EVOLUTIONARY PHYCOLOGY: TOWARDS A MACROALGAL SPECIES CONCEPTUAL FRAMEWORK

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Complete List of Authors:	McCoy, Sophie; Florida State University College of Arts and Sciences, Biological Science Krueger-Hadfield, Stacy; University of Alabama at Birmingham, Biology Mieszkowska, Nova; Marine Biological Association of the UK, Marine Biodiversity & Climate Change; University of Liverpool, Earth, Ocean & Ecological Sciences
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EVOLUTIONARY PHYCOLOGY: TOWARDS A MACROALGAL SPECIES CONCEPTUAL FRAMEWORK[1]

Sophie J. McCoy[2], Stacy A. Krueger-Hadfield[3], Nova Mieszkowska[4,5]

[1] Date of Submission, Date of Acceptance

[2] Department of Biological Science, Florida State University, 319 Stadium Dr., Tallahassee, FL 32312, USA
e-mail: mccoy@bio.fsu.edu
phone: (850) 644-1549
fax: (850) 645-8447
[3] Department of Biology, University of Alabama at Birmingham, 1300 University Blvd, Birmingham, AL 35294, USA
[4] Department of Environmental Sciences, University of Liverpool, L69 3GP, UK
[5] Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, Devon, PL1 2PB, UK

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Abstract

Species concepts formalize evolutionary and ecological processes, but often conflict with one another when considering the mechanisms that ultimately lead to species delimitation. Evolutionary biologists are, however, recognizing that the conceptualization of a species is separate and distinct from the delimitation of species. Indeed, if species are generally defined as separately evolving metapopulation lineages, then characteristics, such as reproductive isolation or monophyly, can be used as evidence of lineage separation and no longer conflict with the conceptualization of a species. However, little of this discussion has addressed the formalization of this evolutionary conceptual framework for macroalgal species. This may be due to the complexity and variation found in macroalgal life cycles. While macroalgal mating system variation and patterns of hybridization and introgression have been identified, complex algal life cycles generate unique eco-evolutionary consequences. Moreover, the discovery of frequent macroalgal cryptic speciation has not been accompanied by the study of the evolutionary ecology of those lineages, and, thus, an understanding of the mechanisms underlying such rampant speciation remain elusive. In this perspective, we aim to further the discussion and interest in species concepts and speciation processes in macroalgae. We propose a conceptual framework to enable phycological researchers and students alike to portray these processes in a manner consistent with dialogue at the forefront of evolutionary biology. We define a macroalgal species as an independently evolving metapopulation lineage, whereby we can test for reproductive isolation or the occupation of distinct adaptive zones, among other mechanisms, as secondary lines of supporting evidence.

Key words: Diversity, Macroalgal, Phycological, Seaweed, Speciation, Species Concept

Introduction

The resolving power of DNA sequences has enabled the identification of a myriad of independently evolving lineages (Pante et al. 2015), and phycology has not escaped the ensuing systematics revolution (Saunders 2005, Le Gall & Saunders 2010, Leliaert et al. 2014, Leliaert et al. 2019). While discussion of species concepts in the scientific literature has increased since the 1960s, little of this discussion has revolved around species concepts, and specifically incorporating evolutionary frameworks (e.g., De Queiroz 2007), for macroalgae (Fig. 1A). Species and speciation are nevertheless two of the most basic elements of evolutionary biology and there are important reasons why we need to pay careful attention to species conceptualization and species delimitation in macroalgae. For higher plants, species have been delimited through the lens of natural history and reproductive mode variation (Grant 1981), even in the modern era of molecular barcoding and phylogenomics that have provided critical lines of evidence for constructing phylogenetic relationships (e.g., Hörandl et al. 2009). Even when taxonomic complexity is accounted for in plants, there are often conservation issues when plant taxa do not fit neatly into a 'species'-based system (e.g., Hollingsworth 2003). Yet, for the macroalgae, we do not possess the same intimate knowledge of mating system and reproductive mode variation that botantists enjoy from a legacy of common garden experiments. Thus, we are often blind as to macroalgal taxonomic complexity that can generate discordances among species concepts as they may be applied to freshwater or marine taxa. Moreover, the profound variation in life cycles exhibited across the red, green, and brown macroalgae suggests that delimiting species may be challenging (Dudgeon et al. 2017) because some algal life cycles have unique eco-evolutionary consequences (e.g., clonality results in an uncoupling of the life cycle, reviewed by Krueger-Hadfield 2020). Thus, incorporating an explicit evolutionary framework into our approach for conceptualizing an algal species should be of great importance to phycologists, especially as we continue to identify new taxa using molecular tools and subdivide existing morphological species into species complexes. Moreover, it will aid in a shift in phycological thinking towards species as hypotheses (*sensu* Pante et al. 2015) and the investigation of different mechanisms that lead to the separation of macroalgal lineages.

The existence of numerous macroalgal cryptic species are of particular concern in this context. While some 'cryptic' species are the result of assigning the same name to morphologically similar taxa throughout the world without the benefit of molecular tools, other cryptic species are now regularly being found in the same habitats, such as the same intertidal zone or reef (e.g., Geoffroy et al. 2015, Montecinos et al. 2017, Gabrielson et al. 2018, Hughey et al. 2019). In the latter case, species are indistinguishable by morphology and are often mistakenly assigned to the same species name, confounding our understanding of their evolutionary ecology (Bickford et al. 2007). This limitation is critical, as our ability to differentiate between cryptic species may have major implications for understanding the ecophysiology, local adaptation, population ecology, evolutionary processes, and community ecology of these taxa (Mayr 1948). From an ecological perspective, cryptic species render experimentation in nature difficult, when there are few diagnostic, visual differences (e.g., Montecinos et al. 2017). Yet, species complexes figure into the ecology of natural systems because life cycle variants, as well as ecotypes within species, matter ecologically (e.g., De Jode et al. 2019). Therefore, before we can test important eco-evolutionary hypotheses, such as how different cryptic species or their life cycle stages may respond to climate change, we have to understand the processes by which variants within species, and species themselves, diversify – which hinges on an evolutionary framework within which to define speciation criteria. These considerations also fuel debates on the importance of functional vs. genetic processes (Bortolus 2008). Thus, it is important to contextualize species complexes with functional differences and similarities between genetic groups to gain an understanding of the basis for speciation in these instances. While the overall study of cryptic species has increased exponentially over the past 30 years, the study of the evolutionary ecology of cryptic algal species has remained sparse (Fig. 1B). Here, we aim to further the discussion and interest in species concepts and speciation processes in macroalgae.

A more formal conceptualization of a macroalgal species that can be separated from the mechanisms that are generated through lineage divergence, that we in turn use as evidence of delimitation (De Queiroz 2007), would facilitate communication and collaboration between taxonomists, evolutionary biologists, ecologists, physiologists, and biogeographers. It is necessary for synergy among these disciplines in order to generate a holistic approach to understanding the mechanisms that underlie phycological biodiversity and ecophysiology. The lack of explicit evolutionary frameworks in phycology poses a problem to our field as we seek a holistic understanding of algal speciation. While the general tenants of our argument below apply to both micro- and macroalgae, we focus here on freshwater and marine macroalgal taxa as a starting point and more tractable taxa with which to understand the challenges associated with macroalgal life cycle complexity and speciation. Future work should expand these ideas and integrate microalgae into these frameworks. Below, we briefly review relevant aspects of macroalgal biology that we need to consider when delimiting species, then outline the evolutionary conceptual framework through which we should assess macroalgal species.

Macroalgal biogeography

Physiologically, macroalgae have limited dispersal compared with marine invertebrates or terrestrial plants, which may be broadcast spawners or dispersed by wind or animals. Most species of macroalgae rely on propagules, defined broadly to include vegetative or sexual reproduction via spores or zygotes, that are either immotile or have limited locomotory capabilities for their reproduction, proliferation, and dispersal (Santelices 1990). Generation time and morphological structure of the propagule stage (Norton 1992), in addition to oceanographic and bathymetric conditions (Breeman 1988, van den Hoek 1982 a,b, Gaylord et al. 2004), determine the distance that propagules can travel from the parent population. In many cases, these factors have led to an overall pattern of isolation-by-distance, where populations regularly exchange migrants with nearby populations (Kimura & Weiss 1964, Brennan et al. 2014). Long-distance dispersal is rare, but does occur, achieved primarily by rafting of detached, reproductive thalli (Norton 1992, Valero et al. 2001, McKenzie & Bellgrove 2008, Fraser et al. 2009, Buchanan & Zuccarello 2012, Provan et al. 2013, Bringloe & Saunders 2018).

Marine macroalgae are distributed along coastal latitudinal clines that correlate with a gradually changing ecological niche space (s*ensu* Hutchinson 1957, Holt 2009). Temperature and photoperiod are thus the primary abiotic factors controlling macroalgal biogeography (Dring 1984, Lüning 1990). Ranges track summer and winter isotherms (Mieszkowska & Sugden

2016), with range edges being set by temperatures exceeding lethal limits of the hardiest life cycle stage or summer temperatures limiting growth or reproduction (Bartsch et al. 2012, Breeman 1988, Hutchins 1947, van den Hoek 1982a). The limited long-distance dispersal of macroalgae effectively reduces their colonization potential to a two-dimensional space that cannot be divorced from concurrent changes in the Hutchinsonian niche.

The long evolutionary history of macroalgae and the multiple origins of macroalgal lineages (Larkum & Vesk 2003) contribute to the ecophysiological versatility, genetic diversity, and latitudinal ubiquity of this group, despite their limited dispersal ability. Patterns of macroalgal diversity within range limits is an area with well-developed theory, but mixed observational evidence. Overall, population sizes and individual fitness metrics decrease as environmental conditions stray from species' optima near range edges (Zardi et al. 2015), consistent with ecological and evolutionary theory (Castro et al. 2004, Hampe 2005, Viejo et al. 2010). However, theory predicts a decline in genetic diversity among populations near range limits, with local marginal populations acting as sink populations (Watkinson and Sutherland 1995). Evidence from macroalgal studies is mixed (Zardi et al. 2015, Assis et al. 2013, Neiva et al. 2012, Krueger-Hadfield et al. 2013b), and populations reveal varying degrees of local adaptation and ecotypic variation in response to environmental conditions (Breeman 1988, Pearson et al. 2009, Kolzenburg et al. 2019). Gene flow among macroalgal populations will become increasingly disrupted in the face of increasing population fragmentation caused by pollution, habitat modification, climate change, algal harvesting, trophic cascades, and other anthropogenic stressors. Thus, it is important to consider patterns of population structure together with the rate of external forcing as we draw conclusions about algal population genetic processes.

Life cycle complexity

The diversity of life cycles found across the macroalgae can be bewildering to the novice and expert alike. Macroalgae can have diplontic (free-living diploid stage; e.g., *Fucus* or *Caulerpa*), haplontic (free-living haploid stages; e.g., *Chara*), or haplodiplontic life cycles (free-living haploid *and* diploid stages; e.g., *Dictyota, Ulva, Gracilaria*). The myriad of variations played upon these three simplified life cycle types across the lineages of macroalgae is truly remarkable (Bell 1994), but can complicate species delimitation when the natural history of the life cycle is unknown. For example, while our understanding of the genetic advantages of diploidy and haploidy are better understood (e.g., Valero et al.1992, Otto and Gerstein 2008), the only way haplodiplontic life cycles can be evolutionarily stable states is when the haploid and diploid stages in the life cycle occupy different niches (Hughes and Otto 1999; see reviews by Thornber 2006, Krueger-Hadfield 2020).

Species delimitation in taxa with biphasic life cycles, in which both the haploid and diploid stages undergo substantial development and are free-living, could be more robust when using both ploidy stages (but see below about coupling this information with mating systems under *Mating system and reproductive mode considerations*). Indeed, for some taxa, heteromorphic haploid gametophytes and diploid tetrasporophytes were classed in different genera before laboratory based culture studies (e.g., *Gigartina* and *Petrocelis* that are now part of the reinstated red algal genus *Mastocarpus*, Guiry et al. 1984). Yet, more recent work on the taxonomy of *Mastocarpus* spp. in the Pacific has not included both life cycle stages, despite the necessary alternation of genetics that is characteristic of the genus *Mastocarpus* (see Lindstrom 2008, Lindstrom et al. 2001, and discussions by Dudgeon et al. 2017). Nevertheless, haplodiplontic species experience evolutionary and ecological constraints because each ploidy stage is linked to the other. Impacts on one stage may cascade through the species' entire life cycle (Thornber 2006, Krueger-Hadfield and Hoban 2016, Krueger-Hadfield 2020). As some species descriptions rely on the heteromorphic or isomorphic alternation of generations, it is critical to assess patterns of gene flow within these life cycles and include both ploidy stages in the gathering of evidence about species delimitation. Understanding these patterns is a necessary component to forecasting how species with complex life cycles will respond to climate change, though macroalgal life cycles are often not included in these assessments (e.g., Pandori and Sorte 2019).

Mating system and reproductive mode considerations

Mating systems exert control over the very lines of evidence we gather to delimit species as they partition the amount of genetic diversity within populations and the amount of genetic differentiation among populations (Hamrick and Godt 1996), thus determining population structure (Tibayrenc and Ayala 1991). Outcrossed mating systems typically result in genetically diverse populations with higher potential for adaptation, while inbreeding (and self-fertilization, its most extreme form) results in reductions in genetic diversity and effective population sizes, potentially reducing adaptive potential (but see Pujol et al. 2009, as selfing can become adaptive). Similarly, clonal (or asexual) populations, in which no recombination or fertilization occurs, incur the same genetic consequences as inbred populations (Halkett et al. 2005). Mating systems not only control, but are in turn controlled by standing genetic variability (e.g., inbreeding reduces genetic variation, reducing mating system variation, and reinforcing inbreeding; Richards 1989), thereby shaping evolutionary trajectories by modulating the relative importance of drift, migration, selection, and mutation.

The algal haplodiplontic life cycle has two critical implications that influence mating system for species delimitation. The life history traits that affect mating systems are evolutionarily labile and likely vary tremendously within and between macroalgal taxa, but data are woefully inadequate, such as basic patterns of the relative rates of outcrossing versus inbreeding and sexual versus asexual reproduction (Valero et al. 2001, Krueger-Hadfield 2020). First, in general, dioecy, or separate sexes, is often used a proxy for outcrossing in higher plants and animals (Krueger-Hadfield et al. 2015), but in haploid-diploid species, separate sexes do not prevent cross-fertilization between male and female haploids that share the same diploid parent (Klekowski 1969). Inbreeding results in smaller effective population sizes with lower genetic diversity and reduced effective recombination, affecting species delimitation (Naciri & Linder 2015). While Olsen et al. (2020) recently included macroalgae in an assessment of inbreeding rates in the sea, the distribution of taxa for which we have robust estimates of inbreeding, and specifically using progeny arrays or paternity analyses is woefully inadequate (see also Krueger-Hadfield 2020).

Second, many macroalgae are partially clonal, a reproductive system in which both clonal and sexual (selfing, inbreeding, and/or outcrossing) reproduction occur (see Sosa et al. 1998, Valero et al. 2001, van der Strate et al. 2002, Guillemin et al. 2008, Krueger-Hadfield et al. 2016, Pardo et al. 2019). The balance between these two reproductive modes strongly influences the ecological success of a species (Halkett et al. 2005, Silvertown 2008) and the ability to track environmental change via phenotypic evolution (Orive et al. 2017). Yet, when asexual reproduction occurs, one of the ploidy stages may be lost (Krueger-Hadfield et al. 2013a, 2016, Dudgeon et al. 2017). Which ploidy stage is lost has important implications for the recovery of the sexual life cycle (see Guillemin et al. 2008, Krueger-Hadfield et al. 2016) and for dispersal potential (see Fierst et al. 2010, Krueger-Hadfield et al. 2013a, Dudgeon et al. 2017). As a consequence, asexuality can facilitate range expansions resulting in different geographic patterns and founder events that can complicate delimitation, particularly when the life cycle is not well characterized (see, as examples, the patterns of geographic parthenogenesis in the red algal genus *Mastocarpus* [Dudgeon et al. 2017] or the geographic separation between haploid and diploid stages in ferns [Nitta et al. 2017]). The impacts of life cycle variation on haplodiplontic systematics are largely unknown, but we need to expand our knowledge of the ecophysiology of different life cycle stages (Krueger-Hadfield 2020).

In ferns and lycophytes, eukaryotes with similar life cycle complexity as found in macroalgae, it has been estimated that 10% of species do not reproduce sexually (Walker 1984). If an asexual lineage is clearly distinct (often morphologically), then Gastony and Windham (1989) proposed a ‘genetic’ species concept that is similar to the concept used for sexually reproducing metapopulation (though it is important to note that models for eukaryotes as sexually reproducing metapopulations is meaningless for asexual taxa, *sensu* Billiard et al. 2012). However, for taxa in which the asexual lineage (which are often triploid) are indistinguishable from their diploid progenitor, Gastony and Windham (1989) proposed to use the term variety. Similarly, there are a whole host of terms employed by other vascular plant taxonomists that could greatly facilitate how phycologists think about species delimitation (Grant 1981).

Bearing these differences between sexual (i.e., both inbreeding and outcrossing) and clonal reproduction and their eco-evolutionary consequence in mind, species-level phylogenetic analyses will require different evolutionary assumptions than those that are appropriate at taxonomic levels of families and above. For example, phylogenetic studies often assume mating systems have a negligible effect on genetic variation within and among species (Naciri & Linder 2015). However, mating systems exert strong influence on patterns of group variability. As a result, evolutionary changes in mating systems are often associated with the development of reproductive isolation and, subsequently, speciation. The frequency of selfing or asexuality can further blur genetic breaks. Dandelions, for example, display taxonomic complexity driven in part by strict asexuality bringing about complete reproductive isolation (Richards 1989). Asexuals confound species delimitation through (i) sequence divergence, (ii) ploidy differences, (iii) linkage of nuclear and organellar genes, (iv) lack of admixture, and (v) differences in generation times between sexual and asexual lineages (Dudgeon et al. 2017). When partially clonal taxa do undergo sexual reproduction, such as in the case of range expansions, they may undergo selfing and/or inbreeding, further generating divergence among populations. Thus, for organisms where detailed mating system data are lacking, species delimitation may be confounded by viable alternative hypotheses when sexual and asexual life cycle variants are analyzed together and treated methodologically as sexual (Dudgeon et al. 2017). Different phylogenetic reconstructions may be retrieved depending on which specimens or loci are sampled, especially among recently diverging species (Naciri & Linder 2015).

A need for phylogenetic networks

As previously discussed, botanical taxonomy developed from breeding studies in common gardens. While there was a period in phycology during which these sorts of experiments were undertaken to understand mating system variation through culturing experiments (e.g., Guiry et al. 1984, Maggs 1988), the molecular revolution has sped up phylogenetic methodologies that have far outstripped our basic natural history knowledge of macroalgal taxa. Nevertheless, macroalgae exhibit tangled taxonomic characters, whereby characters may evolve independently multiple times (e.g., holdfasts, bladders) or be gained then lost within a lineage, such as the crustose morphology of *Crusticorallina* spp. (Hind et al. 2016). Molecular taxonomy may alleviate the pressure to prioritize morphological characters, yet introduces complications of its own. Hybridization is common across macroalgae (e.g., Coyer et al. 2002, 2011, Martins et al. 2019), a situation that is not easily represented in a phylogenetic context. Allopolyploidy, the merger of two different species' genomes, has also been documented in macroalgal evolution (e.g., Neiva et al. 2017, Sousa et al. 2019). Thus, we borrow some inferences from the plant speciation literature, where interspecific hybridization has become recognized as an important creative force in plant evolution - including in the evolutionary history of species which today exhibit strong reproductive isolation (Cronn et al. 2004, Grant 1981). Hybridization may allow the introgression of genes or variation that are later selected on to form true species (e.g., Fig. 2c), possibly leading to an acceleration of speciation due adaptive divergence and cementation of barriers to gene flow during secondary contact, or alternatively impeding speciation altogether (Abbott et al. 2013). Given how common this process seems to be in macroalgal evolution, the ensuing reticulate phylogenies of many species thus require a phylogenetic network model, rather than dichotomously branching trees (Grant 1981).

An open question remains about hybrid fitness in macroalgae, and the degree to which limited gene exchange may occur between species. Evidence from a variety *Fucus* hybrids is mixed (e.g., Billard et al. 2005, Coyer et al. 2002, 2007, 2011), while hybrid vigor has been documented in *Laminaria* hybrids (Martins et al. 2019). Hybrids are certainly a common feature of macroalgal communities, however their stability over time is not well understood. In part, this is because evidence for past hybridization can be conflated with persistence of ancestral polymorphisms (‘gene trees’ divergent from phylogenetic tress). When alleles are shared between taxa in sympatry but not in allopatry, hybridization is ongoing (*sensu* Whittemore and Schaal 1991).

Along with hybrid speciation, incomplete lineage sorting, wherein an ancestor confers some, but not all unique traits to one evolutionary lineage and a different set of unique traits to another lineage, leaves behind a confusing phylogenetic signature (Maddison 1997). Both hybridization and incomplete lineage sorting are likely to occur among closely related species and populations with incomplete reproductive isolation.

A genealogical species has been defined as “a basal, exclusive group of organisms, whose members are all more closely related to each another than they are to any organisms outside the group, and that contains no exclusive groups within it” (Shaw 1998). Exclusivity is further specified as whether the genetic loci of organisms within the group have coalesced most recently only with other organisms within the group (Baum and Shaw 1995), which has been applied as showing reciprocal monophyly with respect to another genealogical species. This criterion ignores situations of incomplete lineage sorting or genetic variability within an ancestral species. Every allele sampled for analysis may be identical within a genetic species, with each allele descended from a shared common ancestor within the group. Importantly, this does not imply that all of these alleles originated from the same original ancestor, and alleles for different loci may have descended from different individuals within the group (Hudson & Coyne 2002). Further, newly speciated groups descendant from one portion of another species – for example, resulting from island invasion or isolation of marginal populations – may lead to individuals from the original population/species being more closely related to the new species than to individuals within their own group, violating the exclusivity clause (Hudson & Coyne 2002).

Phylogenies are typically built using multiple genes, either as a consensus gene tree of phylogenies built using each gene, or as a concatenated sequences tree, which uses a combined ‘super-gene’ alignment of concatenated gene sequences. While most multigene studies employ concatenated sequences to build phylogenies, due to the increased effective sample size of this technique, consensus gene trees account for differences in evolutionary rates or stochastic differences in single gene polymorphisms, for example caused by incomplete lineage sorting (reviewed in Gadagkar et al. 2005). As described above, the most recent common ancestor of sampled individuals may fall within another species, when studying recently diverged groups. In such cases, historical signals of species relationships are likely to be overwhelmed by stochastic genetic processes if gene trees and species trees are assumed to be synonymous, leading to an overestimation of speciation (Carstens & Knowles 2007). Further, varying degrees in a species' ability or propensity to self-fertilize or to reproduce clonally will affect the distribution of these stochastic differences between related lineages (see previous section).

A species conceptual framework for macroalgae

The only 'necessary property of species' is treating an entity as a separately evolving metapopulation lineage (De Queiroz 2007). The unified concept of species advocated by De Queiroz (2007) separates the issues of conceptualization and delimitation of species, whereby the properties advocated by competing species concepts (see Table 1) are no longer at odds with one another, but instead are used as evidence of lineage separation. More lines of evidence will provide more corroboration of a given lineage. Most importantly, however, De Quieroz (2007) states that the 'unified species concept shifts the emphasis away from traditional species criteria, encouraging biologists to develop new methods of species delimitation that are not tied to those properties' (e.g., reproductive isolation or monophyly). Our aim in this perspective is to build on the existing methods used by phycologists, but shift our interpretation to one of a species concept, followed by the interpretation of species delimitation in explicit evolutionary frameworks.

As with all other taxa, macroalgal species are separately evolving metapopulation lineages. In order to begin to build evidence for delimiting algal species, we discuss the utilization of the following lines of evidence often used by phycologists. Phylogenetic species concepts comprise the most appropriate starting point for the development of a macroalgal species conceptual framework, as current taxonomic methods in phycology are based on molecular phylogenies derived from the consensus of gene trees. We advocate for also using the properties outlined in the traditional biological species concept in concert with molecular phylogenies, currently that most often employed in phycology, as this will explicitly incorporate mating systems into species delimitation. In Table 1 and in the text below, we outline existing species concepts, translating them rather into lines of evidence for delimitation, that partially explain our understanding of macroalgal speciation, and finally propose a species conceptual framework for macroalgae.

Multiple phylogenetic species concepts have been formally proposed in the literature, reflecting the difficulty of fitting a continuum of relatedness into discrete categories (Coates et al. 2018). Differences among phylogenetic approaches to species delineation involve (1) a specification of paternal descent (sexual reproduction), (2) monophyly of a the most exclusive group, or (3) greater relatedness of all group members to one another (Table 1; Cracraft 1989, de Queiroz and Donoghue 1988, Baum and Donoghue 1995, Shaw 1998). Hudson and Coyne (2002) have suggested that a proportion of reciprocally monophyletic loci must be specified as a metric for consideration of a group as a species. Quantification of these definitions is appealing and arguably necessary. Yet, such a definition blurs the biological significance of genealogical speciation. By this definition (3) above, speciation could be transitory, allowing for hybridization with sister taxa to create definable species. Simulations using a criterion of at least 50% monophyly and restricted to drift alone can reach speciation in under 200 generations for small populations (Hudson & Coyne 2002), simultaneously making the role for selection unclear and likelihood of local adaptation high, given the biogeography and natural history of macroalgae.

Based on the robust field of speciation within ecology and evolutionary biology, it is critical to maintain biological meaning in our definition of a macroalgal species. Thus, we must take in to account niche partitioning among closely related species. The ecological species concept essentially provides a stipulation that selection must have an axis on which to act during the speciation process. We, thus, propose a macroalgal species conceptual framework that provisions for inclusion of hybridization, life cycle complexity, and mating system variation where there exists trait differentiation by combining critical aspects of the phylogenetic, biological, and ecological species concepts, building on what Simpson (1961) called an evolutionary species. An evolutionary species 'embraces a greater diversity of [mating] systems, and is consequently more general' (Grant 1981). An evolutionary species is a population system which possesses the following characteristics: (i) it is a lineage, in other words there is a sequence of ancestor-descendant relationships among populations that exist in space and time, (ii) the lineage evolves separately from other lineages (i.e., other species), (iii) it fits into its own ecological niche, and

(iv) it can change its evolutionary role over the course of its history (Simpson 1961). Importantly for hybridization under the evolutionary species concept, the question becomes whether the two species that hybridize lose their distinct eco-evolutionary roles. If they do not merge, then they remain distinct species. Combining these elements, we define a **macroalgal species as a lineage that evolves separately from other lineages (i.e., a basal group), and evidence supporting these lineages can comprise but is not limited to the occupation of a distinct adaptive zone (or zones for haplodiplontic taxa), monophyly, or reproductive isolation.** We encourage our fellow phycologists to begin to think more outside the box for reconciling species conceptualization and delimitation, especially for the latter in order to discover new, biologically relevant methods with which to define macroalgal lineages.

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Table 1. Species concepts most relevant to macroalgal diversity and speciation. Modified from Coyne and Orr (2004). Note, the macroalgal species conceptual framework provides an evolutionary lens with which to study macroalgae.

Basis of Concept	Name	Definition
Interbreeding	Biological Species Concept	Species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1995).
Evolutionary cohesion	Ecological Species Concept	A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen 1976).
	Evolutionary Species Concept	A species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies (Simpson 1961).

Evolutionary history	Phylogenetic Species Concept 1	A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a paternal pattern of ancestry and descent (Cracraft 1989).
	Phylogenetic Species Concept 2	A species is the smallest [exclusive] monophyletic group of common ancestry (de Queiroz and Donoghue 1988).
	Phylogenetic Species Concept 3	A species is a basal, exclusive group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group, and that contains no exclusive group within it (Baum and Donoghue 1995; Shaw 1998).
Combination	Macroalgal Species Conceptual Framework	A lineage that evolves separately from other lineages (i.e., a basal group) and evidence supporting these lineages can comprise but is not limited to the occupation of a distinct adaptive zone (or zones for haplodiplontic taxa), monophyly, or reproductive isolation.

Figure Legends

Figure 1. Number of papers returned from a Web of Science search in November 2019. Bars in grey show all papers returned for the base search terms A) "species concept" and B) "cryptic species" in the paper title. In blue, number of papers returned that contained the fragment "alga," and in black, the number of papers returned containing the fragment "phyto" in addition to the base search term. Numbers above bars give the total papers returned containing "alga" and "phyto", respectively. No papers were returned containing the fragment "phyco" in addition to the base search term in either case.

Figure 2. Consider four groups A, B, C, D; A and B share several morphological characteristics and another set is common to B and C and another set to C and D. Different systems of classification will occur based on what characters are given priority by different researchers, such that one system may yield A) A-B and C-D, and another B) A-C and B-D. In C), consider the possibility that a fifth species, E, may have hybridized with the lineage of group A to generate a lineage that was then selected upon to yield groups B, C, and D.

Figures

Figure 1.

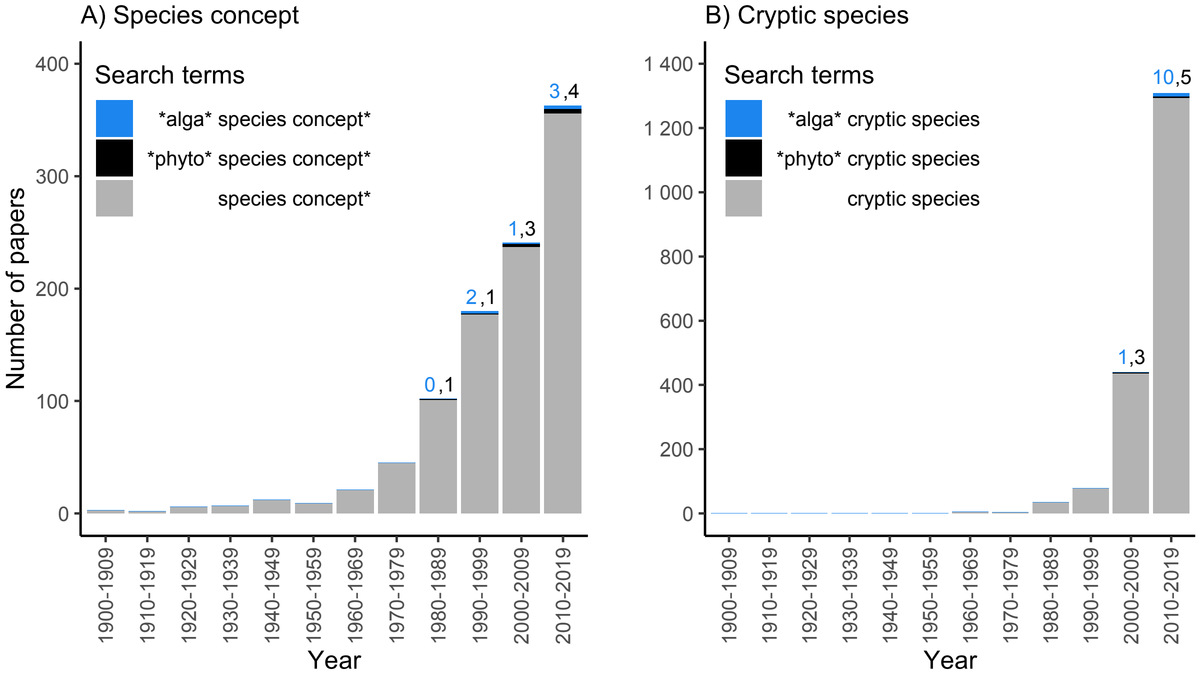
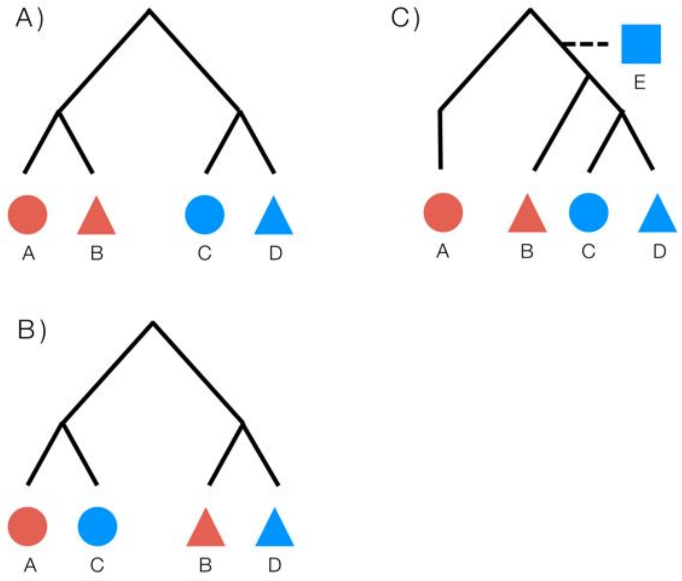
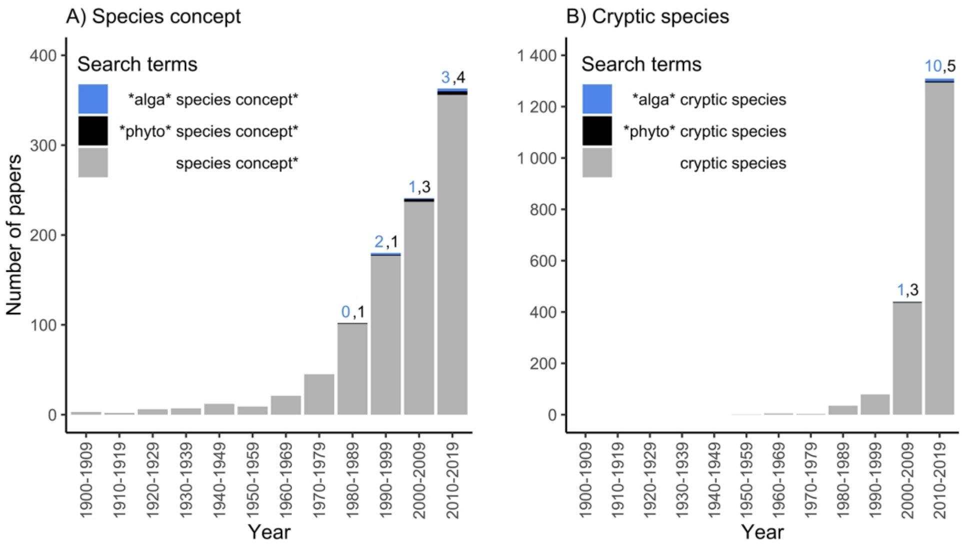


Figure 2.





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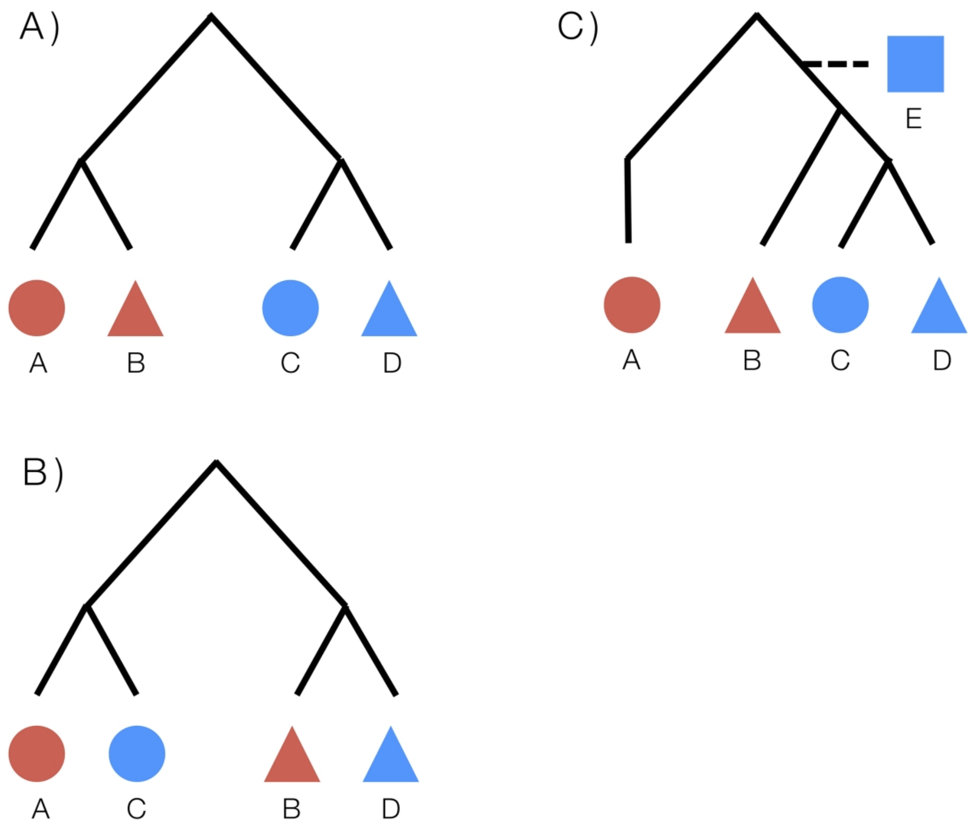

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