

The evolutionary past and the uncertain future of foundational species

Catherine A. Pfister^{a,1}

How do species evolve into foundational roles in ecosystems, and what is the prognosis for them in a changing ocean? Seagrasses, or marine angiosperms, have examples of foundational species that have become widespread throughout the coastal ocean. When flowering angiosperms first entered the ocean, an event dated to 140 million years ago and repeated several times (1, 2), they likely developed or retained a set of traits from flowering plants that would aid their success, including the ability to pollinate in the water (hydrophily) and clonal reproduction. Although only a minor number of species across the flowering plants, seagrasses have had success across the major ocean basins, with ~60 species recognized (1). As seagrasses evolved, the species *Zostera marina* became widespread in the Northern Hemisphere, colonizing the Pacific and eventually the Atlantic, and becoming the most geographically widespread marine angiosperm. Genome duplication and gene loss events likely accompanied it in this new habitat (3). Significant evolutionary events for eelgrass may have occurred during the Pleistocene when the repeated advances and retreats of glaciers removed and added habitat and altered the environment. Through a large-scale and multiauthor effort across the Pacific and Atlantic Oceans, Duffy et al. (4), in PNAS, detect an existing signature of historical events, including these Pleistocene episodes. In their paper entitled “A Pleistocene legacy structures variation in modern seagrass ecosystems,” they find persistent genetic and phenotypic features of seagrass that reverberate through the seagrass ecosystem today, affecting plant shape and density, and the interaction of eelgrass with other key members of the ecosystem.

Marine angiosperms, including *Z. marina*, fix and store immense amounts of carbon, referred to as “blue carbon.” Their widespread abundance and high productivity yield impressive estimates of carbon storage, from 48 Tg per y to 112 Tg per y (5). Marine angiosperms provide critical habitat for myriad species in ocean environments because their blades and their roots modify the environment and provide a surface for other species to thrive. The eelgrass *Z. marina* is a “foundational” species, and Duffy et al. (4) describe how its morphological features differ among ocean basins. Eelgrass in Pacific Ocean locales has a higher stature and lives in sparser aggregations, while the Atlantic Ocean form is shorter and often in more-dense “meadows” (Fig. 1). The shape of eelgrass has effects up the food chain, including the taxa that grow on the blades (periphyton) and the invertebrates that use the plants for habitat. Thus, the growth form characteristic of each ocean basin has ecosystem-level effects.

Growth form, often considered highly plastic in plants, also has a genetic and geographic basis in eelgrass. While morphological differences among eelgrasses might be

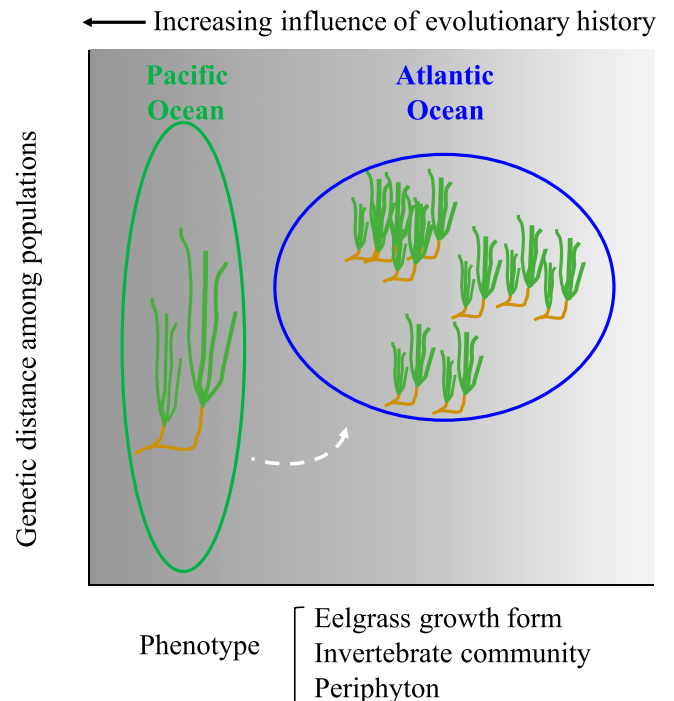


Fig. 1. A representation of the patterns of genetics and phenotype in the eelgrass *Z. marina* as described by Duffy et al. (4). Pacific Ocean eelgrass populations are more genetically disparate and have a more elongate phenotype. Atlantic Ocean eelgrasses are shorter statured and differ in the density of their blades. As younger populations, they are genetically more similar. The darker shading in the Pacific Ocean represents older populations with a greater influence of evolutionary history on present-day phenotype compared with the Atlantic populations. The dashed line represents a colonization event.

ascribed only to the environmental features of each ocean basin, the authors show that these morphological distinctions were set historically through the genome and likely limit the response of the plants to changing environments. Further, the longer evolutionary history of the Pacific Ocean has imparted greater time for mutations and resulted in genetic isolation by distance in Pacific Ocean

Author affiliations: ^aDepartment of Ecology & Evolution, University of Chicago, Chicago, IL 60637

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¹ Email: cpfister@uchicago.edu.

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eelgrass. In contrast, the repeated advance and retreat of glaciers in the Atlantic Ocean increased gene flow and had a homogenizing effect on eelgrass genotypes (Fig. 1). While eelgrass can show high outcrossing rates (6), and reproductive plants can disperse great distances, pollen can also be limited to distances of a few meters (7), leading to genetic structure. *Z. marina* also grows clonally; somatic mutations in these plants lacking a germline mean that mutations can be passed on to the next generation (8). The balance of these opposing genetic processes differed in these oceans, and the signature of past evolutionary events has persisted in the growth form and the ecosystem role of eelgrass in the environment. Further, partitioning the variance in genetic contributions to growth form revealed that the evolutionary history in the Pacific Ocean had a greater and more persistent role than it did in the Atlantic.

The morphological differences in eelgrass and its historical origins bring up a persistent question at the intersection of ecology and evolution: What is the role of evolutionary contingency in the patterns we see in nature (9, 10)? Evolutionary contingency dictates whether events in evolution are repeatable versus unpredictable as a result of chance events that occur. Evolutionary contingency has foundational work in microbial ecology, for example, the surprising evolution of citrate metabolism in *Escherichia coli* (11), but it is a concept difficult to test in nature. Is there contingency in the morphological traits of eelgrass, and does that contingency constrain its response in the future? The continued interplay between the palette of genes and traits available and those that are needed for organisms to persist remain a challenge to identify. The Duffy et al. (4) paper suggests contingency in morphology in the foundational eelgrass, although how it will shape the species responses as ocean conditions change remains an area for investigation.

It is imperative that we understand the underlying constraints for foundational species in changing ecosystems and the role evolutionary history may play in these constraints. Eelgrass fringes some of the most anthropogenically influenced shorelines (12) and occupies shallow marine coastal embayments which are areas of rapid warming (13). The stressors that exist across the two oceans can differ (14). Eelgrass has shown us the capacity for local extinction and the threat of wide-scale extinction. Environmental degradation led to the loss of an eelgrass population in the

North Sea (15), and there are multiple other examples of declining populations. A marine snail that specialized on *Z. marina*, the limpet *Lottia alveus*, is one of the few documented examples of a marine invertebrate extinction (16), underscoring the pivotal role that foundation species play in determining the fate of associated species. The certainty of continued warming in shallow coastal areas and the potential interaction between stress and reduced genetic diversity of restored populations (17) makes the study of evolutionary history and genome features a critical aspect of conservation and restoration.

The study of a global fingerprint of evolution requires a large collaborative effort, and Duffy et al. (4) provide a blueprint for how to do this. The investigators replicate identical research efforts at 50 locales that include 1,000 plots in the Northern Hemisphere to garner insight. Many successful businesses employ a model of scalable and replicable efforts to cover a broad geographic area and garner increased impact and income. The authors have an approach here that is reminiscent of a business model, scaling replicable units of effort over a large area. Their efforts resulted in unique data and a more comprehensive picture. The article serves as an example for how to develop an understanding of a widespread species through a network of scientists.

As we look to the future and the prognosis for the continued adaptation of species to a changing environment, we need to enhance our understanding of evolutionary history and genetic constraints. Eelgrass shows us that evolutionary history is still detectable in this widespread species. But what is the scope for adaptation and change in the future? The current phenotype of an eelgrass individual might prepare or constrain it for future warming, ocean acidification, and pollution. While there has been much attention focused on testing genetic versus plastic responses of species traits across environments (18), we know little about whether those responses differ across a species range due to a template of distinct evolutionary histories. The current study lays the groundwork for determining the scope for adaptation and how it is determined by a species evolutionary history across a species range and in changing coastal environments.

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