

Coevolution of symbiotic mutualists and parasites in a community context

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Recent advances in our knowledge of parasitic and mutualistic associations have confirmed the central role of coevolutionary interactions in population and community ecology. Here, we discuss the potential coevolutionary interdependence of the strength and specificity of symbiotic interactions with the complexity and productivity of their environment. We predict that interactions become less beneficial with increasing environmental quality and that the association of productivity with symbiont specificity depends on the relative strengths of tradeoffs between host range and other life-history parameters. However, as biotic complexity increases, pathogen specificity is predicted to decline, whereas mutualist specificity will increase. Testing these predictions on a geographical scale would contribute significantly to the predictive science of coevolution, and to our ability to manage biological interactions embedded in increasingly fragmented landscapes.

Introduction

Symbiotic parasitic and mutualistic* associations are of major importance as drivers of ecological function and evolutionary processes. These apparently contrasting types of association often exhibit similar features, including asymmetries in body size and deep phylogenetic separation of the interacting species, and high degrees of genetic specialization. These elements are indicative of the intimate nature of these associations, where interacting individuals are generally not immediately injured or killed, but for which the benefits of cheating or evolving heightened virulence leads to selection for adaptations in the affected partner to resist, defend itself, or impose sanctions. Close scrutiny of mutualistic interactions reveals that heterogeneous selection pressures (e.g. adaptation to local habitats, drift and low gene flow) can alter the strength and net fitness effect, causing these interactions to become parasitic under certain conditions [1–5].

Tightly coupled interactions between pairs of species represent only some of the diverse symmetric and asymmetric interactions arrayed along a generalist–specialist continuum, inevitably embedded in community-level

interactions of varying degrees of complexity. Thus, studying host–symbiont dynamics within a community context is a key component of a more general predictive science of coevolution [6–10]. Importantly, complexity does not imply that coevolutionary impacts on communities and vice versa are limited to ‘diffuse’ effects. Rather, it is because most species interact with suites of other species that vary dynamically across geographical landscapes, that coevolutionary processes can be important in organising communities and maintaining variability within specific interactions, such as mutualisms or host–parasite systems [6]. For example, some trematode parasites have strong effects on the evolutionary dynamics of their snail hosts, but themselves are dependent upon waterfowl for completion of their life cycle [11].

An increasing number of studies are exploring how coevolutionary interactions are modified when embedded within communities of varying complexity [12,13]. However, the only synthetic theory is the conceptual framework presented by Thompson [6], based on an array of component mechanisms (e.g. geographical selection mosaics, coevolutionary hotspots and trait remixing). Here, we focus on symbiotic interactions (mutualism and parasitism) to illustrate a complementary way of viewing coevolutionary interactions, based on the integration of environmental quality and community complexity. Specifically, we develop expectations for the evolution of the strength, sign and specificity (the range of host strains or species that can be exploited by parasites or mutualists) of symbiont interactions with their hosts as a function of productivity and biotic complexity (Box 1).

Coevolutionary feedbacks in natural communities

Because symbiotic interactions are set in communities and ecosystems, they are subject to the same ecological and evolutionary pressures as other associations (e.g. competition and predation) and, therefore, are important testing grounds for macroecological and ecosystem patterns. Given the broad features of parasitism and mutualism, some ecological patterns should be specific to symbiotic lifestyles and should also differentiate parasitic and mutualistic systems. There might also be parallels between the evolution of resistance and virulence in host–pathogen associations and the evolution of effectiveness in host–mutualist associations [14] that emerge when viewed within a common conceptual framework. In addition to providing insights into coevolutionary effects on

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* Symbiosis is defined as the protracted, intimate interaction between individuals of two different species as opposed to free-living predator–prey or plant–herbivore interactions. Parasitic associations occur when one symbiont lives at the expense of the other, and mutualisms are situations where both species benefit from the association.

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Box 1. Coevolutionary feedbacks in multilevel ecosystem modules

We define environmental quality as the availability of potential resources that impinge on the growth, survival and reproduction of an organism and, therefore, on population density as well as the potential for disease transmission. Recent theory exploring community dynamics in relation to abiotic stress suggests that quantifying the relative impact of environmental variation on reproductive ability versus mortality is important for understanding spatial patterns of positive and negative interactions [75]. For parasites and mutualists, environmental quality includes the physical environment experienced directly or via the host, as well as factors that correlate with host condition, productivity or ability to tolerate or resist infection [76]. Environmental quality also includes the frequency and amplitude of abiotic stresses (e.g. disturbance regimes), particularly where such processes relate to the predictability of resource availability. Although we do not explicitly consider factors that influence individual host condition (stress) or physiological ability (e.g. metabolic rate) in our definition of environmental quality, such variation is likely to correlate with population measures of productivity.

A definition of community complexity is the number of potential interacting strains or species (e.g. the number of different hosts, herbivores or symbionts) and, thus, the potential for ecological and evolutionary conflicts; more completely, it includes the degree of representation by different 'functional' groups and the phylogenetic relationships among species (e.g. a community of closely related parasites versus a random assemblage or one in which relationships are more distant). Modeling approaches based on the characterization of community food-web topologies [77–79] or the extension of epidemiological contact networks [80] to multiple species could also prove useful in this context.

community dynamics, taking a broader approach to coevolution in studies that encompass large-scale environmental gradients would improve our ability to disentangle the impacts of historical effects from species interactions on community structure [15].

Biotic complexity and environmental quality are often correlated [16–18] and numerous explanations have been offered for this relationship [15,19,20], many of which focus on biotic complexity emerging as a response to productivity. Given that coevolution with symbiotic pathogens and mutualists might contribute to this dependence, we first develop expectations for the shift in symbiont dynamics along a productivity gradient and then add the dimension of biotic complexity.

Evolutionary trajectories of parasites and mutualists along a productivity gradient

Increasing environmental quality should favour exploitation and, therefore, parasites over mutualists (i.e. the relative abundance and virulence of exploiters along the mutualism–parasitism continuum, rather than exclusion of either type of symbiosis). Increased host density enables increased rates of horizontal transmission, which favours virulent pathogen strains or species. This prediction is supported by results from analytical models [2,3,21], which show that more beneficial symbionts are favoured when host productivity is low, whereas more virulent symbionts tend to dominate when host productivity is high. For example, monarch butterflies *Danaus plexippus* vary in migration behaviour and population size across North America. Prevalence and virulence of an

associated protozoan parasite, *Ophryocystis elektroscirrha*, are both greater in the larger non-migratory host populations occurring in regions where resources are available year-round [22].

Increased rates of mixing between hosts associated with increased productivity also favour the spread of cheaters within mutualisms [23]. Using a pairwise Lotka–Volterra approach, Neuhauser and Fargione [21] found that mutualists were favoured when host carrying capacity was low, but that parasites were favoured in more productive environments where host densities were higher; their results further predicted that, in multi-species assemblages with increasing productivity, there would be a shift from systems with only mutualists to mixed symbiont communities to parasites only. Economic models of provider mutualisms (e.g. rhizobial bacteria or mycorrhizal fungi) also suggest that mutualisms decline with increasing nutrient availability [24]. The convergence of results from multiple modelling frameworks suggests that the expected shift from mutualism to parasitism with increasing productivity (Figure 1a) is robust. Similar predictions regarding the expected prevalence of negative interactions in productive environments have been made by other authors [25,26].

By contrast, expectations for the evolution of symbiont specificity across productivity gradients are more complex. From the symbiont perspective, the evolution of specificity is favoured by competition arising from multiple infection and strong tradeoffs in competitive ability on different hosts [27]. Low intrahost competition arising from constraints on transmission [28] and on symbiont population size [29,30] at low productivity, along with increased intrahost competition enabled by higher transmission rates at high productivity, will generate increasing host specificity with increasing productivity (Figure 1b), and this might be exacerbated by the evolution of host defences in response to increased pathogen virulence. However, given weak tradeoffs in growth rates on different hosts, or in intrinsic growth rates or transmission rates, generality will be favoured where alternate hosts are available [31]. As productivity increases, so too does the availability of alternate hosts, which will increase selection for generality [31], generating a negative dependence of host specificity on productivity (Figure 1c). Given these contrasting expectations, the ultimate outcome will depend on the relative strengths of the tradeoffs and host evolutionary and coevolutionary responses. One component of the coevolutionary response is likely to be an increasing diversity of hosts and symbionts over at least some range of productivity [31] (Figure 1e). Thus, further consideration of the evolution of specificity necessarily includes biotic complexity.

Response of pathogens and mutualists to biotic complexity

The trajectory of host–symbiont coevolution depends on multiple dimensions of biotic complexity. Pathogen diversity, particularly within-host genetic variation, will often favour more competitive strains and increased host exploitation, thereby increasing virulence [32], particularly when exploitation is determined by individual infecting

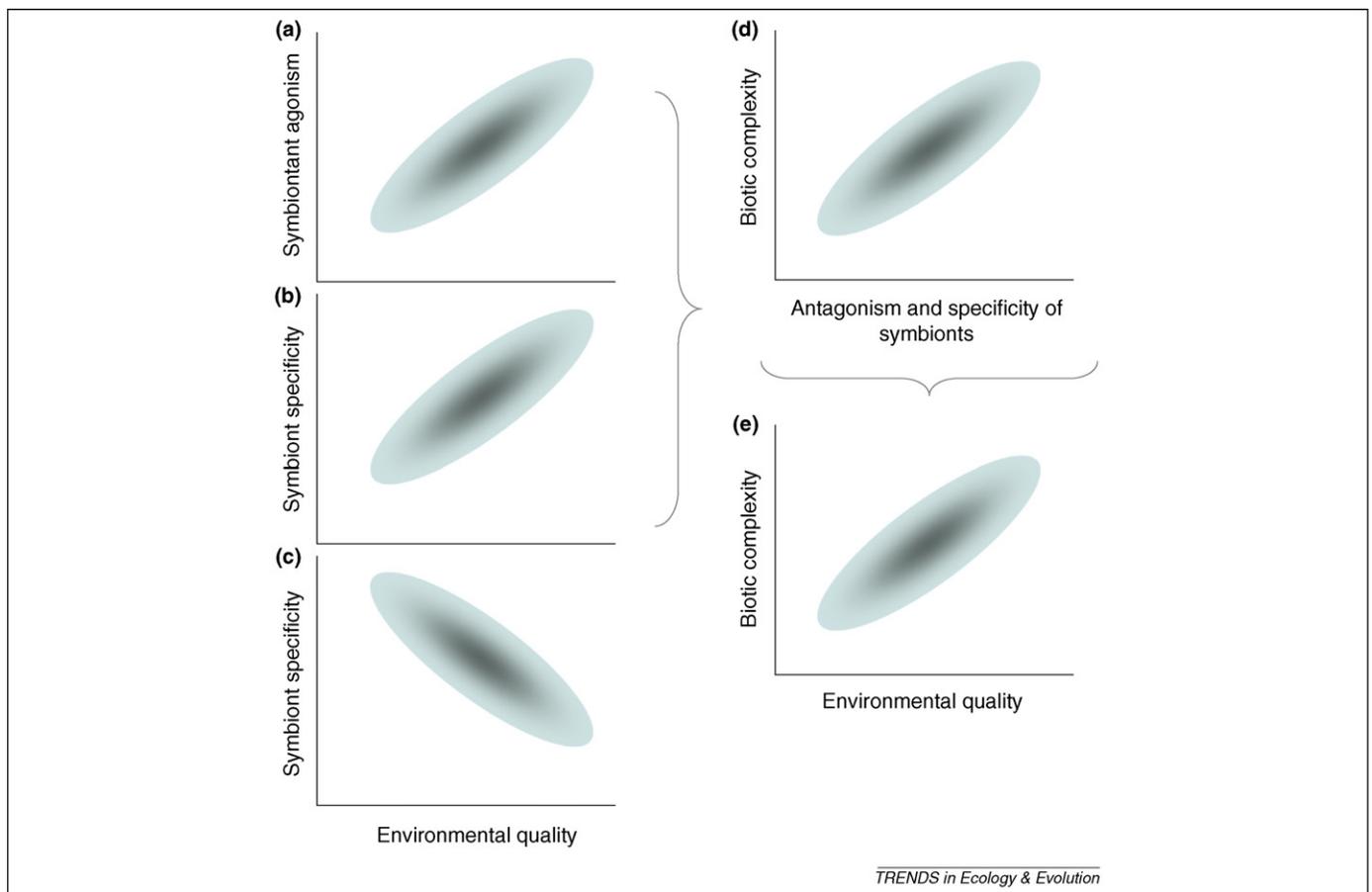


Figure 1. Dependence of virulence, mutualism, specificity and biotic complexity on environmental quality (illustrated by the shaded ovals). With increasing environmental quality, we predict increasing virulence in pathogens and proliferation of cheaters in mutualisms (a). Increasing environmental quality will also reduce minimum population constraints on specialization and increase intrahost competition, both of which will favour the evolution of greater symbiont specificity with higher environmental quality (b). However, increased environmental quality will also increase the availability of alternate hosts, potentially favouring generalism (c). Increased symbiont negativity and specificity in these interactions might generate and maintain greater diversity in associated hosts, thereby increasing biotic complexity (d). This could then create a dependence of biotic complexity on environmental quality (e).

parasites rather than the co-infecting group [33]. Similarly, within-host mutualist diversity will facilitate cheating, thereby decreasing the strength of mutualistic benefits. The expectation of increased virulence and decreased mutualism with increasing symbiont diversity within hosts is supported by theory [23,34], but evolution in the context of other aspects of biotic complexity remains to be fully explored. Pathogen virulence and specialization might either increase or decrease in multi-host communities, depending on whether traits required to infect different hosts successfully are positively or negatively correlated, the relative extent of among-host transmission, and variation in host species abundance [13]. For example, analysis of data from fish–metazoan and mammal–flea host–parasite interaction networks suggests that increased host abundance correlates directly with the proportion of specialist parasites [35].

Importantly, the direction of the evolution of specificity might differ between host–pathogen and host–mutualist systems. Hosts confronted with more parasite species or strains will tend to select for more general all-purpose defences, whereas parasites confronted with more host species will tend to broaden their host range [36], depending on the constraints represented by phylogenetic affinity and availability of new hosts, and the extent to which host range extension represents a direct advantage to the

parasite [37]. We have similar expectations with regard to the evolution of specificity in symbiotic mutualists, suggesting that generalists will increase with the biotic complexity of host communities. If all symbionts were beneficial, we would also expect hosts to be generalists when confronted with more diverse symbiont communities. However, given the demonstrated variability in effectiveness of mutualistic symbioses and the problem of proliferation of cheating symbionts within mutualisms [4,14], we expect hosts to evolve greater specificity in response to increasing diversity within their mutualists.

Mutualistic partners generally share an interest in protecting the mutualism from cheaters [38]. Each might evolve highly specific, sometimes exaggerated characters to protect the interaction (e.g. the complex recognition signals exchanged by legumes and rhizobia before infection; [14]). From this perspective, the specificity of the interaction inhibits the spread of cheaters, which are more likely to be present as biotic complexity increases, particularly if this is linked with productivity. This suggests that the evolution of specificity in symbiotic mutualisms might be driven harder in more productive environments, which also favour parasitic associations and cheaters. Whether this occurs will depend partly on the extent to which the fitness impact of cheaters on mutualist partners is reduced as environmental quality increases.

Overall, there has been less theoretical consideration of the impact of community structure on host–symbiont coevolution. However, results from a theoretical model developed by Jokela *et al.* [39] predict that, as enemy diversity increases, there should be a corresponding shift in host strategy from one of defence (resistance) towards tolerance. In part, this is because increased unpredictability of the interaction is linked to lower effectiveness of more specific defence responses [36], but it could also relate to the potential advantages of tolerance as a ‘biological weapon’ in environments with increased interspecific competition [40]. Recent models have begun to explore coevolution in multi-species interactions [12,13,41], although not focusing on complexity *per se*. Integration of these ideas suggests a synthetic theory of the evolution of host–symbiont interactions as a function of environmental quality and biotic complexity (Figure 2). Although some components of this synthesis have more theoretical support (e.g. shifts from mutualism to parasitism with increasing environmental quality; [21,24]) than others (e.g. predictions with regard to the evolution of specificity; [31]), it provides a basis for developing testable hypotheses regarding the evolution of symbiotic parasites and mutualists.

Hypotheses, predictions and empirical evidence

In addition to some of the examples cited earlier, there is good support for the expectation that provider mutualisms (e.g. rhizobia or mycorrhizae) decline with increasing environmental quality. Nitrogen fertilization, for example,

leads to the proliferation of rhizobial and mycorrhizal strains that are less beneficial to plants [14,42,43]. Similar shifts have been observed in the dependence of hosts on mutualistic symbionts. When derived from infertile sites, big bluestem *Andropogon gerardii*, a dominant grass in central USA, is highly responsive to mycorrhizal fungi, whereas its responsiveness when from fertile sites is reduced [44]. In crop situations, higher rates of fertilizer application often result in increased disease incidence and severity [45,46]. Longer term predictions are also possible. Thus, the observed positive relationships among elevated CO₂, plant growth and yield, and pathogen aggressiveness [47], and between plant species richness and pathogen host range [48] suggest that, in the face of global climate change, more aggressive, host-specific pathogens will be favoured. Clearly, however, trajectories of pathogen community change will depend on the nature of tradeoffs between virulence and transmission [49].

Expectations for patterns of specificity (e.g. the idea that generalist parasites should be favoured in host species-rich productive environments) have less support. For example, microbial mutualisms in species-rich coral reefs appear to be highly host specific [50], whereas many coral diseases are generalists and can infect sets of taxonomically distant hosts [51,52]. Experimental manipulations of plant community diversity have shown that, not only does decreased diversity result in greater pathogen abundance, but it also leads to an increase in the relative prevalence of host-specific foliar pathogens [48]. Analogous to this, at the within-species level, agronomic experiments with crop

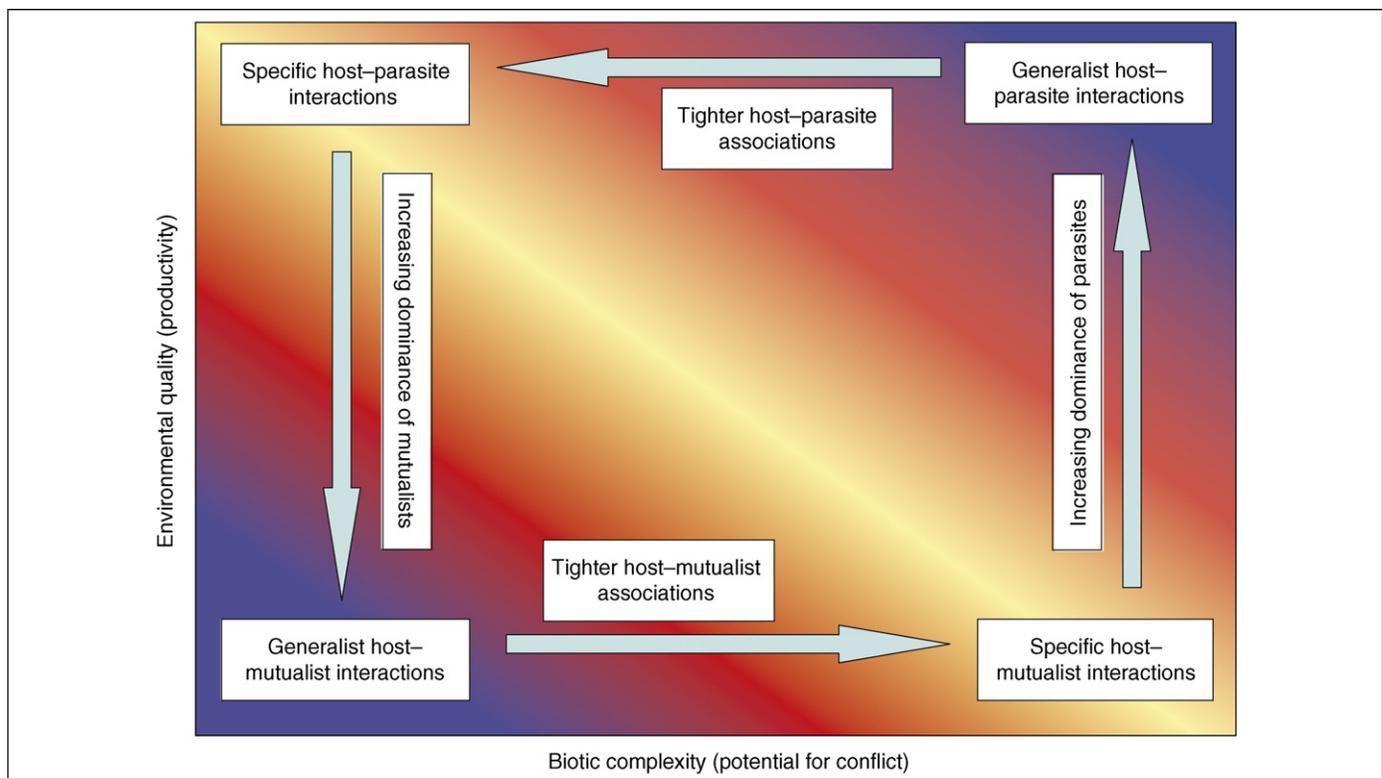


Figure 2. Coevolutionary predictions for parasitic and mutualistic interactions with respect to environmental quality (productivity), and biotic complexity (diversity and/or potential for conflict). We assume that both axes also correlate with predictability; in the case of environmental quality, this can refer to resource availability, whereas in the case of community complexity, this might refer to the likelihood of encounter between particular pairs or subsets of interacting species. The diagonal from upper left to lower right represents the ecological space in which the tightest pairwise coevolutionary interactions are expected (i.e. coevolutionary hotspots in productivity–complexity space).

mixtures [53] as well as studies in natural plant–pathogen systems suggest that more broadly infective pathogen strains are favoured in host populations with a higher diversity of resistance phenotypes (e.g. the rust fungus *Melampsora lini* occurring on the native flax *Linum marginale*; [54]). Perhaps also relevant is the observation that immunological defence strategies vary for finches on large versus small islands in the Galapagos [55]. However, it is unclear whether large islands, where specific antibody responses are favoured, are more species rich compared with small islands in which less specific cellular immune responses predominate.

As well as less-specific parasites, increased complexity might also favour a shift from qualitative resistance (e.g. matching allele or gene-for-gene) to quantitative resistance or to tolerance (representing more generalized defence strategies; [39]). In an empirical study of fungal diseases in a relatively low-diversity shrub community, Roy and co-workers [56] found evidence for high disease tolerance rather than host resistance; they inferred that tolerance had evolved because of the high annual probability of infection. Interestingly, each of the dominant shrub species in this simple community was attacked by a different host-specific rust pathogen.

Assessing the validity of the general predictions illustrated in Figure 2 requires experimental tests in concert with theoretical studies that evaluate explicitly the ways in which interactions between community structure and environmental quality alter coevolutionary outcomes. For example, how do these axes correlate with host and symbiont abundances and, therefore, with the intensity and direction of selection? If, as some studies suggest [57], positive correlations are likely between host and parasite abundances, does this indicate decreased potential for host-specific coevolutionary interactions in complex environments because the average abundance of particular interacting species is lower? Within-host pathogen genetic diversity can lead to the evolution of higher pathogen virulence, and similar patterns are seen at the population level for the effect of host genotypic diversity on pathogen infectivity [54]: are there parallels at the community level? We might predict higher virulence in more diverse host communities or in situations with high numbers of parasite species, particularly if tolerance increases with diversity [39]. A recent model [58] shows that higher pathogen virulence should evolve on hosts that are more tolerant, but this might depend on how among-host transmission patterns are influenced by increased community diversity [13].

Would the average effectiveness of mutualists show similar responses to biotic complexity? For example, would we expect a higher average ability of populations of nitrogen-fixing root-nodule bacteria to promote host plant growth in more diverse legume communities, or would diversity increase the likelihood of degradation of the mutualism [59]? With shifts from simple to more complex community structure, is there evidence for correlated changes in the relative abundance of mutualists and parasites? One empirical approach to answering these questions might be to use successional communities along temporal gradients or even long-term restoration sites

as natural experiments. Interactions between plants and soil symbionts, such as rhizobia, might be particularly good systems in which to test hypotheses regarding interactions between community structure and environmental stress; not only do these symbionts vary in nitrogen-fixing ability and host specificity [60,61], but they also span the continuum from mutualistic to highly parasitic [14].

Mapping ecosystems in coevolutionary space

Plant and animal species diversity, primary productivity and environmental equitability tend to increase with decreasing latitude or altitude [25]. Is it possible to make specific coevolutionary predictions that apply generally to, for example, temperate versus tropical systems? Geographically broad studies of patterns of parasite and pathogen community diversity suggest that the strength and direction of the correlation with latitude depends on the taxonomic group being investigated. The species richness of vector-borne protozoan diseases of free-living primates shows a strong latitudinal gradient, increasing towards the equator [62]; the same study found no such pattern for viruses or helminths. Guernier and colleagues [63] have also shown that parasites affecting humans increase in diversity from temperate to tropical regions. Endoparasite communities of freshwater fish are often richer in temperate regions [64,65], but the reverse is true of marine assemblages of ectoparasites [66,67].

Whereas for purposes of generating ecosystem-specific testable hypotheses it would be useful to map major biomes (e.g. Arctic tundra, temperate grasslands or humid tropical rainforests) to specific regions of productivity–complexity space (Figure 2), for any particular environment there are multiple resource axes (e.g. primary productivity, soil nitrogen, water and solar energy), the relative importance of which will vary for different groups of organisms. For example, the humid tropics are highly productive in terms of solar radiation and aboveground biomass, but are poor in soil nutrient levels. Thus, we might make different predictions for mutualists, parasites and hosts depending on which resource axis was the focus. Overall, we would expect at least some degree of correlation in the responses of different organisms to a particular resource axis (e.g. rainfall or soil fertility), thus providing opportunities to tease these effects apart.

Symbiont life history and community coevolution

Mutualistic symbionts can be classified into two broad types: ‘protectors’ (e.g. against natural enemies), and ‘providers’ (i.e. those that provide some essential reduced or missing component, such as rhizobial bacteria) [3,25]. One example of protecting mutualisms is the diverse group of fungal endophytes that asymptotically infect the leaf tissues of tropical trees. Recent work [68] suggests that these organisms have a significant role in protecting trees from fungal pathogens, such as *Phytophthora* spp; these endophytes appear to show a relatively low level of host specificity [69]. Generally, in the high-quality productive environments that favour antagonistic interactions, we predict a shift in relative abundance from provider to protector mutualisms, whereas the opposite is expected in low-quality environments [3].

Are there class distinctions that can be made among pathogens and parasites that have predictive value in the context of community coevolution? For example, it has been suggested [35,70] that parasites can be divided into castrators, killers and debilitators (e.g. water fleas *Daphnia magna* and the castrating bacterium *Pasteuria ramosa*, damping-off disease of seedlings caused by the fungus *Rhizoctonia solani*, and the common cold respectively); more complex schemes, which extend this idea, have also been proposed [71]. Currently, although it is possible to develop some predictions regarding the evolution of mutualism versus parasitism, host specificity and pathogen virulence in relation to environmental quality and community complexity, it is unclear how other pathogen life-history features (e.g. transmission mode, life-cycle complexity or dependence on free-living stages) would map onto our conceptual framework.

Conclusion

One of the biggest challenges for community ecology is to predict how niche space evolves [72]. Once symbionts are included in the system, they become part of the habitat template and cause other changes (e.g. mutualists can increase the realized niche of their hosts) [2,26], potentially resulting in complex ecological and coevolutionary dynamics. Essentially, this can be viewed as a problem in community assembly where there is an order of invasion. At its simplest, the successful spread of mutualists can shift environments from low to high productivity, thus attracting parasites and cheaters. Enhanced competitiveness of the host of the mutualist might also lead to decreased community diversity; both processes should favour exploiters or more-virulent host-specific pathogens, which might in turn self-limit the spread of the mutualist and its partner. Similarly, in intrinsically productive systems, predators and parasites dominate; this will attract mutualistic protectors, which might in turn, select for more specialized enemies. Such feedbacks might be further complicated by variation in community structure and species richness. For example, soil community abundance and diversity partly determine decomposition processes and nutrient cycles, thus affecting environmental quality. Interestingly, experimental studies of saprotrophic fungi showed that increased diversity resulted in reduced nitrogen and phosphorus availability [73].

From a more applied perspective, understanding successional dynamics (or, conversely, processes associated with ecosystem fragmentation) is central to restoration ecology and the goal of rebuilding biodiverse functioning communities. More specifically, we are interested here in how symbiotic parasite, pathogen and mutualist communities develop over time. What factors determine key characteristics such as host range, pathogen virulence and mutualist effectiveness, or the types of symbionts that predominate? We have highlighted some predictions for symbiotic associations in relation to environmental quality and community complexity. There is theoretical and empirical support for elements of the framework that we present, but there are also significant gaps (e.g. expectations regarding the evolution of specificity). In this context, it is important to compare explicitly predictions for symbiotic and free-living

associations, which appear to be fundamentally different, and might well respond to different axes of selection [74]. There will be value in developing experimental systems in which symbiont dynamics are explored in response to changes in complexity and productivity. Linking such studies with a more-complete theory that accounts for interactions between environmental quality, ecological (e.g. community assembly rules) and coevolutionary processes will be a significant step towards addressing these issues.

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