A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology*

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Abstract. Biodiversity is defined by trait differences between organisms, and biologists have long sought to predict associations among ecologically important traits. Why do some traits trade off but others are coexpressed? Why might some trait associations hold across levels of organization, from individuals and genotypes to populations and species, whereas others only occur at one level? Understanding such scaling is a core biological problem, bearing on the evolution of ecological strategies as well as forecasting responses to environmental change. Explicitly considering the hierarchy of biodiversity and expectations at each scale (individual change, evolution within and among populations, and species turnover) is necessary as we work toward a predictive framework in evolutionary ecology. Within species, a trait may have an association with another trait because of phenotypic plasticity, genetic correlation, or population-level local adaptation. Plastic responses are often adaptive and yet individuals have a fixed pool of resources; thus, positive and negative trait associations can be generated by immediate environmental needs and energetic demands. Genetic variation and covariation for traits within a population are typically shaped by varying natural selection in space and time. Although genetic correlations are infrequently long-term constraints, they may indicate competing organismal demands. Traits are often quantitatively differentiated among populations (local
adaptation), although selection rarely favors qualitatively different strategies until populations become reproductively isolated. Across species, niche specialization to particular habitats or biotic interactions may determine trait correlations, a subset of which are termed “strategic trade-offs” because they are a consequence of adaptive specialization. Across scales, constraints within species often do not apply as new species evolve, and conversely, trait correlations observed across populations or species may not be reflected within populations. I give examples of such scale-dependent trait associations and their causes across taxonomic groups and ecosystems, and in the final section of the paper, I specifically evaluate leaf economics spectrum traits and their associations with plant defense against herbivory. Scale-dependent predictions emerge for understanding plant ecology holistically, and this approach can be fruitfully applied more generally in evolutionary ecology. Adaptive specialization and community context are two of the primary drivers of trade-offs and syndromes across biological scales.

**Key words:** evolutionary ecology; genetic correlations; leaf economics spectrum; local adaptation; milkweeds Asclepias; phenotypic plasticity; strategies and syndromes.

**INTRODUCTION**

**Motivation**

This paper is about trade-offs and strategies, allocation decisions that all organisms face, that impact ecological interactions and ultimately fitness. There has been long-standing interest in trade-offs in the very general sense, stemming from a desire to understand organismal limitations and constraints in evolutionary ecology, with the scale spanning from individuals to species (Futuyma and Moreno 1988, Bolnick et al. 2003). Early on, the study of trade-offs was primarily the domain of evolutionary biologists, but this has changed, with trade-offs becoming more central to understanding phenotypic plasticity, multispecies community interactions, and the comparative ecology of species strategies. Trade-offs are fundamental to the generation and maintenance of diversity at all levels of biological organization (phenotypes, genotypes, populations, species; Antonovics 1976, Vellend and Geber 2005). As such, trade-offs are critical to understanding organisms, their niches, and the ecosystem consequences of diversity.

Ecologists are interested in trade-offs because they highlight limitations, but also because they reveal how natural selection shapes the strategies of organisms. In other words, trade-offs not only show how changes in the environment may impact organisms, but they also provide a lens into how past natural selection has shaped current interactions between species and the environment. At a basic level, most biologists consider the fit of organisms in nature, thinking about which traits appear adaptive, what types of limits organisms face, and how evolution has shaped these attributes. Do sets of coexpressed traits represent the best fit to an organism’s niche? We are often curious to know if some traits, or associations between traits, have been shaped by adaptive evolution, whereas others simply cannot evolve (strong constraint).

My goal here is to arrive at a conceptual and predictive framework for understanding organismal trade-offs, often observed as negative trait associations, across levels of organization from individuals and genotypes to populations and species. Alongside trade-offs, I will consider the coexpression of two or more traits, sometimes called syndromes, which are thought to represent the adaptive expression of trait combinations repeated in independent groups (at any scale from plastic responses to across species). Here the term strategy is synonymous with syndrome, and I refer to strategic trade-offs as a negative association between two traits or sets of traits that have been shaped by natural selection (concordant with Arnold’s 1992 selective constraints). Thus, I will attempt to address when, and between which types of traits, trade-offs are expected. More generally, how should we think about negative trait correlations: are they truly constrained or are they honed by natural selection? And, are the same trait associations predicted to occur across levels of biological organization (through phenotypic plasticity, in genetic correlations, among locally adapted populations, and across species; Figs. 1 and 2)?

**Purview**

It is conventional wisdom that trait expression within species is shaped by different, sometimes conflicting, fitness advantages when organisms are in contrasting environments (Schluter et al. 1991). Accordingly, here I will define trade-offs as the advantage of a phenotype in one ecological context accompanied by a disadvantage in the same or different context; the disadvantage may be due to allocation of a limiting resource, ecological interactions, or the negative impact of one trait on another. Note that this definition is agnostic to level of biological organization; a trade-off may be observed within or between species. At the population or species level, however, the advantages and disadvantages are not accrued to the group (population or species), but should rather be thought of as traits with consequences for individuals within those groups. Although an important pattern, negative interspecific trait correlations are not necessarily generated by within-species trade-offs, but are often a consequence of species-level specialization (Futuyma and Moreno 1988).

Authors have previously disagreed as to whether trade-offs impose strong constraint (i.e., whether the
accompanying disadvantage can or cannot be overcome) and whether trade-offs should be focused exclusively on resource diversion. Constraints of any kind are "restrictions or limitations on the course or outcome of evolution," but with variable persistence across scales (Arnold 1992, Futuyma 2010). Based on my knowledge and review below, I hold the view that nearly all trade-offs can be overcome (except those involving fitness components, defined below), either by being in a different environment or via evolutionary change, and thus most trade-offs should not be considered long-term constraints. Similarly, as discussed below, many organismal limitations occur because of factors other than resource diversion, and thus limiting the purview of trade-offs is undesirable. I propose that we proceed, acknowledging the discomfort of considering multiple types of trade-offs, and use this complexity as a tool to understand the processes that occur at different scales.

In this synthesis, I will focus on phenotypes of ecological importance that go well beyond life-history traits. Following Schluter et al. (1991), I synonymize life-history traits with components of fitness, defined as those traits "correlated with total fitness when all other traits are held constant." Examples of such traits might include survival, fecundity, or early reproduction. Because life-history traits often use a large fraction of total available resources, trade-offs are common among them and ample theory addresses life-history trade-offs (Rose and Charlesworth 1981, Reznick 1985, Stearns 1992, Messina and Fox 2001, Roff 2002). Here I am mostly concerned with those other "functional" traits that typically use fewer resources, are innumerable in most organisms, and yet are central to the mediation of ecological interactions. Most of these traits have context-dependent effects. Examples will stem from my own work and knowledge of the traits of plants and herbivorous insects—but please don’t let that deter you. I will try to generalize as much as possible.

In many cases, trade-offs at one level of organization will provide little insight into what may occur at other levels (Table 1). As a case in point, a nearly universal plastic response of animals to the risk of predation is to hide and eat less. In most cases, this is an adaptive behavioral response that trades off safety from predators with acquisition of resources. Genetic correlations within a species may be expected to look similar, with high-foraging genotypes being subject to greater predation (and vice versa). However, we do not expect species comparisons to show the same trade-off. Animal species that evolve in high-predation environments may exhibit various strategies outside of reduced feeding, including crypsis, aposematism, and escape behaviors. Each of these strategies likely comes with its own set of both positively and negatively associated traits, but these are unlikely to be represented within individual species.

As outlined below, my views are grounded in several assumptions and general conclusions about evolutionary ecology (Box 1). Following the section labeled "Introduction," the paper continues by delving into history, starting with some of the origins of evolutionary ecology and moving to more recent developments, including personal reflections from the past 25 yr. The section labeled "Trade-Offs and Syndromes and Across Scales" includes a more formalized discussion of
definitions and mechanisms of trade-offs and syndromes. There, I outline the scale-dependent evolutionary processes that may lead to different trait associations at each level of biological organization. And finally, in the section “Plant Ecological Strategies and Defense,” I consider empirical work on scale-dependent trait associations using the emerging literature on the “leaf economics spectrum” and my own research on leaf function and defense in the milkweeds, a group of toxic plants with well-known relationships with specialist insect herbivores.

Deep history and Darwin

Johann Wolfgang von Goethe was one of the all-time great natural philosophers, and an early evolutionary ecologist who shed light on trade-offs. He believed that organisms track the environment, adapt to it, and
Within species

<table>
<thead>
<tr>
<th>Where found?</th>
<th>What is the pattern?</th>
<th>Why it does not occur at other levels?</th>
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<tbody>
<tr>
<td>Negative genetic correlation between defense and performance (costs of defense; Züst and Agrawal 2017)</td>
<td>Increased resource availability, acquisition of resources, and niche specialization (strategic trade-offs) reduce the likelihood that highly defended species have extremely slow growth</td>
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<td>High activity is associated with predation risk (Gotthard 2000)</td>
<td>Animal species that evolve in high-predation environments employ a diversity of strategies, including aposematism or escape behaviors to avoid predation</td>
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<td>Timing trades off with the magnitude of reproduction in plants (Dorn and Mitchell-Olde 1991)</td>
<td>Altered resource availability, acquisition, and strategic trade-offs uncouple this association. The pattern is strongest within species, but may be evident at some higher scales</td>
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<td>Larger animals have higher rates of cancer than smaller ones (Caulin and Maley 2011)</td>
<td>Selection in larger species for repair or anticancer defense overweighs the tendency for higher cancer based only on size</td>
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<td>“Pace of life” trade-offs in animal growth and personality (Dammhahn et al. 2018)</td>
<td>Integrated behavioral and physiological phenotypes are less expected within species; resource availability strongly impacts plastic expression of traits, sometimes mirroring species strategies</td>
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<td>Gregarious species have a syndrome of life-history traits less commonly observed in solitary relatives (Hunter 1991)</td>
<td>Trait combinations are less expected among variants within species, even with local adaptation; only when sets of traits evolve (e.g., gregariousness with distastefulness) are the strategies successful</td>
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<td>Resource availability and plant defense trade-off (Hahn and Maron 2016)</td>
<td>A strategy of slow growth in low-resource environments drives high defense because of high value of leaves; such co-adapted sets of traits are not expected to switch within species</td>
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<td>Niche specialized trade-offs such as Grime’s Competitive, Stress tolerant, Ruderal Triangle (Grime 1977)</td>
<td>When specialized to one niche corner of multi-variate space, there is little selection for costly traits in the other corners. Within species, however, there is no expected specialization of traits associated with the corners</td>
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<td>Sometimes across levels</td>
<td>This appears to be quite general across scales, but horn placement has evolved, apparently to differentially impact where the trade-off is experienced</td>
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<td>Beetle horns draw resources from neighboring organs (Emlen 2001)</td>
<td>Life-history traits such as these sometimes trade off within and between species, but trade-offs can be obscured by resource availability and population-level adaptation</td>
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<td>Trade-off between flower size and number (Sargent et al. 2007)</td>
<td>Dictated by physiological relationships, especially when considering body-size variation of several orders of magnitude. However, strong variation exists in these relationships, especially among close relatives of similar body size living in different niches</td>
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<td>Body size, metabolic rate, and ecological consequences (Tilman et al. 2004)</td>
<td>Body plans are often conserved, and thus relationships may hold within and between closely related species; however, relationships are expected to decay at higher taxonomic scales</td>
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<td>Skeletal parameters typically connected by allometry (McGlotten et al. 2018)</td>
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change their morphologies and behaviors to increase their persistence. His thinking was heavily influenced by observations and experiments with plants growing in different environments. In his *Story of My Botanical Studies* from 1831, Goethe wrote of plants having “a felicitous mobility and plasticity that allows them to grow and adapt themselves to many different conditions in many different places” (Teichmann 2005). For Goethe, transmutation within species to the formation of new species was a continuous process, driven by a “law of compensation.” A certain amount of energy is available to organisms, which they may allocate in different ways, depending on the needs of the organism in the environment. Ultimately, he hypothesized that these needs drive individuals and species toward specialization.

Nearly three decades later, Darwin (1859:147) wrote in *On the Origin of Species*: “…as Goethe expressed it, ‘in order to spend on one side, nature is forced to economise on the other side.’” This view indicated that Darwin saw most adaptations as costly: “If under changed conditions of life a structure before useful becomes less useful, any diminution, however slight, in its development, will be seized on by natural selection, for it will profit the individual not to have its nutriment wasted in building up an useless structure.”

In another passage, Darwin wrote about trade-offs “…if nourishment flows to one part or organ in excess, it rarely flows, at least in excess, to another part; thus it is difficult to get a cow to give much milk and to fatten readily. The same varieties of the cabbage do not yield abundant and nutritious foliage and a copious supply of oil-bearing seeds… With species in a state of nature it can hardly be maintained that the law is of universal application; but many good observers, more especially botanists, believe in its truth. …I see hardly any way of distinguishing between the effects, on the one hand, of a part being largely developed through natural selection and another and adjoining part being reduced by this same process or by disuse, and, on the
Many of these come from quantitative genetics research, but this branch of evolutionary biology is currently less focused on such issues and historically lacked a community ecological perspective. Some of these points may be contentious.

**Trait variation is hierarchical**
On average, phenotypic trait variation among individuals that is due to phenotypic plasticity will be relatively small compared to the variation in the same traits that are expressed across related species (expressed in the same environments). Heritable intraspecific variation will often be intermediate compared to plasticity and species variation, especially when multiple populations and environments are considered. The exceptions to this general rule are, of course, interesting, but are nonetheless exceptions.

**Trait correlations at different scales are informative for different reasons**
Our interpretation of a correlation between two traits is different when each point is an individual, a genotype, a population, or a species. Correlations across populations and species represent patterns of the outcome of evolutionary processes, but do not directly bear on future evolution (unlike within-population correlations).

**Much of plasticity (but certainly not all) is adaptive**
When considering trade-offs that are associated with phenotypic plasticity, we are assuming that environmentally induced trait expression is beneficial. If it is not beneficial, then considering trade-offs does not make sense (although there may be important evolutionary consequences in such instances; Ghalambor et al. 2007). In at least some well-studied cases (i.e., inducible defenses of plants and animals), adaptive plasticity can be safely assumed.

**All adaptation is constrained adaptation**
Evolution is “limited by the strength of natural selection, genetic architecture, and fitness costs and benefits, all of which narrow the number of possible evolutionary outcomes” (Agrawal 2017b). The importance of this truism is that most functional traits are shaped by adaptation, but this includes limitations that may be constraining.

**Intraspecific genetic trade-offs are hard to interpret**
Negative genetic correlations within a population may represent limitations that cannot be easily overcome, or they may represent maintained genetic variation along an adaptive axis where alternative positions are favored over space or time via correlational selection (Agrawal et al. 2010).

**Populations show local adaptation**
When gene flow is at least somewhat limited and ecological conditions are different between populations, populations may locally adapt to the biotic or abiotic environment. There are many reasons to expect that trait relationships that emerge across locally adapted populations may not be the same as those among genotypes within populations (Peiman and Robinson 2017).

**Species are reproductively isolated and specialized**
The main point of this trivial observation is to highlight that, because of the time scale and isolation of speciation, trade-offs and trait functionality should not be expected to be the same within as between species. Nearly all pleiotropy or negative genetic correlations within a species can be overcome by strong and persistent selection (save those among life-history traits). The adaptive specialization that occurs at the species level, to habitats or niches, structures a species’ strategy (and trait associations) that may be observed interspecifically.

**Resources are limited, but not really**
Organisms evolve in both their resource-acquisition and -allocation patterns. Under a fixed and limited level of resources, trade-offs will be most observable. However, additional resource acquisition may mask a given trade-off. This recognition revolutionized evolutionary ecological thinking about trade-offs (van Noordwijk and de Jong 1986, Box 2).

**Resource limitation is only half of understanding trade-offs**
The rest is community ecology. Of course, resources are limiting, but the other major driver of phenotypes and negative correlations among them is variation in biotic and abiotic interactions over space and time. Although this seems obvious to most community ecologists, it is less than trivial because in thinking about trade-offs, organisms are balancing resource allocation with the probability of particular interactions (i.e., competition, poisoning, freezing, etc.) occurring and impacting fitness.
other hand, the actual withdrawal of nutriment from one part owing to the excess of growth in another and adjoining part.”

Here Darwin primarily considers two traits showing a negative correlation, either because (1) natural selection has shaped the genetic architecture such that coexpression is not favored (perhaps because the traits are ecologically redundant and yet costly) or because (2) the two traits simply cannot be coexpressed because of resource limitation. In truth, either of these extremes is probably rare. Few, if any, negative or positive correlations among ecologically important traits are unbreakable by long-term selection (Conner 2012). Conversely, two traits are rarely fully redundant (or uniformly experience negative correlational selection) across ecological conditions. Therefore, under the assumption that all adaptation is constrained adaptation (Box 1), most negative correlations between two traits represent making the best of some limited circumstance. In other words, resources are indeed limited, some traits may directly interfere with others, and some traits may be disfavored when others are expressed. The relative importance of these drivers, however, continues to be largely unknown.

Recent history to the present

Zooming past most of the 20th century and the modern synthesis of evolutionary biology, over the last 50 yr, interest in trade-offs has expanded and has helped shape important conceptual areas in evolution ecology. As mentioned above, the constructs of life-history theory and its descendants (e.g., r vs. K selection) have been based in thinking about trade-offs and adaptive strategies. Understanding the evolution of specialization grew from an appreciation of trade-offs (Futuyma and Moreno 1988). The maintenance of diversity, be it genetic variation within a species or species diversity in a community, was heavily influenced by thinking on trade-offs (Antonovics 1976, Vellend and Geber 2005). As the ecologically motivated study of adaptation took hold in the mid-1980s, even greater interest in trade-offs emerged, with an emphasis on within-population costs or limits to adaptation, and a focus on ecologically important traits.

As a graduate student in the mid-1990s at the University of California at Davis (UC Davis), trade-offs were on the tips of a lot of tongues. My graduate advisor, Rick Karban, had become interested in costs of plant defense and local adaptation in insects, both issues being conceptually motivated by the idea of trade-offs. In the fall of 1994, Douglas Futuyma presented a seminar on the topic at UC Davis, evaluating the hypothesis that trade-offs are one of the drivers of specialization, which ultimately leads to evolutionary diversification. Many questions of the day were about finding those key limitations, the trade-off that cannot be avoided and that shape an organism’s niche (Metcalf 2016). Nonetheless, the questions we asked were often very specific and focused on the energetic drain placed on organisms to produce a particular trait. In my case, it was the costs of producing defensive substances in plants. Questions about costs of defense were being asked using phenotypic plasticity (the newly popular “induced defense”), genetic correlations among genotypes within a species, and among species’ strategies.

One day on the way to lunch, a mentor and collaborator, Sharon Strauss, asked me why I thought “we” were interested in costs of defense. I stumbled inarticulately through some garble about how costs were the raw material for evolution. Sharon clarified and said that she thought we were interested in costs of defense because they helped explain the maintenance of variation (or diversity in genotypes). Costs of defense reflected a trade-off, whereby benefits of producing defense in one ecological context (an environment with abundant herbivores) were coupled with a disadvantage in another context (an environment lacking herbivores). With this trade-off and with ecological variation in herbivore pressure over space and time, genetic variation in defense would be maintained within a species. This was certainly the paradigm, although often not explicitly stated, and when evidence failed to support the cost–benefit model, scientists struggled and debated (Fritz and Simms 1992).

That trade-offs were found less often than expected led to all sorts of frustrations and creative explanations. On the one hand, an explanation for the lack of some trade-offs was that experimental conditions might be too resource-rich to reveal the costs; such conditions were often the case in controlled-environment studies (Korcheva 2002). On the other hand, maybe thinking about trade-offs as fitness costs associated with a single trait was shortsighted; although fitness is the ultimate currency, perhaps trade-offs involved two (or more) traits and therefore we may not expect to see a correlation between expression of one trait and reduced fitness (again, especially in controlled conditions; Agrawal et al. 2010). Others emphasized that estimates of phenotypic costs (i.e., those obtained by comparing individuals) were not relevant to evolutionary inference. For example, Reznick (1985) made the influential argument that trade-offs estimated by phenotypic correlations or manipulations of individuals would not necessarily be reflected in trade-offs impacting microevolution; genetic correlations would be the strongest way to infer evolutionary costs that might be reflected in responses to natural selection. Finally, ecological costs, those that are not dependent on energetic drain or two traits, but on single traits that might be favored under some conditions (or by some interactions) but not by others, gained prominence. The notion that particular plant compounds may be both beneficial, in terms of reducing herbivory, and detrimental, in terms of reducing successful pollination, became a paradigm of such ecological costs (Strauss et al. 2002), and paved the way for a community-ecology centered approach to studying trade-offs.
Mathematical and methodological advances introduced several other caveats about trade-offs. First, some models showed that trade-offs were perhaps being overvalued by empiricists, and some patterns being studied did not require trade-offs as an underlying mechanism (Fry 1996, Hubbell 2001). Indeed, conditional neutrality has recently emerged as an important driver of adaptation and specialization (Sexton et al. 2017). Second, the car–house trade-off paradox was revealed and showed how and why trade-offs may be masked in empirical studies (Box 2, Fig. 3). Third, transgenic approaches were initiated and were highly effective at demonstrating trade-offs associated with particular traits (Zavala et al. 2004)—however, questions remained about the evolutionary ecological relevance of such demonstrations. For example, despite showing trade-offs associated with certain phenotypes, it was unclear how natural selection, especially in a community ecological context, would act on natural variation of those same traits. And finally, phylogenetic approaches were introduced, allowing rigorous explorations of the evolution of trait correlations encompassing trade-offs and syndromes at the species (and higher) level (Harvey and Pagel 1991, Silvertown and Dodd 1996, Ackerly and Reich 1999). Although thought of as trade-offs, such patterns across populations and species represent the outcome of evolutionary processes, not differential impacts for individuals. This scale dependence in interpretation is further developed below.

**Box 2. The car–house trade-off paradox**

Trade-offs may not be found because the pools of resources for any given function are not necessarily fixed. Either more absolute resource may be garnered, or the amount available for a function may increase at the expense of some other (hidden or currently unnecessary) function. This issue is especially important when moving across biological scales (from within individuals to between individuals, to among genotypes, populations, or species; Fig. 3). At the lowest scale, trade-offs may be obscured by different resource environments in which an organism is growing (van Noordwijk and de Jong 1986). An economic example about the trade-off between buying houses and cars captures the essence of the environmental resource base obscuring a trade-off. Within any household (individual), money spent on cars cannot be spent on houses; consequently, there is a trade-off. Nonetheless, when we look across households, money spent on houses and cars is typically positively correlated. This is because the resource input (acquisition) varies tremendously, and more so than how much households allocate to either one. For plants and animals, the resource environment where an individual lives can obscure trade-offs when comparing across individuals. Although two traits may trade off at the level of individual expression (because of plasticity or genotype), a survey of a natural population may reveal a positive association among individuals dictated by a gradient of available resources. Trade-offs can similarly be obscured across scales by the evolution of traits directly or indirectly involved in resource capture. Variation in acquisition of a limiting resource can be greater among genotypes than variation in allocation of that resource, resulting in a positive, rather than negative, correlation between traits that actually compete for a limiting resource (Houle 1991). Scaling up, if species variation in acquisition is greater than allocation within species, trade-offs may be obscured across species (Agrawal et al. 2010). The issue is perhaps most acute when considering species strategies, where fundamental changes in how organisms acquire resources and interact with their environment are likely to be more divergent than within species.

**TRADE-OFFS AND SYNDROMES ACROSS SCALES**

**Definitions and an initial example**

In this section, I define different types of trade-offs, their potential mechanisms, and how they may be studied and interpreted across levels of biological organization. Following definitions and an initial example, individual sections are devoted to plasticity, genetic correlations, population-level local adaptation, and species. Each level is developed in terms of outlining the

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**FIG. 3.** Within-group trade-offs may be masked or even reversed when studying higher-scale groupings. A trade-off is shown within each group (same color circles, representing organisms within or between genotypes of a species). Alternate colors represent groups at a higher scale (e.g., groups along a resource gradient, genotypes within species, or different species). [Color figure can be viewed at wileyonlinelibrary.com]
mechanisms and drivers of trait associations and why they may or may not be applicable across scales.

One-trait trade-offs occur where a single trait has benefits and costs to organismal performance (Fig. 1; Agrawal et al. 2010). For example, larger animals typically have high performance, but may also be subject to greater predation pressure or other environmental risks. One-trait trade-offs may be due to environmental selection (i.e., conflicting ecological drivers, or “ecological costs” of one trait) as in the previous example, or due to resource diversion (i.e., energetic cost). In the case of resource diversion, a one-trait trade-off comes at the cost of a fitness component. Many cases of stabilizing selection and polymorphisms are driven by one-trait trade-offs.

In addition, trade-offs often involve two or more traits and are detected as a negative correlation between them. Accordingly, a two-trait trade-off exists when an increase in trait “A” is associated with a decrease in another trait “B,” neither of which is a direct component of fitness (Agrawal et al. 2010). Broadly defined, two-trait trade-offs can be measured among phenotypes, genotypes, populations, or species. Taking the shorthand of simply measuring a negative correlation has its limitations and has been criticized (Zera and Harshman 2001), but as long as the traits are functionally important, and thus can impact fitness, it is a reasonable starting point. This is especially the case if one’s goals are to understand the function of traits, their expression, and their relationships. Two-trait trade-offs may be driven by a number of limiting resources (e.g., energy, space, time) or by direct interference of the traits (elaborated below).

A key limitation in the study of trade-offs is that the traits of interest may be unknown. For example, a meta-analysis of local adaptation found evidence for fitness trade-offs in reciprocal transplant studies, but the traits under selection were typically unidentified (Hereford 2009). Even in classic experimental studies of host adaptation using phytophagous insects, trade-offs may be inferred and genetically identified (Gould 1979, Gompert and Messina 2016), but without understanding the traits associated with adaptation, our understanding of the causes and consequences of trade-offs remains unclear.

When traits underlying a fitness trade-off are known or are themselves the initial focus of investigation, understanding the mechanisms and consequences of trade-offs is possible. Take the production of a specific defensive trait, hydrogen cyanide (HCN), as an exemplar of different mechanisms of trade-offs at different biological levels. HCN is a remarkable compound produced by some animals and many plants, having independently evolved several times across the tree of life (Zagrobelny et al. 2004). HCN functions by inhibiting cellular respiration, making it a very general poison. In plants, HCN production is often quantitatively variable among genotypes (and qualitatively polymorphic in some species). So what limits HCN production? First, HCN is costly in terms of resource diversion away from growth and reproduction (a one-trait trade-off; Kakes 1989, Kooyers et al. 2018). Second, HCN is involved in another one-trait trade-off, whereby the production of HCN makes plants sensitive to self-damage under freezing temperatures (Kooyers et al. 2018). Finally, a two-trait trade-off occurs via direct chemical interference, whereby HCN production directly disrupts the enzymatic activity of polyphenol oxidase, the latter being a mechanism of resistance to fungal pathogens (Ballhorn 2011).

At any one level of organization, some of these mechanistic drivers may be more or less important for shaping the observed trade-offs. It is likely that the nitrogen costs of HCN would be present at all levels, but environmental selection by freezing and pathogens would depend on the geography of populations or species. Plasticity in response to temperatures and pathogen attack could well modulate the trait expression and associated trade-offs. Although these trade-offs have primarily been studied within species, initial forays have been made into the comparative biology of cyanogenic species. An initially proposed trade-off between defense by HCN vs. aggressive ants has not held up among Acacia spp., but variation in HCN production among species is likely to reveal a complex pattern of trait covariation and specialization across the genus (Webber and McKey 2009).

In the sections below, trade-offs, trait correlations, and their mechanisms are considered at each level of biological organization. My goal is to highlight the scale-dependent drivers, profitable areas of future research, and why trait associations may or may not scale across levels.

Trade-offs in phenotypic plasticity

Plasticity allows for rapidly altered phenotypes within an organism, and here I consider trade-offs associated with the adaptive phenotypic responses to environmental signals. As resources are necessarily constrained to what an individual has acquired up to that point in time, energetic drains are often associated with responses to an environmental stimulus (Baldwin and Hamilton 2000). In addition, direct interference of traits and conflicting ecological drivers are also possible trade-offs in response to plastic trait expression. Importantly, the fact that organisms are responding phenotypically to environmental cues suggests that such trade-offs may exist, but are tempered by the plastic expression of traits.

As a means to frame this discussion empirically, I am primarily thinking about organismal responses to risk of attack (herbivory in plants, or predation in animals) and competition, two important biotic interactions with strong evidence for adaptive plastic responses across many systems (Cipollini 2004). Quite remarkably, both plant and animal responses to one of these interactions (enemy attack or competition) tend to make the
organisms more susceptible to the other (Fig. 4; McPeek 1996, Relyea 2002, Relyea and Auld 2005). In this case, a set of correlated trait responses typically occurs when an organism is faced with a new challenge. For example, shaded herbaceous plants typically elongate stems, have larger leaves, fewer trichomes, and higher nitrogen content, increasing carbon gain but making them more susceptible to herbivores than their unshaded neighbors. Palatability to herbivores likely increases due to a reduced physical barrier to feeding and enhanced nutritive quality, respectively (both are one-trait trade-offs). The first two places to look for trade-offs in plastic expression are reproductive effort or a currently unnecessary investment in traits that are otherwise functional. However, evidence for such trade-offs has been harder to come by than expected (Koricheva 2002), and one possible explanation is that we have been looking in the wrong places. I suggest that organisms may have a hierarchy of priorities in which to invest upon receiving environmental cues. Once a particular cue is received, energy may come from other less important functions (i.e., less tied to fitness under the current ecological conditions) that may not be needed in the near future. I elaborate on this below.

Phenotypic plasticity is typically only beneficial because of the information reliability of the initial cues received (Schmidt et al. 2010). Models and evidence suggest that where an environmental cue is reliable about future conditions, a coordinated set of plastic responses makes adaptive sense (Scheiner 1993, Karban et al. 1999). As an example, changes in day length, temperature, and resource availability often jointly signal the onset of winter, which cues plastic responses for dormancy or migration (Agrawal 2017a). For biotic interactions, perhaps the cues are less reliable because of inherent variability in organisms (compared to abiotic conditions), but the smell of predators, the first bite of herbivores, and the altered environmental conditions associated with competition often cue plasticity in anticipation of the changing conditions (Agrawal 2001). What has been missing from work on phenotypic plasticity is whether there is reliable information about what interactions will be less likely or less important when a particular environmental cue is experienced.

Consider a plant that receives initial herbivore damage by species X and is likely to continue to receive damage by X, and thus responds with induced defenses to X. However, is this plant unlikely to be attacked by a different species Y, or unlikely to face new competitive challenges from neighbors if attacked by X? If so, and assuming more than one trait is involved in these interactions, reduced phenotypic expression of traits relevant to Y or neighbors is predicted (and thus, a fitness trade-off may be avoided). This is where knowledge of community ecology can inform expectations for trait expression in plasticity. If the plant experiencing X is still likely to face Y and neighbors, negative trait association may be caused by the fitness decrement due to being eaten by X being greater than that of Y or neighbors. Or, might the response to X be somehow physiologically constraining? In my own work on shade avoidance, plants often become less resistant to herbivores when shaded, but plants in shade tend to receive less herbivory than plants in the sun (Agrawal et al. 2012b). Therefore, although shade avoidance comes with altered trait expression, the detriment associated with these trade-offs may not be experienced by the plant. Indeed, inducing the shade morphology at the cost of reduced resistance may be considered an adaptive negative association, because the likelihood of herbivore attack also decreases in the shade. Addressing such issues is important in evaluating trade-offs and should be applied generally to the different plastic responses in diverse taxa.

A key prediction then is that despite negative trait correlations, many trade-offs may only manifest under certain ecological conditions, and organisms should take advantage of these conditions based on the reliable information of the initial cues. Despite presenting a frustrating level of complexity, adaptive plasticity is presumably shaped by correlations in environment and the relative costs and benefits of particular investments. Accordingly, studying environmental associations (i.e., is
shade associated with reduced herbivory?) and fitness consequences of each is perhaps the most fruitful way to be predictive about trait associations and trade-offs associated with plasticity.

*Genetically based trade-offs*

Most populations harbor variation for ecologically important traits, and the genetic basis of these is often studied by growing individuals of known and varied parentage in a common environment. More recently, natural populations have been surveyed for their phenotypes as well as genomic data, and consequently, heritabilities and genetic correlations can be estimated in nature. Each approach has advantages and disadvantages, the most obvious being differences in the level of control (which is higher in a common environment study; Visscher et al. 2008). In addition, artificial selection experiments have powerfully illustrated the potential for genetic correlations to impact responses to selection (Gompert and Messina 2016). Whatever the method employed, genetic correlations between traits are real associations that represent alternative phenotypes of organisms interacting with the environment.

Negative genetic correlations that represent trade-offs have long been implicated in the evolution of niche specialization (Futuyma and Moreno 1988). For herbivorous insects in particular, experimental evolution proved rewarding (but also frustrating) because phenotypic and genetic analyses were suggestive, but not conclusive, for the role of genetic trade-offs in specialization (Gould 1979, Via and Hawthorne 2002, Gompert and Messina 2016). Perhaps the biggest limitation of this body of work is that the key traits of interest are typically unknown. Although trade-offs in fitness are critical to the pattern, the extent to which genetic correlations are constraining depends on the genetic basis of specific traits. Alternatively, if functional consequences of traits or their resource precursors are known, then a reasonable case can be made that negatively genetically correlated traits represent a trade-off, even if their fitness effects are unknown (Berenbaum et al. 1986, Dorn and Mitchell-Olds 1991, Agrawal et al. 2010).

A large literature over the past 30 yr was devoted to understanding whether genetic correlations might represent strong constraints, that is, limitations on how a population could respond to natural selection (Conner 2012). And although it is certainly the case that when selection is imposed along the line of a genetic correlation, responses are strong and rapid, the bulk of evidence also suggests that genetic correlations are not truly constraining (Conner 2012; Fig. 5). When selection is applied perpendicular to a genetic correlation, some response is typically seen. For the few cases where this has been imposed for a known trade-off, the response to perpendicular selection was weak and took many generations, but was still evident (Dorn and Mitchell-Olds 1991, Stewart and Rice 2018). One means by which selection may break a trade-off is if resource acquisition changes among genotypes, thereby obscuring resource diversion (Box 2). The bottom line is that bivariate genetic correlations do not appear to be long-term constraints. Nonetheless, it is clear that the genetic architecture of organisms is decidedly not bivariate (i.e., involving two traits in isolation). Recent theory and evidence suggest a complex role for multivariate trait associations on evolution. On the one hand, multivariate genetic correlations may be more strongly constraining than previously thought (Blows and Hoffmann 2005). On the other hand, the more traits that contribute to axes of organismal performance, the more likely a bivariate trade-off may be avoided (Holzman et al. 2011).

How then should we interpret negative genetic correlations between ecologically important traits? One approach is to imagine that organisms and their underlying genetic architecture have been subject to natural selection for innumerable generations. As such, genetic variation within populations is that variation which is not fixed, presumably because of spatially and temporally variable selection or nonadaptive processes (gene flow, drift, etc.). Thus, negative genetic correlations, especially those between continuous traits, likely represent the best an organism can do along an axis of frequent change (i.e., alternate phenotypes being favored along that axis across space and time). Nonetheless, I would not go so far as to say that most negative correlations are “adaptive” or represent

![Figure 5](https://example.com/fig5.png)
alternative strategies. Strategic trade-offs observed among species (i.e., r vs. K strategies, competition vs. colonization, or hunting modes among predators) are typically not expected within species because such coarse-level traits tend to be fixed within species (Futuyma 2010).

Negative genetic correlations may represent limitations being shaped by correlational selection, a counterpart to positive genetic correlations representing benefits of concerted trait expression. Indeed, new empirical evidence and population genetic models suggest that genetic elements termed relationship loci (or rQTLs) act to modify trait correlations (Pavlicev et al. 2010). A key prediction emerging from this literature is that genetic correlations among integrated traits (e.g., front and hind limbs in quadrupeds) will be stronger than for functionally unintegrated traits (e.g., front and hind limbs in bats). Although we often think of integration in terms of syndromes or coexpressed traits, functional integration must be as common in the optimization of organismal limitations.

An aspect of within-species trade-offs worthy of special mention is discrete polymorphism. When alternate morphs are maintained in a population, they may indeed represent alternative strategies indicative of trade-offs that are maintained by natural selection. In this case, although the environment-dependent fitness consequences of alternate phenotypes are not always well known, they likely represent one-trait trade-offs. For example, the trade-off between investment in wing musculature and fecundity in grasshoppers and crickets is evident both among discrete morphs (short vs. long winged), but also continuously among genotypes of the long-winged morph (Fig. 2; e.g., Roff and Gélinas 2003). Polymorphisms representing trade-offs are widespread in plants and animals and include those associated with pungency in chili peppers (Haak et al. 2011) and antipredator crypsis, including coat color in mice (Hoekstra et al. 2004), among many others. Such polymorphism allows individuals to specialize, and natural selection shapes the frequency of morphs among populations. The extent to which the mechanisms and consequences of trade-offs are the same for polymorphic vs. continuous traits is an important and open question that bears on the problem of genetic variation and covariation.

Population-level local adaptation

Local adaptation and population specialization can also reveal the importance of trade-offs. At a coarse level, reciprocal transplant experiments that report local adaptation suggest trade-offs, but the mechanisms and traits involved are often unclear (Hereford 2009). For microbial populations, the fitness trade-offs of particular mutations have been studied (Schick et al. 2015) and in field studies, especially of plants, the genetic basis of local adaptation and trade-offs is being increasingly revealed (Prasad et al. 2012, Troth et al. 2018).

In some cases, local adaptation occurs along the lines of genetic correlations within populations. Consider the genetically based trade-off between life-history traits such as early flowering and size at reproduction (discussed above; Fig. 5). This often occurs within populations, and adaptive population divergence can also fall along this same axis (Troth et al. 2018). Thus in some cases, especially where there is a “universal fitness landscape” (Peiman and Robinson 2017), within-population genetic correlations may be reflected in among-population trait associations. For some life-history trade-offs, such as that between early flowering and size at reproduction, patterns may even extend across species, at least among some plant functional groups (Bolmgren and Cowan 2008). As new populations are formed from others and local adaptation occurs, perhaps the common genetic architecture prevents large-scale deviations from the prevalent trade-offs. Nonetheless, it is important to note that the pattern of trait correlations using population means is an outcome of evolutionary processes, but is not itself a constraint or reflective of future evolutionary trajectories (Fig. 6; Futuyma and Moreno 1988, Armbruster and Schwaegerle 1996).

In any particular niche dimension, a species’ qualitative strategy is largely fixed, and we do not expect populations to vary dramatically in the types or classes of adaptations they might have because of the lack of reproductive isolation. Consider the photosynthetic pathways of C3 vs. C4, which are relatively fixed within genera and taxonomic families, and it is the rare case that shows variation in such traits among closely related species (Gowik et al. 2011). The concentration and composition of defensive substances produced by plants or animals certainly vary among populations, but the class of defensive compounds (i.e., cyanides vs. alkaloids) typically does not vary. Among animals, strategies such as “sit-and-wait” vs. “active hunting” are typically fixed within species, with genetic variation present among other axes within the strategy. The key reason for the dearth of local adaptation in strategies among populations is that in order for new strategies to evolve, populations must first have sufficient...
genetic variation and also cross selective “valleys” or low-fitness trait combinations, which usually requires very low gene flow (Futuyma 2010).

Species syndromes and strategies

Trade-offs are most commonly thought of as a within-species, or microevolutionary, phenomena because they can constrain responses to natural selection (Agrawal et al. 2010). Nonetheless, the concept of trade-offs is frequently invoked in comparative biology. For example, r vs. K life-history strategies among closely related species (Reznick et al. 2002), defense syndromes among plant species (Kursar and Coley 2003, Agrawal 2007), and other strategic categorizations of species (Grime 1977, Westoby et al. 2002, Reich 2014) all represent negative associations among functional traits. Among species, the pattern of negative functional trait correlations may be generated during environmental specialization of species, and perhaps is less often determined by limitations of a particular resource or persistent genetic correlations within species (Fig. 6, Schluter 1996).

A pattern reflecting trade-offs (i.e., negative trait correlation) may be more evident across species than within species because there has been substantial evolution creating large differences in trait means that may reveal the trade-off. For example, the trade-off between offspring size and number is often more evident across species than within species. Perhaps more importantly, ecology has driven species to specialize to particular niche axes. If a species has specialized to habitats with high competition, large offspring are often favored, whereas smaller offspring are favored in environments requiring dispersal and colonization.

The above logic was essential to classical interspecific theories of plant specialization such as Grime’s triangle (Grime 1977). Focusing on the trade-offs between specific traits and their contribution to plant strategies, Pierce et al. (2017) proposed a method to classify species into Grime’s scheme, and this has proved useful in predicting the establishment of nonnative species in a global analysis (Guo et al. 2018). As expected, stress-tolerant species were the least likely to establish in new environments. Such modern trait-based and phylogenetic methods have been used to define strategies in other groups including animal species. In a recent study of threatened corals, Darling et al. (2012) used trait data to define species strategies (competitive, weedy, stress-tolerant, and generalist taxa), which was found to be predictive of their responses to environmental change (Fig. 7). Accordingly, negative trait associations inherently associated with niche specialization may be manifested as conditions change and there is community turnover.

When, where, and with what sorts of traits do we expect species-level trade-offs and trait associations? On the one hand, they are expected for traits that are strongly constrained, have little genetic variation, and are closely tied to fitness, and those that are morphological (e.g., associated with body size). More importantly, trait associations among species are associated with niche specialization, where trade-offs may not necessarily be predicted by energetic expenditure, but rather by the many environmental aspects that are not experienced by a specialist (e.g., salinity-adapted species may not cope with particular competitors or predators experienced by freshwater species). And for trade-offs experienced by specialist species, I predict that many of these should not be observed at lower levels of biological organization. Stress-tolerant vs. competitive strategies may be common among species, but this is not expected to be a within-species trade-off axis. The trade-offs within a species will be determined by physiological or genetic connections between traits, and

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**Fig. 7.** Grime’s (1977) triangle of plant strategies applied to reef corals, redrawn from Darling et al. (2012). Left: Conceptualization of how species can be categorized based on the dominant environmental conditions. Right: Ordination of 143 coral species aligning with the three strategies, also with “generalist” taxa in grey. Ruderal is typically a botanical term referring to weedy species. Open circles are Atlantic taxa and filled circles are from the Indo-Pacific. [Color figure can be viewed at wileyonlinelibrary.com]
the many competing ecological demands likely experienced over space and time, but less so by specialization of genotypes on a particular niche axis.

In summary, it is profitable to ask questions about species-level correlations, but also important to be cautious in their interpretation. When taking such an approach, and if correlated evolution is found (i.e., a significant relationship between traits after phylogenetic correction), conclusions can be drawn about the outcome of trait evolution over speciation time. However, ascribing function to those traits or understanding the process that generated the pattern is difficult. Natural history knowledge (ranging from physiology to the habitats that species live in) may help inform hypotheses for the drivers of patterns of correlated evolution. And, comparing comparative and experimental approaches holds promise for deciphering function and evolutionary processes (Weber and Agrawal 2012). Because even closely related species differentially specialize and can have dramatic differences in trait values, examining phylogenetic patterns of trait relationships followed by matching patterns to ecological differences is a strong first step. Subsequently testing the hypothesized drivers experimentally makes for rigorous research.

**A synthesis of trait correlations across scales**

Some trait correlations may be equally strong within and between species. In the simplest case, genetic correlations within a species may bias the phenotypic divergence among descendent species, such that new species occupy phenotypic space along the original axis (Schluter 1996). When is this expected? Trait associations related to body size, such as the allometric relationships between skeletal parameters, organ size and shape, and morphologies may indeed follow the same trait associations within and between species, although the strength of such trait associations typically decays over macroevolutionary time (Schluter 1996, Baker and Wilkinson 2003, Mcclintohlin et al. 2018). Trade-offs between horn size in beetles and adjacent organs (eyes, wings, or antennae) appear to be persistent among phenotypes, genotypes, and species (Nijhout and Emlen 1998, Emlen 2001). In this case, however, although the trait trade-offs are persistent, species have ecologically diverged in ways that appear to minimize the impact (e.g., nocturnal species are less likely to have horns near eyes, reducing the cost of poor vision; Emlen 2001).

For plants, some of the best work on trade-offs across scales comes from studying the relationship between a component of water-use efficiency (carbon isotope discrimination) and relative growth rate in desert annuals (Kimball et al. 2013, Angert et al. 2014). A trade-off between these traits is expected based on water-use efficient plants closing stomata and thus reducing photosynthesis and was reported across four co-occurring species. Nonetheless, at lower levels of organization, when population means, genetic correlations, and phenotypic correlations in natural populations of each species were considered, relatively little consistency in the trade-off pattern was observed (Kimball et al. 2013, Angert et al. 2014). Although natural selection favored highly water-use-efficient and fast-growing phenotypes, a response to selection was apparently not possible. In this case, three of the four species lacked substantial genetic variation for the traits, and the local environment likely masked the trade-off when individuals were in favorable microhabitats.

For plants, stomates are a nexus for the critical trade-off between CO₂ uptake and water loss, with various morphological and physiological traits altering this balance. Within the genus *Asclepias*, species have diverged in the ratio of carbon gain to water loss, suggesting that this trade-off can evolve (Goud et al. 2019). Recent studies of the Solanaceae have shown that the trade-off between leaf thickness (which is beneficial in arid environments) and CO₂ diffusion within leaves (which enhances photosynthesis) is variable among species (Muir et al. 2014a). Remarkably, here too the trade-off itself appears to evolve by genetically determined changes in the distribution of stomates across the top and bottom of leaves (Muir et al. 2014b). More generally for plant physiological traits, it has been suggested that some “leaf economics” traits (i.e., those involved in resource acquisition and allocation) may be fundamentally constrained enough that they experience persistent trade-offs across levels of biological organization. However, the jury is still out, and this will be evaluated in the last section of the paper labeled “Plant Ecological Strategies and Defense.”

If two traits are not correlated within a population, correlational selection may result in a future genetic correlation within the population or a higher-level association between the traits (where populations or species are the unit of replication). As outlined by Armbruster and Schwaegerle (1996) such a result may arise from several different mechanisms. First is the functional dependence of the traits (e.g., fitness is enhanced when Y responds even though selection only acts on X; Fig. 6). Two other scenarios may result in the evolution of correlated sets of traits at the population or species level (Armbruster and Schwaegerle 1996). Selection by one environmental agent (say freezing temperatures or strong herbivory) may result in the evolution of multiple traits independently. Perhaps physical defenses (e.g., trichomes) and chemical defenses (e.g., cyanides) are each favored by herbivory, which may result in populations or species with correlated levels of these two traits. Here, neither a genetic correlation between the two traits within species nor correlational selection (i.e., dependence of the fitness impact of trait X on the expression of trait Y) is required. And finally, certain environments where organisms live may impose selection for distinct traits simultaneously (e.g., perhaps competition and herbivory covary among habitats or along a gradient of succession, latitude, or altitude, thereby imposing
selection on competitive ability and defense, even if genetically uncorrelated; Agrawal et al. 2012a).

When traits are correlated within a population, selection may break the genetic correlations following divergence and reproductive isolation. For example, as new species evolve different strategies, or as they alter resource acquisition for other reasons (e.g., changes in abiotic environment), between-species trait associations are not expected to follow within-species trade-offs. As a case in point, there are costs associated with producing cardenolide toxins in common milkweed (Asclepias syriaca), with genotypes producing higher concentrations having reduced plant growth rate (Züst et al. 2015). Nonetheless, species of Asclepias that produce up to seven times the concentrations of cardenolides as A. syriaca do not have proportionally lower growth rates (Agrawal and Fishbein 2008). Should we necessarily expect the most defended species to grow the slowest? Genotypes within several species of Asclepias also show a quantitative genetic trade-off between constitutive cardenolide production (present before attack) and their inducibility following herbivory, but this pattern is not recapitulated across species (Agrawal and Hastings 2019). I conclude that within a species, the metabolic strategy is largely fixed, and genotypes show trade-offs when deviating from the mean of the species. However, as new species have evolved, the metabolic machinery that acquires and allocates resources to these toxins may have itself evolved, and consequently, the trade-offs are not necessarily expected or evident. Integrative studies to date have not studied the metabolic changes across species that allow circumvention of trade-offs, but this is a promising direction.

In sum, trait correlations may sometimes scale across levels of organization, and when they do, this may represent strong constraint or widely beneficial trait combinations across populations and species. Nonetheless, evolution in response to trade-offs or other trait associations could result in modifications that ameliorate their effects (at higher levels) or that erode genetic diversity such that within-species trade-offs are difficult to study using quantitative genetics (although they could still be studied physiologically). Correlations may emerge and be meaningful at higher levels of organization where they do not occur at lower levels of organization. Adaptation at these higher levels likely results from niche specialization, which, as discussed above, results in a pattern of strategic trait trade-offs that are not necessarily expected at lower levels.

**Plant Ecological Strategies and Defense**

**Evolutionary ecology of the leaf economics spectrum**

In this section I address differences in trait covariation within and between species and their interpretation via scale-dependent evolutionary processes using the burgeoning literature on the leaf economics spectrum (LES) and my own work on milkweeds in the genus Asclepias. The leaf economics spectrum (Wright et al. 2004) has been an important advance in the study of functional ecology and was built on decades of physiological work; comparative ecology; and theory on leaf value, photosynthesis, and defense (Coley 1988, Westoby et al. 2002, Reich et al. 2003). The LES was codified as the trade-off between resource-conservative and -acquisitive strategies for leaves, most typically observed as a pattern across distantly related species (Fig. 8). Resource-conservative species tend to have lower photosynthetic and dark respiration rates, lower nitrogen and phosphorous contents, longer leaf life-spans, and higher leaf mass per area (LMA), whereas acquisitive species tend to have the opposite suite of trait values. A success of this approach has been its remarkable generality, spanning plants from tiny duckweeds to giant sequoia trees. As the paradigm is expanding, the evolution of the LES and possible correlated traits is being addressed within and across scales (Anderegg et al. 2018). This search for generality and expansion of predictions is certainly not unique to plant ecology; for example, this has been recently seen in the animal literature on the pace-of-life hypothesis (Dammahahn et al. 2018).

Importantly, the pattern of the LES was described across diverse taxa and was variously interpreted to be generated by biophysical or genetic constraints, strategic

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**Fig. 8.** The six leaf economics spectrum traits as originally described (top three arrows; Wright et al. 2004) and two additional traits that appear frequently associated (bottom arrow). Arrows indicate low to high trait values pointing to the two ends of the spectrum. Consideration of leaf trichomes, which impact both leaf physiology and herbivory, should be explicitly considered in the future. [Color figure can be viewed at wileyonlinelibrary.com]
adaptation to environmental gradients, and covariation with life-history attributes, with underlying physiology as the driver of the relationships. As with all such large-scale patterns, the question emerges of how it evolved, and whether within-species patterns are consistent with across-species patterns. A review by Donovan et al. (2011) marshaled the evidence that within-species trait covariation and measures of natural selection on these traits were often discordant with the species-level pattern. The authors concluded that constraints are thus unlikely the driver of the LES, but rather selection for and against particular trait combinations is more likely responsible for the pattern across species.

Since the highly influential paper of Donovan et al. (2011), many cross-scale studies of the LES have emerged. These studies have largely taken a phenotypic approach assessing within vs. between species trait associations, typically via field sampling within and between plant communities (Funk and Cornell 2013, Niinemets 2015, Fajardo and Siefert 2018). In particular, local-scale community surveys often lack LES trait correlations, even across species, and this has sometimes been attributed to low variation in leaf life-span within communities (Messier et al. 2017). Anderegg et al. (2018) conclude from a large comparative analysis that variation in the LES is strongest at the level of plant genera and families and that there are frequent reversals of LES trait associations when comparing within to across species. A critical conclusion from Anderegg et al. (2018) was that phenotypic plasticity may be driving reversals in trait correlations across scales. Of course, the role of plasticity in generating (or reversing) trait correlations is inherently interesting, but different from processes affecting within-species genetic variation or patterns across species.

Some early work across broad taxonomic groups used phylogenetic information and corrections to address LES evolution (Flores et al. 2014), although perhaps trait correlations among species are most interesting and interpretable at a lower taxonomic scale (e.g., within a genus). Why? Trait relationships among closely related species are the best indication of the macroevolutionary outcome of selection within species, because relatively recent evolution from a common ancestor resulted in the observed divergences. Evolutionary ecologists are interested in the variation among closely related species, as there is a specific evolutionary process generating diversity within clades. In contrast, the interpretation of larger-scale “universal” patterns is less clear, as the signature of evolutionary processes decays over time. Accordingly, I now consider the evidence for LES genetic correlations within species and phylogenetic correlations among closely related species.

Relatively few studies have conducted common environment studies with different plant genotypes to address the LES, an early point made by Donovan et al. (2011). Although genotypic correlations concordant with the LES were reported for Arabidopsis thaliana (Blonder et al. 2015), in several other species genetic correlations were nonsignificant, were dependent on the environment, or were mismatched with expected outcomes, such as plant growth rate (Poorter et al. 2005, Donovan et al. 2011, Grady et al. 2013). My reading of this literature suggests that although there is superficial concordance of within-species genetic correlations for LES traits, it breaks down in different ways (i.e., different missing trait relationships) for different species. And yet, if the LES across species pattern emerged via evolution driven by constraints or correlational selection, we would expect to see greater consistency among these genetic correlations within species. To be clear, this is not an indictment of the LES, but more so an exploration of what might determine the observed pattern across distantly related species. Is this a case of selection favoring expression of traits only at higher levels (Fig. 6) or fundamental constraints being revealed by broad-scale patterns? The answer appears to be a combination of the two.

Consider the short-range macroevolutionary outcome of selection and divergence within species and how it may be evident on phylogenies of closely related species. Mason and Donovan (2015) conducted such an analysis using 28 species of sunflowers (Helianthus spp.) and report LES correlations similar to the global patterns except for one of the key relationships, that between LMA and leaf life-span. Similar variation was reported for LES trait associations among Solanum species (Muir et al. 2017). Where does this leave us? If multiple LES trait correlations across closely related species represent the outcome of selection, it appears that some rules can be broken, at least at some scales. Of course more data are needed; however, the within-group evolutionary patterns occur within the confines of traits conserved within that group, and this is also where the products of selection are most evident. For example, most Asclepias spp. are herbaceous outcrossing perennials that occur in open habitats. Although diversification occurred into different niches representing different soil types, competition, temperature, and aridity, there is decidedly less variation in size, life-history, and light habitat than seen in broader surveys of herbaceous perennials. Accordingly, it appears that evolution within clades is likely biased away from complete correspondence to the LES because of conserved axes of variation within those clades. Therefore, the leaf economics spectrum is a pattern at the largest biological scale, but its interpretation, especially in an evolutionary context, remains tenuous. As with other patterns of biological scaling, where the most variation is explained at the largest taxonomic scale, both the processes generating the pattern and the ecological interpretation remain surprisingly unclear (Tilman et al. 2004).

Leaf economics and plant defense against herbivores

Despite the caveats discussed above, the LES has been a major advance in ecology that will continue to be central to understanding plant strategies. To push the envelope of understanding these strategies and associated trade-offs across scales, however, it is useful to consider
biotic interactions in addition to resource acquisition and adaptation to abiotic conditions.

As discussed earlier in this paper under the section “Trade-Offs and Syndromes Across Scales,” classic patterns in the literature indicate that phenotypically plastic plant responses to shade induce higher nitrogen content per dry mass, fewer trichomes per area, and lower leaf mass per area compared to plants in full sun. Hence, shaded plants tend to induce resource-acquisitive or “fast” leaves in LES parlance, which makes sense, given that these plants are in reduced light. However, also in response to shade, leaves tend to be of greater quality for herbivores, which is driven by the higher nitrogen, thinner leaves, and fewer trichomes, in addition to reduced defensive compounds. Higher nitrogen represents a one-trait trade-off because the same trait is favored in terms of photosynthesis but is detrimental because it is beneficial to herbivores. Changes in defense compounds represent a two-trait trade-off because responses that enhance resource acquisition result in reduced defensive secondary metabolism. The full set of mechanisms of this plastic trade-off between resource acquisition and defense and the extent to which it is adaptive is unclear, but it is nonetheless quite general.

Across species, a similar set of trait correlations between resource acquisition and defense has emerged, although the way in which this was discovered, the traits originally studied, and the logic behind the observed pattern is entirely different compared to the LES. In particular, Coley’s (1983) early work across diverse tropical trees showed that gap-colonizing (high light) species had a resource-acquisitive strategy, lower defense, and lower leaf life-span, whereas shade-tolerant trees had a more conservative strategy. Not only were gap colonizers fast growers, but they also had lower chemical defenses and were grazed at six times the rate of shade-tolerant species. This work led to the more generalized resource-availability theory of plant defense, which focused on the intersection of plant growth rate as an adaptation to the resource environment and leaf physiological strategies, and the follow-on evolutionary strategy in terms of leaf defense (Coley et al. 1985, Endara and Coley 2011). Most critically, resource-acquisitive species were not only predicted to be less defended intrinsically, but the short leaf life-span was further predicted to dictate reduced investment in defense. Shade-tolerant trees, in contrast, have resource-conservative leaves and tend to invest more in defense to protect these long-lived, high-value leaves.

In summary, the syndrome of LES traits and defense appears to be consistent via phenotypic plasticity (towards shade) and across species (specialized to light environments), but the light drivers are reversed: shade-induced leaves are more resource acquisitive and less defended, whereas shade-adapted species’ leaves are resource conservative and highly defended. A recent phylogenetic analysis of sunflowers found that species with more resource-conservative traits were more defended, although this was apparently not driven by light or other aspects of the resource environment (Mason et al. 2016). Thus, a pattern of LES and defense trait association emerged evolutionarily in this clade, although the drivers were not clear. McManus Chauvin et al. (2018) studied 83 diverse Panamanian trees from one habitat and reported less-consistent patterns of LES traits correlating with measures of defense. A much greater phylogenetic depth was included in this study, and the fact that the species coexist in the same habitat may mean that they have limited variation in some traits. Few, if any, studies have considered genetic or population-level correlations of LES and defense, and an initial attempt at filling this gap is presented below.

Leaf economics and defense in the milkweeds

To address the scale dependence of relationships between LES traits and defense empirically, I summarize

<table>
<thead>
<tr>
<th>Trait 1</th>
<th>Trait 2</th>
<th>Individuals (field; n = 48)</th>
<th>Genotypes (chamber; n = 15)</th>
<th>Populations (chamber; n = 20)</th>
<th>Species (field garden; n = 23)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td>LMA</td>
<td>−0.596***</td>
<td>−0.514*</td>
<td>−0.721***</td>
<td>0.017</td>
</tr>
<tr>
<td>Trichomes</td>
<td>LMA</td>
<td>0.763***</td>
<td>−0.101</td>
<td>0.089</td>
<td>0.684***</td>
</tr>
<tr>
<td>Trichomes</td>
<td>Nitrogen</td>
<td>−0.589***</td>
<td>−0.001</td>
<td>−0.143</td>
<td>0.122</td>
</tr>
<tr>
<td>Latex</td>
<td>LMA</td>
<td>0.191</td>
<td>0.254</td>
<td>−0.110</td>
<td>0.775***</td>
</tr>
<tr>
<td>Latex</td>
<td>Nitrogen</td>
<td>−0.104</td>
<td>−0.256</td>
<td>0.080</td>
<td>0.158</td>
</tr>
<tr>
<td>Cardenolides</td>
<td>LMA</td>
<td>0.369**</td>
<td>−0.223</td>
<td>−0.684***</td>
<td>−0.024</td>
</tr>
<tr>
<td>Cardenolides</td>
<td>Nitrogen</td>
<td>−0.261†</td>
<td>0.273</td>
<td>0.831***</td>
<td>0.153</td>
</tr>
<tr>
<td>Latex</td>
<td>Trichomes</td>
<td>0.188</td>
<td>0.561*</td>
<td>−0.016</td>
<td>0.651***</td>
</tr>
<tr>
<td>Cardenolides</td>
<td>Trichomes</td>
<td>0.542**</td>
<td>−0.284</td>
<td>−0.237</td>
<td>0.027</td>
</tr>
<tr>
<td>Cardenolides</td>
<td>Latex</td>
<td>0.037</td>
<td>0.068</td>
<td>−0.137</td>
<td>0.100</td>
</tr>
</tbody>
</table>

Note: Values for individuals, genotypic means, and population means are all for Asclepias syriaca. LMA is leaf dry mass per area. Shown are correlation coefficients with significant values bolded.

***<0.001.
**<0.01.
*<0.05.
†<0.1.
data from our long-term work on *Asclepias* across four scales (phenotypic variation including plasticity, genetic correlations, differentiated populations, and species correlations) for five leaf traits: nitrogen content (on a dry-mass basis), dry leaf mass per area (LMA), trichome density, cardenolide concentration (on a dry-mass basis), and latex exudation (fresh mass upon clipping the leaf tip). Although the first two traits are considered LES traits and the latter two exclusively defensive, leaf trichomes function both in leaf physiology and defense in *Asclepias* and more widely (Agrawal et al. 2009). Interestingly, trichomes have been rarely considered in the

![Graphs showing correlations among leaf traits of milkweeds](image-url)
LES framework, and one study of sunflowers found trichome density to be unrelated to LES traits (Mason et al. 2016).

All within-species data presented here are from the common milkweed (A. syriaca), with data assembled from Agrawal et al. (2012b) for field-sampled phenotypic correlations, and Agrawal et al. (2015) for population samples grown in a common environment. Genetic correlations were estimated from 15 full-sibling families (n = 10 plants per family) from a single population in Ithaca, New York, grown in a common growth chamber (A. A. Agrawal and A. P. Hastings, unpublished data, plants grown as in Agrawal and Hastings 2019). Initial cross-scale trait relationships for two other Asclepias spp. have also been published (Agrawal et al. 2008, Hahn et al. 2019), but are not used here. Across-species relationships presented here are from 23 species of North American Asclepias (data from Agrawal and Fishbein 2006).

I found the most trait correlations among individuals collected in the field along a gradient of shade, and the least among genetic families when grown in a common environment (Table 2, Fig. 9). In particular, and as expected, LMA was negatively correlated with leaf nitrogen content within species across all three levels of analysis. LMA was also phenotypically correlated (positively) with trichome density, latex exudation, and cardenolide concentration. Indeed, in full sun, not only are leaves more resource conservative (low N investment, high leaf mass per area, and hairy), but they are better defended by several traits. However, this pattern at the phenotypic level did not hold for A. syriaca genotypes or populations (Table 2). The relationship between LMA and cardenolides reversed at the population level (Fig. 9). In this case, populations were from across a substantial latitudinal gradient, which likely imposed selection on plant traits associated with climate and herbivory not represented by the light gradient in field sampling (Woods et al. 2012, Hahn et al. 2019). All significant correlations among defense traits were positive, but there was no consistency across levels.

Overall there were few species correlations, but where significant, they were concordant with the direction of a significant correlation at a lower level (Table 2). The biggest surprise, however, was that the relationship between leaf nitrogen and mass per area, which was consistent at the three levels for A. syriaca, was not significant across species. This result (lack of a species correlation) was confirmed in another study of 30 Asclepias spp. grown in a growth chamber (E. M. Goud et al., unpublished data), as were other key correlations presented in Table 2.

Thus, there is a pattern of trait trade-offs associated with leaf strategies in milkweeds, particularly at lower levels of organization. For example, within species, leaves associated with resource acquisition are often less

Box 3. Suggested research questions for future work. Greater detail on each is presented in the main text

- What are the causes of scale dependence in trait associations? Are across-species relationships fundamentally different than within-species relationships because of reproductive isolation? Are across-genera relationships different than within-genera relationships because of conserved traits within genera (i.e., niche conservatism)?
- What are the mechanisms underlying particular trade-offs or negative correlations (resource diversion, conflicting environmental selection, conditional neutrality, or one trait directly impacting other traits)? Does understanding the relative magnitudes of each mechanism provide insight into the origin and consequences of the correlation, or change predictions for the scales at which they are most prevalent?
- To what extent do plastic phenotypic responses to environmental conditions mirror trait associations at higher scales within species, such as genetic correlations or locally adapted populations? Do trait correlations hold when expressed through plasticity or local adaptation along different environmental axes (e.g., abiotic vs. biotic stress gradients) or spatial scales (e.g., locally vs. across latitude)?
- For phenotypic plasticity, do organisms respond to immediate needs as well as to the interactions or selective conditions that are less likely or less important when a particular environmental condition is experienced? In other words, do apparent trade-offs in response to environmental cues correspond to these less likely or less important conditions?
- To what extent are negative trait correlations adaptive (i.e., shaped by correlational selection)? And what is the relative importance of increasing benefits vs. decreasing costs in the expression of correlated traits?
- For a given trait, what are the benefits and costs of continuous phenotypic expression vs. discrete polymorphism? Are the trade-offs and their mechanisms comparable?
- At the population and species scale, is specialization caused by trade-offs or is the pattern of a trade-off (among populations or species) a consequence of adaptive specialization (including conditional neutrality)?
- To what extent do trait relationships among closely related species change, and are these shifts an indication of the divergent selection between populations of their common ancestor? Relatedly, can comparative analysis of closely related species reveal changes in metabolic machinery that have allowed species to modify or circumvent within-species trade-offs?
well-constructed and poorly defended. However, my interpretation of these relationships is that they are strongest, especially among classically defined traits, when plants are specializing to light conditions through phenotypic plasticity (Agrawal et al. 2012b). For milkweeds growing in a common and seemingly benign growth-chamber environment, genotypic correlations are few and far between (despite substantial genetic variation), revealing relatively little pattern of constraint or adaptive axes of variation. Among populations, trait combinations are likely shaped by local adaptation, and the likely drivers are manifold, spanning biotic and abiotic environmental gradients, the latter including temperature, growing season, and precipitation (Woods et al. 2012, Agrawal et al. 2015, Hahn et al. 2019). Little work to date has addressed local adaptation to sun and shade (but see Schemske 1984), although this would be a profitable direction. Finally, among closely related species, trait associations emerge from a level of divergence on niche

<table>
<thead>
<tr>
<th>Phenotypic plasticity</th>
<th>Response to low light</th>
<th>Response to herbivory</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Resource acquisitive:</strong></td>
<td>Increase in nitrogen</td>
<td>Increase in chemical defense</td>
</tr>
<tr>
<td></td>
<td>Increase photosynthetic rate</td>
<td>Often increases in trichomes</td>
</tr>
<tr>
<td></td>
<td>Decrease in LMA</td>
<td>Sometimes higher LMA</td>
</tr>
<tr>
<td></td>
<td>Reduced trichomes</td>
<td>Often increase in photosynthetic rate</td>
</tr>
<tr>
<td></td>
<td>Reduced toxins</td>
<td>Sometimes increases in nitrogen</td>
</tr>
<tr>
<td></td>
<td>(slow growth, but photosynthesis is high given low light levels)</td>
<td>(plant growth slowed due to diversion of resources; metabolism increased)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Local adaptation</th>
<th><strong>Resource acquisitive:</strong></th>
<th><strong>Induced defense:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LES traits as above; other environmental gradients may decouple correlations</td>
<td>Increase in chemical or physical defenses, including tolerance</td>
</tr>
<tr>
<td></td>
<td>defense may be independent depending on correlated environmental conditions</td>
<td>LES traits may be independent depending on correlated environmental factors</td>
</tr>
<tr>
<td></td>
<td>(plant growth faster?, but depends on environmental conditions)</td>
<td>(plant growth slower relative to populations with low herbivory)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species strategies</th>
<th><strong>Resource conservative:</strong></th>
<th><strong>Higher defense:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low nitrogen</td>
<td>Increase in chemical or physical defenses, including tolerance</td>
</tr>
<tr>
<td></td>
<td>Low photosynthetic rate</td>
<td>LES traits may be independent depending on correlated environmental factors</td>
</tr>
<tr>
<td></td>
<td>High LMA / Long-lived leaves</td>
<td>(plant growth slower relative to populations with low herbivory)</td>
</tr>
<tr>
<td></td>
<td>High toxins</td>
<td>Diversity of potentially equivalent strategies including toxins, undigestible/inedible, highly tolerant, escape, or ephemerality</td>
</tr>
<tr>
<td></td>
<td>Perhaps low trichomes</td>
<td>(a diversity of LES traits should be possible, defense and LES may be uncoupled or interact)</td>
</tr>
<tr>
<td></td>
<td>(extra slow plant growth)</td>
<td></td>
</tr>
</tbody>
</table>

**FIG. 10.** An initial predictive framework for plant plasticity, local adaptation, and species strategies (rows) in response to low light or insect herbivory (columns). Subheadings in green text refer to the adaptive strategy employed. Leaf economics traits and defense may overlap (nitrogen, trichomes) and expression of seemingly independent traits may intersect physiologically. Trait associations may also be generated by correlated environmental variables (e.g., reduced herbivore abundance in shaded habitats). Expected genetic correlations between traits are not shown because they are within-population estimates from the same environmental conditions; these are predicted to be quite variable among populations and species, except those between some leaf economics spectrum (LES) traits such as nitrogen, leaf mass per area (LMA), and photosynthesis. [Color figure can be viewed at wileyonlinelibrary.com]
specialization, given whatever physiological commonalities these *Asclepias* species share. At this level, some trait relationships may emerge (or be conserved), but trade-offs are more likely to be observed on a broad-scale set of strategic axes, including biotic interactions (Agrawal and Fishbein 2006). In summary, a preliminary general framework for the intersection of plant responses to light and herbivory is given in Fig. 10.

**General Conclusion**

A unifying goal in biology is to understand patterns in nature, some of which relate to how organismal traits are expressed, co-expressed, trade off, and how they evolve. Many prominent and long-standing theories are predicated on trade-offs and adaptive trait combinations. Plasticity allows organisms to specialize temporarily in response to environmental challenges, and adaptive responses are typically associated with allocation away from currently less important functions. Within-population variation in traits like defense is maintained because of costs and variable selection in time and space. The extent to which correlational selection is responsible for within-population genetic correlations remains a persistent unknown. Population- and species-level specialization allows organisms to narrow their niche, and with this comes syndromes of adaptive traits and a pattern of strategic trade-offs with other traits that might not allow the species to exist elsewhere.

As we erect new paradigms such as the leaf economics spectrum, of course we should seek generality and test whether associations hold at different levels of organization. As we test classic hypotheses, we should ask whether the predictions are expected to hold across levels of organization—in many cases the answer will be “no.” We will continue to ask how to interpret broad-scale patterns and how they might have emerged through evolution within species. And as we study within-species adaptation, we should address if and why this process may result in different trait associations among closely and distantly related species. In closing, a few take-home messages and suggestions for future research follow (Box 3).

1. Scale-dependent evolutionary processes will often cause trait relationships to diverge across scales from within to among species. Scale-dependent processes should be addressed a priori as well as after patterns are found. The scaling of patterns from within-population genetic correlations, to traits associated with local adaptation, to trait relationships across closely related species are important in connecting constraints, adaptation, and speciation.

2. Even if patterns of trait association are consistent across two levels, it may be very difficult to ascribe the cause. Strong constraint appears uncommon and is often restricted to fundamental traits (e.g., skeletal parameters, mechanisms of photosynthesis, life-history components of fitness); if strong constraint is hypothesized to explain trait correlations at higher levels, it should be challenged experimentally.

3. The line between adaptive strategy (correlated traits evolved to match an environment) and trade-off is pretty fine, and as Darwin recognized, it is especially difficult to disentangle when organisms specialize to their niches. Adaptive plastic responses, polymorphisms maintained by selection, locally adapted populations, and species all represent forms of specialization. Genetic correlations within a population are more ambiguous to interpret.

4. To understand trade-offs and syndromes, we will typically have to step out of our disciplinary bounds (physiology, life-history, species interactions, abiotic environment) because organismal evolution connects these attributes.

**Acknowledgments**

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**Literature Cited**


