Local Adaptation in Marine Foundation Species at Microgeographic Scales

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Abstract. Nearshore foundation species in coastal and estuarine systems (*e.g.*, salt marsh grasses, mangroves, seagrasses, corals) drive the ecological functions of ecosystems and entire biomes by creating physical structure that alters local abiotic conditions and influences species interactions and composition. The resilience of foundation species and the ecosystem functions they provide depends on their phenotypic and genetic responses to spatial and temporal shifts in environmental conditions. In this review, we explore what is known about the causes and consequences of adaptive genetic differentiation in marine foundation species over spatial scales shorter than dispersal capabilities (*i.e.*, microgeographic scales). We describe the strength of coupling field and laboratory experiments with population genetic techniques to illuminate patterns of local adaptation, and we illustrate this approach by using several foundation species. Among the major themes that emerge from our review include (1) adaptive differentiation of marine foundation species repeatedly evolves along vertical (*i.e.*, elevation or depth) gradients, and (2) mating system and phenology may facilitate this differentiation. Microgeographic adaptation is an understudied mechanism potentially underpinning the resilience of many sessile marine species, and this evolutionary mechanism likely has particularly important consequences for the ecosystem functions provided by foundation species.

Introduction and Motivation

Local adaptation—defined here as the higher fitness of local genotypes relative to foreign genotypes in the local environment (Kawecki and Ebert, 2004)—is widely documented in marine organisms (Conover *et al.*, 2006; Sanford and Kelly, 2011; Sotka, 2012), especially across biogeographic and latitudinal scales that exceed the scale of dispersal in a single generation. Local adaptation reflects an ongoing balance between the strength of selection, genetic drift, and the homogenizing effects of gene flow: when gene flow across selective environments is low (*i.e.*, across broad geographic scales), even relatively weak selection can maintain adaptive differences. In contrast, gene flow over steep environmental gradients will swamp local selection (Sultan and Spencer, 2002; Bachmann *et al.*, 2020), unless selection is sufficiently strong to counter the input of maladapted genotypes. Thus, over fine spatial scales, selection is thought to typically favor generalist phenotypes or phenotypically plastic genotypes whose traits depend on local environmental cues (Levins, 1968; Hollander, 2008; Baythavong, 2011). Despite this, there is emerging evidence that local adaptation frequently does occur over microgeographic scales (*i.e.*, well within the species' dispersal neighborhood) (*e.g.*, Hargeby *et al.*, 2004; Antonovics, 2006; Richter-Boix *et al.*, 2013; Yadav *et al.*, 2020), indicating that either selection is stronger or gene flow is more restricted than typically assumed (Richardson *et al.*, 2014).

Microgeographic adaptation is particularly interesting when it occurs in foundation species. Foundation species are numerically abundant, comprising the majority of the biomass in the community; are often primary producers, basal in interaction networks; and are highly connected (both directly and indirectly)

to other species in the community, especially through non-trophic interactions (Dayton, 1972; Ellison, 2019). They provide structural support and habitat complexity for associated organisms, modify abiotic conditions in ways that promote biodiversity (*e.g.*, by ameliorating physical stress, increasing the recruitment and/or retention of propagules), and modulate rates of predation and energy flow in ecosystems (Bruno and Bertness, 2001; Ellison *et al.*, 2005; Ellison, 2019). The presence of a foundation species defines whole community types (*e.g.*, seagrasses in a seagrass meadow, redwoods in a redwood forest). Thus, even though these species do not necessarily fit the typical conservation profile (*i.e.*, not rare or obviously threatened), foundation species have high conservation priority because changes in their demography or resistance or resilience can have profound effects at the community and ecosystem levels (Bruno *et al.*, 2003; Gaston and Fuller, 2008; Degrassi *et al.*, 2019).

There is increasing recognition that intraspecific diversity within foundation species can influence the magnitude and even direction of population-, community-, and ecosystem-level effects (Whitham *et al.*, 2006; Hughes *et al.*, 2008; Des Roches *et al.*, 2018). For instance, across both experimental and natural populations, plant genetic diversity consistently influences the diversity, abundance, and distribution of species associated with these plants (Hughes and Stachowicz, 2004; Crutsinger *et al.*, 2006; Johnson *et al.*, 2006; Crawford *et al.*, 2007; Hughes, 2014). The genetic identity of foundation species can also have far-reaching effects on the abundance and composition of associated communities, as elegantly illustrated in studies of hybridizing *Populus* trees (Whitham *et al.*, 2006; Bangert *et al.*, 2008). In marine systems, eelgrass (*Zostera marina*) provides one of the best case studies for the ecological importance of intraspecific variation, with documented impacts of genotypic identity, diversity, and relatedness on eelgrass density and biomass, associated species abundance and diversity, and ecosystem-level responses to disturbance (Williams, 2001; Hughes and Stachowicz, 2004, 2011; Reusch *et al.*, 2005; Reynolds *et al.*, 2018). These effects are not limited to seagrasses; genetic identity and diversity also affect population and community processes in marine foundation species such as salt marsh plants and oysters (Smee *et al.*, 2013; Hanley *et al.*, 2016; Noto and Hughes, 2020). Despite the solid body of evidence that intraspecific variation in foundation species has community and ecosystem implications, we still have relatively little understanding of the microevolutionary processes that create and maintain within-species genetic variation (Hersch-Green *et al.*, 2011).

In marine environments, foundation species are commonly distributed across strong environmental gradients over relatively small spatial scales. For example, increases in tidal height on a single rocky intertidal shoreline generally yield increases in desiccation, wave energy, and temperature stressors (Menge and Branch, 2001). Similarly, in estuarine and wetland habitats, tidal height alters inundation frequency and duration and drives complex shifts in sediment oxidation, salinity, and nutrient availability (Mendelssohn and Morris, 2002; Mudd and Fagherazzi, 2016). Other notably strong gradients that marine foundation species confront occur horizontally, including tropical lagoons of small *versus* large sizes (Oliver and Palumbi, 2011), inshore-offshore habitats (Lirman and Fong, 2007), protected-exposed intertidal habitat (Johannesson, 2003), estuaries *versus* open coastlines (Zardi *et al.*, 2013), and high- and low-salinity areas within estuaries (Eierman and Hare, 2013; McCarty *et al.*, 2020). Populations may persist across these environmental gradients by a variety of non-exclusive mechanisms, including genotypes with broad physiological tolerance or adaptive phenotypic plasticity (Sultan and Spencer, 2002) and microgeographic adaptation, such that the traits of individual genotypes match local environmental conditions within that gradient (Richardson *et al.*, 2014).

When microgeographic adaptation occurs in foundation species, it can have important effects on their ecological functions. Local adaptation to an environmental gradient can increase a species' distribution along that gradient (Kirkpatrick and Barton, 1997; Barton and Etheridge, 2018; Hargreaves and Eckert, 2019); when the distribution in question is that of a foundation species, this increases the extent of a whole habitat type. However, adaptive differentiation in foundation species may also have more subtle effects, independent of distributional limits. For example, local adaptation in a foundation species can dampen or amplify the existing environmental variation experienced by associated taxa (see Urban *et al.*, 2020). In foundation species, many of the traits that reflect and serve as proxies for fitness (*e.g.*, density, biomass, growth rate) are the same traits that drive and define these species' foundational roles, generating structure and modifying energy flow in an ecosystem. Local adaptation acts to increase mean individual fitness in home environments; this process can decrease spatial variation in fitness-linked traits (*e.g.*, if local adaptation brings low-performing demes closer to the regional mean) or increase it (*e.g.*, if local adaptation further enhances the fitness of high-performing demes).

Importantly, local adaptation shapes spatial patterns of both genetic identity and genetic diversity. As described above, the genotypic identity of clonal foundation plants often matters for associated organisms (*e.g.*, Crutsinger *et al.*, 2006; Whitham *et al.*, 2006; Bangert *et al.*, 2008); thus, any microevolutionary processes that influence the spatial distribution of particular genotypes can influence that species' impact in the community. Moreover, genetic diversity itself can also impact population, community, and ecosystem processes (Whitham *et al.*, 2006; Hughes *et al.*, 2008; Des Roches *et al.*, 2018); and while adaptive differentiation leads to increased genetic variation in selective environments, strong purifying selection may also erode genetic diversity within them (Cvijović *et al.*, 2018). Thus, depending on the relative spatial scales of diversity effects and adaptation, the population-level benefits of increased mean fitness may come with a cost: loss of positive diversity effects

within selective environments. How this conflict might play out across the strong environmental gradients spanned by many foundation species (marine or terrestrial) is unknown.

First, we briefly review current experimental and molecular genetics approaches to studying local adaptation, and we highlight several case studies that provide strong evidence for local adaptation at microgeographic scales in marine foundation species. Next, we discuss the common themes that emerge from these case studies and suggest areas where future work is needed.

Methods: Experimental and Molecular Approaches

At its core, demonstrating local adaptation requires identifying (1) a local fitness advantage that (2) has a genetic component. The two classic experimental approaches to documenting local advantage are reciprocal transplant experiments and common gardens. In the latter, the key idea is to remove phenotypic variance due to differences across environments; thus, this approach is more useful for uncovering genetic differentiation than for explicitly quantifying the adaptive advantage of that differentiation. However, common gardens may include treatments that manipulate a suspected environmental driver (*e.g.*, temperature, pH) to explicitly compare the performance of genotypes from different sources under ecologically relevant conditions. In the field, multiple gardens (called provenance trials in forestry) (Savolainen *et al.*, 2007) can be used to measure plasticity and infer regional adaptation to large-scale gradients (*e.g.*, across a geographic range). Although such studies typically test many fewer environments (gardens) than sources, and gardens may be home to none of the genotypes tested, researchers can quantify the environmental distance between home and outplant sites to explore which characteristics of the home sites best predict performance (*e.g.*, Montalvo and Ellstrand, 2000; Rutter and Fenster, 2007).

Reciprocal transplants have a long history in evolutionary ecology (Turesson, 1922; Clausen *et al.*, 1940; Schemske, 1984) and are still considered the gold standard for demonstrating a fitness advantage. One advantage over other experimental approaches is that reciprocal transplants test all components of the home environment, including subtle environmental differences that may not be obvious. Evidence for local adaptation may be assessed in different ways, usually as the superior performance of local *versus* foreign phenotypes in their home environment (Kawecki and Ebert, 2004; Leimu and Fisher, 2008; Hereford, 2009) or calculated across all source and environment combinations *via* a sympatric *versus* allopatric contrast in a linear model (Blanquart *et al.*, 2013). In fully reciprocal experiments, both analyses are often possible and can lead to different conclusions (Blanquart *et al.*, 2013; *e.g.*, Bucharova *et al.*, 2017), highlighting how scale influences interpretation: a significant proportion of total spatial variance in fitness across a landscape may be attributable to local adaptation, but non-local genotypes may still outperform local ones at particular sites.

Both common gardens and transplant experiments are often severely hindered by the logistics of organismal life history. Many foundation species tend to be long-lived and iteroparous, which greatly complicates any estimate of individual fitness (Orr, 2009). Also problematic is decoupling plastic responses from genetic differences when testing or transplanting adults that have had a long developmental history in a particular microhabitat. While experiments are commonly conducted with field-collected individuals, it is preferable to use propagules rather than adults, and ideally ones that have been maintained in common conditions (*i.e.*, lab or greenhouse) for at least one generation (*e.g.*, Sotka *et al.*, 2003; Sanford and Worth, 2010), because plasticity can persist across generations (*i.e.*, maternal effects: Marshall, 2008; Marshall *et al.*, 2008). Unfortunately, this approach is seldom practical or possible for marine species with complex life cycles and/or long generation times.

For 50 years, molecular methods have played an important role in providing context to experimental studies of local adaptation. Population genetics at putatively neutral loci describe the historical demography of a species (Avise, 2000), that is, patterns of historical and ongoing gene flow, genetic drift, and cryptic genetic differentiation. In marine systems, a large literature on plastid sequencing (*e.g.*, mitochondria, chloroplast) and microsatellite and allozyme genotyping revealed more restricted gene flow between populations than one would predict based on their dispersal capability, although not always (Grosberg and Cunningham, 2001; Hellberg, 2009; Selkoe and Toonen, 2011). In theory, these markers can allow biologists to distinguish between the effects of genetic drift, gene flow, and local selection in explaining patterns of spatial phenotypic differentiation. As an example, Hereford (2009) found that nearly 30% of experimental studies on local adaptation yielded results consistent with maladaptation and suggested that this was due either to gene flow or to strong local genetic drift (Brady *et al.*, 2019); molecular markers may help to delineate these causes. Dispersal is likely broad over the microgeographic spatial scales that are the focus of this review; thus, when putatively neutral molecular markers reveal surprising levels of differentiation over tens to hundreds of meters, drift is less likely than cryptic barriers to gene flow or strong, local selection.

In the last decade, the emergence of genomic tools at relatively lower cost has provided new opportunities for ecologists to survey for genomic signals of local adaptation, with or without experimental studies. Although detecting local adaptation ideally requires measurement of lifetime survival and reproduction (*i.e.*, fitness), genomic studies focus instead on identifying the genetic architecture of phenotypic traits that are proxies for fitness, such as tolerance for abiotic or biotic stressors, height, and growth rate. Such traits typically vary quantitatively and have an underlying genetic architecture that is polygenic, or determined by multiple loci of small or moderate effect (Savolainen *et al.*, 2013; Gagnaire and Gaggiotti, 2016; Hoban *et al.*, 2016; Lind *et al.*, 2018). Three commonly used approaches to detect these polygenic loci include genotyping

for quantitative trait loci (QTL), association mapping (*e.g.*, genotype-wide association mapping [GWAS]), and population genetics of natural populations (*e.g.*, markers or quantitative traits that deviate from neutral genetic structure). There is extensive literature describing these approaches and their benefits and limitations, to which we direct the reader (see reviews above, plus Barrett and Hoekstra, 2011; Tiffin and Ross-Ibarra, 2014). A growing number of studies reveals that local adaptation and ecological speciation events are often accompanied by inversion polymorphisms and shifts within large genomic regions (Wellenreuther and Bernatchez, 2018; Morales *et al.*, 2019; Todesco *et al.*, 2020; Wilder *et al.*, 2020); however, we note that there are relatively few studies of the genomic basis of local adaptation across the microgeographic scales that we focus on here (see *Case Studies*, below). Thus, it remains an open question whether (and how) spatial scale influences the genetic architecture of adaptation across taxa (Hendrick *et al.*, 2016; Morales *et al.*, 2019).

It is important to recognize that different combinations of cross-gradient gene flow and selection can generate the same basic pattern of adaptive differentiation in adults. At one extreme of the connectivity continuum, adaptive genetic structure is maintained only by continuous purifying selection every generation. This process is typically not considered true local adaptation (Kawecki and Ebert, 2004) and instead is referred to as a balanced polymorphism (Grosberg and Cunningham, 2001; Schmidt and Rand, 2001), phenotype-environment mismatch (Marshall *et al.*, 2010), or cohort adaptation (Simon and Hare, 2020). One relatively straightforward approach to deconstruct the timing and contribution of ongoing purifying selection to spatial patterns of differentiation is to sample or experimentally test multiple different life-history stages (*e.g.*, Hilbish and Koehn, 1985; Prada and Hellberg, 2014; Schmidt *et al.*, 2000). While the distinction between local adaptation *sensu stricto* and a balanced polymorphism has important consequences (*e.g.*, for demography and the temporal stability of spatial patterns), either mechanism generates fine-scale adaptive differentiation across space that can impact the ecological function of foundation species (see discussion of balanced selection under *Emergent Themes*, below). Thus, we argue that both require increased attention.

Case Studies

Below we highlight marine foundation species for which there is strong evidence of adaptive differentiation across microgeographic scales. This is not an exhaustive survey of the literature; rather, we focus on case studies that demonstrate the utility of different approaches, particularly the synergy of combining experimental and molecular genetic methods.

The cordgrass Spartina alterniflora

Within most marshes along the Atlantic and Gulf coasts of the United States, *Spartina alterniflora*, the dominant plant,

exhibits pronounced variation in stem height over tens of meters across a natural stress gradient of tidal elevation and associated abiotic conditions (*e.g.*, soil waterlogging, sediment oxidation, salinity, and nutrient availability) (Pennings and Bertness, 2001; Mendelssohn and Morris, 2002; Mudd and Fagherazzi, 2016). Tall-form *S. alterniflora* (~1–2-m stem height) is found in low elevations along creek banks that experience daily inundation, and the short form (<0.5 m) is found at higher elevations that are less consistently flooded (Shea *et al.*, 1975; Valiela *et al.*, 1978; Anderson and Treshow, 1980).

Experimental work in this system demonstrates that both environmental conditions and genetic differences underlie the dramatic phenotypic variation across tidal elevation in *S. alterniflora*. For example, long-term fertilizer experiments in the short zone shifted plant morphology to be consistent with tall-zone plants (Valiela *et al.*, 1978; Morris *et al.*, 2002); and seedlings from the tall form and the short form grew similarly across several temperature and salinity treatments in a common-garden experiment (Mooring *et al.*, 1971), indicating that at least some of the observed differentiation in the field is plastic. However, both a reciprocal transplant experiment (Stalter and Batson, 1969) and a common-garden experiment (Gallagher *et al.*, 1988) conducted with adults detected consistent morphological differences between these two growth forms over a single growing season, suggestive of genetic differentiation. Recent field reciprocal transplant experiments using first-generation seedlings (and thus avoiding the potentially confounding effects of development) detected a significant signal of local adaptation in composite fitness (*i.e.*, survival plus seed production) (Zerebecki *et al.*, 2021). Survival was lower in the tall zone for both short- and tall-form genotypes, indicating a harsh environment for transplants to establish and grow; however, short-form genotypes produced more seeds in the short zone, and tall-form genotypes produced slightly more seeds in the tall zone, consistent with local advantage. In addition, transplanted offspring of tall-form plants grew taller than those of short-form plants in the tall zone, with higher above- to belowground biomass (Zerebecki *et al.*, 2021).

The distance between tall and short zones is within the range that *S. alterniflora* seeds can disperse *via* tides and currents (Taylor *et al.*, 2004; Travis *et al.*, 2004), and early population genetic surveys using allozyme and amplified fragment length polymorphisms (AFLPs) (Shea *et al.*, 1975; Valiela *et al.*, 1978; Foust *et al.*, 2016) found weak to no barriers to gene flow. However, genomic analyses using principal components analysis (PCA) and admixture analysis on 2735 highly variable single-nucleotide polymorphisms (SNPs) detected genetic divergence in zones nested within differentiated sites (Zerebecki *et al.*, 2021). Notably, this pattern was documented at five of six independent marshes, suggesting that adaptive differentiation between tall- and short-form *S. alterniflora* has independently evolved multiple times. The relative strength of and ecological mechanisms underlying

gene flow and selection in maintaining ecotypic divergence remain uncertain.

Mediterranean seagrass Posidonia oceanica

Around the world, seagrasses occur across a nearshore depth gradient such that populations may extend from the intertidal to the subtidal, across a range of depths that differ by species. Environmental conditions such as physical exposure or disturbance, light availability, and temperature thus vary from shallow to deep edges of meadows, generating potential for differentiation in morphology, production, phenology, and reproductive strategy at relatively small spatial scales.

The long-lived and slow-growing Mediterranean endemic *Posidonia oceanica* (Neptune grass) forms extensive monospecific meadows that span up to 40 m in depth (Duarte, 1991; Hemminga and Duarte, 2000; Arnaud-Haond *et al.*, 2012). Across this gradient, shoot density, leaf biomass, and specific leaf area decline from intertidal to subtidal (Olesen *et al.*, 2002). A mesocosm experiment manipulating light availability showed that plants collected from different depths at the same site utilize different photo-adaptive strategies: both gene expression and plant traits differed between shallow and deep *P. oceanica* genotypes in response to changing light environments (Dattolo *et al.*, 2017). Plants growing at the same site (<200 m apart) have also been shown to respond differently to heat stress, with deep plants demonstrating lower tolerance than shallow plants (Marín-Guirao *et al.*, 2016).

Genetic structure across depths has been repeatedly documented within *P. oceanica* populations (Migliaccio *et al.*, 2005; Dattolo *et al.*, 2017; Jahnke *et al.*, 2019), consistent with limited gene flow at these scales. In addition, candidate genes underlying growth and immunity were found to be divergent between shallow and deep individuals: genes associated with metabolism, production of secondary metabolites, and cell wall loosening were differentially expressed; and genes associated with cell wall remodeling were differentially regulated (Jahnke *et al.*, 2019). Interestingly, some candidate loci were associated with multiple gradients in this system—latitudinal as well as bathymetric—which suggests that microgeographic patterns of adaptation to gradients in temperature and light may be driven by some of the same genes contributing to divergence at larger spatial scales (Jahnke *et al.*, 2019).

Temperate seagrass Zostera marina

Zostera marina (eelgrass) is the dominant meadow-forming seagrass in temperate regions worldwide, found intertidally to depths of typically ~5–6 m. Like *P. oceanica*, *Z. marina* shows pronounced trait variation across this gradient, with shallower depths consistently characterized by higher shoot densities than deeper depths, but shoot length and weight varying across depths in different directions, depend-

ing on region and site (Olesen *et al.*, 2017; Krause-Jensen *et al.*, 2000; Hays *et al.*, 2021; von Staats *et al.*, 2021). Reproductive allocation patterns (*i.e.*, vegetative propagation *vs.* sexual reproduction *via* flower and seed production) also often differ across the depth gradient within meadows (Kim *et al.*, 2014; Olesen *et al.*, 2017; Hays *et al.*, 2021; but see von Staats *et al.*, 2021).

While *Z. marina* can be highly plastic (*e.g.*, Backman, 1991; Johnson *et al.*, 2017; Ruesink, 2018), genotypes also show heritable variation in physiological traits (*e.g.*, Hughes *et al.*, 2009; Tomas *et al.*, 2011), including response to light limitation (Salo *et al.*, 2015). Two field transplant experiments directly testing for microgeographic adaptation across the depth gradient in *Z. marina* show mixed results. In one, *Z. marina* seedlings collected from the shallow and transplanted to shallow, intermediate, and deep depths had 100% mortality in the shallow as a result of erosion, despite being transplanted back to their home environment (Olesen *et al.*, 2017). In the other, reciprocal transplant of shallow and deep cores across ~4-m depth found no difference in short-term (four-month) survival but did find differences in growth metrics that were broadly consistent with local adaptation: root, rhizome, and whole-plant production rates were highest for shallow *Z. marina* transplants in the shallow edge of the bed, and deep-origin transplants had higher production rates and photosynthetic capacity (P_{max}) than shallow-origin transplants in the deep (Dennison and Alberte, 1986).

Molecular genetic structure across depths in *Z. marina* has been observed in microsatellite markers (Billingham *et al.*, 2007; Kamel *et al.*, 2012; Hays *et al.*, 2021), SNPs (Oetjen *et al.*, 2010; EES, CGH, TCH, ARH, unpubl. data), and allozymes (Ruckelshaus, 1998), suggesting that gene flow is often limited, consistent with direct measures of pollen and seed dispersal (Orth *et al.*, 1994; Ruckelshaus, 1996). Paternity and pedigree analyses also confirm that pollen flow is largely, though not completely, restricted to <10 m (Furman *et al.*, 2015; Hays *et al.*, 2021), in accord with molecular patterns of kinship structure observed at multiple scales (Hämmerli and Reusch, 2003; Billingham *et al.*, 2007; Kamel *et al.*, 2012; Furman *et al.*, 2015).

Oysters

Like seagrasses, oyster populations span intertidal to subtidal environments, covering gradients in desiccation, heat stress, food availability, predation, competition, and parasitism (Fodrie *et al.*, 2014; Malek and Byers, 2017; Li *et al.*, 2018; Baillie and Grabowski, 2019; Hanley *et al.*, 2019). Experimental work on the eastern oyster, *Crassostrea virginica*, has shown divergence in growth, as well as survival and disease dynamics, across tidal elevations in some systems (Bartol *et al.*, 1999; Fodrie *et al.*, 2014; Malek and Byers, 2017; Baillie and Grabowski, 2019), though not universally (*e.g.*, Malek and Breitburg, 2016); and patterns can vary over time (*e.g.*, Roegner and Mann, 1995; Fodrie *et al.*, 2014) or as a factor of additional microhabitat

characteristics (*e.g.*, Bartol *et al.*, 1999). Whether genetic differences may mediate response to tidal elevation in oysters remains largely unexplored (but see the Pacific oyster, *Crassostrea gigas*; Li *et al.*, 2018). However, the relative contribution of genetic factors in modulating oyster population responses to spatial variation in salinity is being examined in the eastern oyster, *C. virginica* (*e.g.*, Eierman and Hare, 2013, 2016; McCarty *et al.*, 2020), as well as the Olympia oyster, *Ostrea lurida*, which we review below.

Ostrea lurida inhabits intertidal and shallow subtidal estuarine habitat along the west coast of North America, from Baja California to Canada (Polson and Zacherl, 2009; Silliman, 2019). Within San Francisco Bay in northern California, a reciprocal transplant experiment with *O. lurida* using F_1 offspring sourced from sites with different salinity regimes, and separated by ~18 to 40 km, found that juvenile survival 1 month post-outplant was consistent with local advantage for 2 of the 3 sources (Bible and Sanford, 2016). Follow-up common-garden experiments with F_2 offspring showed that these populations differed in both their response to, and tolerance of, low salinity. After exposure to a sublethal low-salinity challenge, survival was greatest for F_2 oysters originating from the field site most consistently exposed to low salinity (Bible and Sanford, 2016). In a paired experiment that included F_2 offspring from the same source populations, Maynard *et al.* (2018) demonstrated differences in gene expression between source populations in both control (ambient salinity) and low-salinity (5 ppt) treatment groups, particularly between the most and least tolerant source populations. Some of the strongest differences in expression came from genes with expected osmoregulatory functions, like the control of ciliary activity in the gill, that may mitigate the adverse effects of low-salinity seawater (Maynard *et al.*, 2018).

Corals

Many species of corals are broadcast spawners with pelagic larval stages that confer high dispersal potential (Hellberg, 2009), consistent with studies showing high genetic connectivity among populations across thousands of kilometers (*e.g.*, Rodriguez-Lanetty and Hoegh-Guldberg, 2002; Goodbody-Gringley *et al.*, 2012). However, coral species also provide evidence of population-level trait and genetic divergence across depths within sites, coincident with environmental gradients in light, water motion, sediment transport, predator and mutualist distributions, and food availability (Prada *et al.*, 2008; Brazeau *et al.*, 2013; Prada and Hellberg, 2013, 2014, 2021; Serrano *et al.*, 2014, 2016; Bongaerts *et al.*, 2017). For example, the broadcast spawner *Montastraea cavernosa* exhibits genetic differentiation from shallow to deep, though the presence and magnitude of this variation and the depth at which it occurs can vary from site to site (Brazeau *et al.*, 2013; Serrano *et al.*, 2014; Studivan and Voss, 2018). There was also evidence for differential dispersal across depth in *M. cavernosa*, with greater gene flow from shallow to deep across all sites (Serrano *et al.*, 2014). Finally, the small percentage of admixed *M. cavernosa* individuals at some sites is consistent with a role of selection in creating and/or maintaining this differentiation (Serrano *et al.*, 2014). Similar patterns of genetic differentiation have been documented in the brooding species *Porites asteroides* (Serrano *et al.*, 2016) and *Agaricia fragilis* (Bongaerts *et al.*, 2017), despite the key differences in brooding *versus* broadcast spawning life-history strategies. Divergence across depth is not uniform, however; in one of the same studies, no evidence for genetic structure between depths or locations was found for the broadcast spawner *Stephanocoenia intersepta* (Bongaerts *et al.*, 2017).

Although not a foundation species, the Caribbean octocoral *Eunicea flexuosa* provides the best evidence for both genetic and trait differentiation across depth in corals and highlights the power of utilizing a combination of experimental and non-experimental approaches (Prada *et al.*, 2008; Prada and Hellberg, 2013, 2014). As with other coral species, *E. flexuosa* exhibits genetic divergence between shallow and deep zones separated by as little as 200 m across multiple sites in the Caribbean, with asymmetrical migration from shallow to deep (Prada and Hellberg, 2013, 2021) and stronger genetic divergence in adults than in juveniles (Prada and Hellberg, 2014). In addition, this genetic differentiation is associated with significant variation in 14 morphological traits (Prada *et al.*, 2008). Field reciprocal transplant experiments confirmed local adaptation to depth (Prada *et al.*, 2008) and also confirmed that selection is strong enough to create the observed segregation, in part due to the long pre-reproductive stage in this species (Prada and Hellberg, 2013).

Emergent Themes

Microgeographic adaptation versus *local adaptation* versus *balanced polymorphism*

This review focused on microgeographic adaptation because this scale is historically understudied (Richardson *et al.*, 2014) and mirrors the within-community scale at which foundation species interact with associated organisms. However, local adaptation in foundation species is also evident and important at larger spatial scales. For example, paired molecular and experimental approaches have discovered (*a*) thermal adaptation in the canopy-forming intertidal seaweed *Hormosira banksii* between sites and regions (Miller *et al.*, 2020), (*b*) latitudinal clines in water use ecophysiology in the mangrove *Avicennia schaueriana* (Cruz *et al.*, 2019), and (*c*) home-site advantage in inshore *versus* offshore populations of the Caribbean coral *Porites asteroides* (Kenkel *et al.*, 2015; Kenkel and Matz, 2017).

Where the line falls, exactly, between balanced polymorphism and local adaptation *sensu stricto* is not clear and is

further complicated by the fact that we often lack sufficient resolution of dispersal kernels to parse very finely. Indeed, even formal definitions of "microgeographic" (within two standard deviations of mean dispersal distance) (Richardson *et al.*, 2014), while inherently appealing, can be difficult to apply. The examples highlighted above span a range of connectivity within the microgeographic framework, and they include broadcast spawning species that trend toward the balanced polymorphism side of the continuum. Balanced polymorphisms are particularly relevant at the fine spatial scales considered here, and arguably in marine systems in general, because many species produce vast numbers of pelagic offspring that disperse over environmental gradients spanning scales from centimeters to hundreds of kilometers (Marshall *et al.*, 2010; Sanford and Kelly, 2011). Polymorphism maintained by strong and continuous purifying selection on immigrants imposes a higher demographic cost than does local, restricted dispersal, but the net outcome (*i.e.*, spatial differentiation of adult genotypes) may be quite similar. Both pre- and post-reproduction selection against immigrants generates a barrier to gene flow and can select for other isolating mechanisms (*e.g.*, habitat or mate choice), if life history allows (Nosil *et al.*, 2005).

Despite similarities in the patterns they generate, the two flavors of differentiation may differ critically in their conservation implications. Local adaptation *sensu stricto* is an important form of intraspecific biodiversity, because locally adapted demes contain unique genetic variation that determines current fitness and can also shape future evolutionary potential (Schneider *et al.*, 1999; Peterson *et al.*, 2018; Di Santo and Hamilton, 2020). If selection pressures change, patterns of differentiation maintained by constant purifying selection will be more labile than in demes showing traditional local adaptation, because these populations may be limited by standing genetic diversity (Linhart and Grant, 1996; Lenormand, 2002).

One assumption in discussions of local adaptation *versus* balanced polymorphism (*e.g.*, Kawecki and Ebert, 2004; Sanford and Kelly, 2011) seems to be that in the latter, local adults are not the only source of locally advantageous alleles. If these alleles exist elsewhere in the larger metapopulation, then the loss of local adults does not decrease the range of phenotypes possible within the species. However, this is not necessarily the case; even under high levels of cross-gradient gene flow typically thought to define balanced polymorphism, local solutions may still be genetically unique and, thus, add to intraspecific biodiversity. Further, marine systems often encompass both patchiness and gradients at different scales, generating potential for both balancing selection and local adaptation for the same trait. For example, the Pacific rockweed *Silvetia compressa* shows variation in embryo emersion tolerance across the intertidal gradient over the scale of meters at some sites (Hays, 2007). While this within-site differentiation is likely maintained only by continuous sorting of phenotypes by selection, the emersion tolerance of upper-limit lineages var-

ies across sites (Hays, 2006), consistent with expected limited dispersal (and greater evolutionary independence) at that scale.

Gradients in elevation

A recurrent theme in our review of differentiation at the microgeographic scale is that elevation (*i.e.*, subtidal water depth or intertidal immersion regime) is likely a common driver of phenotypic and genetic divergence in marine foundation species. The depth gradient spanned by nearshore marine species causes variation in a suite of selective factors, including the quantity and quality of light, the force of waves and currents, sediment load, and the abundance of predators, parasites, and mutualists. Across diverse taxa, individuals found at different depths often vary in traits, including morphology, resistance to natural enemies, and timing of reproduction. Further, these within-species gradients are mirrored by numerous examples of closely related species found at different depths (Prada and Hellberg, 2013), suggesting that depth gradients generate strong selective forces that can ultimately lead to speciation. For example, depth gradients in light are hypothesized as a cause of speciation by sensory drive in cichlids (Seehausen *et al.*, 2008), and factors associated with depth appear to have driven speciation in rockfish (Ingram, 2011).

Similarly, across the intertidal gradient, strong selective pressure associated with emersion differences is repeatedly associated with both intra- and interspecific patterns of differentiation. For example, reciprocal transplants of the habitat modifying brown alga *Fucus vesiculosus* suggest microgeographic phenotypic differentiation across the species' intertidal distribution (Benes and Bracken, 2016, 2020). This result mirrors among-species patterns and cryptic speciation in closely related and co-distributed congeners (*Fucus spiralis* and *Fucus guiry*) that occupy adjacent zones in the intertidal (Cánovas *et al.*, 2011; Zardi *et al.*, 2011). Although they differ in mating system (*F. vesiculosus* is dioecious, and *F. spiralis* and *F. guiry* are hermaphroditic), all three can hybridize (Billard *et al.*, 2005; Engel *et al.*, 2005). Nevertheless, they segregate across tidal heights with distinct differences in allele frequencies (Billard *et al.*, 2010) and physiology (resilience to thermal stress and desiccation) (Zardi *et al.*, 2011), suggesting that the selective gradient across the intertidal zone is stronger than the homogenizing effect of ongoing gene flow.

Elevation gradients in estuarine and nearshore coastal systems have interesting parallels to elevation gradients in alpine and montane systems. Microgeographic adaptation across terrestrial elevation gradients has been demonstrated in a variety of plant species (Halbritter *et al.*, 2018), from perennial forbs such as *Boechera stricta* (Anderson *et al.*, 2015) to deciduous trees such as *Fagus sylvatica* (Gauzere *et al.*, 2020) and *Populus trichocarpa* (Zhang *et al.*, 2019), due to abiotic factors, such as temperature, soil moisture, and growing season covarying with elevation. Moreover, such differentiation within

species by elevation mirrors shifts in species and likely drives speciation with elevation (*e.g.*, Steinbauer *et al.*, 2016). One important difference between elevation gradients in marine systems and those in terrestrial systems is that variation in climatic conditions across elevation parallels climatic gradients across latitude (*e.g.*, 1000 feet of elevation is equal to 10° latitude); in contrast, tidal gradients exist across all latitudes in coastal and estuarine environments, although they differ in amplitude by location.

Phenology as a mechanism restricting gene flow

Another theme that emerges from our review is the likely influence of phenology. Phenological shifts across a selective gradient can result in greater reproductive isolation than predicted based on geographic distance alone and can facilitate adaptation by generating assortative mating within environments (Kirkpatrick and Ravigné, 2002; Gavrilets and Vose, 2007). In the marine foundation species described above, the timing of *Spartina alterniflora* flowering varies across the marsh (Crosby *et al.*, 2015; O'Connell *et al.*, 2020; Daniela Adjunta, College of Charleston, pers. comm.), potentially acting to reduce pollen flow between low- and high-marsh zones. Similarly, the flowering phenology of both *Zostera marina* (von Staats *et al.*, 2021) and *Posidonia oceanica* (Buia and Mazzella, 1991) shifts with depth, such that deeper shoots show delayed flowering and subsequent seed development. *Zostera marina* also shows variation in dichogamy from intertidal to subtidal habitats, leading to spatial differences in the potential for self-pollination (Ruckelshaus, 1995). Whether these phenological differences are entirely plastic or whether they reflect differences between genotypes is unknown. Environment-induced changes in phenology may be a relatively common and under-recognized mechanism that promotes divergence (see reviews by Levin, 2009; Jordan *et al.*, 2015); moreover, if the observed shift in timing is plastic, a partial barrier to gene flow across the selective gradient occurs virtually immediately, unimpacted by the same constraints as evolution (*e.g.*, negative genetic correlations, lack of heritable genetic variation, dissolution by gene flow).

Life history and mating system

Many foundation species share particular life-history traits that influence the likelihood of local adaptation. For example, correlated with their large body size, most foundation species tend to be long lived and iteroparous. Long generation times and overlapping generations are expected to slow the pace of adaptive evolution in a changing environment (Chevin *et al.*, 2010; Kuparinen *et al.*, 2010; Yamamichi *et al.*, 2019). However, along a stable spatial cline, longer life span may increase the window for selection to act before reproduction, countering the influence of maladapted migrants (*e.g.*, Prada and Hellberg, 2013).

Another life-history characteristic common to many marine foundation species (*e.g.*, corals, seagrasses, marsh grasses,

some seaweeds) is a mixed reproductive system that includes both clonal and sexual reproduction. The degree of clonality observed in marine foundation species varies both geographically (*e.g.*, Coyer *et al.*, 2004; Baums *et al.*, 2006; Torres *et al.*, 2020) and across environmental gradients spanned by individual populations (*e.g.*, Hughes and Lotterhos, 2014; Olesen *et al.*, 2017; Hays *et al.*, 2021). Both extrinsic and intrinsic factors contribute to realized mating system differences, such that difference in clonal structure within and across sites may reflect differential reproductive effort (genotypes that allocate more energy to sexual reproduction) or differential reproductive success (environments that favor the establishment of particular types of propagules). Sex is broadly considered to promote adaptation to novel conditions, while clonal lineages are generally expected to evolve more slowly (Felsenstein, 1974; Burt, 2000; Silvertown, 2008; McDonald *et al.*, 2016). However, clonal reproduction has the advantage of preserving and multiplying successful genotypes without the diluting effects of recombination or gene flow: offspring inherit the complete parental genotype, including non-additive genetic effects (*e.g.*, dominance, epistasis). Models suggest that clonality can affect adaptation to a temporally changing environment (*i.e.*, evolutionary rescue). For example, if the environment changes abruptly as a step function, partially clonal populations can outperform fully sexual ones, because clonal reproduction protects well-adapted phenotypes from sex (Orive *et al.*, 2017). However, in a continuously changing environment, partially clonal populations may be less likely to keep pace and persist: when the optimum phenotype was constantly changing, generating novel allele combinations quickly became more important than replicating past winners (Orive *et al.*, 2019). Thus, mixed reproductive systems may be advantageous in spatially heterogeneous environments (Williams, 1975; Eckert *et al.*, 2016; Torres *et al.*, 2020) like those common in coastal and marine systems, especially if allocation of energy to sex is flexible and fitness dependent (Hadany and Otto, 2007, 2009).

Relative strength of abiotic versus biotic selection

Most documented examples of microgeographic differentiation in marine foundation species are attributed to abiotic environmental gradients, rather than biotic factors (*e.g.*, competitors, herbivores, microbial foulers, or parasites) acting as the primary selective forces. A review of local adaptation in marine invertebrates across multiple scales also revealed that abiotic factors, such as temperature, salinity, and wave action, are more commonly identified as the primary selective force than are biotic factors, such as predation, herbivory, and parasitism, though both play a role in marine systems (Sanford and Kelly, 2011). In contrast, recent meta-analyses looking at the strength of abiotic and/or biotic selection across terrestrial and aquatic systems found equivocal results (Urban 2011; Briscoe Runquist *et al.*, 2020; Hargreaves *et al.*, 2020). While biotic factors strongly affect fitness, they do not necessarily result in local

adaptation, perhaps because biotic interactions are more variable and unpredictable at the spatiotemporal scales over which adaptation can occur (Hargreaves *et al.*, 2020). However, a recent meta-analysis across systems and taxa found that local adaptation was greater in the presence of a biotic interactor, particularly for plants (Briscoe Runquist *et al.*, 2020), emphasizing that the relative importance of abiotic and biotic factors in driving population divergence is likely context dependent (Hargreaves *et al.*, 2020). Different abiotic and/or biotic selective forces may drive local adaptation at opposite ends of an environmental gradient (*e.g.*, Morales *et al.*, 2019; Popovic and Lowry, 2020), as in the classic rocky intertidal zonation paradigm (Connell, 1961; Wethey, 1984; Fodrie *et al.*, 2014); whether this is a common feature of microgeographic divergence at smaller scales merits further investigation across systems.

Future directions

Understanding how species respond to spatial variation in their environment is a fundamental question in evolutionary ecology. While microgeographic adaptation remains a relatively understudied phenomenon, an increasing number of case studies across diverse systems and taxa challenges the notion that adaptive genetic differentiation can occur only over spatial scales that greatly exceed that of dispersal (Richardson *et al.*, 2014). We argue that foundation species represent a particularly relevant set of organisms in which to test for and examine microgeographic differentiation, because these species drive ecological functions of entire ecosystems (Ellison, 2019), and because any adaptive phenotypic divergence within populations can have far-reaching impacts on community and ecosystem processes (Norberg, 2004; Whitham *et al.*, 2006; Hughes *et al.*, 2008; Matthews *et al.*, 2011). Notably, the consequences of microgeographic adaptation will depend on the specific traits that underlie fitness and ecological function in foundation species. For example, in the Olympia oyster case study described above, Bible and Sanford (2016) documented differences in *Ostrea lurida* survival after a hyposalinity challenge consistent with local adaptation. Such genetic differentiation may extend the range of salinities over which *O. lurida* can be found and/or allow for more consistent oyster density across parts of estuaries that differ in freshwater input. If the latter, then microgeographic adaption in *O. lurida* will reduce spatial variation in species interactions and ecosystem processes that are linked directly or indirectly to the physical structure that *O. lurida* provides. Conversely, the underlying physiological mechanism that allows low-salinity tolerance is likely a change in ciliary activity in the gill (Maynard *et al.*, 2018); thus, in the same system, local adaptation may also amplify spatial variation for community and ecosystem processes linked to water filtration by *O. lurida*. This example demonstrates the diverse impacts of local adaptation for associated organisms (Urban *et al.*, 2020) and highlights key gaps in our knowledge that

should be the focus of future work. In particular, we need more information on the link between genetics and demography in foundation species across spatial scales—that is, when and where does local adaptation reflect hard *versus* soft selection? We also need to identify the traits underlying both adaptation and ecological function in marine foundation species and to document how these covary over space.

Our review also suggests particular themes that require further exploration and testing: Do the ecological consequences of microgeographic differentiation differ when it is accompanied by broad *versus* restricted dispersal (*i.e.*, balanced polymorphism *vs. sensu stricto* local adaptation)? Are abiotic factors, especially gradients in elevation (water depth, intertidal height), more consistent drivers of genetic differentiation in marine foundation species than biotic factors; and if so, why? Are there particular life-history traits (*e.g.*, mixed clonal and sexual reproduction, plasticity in reproductive phenology) that promote microgeographic differentiation? Effective conservation of biodiversity requires understanding how that diversity is structured and maintained across all relevant spatial scales; we suggest that microgeographic variation may be an important characteristic of many marine foundation species, and further investigations at this scale may inform the management and conservation of critical habitat-forming species and their associated ecosystem functions and services.

Acknowledgments

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