

RESEARCH HIGHLIGHT

The untapped potential of categorical traits in seaweed functional diversity research

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A short introduction to trait-based approaches in seaweeds

Traits are a powerful lens through which to view evolution and ecology. They allow us to examine organisms' ecological strategies, their response to the environment, and understand their effects on ecosystem functions and services (Garnier, Navas & Grigulis 2016). While no panacea, traits remain a central pillar of terrestrial plant ecology, where standardised methods and global databases yield myriad insights (Díaz *et al.* 2016; Carmona *et al.* 2021). Yet, a trait-based ecological understanding of marine macroalgae, or 'seaweed', has lagged behind that of plants. In this issue, Fong *et al.* show how the use of categorical traits can greatly accelerate progress in the emerging field of seaweed trait-based ecology.

A key reason behind the slow emergence of a trait-based approach to seaweeds is their inherent evolutionary and ecological complexity. Seaweeds are a polyphyletic group, with representatives from three major divisions (the Rhodophyta [red], Chlorophyta [green], and Gyrista [brown]) of algae spanning two distinct clades (the stramenopile-alveolate-Rhizaria supergroup and the Archaeplastida), which last shared a common ancestor over a billion years ago. Alongside this deep evolutionary diversity, seaweeds show immense ecological variation: they inhabit diverse environments, from temperate intertidal rocky shores to subtidal deepwater tropical reefs, range in

morphology from rows of single cells to differentiated forest-forming giant kelps, and exhibit diverse life cycles, often with heteromorphic stages (Hurd *et al.* 2014).

Traditionally, seaweed ecologists have dealt with such complexity through frameworks that conceive distinct groups based on gross morphology, such as ‘sheet-like’ or ‘thick and leathery’ (Littler & Littler 1980; Steneck & Dethier 1994; Figure 1). However, these functional groupings overlap considerably and do not correspond well to those based on quantitative traits (Ryznar, Fong & Fong 2020), reducing mechanistic insights, limiting comparisons with similar trait-based approaches to understanding form and function in other producer groups, and constraining flexibility in the use of traits e.g., specific sets for specific functions. Systematic trait-based approaches are at last gaining traction, with, for example, a recent effort in this journal (Mauffrey, Cappelatti & Griffin 2020; Figure 1) characterising continuous variation in a suite of morphological and stoichiometric traits across species. Yet, these emerging approaches have relied on laborious direct trait measurements of collected seaweed specimens, potentially limiting rapid upscaling towards regional or global databases or analyses.

A fresh approach incorporating categorical traits

In this issue, Fong *et al.* break some of the practical constraints of direct trait measurement and make a significant contribution to our understanding of trait-based seaweed ecology (Figure 2). These researchers departed from the use of directly-measured continuous traits, instead focusing on a suite of categorical traits available in the literature. They organised these life history, morphological and physiological traits using an ‘ecological function’ model from the phytoplankton literature (Litchman & Klausmeier 2008). Note that, here, ‘ecological function’ refers to how the trait contributes to individual function (survival, growth, reproduction), rather than ecosystem functions, helping to simplify mechanistic trait-function links. Ultimately, the flexible and practical approach of embracing categorical traits allowed the team to assess over 100 species, from both tropical and temperate regions, and across subtidal and intertidal hard- and soft-bottom communities.

Their results provide important ecological insights. Their analyses revealed 14 *distinct clusters* of species in trait space, or 'emergent groups', that bore little resemblance to traditional groups. Interestingly, unlike recent analyses focused on continuous morphological traits, they showed clear gaps in trait space, illustrative of impossible or inviable trait combinations. Reflecting the strong influence of phylogeny on life cycle variation, 12 of the 14 groups contained species exclusively within the same division (red, green, or brown), which likely reflects reproductive strategies unique to certain algal groups (e.g., triphasic lifecycles in the Rhodophyta). Note, however, that several functional groups contained members of multiple divisions, reflecting similarities in other traits. Importantly, Fong et al. went on to demonstrate the ecological relevance of species' positions in trait space, showing that species associated with different environments occurred in different regions of trait space. Overall, this work shows how categorical traits may allow researchers to integrate distinct aspects of trait variation, crucially embracing life history properties, hints that seaweeds may naturally fall into distinct groups in a gap-filled trait space, and offers a compelling illustration of the potential utility of categorical traits in seaweed functional diversity research (Figure 2).

Five key questions based on our reading of Fong et al.

Looking forward, this contribution by Fong et al. opens the door to new avenues of enquiry. Here, we highlight five key questions that need to be answered as we continue efforts to apply trait-based approaches to seaweed ecology.

1. Is information lost using categorical traits, and does it matter?

Some traits, such as those related to morphology, have traditionally been measured on continuous bases, but Fong et al. show how they can be summarised in categories. Is important information lost in this process, and if so, how does it affect our capacity to explain or predict relevant processes? The answer will likely depend on the scale of analysis and the process in question. But, identifying which traits we can categorise, and which traits and questions will benefit more from continuous measurements, will help streamline and optimise advances moving forward.

2. Which categorical and continuous traits are most ecologically informative in seaweed trait-based ecology?

Trait selection is crucial for understanding topics such as ecological strategies, environmental responses, and effects on ecosystem functions (Griffin-Nolan *et al.* 2018). Armed with a new suite of possible categorical traits, which traits are the most informative for each question (Figure 2)? This analysis includes many previously overlooked aspects, including life cycles and reproductive traits, which are strongly related to phylogeny. While these traits inform on individual function, how do they impact ecosystem processes and services? For specific questions or processes, can we identify a key suite (or a minimum viable set) of traits?

3. How can we catalyse and coordinate global effort towards standardised screening and curation of seaweed trait data?

Fong *et al.* call for global efforts to screen seaweed traits and argue that inclusion of categorical data makes early progress in this area more feasible. Recent efforts have compiled largely categorical traits for European seaweeds (Vranken *et al.* 2023), and databases of continuous traits are available for suites of UK species (<https://seaweedtraits.github.io/>). However, catalysing a global effort, combining categorical and continuous traits, will require coordination across continents and a step-change in international collaboration.

4. What is the trait-space of seaweeds worldwide?

With a more rapid approach using categorical traits, and combined with continuous traits where practical, we may approach a global trait-space for seaweeds, identifying key axes and dimensionality as in plant traits (Laughlin 2014; Díaz *et al.* 2016). However, the interpretation of any such space – and ultimately an understanding of its significance – will require more validation of the ecological relevance of underlying traits.

5. How is global change transforming the trait space of macroalgae?

Ultimately, once a clearer picture of trait variation emerges, we can begin to ask how global change is affecting this variation. Recent work highlights contraction of morphological diversity under canopy loss (Pessarrodona *et al.* 2021). However, how are other axes – now more approachable with this new categorical approach – responding to global change, and what are the possible consequences for ecosystems?

Concluding remarks

This new paper by Fong *et al.* makes an exciting and relevant contribution to the emerging field of trait-based seaweed ecology, leading to new opportunities in trait-based seaweed research. The work establishes a rich connection between categorical traits and individual-level ecological functions and shows how categorical traits have the capacity to allow researchers to efficiently embrace more complete variation in trait space across large numbers of species.

Seaweeds support fisheries, protect coastlines, and store and re-distribute carbon. Yet, this functionally diverse group is variously threatened by ocean acidification, climate change (Koch *et al.* 2013), and food web perturbations (Rasher *et al.* 2020). Understanding the vulnerability of species, whole communities, and indeed functions, is a key challenge, making it an opportune time to develop a trait-based framework for these marine producers. As the nascent field begins to grow, we need more testing of the relevance of traits – both categorical and continuous – to predicting responses to global change and impacts on ecosystem services. Ultimately, researchers should be able to draw on shared databases to handpick well-validated traits to answer their specific research questions. This contribution from Fong *et al.* takes an important step forwards by highlighting the overlooked potential of categorical traits to rapidly advance the field.

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Figures

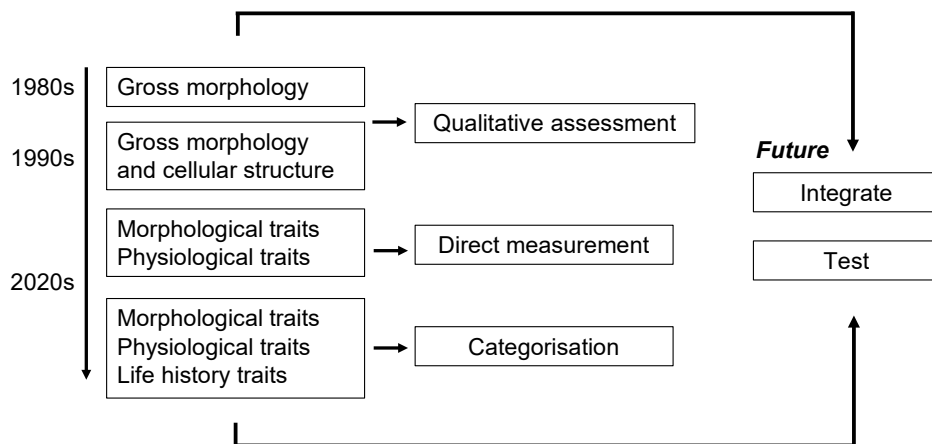


Figure 1. The evolution of trait-based approaches to seaweed ecology. Traditional schemes, developed in the 1980s and 1990s, are based on gross morphology, complemented with consideration of cellular structure. Recent efforts have been made to directly measure continuous functionally-relevant seaweed traits, emphasising morphology and physiology. Fong et al. embrace categorical traits and existing knowledge to explicitly incorporate life history traits. Future efforts must retain insights from earlier schemes, integrate categorical and continuous traits, and crucially continue to test their relevance for a variety of relevant processes.

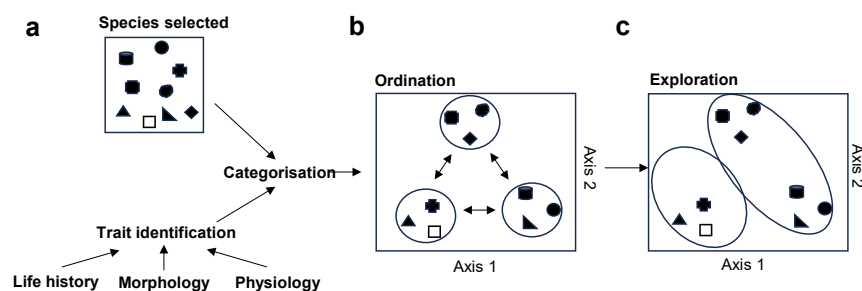


Figure 2. The approach of Fong et al.. Categorisation was used to efficiently incorporate information across many traits (a), identify a resulting seaweed trait space with evident gaps (b) and explore the ecological relevance against environmental types (c)