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Opinion

Embracing Colonizations: A New Paradigm for Species Association Dynamics

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Parasite–host and insect–plant research have divergent traditions despite the fact that most phytophagous insects live parasitically on their host plants. In parasitology it is a traditional assumption that parasites are typically highly specialized; cospeciation between parasites and hosts is a frequently expressed default expectation. Insect–plant theory has been more concerned with host shifts than with cospeciation, and more with hierarchies among hosts than with extreme specialization. We suggest that the divergent assumptions in the respective fields have hidden a fundamental similarity with an important role for potential as well as actual hosts, and hence for host colonizations via ecological fitting. A common research program is proposed which better prepares us for the challenges from introduced species and global change.

Parasites and Phytophagous Insects – Divergent Traditions

Why, how, and when do species associations emerge and change? Trying to answer these questions has always been a key challenge in ecology and evolutionary biology, but might even be crucial for the wellbeing of our own species. After all, the increasing records of emerging infectious diseases (EIDs) [1] result from changing species associations, as an infectious species or virus strain spreads from its previous host species to also attack humans [2,3]. Furthermore, EIDs and new pests also attack other organisms of importance for our existence, such as crops, sources of wood, or livestock [3]. Such changes in associations between infectious agents and their hosts are somewhat mysterious given the traditional assumption in parasitology that parasites are typically highly specialized on a single host species because they need specific adaptations to the host. At first glance, this seems a reasonable expectation given that hosts are both resources and habitat for the parasite [4]. It is even a commonly expressed default expectation for the evolution of associations between parasites and hosts that the associations are so intimate and persistent over time that the interacting lineages should cospeciate, leading to congruent phylogenies [5,6]. This idea has been around for over a century [7], and shows little sign of decreasing in popularity [6,8,9].

Let us first contrast this research tradition in parasitology with the field of insect–plant research (including herbivorous arthropods such as mites). Many phytophagous insects live parasitically on their host plants, so we could expect the two fields to be closely connected when it comes to theory development. Instead, most treatments on parasite–host theory barely mention insect–plant systems and vice versa. Rather, the two fields have developed very divergent research traditions, where for instance, the idea of cospeciation has been an important part of parasitology research but has seldom been taken seriously for associations between insects and plants [10]. Ehrlich and Raven's [11] original and still influential concept of coevolution between butterflies and plants, for

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Parasites are typically assumed to be highly specialized on their hosts and well adapted to them, yet they frequently colonize new hosts – including humans, causing EIDs.

This parasite paradox has caused a growing unease with the traditional assumptions in parasitology, which differ markedly from those in the field of insect–plant studies.

We report the results of a workshop where parasitologists and insect–plant researchers met to explore the possibility that the two systems may be more similar than the divergent research traditions suggest, so that a common research program can be developed to better prepare us for future challenges.

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example, did not suggest cospeciation but rather a diffuse matrix of interactions; later developed by Thompson [12] into the concept of the geographic mosaic of coevolution (it should be noted in passing that we do not deal with or reject coevolution here, and do not accept that cospeciation is the 'hallmark of coevolution' [6]). Insect–plant theory has been more concerned with host colonizations, key innovations, and subsequent adaptive radiations than with cospeciation [13,14], and more with preference and performance hierarchies among multiple hosts than with extreme specialization and specific adaptations to a particular species of host plant [15].

Parasite–Host and Insect–Plant Associations Are Similar

While parasitology and insect–plant research put different emphases on cospeciation and host colonizations, respectively, differences are less apparent in the biology of the systems. Here, we posit that the widespread but divergent assumptions in the respective fields have been a hindrance rather than a help, and that a common research program should instead be developed. The present article stems from a workshop where parasitologists and insect–plant researchers met to explore this idea and found that observed patterns in the two fields are indeed strikingly similar (Table 1 and Figure 1). This suggests that the fields can be integrated and a synthetic understanding can be developed for mutual benefit.

Table 1. Patterns Commonly Observed in Both Insect–Plant and Parasite–Host Systems

Pattern	Examples (insect–plant)	Refs	Examples (parasite–host)	Refs
Specialization common, but host range varies	Nymphalid butterflies	[64]	Malaria-birds	[73]
	Lepidoptera globally	[65]	Unionid mussels–fish	[74]
	Nematinae sawflies	[66]	Nematodes–Artiodactyla	[51]
	Spider mites	[26]	Monogenoida gill parasites-fish	[75]
			Worms-fish	[76]
Wide host ranges are typically apical	Nymphalid butterflies	[64]	Malaria-birds	[77]
	Nematinae sawflies	[66]	Trematodes–snakes, turtles etc.	[33]
	Phyllonorycter moths	[67]		
Relatives share hosts or host clades	Nymphalid butterflies	[64]	Malaria-birds	[73]
	Eois geometrid moths	[68]	Nematodes–Artiodactyla	[51]
	Nematinae sawflies	[66]	Lice-pocket gophers	Box 2
	Phyllonorycter moths	[67]		
Colonizations common via ecological fitting	Nymphalini butterflies	[34]	Malaria–birds	[52]
	California butterflies	[69]	Unionid mussels–fish	[24]
	Nematinae sawflies	[66]	Nematodes–Artiodactyla	[51]
	Spider mites	[26]	Gyrodactylid gill parasites–fish	[78]
	Lycaena salustius butterfly	[70]	Trematodes–snakes, turtles etc.	[33]
			Pomphorynchus worm–amphipods	[21]
			Nematodes–birds	[49]
			Platyhelminths–anurans	[79]
Cospeciation is rare or absent	Nymphalid butterflies	[34]	Malaria–birds	[6]
	Psyllid bugs	[71]	Nematodes–Artiodactyla	[51]
	Phyllonorycter moths	[67]	Lice–pocket gophers	Box 2
	Cynipid gall wasps	[72]		
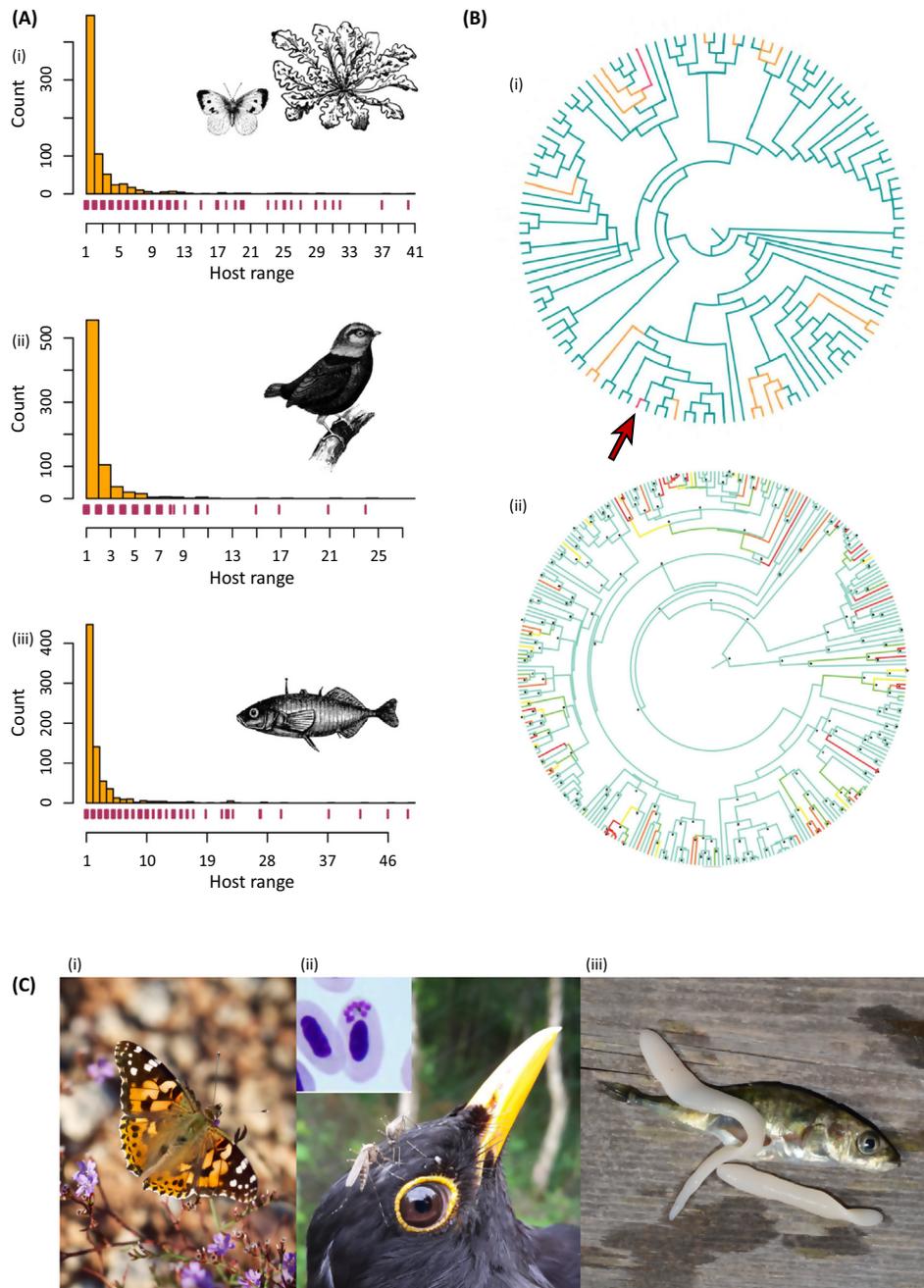
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Figure 1. Examples of Strong Similarities between Ecological and Evolutionary Patterns Observed in Parasite–Host and Insect–Plant Systems. (A) Distribution of host ranges across taxa: (i) number of host plant species for species of Lepidoptera, data from [65]; (ii) number of bird host species for 756 lineages of blood parasites (*Haemoproteus* spp.), data from [73]; (iii) number of fish host species for species of parasitic worms, data from [76]. Lepidoptera and fish parasite data were randomly subsampled to 756 species to make graphs easily comparable. Tick marks below figures highlight individual observations. Note the predominance of narrow host ranges but also the long tail of generalists in each taxon, suggesting that although specialization is the dominant evolutionary process, generalization sometimes occurs, only to later give rise to specialization anew. (B) The phylogenetic position of generalist species: (i) host ranges for butterflies in the subfamily Nymphalinae, with species using seven or more plant orders in red, three or more in

(Figure legend continued on the bottom of the next page.)

In both types of systems, trophic specialization is a predominant pattern, but at the same time there is much variation in host range – a few species have wider host ranges than the others have (Figure 1A). Such species are typically seen apically in phylogenies, and only rarely is wide host range a trait characterizing entire large clades (Figure 1B), suggesting that the degree of specialization varies over evolutionary time, but with a strong trend towards respecialization after episodes of a wider host range [16]. By contrast, related species of parasites and phytophagous insects often share the same specific host species or host clades. This pattern suggests that host colonizations predominantly involve closely related hosts, which generally provide similar resources and defensive challenges to be overcome. Rather than parasites and phytophagous insects remaining on the same lineage of hosts over evolutionary time, speciating when the hosts do, there is a pattern of frequent colonizations of new host lineages when ecological opportunity arises (Box 1). Importantly, there is little evidence of cospeciation in either system (Box 2).

The similarities in observed patterns between the two research fields suggest that the prevalent assumptions of specialization and cospeciation in parasitology may be incorrect and that the alternative explanation where host colonizations account for observed patterns has been largely overlooked. For example, it has often been acknowledged that parasites can sometimes be found on alternative hosts, but with the exception of some universally recognized generalists (e.g., the protist parasite *Toxoplasma gondii*), alternative hosts have tended to be treated as uninteresting deviations from the norm rather than indicators of the potential for host colonizations. Similarly, although cospeciation can immediately be ruled out in many parasite–host systems, theory in the field typically takes this process very seriously as a default model that should always be addressed [6,8,9].

Comparing the Traditional and Revised Paradigms

We believe it is of some value to clearly formulate the pervasive influence of cospeciation thinking in parasitology research, and we will do so here, even though we are aware that such an exercise will be something of a caricature (i.e., real-life parasitologists are typically well aware of the many exceptions to the cospeciation rule). At the core of the traditional paradigm in parasitology is the assumption that parasites are typically highly specialized on a single host species. This expectation follows from the parasitic lifestyle itself: it is an intimate relationship with the host, and the parasite therefore needs to be well adapted to it. The parasite has to overcome any defenses that the host might throw at it, such as a targeted immune system, and will also be selected to become more efficient at utilizing this particular host as a resource for its own survival and reproduction. Thus, it is reasonable from an optimality perspective to expect trade-offs against adaptations enabling the use of other hosts [17], leading the parasite to being trapped in specialization. Under this scenario, genetic change is needed to escape specialization – often in more traits than one – which means that expanding to other hosts will be a rare event. Consequently, specialization is maintained over long time periods during which the host

orange, data from [64]; (ii) host ranges in 303 lineages of avian blood parasites (*Haemoproteus* spp.), calculated with a quantitative approach and labeled by branch color from blue (infecting a single host species) to red (infecting two or more host orders), data and figure reproduced, with permission, from [77]. Note the apical phylogenetic position of generalists in both taxa, again suggesting that this is a transient state and that host ranges oscillate from specialization to generalization over evolutionary time. The arrow in diagram (i) indicates the phylogenetic position of *Vanessa cardui* (see below). (C) (i) The Painted Lady *Vanessa cardui*, a butterfly with an exceptionally wide host range (photo by N. Janz); (ii) The European blackbird *Turdus merula* is a common host for the generalist blood parasite *Plasmodium vaughani* (shown in the corner), with mosquitoes as important vectors (photos: bird by S. Bensch, parasite by P.B. Šivickis Parasitology Laboratory of Nature Research Centre, reproduced with permission); (iii) a three-spined stickleback *Gasterosteus aculeatus*, parasitized by the cestode worm *Schistocephalus solidus* (photo by Bertil Borg, reproduced with permission).

Box 1. Species Associations Are Shaped by Resources and Opportunity

The traditional paradigm in parasitology notes that related species feed on related hosts (circular arrows over clades in Figure I depict such phylogenetically constrained patterns), and from this pattern infers an evolutionary history dominated by cospeciation. However, although both parasite–host and insect–plant species associations are indeed to a large extent shaped by phylogeny, this can be because of historically conserved habitats and ecologies (depicted by blue and red clades in Figure I), similar resources provided by related hosts [47], and similar host defenses [48] rather than because of a tightly shared evolutionary history. Moreover, species associations are also determined by opportunity. Horizontal arrows in Figure I depict colonizations between host clades sharing geographic distribution, habitat, or ecology, providing opportunities for new associations. For instance, a strong effect of geography was shown for the associations of spider mites with plants [26]. In birds, the occurrence of nematode parasite species increases with ecological opportunity resulting from migratory habits and use of multiple aquatic habitats [49]. In general, associations between parasites and hosts are strongly affected by the opportunities given in the community [50].

Any perturbations of species ranges will bring together new parasite–host combinations, seeding opportunities for host colonization through ecological fitting. Well-studied examples come from studies of species introductions, such as the global translocation of sheep and cattle since the 1500s strongly explaining the current host range of *Haemonchus* nematodes [51]. Another example is the malaria-inducing protozoan *Plasmodium relictum*, which was unintentionally introduced to Hawaii in the 1930s [52] and is now highly virulent in the Hawaiian honey creepers.

On macroevolutionary time scales, it is likely that major events such as mass extinctions and global changes in geology and climate have strongly perturbed the distributions of species, across many taxa [53]. We can infer this process from known historical events and recent species associations. Examples include the historical reconstruction of artiodactyl host colonizations by *Haemonchus* nematodes following an ancestral association with antelopes in Africa [51]. Paleontological evidence can be found from the dense fossil record of brachiopods and bivalves, documenting waves of invading species during major paleohistorical events. This resulted in a breakdown of community structure and formation of new species associations via a combination of ecological fitting and new encounters between species [54,55]. The current wave of EIDs is in all probability at least partly a result of similar processes, where climate change and global travel and trade brings new combinations of species into contact.
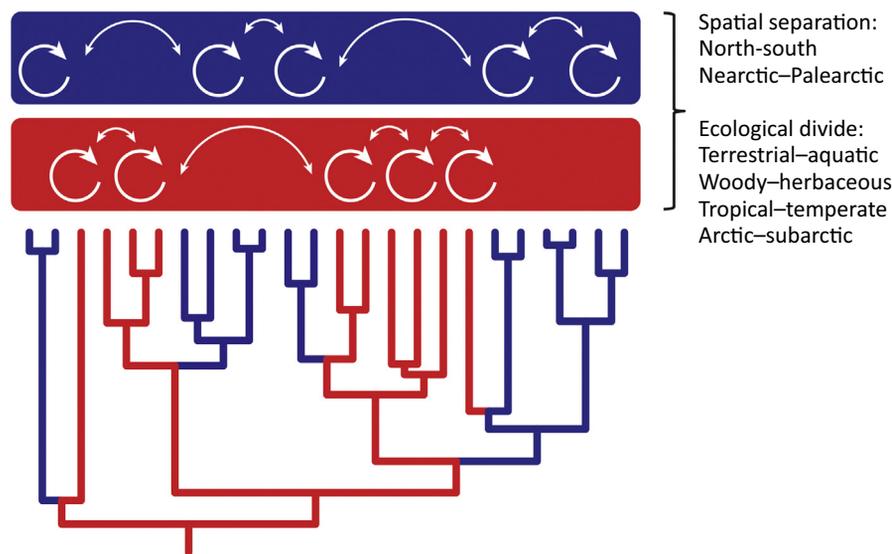

Figure I. Schematic Depiction of How Species Associations of Parasites Are Shaped by Host Phylogeny but also by Ecological Constraints and Opportunities. See Box text for further explanation.

Box 2. Cospeciation Is Rare, Host Switching Is Common

Figure I (redrawn and modified, with permission, from [56,57] by [58], copyright by the Helminthological Society of Washington) shows the classic case of cospeciation between pocket gophers and their parasitic lice; a system that should be unusually prone to such a process because of the host's underground life style and the wingless parasites, promoting reproductive isolation and constraining the opportunities for host colonizations. Even for this iconic case of presumed cospeciation, there is actually much incongruence between the topologies of the host and parasite phylogenies, due to colonizations and host switches (circled in gray). For instance, in the top gray area the parasites *Geomydoecus setzeri* and *Geomydoecus panamensis* are sister species, but their hosts *Orthogeomys underwoodi* and *Orthogeomys cavator* are not, which excludes strict cospeciation. In fact, there is only about 50% cospeciation [58], even if it is assumed that all cases of congruence are due to cospeciation and not a result of phylogenetically constrained resource tracking. Thus, cospeciation may have played some role in this extreme system ([9], and see [59] for a recent similar case), but host colonizations are also evident. This is even truer for many other textbook cases of cospeciation between parasites and hosts, where there is in fact little evidence of such a process [41].

In specialized mutualistic associations such as that between fig trees and fig wasps [60] the picture is similar, with some congruence consistent with cospeciation but also many host shifts and limited evidence that cospeciation was the actual process shaping the congruence [41]. In many systems mutualism repeatedly evolves from parasitism (or other forms of exploitation) or commensalism and can easily be lost, and in other mutualistic systems (such as more typical insect pollinators) the associations are not highly specialized but dependent on the composition of local communities. However, even intimately symbiotic relationships such as lichens [61] and corals [62] are dominated by colonizations and host switches rather than cospeciation. In fact, not even mitochondria always cospeciate with their host cells, and neither do internal cellular symbionts such as *Wolbachia* [63]. Furthermore, even when cospeciation actually occurs, we would suggest that this pattern is more likely to be a passive result of shared vicariance events than due to host-specific adaptations and trade-offs among hosts driving specialization and speciation.


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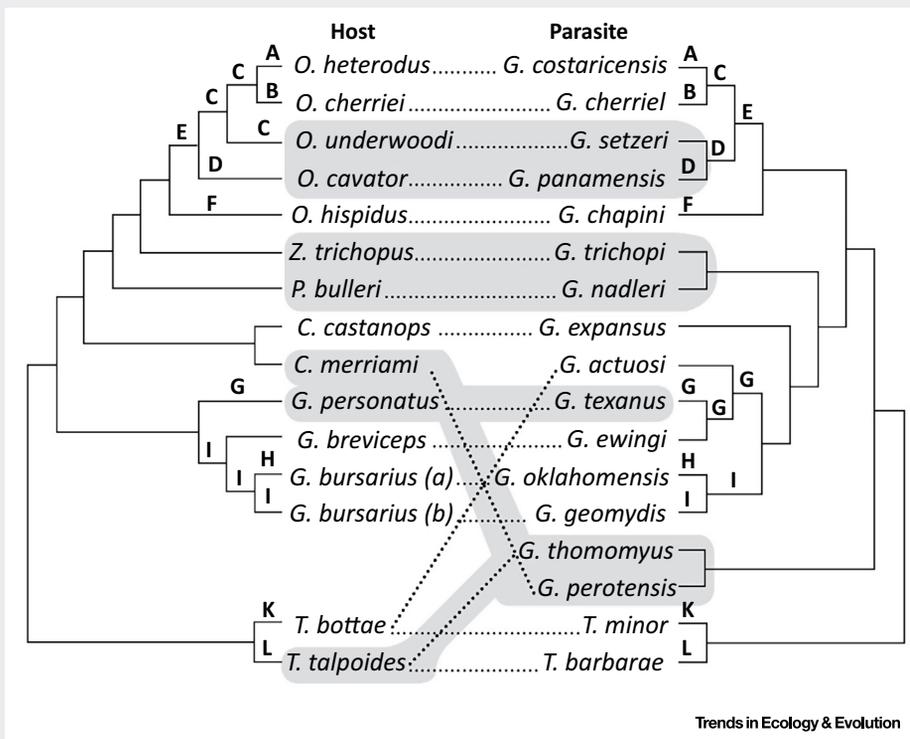
Figure I. Associations between Species of Pocket Gophers (Left) and Lice (Right). Associations are depicted by dotted lines. There is some congruence consistent with cospeciation, but other sections of the phylogenies (marked in grey) are not congruent and other processes must be invoked.

might split into new species. This can lead to reproductive isolation of the respective parasite populations, and recurring events of parasite cospeciation with the host lineage over evolutionary time becomes a possibility or even an expectation.

This paradigm of pervasive cospeciation and 'dead-end' specialization does not, however, match with observations of, for example, EIDs. If the traditional expectations of parasite specificity are true, why and how does a virus go from birds or bats to humans [18,19]? How can squirrels be reservoirs for bacteria causing leprosy in humans [20]? Another example of the same paradoxical situation is the fact that a species colonizing a new geographical area sooner or later (often sooner) is infected with locally resident parasites or conversely infects local species with its own parasites [21–24]. Why and how do the parasite species expand from the host to which they are already well adapted, and on which they are supposedly highly specialized?

There has been a growing unease with the traditional assumptions in parasitology over recent years, fueled by such empirical paradoxes [25], and students of parasitic herbivores have sometimes expressed similar thoughts [26]. We suggest that the time is now ripe for a new common paradigm for parasitology and parasitic herbivory which explicitly acknowledges that parasites should be expected to have the ability to use more hosts than they typically do at any given place or time. In other words they have potential hosts in addition to the actual hosts, analogous to a wider fundamental niche than realized niche. An important consequence of this expectation is that cospeciation should be firmly rejected as a default expectation. Under this new paradigm the aforementioned paradoxes cease to be paradoxes but are instead predictable outcomes in situations in which species distributions and/or the environment changes.

This alternative view has the different assumption that host colonizations will not be particularly rare events. Most importantly, this view does not assume optimality thinking, but rather that host colonizations are possible whenever the parasite is able to persist on an alternative host. Adaptation to use one host does not necessarily exclude other species as hosts; rather, it is to be expected that a parasite can achieve better than zero fitness on other hosts – even in a situation where it is normally specialized on a single host species [27]. This can happen for several nonexclusive reasons: phenotypic plasticity in the parasite allowing for persistence in the alternative environment until selection can modify it enough to become well adapted to the alternate host [28–31], or resource tracking, where the parasite can live on an alternative host because it is similar enough as a resource, regardless of the evolutionary history of the association [32,33]. To this can be added recurrence homoplasy: a parasite should be expected to be more likely to recolonize a host that is ancestrally used in the parasite clade compared to a totally novel host, because of remaining adaptations to the ancestral host [34,35].

From the above, it follows that new species associations will frequently be formed through ecological fitting without specific new adaptations for the use of the novel host, that is, genetic change in the parasite can happen after colonization of a new host rather than before, and loss of the old host is a secondary evolutionary event rather than primary. In other words, the traditional idea of genetic trade-offs among hosts driving host shifts and specialization should not be considered the most parsimonious explanation [36,37]. This is well illustrated with new evidence from butterflies: in the Melissa blue *Lycaeides melissa* a genome-wide association study showed that different loci were associated with different hosts, and genetic variants that affected performance on one host consequently had little effect on the other host [38]. Importantly, the new paradigm is thus best phrased in terms of colonizations of new hosts (i.e., with the old host retained as at least a potential host) rather than in terms of host shifts or

host switches. Moreover, if we appreciate the distinction between realized and fundamental host ranges, host range in parasites is expected to vary in space and time, precisely as we can observe in natural systems (Figure 1 and Table 1).

Finally, under the new paradigm, cospeciation between parasite and host lineages should be rare, particularly as a consistently recurring pattern over evolutionary time, because this is expected to happen only under very limited circumstances: (i) the parasite lineage needs to be consistently specialized on a single host species, that is, lack genetic variance in host-utilization capacities or have no opportunity at all to meet additional potential hosts; (ii) the parasite lineage must speciate when the host does, that is, reproductive isolation must follow, rather than gene flow between the incipient species upholding species integrity; and (iii) the incipient parasite species must then specialize on their respective incipient host species, rather than retain some ability and opportunity to use both species as hosts [39]. These circumstances will rarely apply over several subsequent speciation events if parasites typically have more than one potential host, as the evidence suggests.

When to Expect Cospeciation?

How can our viewpoint be reconciled with the seemingly widespread belief in parasitology that cospeciation is common, and even a reasonable default expectation for host–parasite species associations? We suggest that the endurance of this expectation is an interesting example of how a prevailing paradigm can lead researchers to fit observations into a framework, even when the fit is in fact very poor. If one expects to see cospeciation when comparing the phylogenies of a host lineage with that of a parasite lineage, one will see it – as soon as there is any congruence whatsoever between the phylogenies. Phylogenetic congruence can however occur for other reasons than cospeciation; in particular, because the resources tracked by the parasite often will follow phylogenetic patterns in the host lineage. Related hosts will be similar as a resource in many respects, meaning that a parasite using one taxon can more easily colonize a related host rather than a random taxon (Box 1).

Given this, it is in fact more surprising that most host–parasite systems show so little phylogenetic congruence, meaning that current associations can be explained only by postulating many evolutionary events that do not fit the cospeciation model. These include host switching, extinctions, and extra or missing speciation events [40]. Sometimes this exercise can be reminiscent of the epicycles once needed to fit the movement of planetary bodies into a geocentric paradigm. However, what about the flagship examples of cospeciation where congruence is seemingly evident, such as pocket gophers and their chewing lice? We would argue that even in such cases the new paradigm better explains the patterns observed, although cospeciation may have played some role in such extreme systems (Box 2). Similarly, de Vienne *et al.* [41], from their exhaustive review and reanalysis of published studies, concluded that convincing cases of cospeciation are rare, and that the available evidence clearly suggests that the coevolutionary dynamics of hosts and parasites do not favor long-term cospeciation.

The reason why cospeciation has been considered as an important evolutionary pattern and process for lineages of parasites and their hosts is the intimate nature of such species associations. Conversely, cospeciation can more or less be ruled out beforehand for mutually negative associations – competition – where the interacting species will be selected to leave the association if at all possible; for example, through character displacement [42]. The process is not likely to be invoked for predator–prey associations, either, since predators are rarely, if ever, specialized on a single species of prey.

We suggest that cospeciation would most likely be found in mutualistic associations, since both lineages should to some extent be selected to stay together. However, even for such associations there is in fact limited evidence of cospeciation (Box 2). This is, perhaps, because mutualism is better thought of as mutual exploitation, arising evolutionarily from antagonistic or commensal species relationships, and with partners leaving the association whenever they can do better on their own or together with another partner. Ecological fitting is thus likely to be the first step in the formation of new mutualistic associations as well.

Concluding Remarks and Future Directions

Here we argue that the available evidence suggests that parasite–host associations are not fundamentally different from insect–plant associations in any respect. In other words, both types of systems are affected by the parasite paradox; how can host range be so specialized and yet new hosts be frequently colonized?

The new paradigm that has been developing over recent years (from basic elements that in most cases have been around for some time) removes this paradox, because now parasites and parasitic herbivores alike are expected to have a fundamental capacity for associations with hosts extending well beyond the currently realized associations. This wide capacity arises from phenotypic plasticity and other factors allowing for non-zero fitness on alternative hosts, and has the consequence that colonizations initially occur through ecological fitting, without the need for genetic change. Thus, ecological opportunity rather than capacity is typically what constrains which species associations are observed at a given place and time. Genetic change in performance traits or genetically based performance trade-offs among hosts are not needed for specialization either; only changes in behavior constraining host use to one or a few host species [35,43]. Hence, we should break with the tradition of focusing on host shifts in favor of a more dynamic view of host range ecology and evolution where potential hosts can be colonized, lost, and colonized anew.

Under this new paradigm it is more evident than ever that host range must be seen in relative terms rather than labeling a particular species as either a specialist or a generalist, and indeed we propose that host range is better thought of in terms of a process (specialization and generalization) rather than a state. Current host range is the result of this ongoing process, and should be expected to be dynamic over time. Parasite species should tend to specialize on the hosts that give them the highest fitness, but over time situations will occur when environmental perturbations change the rules of fitness for current host associations to the worse and at the same time open up opportunities for new associations [44]. As a consequence, parasites and parasitic herbivores will for a shorter or longer time generalize their host use, sooner or later followed by them specializing again. In other words there will be oscillations in host range, explaining why specialization is not a dead end in evolution [16,45].

This framework opens up new and exciting areas of research (see Outstanding Questions) with the ultimate aim of improving our ability to predict colonizations of new hosts; not least the EIDs that affect us and the species upon which we depend [2,3]. Thus, EIDs should not be viewed as freak events, but rather as evolutionary accidents waiting to happen as soon as the ecological situation changes and new opportunities for colonization arises [46]. In particular, we propose that more attention must be given to improving our understanding of mismatched realized and potential host ranges of parasitic species: what sets the limits; what are the relative roles of phylogenetic distance and resource similarity (and can they be disentangled from each other)? This can be done through experiments when feasible, but also by careful field inventory that does not ignore unexpected species associations, by the study of new associations involving

Outstanding Questions

How can we make use of existing knowledge to predict EIDs?

How can such predictions be practically used to prevent EIDs?

How can we improve our understanding of the potential host ranges of parasitic species?

What are the relative roles of phylogenetic distance, host defenses, and resource similarity for setting the limits for potential host ranges?

How can these roles be disentangled?

Can new phylogenetic methods be developed that allow for potential as well as actual host associations?

invasive species, and by the development of new phylogenetic methods that allow for potential host associations as well as actual.

In conclusion, we propose that it is now time for a new paradigm: one that unites theory on parasite–host and insect–plant associations; recognizes the empirically grounded evolutionary dynamics of such associations; and accepts that host colonizations by parasites – including our own enemies – are not exceptional events but instead to be expected. This will better prepare us to meet the increasing challenges arising from introduced species and global change.

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