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Editorial

Ecology and evolution along environmental gradients

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Life isn't black and white. It's a million gray areas, don't you find?
–Sir Ridley Scott–

In natural systems, few (if any) environmental factors are truly "binary" (or black and white). This applies to both abiotic factors (e.g., temperature regimes along gradients of altitude, latitude, or longitude), biotic factors (e.g., gradual variation of predation risk along stream gradients), or the impacts entire sets of correlated ecological factors (i.e., multifarious selection) impose onto organisms (e.g., Kraft et al. 2011; Brown 2014; Egea-Serrano et al. 2014; Deacon et al. 2018). The latter occurs when species inhabit starkly different habitat types like forest versus dune habitats (e.g., *Epipactis helleborine* orchids: Jacquemyn et al. 2018) or lakes versus rivers (e.g., three-spine stickleback, *Gasterosteus aculeatus*: Kaeuffer et al. 2011). Exceptions are, of course, the rule, and some environmental factors indeed seem to follow a more clear-cut "binary" pattern. For example, salinity in certain coastal lagoons, landlocked lakes, and estuaries can range from oligo- to hypersaline, with clear differences between individual bodies of water (Laverty and Skadhauge 2015). Nonetheless, temporal variation in salinity can be strong also in some of these environments (Caliman et al. 2010), yet again leading to gradual variation in selective regimes. In other systems, however, salinity forms more continuous gradients, sometimes over large geographic distances (Mück and Heubel 2018).

Historically, the fields of ecology and evolution have often tended to contrast the extremes of selective regimes, such as "low versus high predation" environments (e.g., Reznick and Endler 1982; but see Deacon et al. 2018) or "toxic versus non-toxic" environments (e.g., Riesch et al. 2015; but see Riesch et al. 2016). This approach was driven by the desire to establish general principles of how contrasting environments affect the observed patterns of biodiversity, both in terms of community structures (e.g., through environmental filtering: Kraft et al. 2015; see also Diamond 1975), microevolutionary processes within species (local adaptation: Kawecki and Ebert 2004; Blanquart et al. 2013), and macroevolutionary processes (adaptive or ecological speciation: Nosil 2012).

The same is true for selection imposed by competition (i.e., foraging competition or competition for mates), which may arise from regional differences in population densities, resource availability, operational sex ratios, and so forth (e.g., Winkelmann et al. 2014; Cadotte and Tucker 2017; Mück and Heubel 2018). For example, previous studies have compared behavioral adaptations of males with low versus high sperm competition risk and intensity (e.g., Bierbach et al. 2015; Rouse and Bretman 2016), while various forms of competition-driven selection in reality follow a gradient pattern (Evans and Magurran 1999; Cattelan and Pilastro 2018; Mück and Heubel 2018).

Appreciating that ecological gradients prevail in nature raises a number of conceptual issues, only few of which can be outlined here. In terms of environmental filtering, for example, an important question considers the spatial scale at which environmental gradients affect different taxa. While environmental gradients can be rather steep for some species, others may be affected at a very different geographic scale. This certainly affects the extent to which different taxonomic groups contribute to what has been labeled an "edge-effect," describing higher biodiversity at ecotones (transition zones) due to overlapping species distribution ranges (e.g., Statzner and Higler 1985; Murcia 1995). In terms of microevolutionary processes, questions arise as to whether phenotypic divergence along ecological gradients also follows a gradual pattern (e.g., when trade-offs underlie the adaptive significance of alternative phenotypic trait values, leading to gradually changing local trait optima: Kawakami et al. 2011; Torres Dowdall et al. 2012; Riesch et al. 2016). Alternatively, phenotypic divergence could follow a threshold response, where an increasing strength of selection leads to an all-or-nothing response. The latter could apply, for example, if intermediate phenotypic trait values have a low fitness dependent or independent of the environment (e.g., reduced hybrid fitness: Hatfield and Schluter 1999; Via et al. 2000; Rundle 2002; Jacquemyn et al. 2018), and thus, reaching a new fitness peak requires the full transition toward an entirely different phenotype. Finally, in conjunction

with possible gene-flow along continuous ecological gradients (e.g., Hendry et al. 2002), the question arises as to how the exact nature of a given ecological gradient—in terms of strength of divergent selection, geographic dimensions of the respective gradient for the species under consideration, and so forth—promotes or hampers the emergence of reproductive isolation (Nosil 2012).

Appreciating the diversity of often concomitant ecological gradients in several cases also changes our view of what ecological factors actually drive the aforementioned ecological dynamics and evolutionary processes. When contrasting the extremes of different habitat types, for example, one might be tempted to ascribe any of the observed phenotypic differences to the most obvious, divergent ecological factor(s), such as presence or absence of certain predators, while in reality other, interrelated factors drive parts of the observed phenotypic divergence (Losos 2011; Riesch et al. 2014). Different predatory regimes in streams of Northern Trinidad are, for example, simultaneously characterized by different resource availability and different forms of competition, all of which drive aspects of phenotypic divergence of the inhabiting guppies (*Poecilia reticulata*; Endler 1995; Grether et al. 2001).

Future research on organismal responses to ecological gradients will greatly benefit from high-throughput genomic and transcriptomic analyses. For example, evolutionary replicated ecological gradients inhabited by the same species allow testing for patterns of convergent evolution (e.g., Heinen-Kay and Langerhans 2013; Pfenninger et al. 2014), which can be complemented by comparisons of organismal responses of closely related taxa occurring along the same gradient (Torres-Dowdall et al. 2013; Jourdan et al. 2016). Such an approach can ask whether and to what extent convergent/parallel evolutionary patterns will be found in independent lineages adapting to similar ecological backgrounds at different levels of biological organization, from shared SNPs (Jones et al. 2011) over shared patterns of protein evolution (Pfenninger et al. 2014), pathways (Hu et al. 2017), physiological coping mechanisms (Whitehead 2010), toward gross phenotypic traits like behavior and morphology (Heinen-Kay and Langerhans 2013). Likewise, when comparing community structures along ecological gradients, shared and unique aspects of divergence could be examined not only at the level of species. In analogy to our ideas outlined for evolutionary divergence, (macro-)ecological studies consider shared and unique patterns of divergence in terms of functional groups (e.g., through functional redundancies; e.g., Fetzer et al. 2015), community responses, or even higher levels of ecosystem functioning (e.g., Westneat et al. 2005).

Contributions to This Issue

Linking to the background outlined above, the special column *Ecology and evolution along environmental gradients* acknowledges the complexity and multitude of ecological gradients and the variety of organisms that evolve along them. The different studies are drawn from diverse systems and examine different aspects of diversification along environmental gradients, ranging from physiological and behavioral adaptations to host–parasite interactions to speciation. Our hope is that this special column encourages even more researchers to discard the traditional binary approach to investigating environmental factors (where applicable) and stimulates even more research into nuanced responses along often nuanced environmental gradients.

Alvarez-Ruiz et al. (2018) characterized an elevational gradient for patterns of ecto- and endoparasitization in the lizard *Psammodromus algirus* and reported contrasting patterns of decreasing ecto- but increasing endoparasitism with altitude. Their study further highlights the complexity of selective regimes and especially the role of coevolutionary dynamics along ecological gradients. Cattelan and Pilastro (2018) focus on the relationship between mate availability (in natural systems often a correlate of various ecological factors like resource availability and predation risk) and sperm priming responses in different selection lines of guppies *P. reticulata*. Lines that were selected to produce more sperm showed a comparatively weak response to perceived sperm competition, while lines selected for low baseline sperm production showed a much stronger response. These results raise fascinating new questions about sperm priming responses in natural populations, where multivariate ecological gradients create gradual variation in sperm competition intensity. Deacon et al. (2018) revisit the well-established notion that guppies in Northern Trinidad evolve under different predator regimes, which have classically been categorized as "low predation versus high predation" environments. The authors find compelling evidence for gradual variation in predation risk when comparing different collection sites, and stress the importance of moving away from the binary classification of predation regimes to facilitate a more nuanced understanding of this and similar systems. Diamond and Chick (2018) focus on a long-standing topic in biogeography, assuming that thermal limits could partly explain current species distribution patterns along ecological gradients. The authors examined how both evolutionary history and contemporary ecological conditions affect thermal limits in ants, and found that upper thermal limits are more strongly influenced by evolutionary history than lower thermal limits, which has a much stronger signature of geography. The authors discuss their results also against the background of global climate change and conservation. Gordon et al. (2018) used a natural warming experiment—thermal spring complexes—to investigate the role played by thermal regimes on feeding selectivity in one species of mollusk and two insect species. Their finding of increased feeding selectivity under elevated thermal conditions may provide important new insights into the effects of climate change on various aspects of energy flow and general ecosystem functioning. Keagy et al. (2018) examine an aspect of evolutionary divergence that received little attention in studies on the ecology and evolution along ecological gradients: they examined brain divergence in a fish species, *G. aculeatus*, that serves as a model organism for various questions in evolutionary ecology, such as the mechanisms of sympatric diversification and speciation. Investigating fish from two lakes, the authors found differences in brain regions associated with olfactory (olfactory bulbs) and visual processing (optic tecta) in line with a priori predictions for limnetic and benthic ecotype pairs. Different sensory systems could certainly promote reproductive isolation, for example, via sensory drive mechanisms (Maan and Seehausen 2011). Monier et al. (2018) examined gradients of varying sex ratios and their effects on mate choosiness and mate choice copying in female fruit flies *Drosophila melanogaster*. Females responded to a gradient in mate availability by adapting their choosiness during mate choice. However, females' tendency to copy other females' mate choice was not affected, adding new insights into this widespread aspect of socially dependent mate choice that had previously been reported from an array of species, ranging from insects to humans. Finally, Mück and Heubel (2018) addressed the question of whether correlates of sexual selection, such as mate and nest-site availability, differ systematically along a salinity gradient in common gobies *Pomatoschistus microps*. They found that nest resource quantity and quality decreased with decreasing salinity, but that other variables (e.g., population density and sex ratio)

exhibited more spurious patterns with respect to salinity. These results add another level of complexity to the study of evolutionary divergence along ecological gradients by highlighting the potential impact on sexual selection.

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