



# The evolution of community assembly in marine foundation species

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Community diversity controls ecosystem function, but the supply and replacement of that diversity is ultimately controlled by evolution. Integrating community processes with evolutionary opportunity is therefore central to understanding the future of biodiversity in a changing world. Losos (1996) pointed this out over two decades ago when he showed that we cannot infer mechanisms of community assembly and coexistence without accounting for the evolutionary history constraining the pool of species available to be assembled. There was already evidence that regional species richness could constrain community species richness (Cornell & Harrison, 2014; Cornell & Lawton, 1992; Ricklefs, 1987), but Losos' point spurred new interest in thinking about evolutionary constraints on species' traits in relation to community assembly. Using the assumption of niche conservatism, a community phylogeny could be used to account for evolution and provide a proxy for ecological similarity among species (Webb, Ackerly, McPeck, & Donoghue, 2002). This resulted in an explosion of tests of whether communities are composed of closely related species similarly filtered by the environment, or distantly related species avoiding competitive exclusion by using different resources. However, in systems where much of the community being assembled is drawn from a single lineage that lends itself to careful understanding of trait evolution, it was soon clear that species like oaks (Cavender-Bares, 2019) and anoles (Losos et al., 2003) could evolve convergently to fill available niches. Thus, close relatives cannot be assumed to be the most similar in any particular trait. Furthermore, the failure of close relatives to co-occur locally could simply be the expected signature of allopatric speciation (Pigot & Etienne, 2015; Warren, Cardillo, Rosauer, & Bolnick, 2014) or recent divergence in micro-habitats (Anacker & Strauss, 2014).

So how do we better integrate evolution with community ecology, given this complexity? One major answer is the idea of a 'model lineage' (Cavender-Bares, 2019), where assembling both evolutionary and ecological information about an important group of relatives (like oaks) lets us accurately test questions about the interplay of diversification and coexistence. In this issue of *Functional Ecology*,

Starko and Martone (2020) present the evolution and ecology of kelps (a group of large marine brown algae), providing an excellent first example of a marine 'model lineage'. These authors have traced the diversification of kelps through the evolutionary opportunities of the last 30 million years (Starko et al., 2019) and into the composition of contemporary communities on the eastern Pacific coast (Starko & Martone, 2020). Unlike many marine systems composed of invertebrates from deeply diverged phyla, where important interactions between very distant relatives make it difficult to test community interactions in an evolutionary framework (Wilcox, Schwartz, & Lowe, 2018), kelps have excellent potential as a model lineage for the ocean. The relatively recent history of diversification in this system is much more likely to be influenced by the same selection pressures and environmental gradients relevant for communities observed today, offering important opportunities to do truly integrative work on how species interactions alter evolution (Weber, Wagner, Best, Harmon, & Matthews, 2017) and how evolution shapes species interactions (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Haloin & Strauss, 2008).

Using traits, a phylogeny and community data, Starko and Martone (2020) show that kelp species are filtered by their wave tolerance into communities along a wave exposure gradient. Using specific traits with known functional consequences (Starko & Martone, 2016) strengthens this conclusion relative to analyses of general similarity in community members (Kraft et al., 2015). Then, using ancestral trait reconstructions and tests for phylogenetic signal (the correspondence between time for divergence and actual divergence in traits), the authors show that these wave tolerance traits have evolved convergently across the kelp phylogeny. This convergent evolution is shaped by clear morphological trade-offs, which are central to understanding the evolution of niche specialization in any system (Poisot, Bever, Nemri, Thrall, & Hochberg, 2011). Kelps can adapt to deal with (a) the stress of higher flow and potential dislodgement, either by streamlining their morphology or by investing more energy in the holdfast (Starko & Martone, 2016), or (b) with the stress of still water

and boundary layers that make the uptake of CO<sub>2</sub> and nutrients more difficult (Starko, Claman, & Martone, 2015). As with oaks (Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004), repeated evolution of these strategies across the phylogeny results in the co-occurrence of distant relatives in locations with the same stressors.

As we start to assemble a broader range of 'model lineages' across ecosystems, we can better ask questions about the general rates and constraints of evolution to fill environmental (beta) versus local (alpha) niches. In the few examples starting to accumulate, traits related to environmental tolerances can be more conserved (Ackerly, Schwillk, & Webb, 2006; Silvertown, Dodd, Gowing, Lawson, & McConway, 2006), or less conserved (Cavender-Bares et al., 2004; Emery et al., 2012) than those related to local resource partitioning. This results in the occupancy of stressful habitats either by a few close relatives that can tolerate conditions (Best & Stachowicz, 2014; Kembel & Hubbell, 2006) or convergent specialists from many branches of the phylogeny (Savage & Cavender-Bares, 2012). In kelps, the repeated evolution of wave tolerance could have been facilitated by the availability of wave-swept niches at the time of their radiation (Fukami, 2015; Tanentzap et al., 2015), or patterns of dispersal (Verbruggen et al., 2009), or the relative physiological flexibility of specific traits needed for withstanding wave stress versus accessing light locally available in a multi-species assemblage. Having a greater diversity of systems to test these hypotheses is important because it should help us predict how evolution might contribute new biodiversity to fill new environmental niches opened by anthropogenic change.

In addition to their interesting evolutionary history, kelps also serve an important role as exclusive providers of really three-dimensional marine forest habitat, feeding herbivores and mediating trophic interactions (Steneck et al., 2002). This means that a single lineage captures the full community of foundation species even more so than oaks, which interact with other angiosperms and gymnosperms (Cavender-Bares, Keen, & Miles, 2006). A model lineage in this context offers some very interesting opportunities to explore evolutionary interactions between kelps and invertebrate herbivores, which have preferences for different kelp morphologies as habitat (Stelling-Wood, Gribben, & Poore, 2020) and food (Rhoades, Best, & Stachowicz, 2018) and in turn impact producer performance (Poore et al., 2012). Given that kelps exhibit evolutionary trade-offs between fast growth and defended growth that in some ways parallel those in terrestrial plants (Starko & Marone, 2020), there is great potential for the study of co-diversification across trophic levels in kelp-associated systems, as well as the consequences of ecosystem evolution for ecosystem function (Srivastava, Cadotte, MacDonald, Marushia, & Mirotchnick, 2012). Whether we are interested in the future links between diversity and ecosystem health, or in making more accurate conclusions about the forces shaping coexistence versus extirpation today, systems offering integrated insight about the sources and consequences of biodiversity are extremely valuable.

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