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OPINION PIECE

Missing the marine forest for the trees

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ABSTRACT: Seascapes dominated by large, structurally complex seaweeds are ubiquitous. These critical ecosystems are under increasing pressure from human activities, and conceiving successful management strategies to ensure their persistence and/or recovery is of paramount importance. Currently, ecosystems dominated by large seaweeds are referred to as either 'forests' or 'beds'. We demonstrate how this dual terminology is confusing, is used inconsistently, and reduces the efficiency of communication about the importance and perils of seaweed habitats. As a consequence, it undermines work to alleviate and mitigate their loss and impedes research on unifying principles in ecology. We conclude that there are clear benefits of simply using the more intuitive term 'forest' to describe all seascapes dominated by habitat-forming seaweeds. This is particularly true as researchers scramble to reconcile ecological functions and patterns of change across disparate regions and species to match the increasingly global scale of environmental forcing on these critical ecosystems.

KEY WORDS: Seaweed · Terminology · Kelp · Macroalgae · Communication

1. TREES OF THE SEAS AND MARINE FORESTS

Seascapes dominated by large seaweeds are ubiquitous (Steneck & Johnson 2013, Wernberg et al. 2019; Fig. 1). These 'marine forests' create habitats for fish, crustaceans and other organisms (Graham 2004, Teagle et al. 2017), and provide a suite of valuable ecosystem services for humans (Vásquez et al. 2014, Bertocci et al. 2015, Bennett et al. 2016, Blamey & Bolton 2018). In the past half century, threats to large seaweeds have increased in number and severity, leading to a decline in their abundance in many places globally (Araújo et al. 2016, Krumhansl et al. 2016, Filbee-Dexter & Wernberg 2018).

The juxtaposition of threat and substantial ecological and socio-economic value provides a strong impetus for maximizing the acquisition and dissemination of knowledge about marine forests. However, there is disagreement over which seaweed habitats

can be described as 'forests'. Some experts use this term sparingly, referring only to seaweeds that reach the sea surface (e.g. giant kelp *Macrocystis pyrifera* or bull kelp *Nereocystis luetkeana*; Fig. 1B,F) and calling all other seaweed habitats 'beds' (e.g. Steneck et al. 2002). Others use forests to describe marine plant (sensu Bolton 2016) habitats more broadly (e.g. Krause-Jensen & Duarte 2016, Krumhansl et al. 2016). These different practices are confusing, hamper research on these habitats and hurt communication of their importance.

Due to its intuitive meaning and well established associations on land, we argue that the term 'forest' should be used consistently as a general term to describe structurally complex seascapes created by seaweeds, regardless of specific size and structure. Consequently, we define marine forests as 3-dimensional benthic seascape structures created by seaweeds that modify their local environment to sup-

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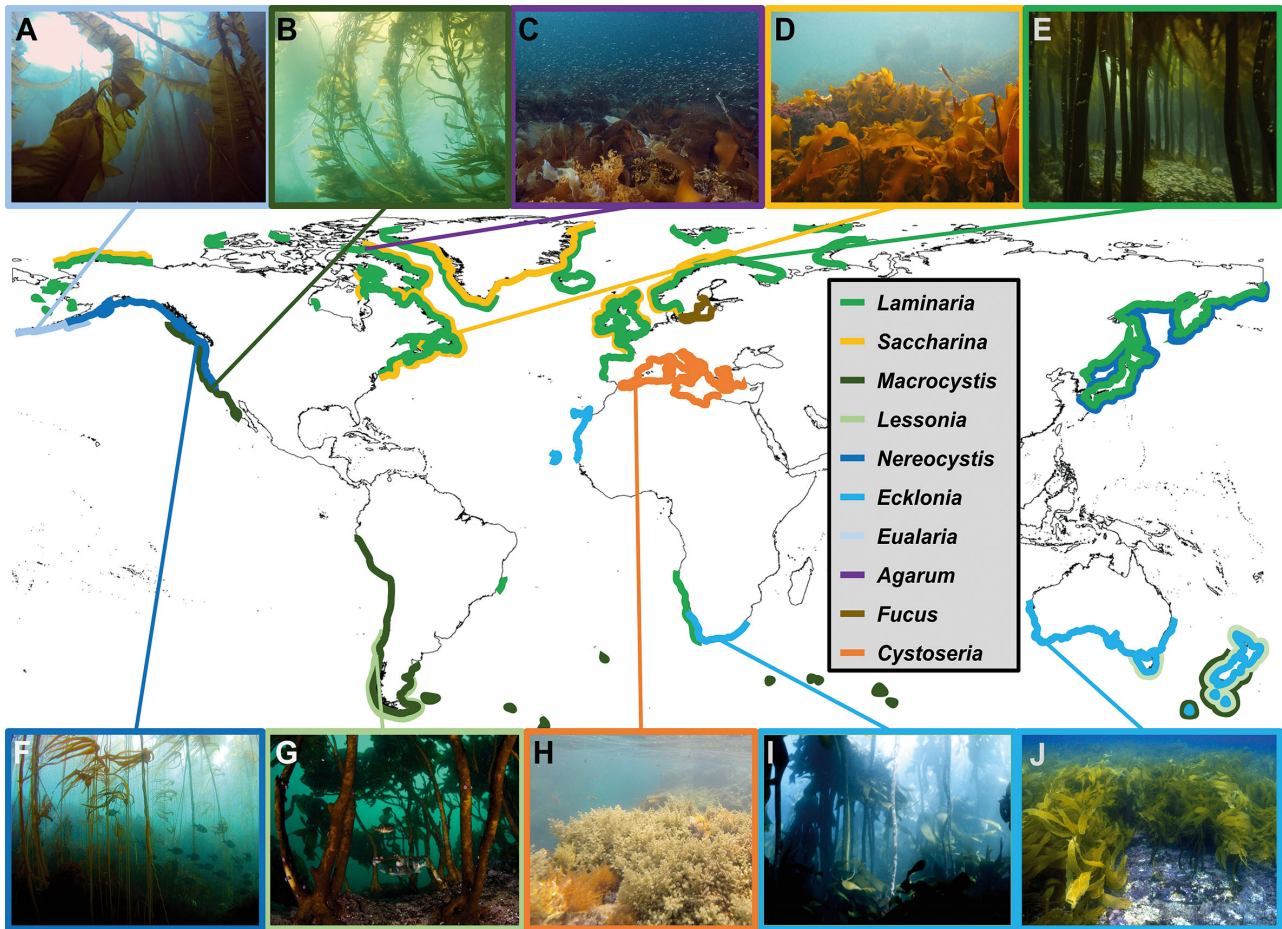


Fig. 1. Diverse marine forests from different regions of the world. Coloured lines show the approximate distribution of key seaweed genera (map adapted from Wernberg et al. 2019). Photographs (photo credits in parentheses) show: (A) *Eualaria fistulosa*, Gulf of Alaska (Pike Spencer); (B) *Macrocystis pyrifera*, western Canada (Jenn Burt); (C) *Saccharina latissima* and *Agarum clathratum*, Canadian Arctic (Frithjof Küpper); (D) *Saccharina latissima*, Atlantic Canada (Kira Krumhansl); (E) *Laminaria hyperborea*, northern Norway (Thomas Wernberg); (F) *Nereocystis luetkeana*, western USA (Jared Figurski); (G) *Lessonia trabeculata*, Chile (Alejandro Pérez Matus); (H) *Cystoseira* spp., Mediterranean Sea (Albert Pessarrodona); (I) *Ecklonia maxima*, South Africa; (J) *Ecklonia radiata*, western Australia (both Thomas Wernberg)

port distinct subtidal communities of plants, invertebrates and vertebrates which would not persist without the seaweed canopy. This definition encompasses both laminarian kelp 'forests' and 'beds' (see Fraser 2012 and Bolton 2016 for discussions of the definition of 'kelp'), as well as other seaweed habitats with similar functional properties, such as those formed by subtidal canopy-forming species of *Cystoseira*, *Durvillaea*, *Fucus*, *Saccorhiza* and *Sargassum* (e.g. Benedetti-Cecchi et al. 2001, Mangialajo et al. 2008, Assis et al. 2016, Coleman & Wernberg 2017).

Seaweeds exhibit a great diversity of growth forms and life strategies, with the largest individuals reaching lengths of more than 30 m and biomasses up to 42 kg (Wernberg et al. 2019). They attain some of the

highest rates of primary production of any natural ecosystem, particularly in cool, nutrient-rich waters (Lüning 1990). Kelps and other large seaweeds are typically competitively dominant and long-lived, and can form canopies over the seafloor that alter their surrounding physical environment (Reed & Foster 1984, Eckman et al. 1989, Wernberg et al. 2005). Some large seaweeds have flexible stipes where the thallus drapes over the sea floor, creating a sweeping prostrate canopy (Fig. 1C,D,H,J), while others have erect stipes that lift the thallus into the water column, creating a dense stipitate canopy several metres above the sea floor (Fig. 1E,G). A few species have very long flexible stipes with one or several blades and gas-filled cavities or bladders, which create a floating canopy on the sea surface (Fig. 1A,B,F,I).

Temperate rocky coastlines of western North and South America, South Africa and parts of Tasmania are dominated by laminarian kelps that form floating canopies at the ocean's surface. In contrast, coastlines throughout Asia, most of Australasia, the South and North Atlantic, the Arctic, and the Mediterranean Sea have seaweed habitats dominated by smaller prostrate, stipitate or buoyant flexible canopies of laminarian kelp or fucoids that drape the sea floor or stand tall but rarely reach the surface (Steneck & Johnson 2013, Wernberg et al. 2019). Regardless of the type of canopy, however, diverse associated and understory communities of smaller algae, invertebrates and fish occur as a consequence of the canopy structure and its effects on the local environment and resource availability.

What is a forest and why should we use this term in the marine realm? On land, a forest is defined simply as 'a large area covered chiefly with trees and undergrowth' (Oxford University Press 2002). According to Wikipedia there are more than 800 precise definitions of what constitutes a forest, incorporating factors such as tree height, density, yield, use and ecological function (Wikipedia, accessed 12.12.2018). Intuitively, however, a key aspect of a forest is that it is made up of trees which create a 3-dimensional canopy that, in turn, creates shade, retains moisture and nutrients, affects soil conditions, reduces wind stress and changes competitive interactions and predation rates (e.g. Blundell & Peart 2001, Caccia et al. 2009, Muscolo et al. 2014). Forests therefore support distinct communities of associated species such as birds, mammals and shade-tolerant plants or young recruits (e.g. van Dorp & Opdam 1987, George & Bazzaz 1999, Blundell & Peart 2001, Ahumada et al. 2011). In the ocean, seaweeds also create 3-dimensional habitats with a canopy and understory, which supports distinct communities of fish, invertebrates and other plants (Graham 2004, Kendrick et al. 2004, Ling 2008). Further, although the term 'tree' is a non-taxonomic term with inconsistent uses and many definitions, it is commonly used to refer to perennial plants that use woody stems or trunks as a way to rise above and shade out other plant species. This resembles the growth strategy and morphology of many (but not all) large seaweeds, which often consist of one or more stipes supporting blades that constitute the tallest biotic component of the seascape, and therefore alter the physical and biological environment in the understory. In this way, large seaweeds can play a functional role similar to that of their terrestrial tree counterparts. In fact, the functional similarity between large seaweeds and trees has been recognized for

close to 2 centuries (Darwin 1839). Of course, some species (e.g. *Laminaria hyperborea*, *Lessonia trabeculata*, *Ecklonia maxima*) fit the common definition of a tree better than others (e.g. *M. pyrifera*, *Saccharina latissima*, *Cystoseria* spp., *N. leutkeana*). Still, when large seaweeds occur in aggregations to form seascape structures, it is often sensible to describe the resulting habitats as marine 'forests'.

There is no specific definition for when a collection of trees becomes a forest. Determining exactly when a group of individual seaweeds becomes a marine forest would be akin to asking how many corals it takes to make a coral reef or the number of oysters required to form an oyster bed. However, in the same way that individual plants or sparse copses do not make up a forest, marine forests should not include seaweeds that are too sparsely distributed or too flattened to the seafloor (e.g. turfs, Connell et al. 2014) to create a distinct subcanopy habitat. For this reason, our definition of a marine forest includes the term 'seascape structure', which implies that the forest is a landscape-scale attribute that alters the spatial pattern of the benthos and canopy-associated species.

2. CONCEPT CONFUSION AND NON-TAXONOMIC TERMS IN ECOLOGY

Kelps are some of the biggest seaweeds, and many are forest-forming. In a seminal review paper, Steneck et al. (2002) described 3 types of kelps: stipitate, prostrate and canopy-forming, stating that canopy-forming kelps create forests, whereas stipitate and prostrate kelps create beds. This was an attempt to retrospectively define 2 terms long in use by kelp ecologists (Fig. 2B). However, we argue that whether one chooses to define kelp forests narrowly as aggregations of surface canopy-forming species or more broadly as aggregations of surface and/or subsurface canopy-forming species is somewhat arbitrary, and that the distinction between surface and subsurface canopy-forming kelps is not strongly founded in functional differences. Both surface and sub-surface kelps are genetically closely related, create similar habitats, require similar environmental conditions and host similar ecological interactions (e.g. grazing, shading) (Teagle et al. 2017, Wernberg et al. 2019). Moreover, along the west coast of North America, surface and subsurface canopies occur in intergrading mosaic patches (Dayton et al. 1984, Reed & Foster 1984, Clark et al. 2004). Clearly there is no unambiguous distinction between 'forests' and 'beds', and these are not binary categories, but exist as gradients

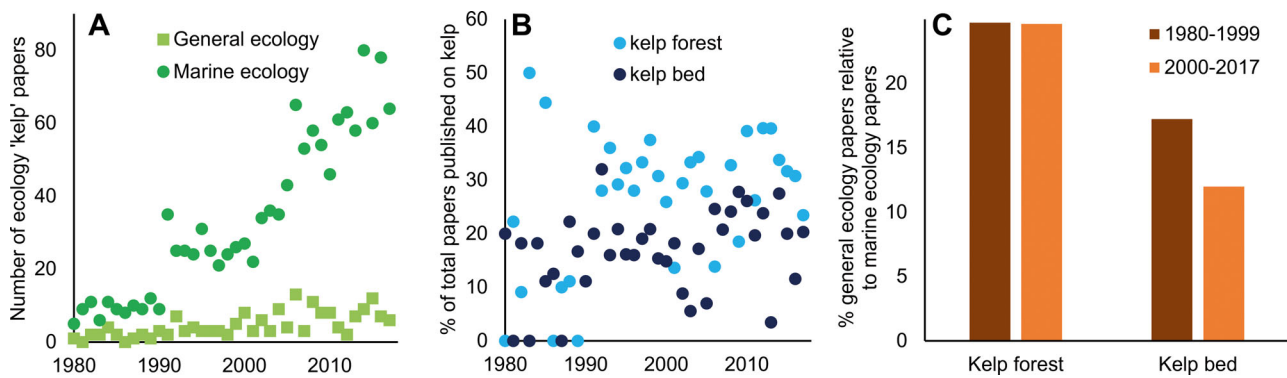


Fig. 2. Use of the terms 'kelp forest' and 'kelp bed' in the general and marine ecology literature. (A) Frequency of 'kelp' papers published over time (1980–2017). (B) Percent of 'kelp forest' and 'kelp bed' papers relative to all 'kelp' papers in marine ecology over time. (C) Percent general ecology papers relative to marine ecology papers on 'kelp forests' and 'kelp beds'

that depend on the relative abundance of different species. We contend that, in the same way that size does not preclude 1–2 m Icelandic birches (Wardle 1965) and 100 m tall redwoods (Koch et al. 2004) from both forming forests on land, it is not the height of the canopy per se, but the function of the ecosystem that determines whether it qualifies as a forest.

When authors and readers associate different meanings for the same term it can cause confusion and can ultimately negatively affect the ability to grow scientific understanding (Peters 1991). In our experience, the excerpt below represents a familiar exchange between marine ecologists who study kelp forests:

"The title was somewhat misleading [...]. First, 'forests' generally refer to kelp that include the surface canopy-formers. This paper is about kelp beds, which include all the sub-surface kelps. This is minor and semantics but I think 'beds' is a more accurate way to describe these communities" (peer review of authors' manuscript for journal publication, July 2018).

The strict use of 'forests' to describe only specific taxa seems to be particularly common where surface canopy-forming seaweeds are common (e.g. California, USA; Reed & Foster 1984, Graham 2004). More broad definitions of kelp forests, and even kelps themselves (Fraser 2012, Araújo et al. 2016, Bolton 2016), are used where sub-surface canopies prevail and many non-laminarian kelps occur (e.g. Japan, Norway, Australia, and eastern North America; Maegawa & Kida 1989, Fagerli et al. 2013, Wernberg et al. 2016, Assis et al. 2018). However, the literature is full of awkward, yet technically 'correct', phrasings such as 'kelp beds and forests' (Goldberg 2007), 'kelp beds/forests' (Balch & Scheibling 2000, Goldberg 2007) and 'kelp beds or forests' (Feehan et al. 2018). There are also examples of inconsistent use within pa-

pers where the authors use both terms synonymously (Gaines & Roughgarden 1987, Konar & Estes 2003) and even many examples of authors referring to 'bed-forming' species as kelp forests (e.g. *Saccharina latisima*, Moy & Christie 2012; *Ecklonia radiata*, Wernberg et al. 2016) or 'forest-forming' species as kelp beds (e.g. *E. maxima*, Levitt et al. 2002; *Macrocystis pyrifera*, Steneck & Johnson 2013). Unfortunately, similar concept confusion is rife in ecological jargon (Peters 1991, Bolton 2016), and this highlights a general need for simplification and clear definitions.

To counter the possible argument that our definition is too broad, an effective solution is to use 'forest' as a general term and add hierarchical classification details (e.g. species, growth form) to describe specific habitats (e.g. a kelp forest dominated by stipitate *Laminaria hyperborea*). There is a wealth of examples in ecology of terms that are used to describe phenomena or groups of species or ecosystems that are neither phylogenetic nor systematic (Bolton 2016). These terms range from groups such as 'plants', 'reptiles', 'turfs' and 'kelp', to concepts such as 'regime shifts' or 'resilience'. While not true classifications, these general terms and concepts have great heuristic value as they can be used to better describe patterns of change on large or global scales, synthesize information from similar habitats in different regions, identify broad functional groups or even explore general principles in ecology (e.g. Folke 2006, Airoldi et al. 2008, Fraser 2012, Connell et al. 2014, Bolton 2016, Noble et al. 2018, O'Brien & Scheibling 2018).

3. CLEAR COMMUNICATION MATTERS

Employing the term 'forest' in the marine context would be a highly effective communication tool.

Forests are well-known by non-experts and are intuitive because they trigger a visual image of a canopy and understorey. The term highlights the key role these foundation species play as habitat formers. In this way, use of 'marine forest' can increase general understanding and awareness of these habitats. Compared to charismatic habitats such as coral reefs, there is an underappreciation of the importance, or even the existence, of supposedly less charismatic habitats such as seaweed forests (Duarte et al. 2008, Bennett et al. 2016). This can have important ramifications, such as reduced research funding or lower conservation priority. A clear example of the power that a broad term can have in science communication is the 'Great Southern Reef' initiative (Bennett et al. 2016). Here the use of an overarching name and identity to describe the extensive series of rocky reefs that extend around Australia's southern coastline has been instrumental in communicating the importance of threats facing these relatively unknown kelp-dominated habitats (<https://www.science.org.au/curious/earth-environment/whos-heard-great-southern-reef>).

A potential benefit of using a terrestrial reference is that it clearly indicates functional similarities between forests on land and in the sea. This may improve the extent to which marine research is used by other ecologists to develop and test broad ecological principles and theory, for example, those associated with succession, disturbances, recovery, resilience and alternative states. In particular, it is well recognized that, in contrast to terrestrial forests, canopy-gap dynamics of marine forests play out on spatio-temporal scales amenable to manipulative experiments (Petraitis & Latham 1999). Despite these similarities, terrestrial ecologists rarely cite marine literature, whereas marine ecologists often cite terrestrial literature (Menge et al. 2009), and this is detrimental to our understanding of general principles in ecology that transcend the marine-terrestrial divide (Thomsen & Wernberg 2014).

The broader appeal of the term 'forest' outside of marine ecology can be demonstrated in the literature (Fig. 2). We obtained data from the Web of Science (21 Sept 2018) by searching for papers containing 'kelp' and 'kelp AND forest' or 'kelp AND bed' in their topic line. For general ecology we searched the journals *Ecological Monographs*, *Ecology*, *Ecology Letters*, *Ecosystems*, and *Journal of Ecology*, and for marine ecology, we searched the journals *Journal of Experimental Marine Biology and Ecology*, *Journal of Phycology*, *Marine Biology*, and *Marine Ecology Progress Series*.

Relative to the number of papers published on kelp in marine ecology journals, the publication rate for 'kelp bed' papers in general ecology is 30–50% lower compared to 'kelp forest' papers, and has decreased in recent times (Fig. 2C). In contrast, although variable, the percent of marine ecology papers using either 'kelp forests' or 'kelp beds' has remained relatively constant over time, with ~40% more papers on kelp forests (mean \pm SE, 28.9 ± 2.0 papers yr^{-1}) compared to kelp beds (16.9 ± 1.4 ; Fig. 2B). For kelps, there has been a substantial increase in the number of papers in the marine ecology literature over the past 4 decades (1980–2017). However, this has not been matched by a similar increase in kelp papers in the general ecology literature, which has remained constant over the same period (Fig. 2A).

Humans are influencing Earth at a planetary scale (Rogelj et al. 2016, Waters et al. 2016), and this is creating broad-scale changes in coastal habitats. Researchers must rise to the challenge of understanding the drivers and dynamics of ecosystem change at these large scales, and here a unified terminology is particularly important. A single term can also be helpful for management, because of the need to effectively communicate needs and outcomes to policy makers and the public and because solutions to broad-scale threats are also being explored at a global scale. In the last decade, several international policy documents (e.g. IPCC supplement on blue carbon, Hiraishi et al. 2014), stakeholder networks (e.g. Norwegian Blue Forest Network: <http://nbf.no/>) and citizen science programmes (e.g. Marine Forests: <https://marineforests.com/>) concerned with habitat restoration, carbon storage and climate change mitigation have referred to any vegetated marine and/or aquatic habitat as marine forests or blue forests. These often include mangroves and seagrasses, and although our focus here is on seaweeds only, an even broader discussion about the use of the term 'blue forest' is probably warranted (e.g. Mcleod et al. 2011, Trevathan-Tackett et al. 2015).

In conclusion, abandoning a confusing vocabulary of habitat classifications that are poorly defined and inconsistently used might reduce our ability to make detailed distinctions between types of seaweed habitats. However, this is far outweighed by the clear benefits of a simpler unified use of the term 'forest' to describe benthic seascapes dominated by large habitat-forming seaweeds. Although we hope that the discussion started here will simplify the jargon surrounding marine forests and improve communication and appreciation of these important but often underappreciated and threatened habitats, we recognize it

also raises questions, which are a result of the qualitative nature and existing ambiguity in descriptions of both forest and seaweed habitats. For example, gray areas include floating *Sargassum* assemblages and intertidal fucoids. Whether or not certain canopy-forming seaweeds support distinct understories may be subjective, and not as evident for some species as for others. Again, we have not presented a rigid classification scheme, but argue for the use of simple, intuitive and consistent terminology when we talk broadly about these habitats. Given the increasing global scale of environmental forcing of seaweed ecosystems and its consequences, consistent terminology, across the diverse range of marine forests, should facilitate research, enhance science communication and be useful in the development of solutions to curb current patterns of decline.

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