OPINION

Towards a new paradigm for species association dynamics

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Abstract:

Parasite-host and insect-plant research have very 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 null model. 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 may even be crucial for the well-being of our own species. After all, the increasing records of “emerging infectious diseases” (EIDs; [1]) depend on changing species associations: for some reason an infectious species or virus strain spreads from its previous host or hosts 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, at first sight a reasonable expectation given that hosts are both resources and habitat for the parasite [4]. It is even a commonly expressed default expectation or even null model 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] (p. 49) [6]. This idea (“Fahrenholz’s rule”) has been around for over a century, but shows little sign of decreasing in popularity.

Let us first contrast this research tradition in parasitology with the field of research studying insect-plant interactions (for simplicity we include similar herbivorous arthropods such as mites among these “insects”). Many phytophagous insects live parasitically on their host plants, so we could expect the two fields to have had close interaction when it comes to theory development. Instead, most treatments on parasite-host theory barely mentions insect-plant systems and vice versa. Rather, the two fields have developed very divergent research traditions, where for instance the idea of cospeciation has seldom been taken seriously for associations between insects and plants [7]. Ehrlich and Raven’s [8] original and still very influential concept of coevolution between butterflies and plants, for example, did not suggest cospeciation but rather a diffuse matrix of interactions, later developed by Thompson [9] 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 certainly do not accept that cospeciation is the “hallmark of coevolution” [6]). Insect-plant theory has been more concerned with host colonizations and subsequent adaptive radiations than with cospeciation (e.g. [10, 11]), and more with preference and performance hierarchies among multiple hosts than with extreme specialization [12].

Parasite-host and insect-plant associations are similar

But to what extent are the differences between the two fields real? Could it be the case that wide-spread but divergent assumptions in the respective fields have been a hindrance rather than a help, and that a common research program could instead be developed? The present article stems from a workshop where parasitologists and insect-plant researchers met to explore this question and found that observed patterns in the two fields are indeed strikingly similar

(Table 1; Fig. 1), meaning that the fields can be successfully integrated and a synthetic understanding is possible.

In both fields specialization is a predominant pattern, but at the same time there is much variation in host range – a few species have considerably wider host ranges than the others (Fig. 1a). Taken together, these patterns suggest that the degree of specialization varies over evolutionary time, but with a strong trend towards re-specialization after episodes of a wider host range [13]. Consistent with this interpretation of wide host range as a transient state is the observation that the widest host ranges are typically seen apically in phylogenies, and only rarely as a trait characterizing large clades (Fig. 1b). The host clades themselves, in contrast, are very often shared between related species of parasites and phytophagous insects. This suggests that host colonizations predominantly involve hosts related to the present ones, but rather than parasites and phytophagous insects staying on the exact same lineage of hosts over evolutionary time, speciating when the hosts do, there is a pattern of frequent colonizations of new host lineages when opportunity arises (BOX1) and little or no evidence of cospeciation (BOX2).

The similarities in observed patterns between the two research fields imply to us that the prevalent assumptions of specialization and cospeciation in parasitology have prevented the field from seeing patterns and processes that do not fit comfortably within this paradigm. The traditional paradigm in parasitology has to our knowledge never been explicitly formulated, and it may well be that no researcher would fully subscribe to it in its extreme form. It has for instance often been acknowledged that parasites can sometimes be found on “alternative” hosts. However, with the exception of some universally recognized generalists (e.g. the roundworm *Trichinella spiralis*) alternative hosts have tended to be treated as rather uninteresting cases of deviations from the norm. We believe it is of some value to clearly formulate this pervasive and influential way of thinking, and we will do so here, even though we are aware that such an exercise will always be something of a caricature. Real-life parasitologists are typically well aware of many exceptions to its “rules” (yet continue to be governed by them in important respects, it would seem).

The “parasite paradox” and its resolution

Returning briefly to EIDs: if the traditional expectations of parasite specificity are true, why and how does a virus go from birds or bats to humans [14, 15]? How can squirrels be reservoirs for bacteria causing leprosy in humans [16]? 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 infect local species with its own parasites (e.g. [17], [18-20]). 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 paradoxes [21], and students of parasitic herbivores have expressed similar thoughts [22]. Now, we suggest that the time is ripe for a new common paradigm for parasitology and parasitic herbivory which explicitly acknowledges that parasites should be *expected* to be able to use more hosts than they typically do at any given place or time. This is because they have *potential* hosts in addition to the actual hosts (analogous to a wider fundamental niche than the realized niche), and because plasticity rather than genetic change is the leader in the evolution of species interactions [23-26]. An important consequence of this expectation is that cospeciation is firmly rejected as a default null model. Under this new paradigm the aforementioned paradoxes cease to be paradoxes but are instead more or less predictable outcomes in situations in which species distributions and/or the environment changes.

Comparing the traditional and revised paradigms

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 may throw at it, such as for instance 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 [27], 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 when the host may split into new species. This can lead to reproductive isolation of their respective parasite populations, and cospeciation with the host lineage becomes a possibility or even an expectation.

The alternative view, suggested by the patterns reported above, has the very different assumption that host colonizations will not be particularly rare events. 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 [28]. An organism does not need to be optimally adapted to its environment, only adapted enough to persist. This, in turn, can happen for several non-exclusive 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, 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 [29, 30]. To this can be added *recurrence homoplasy*: a parasite should be expected to be more likely to recolonize a host that was ancestrally used in the parasite clade compared to a totally novel host, because of remaining adaptations to the ancestral host [31, 32].

From the above follows that new species associations will frequently be formed through *ecological fitting* without specific new adaptations for the use of the novel host, i.e. 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 should be rejected [33, 34]. This is well illustrated with new evidence from butterflies: in the Melissa blue *Lycaeides melissa* a GWAS study showed different loci associated with different hosts, and genetic variants that affected performance on one host consequently had little effect on the other host [35]. Importantly, the new paradigm is thus best phrased in terms of colonizations of new hosts rather than host shifts or host switches, in contrast to both the old paradigm in parasitology and much of the insect-plant literature. Moreover, if we appreciate the distinction between realized and fundamental host ranges, and that the latter will be larger than the former for most species (as they also include potential hosts), *host range in parasites is expected to vary in space and time*, precisely as we can observe in natural systems. Finally, *cospeciation should be rare*, because it is expected to happen only under very special circumstances [36], and these circumstances will be rare indeed if parasites typically have more than one potential host, as the evidence suggests.

When to expect cospeciation?

How can this last expectation 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 [37]. Sometimes this exercise can be reminiscent of the epicycles once needed to fit the movement of planetary bodies into a geocentric paradigm. But 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 our proposed new paradigm better explains the patterns observed, and cospeciation need not be evoked (see BOX2). Similarly, de Vienne et al [38] 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 even been considered as an 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, e.g. through character displacement [39]. 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 be most likely to be found in mutualistic associations, since in this case both lineages should to some extent be selected to stay together. However, even for such associations there is in fact limited evidence of cospeciation (see BOX2). 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.

Conclusions and future directions

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 quite 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 [32, 40]. 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 labelling 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 (“specializa-

tion” 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 highest fitness, but with episodes 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 [41]. 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 [13, 42].

This framework opens up new and exciting areas of research with the ultimate aim of improving our ability to predict colonizations of new hosts, not the least the EIDs that affect us and the species that we depend upon [2] [3]. EIDs are not freak events, but rather “evolutionary accidents waiting to happen” as soon as the ecological situation changes and new opportunities for colonization arises [43]. In particular, we propose that much 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 which does not ignore “unexpected” species associations, by the study of new associations involving 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 there is now time for a new paradigm, one that unites theory on parasite-host and insect-plant associations, recognizes the true evolutionary dynamics of such associations and accepts that host colonizations by parasites – including our own enemies - are not rare events but only to be expected. This will better prepare us for meeting the increasing challenges brought upon us by introduced species and by global change.

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BOX 1: Species associations are shaped by resources and opportunity

Fig. I

Species associations are shaped by phylogeny and host defences [44] but also by spatial separation and ecological parameters such as the type of resource that the potential host provides and the biotope it inhabits (Fig. I). Related species typically feed on related hosts; circular arrows over each separate clade in Fig. I depict such phylogenetic constraints. Horizontal arrows depict host colonizations between clades, with host species sharing habitat and/or ecology, providing opportunities for new associations. For instance, a strong effect of geography was shown for the associations of spider mites with plants [22]. In birds, the occurrence of nematode parasite species increases with ecological opportunity given by migratory habits and use of multiple aquatic habitats [45]. In general, associations between parasites and hosts are affected by the opportunities given in the community [46].

Because parasite communities are structured by both hosts and geography, 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 [47]. Another example is the malaria-inducing protozoa *Plasmodium relictum*, which was unintentionally introduced to Hawaii in the 1930s [48]. It appears to be of low virulence in its native hosts but highly virulent in the Hawaiian honey creepers.

On macro-evolutionary time-scales, it is very likely that major events such as global changes in climate and mass extinctions have been important factors. Such events will have strongly perturbed the distributions of species, across many taxa [49]. We can infer this process indirectly 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 [47]. Paleontological evidence can be found from the dense fossil record of brachiopods and bivalves, where it is possible to document 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 [50, 51]. The current wave of EIDs is in all probability at least partly a result of similar processes, where climate change and global travel/trade brings new combinations of species into contact.

BOX 2: Cospeciation is rare, host switching is common

Fig. II (redrawn and modified from [52, 53] by [54]) shows the classic case of cospeciation between pocket gophers and their parasitic lice. Even for this iconic case of presumed cospeciation, there is much incongruence between the topologies of the host and parasite phylogenies, due to colonizations and host switches (circled in grey). For instance, in the top grey area the parasites *Geomydoecus setzeri* and *G. panamensis* are sister species, but their hosts *Orthogeomys underwoodi* and *O. cavator* are not, which excludes strict cospeciation. In fact, there is only about 50% cospeciation [54], even if it is assumed that all cases of congruence is due to cospeciation and

not a result of phylogenetically constrained resource tracking. The same is true for many other “textbook cases” of cospeciation between parasites and hosts [38].

In specialized mutualistic associations such as that between fig trees and fig wasps [55] 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 [38]. 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 [56] and corals [57] 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* [58].

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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	[59]	Malaria-birds	[62]
	Lepidoptera globally	[60]	Unionid mussels–fish	[63]
	Nematinae sawflies	[61]	Nematodes–Artiodactyla	[47]
	Spider mites	[22]	Monogenoida gill parasites-fish	[64]
			Worms-fish	[65]
Wide host ranges are typically apical	Nymphalid butterflies	[59]	Malaria-birds	[66]
	Nematinae sawflies	[61]	Trematodes-snakes, turtles etc.	[30]
Relatives share host clades	Nymphalid butterflies	[59]	Malaria-birds	[62]
	<i>Eois</i> geometrid moths	[67]	Nematodes-Artiodactyla	[47]
	Nematinae sawflies	[61]	Lice-pocket gophers	Box 2
Colonizations common via ecological fit- ting	Nymphalini butterflies	[31]	Malaria-birds	[48]
	California butterflies	[68]	Unionid mussels-fish	[20]
	<i>Eois</i> geometrid moths	[67]	Nematodes-Artiodactyla	[47]
	Nematinae sawflies	[61]	Gyrodactylid gill parasites-fish	[69]
	Spider mites	[22]	Trematodes-snakes, turtles etc.	[30]
			<i>Pomphorynchus</i> worm-amphipods	[17]
			Nematodes-birds	[45]
			Platyhelminths-anurans	[70]
Cospeciation is	Nymphalid butterflies	[31]	Malaria-birds	[6]

rare
or absent

<i>Eois</i> geometrid moths	[67]	Nematodes-Artiodactyla	[47]
		Lice-pocket gophers	Box 2

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Fig. 1. Examples of the strong similarities between ecological and evolutionary patterns observed in parasite-host and insect-plant systems. A) Distribution of host ranges across taxa: (top) number of host plant families for species of Lepidoptera, data from [60]; (middle) number of bird host species for 756 lineages of blood parasites (*Heaemoproteus* spp.), data from [62]; (bottom) number of fish host species for species of parasitic worms, data from [65]. Bird and fish parasite data was randomly subsampled to 756 species to make graphs easily comparable. Tick marks below figures highlight individual observations. Note the long tail of generalists in each taxon. B) The phylogenetic position of generalist species: (top) host ranges for butterflies in the subfamily Nymphalinae, with species using 7 or more plant orders in red, 3 or more in orange, data from [59]; (bottom) host ranges in 303 lineages of avian blood parasites (*Heaemoproteus* spp.), calculated with a quantitative approach and labelled by branch colour from blue (infecting a single host species) to red (infecting two or more host orders), data and figure from [66], used by permission. Note the apical position of generalists, suggesting a transient state. C) (left) The Painted Lady *Vanessa cardui*, a butterfly with a very wide host range (Photo by N. Janz) and (right) a three-spined stickleback *Gasterosteus aculeatus*, parasitized by the cestode worm *Schistocephalus solidus* (Photo by Bertil Borg, used by permission).