

8

Biological Dynamics and Evolutionary Causation

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Introduction

Why has understanding causation been so difficult in evolution? Perhaps it is because evolutionary biology has the unique role among biological disciplines of interpreting patterns at all levels of biological organization. Each subdiscipline is tasked with investigating how various systems currently function: molecular and cellular biologists at the cellular level, developmental biologists and physiologists at the organismal level, and ecologists at the community and ecosystem level. Evolutionary biologists not only need to understand how these systems function in current time, but they also need to understand how their functioning has changed over time. This requires investigating causal mechanisms that simultaneously span multiple timescales and levels of biological organization.

Studying both current and historical function of biological systems across multiple levels is a truly daunting task, and it is no wonder that a focus on genetic variation and natural selection, which are often measured as statistical summaries of the underlying dynamics of development and ecology, dominates the field. While such summaries of the underlying dynamics, reflected in patterns of genetic, phenotypic, and fitness variation, remain a core component of evolutionary research, they can only indicate correlations and thus should be viewed as a starting point for the determination of evolutionary mechanisms, not an end point. The central thesis of this chapter is that a deeper understanding of how evolution works requires examining system dynamics to determine how the behavior and interaction of biological entities at one scale influence patterns of variation at another scale.

In this chapter, I first discuss approaches to causation from two classic papers in ecology (Levin 1992) and evolutionary biology (Mayr 1961). I suggest that Mayr's proximate/ultimate distinction touches on the fundamental problem of timescale in evolutionary change, but ignores the underlying dynamics of biological systems. In contrast, Levin's perspective, which focuses mainly on ecological timescales, iterates a clear view of how to dissect and understand causation in dynamic systems across scales. I suggest that integrating these two perspectives can provide novel insight into outstanding questions in

evolution and illustrate this with discussion of the mechanisms of micro- and macroevolutionary change. Finally, I draw on nearly two decades of my own work on the dynamics of competition among cavity nesting birds to illustrate how patterns of dynamic stability and robustness in ecological systems are underlain by factors such as niche construction, developmental plasticity, and habitat selection. I suggest more explicit incorporation of these factors in evolutionary biology may be key to explaining patterns of species stasis.

Proximate and Ultimate: A Dichotomy of Timescale and System Dynamics

Levin (1992) argued that the problem of scale is at the crux of how scientists gain a mechanistic understanding of patterns in nature and suggested that it is as fundamental to understanding ecological and evolutionary patterns as it is to understanding the nature and behavior of matter in physics and chemistry. However, despite the widespread importance of the problem of scale across disciplines, explicit discussion of it has been rare in evolution and so it has been relegated mainly to philosophy of science with limited impact on empirical studies of evolution. The one major exception is Ernst Mayr's delineation of proximate and ultimate causation (Mayr 1961), which persists as an important dichotomy of causation in evolutionary biology.

Mayr defined proximate causes as *current* causes of phenotypic variation, and in this category he placed physiology and development; he defined ultimate causes as *historical* causes, and in this category he placed genes and natural selection. Mayr's goal was not to explicitly address the problem of scale in evolution—instead he was more concerned with explaining why functional and evolutionary biologists were often talking past one another and arguing over causation of the phenotype. However, a close reading of Mayr's explanation of this conceptual distinction (Mayr 1961; Mayr 1993) makes it clear that he was using these terms to distinguish between distinct timescales of phenotypic change (Haig 2013). The persistence of this dichotomy, despite many criticisms of it (Francis 1990; Thierry 2005; Laland et al. 2011; Calcott 2013), emphasizes how deeply entrenched it remains in current biological thought.

While the idea of distinguishing between timescales of phenotypic change is central to evolutionary theory, Mayr's placement of genes and natural selection only in the category of "historical causes" burdens his timescale dichotomy with an additional separation of dynamic versus static causes of evolution. This is evident in his treatment of genes as solely a historical cause ignoring the fact that within an individual, gene expression is also a proximate cause of developmental and physiological processes. Mayr put genes only in the category of historical cause because he was focused on inheritance; however, by treating genes as inanimate particles he essentially decoupled the active role of gene expression in current time from evolutionary explanations of phenotypic variation. Similarly, natural

selection as a historical cause is often portrayed as a “force” external to the organism (Endler 1986), but, in reality, it is a summary of the behavioral interactions and resulting ecological dynamics of organisms. Thus, the main problem with the proximate/ultimate dichotomy is not that it delineates distinct timescales for the study of the phenotype, but that it treats the dynamics of biological systems as only relevant for studying current (within generation) timescales of phenotype change and makes inanimate genes and external forces of natural selection the only proper evolutionary causes. Yet, proximate causes of development and physiology in conjunction with ecological interactions are the dynamic processes that unfold each generation that are the building blocks of evolutionary change.

This separation of the dynamics of biological entities from evolutionary causation is problematic because it is the behavior and interactions of biological entities that are key to understanding mechanism (Craver and Bechtel 2006). Levin (1992) writes that “mechanisms operate at different scales than those on which the patterns are observed.” They either emerge “from the collective behavior of large ensembles of smaller scale units ... [Or] the pattern is imposed by larger scale constraints.” The coordinated behavior and interactions of entities at lower scales often lead to emergent properties at higher scales that are not easily predicted from the behavior of an individual entity. This is not because the properties cannot be explained mechanistically, but instead it is because the properties at a higher scale are a statistical summary of the behavior of a group of entities at a lower scale. Constraints place boundaries on the system and limit in some way the variation of the lower scale entities (Bishop 2012). Thus, a complete understanding of causation requires integrating information about the (usually higher scale) constraints, how the component parts of a system (the lower scale entities) interact to produce emergent properties at a higher scale, and how external factors (that act on a different scale) may change these interactions.

Chave (2013), on the 20th anniversary of the publication of Levin’s paper, writes of the impact it has had on the field of ecology: “Few research articles have been more influential to our discipline. ... It has introduced a generation of ecologists to interdisciplinary thinking, and to two crucial concepts for ecology, pattern and scale.” Is it possible to apply Levin’s approach to pattern and scale to evolutionary causation and usher in a similar era of interdisciplinary thinking? If so, what are the “smaller scale units” in evolution whose behavior scales up to produce emergent properties at a higher scale? What are the “larger scale” constraints in the system? There are two important considerations in answering these questions. First, all life is organized hierarchically, where the behavior and interaction of lower-level entities scale up to produce emergent properties at a higher level. While such hierarchical organization of nature makes intuitive sense, working out a theoretical framework that captures the importance of hierarchical thinking for evolution has been challenging. Scale and level are typically treated as distinct concepts, yet they are intimately related (DiFrisco 2016). To be at the same hierarchical level, entities must interact to some extent (Salthe 2012). To interact, they must be on the same scale in multiple

dimensions—at the same spatial, temporal, and size scale. While the nature of the interactions that bind entities to a particular level of biological organization are a matter of debate among biologists and philosophers (see Okasha 2006 for a summary of the main points), Levin essentially sidesteps this debate by treating the whole question as an empirical matter. He writes, “the objective of a model should be to ask how much detail can be ignored without producing results that contradict specific sets of observations, on particular scales of interest. In such an analysis, natural scales and frequencies may emerge, and in these rests the essential nature of the system dynamics.” For Levin, levels are simply natural scales and frequencies that emerge from study of the system. In essence, Levin does not treat biological hierarchies as any different than hierarchies from other disciplines such as what is modeled in “statistical mechanics” and “interacting particle systems.” Most importantly, he makes the point that, “there is no single ‘correct’ scale on which to describe populations or ecosystems” because the importance of a particular scale will vary depending on the focal organism or ecosystem. Similarly, there is no single correct scale at which to study evolution. Evolutionary patterns occur at every scale of biological organization and time—from molecular evolution to evolution of ecological communities to macroevolutionary dynamics—and the most powerful insight into causal mechanisms comes from identifying the constraints and mechanisms acting at one scale above and below the focal scale. The farther one gets from the focal scale, the less direct is the link between cause and effect. This is why the link between genotype and phenotype is such a persistent problem in evolution—it requires crossing multiple levels in the hierarchical organization of life from the transcription of genes that influence processes of cellular metabolism, which in turn influence cell behavior and morphology, to the role of tissue function and size on overall organismal phenotype. As one gets further from the molecular scale, additional system inputs and interactions occur that dilute the direct effects of genes on phenotypes. Thus, the overall organismal phenotype is typically too far removed in scale from the genotype to draw any direct lines of causation.

The second important consideration when applying Levin’s approach to evolutionary patterns is that inheritance complicates assigning a scale to particular entities in evolution. This is because the genome can be either a lower scale entity whose behavior influences higher scale cellular processes or it can be a higher scale constraint in the system. Which of these roles it takes depends on the timescale of interest. Within a generation, the genome directly influences many organismal processes in the current generation by providing a template for cells to produce the raw materials needed for construction and maintenance of an individual organism (Nijhout 1990). In this way, the genome plays an important role in maintaining cellular and organismal stability by internalizing production of a subset of key resources to make the organism less dependent on variable and less predictable external resources. However, the inheritance of a genome across generations acts as a higher scale constraint because it restricts the range of phenotypes possible at the start of each new organism. Thus, genomes have a double role: within a generation, they are a smaller

scale unit whose behavior and interaction with other molecular components influences the phenotype at the cellular and organismal level and across generations they are a larger scale constraint that limits the range of phenotypes possible.

If inheritance is a larger scale constraint in evolution, what then is the role of natural selection? And what are the lower scale entities whose behavior scales up to influence higher scale evolutionary patterns? The most basic unit of evolution is population change each generation, which occurs through processes of birth and death. If births and deaths vary with phenotype, then we may see population-level changes in mean trait values from one generation to the next. It is the interaction and behavior of individuals within populations that cause variation in births and deaths. Thus, patterns of variation in individual behavior are the basis of variable ecological dynamics, which are the mechanisms of natural selection. The idea that ecology is the cause of natural selection has been often made (Eldredge 1985; Van Valen 1989; Okasha 2006). However, there has been less emphasis on the behavior and interaction of individuals in evolutionary processes despite the fact this is what drives ecological dynamics in the first place (Lewontin 1982; Wcislo 1989; Werner 1992; Fryxell and Lundberg 1997; Duckworth 2009).

By behavior, I do not mean only cognitive behavior of animals with a nervous system. Instead, I use behavior in the sense of physics: to describe the movement and action of matter, including its inaction. Behavior is what biological entities (or any entities) do and applies to all biological entities, from the movement of molecules within a cell to the restructuring of the gut after a meal, from the opening of stomatal cells to the growth of branches toward a source of light, from the aggressive defense of a territorial boundary to the construction of a home to live in. In this sense, the behavior of individuals in a population is causally analogous to the behavior of individual water molecules in a pool of water. Just as by determining the principles by which water molecules interact, it is possible to understand the properties of water that influence wave dynamics, by determining the principles by which individuals interact with each other and the environment, it is possible to determine the properties of ecological interactions that influence evolutionary dynamics. This view is not reductionist because it does not suggest that we use the same rules that govern the behavior of molecules or other particles to understand the behavior of individuals. Instead, it requires that we figure out the rules that govern the behavior of individuals (by actually studying the behavior of individuals) to understand the mechanisms of population and community dynamics.

In Levin's view, being able to navigate across scales deftly not only provides insight into causation, but also enables prediction:

... by changing the scale of description, we move from unpredictable, unrepeatably individual cases to collections of cases whose behavior is regular enough to allow generalizations to be made. In so doing, we trade off the loss of detail or heterogeneity within a group for the gain of predictability; we thereby extract and abstract those fine-scale features that have relevance for the phenomena observed on other scales. (Levin 1992, 1947)

Gaining predictability necessitates ignoring some details and focusing on the larger patterns that emerge at a higher scale. For example, natural selection is a statistical summary of the outcome of the ecological dynamics each generation. By tallying the number of individuals that persist, are born and die each generation and seeing whether they differ in phenotype, it is possible to extract and abstract the higher scale pattern of biased survival or reproduction that results from all the detailed actions and interactions that produce ecological dynamics. Such abstraction is useful in pinpointing which traits might be expected to change from one generation to the next. However, it provides little insight into the mechanism by which trait variation is linked to fitness. And without an understanding of mechanism, the outcome of selection cannot be predicted beyond a few generations.

Such lack of understanding of the mechanisms underlying patterns of natural selection may be why it is often difficult to predict when and why natural selection will produce evolutionary change. Even though selection can fluctuate strongly across generations (Grant and Grant 2002; Dingemanse et al. 2004; Siepielski, DiBattista, and Carlson 2009) and can lead to large phenotypic responses on short timescales (Reznick, Rodd, and Nunney 2004), when summed across many empirical examples it is often found to be weak overall (Kingsolver et al. 2001). Such generally weak selection seems at odds with large spatial and temporal environmental variation often observed in nature. Resolution of this paradox comes from the acknowledgment that organisms are not passive entities in evolutionary processes (Lewontin 1983; Bateson 1988; Plotkin 1988; Duckworth 2009). Instead, it is the active strategies and responses of organisms to environmental variation that enables them to survive and reproduce in a variety of circumstances and that makes populations robust to environmental variation.

In essence, a complete understanding of evolutionary causation requires integrating information about inheritance (the higher scale constraint), how the behavior and interaction of individuals (the lower scale units) produce predictable ecological dynamics, and how external environmental factors (often the source of selection) may sometimes disrupt these predictable dynamics. This latter point—the disruption of otherwise predictable ecological dynamics—is the main source of natural selection in populations (Badyaev 2011). Thus, detecting natural selection is easy enough to do statistically, but interpreting its significance in order to predict evolutionary change requires understanding the ecological dynamics of a system enough to know what constitutes a stable and long-term disruption of the system. As an example of the insights that can be gained from applying this perspective, I turn to a long-standing problem of evolution, the link between micro- and macroevolution.

The Problem of Integrating Micro- and Macroevolutionary Dynamics

On the one hand, patterns at the macro and microevolutionary timescales are hypothesized to be causally linked (Charlesworth, Lande, and Slatkin 1982). On the other hand, their dynamics appear to be distinct (Jablonski 2017a). The patterns we observe at the macroevolutionary timescale are many orders of magnitude removed from the timescale of microevolutionary change that can be observed in populations over just a few generations (Ellner, Geber, and Hairston 2011). These same rapid evolutionary changes in phenotype, when viewed over a century or more, may appear as nothing more than stochastic noise. Larger climate-driven divergence among populations, such as those driven by glacial cycles, might produce cycles of local adaptation among populations within a species (Phillimore et al. 2007; Hunt, Hopkins, and Lidgard 2015), but resilient species-wide phenotypic divergence seems to require a timescale of one million years or more (Uyeda et al. 2011).

The idea of gradualism—that natural selection slowly and gradually shapes the phenotype of a species over many millennia or eons—is not supported by the fossil record (Hunt 2007; Eldredge 2016). Instead, species seem largely static in their morphology for the majority of their evolutionary history and this stasis is periodically punctuated by bouts of evolutionary change (Eldredge and Gould 1972; Gould and Eldredge 1977). Widely criticized when it was first proposed, a pattern of punctuated equilibria (if not the proposed mechanisms underlying it) is now largely accepted (Pennell, Harmon, and Uyeda 2014). A study by Uyeda et al. (2011) combined datasets that span different timescales, from field studies to fossil timeseries to phylogenetic datasets, to show that there is a million-year wait for macroevolutionary bursts in body size evolution. They call this the blunderbuss pattern, named for one of these old-fashioned guns with a long narrow barrel that flares out at the end. The Uyeda et al. (2011) study adds to a growing body of evidence that phenotypic change is limited for most of a taxa's evolutionary history (see also Hunt, Hopkins, and Lidgard 2015).

This macroevolutionary pattern of stasis often seems at odds with more recent studies of eco-evolutionary dynamics in which evolutionary changes in traits are observed on timescales of only a few generations (Hendry and Kinnison 1999; Hairston et al. 2005). Not only does significant evolutionary change occur on short timescales, but it is often quite strong (Hereford, Hansen, and Houle 2004). This is emphasized in a classic study by Gingerich (1983), which shows that rates of evolution measured over shorter periods of time are much higher than rates measured over long periods of time (figure 8.1A). One interpretation of this pattern is that evolution follows a weak zigzag pattern with little net directionality (Stanley and Yang 1987; figure 8.1B). In other words, when we scale out to a macroevolutionary timescale, rapid evolution measured in studies of eco-evolutionary dynamics is nothing more than stochastic noise. At moderate scales, perhaps glacial cycles or other climate changes push populations back and forth around a mean, but over very long timescales, there is little net evolutionary change.

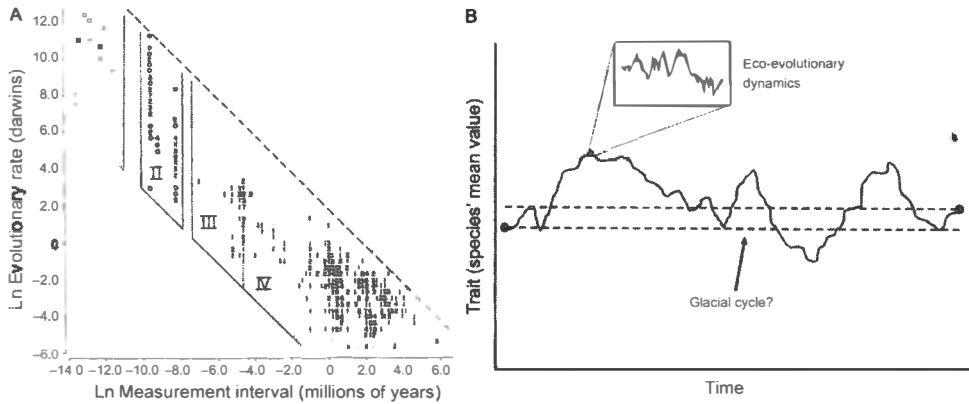


Figure 8.1

Reconciling evolutionary rates and net evolutionary change across diverse timescales. (A) Evolutionary rates scale with measurement interval. Rates are from (i.) laboratory selection experiments (open squares), (ii.) historical colonization events (open circles), (iii.) post-Pleistocene faunal recovery from glaciation, and (iv.) fossil invertebrates and vertebrates. Numbers in (iii.) and (iv.) represent multiple cases falling at the same point. Modified from Gingerich (1983). (B) Changes in a trait over hundreds of thousands of years in a hypothetical lineage. The inset shows trait changes over a randomly selected 50-year period that comprise rapid microevolutionary changes due to eco-evolutionary dynamics. At the macroevolutionary scale these changes are not even visible and resemble stochastic noise. General trends of increases or decreases in trait value on the order of 1000s or 10,000s of years might correspond to glacial cycles or other long-term climate-driven changes. The dots at the ends of the solid line show sampling points from a fossil timeseries and the dashed lines correspond to the amount of net evolutionary change the lineage experiences at the macroevolutionary scale. These types of dynamics at different timescales might produce the relationship observed in A.

In a follow-up to Uyeda et al. (2011), Arnold (2014) proposed that the blunderbuss pattern is consistent with Simpson's idea of quantum evolution in which, for the majority of a species' history, evolution takes place within relatively narrow and bounded adaptive zones, but on rare occasions there are rapid transitions to a new adaptive zone (Simpson 1944). Arnold suggested that the long barrel of the blunderbuss is evolution occurring in adaptive zones and that quantum evolution only occurs during rare events. He noted that the amount of evolution that occurs in the adaptive zones is substantial, on the order of ± 65 percent change in body size. Thus, Arnold referred to the pattern as "bounded evolution" rather than literal stasis. However, whatever the terminology, the pattern of limited evolutionary change for the majority of a lineage's existence remains clear. The most common mechanism proposed for species' adaptive zones is stabilizing selection (Charlesworth, Lande, and Slatkin 1982; Estes and Arnold 2007). But stabilizing selection as a cause can only be half the story—the statistical summary of the underlying dynamics of the system. To gain a mechanistic understanding of the pattern of evolutionary stasis, we must also understand the collective behavior of the smaller scale units to try to discern how lower scale interactions lead to this larger scale pattern.

Dynamic Stability and Robustness of Ecological Systems as Mechanisms of Evolutionary Stasis

The problem of evolutionary stasis is analogous in many ways to the problem of understanding robustness at the molecular, cellular, and organismal scales. Robustness is a ubiquitous property of biological systems (Wagner 2005). A system is robust when its outputs or state can remain stable despite variable inputs (Kitano 2004). Examples include cellular and organismal metabolism, the process of development, gene regulatory systems, and physiological homeostasis. Robustness does not mean that all components of a system stay unchanged in the face of variable inputs—it means the function or output of a system is stable. To achieve this stability at a higher level of organization, the lower scale entities must be in constant action—modifying their behavior and interactions in response to environmental changes. Hence, robust systems maintain a dynamic stability with built-in flexibility that tracks and responds to internal and external changes and maintains the same outputs as long as these changes are within the range of normal conditions (Nijhout and Reed 2014; Badyaev and Morrison 2018). Defining “normal” is the key to predicting how external conditions will influence functioning of the system. Biological systems can be adapted to function in variable environments as long as the variation experienced does not exceed the average or typical variation experienced in its evolutionary history. When it does, the system must either change or cease to function; in evolutionary terms this means evolve or go extinct.

Might Simpson’s adaptive zones be produced by mechanisms of robustness at the population, community, or ecosystem scale? If so, then a species’ adaptive zone is defined by the region of environmental or genetic variation that a species can experience without substantially changing the overall species’ phenotype and large-scale evolutionary changes or extinction would only occur when a species encounters some extreme perturbation. There has long been an interest in the properties that account for stability of ecological communities (May 1974), and recent studies propose that similar properties of communities and ecosystems may account for their dynamic equilibrium state (Borrelli et al. 2015), making community ecology and coevolution perspectives essential to interpretation of patterns of evolutionary stasis (Stenseth and Maynard Smith 1984; Eldredge 1985; Morris et al. 1995; Lieberman, Miller, and Eldredge 2007; Voje et al. 2015). Evolutionary changes that are stable enough to appear in the fossil record may only occur with a major, usually catastrophic, event that pushes entire communities out of their equilibrium (Eldredge 2007). Such events are rare and only occur on the order of a million years or more, and when they occur, species either go extinct or change in profound ways (Gould and Eldredge 1977). Thus, macroevolutionary patterns cannot be understood by simply scaling up microevolutionary changes over a long period of time, because the important evolutionary events, such as those that precipitate mass extinctions, do not occur on a constant gradual basis (Jablonski 2017b). This point is only obvious by explicitly comparing patterns and mechanisms across

multiple timescales (Badyaev 2018). Moreover, given that the clearest pattern in the history of life is one of stasis, this emphasizes that, in order to understand evolutionary processes, it is as important to explain how and why populations don't change as it is to explain how and why they do change.

Fortunately, the general mechanisms that produce robustness at the cellular, developmental, and physiological levels are well-known. These include negative and positive feedbacks, source–sink gradients, redundancy, saturation kinetics, modularity, and the ability of components to switch between bi-stable states (Eldar, Shilo, and Barkai 2004; Kitano 2004; Whitacre and Bender 2010; Nijhout and Reed 2014). There are ecological equivalents of all of these mechanisms. For example, one of the most common negative feedback processes in populations is density dependence. Source–sink gradients at a cellular level seem remarkably like source–sink population dynamics at a larger scale. Saturation kinetics refers to the interaction between enzyme and substrate where the reaction rate is limited by the availability of the substrate. These dynamics are similar to one of the most important relationships in ecology, the population growth curve where growth is limited by the availability of resources. Metapopulation structure of many species might be analogous to modularity within organisms, which confers robustness because it allows changes in one component without disrupting the whole system. This idea is consistent with the observation that species with larger ranges and more subspecies are more resistant to extinction (Vrba 1992; Eldredge et al. 2005). Finally, many robust systems display bi-stability in their components, where system components can switch between different alternative states while maintaining overall system functionality (Badyaev 2018). This might be analogous to alternative strategies at the organismal level where plastic responses enable tracking of variable environments and thus enable species persistence. In sum, any mechanism that allows species to be buffered from environmental changes will contribute to robustness of populations.

Robustness Mechanisms for Ecological Scales: An Empirical Example of Dynamic Stability

Discerning robustness mechanisms in ecological interactions provides a novel way of interpreting the dynamic stability that is often observed in communities and ecosystems. By applying concepts from molecular biology and physiology to higher scale processes, we may begin to observe similarities in the dynamics of biological systems across scales and thus gain deeper insight into evolutionary processes. To show how such dynamics might be studied and how a body of work can be reinterpreted with this novel approach, I draw on my work on the population and community dynamics of cavity nesting birds. Cavity nesting bird populations have been studied extensively in the forest ecosystems of the Northwestern United States. This community of birds depends on habitat that is created

by forest fire, which has a long history of management in the United States, making the ecology of post-fire communities extremely well studied (Hutto 2006). My work has focused on the dynamic interplay of two species that depend on this post-fire habitat.

Mountain and western bluebirds (*S. currucoides* and *S. mexicana*) are two passerine species that compete for territories in areas where their ranges overlap (Duckworth 2014). For successful reproduction and survival, they have two main habitat requirements: open meadows for foraging and nest cavities for breeding. Forest fires generate suitable habitat by opening up understory vegetation and creating dead snags. Primary cavity nesters, such as woodpeckers, excavate nest cavities in these snags that are eventually used by secondary cavity nesters, such as bluebirds. This habitat can last for 20–30 years until regrowth of the forest eliminates the open meadows bluebirds require for insect prey. The successional nature of post-fire habitat means that populations of bluebirds (and the entire post-fire community) have a discrete beginning and end and, at any given time, there are numerous populations of varying ages and successional stages connected by dispersal in a temporally and spatially varying metapopulation structure.

In the bluebird system, the successional dynamics mean that the system is in constant change, but both species of bluebirds have different strategies for maintaining population persistence on a regional scale. Mountain bluebirds are more dispersive than western bluebirds and are among the earliest colonizers of new habitat patches, whereas western bluebirds often show delayed patterns of colonization (Kotliar, Kennedy, and Ferree 2007; Saab, Russell, and Dudley 2007; Duckworth et al. 2017) but are better interference competitors (Duckworth 2014). Mountain bluebirds are eventually displaced by the slower-arriving western bluebirds within a habitat patch, but because they are more dispersive and show a greater flexibility in their nest site and habitat choice (Duckworth et al. 2017; Johnson and Dawson 2019), they can quickly move to new areas when western bluebirds arrive. Western bluebirds, on the other hand, have evolved two distinct strategies that track the rapidly changing environmental conditions across successional stages enabling them to maintain high fitness in distinct competitive environments. Highly aggressive and dispersive western bluebirds are the first to arrive to a new habitat patch and easily displace earlier-arriving heterospecific competitors (Duckworth and Badyaev 2007). These aggressive dispersers excel in populations with low conspecific densities because they acquire large resource-rich territories and thus are able to maintain high fitness (Duckworth 2008; Duckworth 2014); however, they are eventually replaced by a nonaggressive philopatric type that excels in high-density populations because they cooperate with their relatives in territory defense and invest highly in parental care (Duckworth 2006; Aguillon and Duckworth 2015). Eventually, forest succession makes a habitat patch no longer suitable for bluebirds to breed in and the whole cycle—mountain bluebird to aggressive to nonaggressive western bluebird—repeats itself in a new patch. Western bluebird populations display many of the dynamics that characterize robust systems, such as density-dependent fitness leading to negative and positive feedbacks on each behavioral type driven by logistic

growth of newly colonized populations (Duckworth and Aguillon 2015). The predictable increases in western bluebird breeding density over time leads to a predictable decline in the number of available nest cavities (Duckworth et al. 2017), and the switch between the two behavioral types closely tracks changes in population density and resources (Duckworth and Aguillon 2015).

The switch between the two behavioral types is adaptive and is maternally induced via differential allocation of testosterone to clutches. Females in late stage, crowded populations have small territories with few extra nest cavities and experience heightened competition. This induces them to allocate more testosterone to their clutches and produce aggressive sons that colonize new areas. In contrast, aggressive females that colonize new populations acquire large resource-rich territories and have lower stress levels (Duckworth unpub data). As a consequence, they allocate less testosterone to their clutches and immediately start producing nonaggressive offspring that bud off the parental territory and reap the benefits of nest cavity resources their parents acquired (Duckworth, Belloni, and Anderson 2015). The differences in competitive ability of the two types of males produce a type of competitive habitat selection that sets the stage for rapid changes in the cue that induces the maternal effect on offspring aggression allowing a match between behavioral type and the ecological context where they will perform best. Thus, this system provides a clear example of how active responses of organisms to environmental variation can allow for maintenance of high fitness across spatially and temporally varying populations.

Western and mountain bluebirds defend exclusive territories, and the majority of competitive interactions among bluebirds occur in March and April, well before the onset of oogenesis, making them rare during the period when egg production actually occurs. However, bluebirds defend their primary cavity throughout the breeding period from other species, and the peak of these non-bluebird intrusions overlaps with oogenesis (Duckworth, Belloni, and Anderson 2015). Females with more nest cavities on their territory experience fewer intrusions by these other species because one of them typically occupies the extra nest cavity on a bluebird territory and keeps others of its own kind away, effectively buffering the focal bluebird female from further competition. As a result, females on territories with extra nest cavities experience less competition from nest site competitors and produce sons that remain philopatric. Thus, competitive differences in aggressive and nonaggressive birds during settlement of territories lead to a sort of inadvertent niche construction where the outcome of competition over territories has cascading effects on territory quality, maternal effects, and offspring phenotype. These cascading effects are predictable because the extreme limitation of nest cavities for the entire community of secondary cavity nesters means there will always be competitor species intruding on bluebird territories, making competitive interactions over nest sites a reliable cue of the availability of parental resources.

This example shows how predictable higher scale community dynamics can occur despite the contingent nature of local-scale behavioral interactions. While there are many

elements interacting in this system, many of the parts are interchangeable. For example, as long as females on small territories are harassed by competitors for their nest cavity, the particular competitor species doesn't matter. There is a suite of competitor species that can fulfill this role: tree swallows, house sparrows, mountain chickadees, and house wrens are all actively searching for nest cavities while female bluebirds are laying eggs. Thus, species identity of the competitors is a detail that can be extracted and abstracted to understand the larger scale link between population density and maternally induced switches in behavioral phenotype. Another example of interchangeability are the primary cavity nesters, which are a keystone species in this habitat (Martin, Aitken, and Wiebe 2004). They excavate the nest cavities that are then used by numerous species of mammals, birds, reptiles, amphibians, and insects (Bunnell, Kremaster, and Wind 1999). As long as nest cavities are being produced—whether by black-backed woodpeckers, northern flickers, or hairy woodpeckers—this resource will become available to the multitude of secondary cavity nesters that depend on it, fundamentally shaping the community composition of post-fire forests. Such redundancy of functional parts is a common feature of robust systems (Kitano 2004) and of ecological communities (Eldredge 1985).

Other mechanisms of robustness are also evident in this system. The developmental plasticity of dispersal phenotypes in western bluebirds is key to maintaining robustness of fitness across populations and is analogous to the switch between two bistable states of lower scale components that is often observed in robust systems. Moreover, density-dependent fitness of these types (Duckworth and Aguillon 2015) is a common feature of many disturbance-dependent species and is a type of feedback mechanism at the population level that is similar in dynamics to negative feedback mechanisms in molecular and organismal pathways. Thus, this case study shows many features at the population level that are typical of robust systems at the molecular, cellular and organismal levels. However, this is one case study and we can only assess the general importance of such mechanisms by comparing across enough such case studies to determine their prevalence. In other words, we need to change the scale of description and “move from unpredictable, unrepeatable individual cases to collections of cases whose behavior is regular enough for generalizations to be made” (Levin 1992).

One example of such extrapolation is the observation that many plants and animals evolve maternally induced dispersal strategies similar to those expressed in western bluebirds (Harrison 1980; Donohue 1999; Larios and Venable 2015; Duckworth, Potticary, and Badyaev 2018). The similarity across taxa is not in the specific traits linked to dispersal—seed polymorphisms in plants, wing dimorphisms in insects, and distinct personality types in vertebrates—but in the function of the suite of traits that enable the species to escape habitats declining in quality (Harrison 1980; Roff 1994; Cote et al. 2010; Duckworth 2012). Often such dispersal polymorphisms evolve in species that depend on successional or disturbance-prone habitat (Zera and Denno 1997; Armsworth and Roughgarden 2005). In this case, the details that can be extracted and abstracted across species are the specific

traits that enable individuals to stay or go, and the generality is that in successional or disturbance-prone habitat dispersal polymorphisms frequently evolve. Thus, by looking across a wide variety of taxa that experience a similar problem for maintaining meta-population persistence in a constantly changing environment, we can begin to extract and abstract the key repeatable pattern that unites all of these examples.

Given that western bluebirds live in a world that is in constant flux, it seems that they would be resistant to most environmental perturbations. How do we even know what constitutes an environmental perturbation in a system that is constantly changing? The answer is to know enough about the ecology of a species or system to understand which resources and interactions, though constantly changing, are predictable for the species and whose disappearance would constitute a significant perturbation. For western bluebirds, their high competitive ability means that, as long as forests burn, they will have plenty of nest cavities to fight for and win, but take away this key resource and this dominant species becomes vulnerable. When the United States put in place a policy of fire suppression that largely eliminated post-fire habitat (Arno 1980) western bluebirds went extinct from the northern part of their range (Duckworth and Badyaev 2007). In contrast, mountain bluebirds, the subdominant species that evolved greater flexibility in habitat and nest cavity preferences, were able to persist (Duckworth and Badyaev 2007). When humans began to put up man-made nest boxes and fire policy changed in the 1980s to allow fires to burn in wilderness areas once again, western bluebirds quickly returned to the parts of their range where they were formerly extirpated. This human-induced large-scale experiment showed that removal of fire from the landscape was too large of a disruption for western bluebird populations and the species range contracted; if this disruption of their main resource had occurred range-wide, this species would surely have been in danger of extinction.

Conclusion

Applying the robustness concept to ecological systems raises a number of novel questions that have the promise of uniting currently disparate studies in ecology and evolution. What is the role of coevolutionary interactions in the maintenance of community and ecosystem robustness? Do such interactions make systems more or less resilient in the face of environmental change? How is the breadth of environments that a species is buffered against determined? Clearly, species are buffered against the sort of environmental changes that organisms are likely to experience during a lifetime, such as seasonal changes and weather variation across years. But how common and predictable does an environmental change need to be for robustness mechanisms to evolve? Does it depend on the temporal or spatial variability that a species experiences or both? Hunt (2007) found that only 5 percent of fossil timeseries showed directional change with the rest fitting a model of stasis or a

random walk with no net directional change. Is there something different about the taxa that do show directional change? Is there something different about the communities they are a part of? Are they invaders? Do they have a unique role in the community or are they more (or less) likely to be species that show coevolutionary dynamics? All of these questions are at the crux of understanding patterns of stasis—one of the clearest macroevolutionary patterns. To answer them requires greatly expanding the role of ecology, paleontology, and ethology in modern evolutionary biology.

Calls for an Extended Evolutionary Synthesis have often pointed out several factors, such as developmental plasticity, niche construction, and habitat selection, that were left out of the Modern Synthesis but are key to a complete causal understanding of evolution (Laland et al. 2015). What all of these factors have in common is that they encompass the active role of the organism in evolution, and I suggest they are the key mechanisms underlying patterns of stasis. Every time we see organisms taking an active role in responding to or shaping their environment, we are seeing the adaptations that buffer organisms from perturbations—from wing dimorphisms in insects, to maternally induced defensive responses in plants, to helmet formation in daphnia, to habitat selection in birds, to the formation of a biofilm in bacteria, to the construction of elaborate homes in beavers. I suggest that the reasons for one of the most well-documented patterns in evolution—long-term stasis—are the interactions that many organismal biologists and ecologists have been studying all along. But without a unifying principle to tie them together, these studies seem merely a collection of individual case studies. What is now needed is to determine whether the mechanisms conferring robustness at the cellular, physiological, and developmental scale really do work similarly at the population, community, and ecosystem scale.

Each of the subdisciplines within biology—molecular biology, physiology, developmental biology, and ecology—is tasked with figuring out how various biological systems work at different levels of organization. The task of evolutionary biologists is to take this knowledge and use it to determine how these systems change over time so that we can understand how evolution works. Thus, the first step to understanding what processes lead to evolutionary change may be to learn what processes allow populations to stay the same.

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