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NOTE

Why Marine Islands Are Farther Apart in the Tropics

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ABSTRACT: Species diversity of benthic marine organisms is highest in tropical archipelagoes. I hypothesize this is in large part a consequence of the temperature dependence of development times and dispersal distances of planktonic larvae. Metabolic theory predicts and empirical studies confirm that marine larvae develop faster and consequently have shorter durations in the plankton at higher temperatures. Metabolic theory can be extended to predict that species diversity of benthic marine organisms is highest in tropical archipelagoes, because warm temperatures limit dispersal and gene flow and isolated islands provide favorable conditions for speciation and coexistence.

Keywords: dispersal distance, marine larvae, species diversity, temperature, tropical islands.

It is well documented that most groups of animals and plants have highest species diversity in topographically heterogeneous regions of the tropics. For example, diversity of terrestrial animals and land plants is conspicuously high in the Andean region of South America and the Himalayan region of Asia (see examples in Lomolino et al. 2010), and the diversity of marine organisms is highest in the archipelagoes of the Indo-West Pacific and Caribbean (e.g., Roberts et al. 2002; Tittensor et al. 2010; Bowen et al. 2013). Biologists have long recognized that high species diversity is often associated with warm temperatures, aseasonal climates, and topographic heterogeneity, but the causes are still debated.

In 1967, Daniel Janzen published a wonderfully creative paper titled “Why mountain passes are higher in the tropics.” He pointed out that because of the interaction between seasonal variation in climate and thermal sensitivity of organisms, a given change in elevation poses a greater barrier to dispersal of terrestrial organisms in the tropics than at higher latitudes. In the seasonal climates in the temperate zones, a species normally restricted to a low elevation can potentially disperse across mountain passes in summer without encountering temperatures outside the

range that it normally experiences in winter. Similarly, a temperate species endemic to high elevations can disperse across passes in winter without encountering temperatures outside the range that it normally experiences in summer. By contrast, in the tropics where temperatures at a given elevation remain relatively stable throughout the year, a species cannot disperse across a pass at a substantially higher or lower elevation without encountering temperatures that it has never experienced. Moreover, Janzen (1967) suggested that because of the weak seasonality of their thermal environments, tropical species should have evolved narrow thermal niches, reducing their capacities to tolerate extreme temperatures and increasing their “habitat fidelity.”

The Hypothesis for Why Marine Islands Are Farther Apart in the Tropics

I hypothesize that in a somewhat analogous way marine islands are farther apart in the tropics. This hypothesis comes from applying the metabolic theory of ecology (Brown et al. 2004; Sibly et al. 2012) to the larval ecology of marine organisms (O’Connor et al. 2007; O’Connor and Bruno 2012). I introduced it elsewhere (Brown 2014), but I develop it in more detail here. I am aware that parts of it are incomplete, but I hope that others may find it interesting enough to pursue.

The logic flows as follows:

PROPOSITION 1. *Most benthic marine fish, invertebrates, and multicellular algae disperse as larvae and then remain sedentary.*

PROPOSITION 2. *In such ectothermic organisms, metabolic rate, B , scales with body size and temperature as*

$$B = B_0 M^\alpha e^{-E/kT}, \quad (1)$$

where B_0 is a normalization constant; M is body mass, α is the mass-scaling exponent, which is usually close to $-1/4$ for mass-specific metabolic rate; e is the root of the natural logarithm, E is an “activation energy” which gives the temperature dependence; k is Boltzmann’s constant (8.617×10^{-5} eVK $^{-1}$); and T is temperature in Kelvin (Gillooly et al. 2001; Brown et al. 2004; Sibly et al. 2012).

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The value of E is predicted theoretically and measured empirically to usually be approximately 0.65 eV, equivalent to a Q_{10} of approximately 2.5 (Gillooly et al. 2001).

Rate of ontogenetic development, which is controlled largely by metabolic rate, scales similarly (Gillooly et al. 2002; Zuo et al. 2012).

PROPOSITION 3. *Development time, t , is the reciprocal of development rate, so the signs of α and E reversed, giving*

$$t = t_0 M^\alpha e^{E/kT}, \quad (2)$$

where α is approximately 1/4 and $E \approx 0.65$ (Gillooly et al. 2002).

PROPOSITION 4. *The time spent by larvae dispersing in the plankton is largely a function of development time, so larval duration scales as equation (2).* In general, marine larvae can be characterized as either lecithotrophic or planktotrophic, depending on whether development is fueled by metabolizing resources stored in the egg or by feeding on other organisms in the plankton (e.g., Thorson 1950; Strathmann 1985; Hoegh-Guldberg and Pearse 1995). For lecithotrophic larvae, larval duration depends on the time until the stored yolk has been consumed (O'Connor et al. 2007). For planktotrophic larvae, larval duration depends on the rate of development, which scales directly with metabolic rate (Gillooly et al. 2002; O'Connor et al. 2007; Zuo et al. 2012). Empirical studies confirm that the temperature dependence of larval development rate of both lecithotrophic and planktotrophic species scales approximately as equation (2). O'Connor et al. (2007; see also O'Connor and Bruno 2012) collected and analyzed data on the time of development from gamete to settling. They found that the average value of E for larvae of 66 species of invertebrates and 6 species of fish was 0.64.

PROPOSITION 5. *Maximum distance of larval dispersal varies directly with duration in the plankton and inversely with temperature.* Most marine larvae, with the exception of advanced stages of some fish and invertebrates, are too small to travel long distances under their own power, so they drift passively in the plankton. After controlling for other factors, such as mode of development, body size, and currents (see below), the maximal distance dispersed by larvae should vary inversely with temperature as given by equation (2). Substituting into equation (2) allows back-of-the-envelope calculations. Assuming that larval duration has $E = 0.64$ (from O'Connor et al. 2007), a difference in sea surface temperature of 20°C would translate to a more than sixfold greater dispersal distance in the colder waters. This thermal difference approximates that between the tropical Indo-West Pacific or Caribbean Islands compared to the near-polar Aleutian or circum-Antarctic islands.

PROPOSITION 6. *Short dispersal distances facilitate local*

adaptation and lead to restricted geographic distributions and high levels of endemism in warm waters. Short-distance dispersal means that recruitment is local, allowing genetic differentiation and specialized adaptation to local conditions as Janzen proposed. But it also has the consequence of inhibiting colonization of distant sites, resulting in small geographic ranges and high endemism.

PROPOSITION 7. *A low frequency of long-distance dispersal leads to high rates of speciation and high regional (within-archipelago) species diversity.* High speciation rates appear to account, at least in part, for the accumulation and maintenance of high species diversity of marine invertebrates in the tropics (Jablonski et al. 2006; Valentine and Jablonski 2010). For allopatric speciation to build up species diversity within an archipelago, interisland dispersal must be sufficiently low that gene flow does not prevent genetic differentiation but sufficiently high that propagules occasionally colonize other islands. The frequency distributions of typical dispersal distances appear to provide the requisite conditions. The near-exponential distance decay means that the vast majority of individuals settle short distances from their parents, but the “fat tails” of these distributions mean that a tiny minority of individuals are transported great distances (e.g., Clark et al. 1998). Such dispersal dynamics, combined with abundant ecological opportunities for existence and coexistence of specialized species, appear to account for the high rates of speciation and the resulting buildup of both within- and between-island (α - and β -) diversity often observed on archipelagoes. Examples for terrestrial islands include Darwin's finches in the Galapagos and honeycreepers and *Drosophila* flies in the Hawaiian Islands.

Qualifications and Caveats

The logic presented above leads to the hypothesis that marine that islands are effectively farther apart in the tropics. Everything else being equal, warm temperatures result in short larval durations and dispersal distances and high speciation rates and species diversity of benthic marine organisms in tropical archipelagoes. Of course, everything else is never exactly equal. Many complications affect the dispersal and diversification of marine organisms across straights separating tropical islands, just as similar factors affect dispersal and diversification of terrestrial organisms across passes separating tropical mountains.

Actual dispersal distances of marine larvae are affected by many intrinsic biological and extrinsic environmental factors in addition to temperature (e.g., Sponaugle et al. 2002; Leis et al. 2013). For example, equation (2) predicts that body size as well as temperature affects larval duration. For lecithotrophic species, body mass is equivalent to egg mass, because the larvae do not feed. For planktotrophic

species, body mass is less constraining, because the larvae feed and can potentially grow during development. To the extent that marine larvae follow the temperature-size rule—the tendency of ectotherms to develop more rapidly but mature at smaller sizes at higher temperatures (Atkinson 1994; Forster et al. 2012; Zuo et al. 2012; see also Lonsdale and Levinton 1985)—this phenomenon should also affect dispersal. In general, planktotrophic larvae tend to be smaller, to have longer durations in the plankton, and to be more common in warmer tropical waters than nonfeeding larvae (Thorson 1950; Strathmann 1985; Pearse et al. 1991; O'Connor et al. 2007; Valentine and Jablonski. 2010; Marshall et al. 2012). There are additional complications. Some marine invertebrates and fish have aplanktonic larvae; their lecithotrophic eggs are attached to a substrate or brooded by a parent rather than being released into the plankton. This mode of development, at least in invertebrates, is most frequent at high latitudes where it may be an adaptation to limit dispersal (Marshall et al. 2012). In cold waters where larval duration is prolonged and along coastlines where currents are strong, larvae can be carried away from their natal sites, resulting in source-sink population dynamics and limiting local adaptation (Byers and Pringle 2006; Pringle et al. 2011, 2013).

Other abiotic and biotic factors that affect duration in the plankton and dispersal distance include magnitude and direction of currents, productivity of ocean waters, rate of production of larvae (which depends on population size and per capita fecundity rate), rate of mortality of larvae due to starvation and predation, and larval behavior (Marshall et al. 2012). Although tiny marine larvae have limited capacities for active swimming, some exhibit substantial vertical movement in the water column, behavior that can place them in different temperature regimes and currents than surface waters (Sponaugle et al. 2002; Shanks et al. 2003). For these and other reasons, empirical frequency distributions of dispersal distance reflect the interacting effects of multiple variables and are more complex than would be expected on the basis of simple diffusive transport (e.g., Clark et al. 1998; Siegel et al. 2003; Shanks 2009; Pringle et al. 2011). Unfortunately, high-quality data on plankton duration and dispersal distance are available for only a relatively few species—mostly abundant, commercially valuable, invasive, or endangered ones. Nevertheless, empirical studies generally confirm the theoretically predicted relationship between temperature, duration in the plankton, and dispersal distance (Shanks et al. 2003; Siegel et al. 2003; O'Connor et al. 2007; Shanks 2009; Marshall et al. 2012; O'Connor and Bruno 2012).

Janzen emphasized the direct effect of environmental temperature as a barrier to dispersal of terrestrial organisms between tropical mountains. Warm waters present a similar physiological barrier to long-distance dispersal of

marine larvae between tropical islands. In both cases, the barriers due to physiological tolerances are probably exacerbated by biotic resistance from enemies—competitors, predators, herbivores, parasites, and pathogens—that are more diverse and active in the warmer environments of the tropics (e.g., Schemske et al. 2009). This biotic reinforcement should have the effect of increasing the temperature dependence of dispersal distance.

Unlike Janzen, who modestly stated that the mountain-passes phenomenon “is not an attempt to explain tropical species diversity,” I suggest that topographic heterogeneity and associated bioclimatic barriers to dispersal play a major role in tropical species diversity in both marine and terrestrial environments (Brown 2014). The patterns of species diversity with latitude, depth in the ocean, and elevation on land are strongly correlated with climatic or oceanographic gradients of temperature (Fischer 1960; Rohde 1992; Allen et al. 2002; Titensor et al. 2010; Brown 2014). At least four different mechanisms likely operate independently and interactively to generate these patterns; all have a common basis in the pervasive temperature dependence of metabolic rate (eq. [1]): (1) primary productivity (e.g., Hutchinson 1959; O'Brien et al. 1998); (2) rates of biotic interaction and mechanisms of coexistence (e.g., Brown et al. 2004; Brown 2014); (3) rates of evolutionary diversification and coevolution (e.g., Rohde 1992; Storch 2012; Brown 2014); and (4) dispersal (Janzen 1967; Brown 2014). A corollary pattern supporting the effect of dispersal is Rapoport's rule, the tendency of species to be restricted to smaller geographic areas and narrower ranges of abiotic conditions in the tropics than at higher latitudes (e.g., Stevens 1989; McCain 2009). I readily admit, however, that the mechanistic connections between environmental temperature, rates of physiological, ecological, and evolutionary processes, and standing stocks of species richness still need to be clarified, both theoretically and empirically. As David Storch (2012) has written, “a metabolic theory of biodiversity is a work in progress.”

Mechanistic linkages between physiology, ecology, evolution, and biogeography in benthic marine organisms offer promising opportunities to make such progress. It would be interesting to examine effects of temperature, egg size, mode of development, and other variables on geographic variation in dispersal distance, genetic differentiation, and species diversity. The hypothesis introduced here could potentially be generalized to address effects of temperature on dispersal, population dynamics, genetic differentiation, and speciation of pelagic as well as benthic marine organisms, and along gradients of depth as well as latitude. The effects of tropical climates in limiting dispersal should not only promote local adaptation, specialization, and habitat fidelity, as suggested by Janzen (1967), but also lead to higher beta diversity, smaller geographic

ranges, and greater local endemism in topographically heterogeneous regions. The temperature dependence of development and dispersal should also be relevant to more applied issues, such as designing reserves (e.g., Shanks et al. 2003; Marshall et al. 2012) and predicting impacts of climate change (e.g., Munday et al. 2009; Sunday et al. 2012; Thomas et al. 2012).

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