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Apparent Competition

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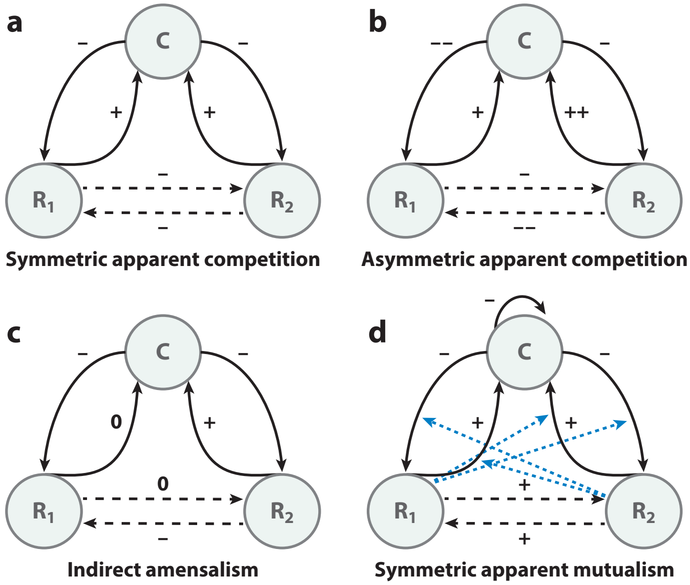
Abstract

Most species have one or more natural enemies, e.g., predators, parasites, pathogens, and herbivores, among others. These species in turn typically attack multiple victim species. This leads to the possibility of indirect interactions among those victims, both positive and negative. The term apparent competition commonly denotes negative indirect interactions between victim species that arise because they share a natural enemy. This indirect interaction, which in principle can be reflected in many facets of the distribution and abundance of individual species and more broadly govern the structure of ecological communities in time and space, pervades many natural ecosystems. It also is a central theme in many applied ecological problems, including the control of agricultural pests, harvesting, the conservation of endangered species, and the dynamics of emerging diseases. At one end of the scale of life, apparent competition characterizes intriguing aspects of dynamics within individual organisms—for example, the immune system is akin in many ways to a predator that can induce negative indirect interactions among different pathogens. At intermediate scales of biological organization, the existence and strength of apparent competition depend upon many contingent details of individual behavior and life history, as well as the community and spatial context within which indirect interactions play out. At the broadest scale of macroecology and macroevolution, apparent competition may play a major, if poorly understood, role in the evolution of species' geographical ranges and adaptive radiations.

BACKGROUND

Organisms are embedded in webs of interactions, including in particular those linking natural enemies (not just predators but also herbivores, omnivores, parasitoids, and pathogens) to their victims. Natural enemies can lower the population abundance and spatial distributions of their victims. Natural enemies can be tightly specialized, but more often they exploit a range of species, leading to the potential for indirect interactions among species inflicted by these shared natural enemies (**Figure 1**). "Apparent competition" is a phrase that today largely refers to an indirect negative interaction between individuals, populations, species, or entire functional groups, mediated through the action of one or more species of shared natural enemies. The term was coined in 1977 in the context of exploring how generalist predators could influence the structure of prey communities (Holt 1977, 1979).

A rich theoretical and empirical literature on this theme has developed over the subsequent 40 years including within the subdisciplines of applied ecology, such as conservation, invasion biology, biocontrol, resource management, and epidemiology. A review of manipulative experiments in



Symmetric apparent competition

Asymmetric apparent competition

Indirect amensalism

Symmetric apparent mutualism

Figure 1

Community modules (sensu Holt 1997a) corresponding to different forms of shared enemy effects. C denotes a natural enemy (e.g., a predator) and R two resource species (e.g., that predator's prey). The + symbol indicates a positive effect on the species at the head of the arrow (and ++ a stronger positive effect), the − symbol indicates negative effects differing in strength, and 0 indicates a negligible effect. So for instance, an increase in the abundance of prey species 1 boosts the food supply of the predator, which then increases in numbers (a + effect). Given straightforward numerical responses by prey and predators to each other (the *solid arrows* in the figure), as in the Lotka-Volterra community models found in Holt (1977, 1984), among others, (*a*) shared enemies are expected to generate the indirect interaction of apparent competition (the *dashed arrows*). (*b*) Asymmetries in this interaction can lead to strong differences in the magnitude of the effects, shading into (*c*) amensalism, where one prey has little direct effect on the predator and so exerts no indirect effect on the alternative prey, while being itself strongly affected by that alternative prey. (*d*) Finally, prey may directly affect predator functional responses (*blue dotted arrows*), and when the predator is in some fashion strongly self-limited (the self-limitation of C on itself), rather than apparent competition under shared predation, one can even observe apparent mutualism, particularly over short timescales but sometimes over long periods, too.

the intertidal zone revealed that approximately 25% of the experiments demonstrated apparent competition (Menge 1995), exceeding even exploitative competition in terms of measurable effects. A previous synthesis (Holt & Lawton 1994) linked apparent competition to the theme of enemy-free space (Jeffries & Lawton 1984). Excellent recent reviews have either focused on apparent competition in particular contexts, such as biological control (Chailleux et al. 2014, Kaser & Ode 2016, Heimpel & Mills 2017), conservation (Wittmer et al. 2013), and infectious disease ecology and invasion (Dunn et al. 2012, Strauss et al. 2012), or provided short overviews aimed at general audiences (Holt 2012, Morris et al. 2017). But there has been no broad synthetic review of apparent competition since 1994. According to the *Web of Science* (on February 6, 2017), there were 1,293 citations of Holt (1977), with over 1,000 appearing after the Holt & Lawton (1994) review, and many additional papers have dealt with apparent competition and related themes without this specific citation. Our goal is to provide a synoptic overview of this sprawling, multifaceted body of literature (emphasizing work since 1994) by highlighting conceptual issues and advances in shared predation theory; noting illustrative basic and applied empirical studies; and bringing out fresh links with infectious disease ecology, biodiversity patterns, and evolutionary biology.

A PRÉCIS OF IDEAS PRESENTED BY HOLT IN 1977, WITH UPDATES

Our review considers dimensions of apparent competition starting at the fine scale of individual organisms, then works up scales of ecological organization in space and time from population dynamics through community organization, and ends with sweeping issues in evolutionary biology and biogeography. But first, we ground our review by highlighting key points made by Holt (1977), which provides a natural springboard for considering recent advances in shared predation theory and practice. As delineated in each of the following sections, there are vital arenas of current research that go well beyond the ideas originally found in Holt (1977).

That paper focused squarely on two central questions of community ecology. First, what determines the composition of communities—in other words, which species coexist, versus which species are excluded from local communities? Second, for those species that do coexist: What factors govern their relative abundances? An ecologist might observe a distributional pattern where two related species do not overlap spatially or might carry out a manipulative experiment in which species A was removed and species B then increased in numbers. It might be reasonable to infer that these patterns reflect competition for resources or direct interference. Yet, Holt conjectured that an alternative class of explanations for such observations might involve the action of natural enemies. A plausible example came from hares on Newfoundland, where the relatively scarce arctic hare (*Lepus arcticus*) once roamed boreal forest but are now only found in tundra, following introduction of the snowshoe hare (*Lepus americanus*). Could this reflect resource competition between the hares? Bergerud (1967) suggested that instead abundant snowshoe hares sustained high lynx numbers, which then eliminated the arctic hare from boreal forest. Since this work, more detailed studies (e.g., Small & Keith 1992) suggest that the natural enemy culprit in this apparent competition tale is not actually lynx (though it may still play a role) but red fox, whose numbers also fluctuate with snowshoe hares. The arctic hare, which is highly susceptible to fox predation, is now restricted to rocky refugia in the tundra, where they can escape prowling foxes.

To explore more formally the idea of indirect interactions emerging from shared predation, Holt (1977) examined a general model for a single predator species feeding on multiple prey:

$$\frac{dR_i}{dt} = F_i(\vec{R}, P) = R_i[g_i(R_i) - f_i(\vec{R})P], \qquad 1.$$

$$\frac{dP}{dt} = G(\vec{R}, P) = PF_P(\vec{R}). \qquad 2.$$

(These equations encompass several specific models presented in Holt 1977.) Here, P and R_i are densities of the predator and prey species i, and the arrow over R denotes a vector of prey abundances, F_i is the total growth rate of prey species i, and G is the growth rate of the predator. In Equation 1, $g_i(R_i)$ is the inherent per capita growth rate of prey i, in the absence of the predator; $f_i(\vec{R})$ is the functional response of the predator to prey i; and the quantity $f_i(\vec{R})P$ is the per capita rate of mortality from predation experienced by prey species i. It is assumed that in each prey species, intraspecific density dependence operates but there is no direct interspecific competition among prey species. The right-hand side of Equation 2 states that the predator is strictly food limited; namely, its per capita growth rate F_P depends only on prey availability. Given that the predator persists, if the system settles to an equilibrium and if $\frac{\partial F_P}{\partial R_i} > 0$ (for each of two prey species), then the zero-growth isocline of the predator feeding on these two prey was shown to have a negative slope (see figure 1 in Holt 1977). Thus, if two prey species coexist at equilibrium, the abundance of each is necessarily lower than if it were alone with the predator (see figure 2 in Holt 2012). Alternatively, if the predator persists and the two prey species cannot coexist, then one prey indirectly excludes the other from the community by sustaining the predator. The qualitative assumptions made about population growth, leading to apparent competition, are simply that an increase in the abundance of each prey i benefits the predator, boosting its numbers, and that an increase in predator numbers then harms each prey. So in some sense, the negative effect one prey species might exert on others, as expressed at least in equilibrial abundances, should be generic to a very wide class of models and should also pertain qualitatively to the many natural systems matching the community module (Holt 1997a) of an effective generalist predator sustained by two or more prey species.

After reaching this general conclusion, Holt (1977) carefully noted that the idea that species could in some sense compete by sharing a predator has had a venerable history in ecology. Williamson (1957) in a single sentence crisply included shared enemies as a kind of competition under the rubric of controlling factors, but he did not elaborate this thought in any detail. Nor did anyone else. Yet one of the founding fathers of ecology, A.J. Lotka (1924, pp. 94–95), had long ago considered the introduction of a second prey species into a predator-prey interaction (which he represented in a model with exponential prey growth and constant attack rates), and he noted:

> A singularly interesting conclusion . . . [is that in] . . . fisheries . . . [the] presence of a common fish may cause the extermination of a rarer species which, were it present alone, would be protected by its very scarcity, since this would make fishing unprofitable. But the more abundant fish continues to render a balance of profit from the trawling operations, and thus the rare species, so long as any of it remains, is gathered in with the same net that is cast primarily for common species.

There it is, a crisp rendition of the basic idea of apparent competition, a half century before the term was coined. Lotka's prescient insight haunts us today. Humans are the dominant generalist predator/omnivore/disturbance agent across the globe, and many of our impacts in essence are manifestations of apparent competition. Branch et al. (2013), for example, describe opportunistic exploitation, where the hunting or logging of a species plunging to extinction remains viable because of the availability of alternative species, which permit continued economically viable harvesting by humans even on increasingly scarce species. Our spread as a species across the globe has led to the extirpation of many species in the vertebrate megafauna, and our ability to drive these species to extinction surely depended in part on the fact that humans also consumed other prey species that persisted and sustained our populations despite relentless exploitation. A multispecies model of Pleistocene overkill in North America makes a plausible case that apparent competition mediated by human predators was a driver of the mass extinction of many large-bodied vertebrates, such as ground sloths, mammoths, and mastodons, leaving behind smaller-bodied prey, such as deer and bison (Alroy 2001).

The above model, although rather general, does make several key assumptions, which when relaxed provide fertile ground for elaborations of theory and application to a broader range of empirical phenomena. One assumption is that predator growth rates are influenced by each prey species. Yet at times, even though a predator's own dynamic is governed by just one set of prey, it can also inflict mortality on species outside that set (a process called incidental predation) (Schmidt 2004, Schartel & Schauber 2016). Human agency leads to much incidental predation (e.g., bycatch in fisheries). Broad-spectrum pesticide and herbicide use is akin, in some ways, to generalist predation: Chemical applications intensify with increasing pest numbers, so the chemical bycatch of other vulnerable, nontarget species also rises (Rohr et al. 2006).

Holt (1977) assumed each of several prey species is harmed because it is consumed, so consumption of one prey species indirectly leads to harm on another species. Connell (1990) suggested that a species might instead provide a refuge for a predator or otherwise facilitate its foraging, aggravating attacks on a focal prey species. Some plant species can provide shelter to herbivores, which then more safely attack their food plants. Cacti grow better in the open than under the shade of shrubs, not because of direct competition from the shrubs, but because insect herbivory is more intense under cover (Burger & Louda 1994). Orrock et al. (2010b) developed a model demonstrating that refuge-mediated apparent competition could reverse the outcome of exploitative competition, permitting an invasive ratchet to unfold across a landscape (Orrock et al. 2010a). Invasion of a chemically defended seaweed species was facilitated because native herbivores found refuge there and then more effectively consumed native species of seaweeds nearby (Enge et al. 2013). In the Argentine Andes, nurse shrubs help tree seedling recruitment by moderating physical stress, but at the same time, they provide refuge for tenebrionid beetles, which consume those seedlings, generating a net negative effect of shrubs on tree recruitment (Chaneton et al. 2010). Refuge-mediated apparent competition can be viewed as one aspect of ecosystem engineering (Jones et al. 1994) and is related to (but not identical with) concepts such as associational resistance and associational susceptibility (Underwood et al. 2014). [In Holt (1977), apparent competition is used for essentially any negative-negative interaction between prey species (however measured), other than exploitative or interference competition; today, unadorned, the term usually denotes one potential effect of shared predation.]

To develop more detailed insights into how predation constrains community membership, Holt (1977; see also 1984) analyzed a special case of Equations 1 and 2, namely, a Lotka-Volterra model with logistic prey growth. The i^{th} prey species has intrinsic growth rate r_i; the predator has linear functional and numerical responses to each prey, with attack rate a_i. When rare, prey i's per capita growth rate is $r_i - a_i P$, so the maximal predator density it can tolerate is $P_i^* = r_i / a_i$. A dominant prey species under apparent competition should thus be one with a high r/a as it can both withstand and support high predator numbers. This suggested a P^* rule of thumb for apparent competition, paralleling the familiar R^*-rule of exploitative competition (Holt et al. 1994); a comparable rule holds in discrete generation host-parasitoid models (Holt & Lawton 1993). Increasing carrying capacity across all prey species indirectly boosts predator numbers, making it more difficult for prey species with low values of r/a to persist (Holt 1984, Holt & Lawton 1994); in a species-rich community, a given species could be excluded by diffuse apparent competition. If prey species vary greatly in r/a, those with low values are more strongly affected by apparent competition, whereas species with high values are resilient to shared predation. Such asymmetries in apparent

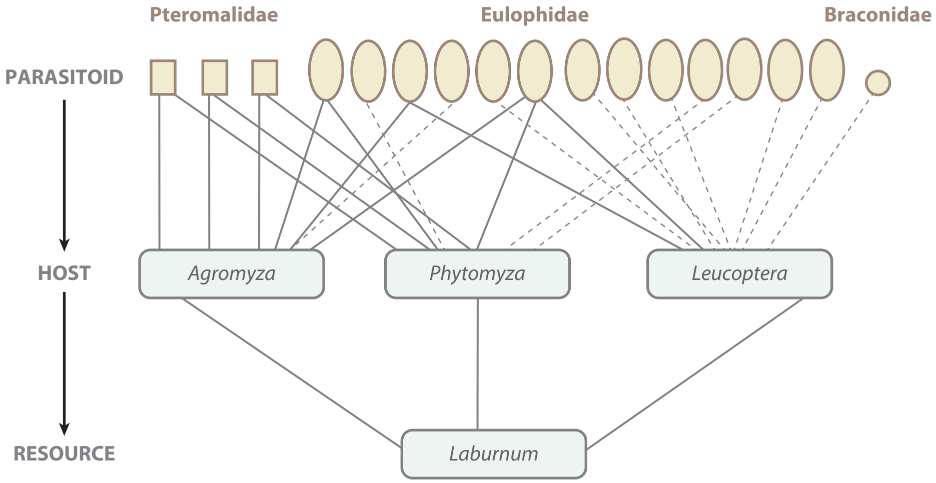


Figure 2

An example of a community subweb describing an insect host-parasitoid system. In this system, 50% of all realized interactions involve shared enemies. Translating food web diagrams into statements about such interactions and into dynamics requires teasing out the aggregative, numerical, and functional responses of shared natural enemies (Holt 1977, Bonsall & Hassell 1999) in the context of other sources of population regulation, such as resource-mediated exploitative competition (Chesson & Kuang 2008, Kuang & Chesson 2009) and nontrophic interactions, all modulated by spatial and temporal heterogeneity. In some empirical cases, shared predation identified from food webs does imply apparent competition, but in others, it actually corresponds to apparent mutualism. Figure crafted using data from Askew (1968).

competition are the norm, not the exception, in empirical studies (Chaneton & Bonsall 2000) and are expected on theoretical grounds (Brassil & Abrams 2004).

In natural systems, shared predation and other modes of interactions among species often act concurrently. In the food web depicted in **Figure 2**, there is likely a blend of exploitative competition, apparent competition, and other shared predation effects among the insect hosts (and if hyperparasitoids are present, a similar array of interactions may govern the dynamics of the parasitoid ensemble). There is a rich literature on the interplay of predation, direct competition, and exploitative competition in determining coexistence (Chase et al. 2002), and here, we only touch on some highlights. Early theoretical studies of community modules (sensu Holt 1997a) of a pair of competing species sharing a predator (e.g., Vance 1978, Armstrong 1979, Noy-Meir 1981, Holt et al. 1994, Leibold 1996, Grover & Holt 1998) demonstrated that predation could permit competitive coexistence if one species is superior at resource competition and the other is more resistant to attack by the shared predator. Weakening predation can then imply the loss of a key coexistence mechanism. Many empirical studies show that top predator removal indeed leads to substantial biodiversity loss and even drastic regime shifts, demonstrating the crucial role of predation for understanding species coexistence (Terborgh 2015). It is becoming increasingly recognized that understanding coexistence in multispecies communities requires food web perspectives.

The one-predator *n*-prey model of Holt (1977) is embedded in much recent theory exploring the food web dimension of species coexistence. Chesson & Kuang (2008) characterized the conditions for coexistence of prey at an intermediate trophic layer in a tritrophic system, where multiple species of top predators and basal resources have logistic growth (predators have resources other than the set of focal prey, and all functional responses are linear). They derived an elegant expression for coexistence of a pair of prey species, paralleling a familiar coexistence condition in Lotka-Volterra competition: $\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho}$. The inner term is the ratio of scaled relative fitness measures for each prey species evaluated at low densities, and ρ measures overlap via both shared resources and predators. The overlap measure involves weights, such as intrinsic growth rates; the net competitive interaction is more heavily influenced by resource competition when resources have slow rates of renewal, and the impact of shared predators is stronger if those predators only weakly depend on other prey outside the focal set. Prey can coexist if they completely share predators given sharp resource partitioning (as in the model of Holt 1977); conversely, multiple prey species, each with its own specialist enemy, can persist on a single resource. If specialist enemies have fast dynamics, this might be represented as direct, intraspecific density dependence, which can permit coexistence of multiple consumers contending for a single resource (McPeek 2012). In a multitrophic context, shared enemies as well as resources provide multiple avenues for niche differentiation via the partitioning of both resources and shared predators, as well as expanding the scope for density-dependent feedbacks (Meszéna et al. 2006). One issue in these results warranting more attention is the persistence of shared species. Abrams (1998) notes that there can at times be abrupt changes in competition coefficients as shared prey species are eliminated by apparent competition. Chesson & Kuang (2008) also assume strict trophic levels. Rossberg (2013) has derived formal expressions for coexistence in food webs, including more complex forms of food web interactions and blurred trophic levels (e.g., intraguild predation). He shows that, even with these more complicated patterns of consumption, apparent competition (which he calls consumer-mediated competition) is strong if direct density dependence among producers is weak and predators are efficient. These findings match the conclusions reached in Holt (1977, 1984).

An enduring issue in ecology is interpreting patterns of species diversity along environmental gradients. Holt (1977) briefly touched on implications of shared predation for diversity patterns. Some ecologists have argued that high diversity would be facilitated when productivity is high or abiotic conditions are benign. In the Lotka-Volterra model of shared predation, however, boosting basal productivity (prey K) or lowering the overall density-independent death rate hampers coexistence. There is substantial evidence (Schemske et al. 2009) for latitudinal gradients in biotic interactions, with higher herbivory, insect predation, and parasitism in the tropics. This might imply that the potential for apparent competition is stronger there. Oksanen (1990; see also Holt 1997a) argued that along gradients in primary productivity, apparent competition for a given set of shared predation relationships might be most evident at intermediate levels of productivity. The reason is that as productivity increases, other limiting factors (e.g., higher-order predators or interference among consumers) can increasingly constrain numerical responses of predators to their prey. To assess hypotheses such as this, it would be valuable (if daunting) to have more cross-system comparisons, comparable to Menge's (1995) pioneering analyses of indirect interactions in the intertidal zone.

Holt (1977) then relaxed some assumptions of this Lotka-Volterra model. Making prey growth nonlogistic does not by itself much matter. However, if prey growth exhibits an Allee effect (positive density dependence at low densities), alternative stable states under shared predation can emerge. Combining resource competition with apparent competition, and assuming a fixed amount of basal resources (Holt et al. 1994, Grover & Holt 1998), can also generate alternative stable states, even without direct Allee effects. Depending on initial conditions, either prey species could coexist with the predator and exclude the other. Chase (1999) extended this model and tested it in a microcosm (Chase 2003), where two pulmonate snails were preyed on by a giant water bug. As predicted by theory, at intermediate levels of enrichment, alternative states arose, reflecting the interplay of resource and apparent competition. This experiment diverges from the assumptions of Holt

(1977) as the snails have a refuge in size (i.e., stage structure). Another form of population structure important to the interaction between natural enemies and their victims is their spatial distributions. Holt (1977) showed that if a prey species has absolute refuges protecting some individuals, this could make persistence more difficult for those prey species lacking refuges. If refuges exist in limited supply, they can also become objects for competition, with emergent consequences for prey species coexistence (Holt 1987). Mentioning refuges was the only consideration of either spatial processes or population structure in Holt (1977); we return to this important topic below in the section titled Population and Community Dynamics.

Important, realistic complications arise if predators have nonlinear functional responses (Holt 1977). With a saturating functional response, "Over short time periods . . . prey species exhibit mutualism" (Holt 1977, p. 215), but at equilibrium, they still experience apparent competition, provided the predator diet choice is adaptive and the predator is food limited. This functional response could be destabilizing; Holt (1977) admits to not knowing what happens then. Subsequent work (e.g., Abrams et al. 1998) has shown how nonlinear functional responses combined with unstable dynamics can weaken apparent competition and in some cases even lead to the emergence of apparent mutualisms. Strong frequency-dependent predation (switching) (Murdoch & Oaten 1975) relaxes constraints on coexistence without necessarily eliminating apparent competition at equilibrium. Altering the assumption about predator food limitation can profoundly change predictions about shared predation (Holt 1977). Predator interference constrains numerical responses and could reduce the functional response to any given prey (Arditi & Ginzburg 2012); predator interference thus tends to weaken apparent competition. If the shared predator is limited to a fixed abundance, say by a higher-order predator or a nontrophic resource, one might not see apparent competition at all; indeed, given saturating functional responses or switching, prey species sharing predators might exhibit "apparent mutualism" (Holt 1977, p. 217) at equilibrium. Examining shared predation with this broader spectrum of possibilities for predator functional and numerical responses has been a major theme in subsequent decades of research on shared predation.

Holt (1977) mainly developed theoretical ideas but did mention illustrative empirical examples: hares on Newfoundland, disjunct distributions of zooplankters, and mites in peach orchards (Holt 1979 discussed many more). Our review cannot possibly discuss the very substantial number of interesting empirical studies in recent years that have shed light on the implications of shared predation, but we should mention a few compelling case studies. Manipulative field experiments provide the most convincing evidence for (or against) apparent competition. On the Åland Islands off Finland, cocoons of a primary parasitoid are hyperparasitized by a generalist parasitoid (van Nouhuys & Hanski 2000). Addition of cocoons of a second noncompeting primary parasitoid led to a sharp decline the next year of the focal species, a clear experimental manifestation of apparent competition. In a hyperdiverse tropical community, Morris et al. (2004) developed a quantitative food web for a guild of leaf-mining insects, identifying which host species shared parasitoids. They then removed a dipteran and coleopteran host and showed that the remaining host species had substantially lower parasitism rates the following year. Molecular techniques now permit investigators to construct food webs that embody much more information about interactions than was possible in the past. One example is a rich tropical assemblage of squash flower–feeding herbivorous insects and their parasitoids (Condon et al. 2014); the structure of this web is consistent with the action of apparent competition (Godfray 2014).

Apparent competition theory has largely focused on interactions among a relatively small number of species (as in the community modules, championed by Holt 1997a, in **Figure 1**). The development of quantitative food webs for complex multispecies communities is a great step forward, going beyond the sort of qualitative food web depicted in **Figure 2** and the simplified modules of **Figure 1**. Quantitative food webs provide plausible hypotheses about which species might experience apparent competition (van Veen et al. 2006), but they really must be interpreted cautiously. Some links may be missing because predation or parasitism is simply too strong, so a species is absent or found only in microhabitats where it enjoys refuge from attack (the dynamic monophagy of Holt & Lawton 1993). Tack et al. (2011) constructed a quantitative food web for leaf miners and parasitoids on oak and then altered the number of one leaf miner species. Instead of apparent competition, the manipulation boosted the numbers of the others—apparent mutualism! In a whole-community manipulation, by contrast, where all lepidopteran larvae were reduced by a lepidopteran-specific insecticide, Frost et al. (2016) showed that quantitative food webs indeed could be used successfully to predict changes in parasitoid attack rates and subsequent host abundances. This study dramatically validates the hypothesis that apparent competition can be an important structuring force in insect communities, but the contrast with the findings of Tack et al. (2011) points out the need to articulate more carefully the contingent features of ecosystems that can promote (or weaken or even eliminate) apparent competition. A particularly important direction for future research is to embed analyses of apparent competition due to shared predation into much broader analyses of complex food web structures to predict such qualitative differences among communities. Roslin et al. (2013), for instance, show that in the high Arctic shared predation syndromes in host-parasitoid interactions suggest much scope for apparent competition. Yet avian predation and spider predation account for at least as much mortality as do these shared parasitoids, and birds, spiders, and parasitoids all in turn engage in intraguild predation, which can weaken interactions due to shared natural enemies among alternative prey/hosts in the food web. A large open challenge is to determine how to relate empirical patterns of food web interactions (e.g., **Figure 2**) to strong quantitative assessments of apparent competition in complex food webs. Resources are always important to organisms, and so resource competition has an ever-present potential to emerge for organisms sharing resources. Resource availability moreover can indirectly influence a prey species' ability to withstand predation; a species with abundant resources may be able to have a high intrinsic growth rate, which allows it to persist in the face of high predation rates. By contrast, as examined in more detail below in the section titled Behavior and Other Plastic Traits, shared predation can at times lead to positive interactions among species (see **Figure 1*d***), and whether this occurs, rather than apparent competition, depends upon many contingent details of particular systems.

We now examine apparent competition across a sweep of biological organization, starting at the most intimate scale—that within individual organisms.

WITHIN-ORGANISM APPARENT COMPETITION

There has been a growing recognition that the internal workings of individual organisms can be fruitfully viewed through the lenses of population and community ecology. Multicellular organisms are ensembles of populations of distinct cell types, and the interactions between these cell populations and invasive pathogens can reflect all the basic processes of population and community ecology. All organisms larger than viruses harbor symbionts (e.g., our microbiome) that can influence organismal fitness (Holt 2007, King & Bonsall 2017). Microcosm studies of microbial assemblages reveal the potential importance of apparent competition effects for driving microbiome dynamics. Chemostat experiments (Bohannan & Lenski 2000) have examined how productivity governs interactions between two populations of *Escherichia coli* sustaining a natural enemy, the bacteriophage T2; one bacterial strain was better at resource exploitation, whereas the other was partially resistant to infection. As theory predicted, with increasing productivity, the latter replaced the former due to apparent competition outweighing resource competition. One could imagine comparable interactions occurring in one of the natural habitats of *E. coli*, namely, the lower intestines of endotherms.

Beyond interactions within the microbiome, given that multicellular organisms are really just complicated sets of interacting cell populations, there are many analogs of apparent competition within the habitat patch of the organism defined by its skin, involving interactions among cell populations. One such interaction is between host cells and hostile populations of invasive pathogens and parasites. The immune system (which acts in many ways like a generalist predator within hosts) can act as a powerful weapon in enhancing or diminishing the effects of alternative pathogens. There is considerable applied interest in this manifestation of apparent competition because of its potential importance in the control of disease organisms and their vectors.

Experiments confirm the role of immune responses in mediating apparent competition among pathogens. Råberg et al. (2006) examined mixed infections of virulent and avirulent clones of the malaria parasite *Plasmodium chabaudi* in both immune-deficient and immune-competent mice. They showed that densities of the avirulent strain of *Plasmodium* were suppressed much more in immune-competent than in immune-compromised hosts due to prior infection with the virulent strain (and the effect was strongly asymmetric, as in field studies of apparent competition) (Chaneton & Bonsall 2000).

Apparent competition could play a role in the evolution of virulence, which is usually measured by the rate of parasite-induced host morbidity or mortality (often associated with increased parasite yield, broadly reflecting resource transfers from hosts to parasites). By creating a novel immunological environment, an invading pathogen may eliminate competing commensals that are not harming their host (Brown et al. 2008); if this provoked, nonspecific immune response is density dependent (i.e., becomes stronger with the abundance of the invasive pathogen), the outcome of this modification of the internal host environment essentially is an apparent competition effect.

Immunity-mediated apparent competition has many nuances, and sometimes indirect positive interactions are observed. For example, consider maternally inherited *Wolbachia*. Infections by this bacterium in *Aedes aegypti* can inhibit *Plasmodium gallinaceum* development by stimulating the immune system and can also inhibit flaviviral infections such as dengue and chikungunya (Moreira et al. 2009). By contrast, some strains of *Wolbachia* enhance infections by other pathogens. The virulence of different *Wolbachia* strains in mosquitoes can affect their interaction within the host: The avirulent wAlbB strain increases *Plasmodium berghei* in *Anopheles gambiae*, whereas the virulent wMelPop strain suppresses *Plasmodium* (Hughes et al. 2012).

We expect that all of the real-world complexities of shared predation we touch on in this review—for instance, the spectrum from apparent competition to apparent mutualism, the role of spatial and temporal variation, controls on species diversity, and eco-evolutionary dynamics—have analogs in the within-host landscape. The biology of *Wolbachia* provides a case in point where the application of ecological theory could help illuminate the already known diversity of outcomes. *Wolbachia* is an intracellular parasite; its replication is linked to the dynamics of the host cell cycle (e.g., Pinto et al. 2013). Cell cycle dynamics are inherently oscillatory, and the interplay of such oscillations with pathogen or commensal population dynamics and immunodynamics could lead to either apparent competition or apparent mutualisms because of the interplay of time-averaging and nonlinear interactions, much as in predator-prey systems (Abrams et al. 1998).

Although the immune system may be treated at first pass as a kind of generalist predator, a mediator of multispecies interactions among pathogens akin in some key respects to generalist predators in a lake, the organismal system in which this interaction plays out is complex and (unlike a lake) presumably has been sculpted as a whole by natural selection. Fuller explication of the molecular/ecological details of the (incredibly ornate) immunological system, coupled with clear ecological theory, could advance our understanding of how the immune system and apparent competition emerging from immune responses can drive parasite dynamics and virulence evolution within individual hosts (e.g., King & Bonsall 2017).

Other dimensions of apparent competition lurk under the skin. Roy & Wodarz (2014) argue that the inherent feedbacks governing cell dynamics within hosts can entail apparent competition dynamics. Complex regulatory processes underlie the homeostasis of cell populations. Viruses and cancers perturb such self-regulation. If stem cells are infected, both uninfected and infected stem cells can produce negative feedback signals that each type responds to, constituting a kind of abstract predator that clamps down on further cell growth. As both cell types can produce such signals, there is the danger that one can go extinct, and indeed considering demographic stochasticity, both might be lost given time lags in cell signaling responses.

Another arena where apparent competition could matter within hosts is the use of viruses to treat cancer. The whole point of oncolytic therapy is to introduce a natural enemy, a virus that attacks cancer cells. Obviously, one would not want such a virus to attack all host cells (one shudders at the thought). But is the optimal therapy achieved with a completely specialized virus that only goes after cancer cells? For single viral inoculations, what one might observe is fade-out, once cancer cells get below a density threshold where viral $R_0 < 1$. In this case, there is a danger the cancer might persist to reemerge later. If instead, the treatment virus can use to some extent healthy host cells, then via apparent competition, the healthy cells of the host can indirectly help drive the cancer population to extinction. Okamoto et al. (2014) developed theory toward this end with models tailored toward an oncolytic vesicular stomatitis virus and an oncolytic herpes simplex virus, both subjects of cancer treatment research. The clinical expectation is that in the short term the ability of the oncolytic virus to infect healthy host cells to a small degree could speed up the near-elimination of cancerous cells via apparent competition. In practice, of course, there are obvious risks of this approach. However, these would have to be balanced against the harm that alternative treatments, such as chemotherapy, entail, and the fact that, for some suffering ill individuals, almost anything is worth trying in the face of imminent death from aggressive cancer.

BEHAVIOR AND OTHER PLASTIC TRAITS

Now we go up one level to individual organisms. Population dynamic models such as those in Equations 1 and 2 are instantaneous expressions of forces acting on the lives of individuals in the here and now. Even with fixed predator populations, behavioral flexibility and other trait-mediated effects can permit alternative prey species to affect a focal prey, mediated through shared predators; such impacts of trait plasticity can scale up to larger spatial and temporal scales, sometimes in surprising ways. Many applied problems mandate answers over short time horizons. For example, a farmer plants her field and wants to know if facilitating a generalist predator such as a ladybird beetle might help prevent a pest outbreak within a single season (and yes, it can) (Harmon et al. 2000). Short-term, nonequilibrial dynamics are then the norm.

Holt & Kotler (1987) examined how alternative prey might interact in a local community via effects on individual predator behavior over relatively short timescales. They noted several spatial and temporal scales relevant to this issue. In a closed community over short timescales, one might gauge how attacks on prey species A are influenced by manipulating the abundance of prey species B (and vice versa). In the simplest case, a predator has fixed encounter rates with prey while foraging and invests a fixed handling time per captured item. These assumptions imply a classical disc equation (Murdoch & Oaten 1975). Instantaneously, increased density of either prey depresses attacks on the other (time spent handling one species is not available for encountering and capturing the other). As Abrams (1987) also notes, this entails short-term mutualism between prey, assessed by instantaneous growth rates. This effect has great practical importance: If predators allocate effort or time to particular prey when they become more common, this weakens predation upon other prey (e.g., in the Gir sanctuary of India, livestock draw lion attacks away from coexisting ungulate prey of conservation concern) (Sundararaj et al. 2012).

In open systems, another short-term behavioral decision predators make is to enter or leave patches. An upsurge in prey numbers in a given patch can lead to an aggregative numerical response, where predators flood there to enjoy increased foraging success. This has several consequences. One simple effect is that if this behavioral response occurs within a predator generation (so predator numbers as a whole are fixed), an increase in predator numbers in the focal patch entails reduction elsewhere in the landscape in predator numbers, relaxing predation elsewhere (Holt 1987). Ergo, there is an emergent landscape-level mutualism. But within the focal patch, a number of interesting potential effects emerge.

As predators aggregate into a patch, prey numbers there become depleted. At some point, predators abandon ship and seek greener pastures elsewhere. If at this point of departure predators satisfy rules of classical optimal foraging theory (i.e., only eat something if it enhances fitness), do not interfere with each other, and are generalists when they leave, the remaining density of each of two prey species in the focal patch is depressed by the presence of the other (Holt & Kotler 1987). In other words, optimal foraging in predators implies an emergent negative-negative interaction among prey within patches. If one conducts an experiment, the immediate effect (before predator numbers change) might be that alternative prey relax predation upon each other (apparent mutualism, e.g., the presence of whiteflies relaxed mite predation upon western flower thrips in short-term experiments in greenhouses) (van Maanen et al. 2012). As time goes on, the potential for apparent competition should grow, either because of aggregative numerical responses by a mobile predator in open systems (within predator generations) or because of reproductive numerical responses (across generations) in both closed and open systems.

Constraints on the predator may prevent these expectations from being realized (Holt & Kotler 1987). For instance, if predators cannot discriminate among prey varying in quality, prey within patches may exhibit a combination of positive and negative interactions. High-quality prey in a patch attract predators, thus increasing mortality on low-quality prey there (a negative indirect effect). Low-quality prey reduce the overall value of foraging in a patch, so predators are more likely to leave (leading to a positive indirect effect on the high-quality prey). An analogous phenomenon in parasitoids is egg wastage, where a female deposits eggs on low-quality hosts. If her egg supply is limited, there are both reduced attacks on high-quality hosts in the current generation and lowered parasitoid population size in the next generation. This can lead to a combination of positive and negative indirect interactions between alternative hosts (Hoogendoorn & Heimpel 2002). If predators enter and leave a patch at random, alternative prey in that patch might exhibit positive-positive (mutualistic) interactions, as there is no numerical response by the predator and time spent feeding on one prey provides a respite from predation for another. Paying attention to the details of predator behavior in terms of diet choice and patch selection, and to the temporal scale of one's inquiry, thus has distinct effects on the strength and even sign of indirect interactions among alternative prey, as almost anything is possible given the right combination of patch use and diet choice strategies by the predator.

An abundance of literature suggests these expectations are often borne out. For instance, an invasive species, the Asian nest mussel, attracted predators such as drilling gastropods to patches even with relatively modest numbers of the invasive species, and these predators then also attacked native clams and depressed their numbers—an aggregative numerical response by predators leading to apparent competition between the invasive and native mussels (Castorani & Hovel 2015).

Modes of behavioral flexibility other than patch use and diet choice can alter the form of the models of Equations 1 and 2 in fundamental ways, with implications for shared predation. Holt (1977) suggested that predator switching relaxes the impact of apparent competition on coexistence, and this conjecture has been confirmed in subsequent theoretical analyses (Krivan 2014). Parasitoid learning in which individuals tend to return to the host on which they were raised permits alternative host species to coexist under shared parasitism (Hastings & Godfray 1999), relaxing the tendency toward exclusion via apparent competition suggested by simpler host-parasitoid theory (Holt & Lawton 1993).

The models in Holt (1977) assumed that functional responses depend solely on prey numbers. There is increasing evidence this need not hold: The functional response can depend on predator density, and this can arise because of labile prey behaviors. Abrams (1987) presented a model in which prey balance rewards of foraging against the risk of predation, and prey can only be caught during time spent foraging (with capture risk increasing with the square of time foraging). If two prey have fixed behaviors, each prey depresses the other's equilibrial abundance. If instead prey adaptively forage, their own consumption rates become functions of predator density, and the rate of predator attack becomes inversely proportional to predator density. In effect, predators indirectly interfere with each other via the prey's adaptive behavior. Abrams (1987) shows that if each prey species can overexploit its own resource the effect of shared predation is mutualistic, as predation keeps overconsumption by each prey in check. Introducing predator interference into the functional response counters increases in predator numbers and so weakens the negative effect of shared predation. In terms of the models of Equations 1 and 2, the predator is no longer strictly food limited, and both the prey growth term and the functional response can be functions of predator density.

Apparent competition can also result from plastic changes in traits other than behavior. The predatory protozoan *Tetrahymena vorax* increased in size when fed *Colpidium kleini*, which then allowed it to also consume and, over time, eliminate *Paramecium aurelia* (Banerji & Morin 2014). There is increasing interest in trait-mediated indirect interactions (Ohgushi et al. 2012), and many of these interactions entail apparent competition.

POPULATION AND COMMUNITY DYNAMICS

To understand the potential implications of apparent competition for species' distributions and abundances—the next level in our ascending hierarchy—requires long-term studies tracking species over time and space. Experimental studies on the long-term population-level outcomes of apparent competition are difficult to undertake. Documenting both the numerical and functional responses of a shared natural enemy, and the responses of its victims, requires long-term, multi-generation experiments. This is a challenge in natural systems and a real advantage for laboratory microcosms (Bonsall & Hassell 2005). Using a simple and well-characterized laboratory system, Bonsall & Hassell (1997) showed that the shared parasitoid, *Venturia canescens*, drove apparent competition effects between two hosts, *Plodia interpunctella* and *Ephestia kuehniella* (the experimental setup precludes direct competition). These population dynamics experiments demonstrated that the inferior apparent competitor, *Ephestia*, was driven extinct because it had a longer development time and hence, overall, a lower growth rate (**Figure 3**). In this example, the dominant apparent competitor did not seem to sustain the higher average parasitoid abundance, suggesting the effects of complexities (in this case, stage structure, nonequilibrial fluctuations in abundance, and spatial dynamics) that were left out of simple models of shared predation such as Equations 1 and 2.

Despite their inherent challenges, a growing number of case studies from natural ecosystems involve a significant apparent competition theme, often using a combination of comparative observations, experimental manipulations, and theory tailored to the details of particular systems. For example, an endangered butterfly, the alcon blue (*Maculinea alcon*), lays its eggs on an endangered gentian, *Gentiana pneumonanthe*, and early instar caterpillars of the butterfly are herbivores

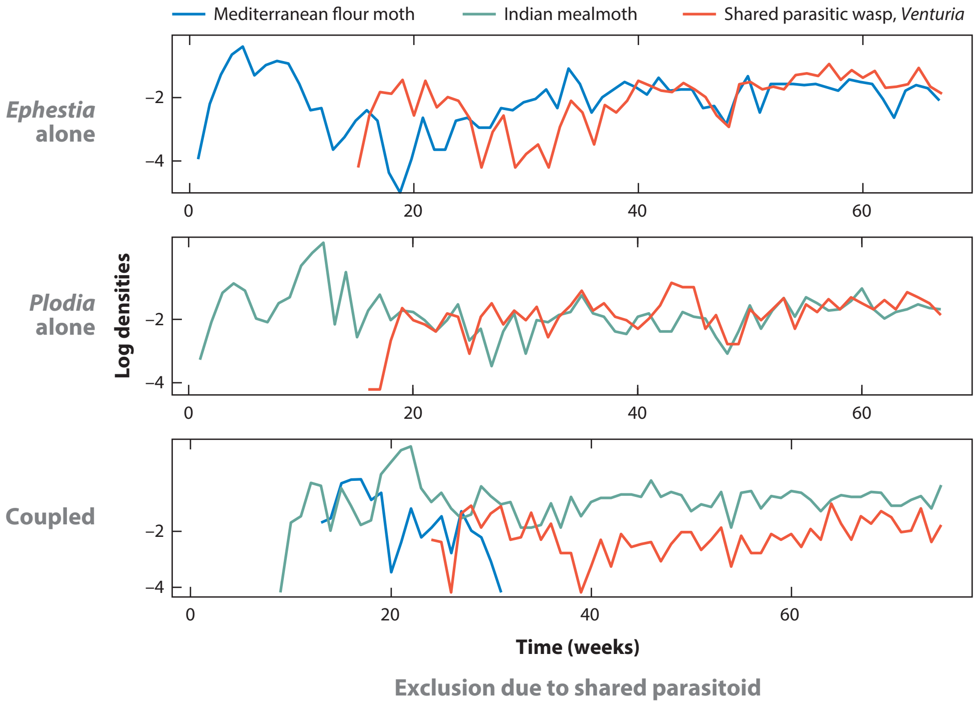


Figure 3

An experimental demonstration of strong exclusion due to apparent competition in a spatially distributed system. The time series are drawn from data from the population cage experiments described in Bonsall & Hassell (1997, 1998, 1999). (*Top*) One host, *Ephestia kuehniella* (Zeller), the Mediterranean flour moth (*blue curve*), coexists with the parasitoid *Venturia canescens* (Gravenhorst), an ichneumonid endoparasitoid wasp (*red curve*), in one cage. (*Middle*) Another host, *Plodia interpunctella* (Hubner), the Indian mealmoth (*teal curve*), coexists with the parasitoid. (*Bottom*) When the two cages are connected, allowing parasitoid movement, *Ephestia* is rapidly excluded. This outcome occurred repeatedly. As noted in the text, this instance of apparent competitive exclusion does not match the P^*-rule of simple theories.

on gentians. After eating gentian leaves, the caterpillars drop to the ground and enter nests of the ant *Myrmica scabrinodis*, where the caterpillars are parasites on the ants (Mouquet et al. 2005). This leads to an apparent competition interaction between the ant and the gentian, mediated through the complex life history of the shared natural enemy. Parameterized models suggest that apparent competition in this field system is strongly asymmetric, with ants more strongly affected, and moreover that apparent competition is quantitatively important only at intermediate successional stages. This work highlights challenges in devising effective conservation strategies for these species because of the many contingent factors influencing the strength of the indirect interaction.

Apparent competition is often evident as an element of the ongoing dynamics in many empirical studies, even if it is not always the dominant theme. Some notable examples of case studies involving apparent competition in complex natural ecosystems include: the wolf-moose-caribou interaction of Canada (Wittmer et al. 2005); the winter moth, interacting with a host of other moths via shared natural enemies (Ammunét et al. 2014); interactions between grouse and voles, both attacked by hen harriers (Barraquand et al. 2015); mink feeding on water voles and rabbits (Oliver et al. 2009); and an interaction between ring-necked pheasant and gray partridge, mediated by a nematode (Tompkins et al. 2000).

Speaking of nematodes, we could have spent this entire review focused entirely on the fascinating consequences of shared parasitism. Examples of pathogen-mediated apparent competition have long been known (Holt 1979), and a growing body of formal theory exists dealing with parasite-mediated apparent competition (an early example is provided in Holt & Pickering 1985). The topic is currently getting increasing attention (e.g., Mordecai 2011) in part because of its great practical importance in public health, conservation, and resource management. Introduced generalist pathogens can have devastating impacts on communities. The introduced soil-borne pathogen *Phytophthora cinnamomi* is wreaking havoc on species-rich plant communities in many habitats across Australia, as it is a hypergeneralist capable of infecting some thousands of host species (Cahill et al. 2008). Some species are more vulnerable than others and are experiencing elevated extinction risk because of this shared pathogen. As with predation, an alternative host can indirectly influence parasitism in a focal host either via numerical effects (e.g., spillover infection, as when some host species when infected transmit many pathogen propagules to susceptible hosts without being harmed themselves, as in the sudden oak death epidemic in California forests; Cobb et al. 2010) or via behavior- and trait-mediated effects on, for example, transmission (Keesing et al. 2006). A consideration of behavior- and trait-mediated effects is likely to be particularly important in shared, vector-borne disease systems, where vector behavior can strongly modulate infectious disease dynamics (Bonsall & Holt 2010).

Holt (1977) assumed predator and prey populations were unstructured. A rich avenue for work on shared predation that is just getting under way is to examine the consequences of different forms of population structure for indirect interactions among prey. Ontogenetic shifts in the size structure of predators can influence the structure of prey communities (e.g., Rudolf & Rassmussen 2013) because key aspects of functional responses (attack rates, handling times) change during ontogeny, often reflecting adaptive responses by both predators and prey. It is well known that enrichment can destabilize predator-prey dynamics. Bonsall & Holt (2003) examined how enrichment influences apparent competitive interactions in a stage-structured system, where alternative prey species were exposed to predation during a vulnerable life stage. The length of this stage was not fixed but varied in accord with resource availability (development was faster with more resources). Each of two prey species was assumed to have a distinct resource base, but both prey were attacked by a shared predator. In contrast to unstructured models (e.g., Holt 1977), exclusion was not more likely at high productivity, and indeed, the coexistence of apparent competitors was helped by unstable dynamics. So introducing stage structure can qualitatively alter expectations about species coexistence under shared predation.

One significant limitation in Holt (1977) was that communities were assumed to reach a stable point equilibrium. This is unlikely to hold in many natural systems, such as those that experience seasonality and stochastic variation as well as those that exhibit unstable or transient population dynamics emerging from nonlinear interactions. In simple models with exponential prey growth and linear functional responses, the winning prey is still simply the one sustaining the greater time-averaged predator population even if growth rates fluctuate (Holt & Lawton 1993, Holt 1997a). This outcome changes, sometimes radically, when prey experience direct density dependence and functional or numerical responses are nonlinear. Abrams et al. (1998), for instance, examined a two-prey, one-predator model with saturating functional responses and direct prey density dependence. Apparent competition is usually weakened by cycling, and sometimes apparent mutualism emerges. Removal of one prey can reduce the time-averaged density of the other, and the short-term effect of abrupt removal of one prey species is often an increase in predation upon another (Serrouya et al. 2015). The introduction of predators can lead to long-term transients and elevated risks of extinction for prey experiencing relatively high attack rates during these transient phases, even in systems where the long-term equilibrium permits prey species coexistence (Holt & Hochberg

2001). Predator switching (which is expected to facilitate coexistence in stable systems) can actually be destabilizing and lead to prey extinction when combined with unstable population dynamics (Abrams & Kawecki 1999).

Phenology and seasonal variation can also drive apparent competition effects. Plants that produce leaves early in a growing season have been suggested to sustain herbivores through the end of a lean winter season, which then permits those herbivores to devour plant species with later leaf production (Smith & Hall 2015).

The spatial structure and dynamics of interacting populations can be critically important for understanding apparent competition (Morris et al. 2005). Holt (1984) argued that given sedentary prey and mobile predators, optimal habitat selection by predators should ameliorate apparent competition among prey that show habitat segregation along axes that predators can use in habitat selection. Interspecific interactions are often sensitive to abiotic conditions (e.g., Schoen et al. 2015), so such axes of differentiation (e.g., along thermal gradients) could be important in understanding regional species coexistence under the influence of shared predation. Understanding the spatial complexities of apparent competition requires separating out the demographic processes associated with dispersal from the action of the shared natural enemy. Building on studies investigating coexistence in direct competition, theoretical studies have revealed how strong apparent competitors can persist even in homogeneous landscapes due to spatial dynamics, with several distinct mechanisms at play. First, inferior apparent competitors (those that suffer higher attacks or have lower host growth rates) may be superior dispersers from patches with the superior apparent competitor and natural enemy. Second, and more surprisingly, even sedentary inferior apparent competitors can persist because the superior species in apparent competition diffuses away from patches containing the natural enemy (Bonsall & Hassell 2000). King & Hastings (2003) note that partial dispersal can lead to a kind of rescue effect, facilitating coexistence; again, this often seems to reflect demographic trade-offs, such as that between fecundity and resistance (a less fecund apparent competitor may coexist with the other prey species if it experiences lower attack rates).

Organisms with complex life histories often move between habitats at metamorphosis (e.g., dragonflies, frogs), providing a conduit for indirect interactions between spatially segregated prey species (Schreiber & Rudolf 2008, McCoy et al. 2009). Many pathogens and parasites require multiple hosts to complete their life cycles, resulting in opportunities for apparent competition. For example, the heteroecious fungus *Puccinia graminis* infects many grasses. It persists through the winter only if alternate hosts are present, in particular the common barberry, *Berberis vulgaris*. In the early twentieth century, approximately 300 million barberry bushes were eradicated in the north-central United States, leading to reduced crop damage of approximately 60% (Fulling 1943; discussed with other examples in Holt 1979). The two kinds of hosts are spatially segregated and are coupled because of aerial dispersal of fungal spores. Predators or prey moving among habitats can likewise lead to spatially mediated apparent competition. This can occur in a metacommunity context because predators colonize patches and drive local extinctions of prey (in theory, as in Holt 1997b, and in practice, as in Cronin 2007). Movement of prey across habitat boundaries can likewise sharpen apparent competition in focal habitats, given predators capable of strong numerical responses to their prey (a spatial subsidy effect) (Polis et al. 1997).

FUTURE DIRECTIONS: APPARENT COMPETITION, EVOLUTION, AND THE ORGANIZATION OF BIODIVERSITY

What is the role of apparent competition in explaining broad biodiversity patterns? Multispecies models help explore this question. In a model of interacting phage and competing bacteria, diversity buildup involves a narrowing of parameter space and a codiversification of phage with bacteria

(Haerter et al. 2014); the interactions are a blend of direct interference among bacteria, resource competition among phage, and apparent competition via the phage among the bacteria. Moreover, there is more to community ecology than understanding species coexistence within trophic levels. Apparent competition plays a role in explanations of why food chain length is typically short in ecological communities (Post & Takimoto 2007) and often lies under the surface in many theoretical explorations of food web dynamics.

Ecologists now recognize that understanding biodiversity patterns requires considering historical and evolutionary processes over a range of temporal and spatial scales from rapid eco-evolutionary dynamics to the slow diversification of clades due to speciation, range shifts, and extinction. Holt (1977) concluded with thoughts about the evolutionary dimensions of apparent competition. An overexploited prey selected to experience lowered attacks could actually boost predator numbers, thereby intensifying predation upon alternative prey. It was suggested that apparent competition could drive character displacement and play a role in adaptive radiation. Finally, it might be anticipated that predators would evolve to increase their attacks on relatively abundant prey, and given trade-offs in attacks across different prey species, this could spare rarer prey. A final thought in Holt (1977) is that to understand the relationship between coevolution and community ecology, one needs to cast evolutionary arguments in the context of explicit population dynamics models.

This latter suggestion is particularly salient if evolutionary and ecological dynamics occur over comparable timescales. Lau (2012) provided an example of how the strength of selection on defenses in an introduced plant in response to a herbivore was strengthened when an alternative host plant sustained greater herbivore numbers. Schreiber et al. (2011) examined in a theoretical model a predator attacking two prey, where the predator has phenotypic and genetic variability in its attack rates and so can evolve (the prey are fixed). Rapid evolution in the predator can fundamentally alter conditions for coexistence between prey species and even lead to positive indirect effects, whereas apparent competition and even exclusion of one prey by the other are expected without predator evolution. The model suggests that the amount of genetic variation has profound and at times surprising consequences. When the amount of genetic variation is low, systems may exhibit long transients with elevated extinction risks even if the ultimate outcome might be a persistent system where all species coexist. When the amount of genetic variation instead is high, unstable dynamics may emerge. In a bitrophic model with both resource and apparent competition, Klauschies et al. (2016) demonstrated that ongoing coevolution permits persistence of hyperdiverse communities with species-rich clusters of similar species separated by phenotypic gaps (emergent neutrality, sensu Holt 2006). However, empirical details confirming these evolutionary dimensions of shared enemies remain rare, and this should be fertile ground for future studies (Estes et al. 2013).

Evolution is not merely about adaptation by natural selection, but it also encompasses maladaptation, such as that due to gene flow. Farkas et al. (2013) demonstrated that in a reticulate landscape gene flow leads to local maladaptation in the crypsis of color morphs of a stick insect. Sites with substantial spillover of maladapted color morphs attracted avian predators, which then incidentally consumed other arthropods and depressed their abundances. Thus, local maladaptation in one prey species can magnify apparent competition upon others. In this example, the links between ecological and evolutionary processes, and the spatial configuration of patches and rates of movement among them (that influence the degree of maladaptation), are critical to determining the magnitude of local apparent competition. In general, spillover of prey among habitats means that predator diets can be supplemented by immigrant prey types, which are not expected to be as well-protected from predation as are resident prey. This may be one reason why spatial subsidies so often seem to lead to apparent competition effects. In

Alaska, salmon show little adaptation to avoid predation on their end-of-life migration upstream to spawn; easily catchable, they provide a large supplement to wolves and other predators in some basins, which then keep moose and other ungulate prey locally rare (Adams et al. 2010).

Phylogenetic perspectives can improve our understanding of the effects of apparent competition. In a California grassland, foliar disease levels were explained better by the summed density of phylogenetically related alternative hosts than by density of just the focal species (Parker et al. 2015). In a tropical system, seedling survival (where seedling mortality is mediated by plant pathogens) is positively affected by phylogenetic seedling diversity at local scales (Webb et al. 2006). Having increased levels of diversity in morphological and biochemical ways to resist infection in the local habitat fosters increased seed survival. One might surmise that apparent competition will be strongest in guilds and communities with low phylogenetic diversity.

Understanding mimicry complexes is a classic problem in evolutionary biology. There are likely commonalities between shared predation theory and mimicry theory that would be worth developing in more detail. The evolutionary emergence of mimicry complexes requires the action of shared predators, and there are many parallels between mimicry theory and apparent competition theory. Although there has to be strong underlying gene control, the phenotypic convergence of similar colorations or other traits (through Batesian or Mullerian mechanisms) arises under the influence of shared enemies. Mimicry is then as much a population dynamic as it is a population genetic process, and recognizing this might help in understanding the evolutionary origins and maintenance of this fascinating phenomenon. Yamauchi (1993) describes a mimicry interaction in which two species (a mimic and a model) share a common generalist natural enemy. The evolutionary origins of mimicry then involve processes parallel to the P^* rule (Holt et al. 1994) where the rules for evolutionary invasion involve a ratio of net births to the level of predation. As with shared predation theory, complications can arise because of other modalities in predator behaviors and other density-dependent processes, but bringing out these relationships could improve our understanding of the evolution of mimicry complexes by placing mimicry theory into the context of apparent competition theory.

Apparent competition may even drive macroevolutionary processes, but how this plays out depends on many contingent details. In evolution experiments, a shared natural enemy (phage) was shown both to enhance prey (bacteria) diversification in homogeneous environments and to depress diversification in heterogeneous environments (Brockhurst et al. 2004). The role of shared predation in character displacement (or convergence) is an open question (Stuart & Losos 2013). Shared predation (in its broadest sense) should provide niche axes along which trait evolution can occur. Models suggest that character divergence in the presence of shared predation is most likely when multiple predators attack multiple prey (Abrams 2000). Multiple predators entail complex trade-offs because when prey evolve defenses against one predator they may become more susceptible to other predators. Abrams (2000) suggested that character divergence is most likely if two prey species have maximal fitness (population growth rates) for different trait values. It is puzzling that the issue of enemy-mediated character displacement has not been the focus of more determined empirical inquiry. Abrams & Chen (2002) observe that displacement resulting from predation may sometimes be mistaken for displacement driven by resource competition (and doubtless, the reverse could happen as well). Shared predation can also in theory lead to character convergence, which may or may not match apparent mutualisms. Whether a given pair of species experiences apparent competition, apparent mutualism, or neither—and whether these translate into character divergence or convergence—depends on the structure of the community. This structure can change over time, and natural enemy numbers can wax and wane.

This could lead to a kind of indeterminacy in trait evolution rather than a strong evolutionary signal.

Adaptive radiations as they unfold across space and time are one evolutionary arena where the hidden players in shared parasitism that leads to apparent competition may be particularly important. Ricklefs (2015) suggests that coevolutionary dynamics between hosts and pathogens could be a key driver in adaptive radiation, at times precluding secondary sympatry. If two taxa have coevolved with their parasite fauna in allopatry, when these taxa come into contact they may be more vulnerable to the parasites of their sister taxa than to their own. This could lead to exclusion via apparent competition. However, such exclusion could weaken as parasites become increasingly specialized to their respective hosts, allowing sympatry (provided the parasites still limit host numbers and thus relax the constraints of resource competition). The shifting impact of apparent competition in the context of complex coevolutionary dynamics could lead to substantial dynamism in species ranges and overlap among clade members. There might be even broader macroevolutionary consequences of apparent competition. For instance, apparent competition has been invoked to explain some aspects of genome evolution in which within-host RNAi defense mechanisms are mounted in a density-dependent fashion against genomic parasites such as transposable elements (Abrusan & Krambeck 2006). As with immune responses, these defense mechanisms may act in fashions comparable to those of generalist predators against these transposable elements.

Many compelling examples of apparent competition come from systems strongly impacted by humans, such as in biocontrol (Janssen & Sabelis 2015), or involve introduced species. As just one of many case studies we could cite, on Santa Cruz Island off Southern California, the endemic Santa Cruz fox was plunging to extinction because of predation from golden eagles, which in turn were motivated to colonize the island by a hyperabundant feral pig population. A determined reduction in pig numbers by managers removed this incentive, and in combination with interference from bald eagles, the golden eagles stopped visiting the island, and fox numbers rebounded (Gibson 2006). One might be tempted to conclude that, given a long shared coevolutionary history, the signal of apparent competition would weaken or might disappear entirely. We believe it is premature to leap to this conclusion. It simply may be easier to study shared predation in systems with just a few species (e.g., islands or disturbed landscapes) or where there are strong societal interests at play (e.g., biocontrol in agriculture). Just as with resource competition, there could be an evolutionary imprint of past strong shared predation, impressed on the traits, species distributions, and community structure of today, even if there is no contemporary apparent competition via local population dynamics (the ghost of apparent competition past). Avian ecologists believe that some high-altitude bird species along altitudinal gradients in the Andes are prevented from colonizing the lowlands by intense nest predation, even in the pristine, indeed paradisiacal, habitat of Manu National Park in southern Peru (S. Robinson, personal communication). The generalist predators leading to this range restriction are obviously sustained by a panoply of alternative prey, which collectively and indirectly may account for this biogeographical signal. Finally, if we return from paradise to the reality we mainly live in, as the world is increasingly impacted by humans, in order to deal with issues ranging from infectious disease dynamics to conservation of endangered species and maintaining the security of our fragile food base, understanding how apparent competition plays out in the Anthropocene may be more important than ever.

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