Week 1: Spatial and Temporal Scale of Environmental Variation

**Discussion Summary:** 13 groups participated in Week 1 discussion. Discussion summaries received from LSU, Hal-Dames Rule, MSC, NEU, UGA/UNH, WSU, USC, RU, FSU, UCONN, Bodega/UCDavis, UCSB/UChicago, UQueensland

84 total participants across groups

**1. Are marine systems more or less variable than terrestrial?**

The Steele et al. paper proposes that variability is greater in the terrestrial biome than the marine biome, and that difference in variability may explain divergent evolutionary trajectories between marine and terrestrial species. In their discussions, three groups rejected this thesis (WSU, UGA/UNH, NEU), four groups said that it depends (UCSB, UCONN, FSU, MSC), and five groups generally supported that marine systems are less variable (Bodega/UCD, RU, USC, Hal-Dames, LSU), although each of the five supportive groups also put forth mitigating factors that tempered support.

Three main themes emerged from the discussions (each discussed in further detail below). 1) Many groups critiqued the oversimplification and generalization in the Steele paper that ignored important sources of variation in marine environments. 2) Several groups pointed out the importance of discriminating between environmental variability and the *predictability* of environmental variability. 3) Groups also questioned the evolutionary consequences of environmental variability given that species also vary in their sensitivity, vulnerability, perception of, and responses to variability in the environment.

1) Ten of the twelve groups commented that the thesis and evidence within the Steele et al. paper was oversimplified and over-generalized. Temporal and spatial scale likely play an important role in whether or not terrestrial and marine biomes differ in variability, as any differences in variability between terrestrial and marine biomes that exist likely become smaller at larger spatial and temporal scales. Moreover, several marine ecosystems including coastal, intertidal, and estuarine systems were overlooked yet are likely as variable as many terrestrial systems, if not more so. Groups also listed several sources of variability that are common and biologically important in marine systems. Currents, gyres, tides, upwelling, offshore advection, pathogens, latitude, temperature, light attenuation, nutrient availability, salinity, pH, dissolved oxygen, season, and substrate stability were all listed as important sources of variation prevalent in marine systems yet not mentioned in the paper. As one group summed up (UCSB/UChicago), among the variables shared by terrestrial and marine environments, terrestrial environments may be more variable. However, the total number of fluctuating selection pressures may be greater in marine systems, which has been shown to strongly affect organismal responses.

The second argument of the Steele paper (i.e., different evolutionary trajectories between terrestrial and marine species evolved in response to differences in variability) was contingent on the first argument being true (i.e., marine systems are less variable than terrestrial systems). The lack of support for the first tenet seemed to weaken support for the second, as few groups even discussed it. The groups that did mention it found that the strategies listed as evidence of evolved differences between marine and terrestrial species (i.e., colonial vs. social systems, life longevity, reproductive mode) were also overgeneralized and insufficient. There is more overlap between marine and terrestrial systems than was alluded to in the text. One group (RU) pointed out that eusociality should not be used as evidence for different evolved strategies given that it is restricted to Hymenoptera and is not a dominant strategy. In addition, several groups disagreed that broadcast spawning and planktonic larvae evolved in response to lower variability, as these life stages are also subject to strong environmental variability and stochasticity. Evolutionary differences between land and sea species may be more likely to be due to differences in the physical and chemical properties of the two environments and the unique challenges posed by each rather than differences in variability.

2) Seven of the twelve groups discussed predictability as an important feature to consider, as predictability changes the nature of variability for the organism. On the whole, oceans may be more predictable than land, but it was generally agreed that unpredictability experienced in marine environments at smaller spatial and temporal scales reduced the likelihood that evolutionary differences are produced by overall differences in predictable variability. For example, the prevalence of high fecundity/low parental care strategies in the ocean may not be a strategy to take advantage of a more predictable environment, as the trajectories of larvae in water are influenced by a wide array of unpredictable factors (such as currents, tides, gyres, or pathogens) and therefore not as predictable as suggested in the paper.

Predictability of a system will have different impact on evolutionary dynamics. For example, intertidal systems are highly variable systems, but a large component of the variation due to tides is predictable, which likely alters the set of adaptations necessary to persist. An example provided by Scott Burgess shows that environmental predictability affects dispersal potential and offspring size in a large-scale survey of marine invertebrates (<https://doi.org/10.1111/ele.12402>). Despite the consensus that predictability is an important factor in adaptation, only one group provided an empirical example of an organismal response correlated to environmental predictability. The lack of examples may mean that the impact of environmental stochasticity on adaptation is an area ripe for further research and exploration.

3.) The organism itself will have a strong impact on how environmental variability will affects evolution. Size arose as an important factor to consider as small, planktonic organisms meet different sets of challenges than larger-bodied organisms therefore require a different set of adaptations. Mobility is another important feature, as sessile organisms may need to rely more on physiological means to persist. The number of stressors encountered by organisms also may drive evolutionary responses. However, multiple stressors may co-vary which could affect selection pressures and possibly lead to unique adaptive strategies. Ecological factors such as the interactions of pathogens or predators further contextualizes the impact of environmental variability. For example, marine organisms may be exposed to pathogens more often since pathogens are suspended in the water column (which is related to how different evolutionary strategies may be the result of differences in physical and chemical properties of environment, as discussed above). Additionally, some hypothesize that marine larval dispersal evolved to exploit lower predator abundance in pelagic water rather than environmental variability.

**2. How can we link the scale of environmental variability to microgeographic adaptation in the ocean? Could other mechanisms be at play?**

This discussion is based the Richardson et al. 2014 paper which reviews adaptation at microgeographic scales. Microgeographic adaptation is not predicted to be common in nature because high amounts of gene flow within small areas is expected to suppress divergent selection. However, authors suggest it may be more common than is currently appreciated. Because the term, “microgeographic” differs according to species, authors use Wright’s dispersal neighborhood metric to standardize across scales.

The majority of group discussions (nine out of eleven posts) centered around defining various requirements for adaptation (apart from dispersal) that are applicable on a microgeographic scale and may be key to understand the potential for microgeographic adaptation. Genetic variation, population size, mutation rate, sexual reproduction, and dispersal rates were mentioned as factors that affect microgeographic adaptation, but environmental variability across scales was the most discussed. Considered spatially, if dispersal kernels exceed the scale of environmental variability, as is expected with many marine organisms with large dispersal or migratory ranges, greater environmental variation may be encountered thus increasing likelihoods of microgeographic adaptation. Environmental variability at temporal or organizational levels may also increase these likelihoods. Dispersal and gene flow remain critical aspects affecting these likelihoods, but the influence of dispersal may be more complicated than discussed in the paper. For example, the influence of dispersal is likely affected if mortality is experienced within certain microhabitats (e.g., high mortality in intertidal systems or high post-settlement mortality). Moreover, potential dispersal is not the same as realized dispersal as certain taxa can exert some control over dispersal range, like crab larvae that control vertical position to increase local retention. Two groups considered different scenarios in which phenotypic plasticity may be a better strategy than microgeographic adaptation. Hal-Dames Rule group suggests that for organisms with limited mobility, plasticity may be a better strategy if the species experiences greater temporal variation, while microgeographic adaptation may be favored if the species experiences greater spatial variation.

Five groups discussed various complicating factors that obfuscate our ability to study or characterize microgeographic adaptation. Typically, data collection practices can be patchy, disjointed, or across coarse scales and therefore may not capture important environmental or evolutionary variability at relevant scales. Additionally, researchers may not know the level that selection is acting, mistake microgeographic variation as phenotypic plasticity, or neglect maternal effects. As a result, microgeographic adaptation may be greatly underappreciated in the literature. Common garden approaches across multiple generations is a suggested solution for these issues. In addition, several groups stated that better efforts should be taken to define scale explicitly in evolutionary studies in terms of population, dispersal, symmetry, time, traits, and genomic basis. For example, the term “population” is commonly used but is a broad scale and poorly defined term that likely overlooks important microgeographic variation. Finally, the UConn group suggests that for studies that seek to test microgeographic adaptation (or other theoretical results), the best systems may be experimentally-tractable systems with strong environmental gradients such as estuaries with salinity gradients. However, many strong gradients are human-induced (e.g., pollution) which could affect or bias results.