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Is dispersal limitation more prevalent in the ocean?

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Fifty years ago, G. Evelyn Hutchinson peered into a pond, and wondered how so many species could co-exist in an apparently homogeneous habitat (Hutchinson 1961). Ecologists continue to grapple with this ‘paradox of the plankton’, but equally perplexing is the opposite question – why don’t all possible species coexist in this habitat? There are three basic types of answer to this second question: dispersal limitation, habitat filtering and biotic filtering. If we put aside habitat filtering for a moment, the world should be divisible into ‘saturated’ communities whose membership is limited primarily by biotic interactions between species, and ‘unsaturated’ communities whose membership is primarily limited by dispersal from the regional pool. The question is, what types of habitats and organisms tend to form either saturated or unsaturated communities?

In their contribution (this issue), Cornell and Harrison (2013) propose three major explanations why stochastic processes of dispersal from the regional pool are recognized to structure marine communities more than terrestrial ones. We agree with their main conclusion that the regional dispersal and recruitment are easier to study in marine than terrestrial environments. This factor most likely had a stronger impact on our understanding of local and regional diversity than the impact of early influential studies. We note that the importance of the production of propagules and their mortality, settlement, and recruitment from regions to local habitats has also been long recognized in the terrestrial literature. For example, the early work on ‘community drift’, which emphasized dispersal and recruitment limitation (Hubbell 1979) and eventually led to the development of ecological neutral theory (Hubbell 2001), was motivated by research in tropical rain forests. In addition to the ease of study and influence of early studies, Cornell and Harrison (2013) outline the case for marine communities actually being more influenced by dispersal from the regional pool than their terrestrial counterparts. We expand upon their line of thought to ask three questions. First, how does dispersal limitation in marine and terrestrial systems differ from the other major realm: freshwater? Second, what general characteristics of habitats and organisms predispose communities to strong dispersal

limitation? Finally, how can experimental and observational evidence for dispersal limitation be usefully combined?

Cornell and Harrison (2013) suggest that dispersal potential may be higher in marine than terrestrial habitats due to the buoyancy of water, and therefore the prevalence of planktonic larval stages in many marine species. The apparent homogeneity of the open ocean may compound these effects as well as facilitate research at regional scale. We have expanded this list by including a comparison with freshwater realm. Generally, buoyancy in freshwater habitats is lower than in oceans but higher than in terrestrial ecosystems (Table 1). Freshwater habitats are characterized by high habitat heterogeneity and their communities are prone to strong trophic interactions. We argue that some other factors linked to dispersal rates need to be considered when comparing the three realms. Some of these factors may work against the generalization that marine systems have the greatest dispersal potential (Table 1). For example, many terrestrial species (especially plants, parasites and mites) use other organisms as dispersal vectors, and thus achieve much greater dispersal distances than would otherwise be possible. Active flying and movement facilitated by wind currents, can modify diversity of terrestrial communities of insect and birds in ways similar to the ocean currents promoting dispersal of marine invertebrates and fish. There is also ample evidence for overland dispersal of freshwater adult insects and plankton (Vanschoenwinkel et al. 2008). Many freshwater species (especially aquatic insects and amphibians) have life cycles that cross ecosystem boundaries, allowing them to disperse in directions other than simply downstream. Finally, habitat disturbance can be extensive in terrestrial and freshwater systems, and the recolonization of disturbed areas can be limited by dispersal: for example, tree distribution in Europe is still rebounding from the last glaciation (Svenning and Skov 2007).

In general, we would expect strong dispersal limitation in communities containing species with low dispersal abilities and narrow habitat affinities, and in heterogeneous habitats where dispersal is impeded in some way. Together, these features ensure that species locate suitable habitat

Table 1. Comparison of main factors known or predicted to affect dispersal limitation in marine, terrestrial and freshwater realms.

Attribute	Marine	Terrestrial	Freshwater
Dispersal barriers	Ocean currents are directional barriers, but effectiveness as barriers highly variable, both spatially and temporally	Geographic and habitat barriers (e.g. mountain ridges and deserts), little variability in effectiveness of barriers	Dispersal often restricted to downstream and to linked bodies of waters although overland dispersal of winged adults and plankton is important especially in temporary habitats, occasional changes in effectiveness of barriers (e.g. to changes in stream course following surge events)
Habitat heterogeneity	Low in deep sea, but high in nearshore areas (e.g. coral reefs, intertidal areas, estuaries)	High except in human-modified landscapes	Very high, reflecting not only variations in water current, substrate, and temperature, but also impacts of watersheds
Habitat buoyancy	Very high	Very low	High
Habitat disturbance*	Buffered in part by the mass of water, but still strong effects of periodic shifts in ocean currents, storms, etc.	Extensive, ranging from recent (hurricanes, fires, human activity) to distant (glaciations)	Extensive and common, in temperate areas includes spring surges in water, freezing in winter, in tropical areas includes landslides and storm-induced changes in stream course
Animal-mediated dispersal	Rare	Common (especially for plants, mites and micro-organisms)	Rare
Life histories spanning multiple realms	Rare (e.g. sea turtles and marine birds, salmon and other anadromous fish)	Only a few groups (amphibians, some insects)	Common (amphibians, most aquatic insects)
High dispersal early life stage	Common (plankton)	Common for plants, but seeds more limited in dispersal distance than plankton	Rare to intermediate, more common at adult life stages

*all realms substantially affected by anthropogenic disturbance.

slowly due to direct limits to the propagule arrival rate, or because of inefficiency in species locating appropriate habitat. Marine systems appear to have many features that allow propagules to move quickly (ocean currents, prevalence of planktonic stages: Carr et al. 2003) and efficiently encounter suitable habitat (apparent homogeneity of benthic and pelagic habitat in deep ocean, although not shallower, nearshore areas: Marshall et al. 2010). Genetic estimates of dispersal distance suggest that marine macroalgae and sessile species disperse orders of magnitude further than terrestrial plants, their ecological analogue (Kinlan and Gaines 2003). Propagules also have longer to disperse in marine environments (e.g. 45–136 d for fish and crustaceans in southern California: Shanks and Eckert 2005) than in many terrestrial or freshwater environments. Once these marine propagules arrive at a site, it is then that two local processes – biotic filtering (e.g. via predation and competition) and habitat filtering (described as ‘phenotype-environment mismatches’ by Marshall et al. 2010) – are effective in weeding out species. Marshall et al. (2010) suggest that habitat filtering may actually be much more important than dispersal limitation in creating strong between-site genetic structure in marine populations. In sum, the high dispersal potential of marine species might argue against marine communities being primarily dispersal limited. Instead, we might predict terrestrial and freshwater communities to be more dispersal limited, despite the strategies (e.g. assisted dispersal, cross-ecosystem lifecycles) that many species have evolved to increase efficiency of their dispersal. Yet decades of marine research have been centered on the idea of strong regional determination of local communities (Carr et al. 2003), and Cornell and Harrison (2013) detail data on coral reefs that also support dispersal limitation.

We believe that an answer to this apparent paradox lies in the ability of ocean currents to both facilitate and obstruct dispersal. We normally think of dispersal barriers as topographic objects, like mountains, but ocean currents may act as strong dispersal barriers by prohibiting dispersal in a particular direction and impeding successful propagule settlement (Bode et al. 2006). The strength and sometimes idiosyncratic nature of ocean currents thus ensures that most early life stages do not get to most places in the ocean, and so enforces dispersal limitation in these systems. Some species are documented to travel with the current during upwelling events, and then follow the current in the opposite direction during relaxation events, returning close to their natal site (Shanks and Eckert 2005). In fact, by moving vertically through the water column to access different layers of water moving in different directions, larvae may be able to control their movement to some degree, resulting in recruitment surprisingly close to their natal site (Morgan et al. 2009, though see Marshall et al. 2010 for an alternate explanation). Finally, long distance marine dispersal is risky – pre-settlement mortality rates can be very high (Marshall et al. 2010) – further decreasing the effectiveness of dispersal.

There are tantalizing hints in the literature of differences in dispersal limitation among realms. Strict dispersal limitation should be apparent as a strong correlation of species turnover with spatial distance between sites, as opposed to correlations with environmental conditions. In a recent meta-analysis, species turnover is more strongly correlated with spatial distance between sites in terrestrial, stream and estuarine communities than in communities occupying marine and lake habitats, suggesting stronger dispersal limitation in the former (Cottenie 2005). However, this result is complicated by the fact that ocean

currents can disrupt the correlation of dispersal probability with linear distance. Another hint of dispersal limitation comes from studies of beta diversity (the spatial turnover of species composition) as all else being equal beta diversity should be higher in saturated than unsaturated communities. A meta-analysis of beta diversity (Soininen et al. 2007) shows a tendency for marine systems to have lower beta diversity than freshwater and terrestrial realms, consistent with marine communities being more regionally controlled. However, many processes besides dispersal limitation influence beta diversity, so it is difficult to ascribe causation. For example, habitat heterogeneity affects beta diversity and differs between realms (Table 1). Beta diversity can also be influenced by characteristics of the organisms in each habitat, including organism metabolic types (exothermic versus endothermic; Qian 2009), body size (Shurin et al. 2009), mobility (Fattorini 2010), trophic position (Soininen et al. 2007), and dispersal type (active versus passive; Cottenie 2005). In addition to habitat type, these organismal characteristics need to be considered when investigating direct relationships between regional and local diversity. Indeed, the influence of dispersal on the occupancy of trait space by ecological communities may be more illuminating than simply counting species.

There is still substantial uncertainty associated with our understanding of mechanisms driving local – regional biodiversity relationships, as most studies to date have been correlational. We join Cornell and Harrison (2013) in calling for research that moves beyond simple documentation of species number at different spatial scales to a more mechanistic approach of testing for dispersal limitation. Evidence for strong dispersal limitation can include statistical techniques, such as identification of vacant niches using niche modeling (Munguia et al. 2008), comparisons of communities with different degrees of isolation (Fattorini 2010), or correlations of species turnover with spatial distance independent of environment-space covariance (Tuomisto et al. 2003). Experimental evidence for dispersal limitation includes demonstrating a local increase in diversity after adding propagules of missing species (most often done in terrestrial systems, but see Lee and Bruno 2009 for an exception in a marine system). Humans are inadvertently creating such experiments by moving species across boundaries through global trade, biocontrol, or accidental introductions, but there has been little comparison of the effects of introduced species across realms. Finally, modeling approaches compare observed species distributions with those predicted from independently derived estimates of dispersal rates (Svenning and Skov 2007, Moore et al. 2008). Research in all realms – marine, terrestrial and freshwater – could benefit from applying the same techniques to separate the relative contributions of local and regional processes to structuring biodiversity.

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