What is sympatric speciation in parasites?

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In a recent article, Karen D. McCoy [1] addresses the question of sympatric speciation in parasites and suggests that the typical definition of sympathy (in the same geographic area) is not widely applicable to parasites. McCoy argues that a speciation resulting from a host shift, even if the two host species are sympatric, should be considered as allopatric if the parasites have no possibility of host choice. The host could represent a geographical locality and the distance between hosts an extrinsic barrier. We agree that sympathy might be a less obvious notion in parasites than in free-living organisms, but the crucial point is the lack of a possibility for host choice. For instance, the passively dispersed parasites that McCoy took as examples, nematodes that have to be eaten by a passing host or fungal spores dispersed by wind or water. Such parasites can end up in any of the hosts existing in sympathy, so the distance between hosts do not constitute an extrinsic barrier. In such cases, there is no possibility of individuals coming from different hosts remaining genetically isolated, unless they evolve intrinsic mechanisms (e.g. host choice, partner choice, gamete recognition, allochronic gamete release) to prevent crosses with individuals coming from different hosts, but this represents classical sympatric speciation. Therefore, it is not whether parasites can choose their host or not, but whether they have a certain probability of ending up in the wrong host without evolving intrinsic mechanisms. Allopatric speciation in parasites with sympatric hosts could occur, but only in cases where, after shifting onto a new host, a parasite cannot disperse to other hosts because of extrinsic barriers. For instance, if parasite transmission takes place vertically (from parents to offspring) or if vectors are strictly different for the different host species. Numerous parasites have a dispersal phase or a possibility of staying alive outside their host, at least for short periods of time, enabling them to end up in any of the host species living in sympathy with their initial host. If the probability of transmission between sympatric hosts is reduced by evolved intrinsic mechanisms (e.g. by the adapted transmission strategies given in Ref. [1]), this means that a behaviour has been selected to impede crosses between individuals from two different hosts, and this represents classical sympatric speciation. The difficulty resides in the fact that some intrinsic mechanisms appear as extrinsic at first sight. Speciation events have been reported, for instance, in parasites from different sympatric hosts by the release of their gametes in different microenvironments or at different hours of the day [2]. Such behaviours could look like extrinsic barriers to gene flow, but they might well be strategies selected to reduce the probability of gene flow between host races of parasites.

Thus, conditions allowing allopatric speciation in parasites that have sympatric hosts could exist, but they are not general. Most speciation events in parasites having sympatric hosts therefore pose the same problems as those for free-living animals: how can a gene pool be separated into two isolated pools without extrinsic barriers? The answer is also the same: they must evolve intrinsic barriers impeding gene flow between incipient species. Those who study parasites are not always aware of this necessity demonstrated by all theoretical models on sympatric speciation [3–5], as shown by the recurrent confusion in the literature between specialization and
Response to Le Gac and Giraud: questioning is a good start

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I agree with the general point made by Le Gac and Giraud that, regardless of the organisms involved, we should focus our attention on identifying the mechanisms leading to speciation – a point that was also emphasized in my recent Opinion article [1]. However, I do not believe that this idea precludes another point (which was also stressed in Ref. [1]): defining sympatry in parasites is not as simple as considering the distribution of their hosts. The addition of the host environment means that sympatry in hosts does not always equate to sympatry in parasites.

There are two points in Le Gac and Giraud’s letter that should be clarified. First, what I consider to be the potential importance of host choice when considering sympatry in parasitic organisms was misinterpreted. Le Gac and Giraud stated my argument as: ‘speciation resulting from a host shift, even if the two host species are sympatric, should be considered as allopatric if the parasites have no possibility of host choice’. This is incorrect. I rather suggested that, for organisms with no ability to select or actively change hosts (a large number of parasitic species), sympatry can be harder to characterize because the probability of a parasite encountering a new host will depend on the details of its transmission and on the microhabitat use of local hosts (see p. 402 in Ref. [1]). This does not mean that no host choice equals allopatry. Indeed, several examples of divergence in sympathy for organisms with no ability to select their host were included in Ref. [1].

The second point concerns the general availability of local hosts to parasites. Le Gac and Giraud commented that only in exceptional cases will allopatric speciation occur in parasites that have sympatric hosts. Clearly, an encounter with a novel host is a necessary prerequisite for a host shift and there are numerous examples of this occurring in Nature. However, as Le Gac and Giraud outline, in order for sympatric divergence to occur, a parasite must have a ‘certain probability of ending up in the wrong host’ and we must therefore distinguish between frequently and rarely encountered host types. Many parasites might be constrained strongly in terms of host encounters, particularly those with complex life cycles (i.e. including intermediate hosts or vectors) or those depending on direct contact between individuals. Such constraints are unlikely to be linked to evolved intrinsic mechanisms of host avoidance in the parasite. Several recent examples have outlined the role of extrinsic factors (or host habitat use) in determining host encounter rates [2–5] and have shown that such ecological constraints can have profound consequences for macroevolutionary patterns [6]. Nevertheless, given the vast diversity of parasites and life cycles, we could find exceptions to any and all of the generalizations. My point is simply that we cannot categorize parasites as being sympatric or allopatric by considering their hosts alone.

References