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# TRADE-OFFS AND BIOLOGICAL DIVERSITY: INTEGRATIVE ANSWERS TO ECOLOGICAL QUESTIONS

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Paul R. Martin

*Department of Biology, Queen's University, Kingston, ON, Canada*

## INTRODUCTION

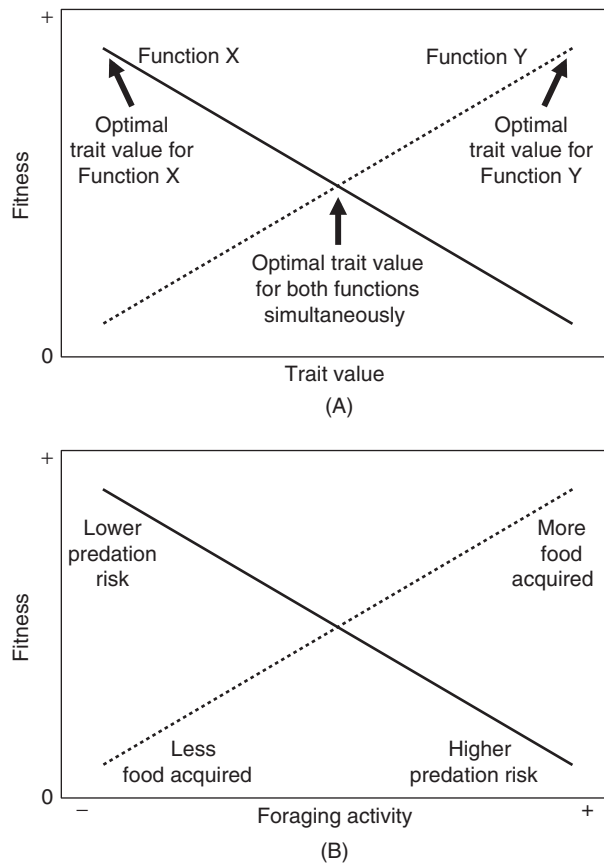
What determines the abundance and distribution of species? This question is paramount to ecology because it encompasses the interactions of individuals, populations, and species with each other, and with their environments – interactions that ultimately create the patterns of biological diversity that we see in nature. Ecological approaches and frameworks have successfully addressed this question across diverse species and contexts, and yet the broader rules that underlie these patterns across environments and taxonomic groups remain elusive (Lawton 1999; Simberloff 2004). In this chapter, I will argue that our difficulties in finding broad answers to this question are, in part, because the answers are not strictly ecological, but broadly biological. Understanding patterns of diversity requires the integration of diverse traits, processes, and selective pressures that span fields, from physiology to biophysics, genetics to biogeography. Importantly, the answers to why species vary in their abundance and distribution benefit from an evolutionary framework that tests ideas from the perspective of the fitness costs and benefits to individuals, and their consequences for populations and species.

An integrative approach within an evolutionary framework helps us to understand species distributions and abundances because of its role in elucidating fundamental trade-offs – adaptations that confer a fitness advantage for performing one function, and simultaneously confer a fitness disadvantage for performing another function (Bohannan *et al.* 2002; Figure 18.1). These trade-offs can be understood from the level of genetics (e.g., antagonistic pleiotropy, linkage; Falconer & McKay 1996) to physiology and

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**Figure 18.1.** (A) A trade-off, where a trait that confers a fitness advantage for performing one function (X), simultaneously confers a fitness disadvantage for performing another function (Y). In the case of allocative trade-offs, the focal trait controls the allocation of limited resources between two (or more) other phenotypic traits. If the selection pressures that create the trade-off vary in space or time, different species may coexist with adaptations that optimize trait values for functions X or Y. For example (B), increased foraging activity increases the rate of food acquisition, but comes at a cost of increased predation. Variation in the risk of predation or availability of resources can lead to coexistence of species whose foraging activity is adapted to either reduce predation risk at the expense of food acquisition, or increase food acquisition at the expense of susceptibility to predation.

development (e.g., trade-offs in allocation of energy, resources; Sibly & Calow 1986) and developed phenotypes (Agrawal *et al.* 2010), and have fundamentally shaped the way biologists think about the evolution of life histories (Stearns 1992), physiologies (Sibly & Calow 1986), behaviors (Krebs & Davies 1997), and adaptation in general (Kawecki & Ebert 2004). Trade-offs are central to the study of diversity because without them, we should expect one species to dominate in all environments (Dobzhansky 1964; Tilman 1982). By forcing the choice between evolutionary paths that cannot be simultaneously taken, trade-offs allow different species to partition energy and other resources, and thus coexist, creating (e.g., Duffy & Forde 2009) and maintaining (e.g., Kneitel & Chase 2004) diversity in nature (Figure 18.1).

The framework of trade-offs for understanding species distributions, interactions, and diversity has a long and productive history in both plant and animal ecology (e.g., Grime 1977; Tilman 1982; Chapin 1980; Holt 1995; McPeck 1996; Chesson 2000). This framework, however, differs from historically common and pervasive approaches to addressing ecological questions that highlight, among other things, the importance of different ecological processes such as competition, predation or parasitism, realized versus fundamental niches, biotic or abiotic factors, and top-down versus bottom-up constraints. By focusing on trade-offs, we no longer emphasize the relative importance of these ecological processes or how species are different, but instead ask why the traits of one species cannot do it all, or in other words, why a trait that is adaptive in one context cannot also excel in another context simultaneously (Box 18.1). By focusing on fundamental trade-offs confronting organisms, we are also forced to understand the mechanisms creating the trade-offs (e.g., Chapin *et al.* 1993; Angert *et al.* 2009), thus promoting the integration of diverse fields often lost in our tendency to specialize in science.

**Box 18.1. Trade-offs and the Niche**

Niches define different ecological strategies of organisms, and thus have direct relevance to the framework of trade-offs. For example, a trade-off in competitive ability versus ability to detoxify heavy metals may result in two different ecological strategies or niches for plants – one adapted to heavy metal soils, and another competitively dominant on soils lacking heavy metals (Macnair *et al.* 2000). A descriptive characterization of the niche, however, tells only part of the story, and misses the most important part: distinct niches occur because of underlying trade-offs confronting organisms, and these trade-offs can be understood from the level of genetics, development, and physiology through to the consequences for species interactions and distributions. Niches also create a narrow view of interactions among species and patterns of coexistence. For example, a recent study suggests that within-species trade-offs involving sexual selection can lead to the coexistence of species without ecological (niche) differentiation (M'Gonigle *et al.* 2012). In this case, the key to coexistence is a trade-off between the costs of searching for suitable mates (that increase with distance) and the costs of competition (that decrease with distance) within a heterogeneous environment. Such patterns of coexistence without ecological divergence challenge a central ecological premise that species can only coexist if they have different ecological niches.

Niches have an inherent appeal because they describe what we can all see – species with different ecological strategies living together, or apart. Understanding these patterns, however, will require more than a study of ecological strategies. It will require an understanding of why one species cannot do it all, and thus the trade-offs that force distinct ecological strategies and create and maintain biodiversity in nature.

Below, I provide select examples to illustrate the importance of key trade-offs and the integration of diverse fields that promote a more mechanistic understanding of the factors underlying the distributions of species and interactions between them. I focus on ecologically similar, closely related populations or species that share most traits in common through recent shared ancestry. Similar trade-offs extend to distantly related species, albeit in more complicated ways as species accumulate divergent traits over evolutionary time. While I focus on trade-offs among populations or species, trade-offs acting within populations can have important consequences for species interactions, distributions, and

patterns of coexistence (e.g., Tessier *et al.* 2000; Agrawal 2001; M'Gonigle *et al.* 2012; see also Clark 2010), and thus understanding within-species trade-offs and variation is also important for our understanding of patterns of diversity (Box 18.2). I begin with case studies and finish with a discussion of why an integrative approach that focuses on trade-offs will advance our understanding of community ecology and biodiversity.

**Box 18.2. Trade-offs, Phenotypic Plasticity, and Specialization among Individuals**

The trade-offs that confront populations and species can act similarly on individuals within populations, with consequences for individual phenotypes. For example, phenotypic plasticity allows individual organisms to match their phenotypes to environmental conditions, such that one individual can settle a trade-off in different ways that corresponds to environmental variation (e.g., McCollum & Van Buskirk 1996). This environmental variation may be current, or predicted to occur in the future (e.g., predicted adaptive responses; Gluckman *et al.* 2005). Phenotypic plasticity frequently mirrors heritable variation among populations and species (e.g., Ruell *et al.* 2013), and can have similar consequences for the abundances and distributions of species because it can determine the relative fitness of individuals in different environments. For example, if individuals in a population cannot adjust their phenotypes to match environmental challenges, then these individuals may be more likely to experience lower fitness, reduced abundance, and a higher risk of population extinction. While phenotypic plasticity can clearly benefit individuals, evidence suggests that plasticity itself may come at a cost (DeWitt *et al.* 1998), presenting its own trade-off that varies with environmental conditions (e.g., Relyea 2002).

While plasticity can allow an individual to settle trade-offs in different ways, variation among individuals within a population can allow different individuals to settle trade-offs in different ways (i.e., individual specialization), with similarly important consequences for community ecology and diversity (Bolnick *et al.* 2003, 2011). Sex-specific and age-related variation in ecological and other traits are common; however, variation among individuals of the same sex and age class is also widespread within populations (Bolnick *et al.* 2003). While gene flow may restrict the evolution of distinct traits within a population, competitive interactions among conspecific individuals are usually more intense (Clark 2010), and may cause the divergence of traits within a population (specialization), even in the face of gene flow. Altogether, trade-offs confront organisms within populations, and commonly favor phenotypic plasticity or individual specialization that parallels divergence among populations and species. These adaptive responses within populations may play an important and underappreciated role in structuring diversity (Agrawal 2001; Bolnick *et al.* 2003; 2011; see also Clark 2010).

**Resource Availability and Environmental Gradients:  
The Importance of Body Size**

All organisms must obtain resources for growth, survival and reproduction, and these resources vary in their availability. Traits that maximize fitness when resources are abundant are often different from those that maximize fitness when resources are scarce (e.g., Chapin 1980), and these traits frequently involve variation in body size. Large body size provides advantages in competitive interactions among diverse groups, including both animals and plants, allowing larger organisms to preferentially acquire limiting resources when interacting with smaller organisms (e.g., Morse 1974; Grime 1977; Schoener 1983; Keddy 2001). Small-bodied organisms, however, require fewer resources for development, growth, survival, and reproduction, providing advantages when resources are too scarce

to sustain large body sizes (Peters 1983; Schmidt-Nielsen 1984; Bonner 2006). These different patterns of resource requirement and use create an important body size trade-off that varies with resource abundance.

Body size trade-offs extend to many other selective pressures beyond resource availability (Peters 1983; Schmidt-Nielsen 1984; Bonner 2006). These selective pressures can be traced back to fundamental biophysical constraints on body size that ultimately help to shape most aspects of an organism's biology (Peters 1983; Schmidt-Nielsen 1984; Bonner 2006). These diverse body size trade-offs create variation in the selective advantage of different body sizes along equally diverse gradients of climatic, chemical, physical, and biotic variation. The important and diverse consequences of body size make size one of the most influential traits for determining the distributions, interactions, and patterns of coexistence of organisms (West *et al.* 1997; Bonner 2006).

### **Body Size Trade-offs and the Segregation of Rodents along a Resource Gradient**

Desert gerbil species (*Gerbillus*) use similar resources but occupy distinct microhabitats and forage at different times of the night in the Western Negev Desert, Israel. Food abundance (seeds) differs among microhabitats and declines over the course of the night as rodents consume seeds made available by strong afternoon winds (Ziv *et al.* 1993). Field experiments reveal a trade-off between two species involving body size. The larger *G. pyramidum* excludes the smaller *G. allenbyi* from preferred seed-rich habitat (semistabilized sand dunes), particularly during seed-rich foraging times (early night). *G. allenbyi*, however, performs well in seed-poor conditions (stabilized sand dunes, foraging later at night) where it typically occurs, because it can harvest seeds profitably at low resource densities. The larger *pyramidum* is a less efficient forager at low seed densities, and prefers high resource habitat and foraging times (Ziv *et al.* 1993). Field and laboratory experiments suggest a trade-off involving size, with large size conferring an advantage to *pyramidum* in aggressive interactions, and small size allowing *allenbyi* to survive and reproduce in low food environments because of reduced energetic demands and thermoregulatory costs (Kotler & Brown 1990; Ziv *et al.* 1993). The two species also differ in other aspects of foraging efficiency (Kotler & Brown 1990), but whether these traits are functionally linked to body size is not clear.

Similar dominance hierarchies among closely related species are common in animals, with larger species typically dominant in aggressive contests for resources (e.g., Morse 1974; Donadio & Buskirk 2006). While gerbils reach adult size relatively early in development, many other organisms (e.g., fish) grow over extended periods through their lifetimes. These changes in size with development can create dynamic interactions and trade-offs that shift over time, complicating interactions among species and between organisms and their environments, and playing an important role in structuring communities (e.g., Werner & Hall 1988).

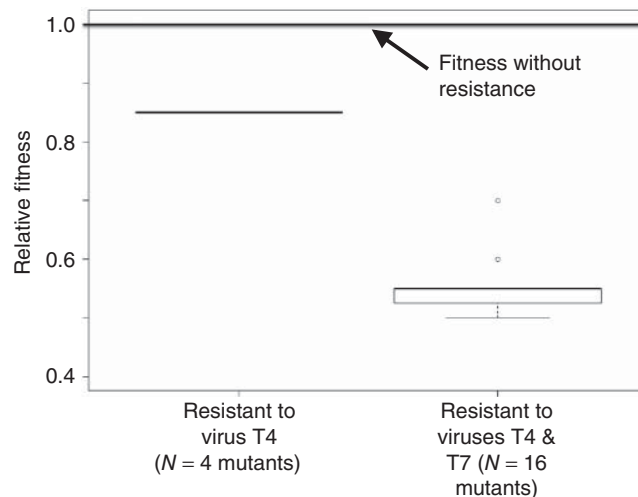
### **Ecological Defense: Guarding against Natural Enemies**

Organisms must guard against being eaten and infected, and most have evolved adaptations for reducing these risks. Adaptations that deter natural enemies are diverse (Edmunds 1974; Coustau *et al.* 2000; Berenbaum 2001) and often costly, creating a trade-off between adaptations that reduce the likelihood of being consumed versus allocation to growth and reproduction (e.g., Strauss *et al.* 2002; Knowles *et al.* 2009; van der Most *et al.* 2011). Trade-offs also occur when organisms encounter multiple threats, such as risk from different predators or threats from predation and disease. For example, behavioral adaptations to reduce predation risk in damselflies (*Enallagma* spp.) vary depending on the predator, and

present a trade-off between reducing predation by fish (e.g., remaining still) versus reducing predation by dragonflies (e.g., swimming away) (McPeck 1990). The importance of natural enemies in nature creates widespread trade-offs confronting hosts and prey, with diverse interactions and investments in adaptations that vary with risk (Raffel *et al.* 2008). These trade-offs can allow species with different strategies to coexist in diverse ways (Raffel *et al.* 2008), increasing diversity.

### **Trade-offs between Viral Defense and Competitive Ability in Bacteria**

Viruses are abundant predators of bacteria in nature (Suttle 2005). Studies of the interactions between *E. coli* and T-type bacteriophage virus have identified *E. coli* that are resistant to viral predation, but their resistance comes at a cost to their growth and competitive ability (Lenski 1988a; Bohannan *et al.* 2002; Figure 18.2). The trade-off between competitive ability and resistance to viral predation typically involves changes to the receptor molecules on the bacteria's cell surface to which the virus initially binds. The changes to the receptor molecules simultaneously compromise aspects of metabolism, such as nutrient uptake, thereby reducing the competitive ability of virus-resistant bacteria (Figure 18.2; Lenski 1988a; Bohannan & Lenski 2000b; Bohannan *et al.* 2002). The magnitude of the trade-off between competitive ability and virus resistance varies (Bohannan & Lenski 2000b), and declines as modifier alleles evolve to mitigate, but not eliminate, the costs of resistance (Lenski 1988b). The cost of viral resistance, and thus the size of the trade-off, also varies with environmental factors such as resource abundance and temperature (Bohannan & Lenski 2000a; Quance & Travisano 2009; Gómez & Buckling 2011), which would alter the distributions of virus-resistant and virus-susceptible bacteria by influencing when they can coexist along environmental gradients.



**Figure 18.2.** The relative fitness of 20 independent *Escherichia coli* mutants that were resistant to virus T4 (but not to virus T7) or to both viruses T4 and T7 (data from Lenski 1988a). The fitness of virus-sensitive *E. coli* is equal to 1. Mutations that altered receptors on *E. coli*'s cell surface prevented viral infection, but compromised metabolism, growth, and competitive ability, illustrating an evolutionary trade-off. This trade-off allows both virus-resistant and virus-susceptible strains of *E. coli* to coexist when viruses are present (Lenski 1988a).

While microbial interactions in the lab provide insight into evolutionary trade-offs, do they inform patterns in nature? Studies of both ocean cyanobacteria (Avrani *et al.* 2011, 2012) and soil bacteria (Gómez & Buckling 2011) and their viruses provide evidence that the evolutionary trade-offs demonstrated in the lab also play an important role in determining the distributions and coexistence of microbial diversity in nature. In nature, however, the costs of resistance are likely to be higher with resource limitation, and extend beyond reduced competitive abilities to trade-offs involving different viruses. In addition, the spatial and temporal complexities of selection, not evident in simplified laboratory settings, may play pivotal roles in maintaining diversity in nature (Avrani *et al.* 2011, 2012; Gómez & Buckling 2011).

### **Abiotic Challenges: The Costs of Adaptation**

Abiotic conditions across most of the Earth's surface significantly challenge the majority of organisms (Russell 1990). Yet some species persist, and even thrive, in the face of these challenges as a result of specific adaptations. These adaptations often come at a competitive cost because allocative or functional trade-offs are required to address the environmental challenge (e.g., Coustau *et al.* 2000). Examples of adaptations to abiotic challenges include ion excretion organs in aquatic organisms that inhabit extremely hyperosmotic environments (e.g., Shimizu & Bradley 1994), physiological adaptations providing resistance to herbicides, pesticides, and antibiotics (e.g., Vila-Aiub *et al.* 2009), and well-developed thermal insulation for homeothermic animals confronting low temperatures (e.g., Scholander 1955).

***Trade-offs during Plant Adaptation to Serpentine Soils*** Serpentine soils represent a challenge to plant growth (Figure 18.3), particularly due to low Ca:Mg ratios (Kruckeberg 2002; Brady *et al.* 2005). Absorption of Ca typically leads to greater absorption of Mg when Ca:Mg ratios are low (Madhok & Walker 1969), with elevated levels of Mg being detrimental to photosynthesis (Marschner 2001). Ca is a vital component of cell walls, and is thus essential for plant growth (Marschner 2001), leaving plants with little option but to maintain adequate Ca uptake while minimizing the problem of Mg. These and other challenges of serpentine soils have led to low productivity, high endemism, and distinct vegetation types in serpentine plant communities (Figure 18.3; Brady *et al.* 2005; Harrison & Rajakaruna 2011).

Despite the challenges of serpentine soils, plants have repeatedly and independently adapted to their hostile conditions (Harrison & Rajakaruna 2011). Several adaptations address the challenge of low Ca:Mg ratios by discriminating Ca and Mg ions during absorption, translocating Mg and other toxins to minimize impacts, and sequestering or chelating Mg and other toxins within the plant (Rajakaruna *et al.* 2003; Brady *et al.* 2005). These adaptations to serpentine soils, however, come at a competitive cost. Many serpentine-adapted populations and species are limited to serpentine soils because they are unable to compete with plant species in nonserpentine environments (Kruckeberg 1954; Moore & Elmendorf 2011) and show reduced growth rates relative to nonserpentine plants, even in the absence of competitors (Brady *et al.* 2005; Wright & Stanton 2011). The reduced competitive ability of serpentine-adapted plants suggests that adaptations to serpentine soils compromise their ability to recolonize and persist in their ancestral habitats (Brady *et al.* 2005). This trade-off allows different plant species to persist on different soil types, increasing local and regional diversity.



**Figure 18.3.** Plant communities on nonserpentine (background) and serpentine (foreground) soils, Snell Valley, Napa County, California. Many different species of plants have adapted to live on serpentine soils, however, adaptations frequently compromise the ability of serpentine plants to compete on nonserpentine soils, illustrating a trade-off. This trade-off allows different species of plants to coexist by using different types of soil. Photo by John McKay. (See plate section for color version.)

## EVOLUTIONARY TRADE-OFFS AND THE DISTRIBUTIONS OF SPECIES

These select studies illustrate integrative approaches to the study of trade-offs and their consequences for diversity. While our understanding of each trade-off is incomplete, the studies collectively illustrate the strength of integrative approaches for the study of evolutionary trade-offs of broad importance – trade-offs that should impact the ecology and evolution of most organisms in nature. The groupings are somewhat artificial (i.e., examples will often fit into multiple categories), but the challenges confronting organisms are real. Still other trade-offs are widespread in nature, such as trade-offs in life history strategies (Stearns 1992), ecological breadth (Futuyma & Moreno 1988), competitive versus colonization abilities (e.g., Violle *et al.* 2010), digestive physiologies (Afik & Karasov 1995), and physiological plasticity (DeWitt *et al.* 1998; Chapter 17, this volume), with important consequences for the distributions of species (Chapter 17, this volume). Furthermore,



some evidence suggests that a diversity of trade-offs, rather than a few, may be the key to explaining the coexistence of rich biodiversity (Clark *et al.* 2007). We may expect such diversity of trade-offs if we consider trade-offs in the context of coevolution among species (cf. Thompson 2005).

Trade-offs allow species to coexist because they prevent any one species from monopolizing energy and other resources, particularly when selective pressures vary over space and time. For example, trade-offs between competitive dominance and herbivory defense may promote the coexistence of diverse plant species on two distinct soil types in Amazonian forest (Fine *et al.* 2004). Without the trade-off (herbivory removed), species adapted to clay soils prevailed across both types of soil (Fine *et al.* 2004). Similarly, trade-offs between minimizing energetic costs of foraging versus minimizing predation allow rodent species to coexist in different microhabitats within the same community (Kotler 1984). Overall, variation in selective pressures, coupled with the inability of species to adapt to all selective pressures simultaneously (trade-offs), create varying opportunities for diverse species. Understanding the mechanistic basis of these trade-offs and their consequences for individual fitness, population dynamics, species interactions, and coexistence will help us to understand how diversity is structured and why it varies (e.g., Bohannan *et al.* 2002; Kneitel & Chase 2004; Angert *et al.* 2009).

The same factors that determine the distributions of species also influence their abundances within their distributions. For example, the size of the trade-off between competitive ability and viral resistance influences the abundance of virus-resistant and virus-susceptible bacteria and their predatory virus. The costs of resistance, and thus the size of the trade-off, vary with both temperature and resources, creating variation in the abundance of coexisting bacteria and their viruses (Bohannan & Lenski 2000a; Quance & Travisano 2009; Gómez & Buckling 2011). Similarly, coexisting species of plants in the Sonoran Desert exhibit temporal variation in their abundance from year to year. This variation is best explained by a fundamental trade-off between the ability to photosynthesize and grow rapidly in wetter years versus the ability to withstand the low resource abundance in drier years. While these species coexist together, their demographic responses, and thus abundances, vary with environmental variation from year to year (Angert *et al.* 2009).

## ARE TRADE-OFFS UNIVERSAL?

Trade-offs confront organisms everywhere we look, and yet when we look for specific or expected trade-offs, we don't always find them (e.g., Strauss *et al.* 2002). Conflicting evidence for trade-offs may be a function of the difficulties of measuring weak selection, the masking of trade-offs by other traits or variation (genetic, environmental), or delayed fitness benefits of different allocation strategies (Van Buskirk 2000; Agrawal *et al.* 2010). Despite these difficulties, simple experiments, such as reciprocal transplants, have been effective at identifying phenotypic traits involved in trade-offs and their consequences for abundances and distributions. Furthermore, the expanding fields of genomics and proteomics will provide new opportunities to understand the mechanistic basis of trade-offs, from genes to phenotypes.

Beyond the mechanics of identifying trade-offs in nature, we should also expect the occurrence of specific trade-offs to vary. Natural selection should strongly favor the evolution of traits that mitigate the costs of trade-offs, especially in the case of functional trade-offs (e.g., Lenski 1988b; Thaler *et al.* 2012). For example, the evolution of weapons (e.g., talons) in smaller species can offset the advantage larger species have in aggressive

contests (Martin & Ghalambor, unpublished data). Allocative trade-offs are less likely to be directly mitigated by other traits because they are dependent upon resource abundance (Lenski 1988b). Allocative trade-offs, however, become more prominent when resources are limiting (e.g., Gómez & Buckling 2011), either in the environment, or because of the poor condition of the individual. In these latter cases, we may find condition-dependent trade-offs that can lead to distinct phenotypes within species (e.g., Emlen *et al.* 2012).

Evolutionary forces, such as gene flow, can constrain divergent evolution in response to trade-offs, potentially explaining why some species respond differently when confronted with similar challenges. For example, trade-offs commonly favor distinct phenotypes, but the evolution of distinct phenotypes is impeded by gene flow. Reproductive isolation creates the evolutionary independence that can free species to settle trade-offs in different ways (Coyne & Orr 2004). This evolutionary independence is a key reason why species formation is so important for adaptation and biodiversity (Coyne & Orr 2004).

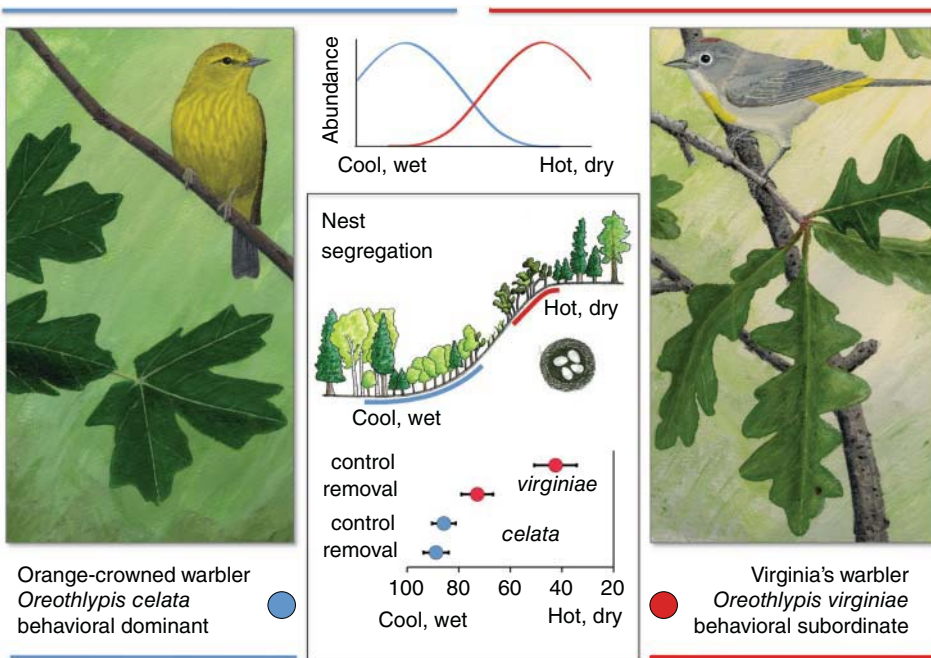
In contrast, evolutionary forces, such as character displacement, can promote divergent evolution in response to trade-offs. The presence of other species can act to shift patterns of evolution from cases where one species optimizes its phenotype in response to a trade-off, to cases where two species optimize their phenotypes to settle a trade-off in different ways (Schluter 2000; Pfennig & Pfennig 2012; Figure 18.1). An illustrative example comes from comparisons of the many *Geospiza* finches found on several of the Galápagos Islands to the one species found on Cocos Island. Similar selective pressures and trade-offs may confront finches on Cocos Island, but without geographic isolation, the evolution of reproductive isolation, or character displacement, the one species has not diverged into distinct, sympatric ecological forms (Grant & Grant 2008; Losos & Ricklefs 2009).

Overall, we should expect variation in the occurrence and importance of specific trade-offs, and expect different trade-offs to determine the distributions and abundances of species under different circumstances (McPeck 1996). Understanding when specific trade-offs occur, including their prevalence at different scales of space and time (Kneitel & Chase 2004), would provide insight into how trade-offs are maintained or lost over time. Some trade-offs may prove to be fundamental across species and difficult to overcome (Tilman 2011), while others may prove fleeting.

## TRADE-OFFS, INTEGRATIVE BIOLOGY, AND MOVING FORWARD

How is a trade-off framework different from other approaches to studying community ecology, given that both approaches focus on the same processes (competition, predation, parasitism, climate) (see also Box 18.1)? To illustrate, I use an example from my own work on wood warblers (Parulidae; Martin & Martin 2001a,b; Figure 18.4), the same family that was the focus of MacArthur's classic study of competition (MacArthur 1958).

Orange-crowned (*Oreothlypis celata*) and Virginia's (*O. virginiae*) warblers are closely related species that segregate their distributions along a temperature and moisture gradient, repeated across multiple spatial scales, but coexist in some areas of sympatry (Figure 18.4). *O. virginiae* occupies hotter, drier regions of North America, and, within regions of sympatry with *celata*, occupies lower elevations that are also hotter and drier. At even finer spatial scales, the two species completely overlap their breeding territories in a zone of geographic and elevational sympatry in central Arizona, USA, where *virginiae* typically nest in hotter, drier nest sites under oak (*Quercus*) or locust (*Robinia*), while *celata* nest in moister regions under maple (*Acer*). The larger *celata* is aggressive to the smaller *virginiae*, but does not fully exclude *virginiae* from its territories. Reciprocal removal experiments revealed high fitness costs of co-occurrence for both species caused by density-dependent nest predation.



**Figure 18.4.** Segregation of Orange-crowned (*Oreothlypis celata*, blue) and Virginia's (*O. virginiae*, red) warblers (Parulidae) along gradients of temperature and moisture during the breeding season. These two species appear to face a trade-off, where the larger *celata* is dominant in aggressive interactions and excludes the smaller *virginiae* from preferred nest sites in cool, moist regions of their breeding territories. The smaller *virginiae*, however, can tolerate hot, dry nesting conditions that *celata* cannot tolerate, leading to spatial partitioning of nest sites where their breeding territories overlap. Experimental removal of the opposite species resulted in *virginiae* shifting their nest sites into cool, wet regions of the gradient in the absence of *celata*, but no shift in *celata* nest sites in the absence of *virginiae* (x-axis is the mean percentage of maple stems near the nest +/- SE). The temperature and moisture gradients that characterize overlapping territories also characterize patterns of elevational and geographic segregation, and temporal variation in abundance, suggesting that these trade-offs may also influence their distributions on broader spatial and temporal scales (Martin 1998, 2001; Martin & Martin 2001a,b). Similar trade-offs between competitive ability and environmental tolerance face barnacles (Connell 1961) and many other closely-related species, from chipmunks to salamanders, cattails to crayfish (Martin & Martin 2001a). (See plate section for color version.)

When *celata* was experimentally removed, *virginiae* shifted their nest sites to sites indistinguishable from *celata*; however, *celata* did not shift their nest sites when *virginiae* had been removed, and appear to be unable to nest successfully in hot, dry conditions. In addition, *O. virginiae* increased their feeding rates at nests with the removal of *celata*, which could reflect competition for food, or shifted time budgets that allow more time for foraging when *virginiae* nest in optimal sites (Martin 1998, 2001; Martin & Martin 2001a,b). The take home message from this study is this: interactions between these species are significant and complicated, involving asymmetric competition for nest sites, high costs of predation, and segregation along a climatic gradient of temperature and moisture to which the species

are differentially adapted. What determines their distributions, abundances, interactions, and patterns of co-occurrence? Is competition more important than predation? Are biotic interactions more important than climate? Are these species constrained by top-down, or bottom-up processes? None of these classic frameworks for studying community ecology can adequately explain these interactions, echoing a sentiment common to many studies of local communities (Lawton 1999).

In contrast, studying trade-offs within an evolutionary context provides a useful and robust framework for understanding interactions and distributional patterns among *Oreothlypis* wood warblers, as it has for many other systems (e.g., Grime 1977; Chapin 1980; Tilman 1982; Petraitis *et al.* 1989; McPeck 1996; Tessier *et al.* 2000; Kneitel & Chase 2004; Angert *et al.* 2009). The two species appear to confront a trade-off between competitive dominance versus tolerance of hot, dry conditions, where *celata* is dominant but unable to tolerate hot, dry environments, while *virginiae* is subordinate but able to tolerate hot and dry climates. The competitively dominant *O. celata* keeps *virginiae* from preferred, moist nest sites, and perhaps from moister regions of the elevational and geographic gradients as well. The two species live together because *celata* does not completely exclude *virginiae*, and *virginiae* benefits from settling with *celata* – *virginiae* nesting in moist habitat with *celata* had similar reproductive success to *virginiae* nesting in dry habitat where *celata* is naturally absent. In other words, the higher quality of moist habitat offsets the costs of living with *celata* and allows these populations of *virginiae* to be sustained. Given density-dependent costs of co-occurrence, we should expect *virginiae* to avoid *celata* when the densities of *celata* reach a threshold (Martin 1998, 2001; Martin & Martin 2001a,b; Clark & Martin 2007; Figure 18.4). Questions remain, such as what adaptations allow *virginiae*, but not *celata*, to use hot and dry environments, and what are the ecological and fitness consequences of aggression by *celata*?

Trade-offs represent evolutionary challenges that play an integral role in ecology. Reviewing examples of widespread trade-offs reveals repeated patterns that suggest fundamental constraints. Among closely-related species, we repeatedly see a trade-off between competitive ability and ability to tolerate diverse environmental challenges, including low resources, high risk of predation, herbivory, parasitism, or pathogens, or hostile conditions such as poisonous soils or extreme climate (Connell 1961; Colwell & Fuentes 1975; Chapin 1980; Wisheu 1998; Keddy 2001; Martin & Martin 2001a; McGill *et al.* 2006). This broad trade-off makes sense from an evolutionary perspective – selective pressures that present significant challenges to a group of organisms require adaptations that should compromise organismal performance and competitive abilities in the context of environments that lack these challenges (e.g., Coustau *et al.* 2000). Importantly, competition does not structure these relationships. Without a trade-off involving diverse selective pressures, these species would be unlikely to coexist (e.g., Lenski & Levin 1985).

We should expect other rules to structure biodiversity, and many have been identified. For example, the extreme variation in body size, from bacteria to large trees and mammals, reveals fundamental scaling laws (West *et al.* 1997) and reflects distinct evolutionary strategies in response to trade-offs in organismal complexity, rates of evolution mediated by generation time, and inertial versus viscous forces (Peters 1983; Bonner 2006). Trade-offs are evident between endothermic and ectothermic strategies – in endotherms, maintaining high body temperatures allows consistently high metabolic rates and performance independent of the thermal environment, but comes at a high energetic cost of maintaining body temperatures (Schmidt-Nielsen 1997). Such a trade-off may explain the success of bird pollinators and bird-pollinated plants on high neotropical mountains where rain and low temperatures constrain bee pollination activity (Cruden 1972).

The evolution of specialized biotic interactions and coevolution could create an abundance of trade-offs, where adaptations that are specific and dependent on another species come at a cost to their function in the absence of that species. For example, adaptations in *Prochlorococcus* cyanobacteria to one set of viruses come at a cost of enhanced susceptibility to a different set of viruses (Avrani *et al.* 2011; 2012). Variation in the occurrence of virus types can lead to the coexistence of bacteria with different patterns of resistance (Avrani *et al.* 2011; 2012). This evolution of traits in response to new and diverse biotic trade-offs could promote speciation and the coexistence of even more species, particularly in species-rich environments (Schemske 2009).

Other trade-offs may also play important roles in the formation of new species. For example, Dobzhansky-Muller incompatibilities – where mutations that function well in the genetic background of their own population, function poorly in the genetic background of another population – can be viewed as a simple trade-off, but one potentially playing an important role in the formation of species by creating costs to hybridizing among populations (Coyne & Orr 2004). Overall, these few examples of fundamental trade-offs represent generalities that can partly explain distributions and diversity – the “rules” for which community ecologists search (Lawton 1999; Simberloff 2004).

In sum, trade-offs provide a productive framework for understanding the distributions and abundance of species in nature, integrating and uniting diverse fields, levels of study, and perspectives in the search to understand broad ecological patterns. This integrative approach yields richer stories, and elucidates mechanisms that help us to identify causal factors shared across diverse taxa and environments. These integrative stories will link together to provide a more complete understanding of how and why organisms live where they do, and ultimately, the factors that structure biological diversity.

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