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Ecological Consequences of Parasitism

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Why are parasites ecologically important? Parasites can shape community structure through their effects on trophic interactions, food webs, competition, biodiversity, and keystone species.
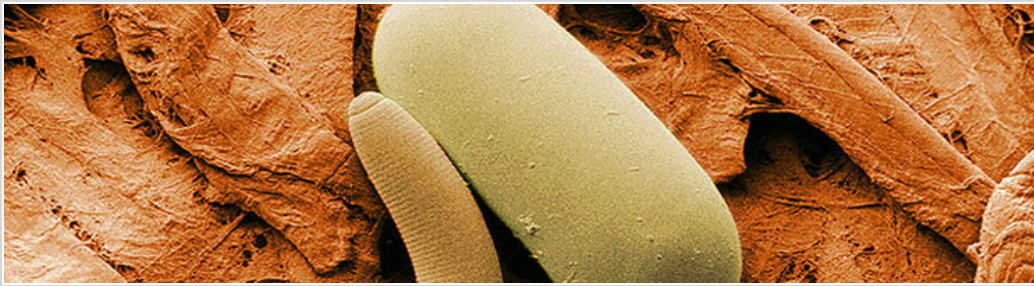
The ecological interactions of parasites (defined here to include both macroparasites and microparasites) are often challenging to observe. Many live their lives secretively, in intimate contact with their host, but invisible to the outside world. With some notable exceptions (e.g., tapeworms), parasites also tend to be very small. It may be easy to assume then, that since parasites are generally inconspicuous, they play less important roles in community ecology than free-living organisms. Yet advances in the field of disease ecology have revealed that parasites are not only ecologically important, but can sometimes exert influences that equal or surpass those of free-living species in shaping community structure. In fact parasitism is more common than traditional predation as a consumer lifestyle (De Meeûs & Renaud 2002), and arguably represents the most widespread life-history strategy in nature (Price 1980). Parasites also influence host behavior and fitness, and can regulate host population sizes, sometimes with profound effects on trophic interactions, food webs, competition, biodiversity and keystone species. These interactions suggest that parasites are integral components in shaping community- and ecosystem structure.

Parasitism and Trophic Interactions

Parasites can function as both predators and prey. Parasites that feed on hosts engage in a special type of predation (Raffel *et al.* 2008). Alternatively, parasites can also serve as important sources of prey (Figure 1). For example, predators on islands in the Gulf of California, including lizards, scorpions and spiders, are one- to two orders of magnitude more abundant on islands with sea bird colonies because they feed on bird ectoparasites (Polis & Hurd 1996). Predators also inadvertently consume parasites during the consumption of infected hosts (Johnson *et al.* 2010). When macroparasites are relatively large, such as nematodes in the gut of vertebrate hosts, the contributions of parasites to the diet of predators can be significant. The roles of parasites as predators and prey suggest that considerable amounts of energy may directly flow through parasites in food webs, despite their small size and cryptic nature.
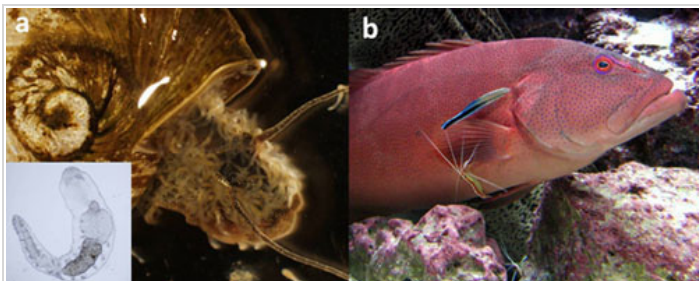

Figure 1: Parasites as prey

(A) Oligochaete worms (Chaetogaster sp., see lower-left inset) feed on trematode parasites
that emerge from an infected freshwater snail host. (B) Cleaner wrasse (Labroides
dimidiatus) and cleaner shrimp (Lysamata sp.) removing ectoparasites from a coral trout.
Parasites may be an important food resource to predators, especially in ecosystems where
parasites are highly productive. (1A courtesy of P. Johnson & S. Orlofske; 1B courtesy of A.
Grutter)

In some cases, predation can serve as a vehicle of transmission, allowing a parasite with a complex life cycle to move from
one host to another. Parasites that infect new hosts via trophic transmission frequently alter their host's behavior or
morphology in ways that increase predation risk, thereby aiding the parasite in reaching the next host in its life cycle (Poulin
et al. 2005). For example, estuarine killifish infected with the trematode *Euhaplorchis californiensis* exhibit erratic
swimming behavior that ultimately makes them up to 30 times more susceptible to bird definitive hosts (Lafferty & Morris
1996). Another trematode endoparasite, *Ribeiroia ondatrae,* causes amphibians to develop severe limb deformities,
including extra or missing limbs (Johnson *et al.* 1999), which impair the host's ability to jump and swim, and presumably
make them more susceptible to predation by bird definitive hosts (Figure 2). The roles of parasites in predator-prey
interactions are rarely obvious, yet they may influence the outcome of trophic interactions at the community scale.

**Figure 2: Pacific chorus frog (Pseudacris regilla) that has three extra hindlimbs due
to infection with a trematode parasite (Ribeiroia ondatrae, see inset).**
Limb deformities reduce the frog's ability to evade predators, possibly making it more
susceptible to being eaten by the definitive host of the trematode. (Courtesy of D.
Herasimtschuk & P. Johnson)

Parasitism, Food Webs, and Ecosystem Energetics

Considering the prominent roles played by parasites in trophic interactions, we might expect parasites to strongly influence
food web characteristics. Recent efforts to include parasites in food webs have revealed sharp changes in the topology of
food webs, including species richness, the total number of links, food chain length (the number of trophic levels in a web),
and connectance (Lafferty *et al.* 2008). In a salt marsh food web in California, parasites were involved in 78% of all links,
and increased estimates of connectance by 93%, which may have implications for web stability (Lafferty *et al.* 2006).
Incorporating parasites into food webs also reveals that mid-trophic levels — rather than the lowest trophic levels — are most
susceptible to natural enemies because this group is at risk from both predators and trophically transmitted parasites.
Integrating parasites into food webs also suggests that the classical Eltonian pyramid (Elton 1927) may need to be revised: if
parasites feed at a trophic level above their hosts, parasites would occupy the pinnacle of this new pyramid (Sukhdeo &
Hernandez 2005), which would be a significant departure from the traditional placement of top predators at the peak of the
food chain.

For decades, parasites were omitted from the study of food web ecology based on the assumption that they contributed
negligible biomass to ecosystems. Measuring biomass, or productivity, allows us to quantify contributions of organisms to
ecosystem energetics. However, when parasite biomass was actually measured on an ecosystem scale, the results challenged
the notion that parasites are unimportant in ecosystem energy flow. In some estuarine systems, the biomass of parasites is
comparable to that of top predators (Kuris *et al.* 2008). Yearly productivity of trematode parasites, for example, was higher
than the biomass of birds. Similarly, the estimated biomass of plant fungal pathogens was comparable to that of herbivores
in experimental grassland plots in Minnesota (Figure 3; Mitchell 2003). In fact, top-down control by fungal pathogens was
more important than herbivory in predicting grass biomass. These studies suggest that parasites can contribute significantly
to ecosystem energetics and exert strong control over the biomass of primary producers. While much remains to be learned

about the roles of parasites in food webs, the classical approach of omitting parasites from considerations of food web ecology could lead to serious errors in our understanding.
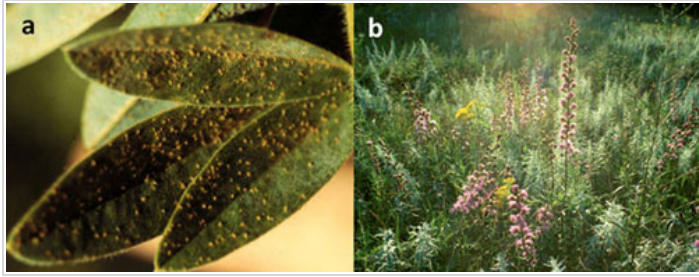

Figure 3: Parasites of plants regulate primary productivity in a grassland ecosystem.
(A) A fungal pathogen (Uromyces lespedezae-procumbenti) on the leaves of a prairie legume. (B) A Minnesota grassland ecosystem. In some grasslands, fungal pathogens can control productivity and biomass more strongly than herbivorous insects, suggesting that parasites play important roles in ecosystem energetics. (3A courtesy of C. Mitchell; 3B courtesy of Cedar Creek Ecosystem Science Reserve)

Parasitism, Competition, and Biodiversity

Parasites can influence biodiversity when they alter the outcome of competitive interactions between host species, a phenomenon termed parasite-mediated competition (Price *et al.* 1986). In some cases, this occurs when a tolerant host species amplifies a parasite's abundance, causing an indirect negative effect on a second, less tolerant host species. For example, the displacement of red squirrels by grey squirrels in Britain may have been facilitated by a parapoxvirus (Tompkins *et al.* 2003). The virus infects both species, but native red squirrels are highly susceptible, whereas invasive grey squirrels experience relatively minor negative effects. In this case, a microparasite has probably facilitated a biological invasion, thereby reducing local biodiversity by eliminating populations of one host species.

Parasites can also positively contribute to biodiversity by allowing a competitively inferior species to coexist with a dominant species. For example, *Anolis gingivinus* outcompetes *Anolis wattsi* everywhere on the Caribbean island of St. Maarten, except the isolated interior of the island. Both lizards host a malarial parasite, *Plasmodium azurophilum*, but the two lizards co-occur only where *A. gingivinus* is heavily parasitized (Figure 4). This suggests that malaria reduces the competitive ability of the dominant lizard, thereby allowing the competitively inferior lizard to coexist (Schall 1992). A similar outcome in a very different system occurs with the pathogenic soil oomycete *Pythium* and its plant hosts. The presence of a particular plant can change the composition of the local soil community such that the growth of that species is diminished, and other colonizing species are given a competitive advantage, which ultimately increases overall plant biodiversity (Mills & Bever 1998).
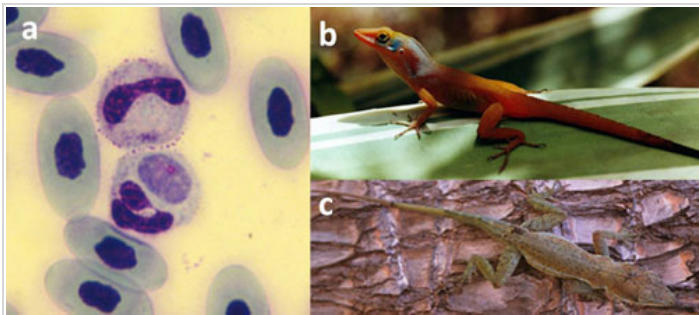

Figure 4: Parasite-mediated competition facilitates species coexistence.
(A) Malarial parasites (Plasmodium azurophilum) in the white blood cells of a lizard; (B) Anolis wattsi; and (C) Anolis gingivinus. Malaria has greater negative effects on the competitively dominant A. gingivinus, allowing A. wattsi to coexist in regions of with high malaria prevalence. (4A and 4C courtesy of J. Schall; 4B courtesy of G. White)

Parasites also influence biodiversity through the direct regulation of host populations. Even though parasites can cause disease, they rarely cause extinctions, because pathogen transmission is usually reduced at low host densities. However, important exceptions can occur, particularly in cases when pathogens invade naïve host populations, or when reservoir hosts allow parasites to persist despite low host densities. The emergence of the amphibian fungal pathogen, *Batrachochytrium dendrobatidis* (Bd), for example, represents a case of a parasite causing mass population

declines, and even extinctions of frogs, on a global scale (Kilpatrick *et al.* 2010). Collectively, the examples described here illustrate how parasites may have opposing net effects on biodiversity, which depend on the context of the parasite–host relationship (e.g., whether host populations are naïve, and whether parasite transmission is density–dependent), and on whether parasites most negatively affect competitively dominant or competitively inferior species in a community.

Parasitism, Keystone Species, and Ecosystem Structure

The effects of parasitism on ecological communities can be particularly pronounced when the hosts are keystone or dominant species with important functions in an ecosystem. For example, *Diadema* urchins in the Caribbean experienced a massive die-off associated with microbial pathogens, eliminating the keystone roles of urchins as grazers and bioeroders on coral reefs (Lessios 1988). Reefs in affected regions became overgrown with algae that displaced mature corals and prevented new coral settlement. In the most extreme examples, algal cover jumped from near 1% prior to the disease outbreak, to 95% in the following two years (Lessios 1988). Nearly twenty years later, *Diadema* populations recovered on some Jamaican reefs, and a shift back to a coral-dominated ecosystem has begun (Edmunds & Carpenter 2001).

Another example involves the introduction and subsequent removal of a viral disease called rinderpest in African ungulates. The virus was introduced to native ungulates from domestic livestock in 1890, and spread throughout the African continent within 10 years, reducing populations of buffalo and wildebeest (also known as gnus) by 80% in some regions. Vaccination of domestic cattle began in the 1950s (Plowright & Taylor 1967) and virtually eliminated the disease in wild African ungulates by 1968. The release of herbivores from parasite control had dramatic cascading effects on the ecosystem: populations of top carnivores, including lions and hyenas increased, and the productivity of grasses decreased (Sinclair 1979; Thomas *et al.* 2005). These examples of parasite introductions and removals provide a rare glimpse into how ecosystem structure can be dramatically altered when parasites regulate populations of functionally important host species.

Concluding Remarks

The prominent roles of parasites in food webs, competitive interactions, biodiversity patterns, and the regulation of keystone species, make it clear that parasites contribute to structuring ecological communities. Yet we have only begun to dissect the complex roles played by parasites in community ecology. Patterns of increased disease emergence in wildlife, with potential implications for human health and wellbeing, make it an especially relevant time to further integrate parasitism into community ecology and improve our understanding of the roles of parasites in nature.

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