upr**	**p adj**		**Species comparisons**	**Diff**	**Lwr**	**Upr**	**p adj**	
U. pinnatifida and *S. latissima*	-0.006	-0.214	0.203	1.000		*S. muticum* and *F. serratus*	-0.065	-0.116	-0.014	**0.011**	
U. pinnatifida and *L. digitata*	-0.002	-0.211	0.206	1.000		*S. muticum* and *F. vesiculosus*	-0.019	-0.070	0.033	0.733	
U. pinnatifida and *S. polyschides*	-0.201	-0.400	-0.001	**0.048**		*S. muticum* and *A. nodosum*	0.005	-0.046	0.056	0.991	
S. latissima and *L. digitata*	0.003	-0.189	0.196	1.000		*F. vesiculosus* and *F. serratus*	-0.047	-0.098	0.005	0.080	
S. polyschides and *S. latissima*	0.195	0.012	0.378	**0.036**		*F. serratus* and *A. nodosum*	0.070	0.019	0.122	**0.006**	
S. polyschides and *L. digitata*	0.198	0.015	0.381	**0.033**		*F. vesiculosus* and *A. nodosum*	0.024	-0.028	0.075	0.563	

Table 7.19 Results of two one-way ANOVA's and associated post hoc tests to investigate the difference in carbon to nitrogen ratio for kelp and fucoid species respectively. Where p<0.05 is shown in bold.

	Kelp species						**Fucoid species**				
	Df	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**		**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**
Species	3	2.057	0.686	32	**<0.001**	Species	3	0.851	0.284	15.12	**<0.001**
Residuals	36	0.771	0.021			Residuals	35	0.656	0.019		
Tukey post hoc test						**Tukey post hoc test**					
Species comparisons	**Diff**	**Lwr**	**Upr**	**p adj**		**Species comparisons**	**Diff**	**Lwr**	**Upr**	**p adj**	
U. pinnatifida and *S. latissima*	-0.296	-0.473	-0.120	**<0.001**		*S. muticum* and *F. serratus*	-0.190	-0.355	-0.025	**0.019**	
U. pinnatifida and *L. digitata*	-0.487	-0.663	-0.311	**<0.001**		*S. muticum* and *F. vesiculosus*	-0.190	-0.355	-0.025	**0.019**	
U. pinnatifida and *S. polyschides*	0.076	-0.100	0.252	0.656		*S. muticum* and *A. nodosum*	-0.424	-0.593	-0.254	**<0.001**	
S. latissima and *L. digitata*	-0.191	-0.367	-0.014	**0.030**		*F. vesiculosus* and *F. serratus*	0.000	-0.165	0.165	1.000	
S. polyschides and *S. latissima*	-0.372	-0.549	-0.196	**<0.001**		*F. serratus* and *A. nodosum*	-0.234	-0.403	-0.064	**0.004**	
S. polyschides and *L. digitata*	-0.563	-0.739	-0.387	**<0.001**		*F. vesiculosus* and *A. nodosum*	-0.234	-0.403	-0.064	**0.004**	

Table 7.20 Results of two one-way ANOVA's and associated post hoc tests to investigate the difference in polyphenolic concentrations for kelp and fucoid species respectively. Where $p<0.05$ is shown in bold.

	Kelp species						**Fucoid species**				
Kelp	**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**	**Fucoid**	**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**
Species	3	15.539	5.180	48.42	**<0.001**	Species	3	2.882	0.9605	9.373	**<0.001**
Residuals	18	1.925	0.107			Residuals	20	2.050	0.1025		
Tukey post hoc test						**Tukey post hoc test**					
Species comparisons	**Diff**	**Lwr**	**Upr**	**p adj**		**Species comparisons**	**Diff**	**Lwr**	**Upr**	**p adj**	
U. pinnatifida and *S. latissima*	1.556	0.997	2.116	**<0.001**		*S. muticum* and *F. serratus*	0.769	0.252	1.286	**0.003**	
U. pinnatifida and *L. digitata*	2.190	1.656	2.723	**<0.001**		*S. muticum* and *F. vesiculosus*	-0.138	-0.655	0.379	0.877	
U. pinnatifida and *S. polyschides*	1.554	0.994	2.113	**<0.001**		*S. muticum* and *A. nodosum*	0.268	-0.249	0.786	0.484	
S. latissima and *L. digitata*	0.633	0.073	1.193	**0.024**		*F. vesiculosus* and *F. serratus*	0.907	0.390	1.424	**<0.001**	
S. polyschides and *S. latissima*	0.003	-0.582	0.587	1.000		*F. serratus* and *A. nodosum*	-0.501	-1.018	0.017	0.060	
S. polyschides and *L. digitata*	0.636	0.076	1.196	**0.023**		*F. vesiculosus* and *A. nodosum*	0.406	-0.111	0.924	0.158	

Table 7.21 Results of a Kruskal Wallis and a one-way ANOVA and associated post hoc tests to investigate the difference in tensile strength for kelp and fucoid species respectively. Where p<0.05 is shown in bold.

	Kelp species				**Fucoid species**				
Kelp	**Kruskal-Wallis chi-squared**	**df**	**p-value**	**Fucoid**	**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**
Species	25.58	3	**<0.001**	Species	3	10.210	3.403	8.556	**<0.001**
				Residuals	33	13.120	0.398		

Dunn post hoc test				**Tukey post hoc test**				
Species comparison	**Z-value**	**p unadj**	**p adj**	**Species comparison**	**Diff**	**Lwr**	**Upr**	**p adj**
U. pinnatifida and *S. latissima*	3.149	0.002	**0.003**	*S. muticum* and *F. serratus*	-0.135	-0.944	0.674	0.969
U. pinnatifida and *L. digitata*	4.605	<0.001	**<0.001**	*S. muticum* and *F. vesiculosus*	-1.351	-2.135	-0.567	**<0.001**
U. pinnatifida and *S. polyschides*	1.496	0.135	0.135	*S. muticum* and *A. nodosum*	-0.621	-1.384	0.142	0.144
S. latissima and *L. digitata*	1.557	0.119	0.143	*F. vesiculosus* and *F. serratus*	1.216	0.387	2.045	**0.002**
S. polyschides and *S. latissima*	1.985	0.047	0.071	*F. serratus* and *A. nodosum*	-0.486	-1.295	0.323	0.379
S. polyschides and *L. digitata*	3.649	<0.001	**0.001**	*F. vesiculosus* and *A. nodosum*	0.730	-0.054	1.514	0.075

Table 7.22 W-values and p-values from Wilcoxon tests to compare percentage dry mass of polyphenolics between samples exposed to herbivory from gastropods and control samples.

Species	W-value	p-value
S. muticum	5	1.00
F. serratus	3	0.70
F. vesiculosus	4	1.00
A. nodosum	5	1.00

Table 7.23 The number of replicates in each experiment which were removed from analysis, either due to incorrect herbivore identification (for the fucoid choice tests), or the sample degrading to the point where the wet weight could not be determined accurately.

Experiment	Taxonomic group	Species	Replicates removed
Choice	Kelp	*U. pinnatifida* and *S. latissima*	4
		U. pinnatifida and *L. digitata*	3
		U. pinnatifida and *S. polyschides*	3
	Fucoid	*S. muticum* and *F. serratus*	1
		S. muticum and *F. vesiculosus*	0
		S. muticum and *A. nodosum*	1
No choice	Kelp	*U. pinnatifida*	2
		S. latissima	1
		L. digitata	1
		S. polyschides	0
	Fucoid	*S. muticum*	0
		F. serratus	0
		F. vesiculosus	0
		A. nodosum	0

Table 7.24 W-values and p-values from unpaired Wilcoxon tests to compare the percentage of change in mass (g) averaged over seven days between samples exposed to artificial herbivory (treatment) and samples which weren't (control).

Species	W-value	p-value
U. pinnatifida	7	0.40
S. latissima	4	0.33
L. digitata	6	0.20
S. polyschides	8	0.20
S. muticum	0	0.67
F. serratus	8	0.20
F. vesiculosus	4	1.00
A. nodosum	3	0.70

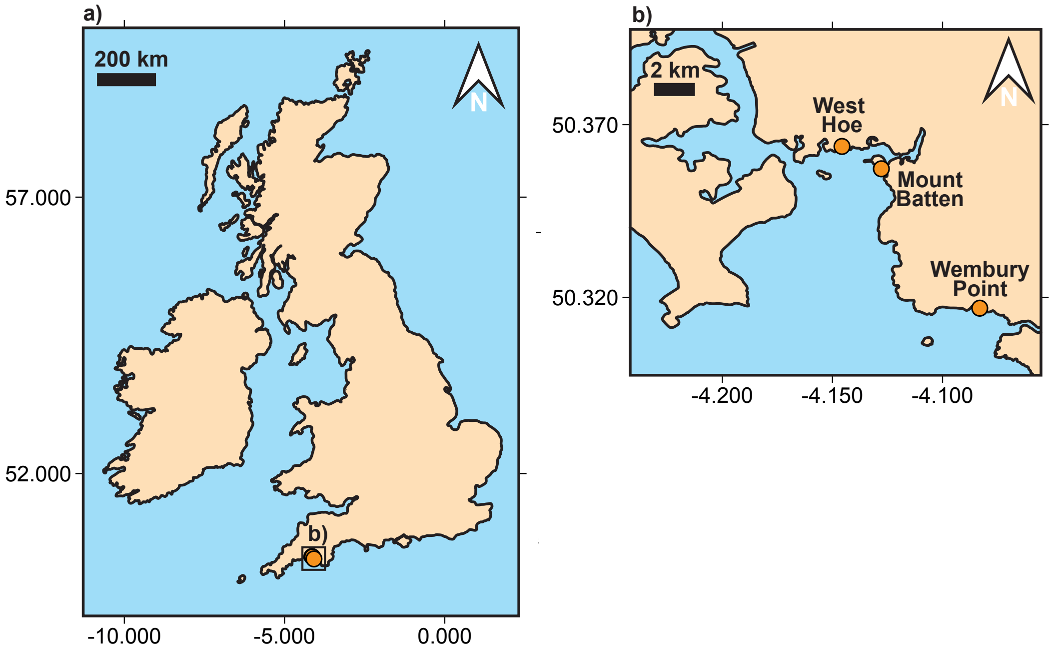

Figure 7.5 Sites in the United Kingdom where field sampling was conducted.

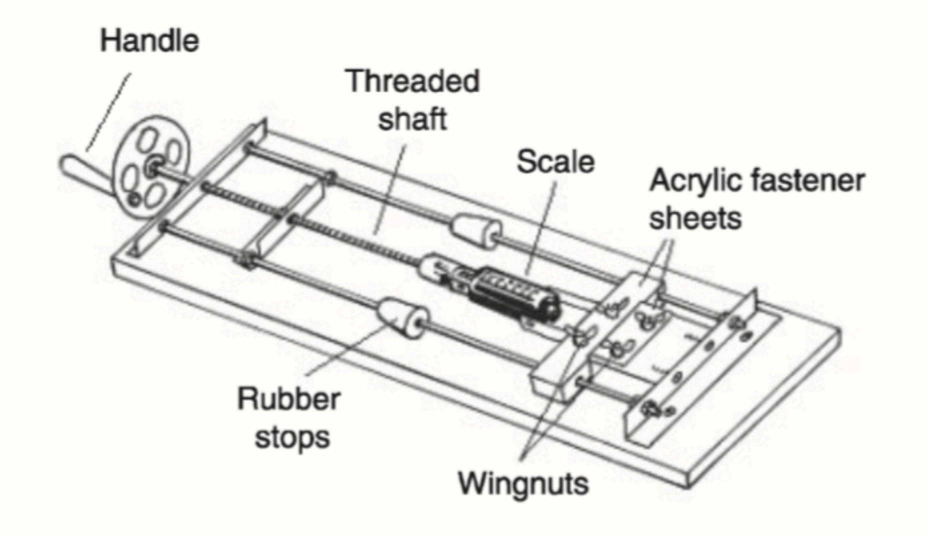

Figure 7.6 Diagram of equipment used to measure tensile strength. Design from Pérez-Harguindeguy *et al.*, (2013).

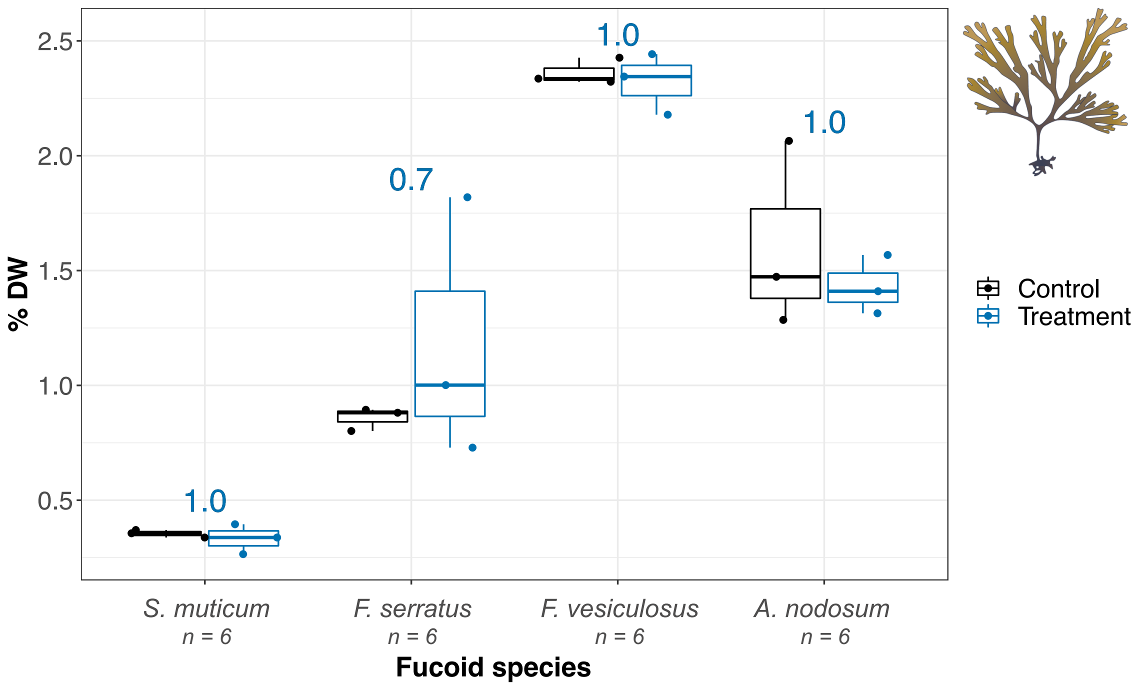

Figure 7.7 Percentage dry weight of polyphenolic concentrations where samples were exposed to herbivory from gastropods during no choice tests (treatment) and some were not (control) in fucoid species. P-values from Wilcoxon tests to determine differences between treatment and control groups for each species are shown. Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/).

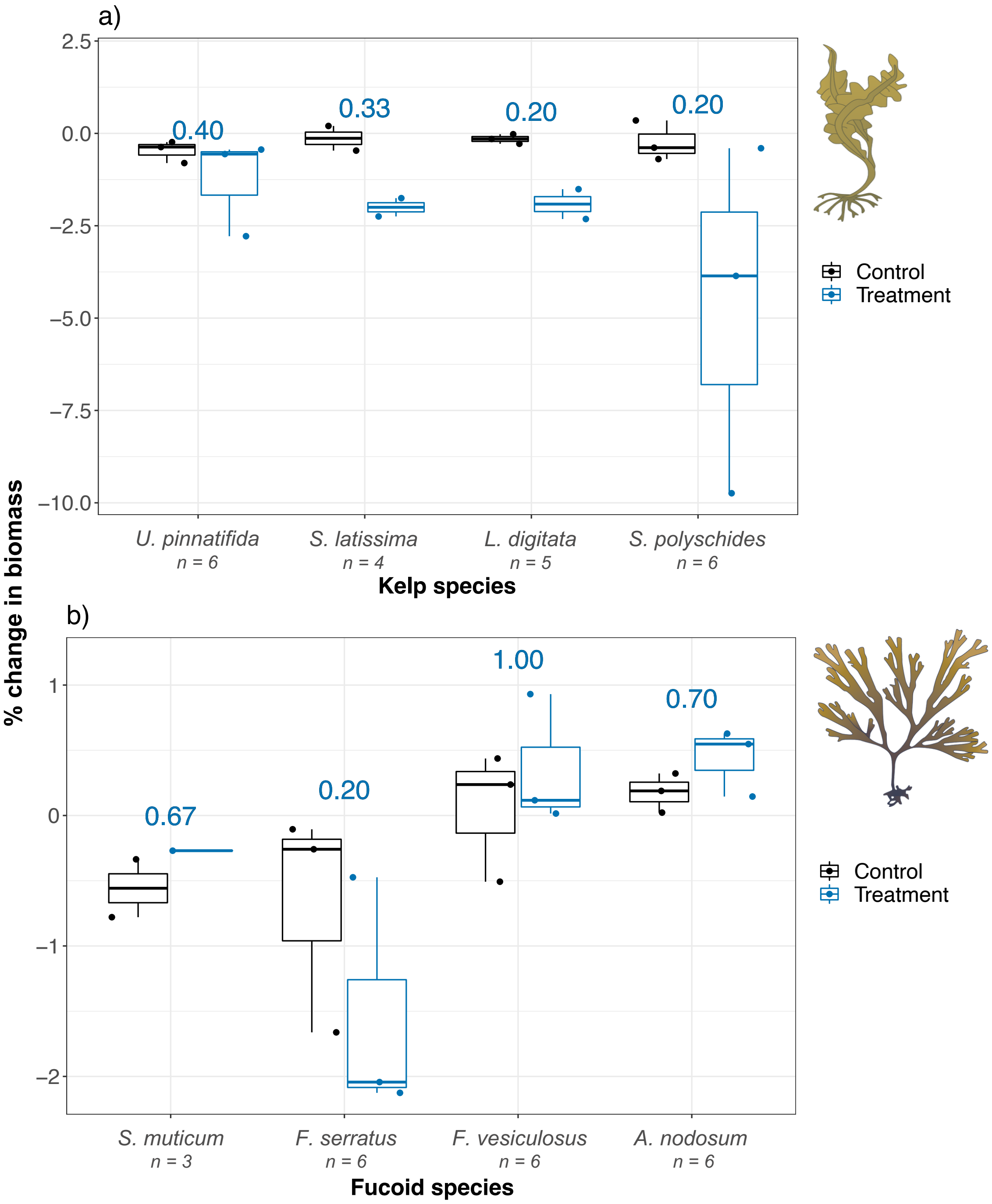

Figure 7.8 Percentage change in mass averaged over seven days where samples experienced artificial herbivory (treatment) or were left alone (control) for a) kelp species and b) fucoid species. P-values from Wilcoxon tests to determine differences between treatment and control groups for each species are shown. Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/).

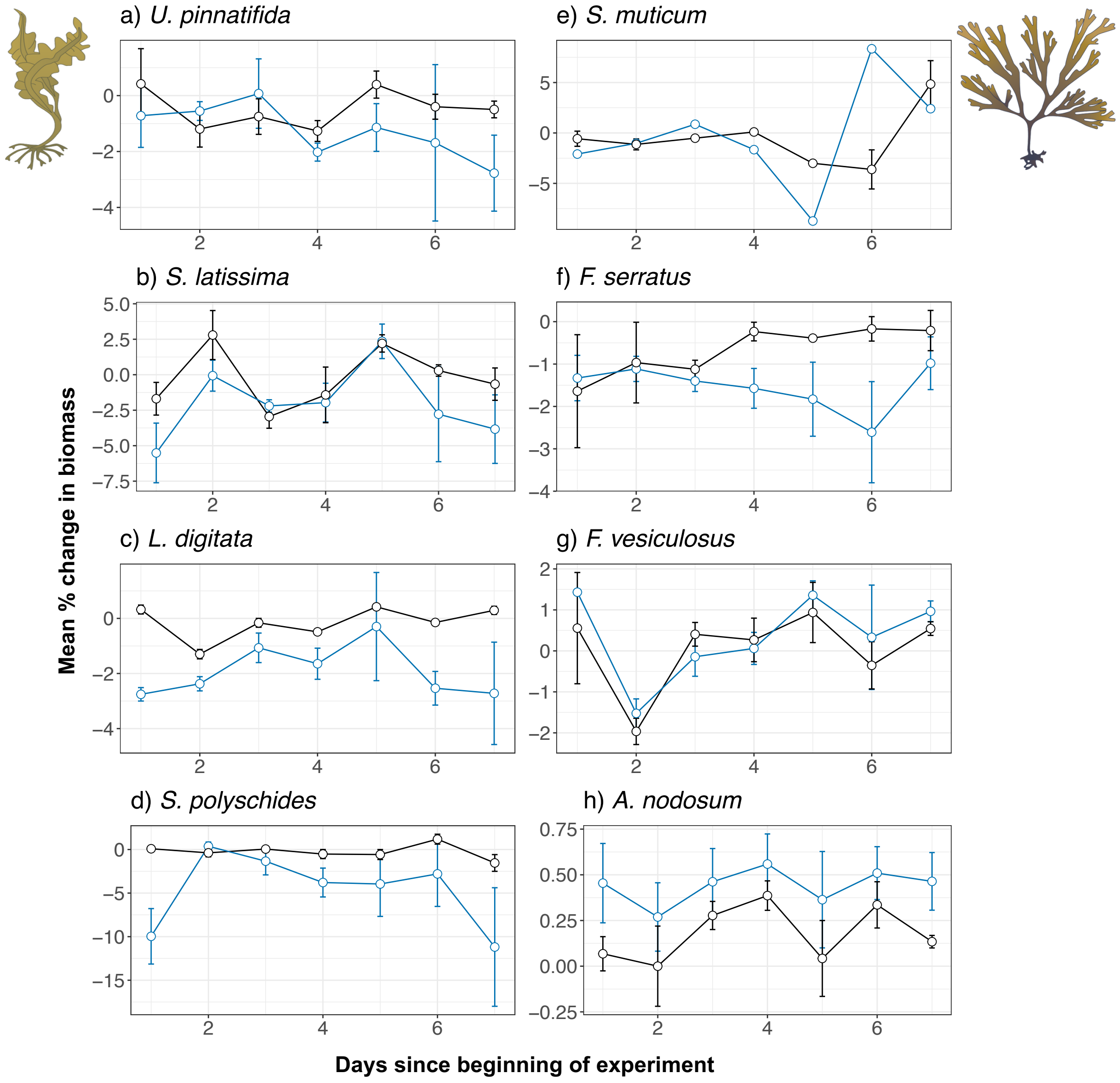

Figure 7.9 Mean percentage change in mass over a seven-day experiment where some samples underwent artificial herbivory (treatment in blue), and others did not (control in black) for a-d) kelp species and e-h) fucoid species. Error bars are standard error.

7.4 Appendices for Chapter 5

Table 7.25 Location of sampled sites and the number of samples of each *Durvillaea* species collected at, and subsequently genetically analysed from, each location.

Site name	**Coordinates**		**Date**	**Number of samples collected**		
	Latitude	**Longitude**		***D. antarctica***	***D. poha***	***D. willana***
Taieri beach	-46.072831	170.201621	01/03/2019	0	9	0
Island bay	-41.349812	174.766412	01/12/2019	1	0	0
Tautuku Peninsula	-46.608552	169.434597	12/02/2020	0	15	3
Smails beach	-45.907749	170.564372	25/02/2020	4	0	0
Brighton	-45.947972	170.335971	25/02/2020	0	13	1
Toko Mouth	-46.223985	170.043312	27/02/2020	2	11	0
Smiths beach	-46.291645	169.927324	27/02/2020	2	0	0
Akatore	-46.112489	170.192227	11/03/2020	13	10	15
Watsons beach	-46.162127	170.153041	11/03/2020	9	15	0

List of References

Aguiar, F. C. F., and M. T. Ferreira. 2013. Plant invasions in the rivers of the Iberian Peninsula, south-western Europe: A review. Plant Biosystems 147:1107–1119.

Aguilera, M. A. 2011. The functional roles of herbivores in the rocky intertidal systems in Chile: A review of food preferences and consumptive effects. Revista chilena de historia natural 84:241–261.

Aguilera, M. A., N. Valdivia, and B. R. Broitman. 2015. Herbivore-alga interaction strength influences spatial heterogeneity in a kelp-dominated intertidal community. PLoS ONE 10:e0137287.

Anderson, S. C., P. R. Elsen, B. B. Hughes, R. K. Tonietto, M. C. Bletz, D. A. Gill, M. A. Holgerson, S. E. Kuebbing, C. McDonough MacKenzie, M. H. Meek, and D. Veríssimo. 2021. Trends in ecology and conservation over eight decades. Frontiers in Ecology and the Environment 19:274–282.

Arnold, T. M., and N. M. Targett. 2003. To grow and defend: lack of tradeoffs for brown algal phlorotannins. Oikos 100:406–408.

Atkinson, J., N. G. King, S. B. Wilmes, and P. J. Moore. 2020. Summer and winter marine heatwaves favor an invasive over native seaweeds. Journal of Phycology 56:1591–1600.

Bacher, S., T. M. Blackburn, F. Essl, P. Genovesi, J. Heikkilä, J. M. Jeschke, G. Jones, R. Keller, M. Kenis, C. Kueffer, A. F. Martinou, W. Nentwig, J. Pergl, P. Pyšek, W. Rabitsch, D. M. Richardson, H. E. Roy, W. Saul, R. Scalera, M. Vilà, J. R. U. Wilson, and S. Kumschick. 2018. Socio-economic impact classification of alien taxa (SEICAT). Methods in Ecology and Evolution 9:159–168.

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pages 147–168 *in* H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species; proceedings. Academic Press, New York, NY.

Bakker, K. 1960. Feeding habits and zonation in some intertidal snails. Archives Néerlandaises de Zoologie 13:230–257.

Baldini, L. M., J. U. L. Baldini, J. N. McElwaine, A. B. Frappier, Y. Asmerom, K. Liu, K. M. Prufer, H. E. Ridley, V. Polyak, D. J. Kennett, C. G. Macpherson, V. V. Aquino, J. Awe, and S. F. M. Breitenbach. 2016. Persistent northward North Atlantic tropical cyclone track migration over the past five centuries. Scientific Reports 6:37522.

Ballabio, C., E. Lugato, O. Fernández-Ugalde, A. Orgiazzi, A. Jones, P. Borrelli, L. Montanarella, and P. Panagos. 2019. Mapping LUCAS topsoil chemical properties at European scale using Gaussian process regression. Geoderma 355:113912.

Barr, D. J., R. Levy, C. Scheepers, and H. J. Tily. 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language 68:255–278.

Bartoń, K. 2020. MuMIn: Multi-Model Inference.

Beattie, D. T., T. Lachnit, E. A. Dinsdale, T. Thomas, and P. D. Steinberg. 2018. Novel ssDNA viruses detected in the virome of bleached, habitat-forming kelp *Ecklonia radiata*. Frontiers in Marine Science 4:441.

Bellard, C., W. Thuiller, B. Leroy, P. Genovesi, M. Bakkenes, and F. Courchamp. 2013. Will climate change promote future invasions? Global Change Biology 19:3740–3748.

de Bello, F., J. N. Price, T. Münkemüller, J. Liira, M. Zobel, W. Thuiller, P. Gerhold, L. Götzenberger, S. Lavergne, J. Lepš, K. Zobel, and M. Pärtel. 2012. Functional species pool framework to test for biotic effects on community assembly. Ecology 93:2263–2273.

Belluau, M., and B. Shipley. 2018. Linking hard and soft traits: Physiology, morphology and anatomy interact to determine habitat affinities to soil water availability in herbaceous dicots. PLoS ONE 13:e0193130.

Bermejo, R., M. MacMonagail, S. Heesch, A. Mendes, M. Edwards, O. Fenton, K. Knöller, E. Daly, and L. Morrison. 2020. The arrival of a red invasive seaweed to a nutrient over-enriched estuary increases the spatial extent of macroalgal blooms. Marine Environmental Research 158:104944.

Birks, H. J. B. 2020. Reflections on the use of ecological attributes and traits in Quaternary Botany. Frontiers in Ecology and Evolution 8:166.

Blackburn, T. M., P. Cassey, and J. L. Lockwood. 2009. The role of species traits in the establishment success of exotic birds. Global Change Biology 15:2852–2860.

Blackburn, T. M., J. L. Lockwood, and P. Cassey. 2015. The influence of numbers on invasion success. Molecular Ecology 24:1942–1953.

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26:333–339.

Blake, C., M. Thiel, B. López, and C. Fraser. 2017. Gall-forming protistan parasites infect southern bull kelp across the Southern Ocean, with prevalence increasing to the south. Marine Ecology Progress Series 583:95–106.

Blight, O., R. Josens, C. Bertelsmeier, S. Abril, R. Boulay, and X. Cerdá. 2017. Differences in behavioural traits among native and introduced colonies of an invasive ant. Biological Invasions 19:1389–1398.

Blossey, B., and R. Nötzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. Journal of Ecology 83:887–889.

Boalch, G. T., and G. W. Potts. 1977. The first occurrence of *Sargassum muticum* (Yendo) Fensholt in the Plymouth area. Journal of the Marine Biological Association of the United Kingdom 57:29–31.

Borell, E. M., A. Foggo, and R. A. Coleman. 2004. Induced resistance in intertidal macroalgae modifies feeding behaviour of herbivorous snails. Oecologia 140:328–334.

Braga, R. R., L. Gómez-Aparicio, T. Heger, J. R. S. Vitule, and J. M. Jeschke. 2018. Structuring evidence for invasional meltdown: broad support but with biases and gaps. Biological Invasions 20:923–936.

Britton-Simmons, K. H. 2004. Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. Marine Ecology Progress Series 277:61–78.

Britton-Simmons, K. H., B. Pister, I. Sánchez, and D. Okamoto. 2011. Response of a native, herbivorous snail to the introduced seaweed *Sargassum muticum*. Hydrobiologia 661:187–196.

Bulleri, F., and F. Malquori. 2015. High tolerance to simulated herbivory in the clonal seaweed, *Caulerpa cylindracea*. Marine Environmental Research 107:61–65.

Burge, C. A., C. Mark Eakin, C. S. Friedman, B. Froelich, P. K. Hershberger, E. E. Hofmann, L. E. Petes, K. C. Prager, E. Weil, B. L. Willis, S. E. Ford, and C. D. Harvell. 2014. Climate change influences on marine infectious diseases: Implications for management and society. Annual Review of Marine Science 6:1.1-1.29.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33:261–304.

Byun, C., and E. J. Lee. 2017. Ecological application of biotic resistance to control the invasion of an invasive plant, *Ageratina altissima*. Ecology and Evolution 7:2181–2192.

Cacabelos, E., C. Olabarria, M. Incera, and J. S. Troncoso. 2010. Do grazers prefer invasive seaweeds? Journal of Experimental Marine Biology and Ecology 393:182–187.

Cadotte, M. W., C. A. Arnillas, S. W. Livingstone, and S.-L. E. Yasui. 2015. Predicting communities from functional traits. Trends in Ecology & Evolution 30:510–511.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services: Functional diversity in ecology and conservation. Journal of Applied Ecology 48:1079–1087.

Campbell, A. H., T. Harder, S. Nielsen, S. Kjelleberg, and P. D. Steinberg. 2011. Climate change and disease: bleaching of a chemically defended seaweed. Global Change Biology 17:2958–2970.

Campbell, A. H., A. Vergés, and P. D. Steinberg. 2014. Demographic consequences of disease in a habitat-forming seaweed and impacts on interactions between natural enemies. Ecology 95:142–152.

Carboni, M., T. Münkemüller, S. Lavergne, P. Choler, B. Borgy, C. Violle, F. Essl, C. Roquet, F. Munoz, DivGrass Consortium, and W. Thuiller. 2016. What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. Ecology Letters 19:219–229.

Cardoso, A. C., F. Arenas, I. Sousa-Pinto, A. Barreiro, and J. N. Franco. 2020. Sea urchin grazing preferences on native and non-native macroalgae. Ecological Indicators 111:106046.

Carlton, J. T., J. W. Chapman, J. B. Geller, J. A. Miller, D. A. Carlton, M. I. McCuller, N. C. Treneman, B. P. Steves, and G. M. Ruiz. 2017. Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. Science 357:1402–1406.

Casas, G. N., M. L. Piriz, and E. R. Parodi. 2008. Population features of the invasive kelp *Undaria pinnatifida* (Phaeophyceae: Laminariales) in Nuevo Gulf (Patagonia, Argentina). Journal of the Marine Biological Association of the United Kingdom 88:21–28.

Case, R. J., S. R. Longford, A. H. Campbell, A. Low, N. Tujula, P. D. Steinberg, and S. Kjelleberg. 2011. Temperature induced bacterial virulence and bleaching disease in a chemically defended marine macroalga. Environmental Microbiology 13:529–537.

Catford, J. A., J. B. Baumgartner, P. A. Vesk, M. White, Y. M. Buckley, and M. A. McCarthy. 2016. Disentangling the four demographic dimensions of species invasiveness. Journal of Ecology 104:1745–1758.

Catford, J. A., C. C. Daehler, H. T. Murphy, A. W. Sheppard, B. D. Hardesty, D. A. Westcott, M. Rejmánek, P. J. Bellingham, J. Pergl, C. C. Horvitz, and P. E. Hulme. 2012. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. Perspectives in Plant Ecology, Evolution and Systematics 14:231–241.

Catford, J. A., and R. Jansson. 2014. Drowned, buried and carried away: effects of plant traits on the distribution of native and alien species in riparian ecosystems. New Phytologist 204:19–36.

Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15:22–40.

Catford, J. A., A. L. Smith, P. D. Wragg, A. T. Clark, M. Kosmala, J. Cavender-Bares, P. B. Reich, and D. Tilman. 2019. Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. Ecology Letters 22:593–604.

Catford, J. A., J. R. U. Wilson, P. Pyšek, P. E. Hulme, and R. P. Duncan. 2022. Addressing context dependence in ecology. Trends in Ecology & Evolution 37:158–170.

Cerda, O., U. Karsten, E. Rothäusler, F. Tala, and M. Thiel. 2009. Compensatory growth of the kelp *Macrocystis integrifolia* (Phaeophyceae, Laminariales) against grazing of *Peramphithoe femorata* (Amphipoda, Ampithoidae) in northern-central Chile. Journal of Experimental Marine Biology and Ecology 377:61–67.

Chandrasekaran, S., N. A. Nagendran, D. Pandiaraja, N. Krishnankutty, and B. Kamalakannan. 2008. Bioinvasion of *Kappaphycus alvarezii* on corals in the Gulf of Mannar, India. Current Science 94:7.

Chefaoui, R. M., A. Serebryakova, A. H. Engelen, F. Viard, and E. A. Serrão. 2019. Integrating reproductive phenology in ecological niche models changed the predicted future ranges of a marine invader. Diversity and Distributions 25:688–700.

Choi, H. G., Y. S. Kim, S. J. Lee, and K. W. Nam. 2007. Growth and reproductive patterns of *Undaria pinnatifida* sporophytes in a cultivation farm in Busan, Korea. Journal of Applied Phycology 19:131–138.

Chung, Y., S. Rabe-Hesketh, V. Dorie, A. Gelman, and J. Liu. 2013. A Nondegenerate Penalized Likelihood Estimator for Variance Parameters in Multilevel Models. Psychometrika 78:685–709.

Chytrý, M., J. Danihelka, Z. Kaplan, J. Wild, D. Holubová, P. Novotný, M. Řezníčková, M. Rohn, P. Dřevojan, V. Grulich, J. Klimešová, J. Lepš, Z. Lososová, J. Pergl, J. Sádlo, P. Šmarda, P. Štěpánková, L. Tichý, I. Axmanová, A. Bartušková, P. Blažek, J. Chrtek, F. M. Fischer, W.-Y. Guo, T. Herben, Z. Janovský, M. Konečná, I. Kühn, L. Moravcová, P. Petřík, S. Pierce, K. Prach, H. Prokešová, M. Štech, J. Těšitel, T. Těšitelová, M. Večeřa, D. Zelený, and P. Pyšek. 2021. Pladias Database of the Czech flora and vegetation. Preslia 93:1–87.

Chytrý, M., L. C. Maskell, J. Pino, P. Pyšek, M. Vilà, X. Font, and S. M. Smart. 2008. Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. Journal of Applied Ecology 45:448–458.

Cohen, R., C. James, A. Lee, M. Martinelli, W. Muraoka, M. Ortega, R. Sadowski, L. Starkey, A. Szesciorka, S. Timko, E. Weiss, and P. Franks. 2018. Marine host-pathogen dynamics: Influences of global climate change. Oceanography 31:182–193.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7:721–733.

Colautti, R., J. D. Parker, M. W. Cadotte, P. Pyšek, C. S. Brown, D. Sax, and D. Richardson. 2014. Quantifying the invasiveness of species. NeoBiota 21:7–27.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126.

Coviella, C. E., R. D. Stipanovic, and J. T. Trumble. 2002. Plant allocation to defensive compounds: interactions between elevated CO_2 and nitrogen in transgenic cotton plants. Journal of Experimental Botany 53:323–331.

Crawley, M., S. Brown, M. Heard, and Edwards GR. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters 2:140–148.

Crawley, M., P. Harvey, and A. Purvis. 1996. Comparative ecology of the native and alien floras of the British Isles. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 351:1251–1259.

Critchley, A. T., P. R. M. De Visscher, and P. H. Nienhuis. 1990. Canopy characteristics of the brown alga Sargassum muticum (Fucales, Phaeophyta) in Lake Grevelingen, southwest Netherlands. Hydrobiologia 204–205:211–217.

Crooks, J. A., A. L. Chang, and G. M. Ruiz. 2011. Aquatic pollution increases the relative success of invasive species. Biological Invasions 13:165–176.

Dalla Vecchia, A., P. Villa, and R. Bolpagni. 2020. Functional traits in macrophyte studies: Current trends and future research agenda. Aquatic Botany 167:103290.

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9:772–772.

Dawson, S. K., L. Boddy, H. Halbwachs, C. Bässler, C. Andrew, T. W. Crowther, J. Heilmann-Clausen, J. Nordén, O. Ovaskainen, and M. Jönsson. 2019. Handbook for the measurement of macrofungal functional traits: A start with basidiomycete wood fungi. Functional Ecology 33:372–387.

Dawson, S. K., C. P. Carmona, M. González-Suárez, M. Jönsson, F. Chichorro, M. Mallen-Cooper, Y. Melero, H. Moor, J. P. Simaika, and A. B. Duthie. 2021. The traits of “trait ecologists”: An analysis of the use of trait and functional trait terminology. Ecology and Evolution:ece3.8321.

Dawson, W., M. Fischer, and M. van Kleunen. 2012. Common and rare plant species respond differently to fertilisation and competition, whether they are alien or native. Ecology Letters 15:873–880.

De Leij, R., G. Epstein, M. P. Brown, and D. A. Smale. 2017. The influence of native macroalgal canopies on the distribution and abundance of the non-native kelp *Undaria pinnatifida* in natural reef habitats. Marine Biology 164:156.

Delaney, A., K. Frangoudes, and S.-A. Ii. 2016. Society and seaweed: Understanding the past and present. Pages 7–40 *in* J. Fleurence and I. Levine, editors. Seaweed in health and disease prevention. Elsevier.

Demes, K. W., C. D. G. Harley, L. M. Anderson, and E. Carrington. 2013. Shifts in morphological and mechanical traits compensate for performance costs of reproduction in a wave-swept seaweed. Journal of Ecology 101:963–970.

Desmond, M. J., D. W. Pritchard, C. L. Hurd, D. K. Richards, K. Schweikert, S. Wing, and C. D. Hepburn. 2019. Superior photosynthetic performance of the invasive kelp *Undaria pinnatifida* may contribute to continued range expansion in a wave-exposed kelp forest community. Marine Biology 166:139.

Di Marco, M., S. Chapman, G. Althor, S. Kearney, C. Besancon, N. Butt, J. M. Maina, H. P. Possingham, K. Rogalla von Bieberstein, O. Venter, and J. E. M. Watson. 2017. Changing trends and persisting biases in three decades of conservation science. Global Ecology and Conservation 10:32–42.

Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science 9:113–122.

Diepeveen, E. T., and W. Salzburger. 2012. Two decades of molecular ecology: where are we and where are we heading? Molecular Ecology 21:5656–5659.

Diez, J. M., C. M. D’Antonio, J. S. Dukes, E. D. Grosholz, J. D. Olden, C. J. Sorte, D. M. Blumenthal, B. A. Bradley, R. Early, I. Ibáñez, S. J. Jones, J. J. Lawler, and L. P. Miller. 2012. Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment 10:249–257.

Dijkstra, J. A., A. Litterer, K. Mello, B. S. O'Brien, and Y. Rzhanov. 2019. Temperature, phenology, and turf macroalgae drive seascape change: Connections to mid-trophic level species. Ecosphere 10.

Divíšek, J., M. Chytrý, B. Beckage, N. J. Gotelli, Z. Lososová, P. Pyšek, D. M. Richardson, and J. Molofsky. 2018. Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nature Communications 9:4631.

Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16:646–655.

Donaldson, J. E., C. Hui, D. M. Richardson, M. P. Robertson, B. L. Webber, and J. R. U. Wilson. 2014. Invasion trajectory of alien trees: the role of introduction pathway and planting history. Global Change Biology 20:1527–1537.

Duffy, G. A., B. W. T. Coetzee, G. Latombe, A. H. Akerman, M. A. McGeoch, and S. L. Chown. 2017. Barriers to globally invasive species are weakening across the Antarctic. Diversity and Distributions 23:982–996.

Duffy, J. E., and M. E. Hay. 1990. Seaweed adaptations to herbivory. BioScience 40:368–375.

Duffy, J. E., and M. E. Hay. 1991. Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286–1298.

Dufour, C., P. Probert, and C. Savage. 2012. Macrofaunal colonisation of stranded *Durvillaea antarctica* on a southern New Zealand exposed sandy beach. New Zealand Journal of Marine and Freshwater Research 46:369–383.

Dworjanyn, S. A., J. T. Wright, N. A. Paul, R. de Nys, and P. D. Steinberg. 2006. Cost of chemical defence in the red alga *Delisea pulchra*. Oikos 113:13–22.

Ebeling, A., S. T. Meyer, M. Abbas, N. Eisenhauer, H. Hillebrand, M. Lange, C. Scherber, A. Vogel, A. Weigelt, and W. W. Weisser. 2014. Plant diversity impacts decomposition and herbivory via changes in aboveground arthropods. PLoS ONE 9:e106529.

Edwards, K. F., E. Litchman, and C. A. Klausmeier. 2013. Functional traits explain phytoplankton community structure and seasonal dynamics in a marine ecosystem. Ecology Letters 16:56–63.

Eggertsen, M., S. A. Tano, D. H. Chacin, J. S. Eklöf, J. Larsson, C. Berkström, A. S. Buriyo, and C. Halling. 2021. Different environmental variables predict distribution and cover of the introduced red seaweed *Eucheuma denticulatum in two geographical locations*. Biological Invasions 23:1049–1067.

Enders, M., F. Havemann, F. Ruland, M. Bernard-Verdier, J. A. Catford, L. Gómez-Aparicio, S. Haider, T. Heger, C. Kueffer, I. Kühn, L. A. Meyerson, C. Musseau, A. Novoa, A. Ricciardi, A. Sagouis, C. Schittko, D. L. Strayer, M. Vilà, F. Essl, P. E. Hulme, M. van Kleunen, S. Kumschick, J. L. Lockwood, A. L. Mabey, M. A. McGeoch, E. Palma, P. Pyšek, W.-C. Saul, F. A. Yannelli, and J. M. Jeschke. 2020. A conceptual map of invasion biology: Integrating hypotheses into a consensus network. Global Ecology and Biogeography 29:978–991.

Enge, S., J. Sagerman, S. A. Wikström, and H. Pavia. 2017. A review of herbivore effects on seaweed invasions. Oceanography and Marine Biology 55:421–440.

Engelen, A., A. Serebryakova, P. Ang, K. Britton-Simmons, F. Mineur, M. Pedersen, F. Arenas, C. Fernández, H. Steen, R. Svenson, H. Pavia, G. Toth, F. Viard, and R. Santos. 2015. Circumglobal invasion by the brown seaweed *Sargassum muticum*. Pages 81–126 *in* R. Hughes, D. Hughes, I. Smith, and A. Dale, editors. Oceanography and Marine Biology. 1st Edition. Boca Raton.

Epstein, G., A. Foggo, and D. A. Smale. 2019. Inconspicuous impacts: Widespread marine invader causes subtle but significant changes in native macroalgal assemblages. Ecosphere 10:1–15.

Epstein, G., and D. A. Smale. 2017. *Undaria pinnatifida*: A case study to highlight challenges in marine invasion ecology and management. Ecology and Evolution 7:1–19.

Eschtruth, A. K., and J. J. Battles. 2011. The importance of quantifying propagule pressure to understand invasion: an examination of riparian forest invasibility. Ecology 92:1314–1322.

Farrell, P., and R. Fletcher. 2000. The biology and distribution of the kelp, *Undaria pinnatifida* (Harvey) Suringar, in the Solent. Pages 311–314 *in* M. Collins and K. Ansell, editors. Solent science - a review. Elsevier.

Felker-Quinn, E., J. A. Schweitzer, and J. K. Bailey. 2013. Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). Ecology and Evolution 3:739–751.

Fernández-Pascual, E., A. Pérez-Arcoiza, J. A. Prieto, and T. E. Díaz. 2017. Environmental filtering drives the shape and breadth of the seed germination niche in coastal plant communities. Annals of Botany 119:1169–1177.

Fick, S.E. and Hijmans. 2017. WorldClim 2: new 1 km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12): 4302-4315.

Fischhoff, I. R., T. Huang, S. K. Hamilton, B. A. Han, S. L. LaDeau, R. S. Ostfeld, E. J. Rosi, and C. T. Solomon. 2020. Parasite and pathogen effects on ecosystem processes: A quantitative review. Ecosphere 11:1–12.

Flagella, M., N. Andreakis, M. Hiraoka, M. Verlaque, and M. Buia. 2010. Identification of cryptic *Ulva* species (Chlorophyta, Ulvales) transported by ballast water. Journal of Biological Research 13:47–57.

Ford, S. E., N. A. Stokes, K. A. Alcox, B. S. F. Kraus, R. D. Barber, R. B. Carnegie, and E. M. Burreson. 2018. Investigating the life cycle of *Haplosporidium Nelsoni* (Msx): A review. Journal of Shellfish Research 37:679–693.

Fournier, A., C. Penone, M. G. Pennino, and F. Courchamp. 2019. Predicting future invaders and future invasions. Proceedings of the National Academy of Sciences 116:7905–7910.

Fowler, A. E., A. M. H. Blakeslee, J. Canning-Clode, M. F. Repetto, A. M. Phillip, J. T. Carlton, F. C. Moser, G. M. Ruiz, and A. W. Miller. 2016. Opening Pandora's bait box: a potent vector for biological invasions of live marine species. Diversity and Distributions 22:30–42.

Fox, J., and S. Weisberg. 2019. An {R} Companion to Applied Regression. Third. Sage, Thousand Oaks CA.

Fraser, C. 2012. Is bull-kelp kelp? The role of common names in science. New Zealand Journal of Marine and Freshwater Research 46:279–284.

Fraser, C. I., A. K. Morrison, A. McC Hogg, E. C. Macaya, E. van Sebille, P. G. Ryan, A. Padovan, C. Jack, N. Valdivia, and J. M. Waters. 2018. Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. Nature Climate Change 8:704–708.

Fraser, C. I., R. Nikula, and J. M. Waters. 2011. Oceanic rafting by a coastal community. Proceedings of the Royal Society B: Biological Sciences 278:649–655.

Fraser, C. I., M. Velásquez, W. A. Nelson, E. C. Macaya, and C. H. Hay. 2020. The biogeographic importance of buoyancy in macroalgae: A case study of the southern bull-kelp genus *Durvillaea* (Phaeophyceae), including descriptions of two new species. Journal of Phycology 56:23–36.

Fraser, C. I., and J. M. Waters. 2013. Algal parasite *Herpodiscus durvillaeae* (Phaeophyceae: Sphacelariales) inferred to have traversed the Pacific Ocean with its buoyant host. Journal of Phycology 49:202–206.

Fraser, L. H. 2020. TRY—A plant trait database of databases. Global Change Biology 26:189–190.

Fristoe, T. S., M. Chytrý, W. Dawson, F. Essl, R. Heleno, H. Kreft, N. Maurel, J. Pergl, P. Pyšek, H. Seebens, P. Weigelt, P. Vargas, Q. Yang, F. Attorre, E. Bergmeier, M. Bernhardt-Römermann, I. Biurrun, S. Boch, G. Bonari, Z. Botta-Dukát, H. H. Bruun, C. Byun, A. Čarni, M. L. Carranza, J. A. Catford, B. E. L. Cerabolini, E. Chacón-Madrigal, D. Ciccarelli, R. Ćušterevska, I. de Ronde, J. Dengler, V. Golub, R. Haveman, N. Hough-Snee, U. Jandt, F. Jansen, A. Kuzemko, F. Küzmič, J. Lenoir, A. Macanović, C. Marcenò, A. R. Martin, S. T. Michaletz, A. S. Mori, Ü. Niinemets, T. Peterka, R. Pielech, V. Rašomavičius, S. Rusina, A. S. Dias, M. Šibíková, U. Šilc, A. Stanisci, S. Jansen, J.-C. Svenning, G. Swacha, F. van der Plas, K. Vassilev, and M. van Kleunen. 2021. Dimensions of invasiveness: Links between local abundance, geographic range size, and habitat breadth in Europe’s alien and native floras. Proceedings of the National Academy of Sciences 118.

Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C. Laughlin, A. E. Sutton-Grier, L. Williams, and J. Wright. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological Reviews 92:1156–1173.

Gallagher, R. V., R. P. Randall, and M. R. Leishman. 2015. Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. Conservation Biology 29:360–369.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/heirarchical model. Cambridge University Press, Cambridge, United Kingdom and New York, USA.

Gennaro, P., L. Piazzi, E. Persia, and S. Porrello. 2015. Nutrient exploitation and competition strategies of the invasive seaweed *Caulerpa cylindracea*. European Journal of Phycology 50:384–394.

Geoffroy, A., L. Le Gall, and C. Destombe. 2012. Cryptic introduction of the red alga *Polysiphonia morrowii* Harvey (Rhodomelaceae, Rhodophyta) in the North Atlantic Ocean highlighted by a DNA barcoding approach. Aquatic Botany 100:67–71.

Gioria, M., and B. A. Osborne. 2014. Resource competition in plant invasions: emerging patterns and research needs. Frontiers in Plant Science 5.

Goecke, F., J. Wiese, A. Núñez, A. Labes, J. F. Imhoff, and S. Neuhauser. 2012. A novel phytomyxean parasite associated with galls on the bull-kelp *Durvillaea antarctica* (Chamisso) Hariot. PLoS ONE 7:e45358.

Gollan, J. R., and J. T. Wright. 2006. Limited grazing pressure by native herbivores on the invasive seaweed *Caulerpa taxifolia* in a temperate Australian estuary. Marine and Freshwater Research 57:685.

Gordon, D. R., C. A. Gantz, C. L. Jerde, W. L. Chadderton, R. P. Keller, and P. D. Champion. 2012. Weed risk assessment for aquatic plants: Modification of a New Zealand system for the United States. PLoS ONE 7:e40031.

Green, P. T., D. J. O'Dowd, K. L. Abbott, M. Jeffery, K. Retallick, and R. Mac Nally. 2011. Invasional meltdown: Invader–invader mutualism facilitates a secondary invasion. Ecology 92:1758–1768.

Grewell, B. J., M. J. Skaer Thomason, C. J. Futrell, M. Lannucci, and R. E. Drenovsky. 2016. Trait responses of invasive aquatic macrophyte congeners: colonizing diploid outperforms polyploid. AoB Plants 8:1–11.

Groner, M. L., J. Maynard, R. Breyta, R. B. Carnegie, A. Dobson, C. S. Friedman, B. Froelich, M. Garren, F. M. D. Gulland, S. F. Heron, R. T. Noble, C. W. Revie, J. D. Shields, R. Vanderstichel, E. Weil, S. Wyllie-Echeverria, and C. D. Harvell. 2016. Managing marine disease emergencies in an era of rapid change. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150364.

Gross, N., L. Börger, R. P. Duncan, and P. E. Hulme. 2013. Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands? Functional Ecology 27:1262–1272.

Grubb, P. J. 1998. A reassessment of the strategies of plants which cope with shortages of resources. Perspectives in Plant Ecology, Evolution and Systematics 1:3–31.

Gu, Z., L. Gu, R. Eils, M. Schlesner, and B. Brors. 2014. circlize implements and enhances circular visualization in R. Bioinformatics 30:2811–2812.

Guindon, S., J.-F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk, and O. Gascuel. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Systematic Biology 59:307–321.

Guiry, M. D. 2012. How many species of algae are there? Journal of Phycology 48:1057–1063.

Guiry, M. D., and G. M. Guiry. 2022. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. https://www.algaebase.org.

Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions: Conceptual frameworks for biological invasions. Ecology Letters 14:407–418.

Haavisto, F., R. Koivikko, and V. Jormalainen. 2017. Defensive role of macroalgal phlorotannins: benefits and trade-offs under natural herbivory. Marine Ecology Progress Series 566:79–90.

Hagerman, L. 1966. The macro- and microfauna associated with *Fucus serratus* L., with some ecological remarks. Ophelia 3:1–43.

Hanspach, J., I. Kühn, P. Pyšek, E. Boos, and S. Klotz. 2008. Correlates of naturalization and occupancy of introduced ornamentals in Germany. Perspectives in Plant Ecology, Evolution and Systematics 10:241–250.

Hargrave, M. S., A. Foggo, A. Pessarrodona, and D. A. Smale. 2017. The effects of warming on the ecophysiology of two co-existing kelp species with contrasting distributions. Oecologia 183:531–543.

Harley, C. D. G., K. M. Anderson, K. W. Demes, J. P. Jorve, R. L. Kordas, T. A. Coyle, and M. H. Graham. 2012. Effects of climate change on global seaweed communities. Journal of Phycology 48:1064–1078.

Harries, D. B., E. Cook, D. W. Donnan, J. M. Mair, S. Harrow, and J. R. Wilson. 2007. The establishment of the invasive alga *Sargassum muticum* on the west coast of Scotland: Rapid northwards spread and identification of potential new areas for colonisation. Aquatic Invasions 2:367–377.

Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann, E. K. Lipp, A. D. M. E. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith, and G. R. Vasta. 1999. Emerging marine diseases - climate links and anthropogenic factors. Science 285:1505–1510.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296:2158–2162.

Hay, C. H. 2020. Seashore uplift and the distribution of the bull kelp *Durvillaea willana* Lindauer in New Zealand. New Zealand Journal of Botany 58:94–117.

Hay, M. E., and P. D. Steinberg. 1992. The chemical ecology of plant herbivore interactions in marine versus terrestrial communities. Pages 371–413 *in* G. A. Rosenthal and M. R.

Berenbaum, editors. Herbivores: their interactions with secondary plant metabolites. Academic Press, New York.

Heger, T., and J. M. Jeschke. 2014. The enemy release hypothesis as a hierarchy of hypotheses. Oikos 123:741–750.

Heiser, S., J. M. Hall-Spencer, and K. Hiscock. 2014. Assessing the extent of establishment of *Undaria pinnatifida* in Plymouth Sound Special Area of Conservation, UK. Marine Biodiversity Records 7:e93.

Helsen, K., H. Matsushima, B. Somers, and O. Honnay. 2021. A trait-based approach across the native and invaded range to understand plant invasiveness and community impact. Oikos 130:1001–1013.

Henkel, S. K., and G. E. Hofmann. 2008. Thermal ecophysiology of gametophytes cultured from invasive *Undaria pinnatifida* (Harvey) Suringar in coastal California harbors. Journal of Experimental Marine Biology and Ecology 367:164–173.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: To grow or defend. The Quarterly Review of Biology 67:283–335.

Hess, M. C. M., E. Buisson, R. Jaunatre, and F. Mesléard. 2020. Using limiting similarity to enhance invasion resistance: Theoretical and practical concerns. Journal of Applied Ecology 57:559–565.

Hewitt, C. L., M. L. Campbell, and B. Schaffelke. 2007. Introductions of seaweeds: accidental transfer pathways and mechanisms. Botanica Marina 50:326–337.

Hodgson, J., P. Wilson, R. Hunt, J. Grime, and K. Thompson. 1999. Allocating C-S-R plant functional types: A soft approach to a hard problem. Oikos 85:282–294.

Hoffmann, B. D., and L. M. Broadhurst. 2016. The economic cost of managing invasive species in Australia. NeoBiota 31:1–18.

Honjo, M. N., N. Emura, T. Kawagoe, J. Sugisaka, M. Kamitani, A. J. Nagano, and H. Kudoh. 2020. Seasonality of interactions between a plant virus and its host during persistent infection in a natural environment. The ISME Journal 14:506–518.

Houssard, C., and J. Escarré. 1991. The effects of seed weight on growth and competitive ability of Rumex acetosella from two successional old-fields. Oecologia 86:236–242.

Hovick, S. M., and K. D. Whitney. 2019. Propagule pressure and genetic diversity enhance colonization by a ruderal species: a multi-generation field experiment. Ecological Monographs 89.

Humair, F., L. Humair, F. Kuhn, and C. Kueffer. 2015. E-commerce trade in invasive plants: E-commerce Scanning for Invaders. Conservation Biology 29:1658–1665.

Incera, M., C. Olabarria, E. Cacabelos, J. César, and J. S. Troncoso. 2011. Distribution of *Sargassum muticum* on the North West coast of Spain: Relationships with urbanization and community diversity. Continental Shelf Research 31:488–495.

Ingólfsson, A. 2008. The invasion of the intertidal canopy-forming alga Fucus serratus L. to southwestern Iceland: Possible community effects. Estuarine, Coastal and Shelf Science 77:484–490.

IPBES. 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretatiat, Bonn, Germany.

IUCN. 2000. Guidelines for the prevention of biodiversity loss caused by alien invasive species. IUCN, GLAND SWITZERLAND.

James, G., D. Witten, T. Hastie, and R. Tibshirani. 2013. An Introduction to Statistical Learning. Springer New York, New York, NY.

Jaramillo, E., R. D. L. Huz, C. Duarte, and H. Contreras. 2006. Algal wrack deposits and macroinfaunal arthropods on sandy beaches of the Chilean coast. Revista Chilena de Historia Natural 79:337–351.

Jarošík, V., M. Kenis, A. Honěk, J. Skuhrovec, and P. Pyšek. 2015. Invasive insects differ from non-invasive in their thermal requirements. PLOS ONE 10:e0131072.

Jaspers, C., B. Huwer, E. Antajan, A. Hosia, H.-H. Hinrichsen, A. Biastoch, D. Angel, R. Asmus, C. Augustin, S. Bagheri, S. E. Beggs, T. J. S. Balsby, M. Boersma, D. Bonnet, J. T. Christensen, A. Dänhardt, F. Delpy, T. Falkenhaug, G. Finenko, N. E. C. Fleming, V. Fuentes, B. Galil, A. Gittenberger, D. C. Griffin, H. Haslob, J. Javidpour, L. Kamburska, S. Kube, V. T. Langenberg, M. Lehtiniemi, F. Lombard, A. Malzahn, M. Marambio, V. Mihneva, L. F. Møller, U. Niermann, M. I. Okyar, Z. B. Özdemir, S. Pitois, T. B. H. Reusch, J. Robbens, K. Stefanova, D. Thibault, H. W. van der Veer, L. Vansteenbrugge, L. van Walraven, and A. Woźniczka. 2018. Ocean current connectivity propelling the secondary spread of a marine invasive comb jelly across western Eurasia. Global Ecology and Biogeography 27:814–827.

Jeschke, J. M. 2014. General hypotheses in invasion ecology. Diversity and Distributions 20:1229–1234.

Jiménez, R. S., C. D. Hepburn, G. A. Hyndes, R. J. McLeod, R. B. Taylor, and C. L. Hurd. 2015. Do native subtidal grazers eat the invasive kelp *Undaria pinnatifida*? Marine Biology 162:2521–2526.

Jones, G., and W. Farnham. 1973. Japweed: new threat to British coasts. New Scientist 60:394–395.

Josse, J., and F. Husson. 2016. **missMDA** : A Package for Handling Missing Values in Multivariate Data Analysis. Journal of Statistical Software 70.

Jung, V., C. Violle, C. Mondy, L. Hoffmann, and S. Muller. 2010. Intraspecific variability and trait-based community assembly: Intraspecific variability and community assembly. Journal of Ecology 98:1134–1140.

Kassambara, A., and F. Mundt. 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Keane, R. M., and M. Crawley J. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17:164–170.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, and A. Drummond. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647–1649.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Kelly, B. J., and M. T. Brown. 2000. Variations in the alginate content and composition of *Durvillaea antarctica* and *D. willana* from southern New Zealand. Journal of Applied Phycology 12:317–324.

Kimbro, D. L., B. S. Cheng, and E. D. Grosholz. 2013. Biotic resistance in marine environments. Ecology Letters 16:821–833.

van Kleunen, M., O. Bossdorf, and W. Dawson. 2018. The ecology and evolution of alien plants. Annual Review of Ecology, Evolution, and Systematics 49:25–47.

van Kleunen, M., W. Dawson, D. Schlaepfer, J. M. Jeschke, and M. Fischer. 2010a. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness: Comparisons on determinants of invasiveness. Ecology Letters 13:947–958.

van Kleunen, M., E. Weber, and M. Fischer. 2010b. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13:235–245.

Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. van Groenendael, L. Klimeš, J. Klimešová, S. Klotz, G. M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J. G. Hodgson, A.-K. Jackel, I. Kühn, D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266–1274.

Klinerová, T., K. Tasevová, and P. Dostál. 2018. Large generative and vegetative reproduction independently increases global success of perennial plants from Central Europe. Journal of Biogeography 45:1550–1559.

Koerich, G., J. Assis, G. B. Costa, M. N. Sissini, E. A. Serrão, L. R. Rörig, J. M. Hall-Spencer, J. B. Barufi, and P. A. Horta. 2020. How experimental physiology and ecological niche modelling can inform the management of marine bioinvasions? Science of The Total Environment 700:134692.

Kooyman, R., W. Cornwell, and M. Westoby. 2010. Plant functional traits in Australian subtropical rain forest: partitioning within-community from cross-landscape variation. Journal of Ecology 98:517–525.

Krumins, J. A., V. Krumins, E. Forgoston, L. Billings, and W. H. van der Putten. 2015. Herbivory and stoichiometric feedbacks to primary production. PLoS ONE 10:e0129775.

Kubát, K., L. Hrouda, J. jun. Chrtek, Z. Kaplan, J. Kirchner, and J. Štěpánek, editors. 2002. Klíč ke květeně České Republiky. [Key to the Flora of the Czech Republic]. Academia, Praha.

Kubešová, M., L. Moravcová, J. Suda, V. Jarošík, and P. Pyšek. 2010. Naturalized plants have smaller genomes than their non-invading relatives: a flow cytometric analysis of the Czech alien flora. Preslia 82:81–96.

Kueffer, C., P. Pyšek, and D. M. Richardson. 2013. Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytologist 200:615–633.

Kumar, V., E. Zozaya-Valdes, S. Kjelleberg, T. Thomas, and S. Egan. 2016. Multiple opportunistic pathogens can cause a bleaching disease in the red seaweed *Delisea pulchra*. Environmental Microbiology 18:3962–3975.

Kurr, M., and A. J. Davies. 2018. Time-since-invasion increases native mesoherbivore feeding rates on the invasive alga, *Sargassum muticum* (Yendo) Fensholt. Journal of the Marine Biological Association of the United Kingdom 98:1935–1944.

Lai, H. R., M. M. Mayfield, J. M. Gay-des-combes, T. Spiegelberger, and J. M. Dwyer. 2015. Distinct invasion strategies operating within a natural annual plant system. Ecology Letters 18:336–346.

Lajeunesse, M. J. 2016. Facilitating systematic reviews, data extraction and meta-analysis with the metagear package for R. Methods in Ecology and Evolution 7:323–330.

Langar, H., A. S. Djellouli, F. Sellem, and A. El Abed. 2002. Extension of two *Caulerpa* species along the Tunisian coast. Journal of Coastal Conservation 8:163–167.

Lapointe, B. E., and B. J. Bedford. 2011. Stormwater nutrient inputs favor growth of non-native macroalgae (Rhodophyta) on O’ahu, Hawaiian Islands. Harmful Algae 10:310–318.

Latombe, G., S. Canavan, H. Hirsch, C. Hui, S. Kumschick, M. M. Nsikani, L. J. Potgieter, T. B. Robinson, W. -C. Saul, S. C. Turner, J. R. U. Wilson, F. A. Yannelli, and D. M. Richardson.

2019. A four-component classification of uncertainties in biological invasions: implications for management. Ecosphere 10:e02669.

Laughlin, D. C., R. T. Strahan, D. W. Huffman, and A. J. S. Meador. 2017. Using trait-based ecology to restore resilient ecosystems: historical conditions and the future of montane forests in western North America. Restoration Ecology:12.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail: *Plant response and effect groups*. Functional Ecology 16:545–556.

Le Cam, S., C. Daguin-Thiébaut, S. Bouchemousse, A. H. Engelen, N. Mieszkowska, and F. Viard. 2020. A genome-wide investigation of the worldwide invader *Sargassum muticum* shows high success albeit (almost) no genetic diversity. Evolutionary Applications 13:500–514.

Lê, S., J. Josse, and F. Husson. 2008. **FactoMineR** : An *R* Package for Multivariate Analysis. Journal of Statistical Software 25.

Leclerc, J., P. Riera, C. Leroux, L. Lévêque, and D. Davoult. 2013. Temporal variation in organic matter supply in kelp forests: linking structure to trophic functioning. Marine Ecology Progress Series 494:87–105.

Lees, L. E., S. A. Krueger-Hadfield, A. J. Clark, E. A. Duermit, E. E. Sotka, and C. J. Murren. 2018. Nonnative *Gracilaria vermiculophylla* tetrasporophytes are more difficult to debranch and are less nutritious than gametophytes. Journal of Phycology 54:471–482.

Leffler, A. J., J. J. James, T. A. Monaco, and R. L. Sheley. 2014. A new perspective on trait differences between native and invasive exotic plants. Ecology 95:298–305.

Leger, E. A., and E. K. Espeland. 2010. Coevolution between native and invasive plant competitors: implications for invasive species management: Managing coevolution. Evolutionary Applications 3:169–178.

Leishman, M. R., and B. R. Murray. 2001. The relationship between seed size and abundance in plant communities: model predictions and observed patterns. Oikos 94:151–161.

Leung, B., D. M. Lodge, D. Finnoff, J. F. Shogren, M. A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:2407–2413.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions: Biotic resistance to plant invasion. Ecology Letters 7:975–989.

Liu, H., P. Stiling, and R. W. Pemberton. 2007. Does enemy release matter for invasive plants? evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. Biological Invasions 9:773–781.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20:223–228.

Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distributions 15:904–910.

Lowry, E., E. J. Rollinson, A. J. Laybourn, T. E. Scott, M. E. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3:182–196.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. The American Naturalist 112:23–39.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annual Review of Ecology and Systematics 12:405–437.

Lüdecke, D. 2018. ggeffects: Tidy data frames of marginal effects from regression models. Journal of Open Source Software 3:772.

Lüdecke, D. 2021. sjPlot: Data visualization for statistics in social science.

Lüdecke, D., M. Ben-Shachar, I. Patil, and D. Makowski. 2020. Extracting, computing and exploring the parameters of statistical models using R. Journal of Open Source Software 5:2445.

Ludlow, M. M. 1989. Strategies of response to water stress. Pages 269–281 *in* K. H. Kreeb, H. Richter, and T. M. Minckley, editors. Structural and functional responses to environmental stress. SPB Academic, The Hague, the Netherlands.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

MacLeod, A., E. J. Cook, D. Hughes, and C. Allen. 2016. Investigating the impacts of marine invasive non-native species. Page 59. A report by Scottish Association for Marine Science Research Services Ltd for Natural England & Natural Resources Wales, Natural England Commissioned Reports.

Maier, I., E. Parodi, R. Westermeier, and D. G. Müller. 2000. *Maullinia ectocarpii* gen. et sp. nov. (Plasmodiophorea), an intracellular parasite in *Ectocarpus siliculosus* (Ectocarpales, Phaeophyceae) and other filamentous brown algae. Protist 151:225–238.

Mangiafico, S. 2021. rcompanion: Functions to support extension education program evaluation.

Mannino, A. M., and C. Micheli. 2020. Ecological function of phenolic compounds from Mediterranean fucoid algae and seagrasses: An overview on the genus *Cystoseira sensu lato* and *Posidonia oceanica* (L.) Delile. Journal of Marine Science and Engineering 8:19.

Martín-Vélez, V., C. H. A. van Leeuwen, M. I. Sánchez, F. Hortas, J. Shamoun-Baranes, C. B. Thaxter, L. Lens, C. J. Camphuysen, and A. J. Green. 2021. Spatial patterns of weed dispersal by wintering gulls within and beyond an agricultural landscape. Journal of Ecology 109:1947–1958.

Mathakutha, R., C. Steyn, P. C. le Roux, I. J. Blom, S. L. Chown, B. H. Daru, B. S. Ripley, A. Louw, and M. Greve. 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. Journal of Vegetation Science 30:994–1006.

Matteodo, M., S. Wipf, V. Stöckli, C. Rixen, and P. Vittoz. 2013. Elevation gradient of successful plant traits for colonizing alpine summits under climate change. Environmental Research Letters 8:024043.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

Mauffrey, A. R. L., L. Cappelatti, and J. N. Griffin. 2020. Seaweed functional diversity revisited: Confronting traditional groups with quantitative traits. Journal of Ecology 108:2390–2405.

Maurel, N., J. Hanspach, I. Kühn, P. Pyšek, and M. van Kleunen. 2016. Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success: Introduction bias and naturalization success. Global Ecology and Biogeography 25:1500–1509.

McCallen, E., J. Knott, G. Nunez-Mir, B. Taylor, I. Jo, and S. Fei. 2019. Trends in ecology: shifts in ecological research themes over the past four decades. Frontiers in Ecology and the Environment 17:109–116.

McCallum, H., D. Harvell, and A. Dobson. 2003. Rates of spread of marine pathogens. Ecology Letters 6:1062–1067.

McGeoch, M. A., and G. Latombe. 2016. Characterizing common and range expanding species. Journal of Biogeography 43:217–228.

McGeoch, M. A., D. Spear, E. J. Kleynhans, and E. Marais. 2012. Uncertainty in invasive alien species listing. Ecological Applications 22:959–971.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–185.

McKnight, E., E. García-Berthou, P. Srean, and M. Rius. 2017. Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems. Global Change Biology 23:1861–1870.

McLaughlan, C., B. Gallardo, and D. C. Aldridge. 2014. How complete is our knowledge of the ecosystem services impacts of Europe’s top 10 invasive species? Acta Oecologica 54:119–130.

Menge, J. L. 1975. Effect of herbivores on community structure of the New England rocky intertidal region: distribution, abundance and diversity of algae. PhD diss., Harvard University.

Meyerson, L. A., and H. A. Mooney. 2007. Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5:199–208.

Mitchell, C. E., and A. G. Power. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421:625–627.

Moles, A. T., and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. Journal of Ecology 92:372–383.

Moles, A. T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. Oikos 113:91–105.

Monteiro, C. A., A. H. Engelen, and R. O. P. Santos. 2009. Macro- and mesoherbivores prefer native seaweeds over the invasive brown seaweed *Sargassum muticum*: a potential regulating role on invasions. Marine Biology 156:2505–2515.

Moore, L. B., and A. B. Cribb. 1952. The brown alga *Durvillea antarctica* in Australian waters. Nature 169:1101–1102.

Morais, P., and M. Reichard. 2018. Cryptic invasions: A review. Science of The Total Environment 613–614:1438–1448.

Moravcová, L., P. Pyšek, V. Jarošík, V. Havlíčková, and P. Zákravský. 2010. Reproductive characteristics of neophytes in the Czech Republic: Traits of invasive and non-invasive species. Preslia 82:365–390.

Moravcová, L., P. Pyšek, V. Jarošík, and J. Pergl. 2015. Getting the right traits: Reproductive and dispersal characteristics predict the invasiveness of herbaceous plant species. PLOS ONE 10:e0123634.

de Moura Queirós, A., J. G. Hiddink, G. Johnson, H. N. Cabral, and M. J. Kaiser. 2011. Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. Biological Invasions 13:1059–1075.

Mouritsen, O. G., P. Rhatigan, and J. L. Pérez-Lloréns. 2018. World cuisine of seaweeds: Science meets gastronomy. International Journal of Gastronomy and Food Science 14:55–65.

Muff, S., E. B. Nilsen, R. B. O’Hara, and C. R. Nater. 2021. Rewriting results sections in the language of evidence. Trends in Ecology & Evolution:S0169534721002846.

Muller-Landau, H. C. 2010. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. Proceedings of the National Academy of Sciences 107:4242–4247.

Murúa, P., F. Goecke, R. Westermeier, P. van West, F. C. Küpper, and S. Neuhauser. 2017. *Maullinia braseltonii* sp. nov. (Rhizaria, Phytomyxea, Phagomyxida): A cyst-forming parasite of the bull kelp *Durvillaea* spp. (Stramenopila, Phaeophyceae, Fucales). Protist 168:468–480.

Muthukrishnan, R., and D. J. Larkin. 2020. Invasive species and biotic homogenization in temperate aquatic plant communities. Global Ecology and Biogeography 29:656–667.

Najdek, M., M. Korlević, P. Paliaga, M. Markovski, I. Ivančić, L. Iveša, I. Felja, and G. J. Herndl. 2020. Effects of the invasion of *Caulerpa cylindracea* in a *Cymodocea nodosa* meadow in the Northern Adriatic sea. Frontiers in Marine Science 7:602055.

Nathan, R. 2006. Long-distance dispersal of plants. Science 313:786–788.

Naylor, R. L., S. L. Williams, and D. R. Strong. 2001. Aquaculture - A gateway for exotic species. Science 294:1655–1656.

Nejrup, L., and M. Pedersen. 2010. Growth and biomass development of the introduced red alga *Gracilaria vermiculophylla* is unaffected by nutrient limitation and grazing. Aquatic Biology 10:249–259.

Neuhauser, S., M. Kirchmair, and F. H. Gleason. 2011. Ecological roles of the parasitic phytomyxids (plasmodiophorids) in marine ecosystems - a review. Marine and Freshwater Research 62:365–371.

Neuwirth, E. 2014. RColorBrewer: ColorBrewer Palettes.

Norton, T. A. 1977. The growth and development of *Sargassum muticum* (Yendo) Fensholt. Journal of Experimental Marine Biology and Ecology 26:41–53.

Norton, T. A., S. J. Hawkins, N. L. Manley, G. A. Williams, and D. C. Watson. 1988. Scraping a living: a review of littorinid grazing. Pages 117–138 *in* K. Johannesson, D. G. Raffaelli, and C. J. Hannaford Ellis, editors. Progress in littorinid and muricid biology. Springer Netherlands, Tjärnö Marine Biological Laboratory, Sweden.

Novoa, A., D. M. Richardson, P. Pyšek, L. A. Meyerson, S. Bacher, S. Canavan, J. A. Catford, J. Čuda, F. Essl, L. C. Foxcroft, P. Genovesi, H. Hirsch, C. Hui, M. C. Jackson, C. Kueffer, J. J. Le Roux, J. Measey, N. P. Mohanty, D. Moodley, H. Müller-Schärer, J. G. Packer, J. Pergl, T. B.

Robinson, W.-C. Saul, R. T. Shackleton, V. Visser, O. L. F. Weyl, F. A. Yannelli, and J. R. U. Wilson. 2020. Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management. Biological Invasions 22:1801–1820.

Nurjanah, M. Nurilmala, T. Hidayat, and F. Sudirdjo. 2016. Characteristics of seaweed as raw materials for cosmetics. Aquatic Procedia 7:177–180.

Nyberg, C. D., and I. Wallentinus. 2005. Can species traits be used to predict marine macroalgal introductions? Biological Invasions 7:265–279.

Ogle, D. H., J. C. Doll, P. Wheeler, and A. Dinno. 2021. FSA: Fisheries Stock Analysis.

Oróstica, M., R. Otaíza, and P. Neill. 2012. Blades and papillae as likely dispersing propagules in Chilean populations of *Mastocarpus* sp. (Rhodophyta, Gigartinales). Revista de Biología Marina y Oceanografía 47:109–119.

Padgham, M., and M. D. Summer. 2021. geodist: Fast, Dependency-Free Geodesic Distance Calculations.

Palma, E., A. L. Mabey, P. A. Vesk, and J. A. Catford. 2021a. Characterising invasive species. Page *in* K. Barker and R. A. Francis, editors. Routledge Handbook of Biosecurity and Invasive Species.

Palma, E., P. A. Vesk, M. White, J. B. Baumgartner, and J. A. Catford. 2021b. Plant functional traits reflect different dimensions of species invasiveness. Ecology 102:e03317.

Parodi, E. R., E. J. Cáceres, R. Westermeier, and D. G. Müller. 2010. Secondary zoospores in the algal endoparasite *Maullinia ectocarpii* (Plasmodiophoromycota). Biocell 34:45–52.

Paula, S., M. Arianoutsou, D. Kazanis, Ç. Tavsanoglu, F. Lloret, C. Buhk, F. Ojeda, B. Luna, J. M. Moreno, A. Rodrigo, J. M. Espelta, S. Palacio, B. Fernández-Santos, P. M. Fernandes, and J. G. Pausas. 2009. Fire-related traits for plant species of the Mediterranean Basin: *Ecological Archives* E090-094. Ecology 90:1420–1420.

Pearson, D. E., Y. K. Ortega, Ö. Eren, and J. L. Hierro. 2018. Community assembly theory as a framework for biological invasions. Trends in Ecology & Evolution 33:313–325.

Pedersen, M. F., K. L. Johnsen, L. L. Halle, N. D. Karling, and T. Salo. 2016. Enemy release an unlikely explanation for the invasive potential of the brown alga *Sargassum muticum*: experimental results, literature review and meta-analysis. Marine Biology 163:1–14.

Pejchar, L., and H. A. Mooney. 2009. Invasive species, ecosystem services and human well-being. Trends in Ecology & Evolution 24:497–504.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. B. Reich, L. Poorter, I. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. de Vos, N. Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti, G. Conti, A. C. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61:167–234.

Pessarrodona, A., A. Foggo, and D. A. Smale. 2019. Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests. Journal of Ecology 107:91–104.

Pheloung, P. C., P. A. Williams, and S. R. Halloy. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57:239–251.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

Pinteus, S., M. F. L. Lemos, C. Alves, J. Silva, and R. Pedrosa. 2021. The marine invasive seaweeds *Asparagopsis armata* and *Sargassum muticum* as targets for greener antifouling solutions. Science of The Total Environment 750:141372.

Pinteus, S., M. F. L. Lemos, M. Simões, C. Alves, J. Silva, H. Gaspar, A. Martins, A. Rodrigues, and R. Pedrosa. 2020. Marine invasive species for high-value products’ exploration – Unveiling the antimicrobial potential of *Asparagopsis armata* against human pathogens. Algal Research 52:102091.

Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E. E. Sotka, J. J. Stachowicz, R. B. Taylor, M. A. Vanderklift, and J. Emmett Duffy. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecology Letters 15:912–922.

Poore, A. G. B., and N. A. Hill. 2006. Sources of variation in herbivore preference: among-individual and past diet effects on amphipod host choice. Marine Biology 149:1403–1410.

Price, P. W., M. Westoby, B. Rice, P. R. Atsatt, R. S. Fritz, J. N. Thompson, and K. Mobley. 1986. Parasite mediation in ecological interactions. Annual Review of Ecology and Systematics 17:487–505.

Primo, C., C. L. Hewitt, and M. L. Campbell. 2010. Reproductive phenology of the introduced kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) in Port Phillip Bay (Victoria, Australia). Biological Invasions 12:3081–3092.

Pyšek, P., M. Chytrý, J. Pergl, J. Sádlo, and J. Wild. 2012a. Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. Preslia 84:575–629.

Pyšek, P., J. Danihelka, J. Sádlo, J. Chrtek Jr., M. Chytrý, V. Jarošík, Z. Kaplan, F. Krahulec, L. Moravcová, J. Pergl, K. Štajerová, and T. Lubomír. 2012b. Catalogue of alien plants of the

Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. Preslia 84:155–255.

Pyšek, P., and P. E. Hulme. 2005. Spatio-temporal dynamics of plant invasions: Linking pattern to process. Écoscience 12:302–315.

Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, J. T. Carlton, W. Dawson, F. Essl, L. C. Foxcroft, P. Genovesi, J. M. Jeschke, I. Kühn, A. M. Liebhold, N. E. Mandrak, L. A. Meyerson, A. Pauchard, J. Pergl, H. E. Roy, H. Seebens, M. Kleunen, M. Vilà, M. J. Wingfield, and D. M. Richardson. 2020. Scientists' warning on invasive alien species. Biological Reviews 95:1511–1534.

Pyšek, P., and V. Jarošík. 2005. Residence time determines the distribution of alien plants. Pages 77–69 *in* Inderjit, editor. Invasive Plants: Ecological and Agricultural Aspects. Birkhäuser Verlag-AG.

Pyšek, P., V. Jarošík, and J. Pergl. 2011. Alien plants introduced by different pathways differ in invasion success: Unintentional introductions as a threat to natural areas. PLoS ONE 6:e24890.

Pyšek, P., M. Křivánek, and V. Jarošík. 2009. Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90:2734–2744.

Pyšek, P., A. M. Manceur, C. Alba, K. F. McGregor, J. Pergl, K. Štajerová, M. Chytrý, J. Danihelka, J. Kartesz, J. Klimešová, M. Lučanová, L. Moravcová, M. Nishino, J. Sádlo, J. Suda, L. Tichý, and I. Kühn. 2015. Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96:762–774.

Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: Where do we stand? Pages 97–125 *in* W. Nentwig, editor. Biological Invasions. Springer Berlin Heidelberg, Berlin, Heidelberg.

Pyšek, P., D. M. Richardson, and V. Jarošík. 2006. Who cites who in the invasion zoo: insights from an analysis of the most highly cited papers in invasion ecology. Preslia 78:437–468.

Pyšek, P., J. Sádlo, and B. Mandák. 2002. Catalogue of alien plants of the Czech Republic. Preslia 74:97–186.

Pyšek, P., H. Skálová, J. Čuda, W.-Y. Guo, J. Suda, J. Doležal, O. Kauzál, C. Lambertini, M. Lučanová, T. Mandáková, L. Moravcová, K. Pyšková, H. Brix, and L. A. Meyerson. 2018. Small genome separates native and invasive populations in an ecologically important cosmopolitan grass. Ecology 99:79–80.

Questad, E. J., and B. L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. Ecology Letters 11:717–726.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ragan, M. A., and A. Jensen. 1978. Quantitative studies on brown algal phenols. II. Seasonal variation in polyphenol content of *Ascophyllum nodosum* (L.) Le Jol. and *Fucus vesiculosus* (L.). Journal of Experimental Marine Biology and Ecology 34:245–258.

Redding, D. W., A. L. Pigot, E. E. Dyer, Ç. H. Şekercioğlu, S. Kark, and T. M. Blackburn. 2019. Location-level processes drive the establishment of alien bird populations worldwide. Nature 571:103–106.

Rejmánek, M. 1996. A theory of seed plant invasiveness: The first sketch. Biological Conservation 78:171–181.

Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655–1661.

Ricciardi, A., T. M. Blackburn, J. T. Carlton, J. T. A. Dick, P. E. Hulme, J. C. Iacarella, J. M. Jeschke, A. M. Liebhold, J. L. Lockwood, H. J. MacIsaac, P. Pyšek, D. M. Richardson, G. M. Ruiz, D. Simberloff, W. J. Sutherland, D. A. Wardle, and D. C. Aldridge. 2017. Invasion science: A horizon scan of emerging challenges and opportunities. Trends in Ecology & Evolution 32:464–474.

Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress towards understanding the ecological impacts of nonnative species. Ecological Monographs 83:263–282.

Ricciardi, A., J. C. Iacarella, D. C. Aldridge, T. M. Blackburn, J. T. Carlton, J. A. Catford, J. T. A. Dick, P. E. Hulme, J. M. Jeschke, A. M. Liebhold, J. L. Lockwood, H. J. MacIsaac, L. A. Meyerson, P. Pyšek, D. M. Richardson, G. M. Ruiz, D. Simberloff, M. Vilà, and D. A. Wardle. 2021. Four priority areas to advance invasion science in the face of rapid environmental change. Environmental Reviews 29:119–141.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Robuchon, M., S. Vranken, L. Vandepitte, S. Dekeyzer, R. Julliard, L. Le Gall, and O. De Clerk. 2015. Towards a seaweed trait database for European species.

Russell, L. K., C. D. Hepburn, C. L. Hurd, and M. D. Stuart. 2008. The expanding range of *Undaria pinnatifida* in southern New Zealand: distribution, dispersal mechanisms and the invasion of wave-exposed environments. Biological Invasions 10:103–115.

Salvaterra, T., D. S. Green, T. P. Crowe, and E. J. O’Gorman. 2013. Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure. Biological Invasions 15:2563–2576.

Santamaría, J., F. Tomas, E. Ballesteros, J. M. Ruiz, J. Bernardeau-Esteller, J. Terrados, and E. Cebrian. 2021. The role of competition and herbivory in biotic resistance against invaders: a synergistic effect. Ecology 102.

Sapsford, S. J., A. J. Brandt, K. T. Davis, G. Peralta, I. A. Dickie, R. D. Gibson, J. L. Green, P. E. Hulme, M. A. Nuñez, K. H. Orwin, A. Pauchard, D. A. Wardle, and D. A. Peltzer. 2020. Towards a framework for understanding the context dependence of impacts of non-native tree species. Functional Ecology 34:944–955.

Sardain, A., E. Sardain, and B. Leung. 2019. Global forecasts of shipping traffic and biological invasions to 2050. Nature Sustainability 2:274–282.

Schade, F. M., M. J. Raupach, and K. Mathias Wegner. 2016. Seasonal variation in parasite infection patterns of marine fish species from the Northern Wadden Sea in relation to interannual temperature fluctuations. Journal of Sea Research 113:73–84.

Schaffelke, B., J. E. Smith, and C. L. Hewitt. 2006. Introduced macroalgae – a growing concern. Journal of Applied Phycology 18:529–541.

Scheibling, R. E., and R. A. Melady. 2008. Effect of water movement and substratum type on vegetative recruitment of the invasive green alga *Codium fragile ssp. tomentosoides*. Botanica Marina 51.

Schiel, D. R. 2006. Rivets or bolts? When single species count in the function of temperate rocky reef communities. Journal of Experimental Marine Biology and Ecology 338:233–252.

Schleuning, M., E. L. Neuschulz, J. Albrecht, I. M. A. Bender, D. E. Bowler, D. M. Dehling, S. A. Fritz, C. Hof, T. Mueller, L. Nowak, M. C. Sorensen, K. Böhning-Gaese, and W. D. Kissling. 2020. Trait-based assessments of climate-change impacts on interacting species. Trends in Ecology & Evolution 35:319–328.

Schwartz, N., S. Rohde, S. Hiromori, and P. J. Schupp. 2016. Understanding the invasion success of *Sargassum muticum*: herbivore preferences for native and invasive *Sargassum* spp. Marine Biology 163:181.

Seebens, H., N. Schwartz, P. J. Schupp, and B. Blasius. 2016. Predicting the spread of marine species introduced by global shipping. Proceedings of the National Academy of Sciences 113:5646–5651.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions 1:21–32.

Slavík, B. 1998. Phytocarographical syntheses of the Czech Republic. Academia, Praha.

Smit, A. J. 2004. Medicinal and pharmaceutical uses of seaweed natural products: A review. Journal of Applied Phycology 16:245–262.

Sobel, A. H., S. J. Camargo, T. M. Hall, C.-Y. Lee, M. K. Tippett, and A. A. Wing. 2016. Human influence on tropical cyclone intensity. Science 353:242–246.

Sotka, E. E., A. W. Baumgardner, P. M. Bippus, C. Destombe, E. A. Duermit, H. Endo, B. A. Flanagan, M. Kamiya, L. E. Lees, C. J. Murren, M. Nakaoka, S. J. Shainker, A. E. Strand, R. Terada, M. Valero, F. Weinberger, and S. A. Krueger-Hadfield. 2018. Combining niche shift and population genetic analyses predicts rapid phenotypic evolution during invasion. Evolutionary Applications 11:781–793.

Sotka, E. E., R. B. Taylor, and M. E. Hay. 2002. Tissue-specific induction of resistance to herbivores in a brown seaweed: the importance of direct grazing versus waterborne signals from grazed neighbors. Journal of Experimental Marine Biology and Ecology 277:1–12.

South, P. M., S. A. Lilley, L. W. Tait, T. Alestra, M. J. H. Hickford, M. S. Thomsen, and D. R. Schiel. 2016. Transient effects of an invasive kelp on the community structure and primary productivity of an intertidal assemblage. Marine and Freshwater Research 67:103.

Speek, T. A. A., L. A. P. Lotz, W. A. Ozinga, W. L. M. Tamis, J. H. J. Schaminée, and W. H. van der Putten. 2011. Factors relating to regional and local success of exotic plant species in their new range: Invasiveness at regional and local scales. Diversity and Distributions 17:542–551.

Steinberg, P. D. 1984. Algal chemical defense against herbivores: Allocation of phenolic compounds in the kelp *Alaria marginata*. Science 223:405–407.

Steinberg, P. D. 1988. Effects of quantitative and qualitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. Journal of Experimental Marine Biology and Ecology 120:221–237.

Steinberg, P. D. 1995. Seasonal variation in the relationship between growth rate and phlorotannin production in the kelp *Ecklonia radiata*. Oecologia 102:169–173.

Stekhoven, D. J., and P. Bühlmann. 2012. MissForest-non-parametric missing value imputation for mixed-type data. Bioinformatics 28:112–118.

Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. Marine Biology 68:299–319.

Strong, J. A., C. A. Maggs, and M. P. Johnson. 2009a. The extent of grazing release from epiphytism for Sargassum muticum (Phaeophyceae) within the invaded range. Journal of the Marine Biological Association of the United Kingdom 89:303–314.

Stuart, M. D. 2004. Review of research on *Undaria pinnatifida* in New Zealand and its potential impacts on the eastern coast of the South Island. Pages 1–40. Department of Conservation, Wellington.

Suding, K. N., and L. J. Goldstein. 2008. Testing the Holy Grail framework: using functional traits to predict ecosystem change. New Phytologist 180:559–562.

Sutton-Grier, A. E., and J. P. Megonigal. 2011. Plant species traits regulate methane production in freshwater wetland soils. Soil Biology and Biochemistry 43:413–420.

Swanson, A. K., and L. D. Druehl. 2002. Induction, exudation and the UV protective role of kelp phlorotannins. Aquatic Botany 73:241–253.

Swenson, N. G., B. J. Enquist, J. Pither, A. J. Kerkhoff, B. Boyle, M. D. Weiser, J. J. Elser, W. F. Fagan, J. Forero-Montaña, N. Fyllas, N. J. B. Kraft, J. K. Lake, A. T. Moles, S. Patiño, O. L. Phillips, C. A. Price, P. B. Reich, C. A. Quesada, J. C. Stegen, R. Valencia, I. J. Wright, S. J. Wright, S. Andelman, P. M. Jørgensen, T. E. Lacher Jr, A. Monteagudo, M. P. Núñez-Vargas, R. Vasquez-Martínez, and K. M. Nolting. 2012. The biogeography and filtering of woody plant functional diversity in North and South America: Functional trait biogeography. Global Ecology and Biogeography 21:798–808.

Taylor, D., and D. Schiel. 2005. Self-replacement and community modification by the southern bull kelp *Durvillaea antarctica*. Marine Ecology Progress Series 288:87–102.

Teagle, H., S. J. Hawkins, P. J. Moore, and D. A. Smale. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. Journal of Experimental Marine Biology and Ecology 492:81–98.

Thiel, M., and L. Gutow. 2005a. The ecology of rafting in the marine environment. I. The floating substrata. Pages 181–263 *in* R. Gibson, R. Atkinson, and J. Gordon, editors. Oceanography and Marine Biology. CRC Press.

Thiel, M., and L. Gutow. 2005b. The ecology of rafting in the marine environment. II. The rafting organisms and community. Pages 279–418 *in* R. Gibson, J. Gordon, and R. Atkinson, editors. Oceanography and Marine Biology. CRC Press.

Thompson, K., K. J. Gaston, and S. R. Band. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. Journal of Ecology 87:150–155.

Thomsen, M. S., L. Mondardini, T. Alestra, S. Gerrity, L. Tait, P. M. South, S. A. Lilley, and D. R. Schiel. 2019. Local Extinction of Bull Kelp (*Durvillaea* spp.) due to a Marine Heatwave. Frontiers in Marine Science 6:1–10.

Thornalley, D. J. R., D. W. Oppo, P. Ortega, J. I. Robson, C. M. Brierley, R. Davis, I. R. Hall, P. Moffa-Sanchez, N. L. Rose, P. T. Spooner, I. Yashayaev, and L. D. Keigwin. 2018. Anomalously weak Labrador Sea convection and Atlantic overturning during the past 150 years. Nature 556:227–230.

Thornber, C. S., B. P. Kinlan, M. H. Graham, and J. J. Stachowicz. 2004. Population ecology of the invasive kelp *Undaria pinnatifida* in California: environmental and biological controls on demography. Marine Ecology Progress Series 268:69–80.

Tobias, J. A., C. Sheard, A. L. Pigot, A. J. M. Devenish, J. Yang, F. Sayol, M. H. C. Neate-Clegg, N. Alioravainen, T. L. Weeks, R. A. Barber, P. A. Walkden, H. E. A. MacGregor, S. E. I. Jones, C. Vincent, A. G. Phillips, N. M. Marples, F. A. Montaño-Centellas, V. Leandro-Silva, S. Claramunt, B. Darski, B. G. Freeman, T. P. Bregman, C. R. Cooney, E. C. Hughes, E. J. R. Capp, Z. K. Varley, N. R. Friedman, H. Korntheuer, A. Corrales-Vargas, C. H. Trisos, B. C. Weeks, D. M. Hanz, T. Töpfer, G. A. Bravo, V. Remeš, L. Nowak, L. S. Carneiro, A. J. Moncada R., B. Matysioková, D. T. Baldassarre, A. Martínez-Salinas, J. D. Wolfe, P. M. Chapman, B. G. Daly, M. C. Sorensen, A. Neu, M. A. Ford, R. J. Mayhew, L. Fabio Silveira, D. J. Kelly, N. N. D. Annorbah, H. S. Pollock, A. M. Grabowska-Zhang, J. P. McEntee, J. Carlos T. Gonzalez, C. G. Meneses, M. C. Muñoz, L. L. Powell, G. A. Jamie, T. J. Matthews, O. Johnson, G. R. R. Brito, K. Zyskowski, R. Crates, M. G. Harvey, M. Jurado Zevallos, P. A. Hosner, T. Bradfer-Lawrence, J. M. Maley, F. G. Stiles, H. S. Lima, K. L. Provost, M. Chibesa, M. Mashao, J. T. Howard, E. Mlamba, M. A. H. Chua, B. Li, M. I. Gómez, N. C. García, M. Päckert, J. Fuchs, J. R. Ali, E. P. Derryberry, M. L. Carlson, R. C. Urriza, K. E. Brzeski, D. M. Prawiradilaga, M. J. Rayner, E. T. Miller, R. C. K. Bowie, R. Lafontaine, R. P. Scofield, Y. Lou, L. Somarathna, D. Lepage, M. Illif, E. L. Neuschulz, M. Templin, D. M. Dehling, J. C. Cooper,

O. S. G. Pauwels, K. Analuddin, J. Fjeldså, N. Seddon, P. R. Sweet, F. A. J. DeClerck, L. N. Naka, J. D. Brawn, A. Aleixo, K. Böhning-Gaese, C. Rahbek, S. A. Fritz, G. H. Thomas, and M. Schleuning. 2022. AVONET: morphological, ecological and geographical data for all birds. Ecology Letters 25:581–597.

Tuanmu, M.-N., and W. Jetz. 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Global Ecology and Biogeography 23:1031–1045.

Turnbull, L. A., C. D. Philipson, D. W. Purves, R. L. Atkinson, J. Cunniff, A. Goodenough, Y. Hautier, J. Houghton, T. R. Marthews, C. P. Osborne, C. Paul-Victor, K. E. Rose, P. Saner, S. H. Taylor, F. I. Woodward, A. Hector, and M. Rees. 2012. Plant growth rates and seed size: a re-evaluation. Ecology 93:1283–1289.

Turner, S. J., and C. D. Todd. 1991. The effects of *Gibbuia cineraria* (L.), *Nucella lapillus* (L.) and *Asterias rubens* L. on developing epifaunal assemblages. Journal of Experimental Marine Biology and Ecology 154:191–213.

Uyà, M., F. Bulleri, and P. E. Gribben. 2018. Propagules are not all equal: traits of vegetative fragments and disturbance regulate invasion success. Ecology 99:957–965.

Uyà, M., E. Maggi, G. Mori, C. Nuccio, P. E. Gribben, and F. Bulleri. 2017. Carry over effects of nutrient addition on the recovery of an invasive seaweed from the winter die-back. Marine Environmental Research 126:37–44.

Valéry, L., H. Fritz, J.-C. Lefeuvre, and D. Simberloff. 2009. Invasive species can also be native…. Trends in Ecology & Evolution 24:585–585.

Van Alstyne, K. L. 1988. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus Distichus*. Ecology 69:655–663.

Van Alstyne, K. L., S. L. Whitman, and J. M. Ehlig. 2001. Differences in herbivore preferences, phlorotannin production, and nutritional quality between juvenile and adult tissues from marine brown algae. Marine Biology 139:201–210.

Vasconcelos, M. A., C. L. Q. Schubart, and M. T. M. de Széchy. 2011. Temporal variation in vegetative development of *Caulerpa scalpelliformis* (Chlorophyta) from Baleia beach, Ilha Grande bay (Rio de Janeiro, Brazil). Brazilian Journal of Oceanography 59:145–152.

Vedder, D., L. Leidinger, and J. Sarmento Cabral. 2021. Propagule pressure and an invasion syndrome determine invasion success in a plant community model. Ecology and Evolution 11:17106–17116.

Veiga, P., M. Rubal, and I. Sousa-Pinto. 2014. Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species. Marine Environmental Research 101:115–123.

Venette, R. C., D. R. Gordon, J. Juzwik, F. H. Koch, A. M. Liebhold, R. K. D. Peterson, S. E. Sing, and D. Yemshanov. 2021. Early intervention strategies for invasive species management: Connections between risk assessment, prevention efforts, eradication, and other rapid responses. Pages 111–131 *in* T. M. Poland, T. Patel-Weynand, D. M. Finch, C. F. Miniat, D. C. Hayes, and V. M. Lopez, editors. Invasive Species in Forests and Rangelands of the United States: A Comprehensive Science Synthesis for the United States Forest Sector. Springer International Publishing, Cham.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Violle, C., P. B. Reich, S. W. Pacala, B. J. Enquist, and J. Kattge. 2014. The emergence and promise of functional biogeography. Proceedings of the National Academy of Sciences 111:13690–13696.

Walsh, J. R., S. R. Carpenter, and M. J. Vander Zanden. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences 113:4081–4085.

Walsh, P., D. Metzger, and R. Higuchi. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques 10:506–513.

Walther, G.-R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pyšek, I. Kühn, M. Zobel, S. Bacher, Z. Botta-Dukát, and H. Bugmann. 2009. Alien species in a warmer world: risks and opportunities. Trends in Ecology & Evolution 24:686–693.

Wang, H., S. P. Harrison, I. C. Prentice, Y. Yang, F. Bai, H. F. Togashi, M. Wang, S. Zhou, and J. Ni. 2018. The China plant trait database: toward a comprehensive regional compilation of functional traits for land plants. Ecology 99:500–500.

Watanabe, S., A. Metaxas, and R. E. Scheibling. 2009. Dispersal potential of the invasive green alga *Codium fragile ssp. fragile*. Journal of Experimental Marine Biology and Ecology 381:114–125.

Waters, J. M., T. M. King, C. I. Fraser, and D. Craw. 2018. Crossing the front: contrasting storm-forced dispersal dynamics revealed by biological, geological and genetic analysis of beach-cast kelp. Journal of The Royal Society Interface 15:20180046.

Watkins, H. V., H. F. Yan, J. C. Dunic, and I. M. Côté. 2021. Research biases create overrepresented “poster children” of marine invasion ecology. Conservation Letters 14.

Watson, D. C., and T. A. Norton. 1985. Dietary preferences of the common periwinkle, *Littorina littorea* (L.). Journal of Experimental Marine Biology and Ecology 88:81–91.

Weber, J., F. Dane Panetta, J. Virtue, and P. Pheloung. 2009. An analysis of assessment outcomes from eight years’ operation of the Australian border weed risk assessment system. Journal of Environmental Management 90:798–807.

Weinberger, F., B. Buchholz, R. Karez, and M. Wahl. 2008. The invasive red alga *Gracilaria vermiculophylla* in the Baltic Sea: adaptation to brackish water may compensate for light limitation. Aquatic Biology 3:251–264.

Weis, I. M. 1982. The effects of propagule size on germination and seedling growth in *Mirabilis hirsuta* . Canadian Journal of Botany 60.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33:125–159.

White, L. F., and J. B. Shurin. 2011. Density dependent effects of an exotic marine macroalga on native community diversity. Journal of Experimental Marine Biology and Ecology 405:111–119.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Williams, S. L., M. E. S. Bracken, and E. Jones. 2013. Additive effects of physical stress and herbivores on intertidal seaweed biodiversity. Ecology 94:1089–1101.

Williamson, M., K. Dehnen-Schmutz, I. Kühn, M. Hill, S. Klotz, A. Milbau, J. Stout, and P. Pyšek. 2009. The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. Diversity and Distributions 15:158–166.

Williamson, M. H., and A. Fitter. 1996. The characters of successful invaders. Biological Conservation 78:163–170.

Williamson, M., P. Pyšek, V. Jarošík, and K. Prach. 2005. On the rates and patterns of spread of alien plants in the Czech Republic, Britain, and Ireland. Écoscience 12: 424-433.

Wilson, J. R. U., C. Gairifo, M. R. Gibson, M. Arianoutsou, B. B. Bakar, S. Baret, L. Celesti-Grapow, J. M. DiTomaso, J.-M. Dufour-Dror, C. Kueffer, C. A. Kull, J. H. Hoffmann, F. A. C. Impson, L. L. Loope, E. Marchante, H. Marchante, J. L. Moore, D. J. Murphy, J. Tassin, A. Witt, R. D.

Zenni, and D. M. Richardson. 2011. Risk assessment, eradication, and biological control: global efforts to limit Australian acacia invasions: Pro-active management of Australian acacias. Diversity and Distributions 17:1030–1046.

Yokomizo, H., H. P. Possingham, M. B. Thomas, and Y. M. Buckley. 2009. Managing the impact of invasive species: the value of knowing the density–impact curve. Ecological Applications 19:376–386.

Zanolla, M., M. Altamirano, R. Carmona, J. De La Rosa, A. Sherwood, and N. Andreakis. 2015. Photosynthetic plasticity of the genus *Asparagopsis* (Bonnemaisoniales, Rhodophyta) in response to temperature: implications for invasiveness. Biological Invasions 17:1341–1353.

Zenni, R. D., F. Essl, E. García-Berthou, and S. M. McDermott. 2021. The economic costs of biological invasions around the world. NeoBiota 67:1–9.