APPARENT COMPETITION

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Apparent competition is an indirect negative interaction between species mediated through the action of a shared natural enemy. The concept of apparent competition illuminates how natural enemies at times constrain the species richness of communities but at other times help maintain diversity. It is an integral part of any community theory focused on predators and their prey, parasites and their hosts, herbivores and the plants they consume, or entire food webs. In applied ecology, apparent competition can influence conservation risks, the success of invasive species, epidemiological patterns, and the efficacy and dangers of pest control. Finally, apparent competition exemplifies the general theme that ecological communities are not a haphazard assemblage of species, each interacting separately with the external environment, but instead exhibit complex and at times surprising chains of interactions.

ECOLOGICAL THEORY CAN HELP UNIFY ECOLOGICAL UNDERSTANDING OF DISPARATE SYSTEMS

Natural historians glory in life's rich diversity. Ecological theory can help tease out commonalities among disparate systems and thus help unify understanding. What do the following real-world stories have in common, and how can theory help explain the patterns they reveal?

Case Studies: Ecological Puzzles from Studies of Interacting Species

DO RABBITS "EAT" VOLES?

In the Grampian Mountains of Scotland, the native water vole, *Arvicola amphibius,* resides in lush vegetation along streams and other water bodies. During the eighteenth century, the European rabbit, *Oryctolagus cuniculus,* colonized the area, and its warrens of deep burrows are mainly found in dry fields of short grass. The two species live in different habitats and have different diets, and the rabbit invasion had no obvious impact on the water vole. Sadly, the water vole has plummeted in abundance over the last 50 years from millions to a few hundred thousand across the entire UK. In the Grampians it has disappeared from sites near upland fields containing rabbits. If the two species do not compete, how can the presence of one affect the fate of the other?

ANOTHER PUZZLE IN AN INVASION

In the United Kingdom, the native red squirrel, *Sciurus vulgaris*, once widespread, has been largely supplanted by the introduced grey squirrel, *Sciurus carolinensis*. The two squirrel species overlap in diet and habitat and so probably compete. But there are puzzling aspects of the decline: sometimes the red squirrel disappears from a locale even before the grey squirrel has built up its numbers. Is this just a straightforward story of competitive exclusion?

COUNTERINTUITIVE EFFECTS OF PROTECTING WILDLIFE

In the dry savanna of northern Kenya, humans, livestock, and wildlife have coexisted for millennia. To boost ecotourism, there have been localized shifts from cattle ranching to wildlife conservation. Some species, in particular the plains zebra, *Equus quagga burchellii*, increased greatly post-protection, but other ungulates such as hartebeest (*Alcelaphus buselaphus*) have severely declined. Are these declines driven mainly by competitive interactions among these large mammalian herbivores, or something else?

AN ENDANGERED ISLAND SPECIES

Feral pigs (*Sus scrofa*) were introduced into the California Channel Islands, which later saw abrupt crashes toward near-extinction of an endemic predator, the island fox, *Urocyon littoralis*. How did the pig introduction endanger the fox—could it for instance be habitat degradation driven by the destructive rootings of the pigs?

Simple Models of Apparent Competition

NATURAL ENEMIES ARE SIGNIFICANT FACTORS IN MOST SPECIES' LIVES

At first glance, several of these case studies are consistent with the hypothesis that species are directly competing—and this may be true. But to understand what forces drive these systems, it turns out one must consider species or populations beyond those that at first glance seem to be the main players—and all these empirical patterns reflect apparent competition.

Communities are complex webs of interacting species, affecting each other not just one on one but via interlocking chains of indirect interactions mediated through other species. Most species suffer from natural enemies—a term broadly encompassing predators, herbivores, parasites, pathogens, and indeed any species that to make a living inflicts harm on other species, taking resources (energy and nutrients) from living organisms so as to survive or reproduce itself. Even the fiercest top predator—lion, tiger, or bear—can be laid low by an infectious disease agent, and the smallest quasi-organisms of all—viruses—themselves can be attacked by other viruses or consumed when their infected hosts fall prey to natural enemies.

Many natural enemies are generalists, exploiting more than just one victim species (prey or host). The level of damage imposed on any particular prey or host species (as assessed by reduced growth rates, fitness, or abundance) may depend upon the availability, traits, and productivity of alternative prey or hosts. In other words, there is an indirect interaction between these species. Formally, in a mathematical model, an indirect interaction exists between species I and III, mediated through II, if the dynamical equation describing growth rates in I contains a variable referring to II (e.g., abundance), and the equation for II has a variable referring to III. Changes in III lead to changes in II, which in turn affects I. When an indirect interaction between two victims mediated by a natural enemy is negative, it is called apparent competition. This term was coined by the author in 1977 because ecological patterns that appear to be due to competition for resources, such as nonoverlapping spatial distributions, can also emerge from impacts of a shared natural enemy.

A COMPARISON OF EXPLOITATIVE AND APPARENT COMPETITION

Figure 1 depicts community modules corresponding to exploitative competition and apparent competition. Each node represents a species, and arrows represent directions of effects. On the left, two natural enemies are consumers of the same resource, and any resource gathered by

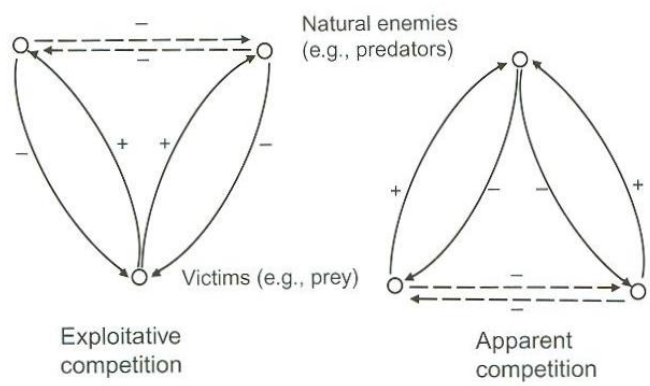

FIGURE 1 Exploitative and apparent competition. Each node is a species. Solid arrows are signed direct interactions; dashed arrows, emergent indirect interactions. Higher species in the figure are higher in the food web. On the left, two consumers (e.g., predators) share a resource. Multiplying the signs, each consumer has a negative indirect effect upon the other—competition for resources. On the right, two victim species (e.g., prey) share a natural enemy (predator). Again, multiplying the signs shows that each victim indirectly harms the other, via their shared natural enemy.

species A is thus unavailable to species B, which therefore suffers a reduction in its growth rate. Apparent competition is a mirror image of this familiar indirect interaction. Victim species A has a positive effect on the abundance or activity of a natural enemy, and because the natural enemy has a negative effect upon species B, species A indirectly has a negative effect upon species B.

A GRAPHICAL MODEL OF APPARENT COMPETITION

A simple graphical model exploring this process provides one step towards a formal theory of apparent competition. Assume a predator of abundance P has an instantaneous population growth rate dependent only on availability of two prey species, of abundance R_1 and R_2:

$$\frac{1}{P}\frac{dP}{dt} = F_P(R_1, R_2). \tag{1}$$

Assume the system reaches equilibrium, so $F_P(R_1, R_2) = 0$. We plot this (the predator zero-growth isocline) as a curve on a graph with axes of prey abundance (Fig. 2A). Outside the isocline, the predator grows; inside, it declines.

Assume each prey species when alone can sustain the predator. The predator reaches equilibrium when prey abundances match the open circles in the figure. Now assume an equilibrium exists with both prey species present. This equilibrium must lie on the predator isocline, for instance at the closed circle. If we compare the equilibrial abundance of each prey when alone to its abundance when the two coexist, note that at the joint equilibrium each prey species is depressed in abundance. The little arrows in the figure show that adding a small amount of either prey to the system permits predator growth. Mathematically, this is equivalent to saying the predator isocline has negative slope. Thus, each prey species indirectly depresses the equilibrial density of the other because each benefits the predator, increasing its numbers and thus predation upon the alternative prey.

A SIMPLE RULE FOR DOMINANCE IN APPARENT COMPETITION

But maybe no equilibrium exists with both prey species. Imagine the predator depresses prey species i to a level where it experiences only density-independent per capita growth at rate r_i and predation at rate a_iP (a_i is the attack rate, and P predator abundance). The net per capita growth of species i is $r_i - a_iP$. For equilibrium, the predator must settle to $P_i^* = r_i/a_i$ (the asterisk indicates equilibrium, and the index on P indicates just prey i is present). Suppose prey 1 is at equilibrium with the predator, and prey 2 tries to invade. Invasion succeeds only if $r_2 - a_2P_1^* > 0$, which implies $P_2^* > P_1^*$. But if this holds, then when prey species 2 in turn is present at equilibrium, and prey species 1 tries to invade, it cannot—predation upon it exceeds its intrinsic $>k$ growth rate.

If attack rates are constant but intrinsic growth rates and predator densities vary over time, one can replace the

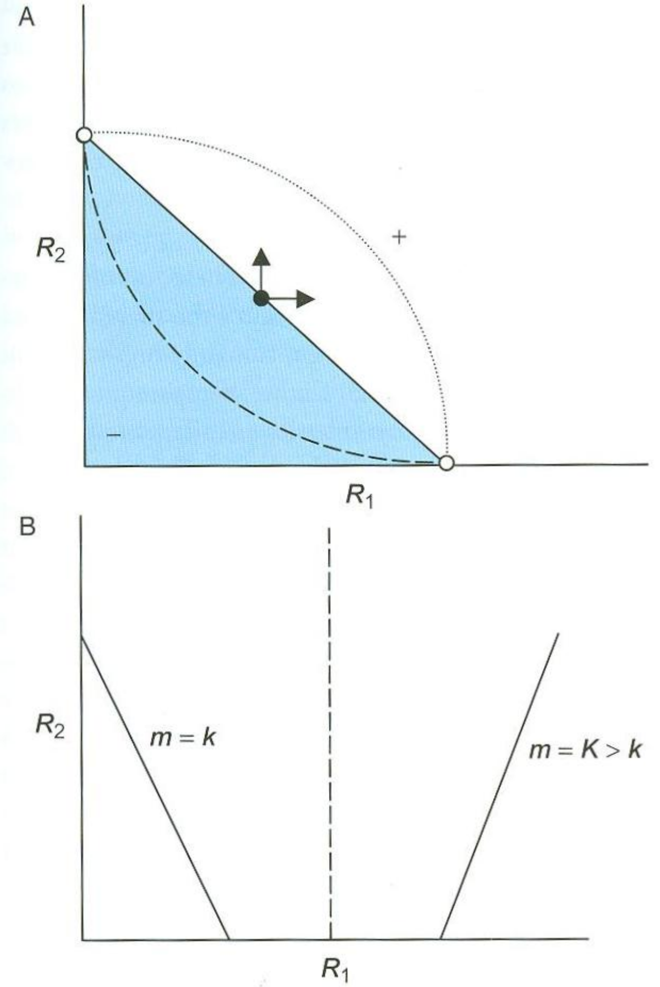

FIGURE 2 A graphical model of shared predation. (A) The solid straight line is the zero growth isocline of a predator. Between this line and the origin, the predator declines in abundance because of a shortage of food; outside the line, it thrives and grows in numbers. The small arrows show that increases in either prey leads to predator growth, and this leads to a negative isocline slope, and apparent competition (compare open circles to closed circles; see text). Apparent competition is even stronger if the predator thrives better on a mixed diet (dashed line), and weaker if it does not benefit from the mix (dotted line). (B) The model is for a food-limited predator with a saturating response to each of two prey:

$$\frac{1}{P}\frac{dP}{dt} = F_P(R_1, R_2) = \sum_{i=1}^{2} \frac{a_i b_i R_i}{1+a_1 b_1 R_1 + a_2 b_2 R_2} - m,$$

where P and R_i are respectively the abundances of the predator and prey species i; a_i, b_i, h_i are attack rates on prey i, the benefit the predator gains per prey caught, and handling times; and m, the predator death rate. We assume one prey is better than the other (as measured in b/h, benefit gained per unit handling time). If the predator is a generalist for all prey densities, at low abundances it benefits from each prey, so the isocline has a negative slope, but at high abundances, it can waste time on the poor prey (see text). At low predator mortality (the line indicated with $m = k$), the two prey experience apparent competition, but at higher mortality (marked by $m = k$), the isocline has a positive slope, so the indirect interaction between prey is $(-, +)$.

r's and P's with time averages, and this conclusion still holds. In other words, if the predator is the only regulatory factor limiting each prey species, one expects to see exclusion of one prey species by the other, and that prey which sustains higher average predator abundance wins in apparent competition. Shared predation can constrain prey species diversity.

All the Above Ecological Puzzles Involve Apparent Competition.

Apparent competition arises in many different ecological systems. The solution to each ecological puzzle above turns out to involve apparent competition. Each illuminates different features and realistic complications of apparent competition and points out directions for theory development.

RABBITS DO NOT EAT VOLES—BUT MINK DO

In the first example above, there is another invasive species that also moved into Scotland, but well after the rabbits—the American mink, *Neovison vison*. This species is a smart, voracious predator, and it can follow the water vole into all its normal refuges. Minks do consume rabbits, but they cannot readily eliminate them from their protective warrens. In short, mink numbers get boosted by a species that they cannot control—the rabbit—which then permits the mink to impose very heavy mortality on a more vulnerable species—the water vole. Rabbits in no way directly compete with water voles, but nonetheless by sustaining a predator—the mink—they have a strong, albeit indirect, deleterious impact upon the persistence of water voles. This appears to be an excellent (if sad) example of apparent competition in action.

The water vole–rabbit–mink interaction matches expectations of our simple model. Mink populations respond strongly to increased food availability, so are food-limited. Rabbits have notoriously high fecundity and can reach high abundance; they have a high intrinsic growth rate. Many rabbits are protected from mink predation in their warrens and so have an average lower (but nonzero) attack rate than the water voles. Rabbits, we can reasonably infer, have a higher r/a than do water voles and so should tend to dominate in apparent competition. This appears to be what happens—the water vole is excluded from sites near rabbit warrens.

Spatial Processes and Apparent Competition This example can be used to glean other insights that have been explored in theoretical models. The theory of apparent competition has been extended from closed to open communities, comprised of habitat patches linked by dispersal. If different prey species occupy different habitats (and so do not compete), their dynamics may be nonetheless coupled by predator movement. It turns out that alternative prey species can coexist, if prey species segregate among habitats and predator mobility is constrained. Water voles and rabbits do live in quite different habitats. The reason their fates are joined at all in the Scottish landscape is that minks are highly mobile. The farther a water vole population is located from rabbit populations, the less likely it is that mink (sustained by feeding on rabbits) will wander through. Remnant populations of water voles in the Grampians tend to be those at some distance from rabbit habitat, presumably because they suffer less "spillover" predation.

A critical dimension of apparent competition is thus the nature of spatial processes connecting different habitats. Natural enemies are often mobile, permitting apparent competition to act at a distance. This effect has been studied in laboratory microcosms consisting of patch arrays containing two moth species. Arrays were set up so that moths lived in different patches and did not directly compete, but a mobile wasp parasitoid could move freely among them. The wasp coexisted just fine with either host when alone, but the three-species combination collapsed, and one host species went extinct from elevated parasitism—apparent competition. In like manner, movement of prey across space can subsidize predators in a community, permitting them to more effectively limit resident prey.

WITH A LITTLE HELP FROM MY FRIENDS

Apparent competition is implicated in the conservation risks experienced by many endangered species, including the replacement of red by grey squirrels. The squirrels do seem to compete for resources, and the grey squirrel seems more effective at using acorn resources. Hence, grey squirrels can potentially have a higher carrying capacity and so may dominate in competition for shared resources. But on top of this, the grey squirrel harbors a poxvirus (SQPV)—an infectious disease agent to which they are seemingly immune but to which the red squirrel is highly vulnerable. Mathematical models suggest this shared pathogen greatly speeds up the demise of the red squirrel, even in advance of an increase in grey squirrel numbers.

Apparent Competition Mediated by Parasitism This example illustrates the potential importance of pathogens as conduits of apparent competition. This is a very important issue for conservation and public health. In California, the invasive pathogen *Phytophthora ramorum* is a highly generalized natural enemy, inflicting serious damage on many native tree species. The California bay laurel (*Umbellularia californica*) is a heavy producer of pathogen spores but is not itself greatly harmed. The spillover of spores from this species onto more vulnerable species such as tanoak (*Lithocarpus densiflorus*) leads to high mortality. Because trees compete, as vulnerable trees decline the bay laurel increases and hammers its competitors via the pathogen even harder.

Asymmetric Apparent Competition These examples reveal strong asymmetry in the effect of the shared natural enemy—the indirect interaction is mainly one-way. This is a common (not universal) feature of apparent competition. Explaining why asymmetries are often strong is still an open question and probably reflects both ecological factors and evolutionary history. In general, whichever species has the highest productivity (high r) and is not limited strongly by factors other than predation tends to dominate. If grey squirrels more effectively utilize a resource such as acorns, this could accentuate their dominance over reds in apparent competition. A full explanation of species extinctions from local communities often involves both competition (in the usual sense of the term) and apparent competition. These are not alternative, incompatible explanations but processes that can occur simultaneously and interact in various ways.

PROTECTING PREDATORS CAN PERMIT APPARENT COMPETITION TO OCCUR AMONG PREY

In the Kenyan example, humans historically suppressed zebras (which compete with livestock) and predators such as lions. Limiting livestock and reducing hunting in the interest of wildlife conservation allowed zebras to surge to high numbers, and predators such as lions reappeared. Predators do not substantially limit zebra numbers; zebras form large herds that provide protection from predation. But these herds do provide a steady supply of young, sick, or injured individuals that are easy pickings and can sustain predator populations. Other ungulates do not necessarily enjoy this kind of protection, and intensified predation appears to account for their declines.

Apparent Competition Does Not Arise Only in Disturbed Ecosystems In contrast to the invasion case studies, this African system involves species that have lived together for a very long time. Apparent competition is not just a process that shows up as a brief transient in unnatural situations created by human disturbance and transplantation of species around the globe but can be important in natural ecosystems. The reason it was detected was that there was in effect a large-scale inadvertent experiment driven by a shift in land use patterns by humans. Stronger evidence for apparent competition in natural assemblages comes from deliberate experimental manipulations. In the rain forests of Belize, a rich community of leaf-mining insects (flies and beetles) sustains a high diversity of parasitoids. Experimental removal of some hosts led to lower parasitism in the remaining hosts, showing strong apparent competition in this natural community of herbivorous insects. Apparent competition could play a significant role in the dynamics of biodiversity over evolutionary time scales as well. Shared predation provides novel niche axes for specialization and diversification, and localized coadaptation of natural enemies and victims can lead to a sorting out of species among habitats or along gradients. Understanding the evolutionary dimensions of apparent competition is a largely unexplored area of theory.

Availability of Refuges Is a Key Element in Apparent Competition Another general message can be gleaned from the Kenyan example: the zebra has a partial refuge from predation by virtue of grouping behavior. Refuges come in many forms, ranging from permanent physical locations providing escape (e.g., rabbit warrens), to transient refuges in space (as in metapopulation dynamics), to escapes in time, to plastic adaptations that lower predation or parasitism rates. Stage structure (e.g., an invulnerable adult class) provides a particularly important form of refuge in some systems, and leads to rich complexities in theoretical models, because of the multiplicity of feedbacks that are possible (e.g., alternative stable states, and complex dynamics). If refuges protect some but not all individuals in a species, natural enemies can be sustained by this species without endangering it. Such species can dominate in apparent competition over species lacking refuges. Hosts can evolve to tolerate parasites or herbivores, without eliminating them. Such hosts could then exert strong apparent competition on alternative hosts that are not so well adapted. Understanding how population structure and evolutionary processes affect the strength of interspecific interactions, including apparent competition, is an active and growing area of ecological theory.

Multiple prey or host species can coexist, despite strong apparent competition, if each has its own refuge—a kind of niche partitioning in enemy-free space. An important subtlety is that this works if species are more likely to be in such a refuge when rare than when common. Theoretical models suggest that such refuge-mediated coexistence is greatly amplified if natural enemies behaviorally aggregate, spending more time where their victims are common.

PREDATOR BEHAVIOR GENERATES OTHER MECHANISMS OF APPARENT COMPETITION

Behavior—foraging tactics of predators and escape maneuvers of prey—is an important element in apparent competition. In the Channel Islands story, the presence of an abundant prey species, feral pigs, led to colonization by a few pairs of Golden Eagles, *Aquila chrysaetos*. Foxes on their own are far too scarce to warrant eagles setting up house on the island, but they are easy to casually catch as tasty morsels by eagles lured to the islands by an abundant alternative prey. This is called incidental predation in the literature.

In this case study, predator behavior is a key driver of apparent competition. The handful of Golden Eagles present could have nested on the mainland but instead chose to reside on the islands. In Figure 2, rather than interpreting the isocline as describing the dynamics of an entire predator population (births and deaths), we can view it as a model of predator use of a small habitat patch (i.e., numbers change via immigration and emigration). When prey are scarce, predators leave; when prey are flush, predators arrive and stay. This aggregative numerical response is expected from optimal foraging theory; models predict that it leads to apparent competition between prey species within a patch, even if predator populations as a whole do not respond to shifts in prey numbers.

Flexible behavior (including patch use) can lead predators to ignore rare prey species, at least if those prey require special foraging tactics or specific recognition cues (search images), or if they are found in sites lacking other, more common prey. Many mechanistic processes lead to such switching by generalist predators. Theoretical models suggest that switching often promotes the persistence of multiprey assemblages. But counterexamples are also suggested by theory, dependent on the temporal scale and accuracy of switching relative to changes in prey abundance.

Changes in predator behavior that alter the indirect interaction between alternative prey exemplify what are called trait-mediated indirect interactions. There can be a range of effects alternative species have on each other, and the net effect is often context specific. One species can indirectly negatively impact another not by feeding a natural enemy but instead by in some other way facilitating its presence or activity levels. Invasive shrubs can foster their own invasion by sheltering native herbivores from predators, so the herbivores more effectively reduce their native food plants, freeing resources for the invader. This is still apparent competition, albeit via a kind of ecological engineering. One direction for future theory will be to develop mechanistic models incorporating the multiplicity of potential channels of interactions among species.

A KIND OF APPARENT COMPETITION CAN OCCUR WITHIN INFECTED HOSTS

A major defense that vertebrates have against parasites is acquired immunity. To boil a complex story down to some basic elements, the immune system works by the stimulation of the proliferation of particular cell lines—a population of predatory cells—tailored in their attacks to parasites with certain attributes. If parasite A invades a host body and that host mounts an immune response, this may help fend off invasion by a relatively similar parasite B if it is recognized as being hostile by the host immune system. In this case, the natural enemy is the host immune system, and its numerical response (comparable to Eq. 1) is the growth of a particular population of defensive cells. The victims are different species or categories of parasites attempting to invade the host. Such apparent competition among similar strains of parasites is a powerful force selecting for parasite diversity.

This example illustrates the general point that abstract theoretical models can help illuminate comparable processes found in seemingly radically different systems. There are important differences between theoretical immunology and the theory of, say, vertebrate predator–prey interactions, but recognizing commonalities can help point to a unification of perspectives and approaches across levels of biological organization guided by powerful theoretical insights.

APPARENT COMPETITION IS ONLY PART OF THE STORY OF SHARED PREDATION

Does shared predation *always* lead to apparent competition? When it does, does it always tend to reduce prey species diversity? The short answer to both questions is "No!"

Let us go back to the basics. The simple theoretical model sketched above, part of which is shown in Figure 2A, makes many assumptions. Relaxing these assumptions can lead to a shift in theoretical predictions.

First Assumption We assumed an increase in prey numbers, for either of two prey species, benefits the predator (as assessed by a boost in its per capita growth rate). This might not hold, and for two reasons, one having to do with the prey themselves, and one having to do with the predator, largely independent of its prey.

Equation 1 assumes predator growth depends on prey availability. More generally, predator dynamics can depend on its own density. For instance, for successful reproduction weasels might require specialized nest sites, which could be in short supply and lead to direct competition. This could constrain the numerical response of weasels to mice and shrews, weakening apparent competition between these prey. Even if this is not the case, higher-order predators such as owls might limit weasel abundance. A pulse in mouse numbers might lead to a temporary increase in weasels, suppressing shrews, but in the long-term owl predation might bring the weasels back to their original levels. So food-web interactions can at times temper apparent competition or make it a transient response in system dynamics.

Equation 1 and Figure 2A assume consumption of each prey benefits the predator. This is not always true. Some prey contain toxins, harming consumers. Fish that die in the mass fish kills of red tides presumably are not very good at discriminating poisoned food from safe food. More subtly, even if a certain prey species is not absolutely bad, it might be bad in a relative sense, compared to other prey types. One generality about predators is that the rate at which they feed always saturates, due to limitations in handling time, gut capacity, or attention span. When food is abundant, time spent handling a low-quality prey type is in a sense wasted; there is an opportunity cost, because higher-quality prey are being ignored. Figure 2B shows how this alters the slope of the predator isocline. At sufficiently high abundance of the good prey, boosting numbers of the poor prey actually depresses predator growth; the indirect interaction shifts from $(-, -)$ to $(-, +)$.

This may seem unlikely, but something like this is believed to be of great importance in vector-borne infectious diseases involving multiple potential host species for the vector. Isoclines with partial positive slopes arise quite naturally in theoretical models of such systems. Some hosts are poor for pathogen reproduction, and if they can draw off attacks by vectors from more competent hosts, the net effect is a reduction in pathogen load across the entire system. Biodiversity can thereby moderate the risk of infectious disease.

Second Assumption We assumed interacting species reach equilibrium. Saturating responses, demographic stochasticity, and environmental fluctuations can lead to sustained oscillations. Theoretical studies show that alternative prey can sometimes boost each other's average numbers, when one averages over the nonequilibrial dynamics of these highly nonlinear systems. Understanding how environmental variability and complex dynamics modify indirect interactions is a largely open area of theoretical ecology.

Third Assumption In our examples, apparent competition drove particular prey species to lower abundance or even extinction. Apparent competition via shared natural enemies can sometimes facilitate coexistence—if prey species also compete by interference or exploitatively for limiting resources. For instance, two prey species can persist on a single resource if a predator is present and one prey is better at resource competition and the other is better at apparent competition.

For a single generalist predator to enhance prey diversity beyond this effect requires some mechanism in effect permitting prey species to each have its own refuge from shared predation. As noted above, switching behavior by the predator is one such mechanism, as is habitat segregation among prey (given limited predator mobility). Another is to imagine that there is not just one predator species but instead a number, each to a degree specialized in its attacks to different prey. There can then be a kind of codependence of diversity across different trophic levels, and coexistence of numerous species in each trophic level becomes possible. Recent theoretical studies have explored this idea in some detail, highlighting the symmetry between shared predation and exploitative competition illustrated in Figure 1.

The symmetry is, however, incomplete. All species need resources, so there is always a potential for competition, within or among species. Whether or not shared predation leads to apparent competition is contingent (as we have seen) on many details. Moreover, there can be a difference in time scales over which dynamics play out. Resource levels can change very rapidly in response to changes in consumption (e.g., plants competing for light), whereas there can be significant time lags in responses of predators to their prey. Pathogen loads, however, can change rapidly, relative to host generation lengths, and for some purposes the impacts of shared pathogens and parasites might almost be viewed as a form of interference competition.

APPARENT COMPETITION PLAYS A ROLE IN HUMAN HISTORY AND OUR IMPACTS ON THE BIOSPHERE

Ecological theories such as apparent competition have implications for understanding ourselves and our impacts upon the rest of the biosphere. All the above case studies exemplify important problems in applied ecology. A clear appreciation of apparent competition theory can inform issues and management strategies in many practical disciplines, from conservation, to natural resource management, to pest control, to epidemiology, to invasion biology.

Apparent competition among peoples arguably has carved major channels in our own history. Parallel to the interaction between red and grey squirrels of the United Kingdom, plagues (in combination with other forms of more direct competition) have tragically influenced the waxing and waning of different peoples around the globe. For instance, as western Europeans conquered much of the world they had a hidden weapon—shared infectious diseases such as smallpox, to which indigenous populations were much more vulnerable. Further back in time, one hypothesis to explain the mass extinction of large mammals in North America is that it was overkill by a wave of colonizing people sweeping across the continent. Theoretical models suggest this hypothesis may work, if smaller species with a higher reproductive rate sustained the population of hunters, who could continue to preferentially attack large mammals such as mastodons even when the latter became vanishingly rare. In other words, apparent competition, mediated through humans, may be implicated in sculpting major features of the current fauna of entire continents.

Nearer the present, the ability of humans to hunt to extinction the Passenger Pigeon and Dodo reflects the fact that we do not depend on these species alone for sustenance. Humans are the ultimate generalist consumer, able to crack almost any victim's defenses, and our burgeoning population is sustained in terms of calories and nutrients by a quite small number of species, permitting us to wreak havoc upon the rest. The biodiversity crisis across the globe, seen through the lenses of ecological theory, may be an example of apparent competition, writ large.

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APPLIED ECOLOGY

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Applied ecology aims to relate ecological concepts, theories, principles, models, and methods to the solving of environmental problems, including the management of natural resources, such as land, energy, food or biodiversity.

DEFINITION AND SCOPE

What Is Applied Ecology?

Despite its somewhat restrictive name, applied ecology is more than simply the application of fundamental ecology. In a nutshell, ecological management requires prediction, and prediction requires theory. Applied ecology is a scientific field that studies how concepts, theories, models, or methods of fundamental ecology can be applied to solve environmental problems. It strives to find practical solutions to these problems by comparing plausible options and determining, in the widest sense, the best management options.

One particular feature of applied ecology is that it uses an ecological approach to help solve questions concerned with specific parts of the environment, i.e., it considers a whole system and aims to account for all its inputs, outputs, and connections. Of course, accounting for everything is no more possible in applied ecology than it is in fundamental ecology, but the ecosystem approach of applied ecology is both one of its characteristics and one of its strengths.

Indeed, one could view the overall objective of applied ecology as to maintain the focal system while altering either some of the elements we take from the system (i.e., ecosystem services or exploitable resources) or some of those we add to the system (i.e., exploitation regimes or conservation measures) through an educated management strategy. Since those two types of elements are not mutually independent, long-term management strategies are best aimed at optimizing rather than maximizing exploited items. This is more efficiently achieved through an adequate understanding of theoretical ecology, which generally considers all parts of the system rather than a limited set of its components.

What Are the Fields Covered?

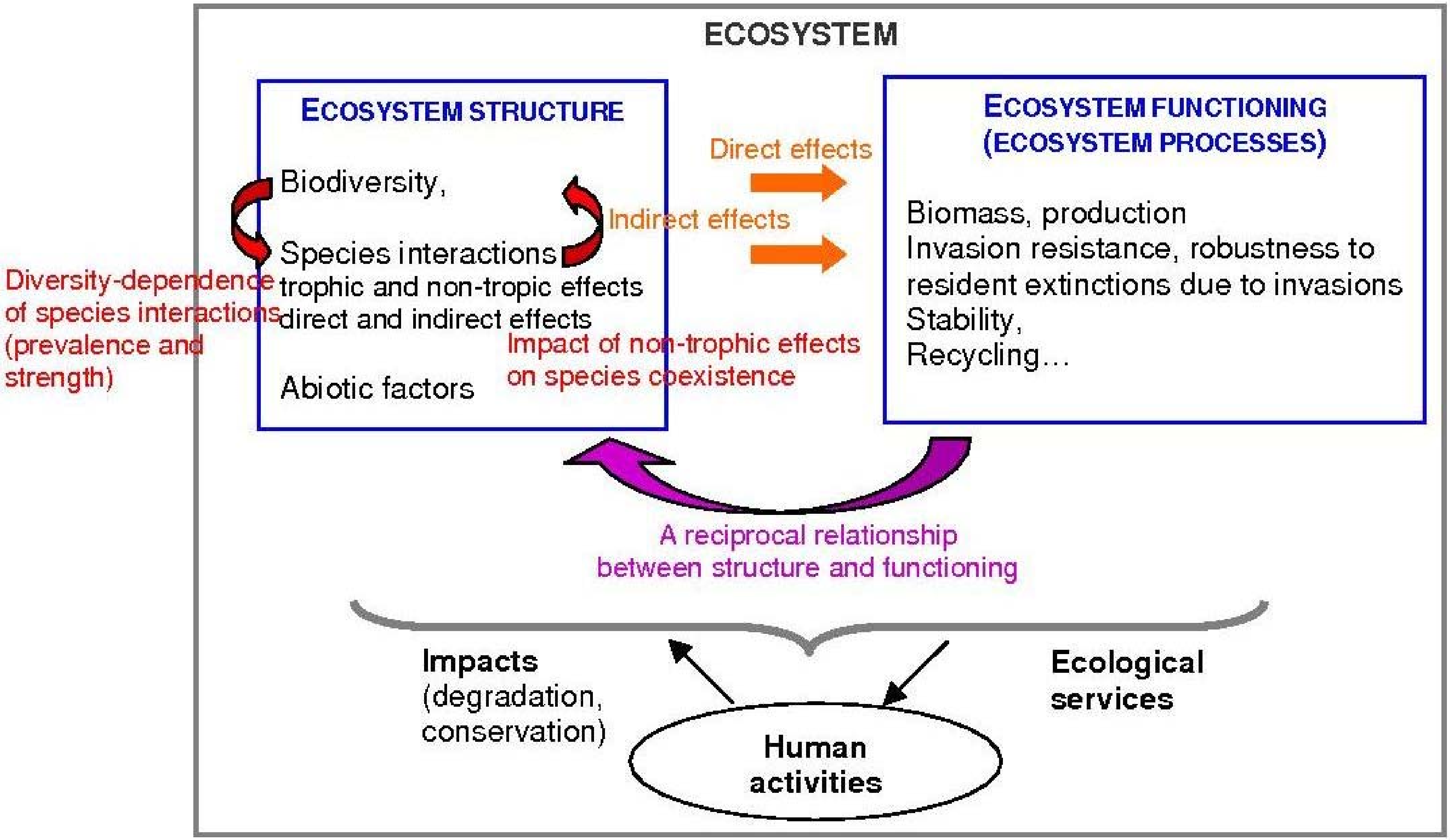
The word "applied" implies, directly or indirectly, human use or management of the environment and of its resources, either to preserve or restore them or to exploit them. Humans influence the Earth at all levels: the atmosphere, the hydrosphere (oceans and fresh water), the lithosphere (soil, land, and habitat), and the biosphere. Understandably, questions related to human populations (notably its demography) fall within the scope of applied ecology, as most impacts on ecosystems are directly or indirectly anthropogenic.

Aspects of applied ecology can be separated into two broad study categories: the outputs and the inputs (Fig. 1). The first contains all fields dealing with the use and management of the environment for its ecosystem services and exploitable resources. These can be very diverse and include energy (fossil fuel or renewable energies), water, or soil. They can also be biological resources—for their exploitation—from fish to forests, to pastures and farmland. They might also, on the contrary, be species we wish to control: agricultural pests and weeds, alien invasive species, pollutants, parasites, and diseases. Finally, they can be species and spaces we wish to protect or to restore.

The fields devoted to studying the outputs of applied ecology include agro-ecosystem management, rangeland management, wildlife management (including game), landscape use (including development planning of rural, woodland, urban, and peri-urban regions), disturbance management (including fires and floods), environmental engineering, environmental design, aquatic resources management (including fisheries), forest management, and so on. This category also includes the use of ecological knowledge to control unwanted species: biological invasions, management of pests and weeds (including biological control), and epidemiology.

The inputs to an applied ecology problem consist of any management strategies or human influences on the target ecosystem or its biodiversity. These include conservation biology, ecosystem restoration, protected area design and management, global change, ecotoxicology

Figure 6. Importance of non-trophic interacions and trait-mediated effects in the relationship between ecosystem structure and functioning




Map
Traffic
A
Wild Horse Rd
278
19794
Snake Farm Rd
Snake Farm Rd
N2100 Rd
N2100 Rd
N2100 Rd
200 ft
100 m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Photograph by Brian Skerry