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The use of species traits in invasive seaweed research: a systematic review

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Abstract

Species traits have been used extensively in invasion science, providing common metrics across taxa and ecosystems that enable comparisons based on the functional responses and effects of biota. However, most work on traits in invasion science has focused on terrestrial plants, despite the vulnerability of aquatic ecosystems to invasive species, such as invasive seaweeds. Research that focuses on individual species of invasive seaweeds has intensified in recent years, yet few studies have synthesised the information learned on species traits to identify commonalities or knowledge gaps in invasion science. Through a systematic review of 322 papers that investigate the traits of seaweed species from across the globe, here we ask – what are the trends and gaps in research that investigates traits of invasive seaweeds? To address this question, we aimed to: (1) identify publication rates and characteristics of the studies examining traits of invasive seaweeds; (2) clarify which and how many species have been investigated; and (3) assess which traits have been measured and how those traits have been used. Our review revealed that study regions for research on invasive seaweed traits were concentrated in Europe and North America. In addition, we found a total of 158 species that have been investigated, with a large proportion of studies (35%) focusing on just two species, *Sargassum muticum* and *Undaria pinnatifida*. Our study revealed that the most researched traits were morphological, which were used to address a wide range of research questions. Key research gaps included relatively few studies from Africa, Asia and South America, a lack of papers researching more than one species and a lack of measurements of biomechanical traits. Altogether, this review provides a thorough overview of research progress on species traits of invasive seaweeds and highlights the existing knowledge gaps that may lead to new ways in which the traits of invasive seaweeds can be used to answer important ecological questions.

Keywords
Characteristics, functional traits, macroalgae, non-indigenous, non-native

Introduction

Species traits can be defined as measurable features of an organism that potentially affect performance or fitness and that can be measured at the individual level (Cadotte et al. 2011; Dawson et al. 2021). Traits provide a common metric, comparable across taxa and systems, that allow ecologists to move from taxonomic assessments and comparisons to studies based on functional responses and effects (Funk et al. 2017). Species traits have been widely used across a variety of disciplines, including community ecology, evolutionary biology 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; Birks 2020; Schleuning et al. 2020). They have become an especially valuable tool in invasion science and biosecurity (Palma et al. 2021a).

Non-native species are those that are transported to areas beyond their native range through accidental or intentional human mediated transport of species (Pimentel et al. 2005; Hewitt et al. 2007; Aguiar and Ferreira 2013). Some of these non-native species may become invasive through dispersing from their point of introduction and increasing their population and range sizes (Blackburn et al. 2011). 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). Indeed, a systematic review undertaken by Dalla Vecchia et al. (2020) on functional traits in aquatic plants found an increasing trend in the number of published papers investigating functional traits of macrophytes over time, with invasiveness being the third most investigated topic.

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), continued rapid expansion of aquaculture (Ahmed and Thompson 2019) and ocean warming facilitating the spread of invasive species (Bellard et al. 2013; McKnight et al. 2021). 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.

One of the largest investigations of traits of invasive seaweeds was carried out by Nyberg and Wallentinus (2005), who examined 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 in research investigating traits of invasive seaweeds, combined with the growing availability of seaweed trait data shared via databases (Mauffrey et al. 2020; Vranken et al. 2022), suggests that there is great potential for the use of seaweed traits to address 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. To the best of our knowledge, this is the first systematic review that examines the use of traits in invasive seaweed research. Using a systematic and reproducible methodology (based upon the principles outlined in Moher et al. (2009)), we screened the scientific literature to find relevant papers to address the research question 'what are the trends and gaps in research that investigates traits of invasive seaweeds'? Our study had three main aims: (1) to identify the rate of publications and characteristics of the studies examining the 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. This systematic review aims to provide an overview of this subject. This will include providing insights into how rapidly this field is expanding, what species are being investigated the most and which traits are being studied. We conclude by highlighting research gaps and providing recommendations for further work.

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 (Suppl. material 1: table S1) and, in total, 19,954 records were downloaded from all three databases (Suppl. material 1: fig. S1). 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. From this, 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. A total of 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 that 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. At each stage of screening, records were only accepted if they were published in English. This resulted in 322 papers being included in the analysis (Suppl. material 1: fig. S1).

For each paper included in this review, 15 categories were used to collect data, similar to those adopted by Dalla Vecchia et al. (2020) in a systematic review of the use of functional traits in macrophyte studies. Each category contributed to 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 by 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 from which the invasive species were collected. The second aim (2) to clarify which and how many species have been investigated was met by collecting 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. (2010)]. 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 each individual study.

The geographic area of first author was recorded as the country or countries of the associated institutions 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 from where the population of the invasive species was collected. 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 were 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 following the classification found in the World Register of Marine Species (Ahyong et al. 2023). 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 (Palma et al. 2021b). To investigate whether studies accounted for this, we recorded if criteria for invasiveness were noted in the paper and, if so, what criteria were used. We found that the criteria used in the studies corresponded with the four demographic dimensions of invasiveness, which were previously identified by Catford et al. (2016). These were local abundance, geographic range size, environmental range size and spread rate, which can be combined to give 15 forms of invasiveness. We accordingly recorded what combination of the four demographic dimensions each study used. 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. We chose to note this aspect of a study because some studies may just examine traits of invasive species in isolation, whereas others have used comparisons between invasive species and native species (here referred to as a baseline) to investigate whether invasive species have different traits from those of non-invasive species (van Kleunen et al. 2010).

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. Reproduction 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. Season/time 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 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 that 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 that investigated how traits changed with the invasive process, such as propagule pressure or differences between native and invasive populations. Other included any main aims that 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, respectively) and 'circlize' for the chord diagrams (Gu et al. 2014).

Given our focus on trends in literature, we re-ran the search on 6 November 2022 in Web of Science and EBSCO*host* Greenfile to estimate how many new papers may have been excluded from our systematic review. Since our initial search date of 21 January 2021, we estimate that approximately 31 additional papers could be included if we had used a November 2022 search date. This accounts for < 10% of the 322 papers used in our review and is, thus, not expected to significantly change the results presented here (Suppl. material 1: appendix 1).

Data availability

All data generated or analysed during this study are included in this published article and its Suppl. materials 1, 2.

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 risen, as 39% of the 322 papers included in this review were published between 2014 and 2021. This reflects trends in the wider literature, as the number of publications that mention ecology, invasive species and traits in the title, abstract or keywords has also increased since 1985 (Fig. 1a; Suppl. material 1: appendix 2, fig. S2a). The papers included in this review were published in a wide range of journals (Suppl. material 1: table S2), with the journal Botanica Marina being the most common (35% of papers in this review) (Fig. 1b; Suppl. material 1: fig. S2b).

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%) (Fig. 2a). 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

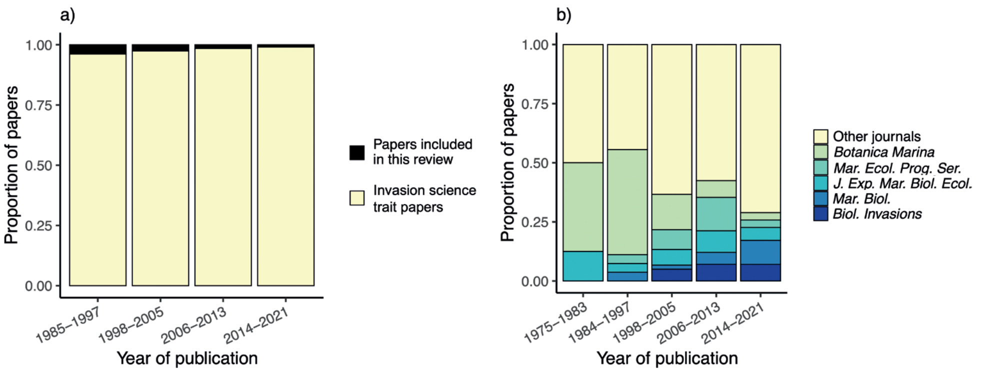

Figure 1. a The proportion of invasion science papers published on species traits (see Suppl. material 1: appendix 2) over time, alongside the number of papers that met the criteria to be included in this review and **b** stacked bars showing the proportion of papers included in this review published over time, showing the five most common journals where the papers were published.

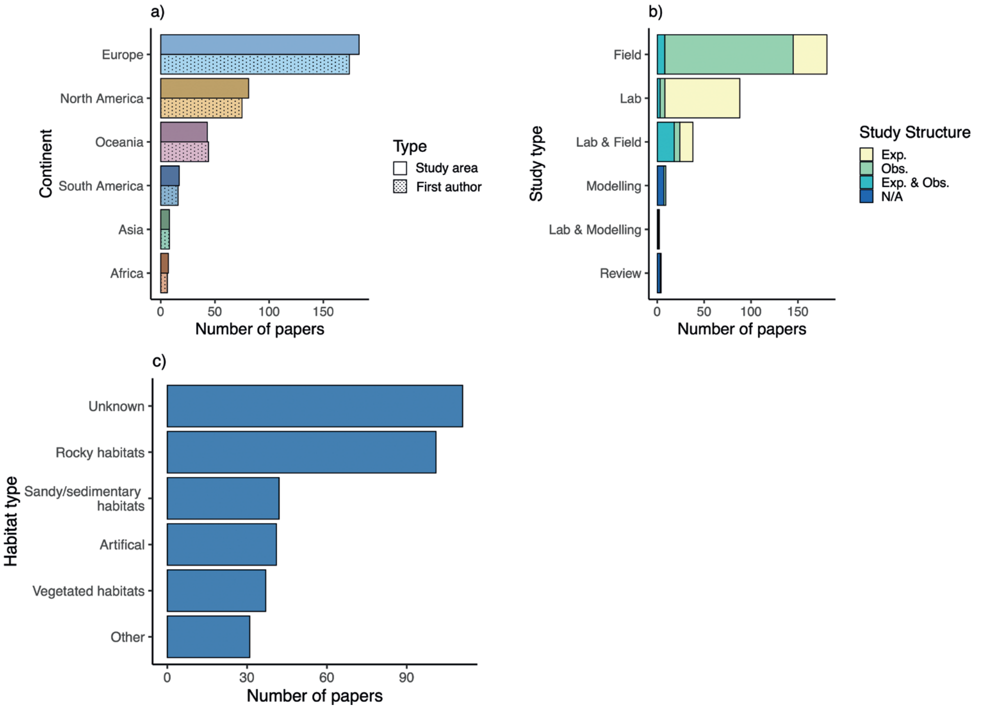

Figure 2. The **a** geographic area of first author affiliation and the study area (where the invasive species were sampled from) (two papers had a global study area and two had a study area of the Northern Hemisphere which are not shown). Multiple geographic areas were recorded for both first author and study locations, but more so for the latter. 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 from where the invasive species were collected.

lab and field studies (12% of all papers) (Fig. 2b). Whilst many papers did not record the habitat type from where seaweed samples were collected (n = 111, 34%), for those which did, the majority were taken from rocky habitats (31%) (Fig. 2c).

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

The 322 papers included in this review measured traits of 158 seaweed species. Of these, the most investigated taxonomic classification was Rhodophyta (65% of all species) and Chlorophyta was the least studied (11%) (Fig. 3a), following broader trends in both the number of orders and the proportion of orders that include a non-native species (Schaffelke et al. 2006) (Fig. 3c). However, the most investigated seaweed species (*Sargassum muticum* and *Undaria pinnatifida*) both belong to the Phaeophyceae (Fig. 3b). Eight papers (2%) included species classified as invasive within their native range.

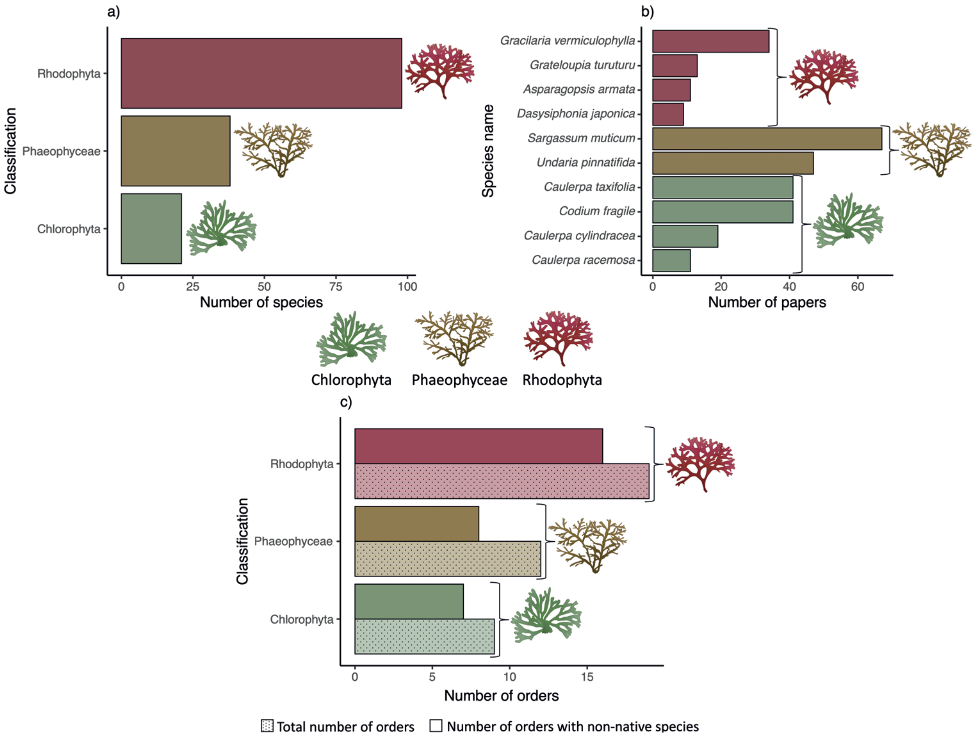

Figure 3. The number of **a** invasive species in each taxonomic group investigated across all papers in this review [two papers each investigated one charophyte species, (see Nyberg and Wallentinus (2005); Sahlin et al. (2011)) which are not shown], **b** the number of papers that investigated the ten 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/).

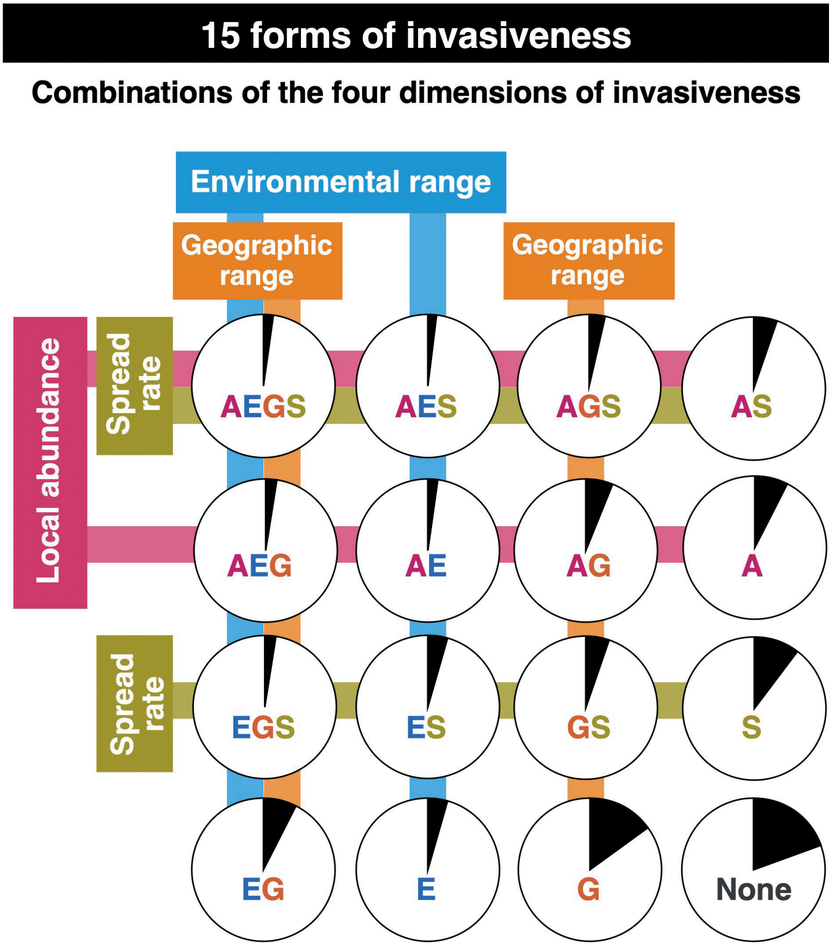

Figure 4. Proportion of 322 trait-based studies that classify invasive seaweed species into 15 forms of invasiveness, based on the dimensions of invasiveness (local abundance, geographic range size, environmental range size and spread rate) and their combinations, as described in Catford et al. (2016). 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).

All 15 forms of invasiveness were represented amongst the 322 studies, i.e. all possible combinations of the four demographic dimensions were used to define invasive species, with geographic range size (15%) and spread rate (10%) being the most frequently used criteria (Fig. 4). However, 20% of papers did not describe the criteria used for classifying species as invasive.

We found that the majority of papers did not include comparisons to a baseline of native species or populations (61% of all papers), suggesting that they are not

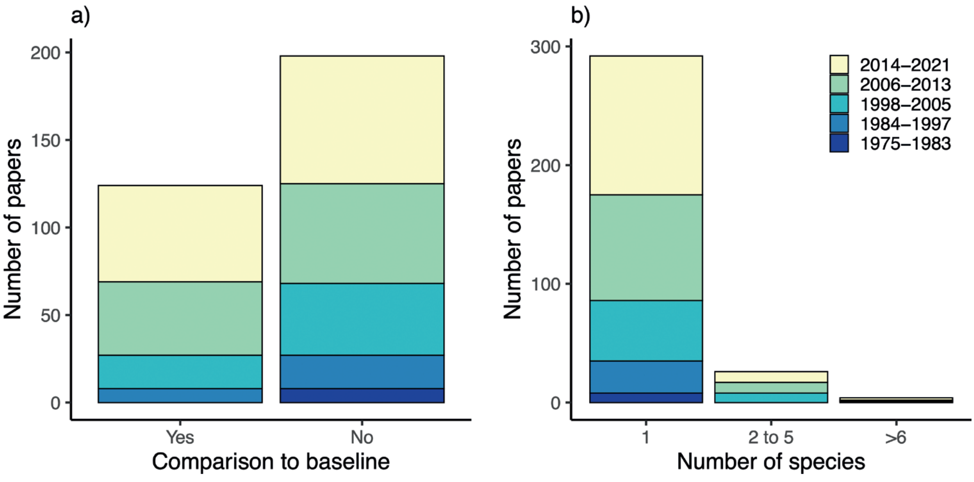

Figure 5. The number of papers which **a** compared the invasive species to a baseline (either a native species or a native population of the invasive species) and the number of papers which **b** studied one, two-five or more than six invasive species within the same paper. Stacked bars show the years of publication.

investigating differences between invasive species and native species or populations of the invasive species in its home (native) and invaded (non-native) range (Fig. 5a). Papers published between 1975 and 1983 did not compare the invasive species to a baseline (either a native species or a native population of the invasive species) (Suppl. material 1: fig. S3a). Most papers investigated one invasive species (91%) and 1% investigated more than six (Fig. 5b). All papers published between 1975 and 1983 included in this systematic review investigated a single invasive species (Suppl. material 1: fig. S3b).

(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 (Fig. 6a). Biomechanical traits were the least investigated (3%). 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) (Fig. 6b). Environmental gradients were the primary main aim investigated by a large margin (31%). Papers which investigated environmental gradients were published in all five time-frames (from 1975 to 2021) (Suppl. material 1: fig. S4c). Commercial application was the least investigated (8%); however, most of these studies were published between 2014 and 2021 (Fig. 6c). Regarding the purpose of the research and, therefore, the reason for measuring traits, the majority of papers investigated one main aim (83%) (Suppl. material 1: fig. S5).

There were no clear trends in which traits were used to investigate certain environmental variables (Fig. 7a) or certain main aims (Fig. 7b). In general, nearly all trait categories were used to investigate all other aims, except for commercial application, which was exclusively investigated using biochemical traits.

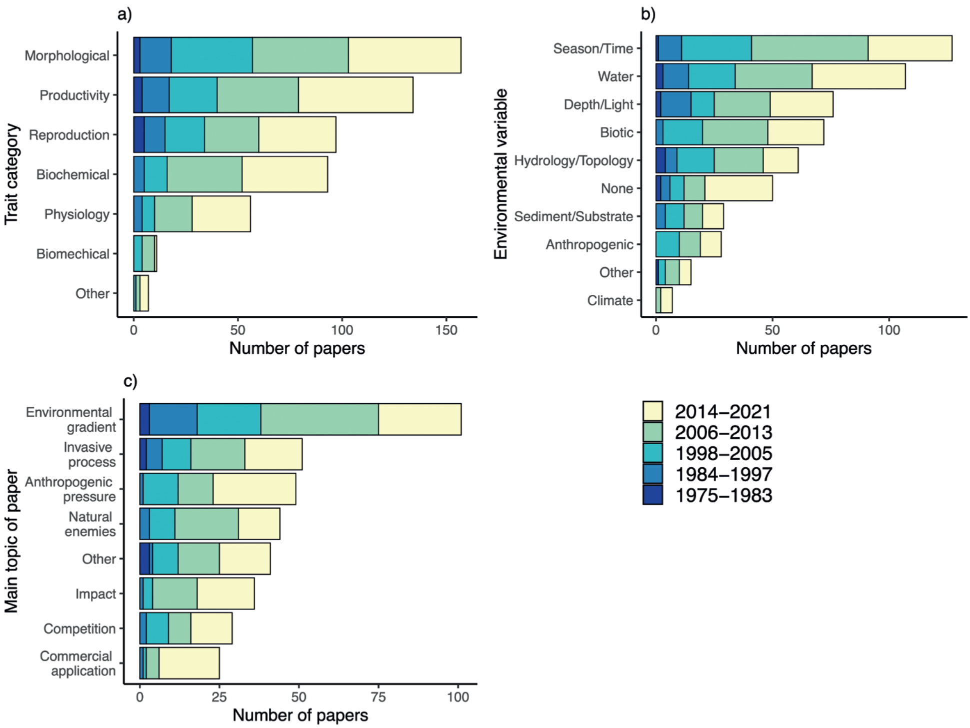

Figure 6. Number of papers which measured **a** categories of traits and **b** environmental variables to reach the **c** main aims of the paper, out of a possible 322 papers.

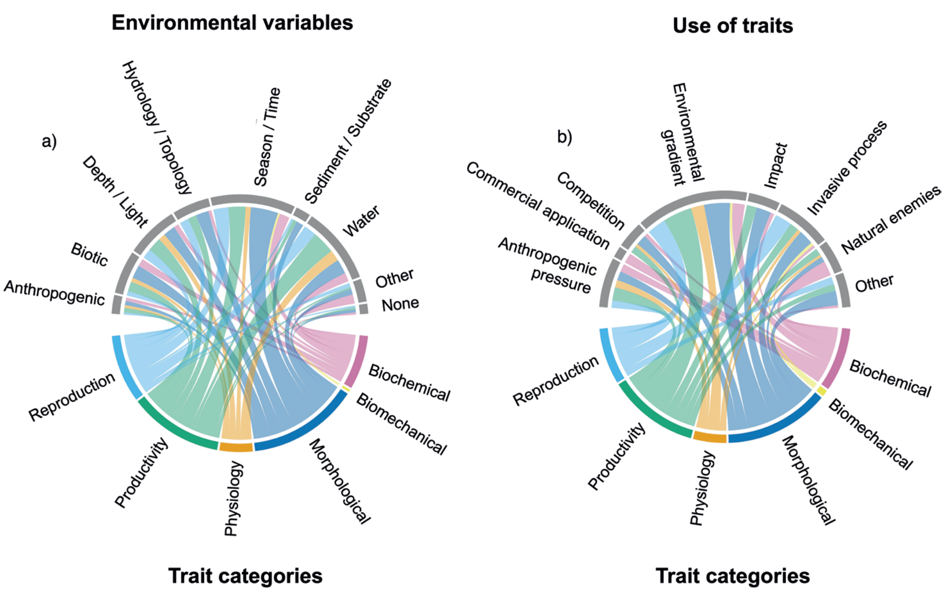

Figure 7. The proportion of papers in which trait categories were investigated **a** alongside environmental variables or **b** how the traits have been used. For clarity, links with less than five connections are not shown in this figure.

Discussion

In this systematic review of 322 papers, we identified several key trends in how studies have investigated traits of invasive seaweeds. These included an increase in publications over time (although this increase did not exceed the background publication rate) and a higher research effort in Europe and North America. We also found a research focus on two brown seaweeds, *Sargassum muticum* and *Undaria pinnatifida*. Finally, morphological and productivity traits were 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 invasion science literature (Rius et al. 2015), 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). We find that, over time, papers included in this review made up a smaller proportion of the invasion science trait literature (Fig. 1a). The increasing number of papers suggests that traits of invasive seaweeds will continue to be used to answer ecological questions in marine ecosystems; however, we do not find evidence that this increase in publications over time exceeds the background publication rate.

The papers included in this systematic review were published in a wide range of journals, but the five journals in which these were most frequently published were Botanica Marina, Marine Ecology Progress Series, Journal of Experimental Marine Biology and Ecology, Marine Ecology and Biological Invasions. Although papers in these journals investigated an invasive species, only one of these top-5 journals specifically focuses on invasion science. This indicates that, for the topic of invasive seaweed traits, a large body of work may be associated with marine biology and ecology topics, rather than exclusively invasion science.

The most studied geographic areas were in Europe, North America and Oceania, with Africa and Asia being extremely under-represented in the papers included in this review. A similar geographical bias was also apparent in the greater research output in Europe and North America which has also been noted in conservation and invasion science literature previously (Pyšek et al. 2006; Lowry et al. 2013; Di Marco et al. 2017; Watkins et al. 2021). This pattern is also reflected in the location of the first author's affiliation, with the majority located within Europe and North America. This consistent trend may reflect the greater amount of funding available, number of researchers and policy-makers' priorities in these areas, amongst other factors, including language. Papers in this review were only included if they were in published English. This may have influenced the geographic distribution observed particularly for under-represented regions, as studies from those regions may have been published in languages other than English and, therefore, be excluded from our review. Based on our search terms, only 3% of the records screened by full paper were excluded because they were not written in English, so we do not expect the results to be substantially affected. However, a recent study that explicitly examined the effect of language choice on invasive species research findings showed that 83% of documents that met particular search criteria were published in English and 17% were published in one of 15 other languages (Angulo et al. 2021). It is, thus, important to acknowledge that this systematic review and the conclusions drawn from it, are based on English-language publications only.

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

Species belonging to 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) (Fig. 3c). 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), are of commercial interest (Yamanaka and Akiyama 1993; Silva et al. 2019), their individuals are relatively large in size and they 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 may be more likely to be noticed, may be easier to collect and measure for functional traits and, therefore, be prioritised for research. In contrast, invasive species that are undetected or are misidentified as a native species or another invasive species [known as cryptic invaders (Morais and Reichard 2018)] are less-well 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 (Fig. 5b), likely due to limitations in the logistics of 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, 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 95 species in the UK (Mauffrey et al. 2020) and a larger pan-European database of 21 traits spanning 1745 species (Vranken et al. 2022). 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 criteria for why species were considered invasive and papers often used non-native and invasive as interchangeable terms. Given the wide remit of invasion science 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. However, going forward, it is vital that papers explicitly state the criteria they use to define a species as invasive or non-native. This transparency would facilitate appropriate comparisons across taxa (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 fast spread rate). If the species is not considered invasive, then authors should clarify that the species is at an earlier stage of the invasion process and refer to it as non-invasive (or a synonym of). Explicit use of clear definitions will enable more meaningful and appropriate comparisons across studies, thus helping to reduce the prevalence of apparent context dependence that can stem from comparing studies that differ in methodological approach, including study metrics (Catford et al. 2022).

(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 that 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 freshwater and marine 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 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 that 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 changed 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). This trend may also be due to the use of non-native species to fulfil anthropogenic needs. For example, the invasive species *S. muticum* has been identified as having several commercial uses, including agricultural applications (e.g. fertiliser) or in a pharmaceutical capacity using bioactive compounds isolated from the seaweed (Milledge et al. 2016). Both of these commercial applications were found as main aims for the papers within our review (Balboa et al. 2016; Sanjeewa et al. 2019; Thompson et al. 2020). We also found papers that focused on the use of invasive seaweed compounds in cosmetics and anti-fouling (Félix et al. 2020; Flórez-Fernández et al. 2021; Pinteus et al. 2021). This reflects the wide range of commercial uses to which seaweeds can be applied and may be of use for managing invasive seaweeds (Milledge et al. 2016). As pressures such as climate change, pollution and habitat degradation increase, these research areas may become more important to understand the relationships between anthropogenic pressures and invasive seaweeds and their potential uses in industry.

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 given the expected increase in the rate of marine introductions. By 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 urgently required in under-studied regions, especially Africa, Asia 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 explicit definitions and criteria should be included in the paper where species are considered invasive. This will be more challenging for species that have not been researched extensively, but providing a definition of invasiveness will still help maintain consistency across papers and, therefore, facilitate meaningful inter-study comparisons (Catford et al. 2022).

iii) One of the benefits of a trait-based approach is that comparisons can be made across species and functional groups. However, most of the 322 papers investigated only one invasive species and did not compare it to a native species or with the same species in its native range. 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 facilitate 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 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 as they may be important attributes which influence species distributions.

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. By providing a concise summary of the research so far, this review has identified knowledge gaps and future research directions for invasive seaweed research.

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Supplementary material 1

Supplementary information

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Data type: NA (PDF file)

Explanation note: Supplementary information referenced throughout the paper.

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Supplementary material 2

Associated data

Authors: Abigail L. Mabey, Marc Rius, Dan A. Smale, Jane A. Catford

Data type: Categorical data collected from published papers (excel document)

Explanation note: Data collected from 322 papers included in this review, and the relevant bibliographic information.

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