

**IJEE SOAPBOX:
IN ECOLOGY AND EVOLUTION,
WHEN I SAY “I”, SHOULD I MEAN “WE”?**



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PREAMBLE

I am honored that the editors of the *Israel Journal of Ecology and Evolution* have invited me to write a series of essays with a style that differs from the standard cut-and-dried journal article. My broad aim in these essays will be to reflect on puzzles that strike me as providing likely directions for profitable inquiry in the areas of ecology and evolution, and often their interface, as well as on more general issues concerning the rhythm and direction of our science. Israeli scientists have long been at the forefront of fundamental advances in these disciplines, and it is a privilege to have this opportunity. Some of these essays will spring from my own work, and others will be reflections on issues and themes far from my own specialized interests.

HIDDEN PLAYERS

As a student in the 1970s, I recall being fascinated by sinister tales of parasites manipulating host behavior, like a fifth column lurking within one’s own body, so as to foster transmission to other hosts while incidentally harming or even killing their hosts (Holmes and Bethel, 1972; Shapiro, 1976). Digeneans, for instance, are consumed as eggs by terrestrial snails, which then exude gooey masses carried by ants to their nest, where they are gobbled up. The ants then do something peculiar for an ant—in the cool of the evening they climb to the tops of grass stems, where they can be accidentally ingested by large herbivorous mammals. At that point the parasites complete their life cycles in their mammalian hosts. Some examples of parasite manipulation are visually conspicuous (e.g., galls on plants, Stone and Cook, 1998), and Janice Moore’s book (Moore, 2002) is full of examples of dramatic modifications in host behavior and life history induced by parasites.

The IJEE Soapbox provides an informal forum for leading ecologists and evolutionary biologists to expound on issues that they find particularly exciting, thought provoking, and novel.

Robert D. Holt is our first invited *IJEE Soapbox* essayist. Bob is Professor of Zoology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

I was reminded of these stories a short while back when I came across a new perspective on the phenomenon of superparasitism (Gandon et al., 2006). Many parasitoids (e.g., ichneumonid wasps) are “solitary”, in that only a single larva can develop within a single individual host. Superparasitism occurs when two or more females lay eggs in the same host. The developing larvae duke it out, and just one emerges as a fresh adult. Various hypotheses have been proposed to account for this seemingly maladaptive behavior. For instance, maybe wasps have constraints on their sensory systems, so they simply cannot tell if a host already has an egg in it. There is surely some truth to this constraint hypothesis, but in many cases wasps have indeed been shown to discriminate against parasitized hosts, so it cannot be the full explanation. There are also costs and benefits to a female wasp of its laying in a previously parasitized host. The most obvious benefit is that if hosts are scarce, and a female has limited time to search for hosts, it may pay to take a risk in laying an egg—even given a low probability of having offspring successfully emerge from a parasitized host that is encountered—if there is an even lower probability of continuing to search and finding an unparasitized host. Sophisticated optimality and evolutionary stable strategy (ESS) models have been sculpted around this idea (Charnov and Stephens, 1988; Visser et al., 1992), with some empirical success.

But Varaldi et al. (2003) have recently uncovered a potentially quite different kind of explanation. It turns out that in at least one species of parasitoids, the wasps are infected by a virus. The virus can be transmitted either vertically (i.e., from the mother wasp to her eggs), or horizontally among larvae in an infected host. Female wasps emerging infected with the virus have a greater tendency to superparasitize, which facilitates horizontal transmission. Like the ant nursing its digenean, the oviposition behavior of the wasp may not be its own (or at least not just its own). Thus, superparasitism may express manipulation of the parasitoid by the virus, and the degree of superparasitism in turn may be the outcome of a coevolutionary struggle, rather than a straightforward adaptation fitting the usual kind of optimality or even ESS model. [Gandon et al. (2006) provide an interesting theoretical framework for considering this particular coevolutionary dynamic.]

Stepping back from all the details of this fascinating tale, I think this story exemplifies a larger rumbling that one can dimly sense in both ecology and evolution, a conceptual disturbance that we are just beginning to fathom in all its complexities. This past semester, I taught a graduate seminar at the University of Florida on the “Frontiers of Community Ecology”, focused on the themes sketched by Thompson et al. (2001). One frontier noted by these authors was the growing evidence for the importance of “hidden players”—cryptic invertebrates, microbes, and mycological groups living freely, or as parasitic or mutualistic symbionts—for community interactions and ecosystem processes. Many of these taxa were not even recognized until very recently, and every day seems to bring an account of new discoveries in this microrealm.

Part of the “hidden player” issue is a straightforward, in principle (if challenging in practice), observational problem. A standard complaint about classical descriptions of food-web dynamics is that they ignore many species relevant to flows of energy and nutrients in ecosystems, particularly vast numbers of smaller and less obvious taxa.

Many microbial species are not culturable, so before the advent of molecular tools it was difficult to even recognize their presence, much less articulate their functional roles. Dealing with this issue of incompleteness in community ecology is clearly an important challenge. But an even more important challenge may be dealing with the implications of such hidden players as perturbations on basic conceptual elements of ecological and evolutionary theory.

Think for a moment about how in community ecology, there was a historical clash between the world view of Clements (1916), and that of Gleason (1926) and Tansley (1935). Clements viewed communities as ensembles of species comparable in many ways to individual organisms, with homeostasis and other adaptations at the level of the entire community. (Parenthetically, please do not read me as meaning to beat on a scientist who lived nearly a century ago; his views may, in any case, have actually been more subtle than the usual textbook caricature, and so his name stands for a somewhat uncritical vein in ecological thinking.) Gleason, by contrast, argued that it was deeply misleading to think of communities as akin to individual organisms. This is not to say that one cannot make sense of the structure of communities (e.g., patterns in species diversity, or constraints on food chain length), but these explanations do not depend upon viewing these emergent features of communities as *adaptations* in the Darwinian sense. So when an ecologist studies the food web in a pond, the Gleasonian perspective is that it is not useful to think of the structure of the food web in that pond as an adaptation of the web as a holistic whole to its local environment. There is still some debate about this issue (e.g., Wilson, 1986), but I think it is fair to say this is the stance of most ecologists today.

But what about the traits of the individuals comprising the nodes in that food web—from the macrophytes cloaking the pond benthos, to the tadpoles in the shallows, to the bass at the top of the food web? A powerful conceptual framework has evolved over the last several decades that governs how we think about individuals, and that then feeds into how we envisage individuals are put together to make larger systems (communities, ecosystems). This framework basically asserts that the dynamics of populations, communities, and indeed entire ecosystems bear the imprint of individual traits, and that these traits in turn can be understood as Darwinian adaptations of individual organisms. Coulson et al. (2006) have recently laid out a formal procedure relating genes to traits, to vital rates, to fitness. The development of individual-based models in ecology is a veritable growth industry. The “phenotypic gambit” assumes that one can, to a first approximation, ignore the details of genetic architecture. Basically, for each suite of traits of an organism in a given environment, there is a function describing how fitness varies with the values of those traits. For instance, Vincent and Brown (2005) provide a formulation of Darwin’s postulates of evolution by natural selection in the perspective of game theory as follows: An individual organism possesses a heritable strategy drawn from a set of potential strategies (the G-function); the individual has an expected per capita growth rate (its fitness) that depends on both this inherited strategy, and the arrays of strategies that surround it (and their densities).

This world view has, of course, proven enormously productive, and there is a great

deal remaining to be done in working it out. But all world views have their limits. The word “limit” here is not meant in a pejorative sense, but rather in the sense that there may be ways the world view can be refined, clarified, or broadened. One could imagine a number of ways to enrich this world view. For instance, fitness functions are usually defined as growth rates, but in small populations demographic stochasticity looms large, and measures such as fixation probabilities may provide more accurate portrayals of the outcomes of selection. Non-selective evolutionary forces, such as drift, mutation, and gene flow, can lead to perturbations of populations from local adaptive optima, particularly in small, marginal populations (Holt, 1987; Rice, 2004).

These are all interesting and important topics, but what I want to focus on here is another potential limitation. Namely, note that the formulation of Vincent and Brown makes the primitive (in the sense of unexamined) assumption that the Darwinian logic applies to individual organisms. Ecologists almost always assume that the organisms revealed in standard surveys—lions, tigers, and bears—are unitary beings, to which it makes unquestioned sense to attach a single fitness function.

Yet, there is increasing evidence that just like the parasitoid with a hidden virus manipulating its oviposition behavior, the organism as a unit is a kind of approximation, under the surface of which is a seething reality of potential and realized competitive microunits. These squabbling intraorganismal players come in two basic forms.

First, the existence of sex itself makes organisms vulnerable to the proliferation of selfish genetic elements that can influence organismal traits. The term “selfish gene” has been familiar to all ecologists and evolutionary biologists since the publication of Richard Dawkins’ famous book, *The Selfish Gene* (Dawkins, 1976). Burt and Trivers (2006) have authoritatively reviewed our understanding of how genes within an organism can be in conflict over how the resources of that organism are to be expended. These conflicts can lead to maladaptations at the level of the entire organism. Individual traits may thus reflect, in part, the outcome of multidirectional, coevolutionary struggles between these competing selfish genetic units. The consequences of such struggles for overall measures of organismal adaptation, and issues such as scaling up from individuals to ecosystems, have barely been touched on to date.

Second, many species harbor an array of smaller-bodied taxa, whose very existence was not recognized until quite recently, and which are still poorly understood. Many phenotypic traits of macroorganisms such as vertebrates and terrestrial plants likely reflect the interaction of host genotypes with those of symbiotic microbes. The May 5, 2007 issue of *The Economist* (Anon., 2007, p. 100) reports that “besides the 10 trillion human cells in a body, there are another 100 trillion bacterial cells....the numerous species that make up this luxuriant community are estimated to contain about 100 times as many genes as the human genome proper” spread around the digestive, respiratory, and reproductive tracts, and the skin. The article goes on to note that the kind of bacteria present can influence the likelihood of contracting a wide range of disease syndromes, from diabetes, to autism, to cancer, to cardiovascular diseases. The diverse gut microbiota is also intimately involved in normal dimensions of healthy life, including in humans the pattern of maturation of our gut, energy metabolism, and resistance to patho-

gens (Dethlefsen et al., 2006). McFall-Ngai (2005) notes that humans, for instance, may contain thousands of species of bacteria (not to mention other taxa). This seems to be typical in vertebrates. Invertebrates, by contrast, by and large have simpler associations with microbes, more typically with a small number of commensal species (McFall-Ngai, 2005). One would, in general, expect the diversity of microbial commensals to scale with host body size, and with other factors such as generation length and foraging adaptations (Hall et al., 2007). It is tempting to speculate that such relationships could lead to systematic trends in the degree to which the host phenotype reflects coevolutionary compromises among many potentially competing entities, which might then influence, say, allometric scaling relationships in digestive traits.

As noted at the outset of this essay, the host–parasite literature is replete with tales about how parasites manipulate their host behavior so as to facilitate transmission of the parasite to other hosts. For instance, a trematode eye fluke (*Diplostomum spathaceum*) makes its intermediate host the rainbow trout (*Ocorhynchus mykiss*) more vulnerable to avian predation (Seppala et al., 2006). I think that the impacts of symbiotic microorganisms on host fitness and phenotypes may go well beyond obvious cases of parasitism.

Many healthy plants, for instance, have a rich ensemble of endophytes (fungi or bacteria) that live within plant tissues, including foliar endophytic fungi (FEF) and arbuscular mycorrhizal fungi (AMF) (Herre et al., 2007). When one sees a leaf, what is present is really a mosaic of fungal and “real” plant tissues. Herre et al. (2007) describe experiments showing that FEF in healthy host leaves, and AMF in roots, can both reduce foliar damage by pathogens in cacao. The diversity of FEF in leaves can be very high. Endophytes provide both direct defenses (e.g., antibiotics), and indirect effects via the host. The latter can occur because of impacts on overall host vigor (e.g., because the endophytes help acquire limiting nutrients), or because of shifts in the expression of host genes. If fungal effects on hosts are large, then as Herre et al. (2007) note, many familiar “plant” characteristics may in fact reflect emergent features of these intimate ensembles. Understanding basic traits such as the phenology of leaf shedding could require a consideration of the impact of microbial symbionts (van den Berg and van den Bosch, 2004).

A standard protocol in relating evolution to ecology is to assume that genes in an individual interact in complex networks to determine phenotypes, which then determine fitness in a particular environment. This is a “many-to-one” relationship. Maybe for many “organisms”, a more complex “many-to-many” relationship is required to describe the relationship between heritable units and phenotypic traits; when this is not the case, questions should focus on the specific mechanisms and evolutionary pathways that dampen out these inherently competitive relationships (Leigh, 1972; Buss, 1982). The “hidden players” of parasites and microbial mutualists are now recognized as playing important roles in governing dynamics of communities and ecosystems (Hudson et al., 2006). I suspect that in the decades ahead, an increasing number of organismal phenotypes will likewise be recognized to reflect coevolutionary struggles between “hidden players” and the macroorganisms that harbor them, more complex than the gene-to-phenotype-to-fitness mapping of standard accounts of adaptation. The traits of the macrophytic plants,

tadpoles, and bass in the Gleasonian pond noted above might themselves reflect the microbial communities they contain, and so, to some degree, the nature of these traits may be conceptually akin to the structure of community organization that emerges from the coevolutionary struggle among multiple species. To paraphrase a famous story involving William James, maybe “it is communities, all the way down.”

So, when I say “I”, maybe I really should say “we”, and when I say “you”, I should likewise say “you all” (I am from Tennessee, so can occasionally get away with that). Each of us contains multitudes.

ACKNOWLEDGMENTS

I again thank the editors for their invitation to write this series of essays, and the University of Florida Foundation for its support.

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