DO TRADE-OFFS HAVE EXPLANATORY POWER FOR THE EVOLUTION OF ORGANISMAL INTERACTIONS?

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The concept of a trade-off has long played a prominent role in understanding the evolution of organismal interactions such as mutualism, parasitism, and competition. Given the complexity inherent to interactions between different evolutionary entities, ecological factors may especially limit the power of trade-off models to predict evolutionary change. Here, we use four case studies to examine the importance of ecological context for the study of trade-offs in organismal interactions: (1) resource-based mutualisms, (2) parasite transmission and virulence, (3) plant biological invasions, and (4) host range evolution in parasites and parasitoids. In the first two case studies, mechanistic trade-off models have long provided a strong theoretical framework but face the challenge of testing assumptions under ecologically realistic conditions. Work under the second two case studies often has a strong ecological grounding, but faces challenges in identifying or quantifying the underlying genetic mechanism of the trade-off. Attention is given to recent studies that have bridged the gap between evolutionary mechanism and ecological realism. Finally, we explore the distinction between ecological factors that mask the underlying evolutionary trade-offs, and factors that actually change the trade-off relationship between fitness-related traits important to organismal interactions.

KEY WORDS: Antagonistic pleiotropy, evolution of increased competitive ability, host range, mutualism, parasitism, Y-model.

The concept of a trade-off is deeply embedded in thinking across biology because the balance between fitness benefits and costs often provides a basis for predicting the evolutionary process. For example, the trade-off between fecundity and longevity is central to understanding life-history variation within a species (Stearns 1992). Although trade-offs underlie much of the theory for interactions between species as well, the greater biological complexity of organismal interactions makes empirical evaluation of trade-offs more difficult, and their value for predicting evolutionary trajectories has been questioned (e.g., Ebert and Bull 2003). In this perspective, we find that trade-offs often generate constraints on the evolution of traits important to the fitness of interacting organisms. Although measurement of trait values under ecologically relevant conditions is challenging, such studies are necessary for identifying the shape and magnitude of trade-off relationships and to give insight into sources of selection. The genetic analysis of traits and their correlation across ecologically relevant environments is especially germane to organismal interactions because

in many cases, other organisms constitute the environment of interest.

Rather than providing an exhaustive literature review, we focus on exemplary research in four case studies to examine the importance of ecological context for understanding evolutionary trade-offs: (1) resource-based mutualisms, (2) parasite virulence and transmission, (3) invasive plant populations, and (4) host range in parasitic organisms. The four case studies allow us to examine several types of trade-offs such as those based on resource allocation or those based on antagonistically pleiotropic traits not involving resources. For example, in mutualistic interactions between nitrogen-fixing bacteria and their legume hosts, fixed carbon can be deployed for bacterial multiplication inside the nodule or for nitrogen fixation, an activity that directly benefits the plant partner and only indirectly benefits the bacterium (Ratcliff et al. 2008). Similarly, a key research paradigm in plant invasion biology emphasizes the importance of an individual's allocation of resources to competitive ability versus defense against natural enemies (Blossey and Nötzold 1995). In contrast, parasite virulence toward a host is commonly viewed as a necessary cost of within-host reproduction. Thus, transmission and virulence are antagonistically pleiotropic traits not related to alternative uses of a resource pool (Anderson and May 1982). Similarly, generalist parasites may evolve increased fitness across a number of shared hosts, but cannot simultaneously maximize fitness on a single host, again, likely due to antagonistic pleiotropy (Legros and Koella 2010).

The greatest challenge to using trade-off relationships to predict evolutionary trajectories of interacting organisms is that of understanding ecological context. For example, invasive plant studies often incorporate ecological context into experimental design and experiments to determine the host range of parasites may evaluate the constraints on biological control agents in specific ecological contexts. However, in both these areas of study, experiments evaluating the relative fitness of different genotypes or species across differing environments have less often been conducted. In contrast, a major challenge for evolutionary studies of mutualism or parasitism has been to move out of controlled laboratory studies and conduct experimental genetic studies in field settings. In all four case studies, understanding constraints generated by trade-offs is important to management of human systems, and accounting for ecological sources of "noise" is necessary to uncovering the underlying trade-off (Roff and Fairbairn 2007).

In all cases, a more thorough understanding of evolutionary responses in ecologically relevant contexts enriches our ability to discern the processes and underlying mechanisms of evolution in organismal interactions (Thompson 1999). Recent reviews have argued for the value of trade-off models to predict evolutionary outcomes for resource allocation (Roff and Fairbairn 2007), for host–parasite interactions (Alizon et al. 2009), and for

ecological specialization (Poisot et al. 2011), despite challenges arising from ecological complexity or the difficulty of placing costs and benefits into a common currency (Hutchings et al. 2006). Here, we focus on assessing the explanatory power of trade-off models for interacting species, and use four case studies to review differing types evolutionary of trade-off models. In contrast to the more singular focus of previous reviews, the case study approach allows comparison and broader synthesis across systems regarding the effects of ecological factors on the evolutionary trajectories predicted by such models.

Case Study No. 1: Resource-Based Mutualisms—Benefit to Self or Partner

A trade-off between allocation of resources directly to symbiont reproduction, versus allocation to a mutualistic partner, plays a key role in the evolution of mutualisms. However, the negative correlation expected between resources allocated to reproduction versus to a partner is not always found and in some cases, positive correlations have been observed (Bronstein 1988; Reznick et al. 2000). Here, we discuss the importance of ecological context for uncovering the role of trade-offs in the evolution of two well-studied mutualisms: the interactions of figs and pollinating fig wasps, and of rhizobia and their legume plant hosts.

THE "Y-MODEL" AND RESOURCE ALLOCATION IN MUTUALISMS

The "Y-model" describes resource allocation to two traits within an individual from a resource pool acquired from the environment. Here, allocation of the resource to one trait (at proportion P of the total) comes at the cost of allocation to the second trait (at proportion 1-P), thus trait values should demonstrate a negative correlation. A key insight arising from the Y-model is that variation in resource acquisition across individuals and populations can mask an underlying and potentially predictive resource allocation trade-off (de Jong and Van Noordwijk 1992; Roff and Fairbairn 2007) (Fig. 1).

A classic example of a putative resource allocation trade-off within the context of a mutualism involves the association between figs and their pollinating wasps (Herre and West 1997). Here, individual flowers in an enclosed fig inflorescence (synconium) either develop a seed or are consumed by a developing wasp. The trade-off for the plant is between fitness benefits of seed production (female function) versus support of wasps that may transmit its pollen (male function). Given that a single resource, the fig flower, must be allocated to either a seed or a wasp, Herre and West (1997) predicted, but did not find, a negative correlation between the number of seeds and the number of wasps emerging
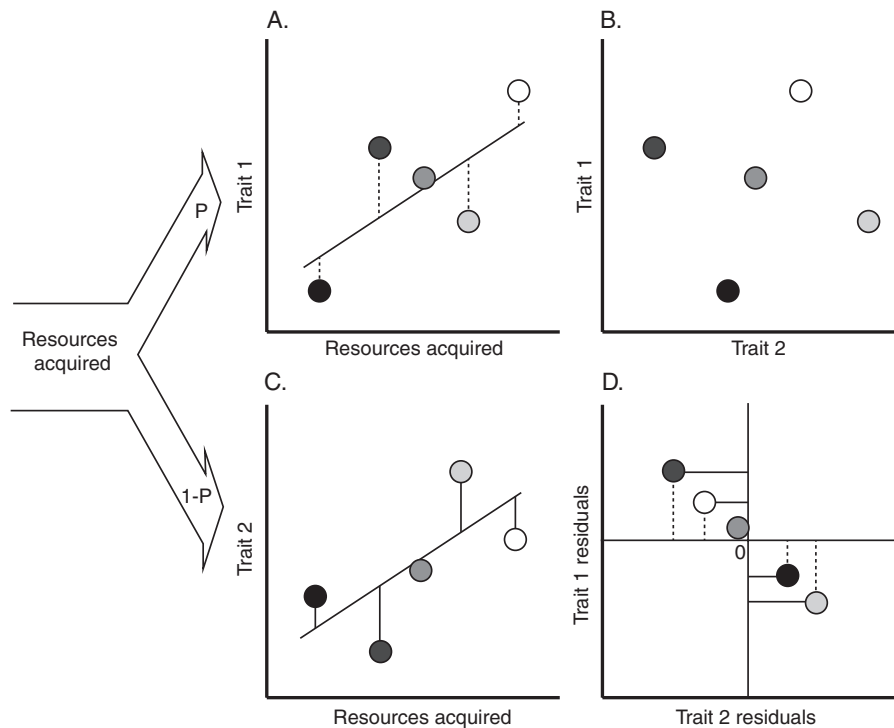
Figure 1. A resource allocation trade-off may be masked by ecological factors if such factors are not accounted for. Dots represent individual measures; each individual is the same shade of gray in all panels. We use a phenotypic expression of the Y-model for resource allocation trade-offs defined as the proportion, P, of acquired resources going to one trait, and 1-P as the proportion going to the second trait. Hence, a negative correlation between the trait values is expected (de Jong and Van Noordwijk 1992; Roff et al. 2002). However, the amounts of resource reaching both traits are positively related to the amount of resource acquired by an individual (A, C). Variation in resource acquisition across individuals and populations can mask the inherent negative relationship and yield zero net or even positive correlations between the two traits (B). Intuitively then, the underlying negative correlation in resource allocation to the two traits can be understood by plotting the residuals of the relationships between traits against the amount of resource acquired (D).

from the synconium. Is the hypothesized trade-off absent or are there other factors that mask the resource allocation trade-off?

Using an approach similar to the Y-model, Herre and West (1997) were able to uncover the expected allocation trade-off between seed and wasp production only after they accounted for variation in resources available to the synconium and individual flowers. Such differences included the effects of variation in the number of flowers per synconium, and the size of leaves subtending the synconium. This example demonstrates how accounting for ecological factors external to the direct organismal interaction can be essential for identifying trade-offs influencing the evolution of the interaction.

An allocation-based trade-off also affects the evolution of interactions of symbiotic rhizobia with their legume host plants. The photosynthate that rhizobia acquire from their plant hosts can either be stored as polyhydroxybutyrate (PHB), which supports rhizobial reproduction and survival (Ratcliff et al. 2008), or it can be respired in fixation of atmospheric nitrogen. Most nitrogen fixed by rhizobia is transferred to the host, where it may lead to increased photosynthesis and thus indirectly increased photosynthate supply to rhizobia. Genetic evidence for a trade-off between

PHB accumulation versus nitrogen fixation includes increased nitrogen fixation by a PHB-minus strain (Cevallos et al. 1996), and greater PHB accumulation by a nonfixing mutant relative to a wild-type strain in the same nodule (Hahn and Studer 1986). The trade-off between using photosynthate for self-reproduction or for nitrogen fixation might be expected to undermine the stability of the mutualism unless the plant has a mechanism of sanctioning cheaters, as we discuss below.

THE CHALLENGE OF MULTIPLE INFECTIONS AND HOST EXPLOITATION

A key challenge in many mutualisms is that of understanding how a host's interactions with more than one partner affects the evolutionary interaction between partners. In the rhizobia–legume example, infection of individual plants by more than one strain potentially reduces the net benefits to a rhizobial strain of investing in nitrogen fixation. Improving host-plant nitrogen status increases photosynthesis, but what if photosynthate is shared with nonfixing strains, a "tragedy-of-the-commons" situation (Hardin 1968)? If allocation of photosynthate among rhizobial strains is independent of their nitrogen contributions (i.e., if there are no

host sanctions), then individual benefits from each strain's share in the increased photosynthate resulting from its investment in nitrogen fixation are exceeded by the opportunity cost of forgoing additional PHB accumulation. In this situation, the predicted evolutionarily stable allocation of photosynthate by rhizobia to nitrogen fixation is zero (West et al. 2002).

Given that multiple infections are observed in nature (Dowling and Broughton 1986), and that nitrogen fixation only indirectly benefits the symbiont, what evolutionary pressures maintain allocation of fixed carbon to rhizobial nitrogen fixation? One possible answer involves the imposition of sanctions on underperforming nodules by legumes, such as allocating less photosynthate to nonfixing nodules (West et al. 2002; Oono et al. 2011). Sanctions eliminate the fitness benefit that strains fixing less nitrogen would otherwise obtain.

However, rhizobia that fix some nitrogen but divert significant photosynthate to their own reproduction or to PHB may escape sanctions, especially if they occur in mixed infections with a strain fixing more nitrogen (Friesen and Mathias 2010). Similarly, in the fig–fig wasp mutualism discussed above, some fig species may impose sanctions on wasps that fail to pollinate their flowers. Selective abortion of nonpollinated syconia, or inhibition of wasp development in nonpollinated synconia will effectively sanction nonpollinating wasps (Jandér and Herre 2010). However, as in the case of nonfixing rhizobia, nonpollinating wasps may not have lower fitness than pollinators if they are present together in the fig syconium and sanctions are imposed on the level of the entire nonpollinated syconium (Jandér and Herre 2010). Currently, the spatial scales at which sanctions are imposed, and the genetic and species diversity of partners at that scale, remain key open questions in these and other mutualisms (Stanton 2003; Jandér and Herre 2010).

The examples of trade-offs in resource allocation faced by rhizobia and by figs highlight the importance of considering the ecological context of organismal interactions, such as the presence of diverse symbionts within the host or variation in resource acquisition, for understanding how trade-offs influence the evolution of mutualistic interactions. Similarly, understanding the dependence of trade-off relationships on ecological context also challenges our understanding of the evolution of host–parasite interactions.

Case Study No. 2: Parasite Virulence—Transmission at a Cost

As in the mutualism case study above, a trade-off between immediate reproduction by the symbiont and more prudent behavior that increases the host's population viability likely plays a key role in the evolution of parasite populations. Anderson and May's

(1982) mathematical model formalized the key trade-off between parasite virulence and transmission:

$R_0 = \frac{\beta S}{\mu + \alpha}$, where R_0 is the parasite reproductive rate in terms of the number of new infections generated by a single infected host, β is the between-host transmission rate, S is the number of susceptible hosts, and μ is the background host mortality rate. Virulence (α) is the additional mortality caused by pathogen infection, and can also be defined as a reduction in host fitness due to growth of the pathogen within the host (Sacristan and Garcia-Arenal 2008). The trade-off between transmission and virulence arises if decreased host viability also reduces the duration of pathogen transmission. In other words, the Anderson and May model makes explicit the assumption that traits associated with greater parasite growth within the host will have the antagonistically pleiotropic effect of increased transmission but decreased host viability. Given assumptions for the shape of the trade-off, the model predicts that pathogens should evolve an intermediate level of virulence (see Alizon et al. 2009). Although later models incorporated host recovery rates (γ) and host species coevolution (Alizon et al. 2009), Anderson and May's model set the fundamental questions for the field.

Implicit in the Anderson–May model are two key assumptions: first, as described above, growth and reproduction of the pathogen within the host are positively correlated with between-host transmission rate (β) and negatively correlated with host fitness (α), and second, that transmission and virulence are under pathogen control whereas the number of hosts remains constant. Empirical tests of expectations arising from the transmission–virulence trade-off have been fruitful. Across diverse pathogen systems, within-host growth (parasite load) has been correlated with reproductive capacity in phage viruses (Messenger et al. 1999), and with transmission to new hosts in a number of systems: rodent malaria (Mackinnon and Read 1999), protozoan parasites of monarch butterflies (de Roode at al. 2008), the human immunodeficiency virus (Fraser et al. 2007), and plant viruses (Banik and Zitter 1990; Ng and Falk 2006). Nonetheless, because between-host transmission is subject to considerable environmental variation including effects of host genotypic variation, and is difficult to measure, the relationship between transmission and virulence has not been established in many systems (Froissart et al. 2010).

ADDING ECOLOGICAL CONTEXT: DO TRADE-OFF PREDICTIONS CHANGE?

Ecological factors such as abiotic conditions (Laine 2007), genetic structure of host and pathogen populations (Jarosz and Burden 1991; Krist et al. 2000; Thrall et al. 2005), and community composition (de Roode et al. 2011) all likely affect the expression of virulence and transmission traits. The challenge is this: if environmental factors increase variation in virulence and transmission,

the power of selection to cause a shift in trait values will be reduced but the predicted optimal virulence will not differ. Alternatively, if the trade-off relationships and optimal virulence levels change across environmental variables, selection might move the interaction in new directions. In either case, teasing out the specific effects of ecological context, and the extent to which organismal responses to environment have a genetic component, is critical if we hope to use trade-offs to predict and manage virulence evolution. We illustrate promising approaches using rodent malaria and monarch butterfly parasites in which the genetic basis of trade-off is well understood, and the impact of ecological factors on the shape of the trade-off relationship has been assessed.

Similar to "tragedy of commons" arguments made for mutualisms above, infection by different parasite strains should select for increased virulence because the cost of virulence is shared among all strains and the benefits to the more prudent parasite individual decrease (Levin and Bull 1994). Assuming that better competitors within the host are more virulent, the evolution of transmission rate might be constrained by selection for increased competitive ability rather than a direct cost of virulence. For the rodent malaria parasite *Plasmodium chabaudii*, Bell et al. (2006) found support for the correlation of competitive ability and virulence during some infection phases and evidence for facilitation among strains during other stages of infection. Because transmission to the mosquito is indeed proportional to a clone's prevalence in the host (de Roode et al. 2005), a simple negative correlation of virulence and transmission could yield apparent support for the transmission–virulence trade-off but in this example that trade-off has little explanatory power for the evolution of virulence. Moreover, not all host–parasite systems behave the same way. Garbutt et al. (2011) found that multiple infections of the bacterial insect pathogen *Bacillus thuringiensis* selected for lower virulence as strong antagonistic interactions among strains reduced transmission rate. Together, these and other studies argue that understanding underlying mechanisms of parasite competition and its effect on virulence and transmission will improve predictions for virulence evolution (e.g., Mideo 2009).

Likely the greatest challenge is to put the study of trade-offs into a community ecological context and here work has just begun. Building on previous work demonstrating the genetic basis of the trade-off between virulence and transmission in a butterfly parasite, de Roode and Altizer (2010) showed that specific pathogen by host genotypic interactions led to increased variation and decreased heritability of virulence and transmission traits, but that such variation did not affect the optimal virulence level predicted by the trade-off model. The value of understanding trade-off relationships in an ecological context is further illustrated by recent results showing the effects of a third interacting species, the oleander aphid, which alters the chemical composition of the plant host shared by aphid and butterfly. Interestingly, the presence of

the aphid indirectly increases both the virulence and the transmission potential of the butterfly parasite (de Roode et al. 2011). The slope of the trade-off is unaltered, so the aphid's presence has the effect of moving the virulence and transmission to a higher point on the trade-off surface (to the right in Fig. 2B).

The empirical examples discussed above illustrate the value of approaches that combine genetic and ecological approaches to better distinguish between factors that might mask an underlying trade-off, and those that affect the shape and intensity of the trade-off. We turn now to a trade-off that has been steeply grounded in ecological realism since its inception—the hypothesis for the evolution of increased competitive ability (EICA) in invasive plant populations.

Case Study No. 3: Invasive Plants—Competition Versus Defense

We focus on work evaluating the EICA hypothesis as a case study for a trade-off between competition and defense in invasive plant species. The strength of research in this field is that investigators often conduct studies in relevant ecological settings, although key evolutionary questions remain understudied.

The EICA hypothesis predicts that during invasion, plants are released from the herbivores of the native range and will evolve to shift resources from herbivore defense to vigor, resulting in increased competitive ability in the invasive range (Blossey and Nötzold 1995). The problem has been approached primarily from the perspective of resource allocation, as resource investment in herbivore defense is thought to engender costs to plant growth and reproduction (Bazzaz et al. 1987; Koricheva 2002). Assuming such costs, investment in defense is only advantageous in environments with significant herbivore pressure. Because introduction into a new range exposes a plant population to a new herbivore community not adapted to the host's defenses, allocating fewer resources to defense and more toward growth, reproduction and other components of competitive ability may represent an adaptive shift.

Empirical evaluations of EICA are most often conducted in a common garden by direct comparisons of phenotypic differences between native and invasive genotypes (Bossdorf et al. 2005; Atwood and Meyerson 2011). These experiments typically measure growth and fecundity as response variables, with fewer studies quantifying differences in herbivore performance (e.g., Rapo et al. 2010), the host's tolerance to herbivory (e.g., Zou et al. 2008), or defensive chemistry (e.g., Cano et al. 2009). In fact, only 26% of studies aimed at testing the EICA hypothesis measured both growth and defense traits (Atwood and Meyerson 2011). Given the variety of mechanisms by which investment in defense might
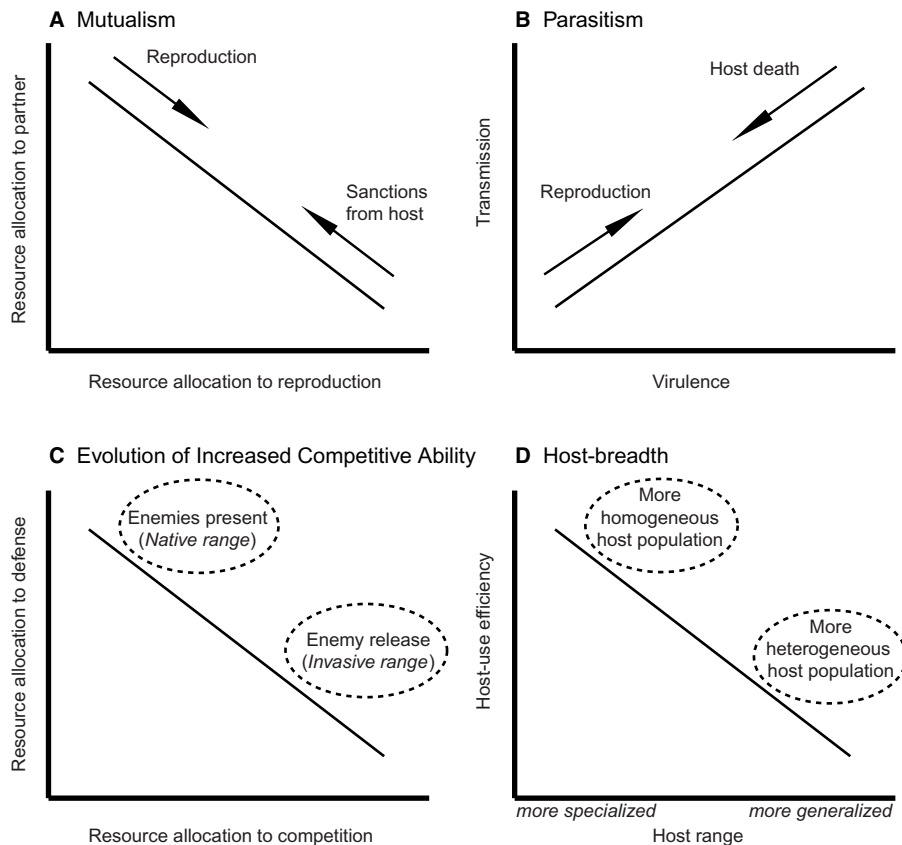
A Mutualism

B Parasitism

C Evolution of Increased Competitive Ability

D Host-breadth

Figure 2. Trade-off models predict different evolutionary outcomes depending on the type of organismal interaction and ecological context. Models for trade-offs faced by obligate symbionts such as mutualists (A) and parasites (B) often predict evolution toward intermediate, optimum trait values in response to opposing selective pressures, whereas the models for trade-offs underlying the evolution of increased competitive ability (C) and host-breadth (D) predict differing optima depending on ecological context. (A) For the mutualist partner of a host, selection for increased allocation of resources to mutualist reproduction is countered by host sanctions; (B) selection for increased parasite transmission is countered by elevated host death rates. Note that here we present simple linear forms of trade-offs. Arrows indicate direction of selection. (C) Selective pressure from natural enemies differs between the native and invasive ranges, predicting evolutionary changes in resource allocation; (D) selection pressures differ for homogeneous and heterogeneous host populations, predicting evolutionary changes in host specialization.

limit plant growth such as autotoxicity from defensive compounds or physical limitations related to structural defenses (Poorter and de Jong 1999), it is perhaps not surprising that tests of the EICA hypothesis have produced mixed results. Although some studies have shown support for evolution of increased vigor or reduced herbivore defense following release from specialist herbivores (reviewed by Bossdorf et al. 2005; Dlugosch and Parker 2008, reviewed by Atwood and Meyerson 2011), other studies have shown that an increase in size or abundance of plant species following introduction is not a universal outcome (e.g., Rejmánek 1996; Firn et al. 2011).

Nonetheless, progress has been made. The EICA hypothesis has been refined to account for differences between specialist and generalist herbivores (Hull-Sanders et al. 2007), experimental studies have accounted for ecological setting and abiotic factors (Colautti et al. 2009), and competitive strategies other than

reallocation of resources have been evaluated (Callaway and Ridenour 2004). We illustrate these advances by discussing recent work on the highly invasive Crofton weed.

PROGRESS TOWARD MECHANISM AND CHALLENGES MOVING FORWARD

Crofton weed, *Ageratina adenophora*, is native to Mexico and has been identified as an invasive plant throughout the world (Cronk and Fuller 1995). The evolution of increased vigor and decreased herbivore defense in the invasive range has been documented for Crofton weed using common gardens (Feng et al. 2009). Based on differentiation between phenotypes in the invasive and native ranges, Feng et al. (2009) show that invasive genotypes allocate increased nitrogen toward photosynthetic structures at the expense of allocation to structural defenses in cell walls, resulting in increased growth. Furthermore, increased nitrogen

allocation in photosynthetic machinery results in higher photo-synthetic energy-use efficiency in invasive plants than in their native range counterparts (Feng et al. 2011).

Despite advancements in our understanding of plant invasions and evolution, challenges remain to testing the EICA hypothesis. A key problem is that few studies have exhaustively tested both defense and competitive ability, even though the trade-off between these two traits is at the heart of the hypothesis. Plant competitive ability is often evaluated using a wide range of plant traits such as growth rate as proxies for competition, which is in itself an oft-debated topic in ecology (Grace 1991). As described above, Feng et al. (2009, 2011) were able to illustrate a potential mechanism producing the observed phenotypic differences between native and invasive populations in allocation to growth and defense traits, although a direct measure of competitive ability is lacking. Tying underlying mechanism to measurements of competition clearly remains the most difficult challenge to testing the EICA hypothesis, setting the stage for the next major research breakthrough in this field.

The strengths of EICA research stem from a foundation in observed ecological phenomena, and a motivation to understand and mitigate species invasions, a clear threat to global biodiversity. Tangible steps toward the accurate prediction of biological invasions are found in exemplary studies that have quantified evolution of increased growth rates in invasive populations and uncovered their underlying physiological mechanisms. Although we are often unable to predict the evolution of invasiveness, direct measures of quantitative genetic variation for traits associated with competitive ability and defense will likely be most informative as such approaches have yielded progress in understanding other traits important to invasive populations (e.g., Lee et al. 2007; Colautti and Barrett 2011). Recent methods allow explicit consideration of constraints on the evolution of quantitative traits (Bacigalupe 2009; Gomulkiewicz and Houle 2009). In moving toward a more complete understanding the evolution of invasive plants, we recommend that such methods be employed in combination with common garden experiments designed to mimic ecologically relevant settings (Moloney et al. 2009). We now turn to an evolutionary trade-off that, like EICA, has a strong ecological foundation, host range in parasites and parasitoids.

Case Study No. 4: Host Range in Parasitic Organisms—Is the Jack-of-All-Trades a Master of None?

The "jack-of-all-trades is a master of none" hypothesis asserts that increased parasite performance on one host comes at the cost of decreased performance on other hosts (Futuyma and Moreno

1988). A trade-off of host use efficiency and specialization is an intuitively pleasing way to think about host breadth because if a consumer could utilize all hosts within its range without constraints, the evolution of specialization would seem highly unlikely. Of the four topics highlighted in this perspective, studies of trade-offs in host use efficiency perhaps best exemplify the value of including both evolutionary and ecological approaches. Although we restrict our focus primarily to parasites and parasitoids, many of the issues discussed are applicable to other consumers with "parasite-like" host interactions, such as phytophagous insects (Price 1997).

AN EVOLUTIONARY APPROACH—EXPERIMENTAL EVOLUTION IN MICROSPORIDIAN PARASITES

In experimental evolutionary approaches to the study of trade-offs in host use efficiency (see Fry 2003 for an in-depth discussion), conspecifics are reared on different host strains over a number of generations. Individuals from these selected lines are screened for fitness components against both the host strain on which they were reared (the "matched" host) and on the alternative host strains (the "nonmatched" hosts). If a trade-off in host use efficiency exists, lines that show adaptation to their matched host should also show a concomitant decrease in fitness on nonmatched hosts.

Legros and Koella (2010) examined the fitness effects of host use in *Brachiola algerae*, a microsporidian parasite. Here, parasites were reared on different strains of its mosquito host (*Aedes aegypti*) in one of three selection regimes: single (one host strain), mixture (equal mixture of all host strains), and alternating (a single host strain that changes each generation). After 13 generations of selection, infectivity of the parasite populations against the different host lines was examined and results conformed to predictions of a trade-off in host use efficiency. Single line parasites showed increased infectivity on matched hosts and decreased performance on nonmatched hosts, whereas the generalist lineages showed intermediate infectivity across all host strains. Further, the results of the above experimental evolution study also gave insight into the genetic architecture of the trade-off. Because changes were observed over relatively few generations, the results are more consistent with selection on existing variation and antagonistic pleiotropy among traits, rather than the accumulation of deleterious mutations.

The Legros and Koella (2010) study illustrates the power of an experimental evolutionary approach to directly assess the fitness effects of host adaptation on host use efficiency. A key limitation of this experimental evolutionary approach is that the potential dependence of trade-offs on ecological context is left unexplored in the confines of a controlled environment. For example, growth of the generalist caterpillar *Estigmene acrea* is greater on the less well-defended plant host *Viguiera dentata* than on a more toxic plant *Senecio longilobus* in the absence of parasitoid flies.

However, with increased risks of parasitism, caterpillar population growth increases when it feeds on *S. longilobus* and sequesters plant toxins for its own defense (Singer et al. 2004).

AN ECOLOGICAL APPROACH—ABUNDANCE AS A PROXY FOR HOST USE EFFICIENCY

An alternative approach to experimental evolution is to use relative abundance on shared hosts as a proxy measure for host use efficiency, and thus gain estimates of relative fitness of the parasites in relevant ecological contexts (e.g., Poulin 1998, 2005). If a trade-off in host use efficiency exists, then specialists should be more efficient than generalists in attacking shared hosts, and demonstrate greater relative abundance on their "well-matched" host. Here, we summarize two studies utilizing this approach but which differ strongly in their conclusions. Straub et al. (2011) compared the abundance of specialist and generalist parasitoid wasps on shared aphid hosts. After accounting for aphid taxonomy, they found that specialist parasitoids are indeed more abundant than generalists on hosts they share in common. In contrast, a study of avian blood parasites paints a different picture. Here, *Plasmodium* and *Haemoproteus* parasites with broad host ranges were also most abundant on shared host species (Hellgren et al. 2009). Hellgren et al. suggest an explanation for this apparent departure from expectations: in heterogeneous host environments, vectored generalist parasites are more likely to encounter suitable hosts than are specialists. As these generalists reproduce and disperse more frequently, they may become more abundant on the shared hosts as a result of increased transmission, even if they have lower relative performance on the shared hosts.

We raise the question of whether or not abundance is an appropriate proxy for host use efficiency in systems that differ strongly in the biology of host location, especially those that locate hosts by free-searching (e.g., parasitoid wasps) rather than by vectors. If abundance is actually more accurately predicted by the efficiency of host location rather than the efficiency of host utilization, then the actual trade-off measured by Straub et al. (2011) may be one of searching efficiency. Thus, the proxy of abundance for relative fitness must be viewed with caution when generally applied across parasitic lineages.

We believe that the evolutionary and ecological approaches discussed above can be used in a complementary fashion to better detect trade-offs in host use efficiency, and more accurately assess their explanatory power in nature. From the evolutionary perspective, artificial selection studies on multiple parasite traits, such as host recognition and physiological host use efficiency, are necessary to determine how these traits respond to selection. If selected lines were then exposed to varying environmental conditions such as resource limitation or predation pressure within a microcosm, invaluable insight could be gained on the context-dependence of

trait values and constraints on their evolution. This, in turn, may lead to the development of more suitable proxy measures in the field.

Throughout this perspective, we have examined the trade-offs represented in differing case studies with an eye toward understanding the manner in which ecological context may affect evolutionary outcomes. It is in this light that we now compare and contrast insights gleaned from the highlighted case studies to develop themes and suggest alternative approaches to studying fitness trade-offs.

Discussion

A more thorough understanding of both the genetic mechanism and the effects of environment on trait expression strengthens the power of trade-off models to predict the evolutionary trajectories of interacting species. Achieving this goal is critical to evolutionary biologists on two fronts. First, organismal interactions present some of the most puzzling challenges to evolutionary thought, for example, the evolutionary stability of mutualism, limits on parasite virulence or on organismal invasions, or the pervasiveness of dietary specialization in an uncertain world. Although trade-off models provide a strong hypothesis-testing framework by which we explore complex evolutionary processes, they are only valuable if underlying assumptions are critically evaluated under realistic ecological conditions. The second front lies in the applied arena. Reliable prediction of evolutionary processes is critical as we wrestle with management decisions regarding human ecological impacts, for example, invasive and exotic organisms (including intentionally released biological control agents), adaptation to climate change, and the spread of infectious disease. Accurate prediction of evolutionary trajectories requires understanding the effects of an often changing ecological context on the strength and shape of trade-offs.

THEMES ACROSS THE FOUR CASE STUDIES

Of the four case studies examined here, the most intense organismal interactions are found in the symbiotic systems such as mutualism and parasitism. Obligate symbionts are both directly dependent on hosts for short-term reproduction, and dependent on host population viability for long-term maintenance of the symbiont population. Consequently, over the history of symbioses studies, trade-offs between symbiont reproduction and traits associated with host viability have been predicted to push the evolution of symbionts' fitness-related traits toward an intermediate optimum (Fig. 2). Given this clear conceptual underpinning, it is not a coincidence that studies of symbiont–host trade-offs have long employed strong mechanistic models. Moreover, the relative ease with which many of these organisms can be manipulated in the laboratory permits use of varied genotypes and

quantification of phenotypic trait values in controlled experimental tests of model predictions.

However, studies of trade-offs in symbiotic interactions face a common challenge—much research is yet needed on the effects of ecological context. Although we recognize the difficulties associated with conducting genetic studies in realistic ecological settings, our symbiont case studies reveal the promise for greater understanding of selective forces pushing trait evolution. For example, in an environment in which a legume host gains a higher proportion of its nitrogen by soil uptake or provides weaker sanctions (Kiers et al. 2007), the trade-off between using photosynthate for rhizobial reproduction and for nitrogen fixation benefiting the host predicts that rhizobia should evolve to allocate more photosynthate to self-reproduction (West et al. 2002).

The organismal interactions embodied by the last two case studies of plant invasion and host range are arguably less constrained by trade-offs between self-reproduction and the viability of a partner population, and are more highly dependent on ecological context. Here, trade-off relationships have often predicted shifts in phenotypic optima of populations exposed to different environmental conditions, rather than an intermediate optimum (Fig. 2). For example, under the EICA hypothesis, allocation of resources toward competitive ability and away from herbivore or parasite defense is predicted upon introduction into novel habitats (Fig. 2C). The direction and intensity of such shifts must depend on the particular co-occurring species. In studies of host use efficiency, homogeneous host landscapes are expected to provide selection for highly efficient specialists, whereas greater host heterogeneity should provide selection for intermediate-performing generalists when the parasite species moves across environments (Fig. 2D) (Kassen 2002).

Across all the case studies, accounting for interactions of multiple species or genotypes generates experimental challenges but is a necessary "next step" to identifying factors affecting the shape and magnitude of trade-off relationships, and thus, their predictive power. Biotic interactions provide a different type of context-dependence, one in which the benefits and costs to self versus other are less direct than in obligate, pairwise symbioses. Although "diffuse coevolution" in the strict sense has proven difficult to evaluate (Janzen 1980; Iwao and Rauscher 1997), the broader conceptual paradigm of a geographical mosaic provides a comparative framework with which to examine the context-dependence of selection and coevolutionary outcomes (Thompson 1999; Strauss et al. 2005; Hoeksema 2010). For example, results of the case studies we examine here suggest that even if the focal organismal interaction and underlying trade-offs are constant, the presence and identity of competitors may drive differing evolutionary outcomes.

To capture that biological complexity, a research program might profitably use field observations and the field proxy measures discussed above to gain insight into interacting species networks (Poisot et al. 2011). Inferences from such field studies could then be tested using experimental evolution, or quantitative genetic analyses to evaluate phenotypic trait correlations and genotype by environment interactions in controlled laboratory settings. Genetic families may then be evaluated in classic common garden or "home" and "away" experiments, either in the field or in microcosm experiments. Each of these approaches varies in the degree to which genetic mechanism and ecological realism are captured, such that reliance on any one of these methods constitutes a "trade-off" in its own right between two factors critical to the predictive power of evolutionary hypotheses. Ultimately, although genetic analyses are not trivial to conduct, the reward of combining genetic analyses with ecological realism will be to gain a better understanding of mechanism, and with that, the shape and magnitude of the trade-off surface.

MASKING VERSUS COMPENSATORY FACTORS

It is critical to underscore the distinction between masking factors that increase variation in trait values and thus decrease the likelihood of detecting the underlying trade-off, and compensatory factors that may "flatten" the trade-off and thus decrease its predictive power. An example of masking factors is found in the discussion of the fig–fig wasp mutualism: the size and proximity of leaves to fig fruits affect resource availability to the developing syconium and may mask an underlying trade-off between seed number and pollinating fig wasp development (Herre and West 1997). Here, we saw that a trade-off between seed and wasp production appeared absent if variation in resource availability was left unaccounted. In contrast, compensatory mechanisms also decrease the likelihood of detecting trade-offs but do so by altering the trade-off surface for the traits under study. For example, in heterogeneous host environments, an increased encounter rate by generalist avian parasites may compensate for poorer host use efficiency, flattening the trade-off between host range and host use efficiency, and making fitness predictions based on host use efficiency less certain. A more complete understanding of masking and compensatory factors is critical to assessing the power of trade-off relationships to predict evolutionary processes.

CONCLUDING REMARKS

Throughout this perspective, we have stressed the importance of a more complete consideration of both genetic mechanism and ecological context in studies of evolutionary trade-offs in organismal interactions. Future work to understand the evolution of organismal interactions can profit from advances in both arenas. For example, the Y-model could be deployed more broadly in evolutionary studies of multispecies interactions, or, experimentally evolved populations might be used in field population-level experiments. The exemplary research we highlight in this

perspective illustrates the challenges and rewards of addressing biological complexity. Although designing experiments to handle an inevitable increase in the level of statistical "noise" is anything but trivial, we gain a better understanding of mechanisms underlying the shapes and intensity of trade-off relationships.

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