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# Sympatric speciation in parasites – what is sympatry?

Karen D. McCoy

Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6

**Parasites account for a large part of known species diversity and are considered to have a high potential for sympatric speciation. However, the frequency of sympatric divergence in these organisms will depend on the definition of sympatry that one uses. Like many of our current species concepts, the typical definition of sympatry is not widely applicable to parasites. Revisiting the historically defined conditions for sympatric speciation and considering the situations in which we might regard parasites as being sympatric leads us to question the classic prediction that parasites have a greater tendency to speciate in sympatry than do free-living organisms.**

Species concepts borne from a consideration of vertebrate animals are difficult to apply to many parasites and no one definition seems to be widely appropriate for this group [1,2]. However, the species concept is not the only biological notion that is problematic for parasites. In a recent Opinion article by Kunz [2] on defining a parasite 'species', he mentions the common prediction that parasites have a greater tendency to speciate in sympatry than do free-living organisms (see, for example, Refs [1,3–5]). This idea is based on the premise that a subgroup of a parasite population can become isolated from the parent population when it occupies a new host. The high potential for parasites to colonize new host types should result in sympatric speciation occurring more commonly in parasitic organisms. In line with typical definitions, Kunz defines sympatric speciation as 'the origin of new species in the same geographic area', with sympatry itself defined as 'the occupation of the same geographic area by different populations'. Putting aside the recognized difficulty of defining a parasite 'species' for asexual or obligate selfing organisms [1,2], these definitions do not generally work for parasites. As with the species concept that is employed, when discussing speciation modes, it is important to consider the particular characteristics of the phyla concerned. The general case of sympatric speciation of parasites outlined by Kunz could be considered as allopatric (or geographically isolated) speciation. For sympatric speciation to occur, the incipient species must be in sympatry during the initial stages of divergence – sympatry, however, is not always easy to define.

## Historical definitions of sympatry

Despite strong debate over the past half century, sympatric speciation is now widely recognized as a plausible and potentially important process of species diversification (Box 1) [6]. The historical concept embodies the idea that divergence occurs without geographic isolation, such that individuals have the opportunity to encounter each other in the environment with a moderately high frequency [7]. For sexual organisms, reproductive isolation between groups occurs due to attributes intrinsic to the organisms involved rather than to factors external to the biological system (or extrinsic factors). When populations are geographically separated by some extrinsic force (i.e. allopatry), they become isolated as a by-product of independent evolution in each location [8]. In these instances, gene flow is overcome by the force of genetic drift resulting in the accumulation of differences between populations at neutral sites in the genome. Under sympatric conditions, such differences will only occur once populations are sufficiently diverged to have eliminated the influence of gene flow. However, despite the rapid development of new methods, it remains difficult to infer historical situations using contemporary genetic patterns, and the decision about whether or not populations were initially sympatric still remains largely subjective [6].

Some of the debate linked to the concept of sympatric speciation has arisen from a problem of terminology and, in particular, to the spatial limits implied by the terms 'sympatry' and 'allopatry' [9]. Several definitions have been suggested. White [3] considered that '[one can] regard two populations as sympatric if their ranges overlap in such a manner that inter-mating could occur with a genetically significant frequency, unless prevented by genetic isolating mechanisms of some kind'. A more precise definition considers that speciation should take place within the dispersal range of the offspring of a single deme [5,7]. Kondrashov and Mina [9] considered speciation as sympatric if, in its course, the probability of mating between two individuals depended only on their genotypes and provided that genes were dispersed throughout the range of the population during the period of reproduction. From these different definitions, it can be seen that, regardless of precise geographic limits or whether species are sexual or asexual, a key prerequisite for speciation in sympatry is the possibility for individuals to find themselves in the same population.

Corresponding author: Karen D. McCoy (mccoyk@biology.queensu.ca).

## Glossary

**Allochronic speciation:** speciation in which the initial separation of populations is in time rather than space.

**Assortative survival:** only the presence of certain genes allow a parasite to survive to reproduce in a given host type, thus favoring assortative mating [15].

**Host choice:** the ability of an individual parasite to select among available hosts.

**Host shift:** the colonization of a new host species.

**Homogamy:** assortative mating between similar phenotypes.

**Dispersal:** the movement of an individual from its natal population to a new population where it undergoes reproduction.

**Propagule pool:** an aggregation of parasite infective stages available for transmission.

**Synxenic speciation:** speciation of parasites due to a niche shift in the within-host environment [29].

**Transmission:** the passage of a parasite from a source of infection to a host individual.

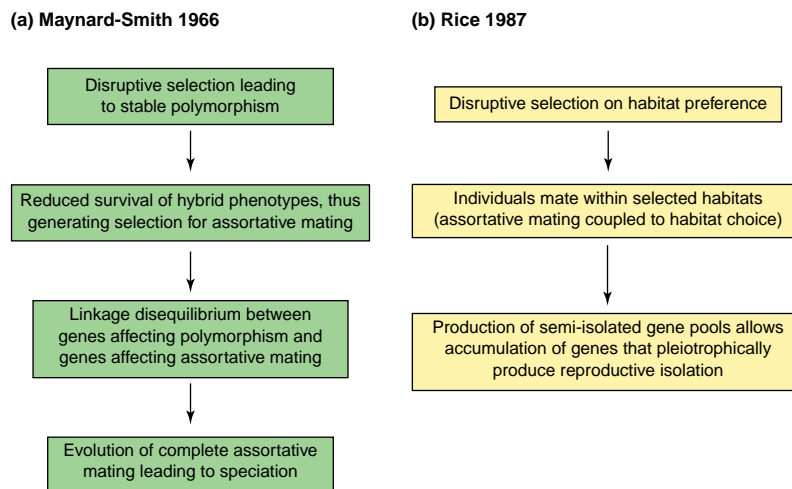
## Sympatry and the problem of host choice

In parasites, Price [4] hypothesized that sympatric speciation occurred predominantly via HOST SHIFTS (see Glossary). Indeed, sympatric speciation through host race formation is thought to be an important process, explaining the vast diversity of some parasitic organisms and, most notably, the great number of phytophagous insects [10]. The classic example of this type of divergence is the host race formation of the haw fly (*Rhagoletis pomonella*). Following the introduction of old world apples (*Malus pumila*) to north-eastern USA, a host shift occurred from the fly's native hawthorn hosts (*Crateagus* spp.) to the new apple host [11]. Later studies confirmed genetic differentiation between co-occurring hawthorn and apple populations of *R. pomonella* consistent with a sympatric mode of divergence (see, for example, Ref. [12]). Compared with the theoretical conditions for sympatric speciation outlined by early work largely aimed at vertebrates, the

### Box 1. Theoretical models of sympatric speciation

The early advocates of sympatric speciation were entomologists, who felt that the existence of host races in phytophagous insects was a possible first step toward distinct species. However, the concept of speciation in sympatry was strongly criticized by Mayr [7], who largely dismissed it in favour of allopatric models. In the case of internal parasites, he felt that speciation was almost strictly allopatric, not believing that different sympatric intermediate or final hosts of a local parasite could lead to its speciation. Maynard-Smith [31] developed the first genetic model of sympatric speciation; this entailed two main steps. The first requirement was the establishment of a stable polymorphism through disruptive selection (e.g. on resource use). The evolution of reproductive isolation then followed as a consequence of linkage disequilibrium between genes affecting the polymorphism and genes affecting assortative mating (Fig. 1a). Felsenstein [36] demonstrated that the selection necessary to build this prerequisite disequilibrium was unrealistically high because of the influence of recombination. Rice [37] circumvented the selection–recombination antagonism by suggesting that selection applied to a trait that produced assortative mating as a correlated character could more easily lead to reproductive isolation. For example, disruptive selection on habitat preference, where mating is linked to habitat choice, would allow the accumulation of genes that

would lead indirectly to prezygotic reproductive isolation without strong selection (Fig. 1b). Diehl and Bush [38], using a modified version of Felsenstein's model that incorporated habitat selection as a mechanism of intrinsic isolation, demonstrated that the conditions allowing speciation in sympatry were indeed less extreme than those outlined by Maynard-Smith and that non-allopatric speciation could occur much more readily when mate choice was directly linked to habitat preference. More recent models further suggest that the conditions required for sympatric speciation are, in general, less stringent than previously thought. Habitat (host) races, the initial step towards potential reproductive isolation, might form through the accumulation of mutations with habitat-specific beneficial or deleterious effects without the need for trade-offs in habitat adaptation [39,40]. Likewise, using an adaptive dynamics framework, sympatric speciation has been shown to evolve through stochastic processes and competition for resource use, even when it requires the evolution of genetic associations between ecologically important traits and neutral markers for mate discrimination [41]. Thus, it seems that, despite early arguments on the limited conditions favoring speciation in sympatry, the possibility of it occurring in both parasitic and non-parasitic organisms is becoming more plausible with time.



TRENDS in Parasitology

Fig. 1.

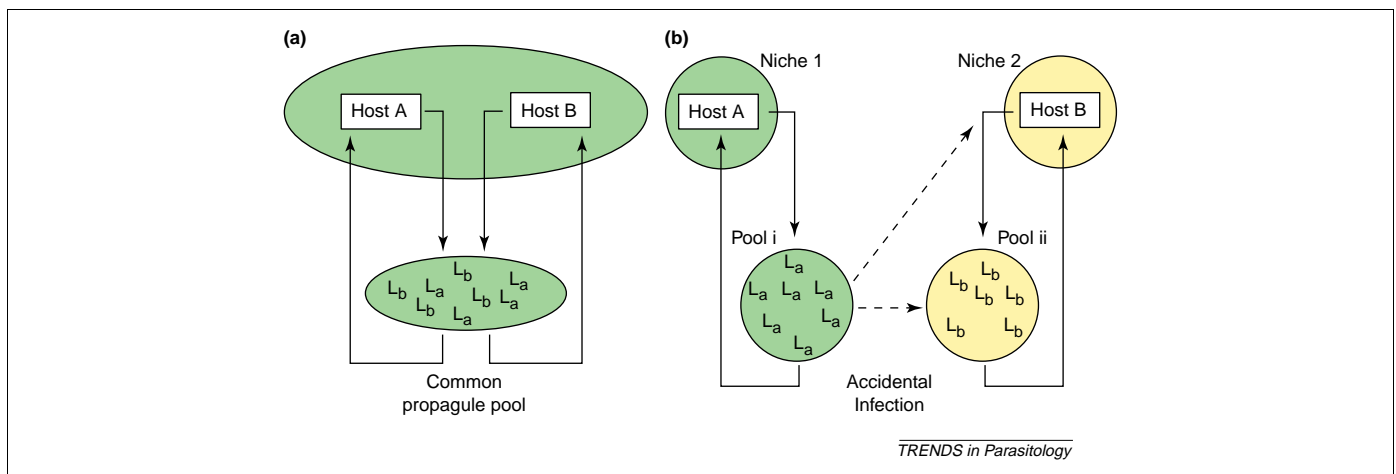
incorporation of organisms with the life history characteristics of phytophagous insects into models (i.e. the host as the mating site) greatly broadened the circumstances favoring this mode of speciation (Box 1). However, phytophagous insects account for only part of parasite biodiversity [13] and are particular among parasites, in that they are actively able to choose their host. For most of what we consider as more typical parasites, there is no HOST CHOICE; the parasite is constrained to the host that it ends up with. For example, parasite TRANSMISSION and DISPERSAL is often passive, such as through direct contact (e.g. influenza virus), by wind or water (e.g. fungal spores), via a vector (e.g. *Plasmodium* spp.), or by ingestion (e.g. many trematodes, cestodes and nematodes). In these instances, a parasite individual does not have a choice about whether to stay or leave the newly infected host. This lack of host choice means that not all local host types will necessarily be available to parasite individuals and thus questions the general applicability of models of sympatric speciation to parasites other than phytophagous insects.

When parasites lack the ability to choose their hosts actively, a subgroup that infects a new host type might have a reduced probability of encountering individuals of the parental population and thus could effectively find itself in allopatry. For example, major groups of nematodes are transmitted directly between hosts and facilitate this transmission by releasing larvae into the general environment that are ingested by new host individuals [14]. These larvae might be isolated from alternative host types, depending on the degree of aggregation of infective stages and the spatial heterogeneity of the host habitat (Fig. 1); for example, infected sympatric hosts that use different resources important to parasite transmission could result in the formation of separate parasite PROPAGULE POOLS. This isolation could be particularly common, given that most parasites have adapted transmission strategies that match certain predictable characteristics of their hosts to reduce the probability of ending up in the wrong host [15].

For parasites transmitted through direct contact, an accidental infection of a new host type could have a high probability of isolating the parasite from the source population because the probability of horizontal transmission to conspecifics or vertical transmission to offspring will be much greater than the probability of heterospecific transmission [16]. Indeed, there are currently several examples of emerging infectious diseases in humans that are thought to have originated by jumping the species barrier (e.g. severe acute respiratory syndrome [17], avian influenza [18]). Allopatry after an accidental host shift could also result if transmission occurs indirectly, via an intermediate host or a vector. Unless the vector is commonly encountered during the life cycles of both host types, parasites in the new host will be effectively isolated from the original population [19].

We could question the ability of parasites to colonize successfully a new host after an accidental transmission event, particularly for sexual species that require the presence of a mate to reproduce. However, infective stages are often clumped within the environment or intermediate host [20], meaning that a single transmission event will frequently involve several parasite propagules and could therefore enable the establishment of a new population. For example, mosquitoes that bite a single malaria-infected host will often ingest several *Plasmodium* gametocytes during the meal. This ensures that the parasite can complete its sexual reproductive phase in the mosquito and that the resultant infective stages (sporozoites) can be transmitted to a new host during subsequent bloodmeals. It has recently been shown that certain species in the phylum Apicomplexa, including *Plasmodium* spp, can even produce double gametocyte infections within a single erythrocyte that could further enhance transmission success [21].

The isolation of parasite groups after a host shift has been discussed by several authors over the years [1,15,22,23]. Brooks and McLennan [23] suggested that speciation through host switching should be considered as



**Fig. 1.** Transmission of parasites with no host choice between sympatric hosts in (a) homogeneous and (b) heterogeneous environments. In (a), propagules released into the environment mix in a common propagule pool [propagules from host A ( $L_a$ ) and host B ( $L_b$ )] and have similar probabilities of being transmitted to each host type. Genetic isolation of parasites infecting different host types will occur only if selection within the host (e.g. by the host immune response) is strong enough to produce homogeneity. This situation could result in sympatric speciation. In (b), host types use different niches (or resources) within the local environment. In this case, the colonization of a new host type can result in partial or complete isolation of propagule pools [defined as pool i and pool ii] and provides only a limited probability of transmission back to the parental population. Isolation and selection combine to produce genetic divergence between populations. The physical barrier is the distance between hosts. This should be considered as allopatric speciation.

an example of peripheral isolates allopatric speciation (or Mayr's peripatric speciation [7]) rather than sympatric speciation. Combes and Théron [15] made a clear distinction between habitat preference genes that alter the probability of host-parasite encounters and genes that act on parasite survival after encounter. In a review of parasite diversity, de Meeûs *et al.* [1] attempted to clarify cases of true sympatric and true allopatric speciation in parasites. However, they did not consider the specific problem posed by limited host choice when hosts are on sympatric ranges.

In general, when a parasite can choose among host types, local host shifts can be considered as sympatric. However, as outlined above, a successful host shift in parasites with no choice could result in allopatric conditions, even if hosts are on overlapping ranges (i.e. sympatry). In these cases, the host represents a geographic locality for the parasite, and the distance between hosts, an extrinsic barrier (see Fig. 1a,b). A good illustration of this could be found in lice. Louse species tend to be highly host specific, with each species restricted to a single, or few, host species [24]. Much of this specificity is linked to patterns of cospeciation between host and parasite, but host switching does occur [25]. Although lice can actively disperse between hosts when they are in close contact, significant genetic differentiation can be found between lice species infesting different sympatric hosts. Johnson *et al.* [26] found that feather lice species with a high capacity to disperse among available host species (via phoresis on generalist hippoboscids) showed lower differentiation between sympatric host species than those that relied only on direct contact. This suggests that limited dispersal between sympatric host types could play an important role in the speciation of this group. Indeed, Clay [22] considered that interspecific infestation by lice was essentially allopatric, host isolation being equivalent to geographic isolation. She suggested that opportunities for louse dispersal between different host types are so limited, that even if hosts are sympatric, their lice are not. From this example and those discussed above, it can be seen that the divergence of parasite groups following local host shifts might or might not be sympatric, depending on the nature of the organism being considered. Given this, parasite speciation should not necessarily be called sympatric simply because host types are in the same geographical area.

### Conditions for sympatric speciation in parasites

This is not to say that sympatric speciation does not occur in parasites. There are several observations that support speciation in parasitic organisms in situations where it is intrinsic factors that lead to divergence. As mentioned above, speciation by disruptive selection for host choice in phytophagous insects provides the strongest evidence available that sympatric speciation could be an important diversification force in nature [6]. For other types of parasites, this can also be a pathway to diversification. In instances where the parasite is able to choose its host actively (e.g. some free-living stages of nematodes and trematodes, or ectoparasites such as ticks or fleas), speciation by means of local host preference can occur. For example, strong host choice is thought to maintain

isolation between the closely related species of parasitic copepods *Lepeophtheirus thompsoni* and *L. europaensis* infesting sympatric species of flatfish [27]. Host choice could also be linked to sympatrically occurring races of the seabird tick *Ixodes uriae* [28].

Similarly, sympatric speciation could occur through habitat selection, but on a different scale to that in the case of between-host types, when a parasite actively shifts habitats within a given host (SYNXENIC SPECIATION) [29]. Monogeneans provide some of the best examples of diversification due to within-host habitat selection (e.g. Ref. [30]). However, there are also cases of presumed synxenic speciation for internal parasites [15].

Other examples of sympatric speciation might be related to strong selection in the host before mating occurs, such that only certain genotypes have the opportunity to mate (ASSORTATIVE SURVIVAL) [15]. In this situation, all genotypes are transmitted to all available host types (Fig. 1a), but only certain genotypes enable survival in a given host type. In the extreme case, only individuals of the same genotype survive in the host and are available for mating (HOMOGAMY). Thus, depending on the strength of selection, this form of premating isolation could lead to sympatric speciation through divergent selection on different host types (*sensu* Maynard Smith [31]). An adaptation to a given host type under these circumstances could then lead to the evolution and fixation of host preference (or differential encounter) genes [32]. Despite the potential importance of this form of divergence for parasitic organisms, there appears to be no explicit examples in the literature and it remains to be more fully explored.

White [3] identified a special variant of the sympatric model of speciation, ALLOCHRONIC SPECIATION, in which two populations develop genetic isolation without geographic separation through the acquisition of different breeding cycles. Indeed, hosts with different phenologies (rhythms or breeding cycles) could eventually isolate their parasites in time and could play an important part in sympatric speciation [33]. The adoption of different breeding cycles linked to host choice is thought to be responsible for the rapid divergence of haw fly races, *R. pomonella* [11]. Host race formation of the trematode *Schistosoma mansoni* in Guadeloupe is also thought to have occurred via allochronic divergence [34]. The emergence of infective stages of the parasite (cercariae) from the aquatic snail intermediate host is heritable. The frequent use of water by two host types, rats (*Rattus rattus*) in the evening and humans during the day, selectively separated the parasite into groups with different rhythms of cercarial emergence [34].

Finally, chromosomal rearrangements or key morphological changes could also be important, instantaneous modes of speciation in parasites [1,35]. For example, the characid fish *Brycinus nurse* in the Chad Basin (Africa) is known to host at least eight monogenean species of the *Annulotrema* genus on its gills. These species are all hermaphroditic out-crossers, each possessing unique genitalia that prevent hybridization. As both host and parasite are known only from this area, speciation is likely to have

occurred in sympatry through key morphological changes that affected both male and female genitalia [29,35].

### Conclusions

Parasites make up over 30% of known species diversity [13] and are considered to have a high potential for diversification. As such, they are ideal models for studying the processes linked to species divergence. However, because of the particular nature of their lifestyle, parasites present challenges for many of the concepts borne from a consideration of free-living organisms. The notion of sympatry represents such a challenge. Simply because hosts are present on sympatric ranges does not necessarily mean that this is also true of their parasites. Thus, the definition of sympatry that should be used must come from consideration of the organisms concerned. Like the idea of the species itself [2], it is important to consider the evolutionary processes behind species divergence in the light of parasitic lifestyles. To do this, it is necessary to clarify the terminology used in relation to the group being considered, so as not to compare apples with oranges. For example, if only 'true' cases of sympatry are considered, do parasites really have a greater tendency to undergo sympatric divergence than do free-living organisms?

### Acknowledgements

K.D.M. thanks Thierry de Meeûs, Troy Day, Thierry Boulinier and the anonymous referees for helpful comments on this article. Financial support for K.D.M. was provided by a post-doctoral fellowship award from the Natural Sciences and Engineering Research Council of Canada.

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