REVIEW
What, if anything, is sympatric speciation?

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Abstract

Sympatric speciation has always fascinated evolutionary biologists, and for good reason; it pits diversifying selection directly against the tendency of sexual reproduction to homogenize populations. However, different investigators have used different definitions of sympatric speciation and different criteria for diagnosing cases of sympatric speciation. Here, we explore some of the definitions that have been used in empirical and theoretical studies. Definitions based on biogeography do not always produce the same conclusions as definitions based on population genetics. The most precise definitions make sympatric speciation an infinitesimal end point of a continuum. Because it is virtually impossible to demonstrate the occurrence of such a theoretical extreme, we argue that testing whether a case fits a particular definition is less informative than evaluating the biological processes affecting divergence. We do not deny the importance of geographical context for understanding divergence. Rather, we believe this context can be better understood by modelling and measuring quantities, such as gene flow and selection, rather than assigning cases to discrete categories like sympatric and allopatric speciation.

Sympatric speciation is of great interest to evolutionary biologists, in part because it has been consistently controversial since the inception of our field (Sulloway, 1979; Mayr, 1982; Bush, 1998; Feder, 1998; Berlocher & Feder, 2002; Coyne & Orr, 2004; Bolnick & Fitzpatrick, 2007), and in part because it challenges us to synthesize ecology, genetics and behaviour when attempting to understand how it might occur in nature. Both proponents and skeptics agree on the importance of understanding the contexts and processes influencing the likelihood of sympatric divergence, and of identifying the kinds of evidence necessary to diagnose individual case studies. However, sympatric speciation is not always clearly defined, and not all clear definitions describe the same set of phenomena. In fact, some of the disagreement over the prevalence and importance of sympatric speciation rests on disagreement over what sympatric speciation is. Such arguments do little to advance the study of evolution, and we advocate research aimed at understanding mechanisms of divergence, rather than

classifying cases into a taxonomy of 'modes of speciation' (*sensu* Mayr, 1942, 1963).

The problem is most severe in host-specific parasites, phytophagous insects and other situations where ecological differentiation necessarily involves spatial structure. Differentiated populations, 'host races' or descendant species that occur in different, discrete habitat patches may have broadly overlapping geographical ranges and yet never encounter one another at the same time and place because of their distinct ecological niches. Such situations were dubbed 'microallopatric' by Smith (1955, 1965), who was dissatisfied with the simple dichotomy between allopatry and sympatry advocated by Mayr (1942, 1963). Several recent authors have raised concerns over conceptual and evidential confusion between 'microallopatry' and 'sympatry' (Berlocher & Feder, 2002; Dres & Mallet, 2002; Dieckmann & Doebeli, 2004; Provine, 2004; Mallet, 2005).

The definition of sympatric speciation is important in the interpretation of case studies. For example, regarding Rice & Salt's (1990) classic experimental demonstration of speciation by habitat selection in *Drosophila*, Coyne & Orr (2004, pp. 140–141) argued that the strong selection levied against females that switched habitats made the

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scenario effectively allopatric by reducing gene flow. Another example is a recent case of proposed sympatric speciation of palms on an oceanic island (Savolainen *et al.*, 2006). The authors emphasized the importance of an environmentally induced shift in flowering for facilitating genetic divergence. However, if this effect was indeed present, then speciation was not sympatric but parapatric at least according to some definitions (Gavrilets & Vose, 2007).

The most famous case study associated with sympatric divergence is the recent evolution of apple-infesting *Rhagoletis pomonella* from hawthorne-investing populations (Bush, 1969; Feder, 1998; Berlocher & Feder, 2002; Coyne & Orr, 2004). The two forms presently co-occur through much of northern North America, but recent analyses indicate that important pre-adaptations for apple infestation probably arose in Mexico (Feder *et al.*, 2003), leading some authors to advocate a mixed geography model of divergence (Bolnick & Fitzpatrick, 2007; Xie *et al.*, 2007). Coyne & Orr (2004) point out the difficulty of ruling out a nonsympatric phase in the time course of any example of divergence; for example, see Stuessy's (2006) comment on the Savolainen *et al.* (2006) study on oceanic palms.

Disagreements about cases from nature often depend on grain. Grain describes the resolution at which patterns are observed. Populations might overlap at a coarse grain if they occupy the same geographical region, but not co-occur at a finer grain if they occupy different habitats within that region. Thus, whether populations are described as sympatric is at the discretion of the observer who defines the grain. For example, White (1978) suggested that the weevils of Rapa represent a sympatric adaptive radiation, whereas Paulay (1985) argued that satellite islets and isolated mountain ranges provide ample opportunity for allopatric divergence. Mayr (1963, p. 460) suggested that apple and walnut infesting codling moths might be 'microgeographic races' rather than sympatric host races because apple and walnut orchards are spatially separated. Likewise, host races of *Eurosta solidaginis* have been considered an example of sympatric divergence (Craig *et al.*, 1993; Stireman *et al.*, 2005), but others think the naturally patchy distribution of the host plant implies an important role for geographical isolation (Coyne & Orr, 2004). Savolainen *et al.* (2006) argued for sympatric speciation of palms on Lord Howe Island, even though the daughter species are generally found on distinct soil types necessarily occupying nonoverlapping portions of the island; they argue that this spatial structure is too fine grained to have a significant effect on the probability of cross fertilization; so, the groups are sympatric at the spatial scale that is relevant for population processes.

The definition of sympatric speciation is also important in the interpretation of mathematical models. For example, in the very first model of sympatric speciation (Maynard Smith, 1966), the fact that females do not move between the two habitats is crucial for speciation to occur (Gavrilets, 2006). This means the spatial structure is important genetically and, thus, makes speciation nonsympatric according to Kondrashov & Mina's (1986) definition (Table 1). However, according to Gavrilets (2003) definition, speciation in the Maynard Smith model is sympatric because males are equally likely to mate with females in either habitat.

These examples illustrate the importance of definitions and of precise statements of evidential criteria. Several definitions of sympatric speciation have appeared in the literature (Table 1). These definitions generally fall into two conceptual categories: biogeographical and population genetic. They sometimes imply different criteria for distinguishing sympatric from nonsympatric speciation, and only a few are precise enough to specify mathematical models. The most precise definitions may be so difficult to apply to real populations that attempts to diagnose cases of sympatric divergence in the wild are much less likely to yield important insights compared with research aimed at estimating parameters relevant to the interplay of selection, drift and recombination in the evolution of genetic incompatibility, local adaptation and nonrandom mating.

Biogeographical vs. population genetic concepts of sympatry

Definitions of sympatric speciation that focus on explicit geographical patterns are categorized here as biogeographical. Definitions focusing on explicit demographic conditions (probabilities of movement or mating) are categorized here as population genetic. As a geographical concept, sympatric speciation is divergence within a single geographical region such that the range of one nascent species completely overlaps the other. These diverging groups are not separated by a geographical barrier (allopatric speciation) nor do they occupy exclusive subdivisions of the ancestral range (parapatric speciation). Gavrilets (2003) pointed out that such a geographical definition is not precise enough for modelling purposes because it does not specify the population structure of the ancestral population. More demographically precise definitions rely on concepts from population genetics and ecology, and often are not explicitly spatial or geographical. Instead, models usually specify an initial condition of panmixia. An association between birthplace and mating may emerge as an evolutionary consequence of selection for habitat choice, but in the initial population, pairing of sexual partners is causally independent of their respective birthplaces.

These more precise population genetic definitions are also more restrictive, creating a minor battleground between skeptics and advocates of sympatric speciation (Mallet, 2005). In the population genetic view, any case in which the spatial structure of populations affects

Table 1 Definitions.

General terms

Speciation refers to any process of divergence that results in distinct groups of organisms that could be recognized as taxonomic species. In sexually
reproducing organisms, the coexistence of such groups requires substantial reproductive isolation. The evolution of reproductive isolation is generally
considered the crucial and most difficult aspect of divergence (Coyne & Orr, 2004; Gavrilets, 2004).

Sympatry, allopatry and parapatry. These terms describe spatial relationships among geographical ranges.

Sympatry (Poulton, 1903) is the state of being in the same place (from the Greek words *sym* meaning same and *patra* meaning 'fatherland' or country).
Groups of organisms may be entirely sympatric (the range of one is entirely included in the range of the other such that the union of the two ranges is equal to
the larger of the two ranges) or partially sympatric (there is an area in which the two geographical ranges overlap but also areas where only one of the two
groups is found; the intersection of the two ranges is less than either range). Smith (1955) proposed 'macrosympatry' to describe overlapping
geographical ranges and 'microsympatry' for groups co-occurring in the same habitat. Rivas (1964) preferred 'syntopy' for the latter situation.

Allopatry (Mayr, 1942) is the state of being in different places (from the Greek *allos* meaning different). Geographical ranges are allopatric if they are entirely
separate; their intersection is zero. Geographical ranges of groups showing partial sympatry may be said to include both sympatric and allopatric portions or
subpopulations (Cain, 1954; Dayan & Simberloff, 2005).

Parapatry (Smith, 1955) is the state of being in contact but not overlapping (from the Greek *para* for 'beside' or 'next to'). Parapatric distributions share a
border but do not intersect (Smith, 1955, 1965).

Some biogeographical definitions of sympatric speciation

Endler (1977): 'In *sympatric* speciation, there is neither spatial segregation nor spatial divergence'.

Diehl & Bush (1989): Populations in different habitats are sympatric if 'all individuals can readily move between habitats within the lifetime of an
individual.', i.e. there are no extrinsic barriers.

Ridley (1993): Speciation is sympatric if 'a new species…evolves within the geographic range of its ancestor' or 'a species splits into two without any
separation of the ancestral species' geographic range'.

Berlocher & Feder (2002): 'Sympatric speciation is the splitting of one evolutionary lineage into two in the absence of geographic isolation'. 'All stages of
divergence occur within an undivided geographic area'.

Coyne & Orr (2004): 'sympatric speciation involves the evolution of reproductive isolation within the average dispersal distance ("cruising range") of a
single individual'.

Kawecki (2004): Speciation is sympatric if 'the restriction and eventual elimination of gene flow between the two species occurs gradually as a
consequence of evolutionary (i.e. genetically based) change', and 'the entire process takes place diffusively over a large area, isolation by distance is
not important, and all important events that lead to speciation occur in the area where the ranges of the incipient species overlap'.

Some population genetic definitions of sympatric speciation

Mayr (1942): Sympatric speciation is the evolution of reproductive isolation '…within a single local population, that is within a single interbreeding unit'.

Futuyma & Mayer (1980): 'Sympatric speciation is the origin of an isolating mechanism (i.e. the evolution of a barrier to gene flow) among the members of
an interbreeding population'.

Kondrashov & Mina (1986): Sympatric speciation is the 'formation of species out of a population whose spatial structure is not important genetically'. 'We
shall call speciation 'sympatric' if in its course the probability of mating between two individuals depends on their genotypes only'.

Tauber & Tauber (1989): Sympatric speciation is initiated in a panmictic population, but it seems reasonable that some spatial/physical separation will
arise as a consequence of ecological divergence.

Futuyma (1998): 'Speciation would be sympatric if a biological barrier to gene exchange arose within the confines of a panmictic (randomly mating)
population without any spatial segregation of the incipient species – that is, if speciation occurred despite high initial gene flow'.

Johnson & Gullberg (1998): Sympatric speciation is 'speciation in the face of gene flow that is uninhibited except by genetic isolating mechanisms'. That
is, when the '…probability of mating between two individuals depends only on their genotypes'.

Gavrilets (2003): Sympatric speciation is the 'emergence of new species from a population where mating is random with respect to the birthplace of the
mating partners'.

Coyne & Orr (2004): Sympatric speciation describes instances of 'speciation occurring between two populations that show free migration (i.e. $m = 0.5$)'.

Nonsympatric modes of speciation

Allopatric speciation is the origin of new species from geographically isolated populations, i.e. gene flow between the incipient species is zero from the
beginning (Mayr, 1942; Gavrilets, 2003, 2004; Coyne & Orr, 2004).

Divergence-with-gene-flow is the complement of allopatric speciation; it includes any mode of speciation where gene flow occurs between incipient species
during the process of speciation and includes parapatric and sympatric speciation (Rice & Hostert, 1993).

Parapatric speciation is the origin of new species from populations that share some gene flow, i.e. between which the probability of dispersal is between zero
and 1/2 (Gavrilets, 2003; Coyne & Orr, 2004). A more traditional biogeographical definition specifies that gene flow occurs across a spatially restricted
contact zone such that only a fraction of each population has a high probability of emigrating or of interacting with immigrants (Smith, 1955; Endler,
1977; Futuyma & Mayer, 1980).

mating is not sympatric speciation. For example, divergence between host races of phytophagous insects is not genetically sympatric if: (i) individuals are philopatric at the level of individual plants or trees so that dispersal between host species is restricted simply because dispersal between host individuals is restricted; or (ii) the

relative density of alternative hosts varies on a large enough scale that an individual's birthplace affects the probability of encountering the alternative host. By contrast, the biogeographical perspective does consider host race formation sympatric as long as dispersing individuals are likely to encounter both hosts, i.e. they are within 'cruising range' (Mayr, 1963; Berlocher & Feder, 2002). In this case, restricted gene flow between host species relative to dispersal between individual hosts of the same species is caused by intrinsic biological differences between host races rather than between extrinsic barriers (Futuyma & Mayer, 1980).

Some of the differences between biogeographical and population genetic concepts are illustrated in Fig. 1. When individuals belonging to diverging subpopulations are literally in the same places at the same times, they are sympatric under both biogeographical and population genetic concepts (Fig. 1a). When the diverging populations occupy niches that are spatially exclusive but scattered in a mosaic across the landscape, they are biogeographically sympatric, but may not meet the criterion of panmixia (such configurations are sometimes referred to as 'macrosympatric' or 'microallopatric', a term we find misleading, see below). Panmixia is satisfied only when individuals are equally likely to breed in any patch (or on any host), including the one in which they were born (Fig. 1b). Under the initial condition illustrated in Fig. 1b, the evolution of host/habitat choice can contribute to sympatric speciation by causing nonrandom mating (Fig. 1c). By contrast, when dispersal between patches is restricted, the initial population is spatially structured and subsequent divergence is not sympatric under the population genetic view because individuals experiencing the same selective pressures are more likely to mate simply because they are more likely to encounter one another by chance (Fig. 1d). By the same token, populations on separate islands appear geographically segregated but can be genetically sympatric if individuals are equally likely to emigrate as they are to remain on their natal island (Fig. 1e).

The biogeographical and population genetic concepts also differ in their treatment of restrictions to gene flow due to nongenetic factors other than geography. For example, imprinting may cause animals to choose breeding habitats that resemble the habitat in which they were born, or habitat-induced differences in phenology may restrict opportunities for interbreeding or cross-pollination. Populations with environmentally induced constraints on gene flow may be geographically sympatric, but the genetic models describing divergence in such scenarios will be equivalent to models with spatial restrictions on gene flow (Gavrilets & Vose, 2007). Thus, whether allochrony is tantamount to allopatry depends on whether temporal isolation is environmentally induced or genetically based.

One consequence of adopting rigorous population genetic definitions of the geographical modes of speciation

is that divergence-with-gene-flow is the most general model (Rice & Hostert, 1993; Gavrilets, 2003, 2004). Because most case studies will fail to satisfy the precise conditions for sympatric speciation, cases of nonallopatric speciation will fall into the broad category of divergence-with-gene-flow. Divergence may depend critically on restricted gene flow if the cause of divergence is genetic drift or relatively weak natural selection. However, strong divergent selection can overcome very high rates of gene flow; for example, models indicate that differentiation can occur if the average selection coefficient is greater than the average fraction of immigrants per generation (Haldane, 1930; Wright, 1931; Bulmer, 1972; Slatkin, 1987). Thus, rejecting the plausibility of strict allopatric and/or sympatric divergence does little to inform us about the importance of geographical structure.

What, if anything, is microallopatry?

The term *microallopatry* requires special attention because it has been used in two very different ways. In one, it is allopatry on a very small geographical scale. For example, flightless insects on small oceanic islands may be isolated by minor ridges (Paulay, 1985) or fish populations in large lakes may be isolated by habitat discontinuities (Rico and Turner, 2002). This is no different from allopatry; the prefix *micro* simply emphasizes that geographical isolation between parts of a 40-km^2 island or by a few meters of inhospitable habitat seems very small to human biologists. But the original use of the term microallopatry was to characterize populations that are sympatric at a coarse geographical grain and segregated at a finer grain (Smith, 1955, 1965). This usage is misleading because it confuses geographical and ecological concepts. Species with broadly overlapping geographical ranges are not allopatric, even when they never encounter one another due to divergent habitat choice or circadian activity patterns. The defining characteristic of allopatric speciation is that isolation is achieved by an extrinsic geographical barrier to dispersal, not by any difference in the intrinsic biological traits of the organisms (Futuyma & Mayer, 1980). If 'microallopatry' is caused by intrinsic differences in habitat use or breeding phenology, then it is not allopatry at all because biological differences rather than geography restrict gene flow. Whether the situation should be described as sympatry depends on how important the spatial structuring of habitats is for dispersal rates and on whether a population genetic or biogeographical concept of sympatric speciation is applied.

Criteria for ascertaining sympatric speciation

The problem for empiricists is that biogeographical sympatry is relatively straightforward to diagnose, but the initial condition of panmixia specified by population genetic models is virtually impossible to test.

(a) Complete range overlap at coarse grain and co-occurrence at fine grain (purple represents thorough intermingling of red and blue individuals) is sympatry by most criteria.

(b) When red and blue habitat patches are spatially segregated at fine grain, but individuals disperse and mate at random, favoring neither their natal patches nor a particular habitat type, the groups are sympatric according to population genetic concepts. Biogeographically, they may be seen as sympatric or not, depending on the grain.

(c) Intrinsic habitat isolation occurs when $X > Y$ (where $2X + 2Y = 1$ in the 4-patch case); dispersal and mating are nonrandom owing to habitat choice alone and not affected by the spatial structure.

(d) Patches that are intermingled at fine grain may be said to have overlapping distributions, but if individuals tend to stay and breed in their natal patches, gene flow between patch types is reduced simply because gene flow between patches is reduced. These populations may be geographically sympatric but genetically parapatric.

(e) Geographically disjunct populations can be genetically sympatric if individuals disperse and breed without regard to their places of origin.
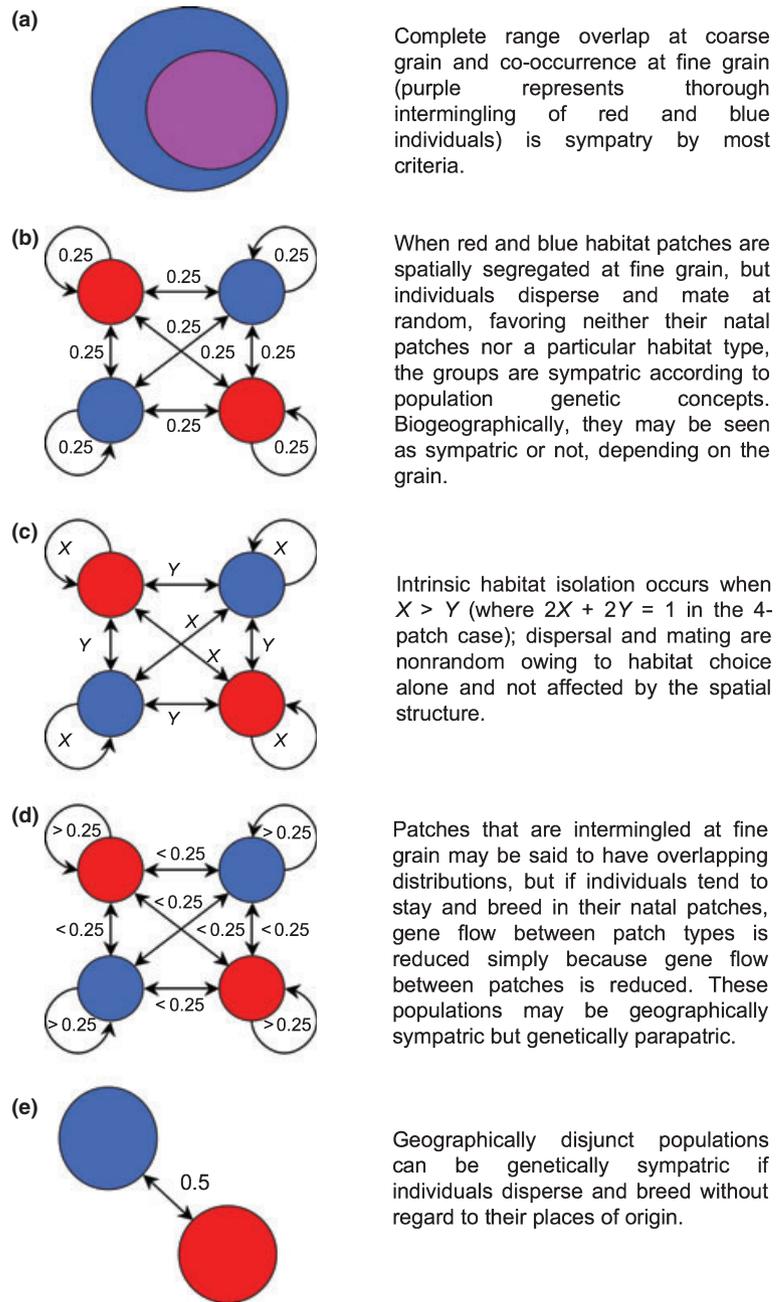
Fig. 1 Scenarios illustrating differences between geographical and genetic concepts of sympatry. Red and blue are abstract representations of distinct niches or populations. The purple colour in (a) indicates thorough mixture of red and blue individuals or their niches. (b–d) represent fine grain geographical or ecological structure with numbers giving dispersal probabilities. For example, using the well-known *Rhagoletis* system, a red dot could represent an apple tree and a blue dot a hawthorn tree. In (b), spatial structure does not affect population processes because individuals are equally likely to breed in any patch, including the one in which they were born; i.e. mating is random with respect to birthplace. In (c), spatial structure still does not affect gene flow because dispersal is based entirely on choice and not at all on position or distance. In (d), because individuals are more likely to stay in their natal patches, gene flow between patches is restricted; as a by-product, gene flow between patches of different habitat types is restricted owing to spatial structure alone. (e) represents regions that appear disjunct at a coarse geographical scale, but the individuals inhabiting those regions constitute a single panmictic population.

Coyne & Orr (2004) listed four criteria for inferring that a particular case is best explained by sympatric speciation:

1 Species thought to have arisen via sympatric speciation must have largely overlapping geographical ranges. In principle, sympatrically derived species could become allopatric over time, but it is not clear how to demonstrate such secondary allopatry.

2 Speciation must be complete. We cannot declare a case of sympatric speciation if speciation has not occurred. In practice, whether or not speciation is complete is a taxonomic decision that is contingent on the definition of 'species' (the biological species concept in Coyne and Orr's case).

3 Clades thought to arise via sympatric speciation must be sister species or monophyletic groups; i.e. we can support sympatric speciation only when the evidence has not been obscured by subsequent nonsympatric diversification.

4 According to Coyne and Orr, 'the biogeographic and evolutionary history of the groups must make the existence of an allopatric phase *very unlikely*' (p. 142,

their italics). This is not so much a criterion as a statement that the first three criteria are necessary but not sufficient, in their view, to reject alternatives to sympatric speciation.

These criteria clearly relate to the biogeographical concept of sympatric speciation. To infer sympatric speciation under the population genetic concept, an additional condition must be met: *Evidence must support panmixia of the ancestral population.* One approach is to evaluate the population structure of the daughter species. If each of the sympatric daughter species is panmictic, we may reasonably infer that they descended from a single panmictic population. For example, Barluenga *et al.* (2006) found no evidence of genetic structure among sampling localities of two sympatric cichlids, and concluded that spatial structure within the lake was unimportant for speciation. However, actually inferring panmixia is problematic because panmixia is usually a null hypothesis in statistical analyses of population structure. Failing to reject the null hypothesis is very different from supporting panmixia over some biologically significant level of population structure; therefore, a power analysis or goodness-of-fit approach (Edwards, 1972) would be desirable to quantify the strength of support for panmixia. On the other hand, extensive population structure in *Rhagoletis* fruit flies has caused investigators to re-evaluate the usefulness of a simple sympatric speciation model for this classic case study (Xie *et al.*, 2007).

Conclusion and prospectus

Different concepts of sympatric speciation imply different criteria for inferring cases of sympatric speciation. This situation contributes to the ongoing debate over the prevalence and importance of sympatric speciation in nature. Further, the precise population genetic concept used by most models of sympatric speciation is rarely (if ever) applied to empirical studies. The initial condition of panmixia that characterizes models may be impossible to demonstrate in case studies. Further, the data from natural populations indicate that most species have some spatial genetic structure and complex biogeographical histories of range shifts and fragmentation (e.g. Avise *et al.*, 1987; Lyons, 2003; Fitzpatrick & Turelli, 2006).

The geography of divergence remains extremely important for understanding the evolution of diversity. Geographical structure influences what mechanisms can operate, and how important they are in causing reproductive isolation and ecological divergence. However, it may be that the most interesting and relevant kinds of geographical structure have been ignored because of a focus on the extreme cases known as sympatric and allopatric speciation. While having the term 'sympatric speciation' in the title of a manuscript may improve its chances of publication in a high-profile journal, we question whether an obsession with

identifying true cases of sympatric speciation is the best way to advance the science.

It has been suggested before that we abandon the geographical classification of modes of speciation (Via, 2001; Kirkpatrick & Ravigné, 2002). So far, this suggestion has had little obvious influence. So, is sympatric speciation too useful a term to be defined away? What remains useful about the old classification of geographical modes of speciation is its representation of biogeographical (not genetic) scenarios. Sympatric, allopatric and parapatric ranges can be drawn on a map (e.g. Mayr, 1942; Futuyma, 2005). However, we have argued that these geographical concepts cannot be translated directly into the language of population genetics without specifying a precise relationship between location (at the appropriate grain) and probability of mating.

Precise and rigorous definitions of sympatric and allopatric speciation identify them as infinitesimal points at the limits of the range of possibilities for speciation (Rice & Hostert, 1993; Gavrilets, 2003, 2004). Divergence-with-gene-flow is the most general model of divergence (excluding only strict allopatric speciation) and may be the most common process of divergence in nature. Populations may diverge in the face of continuous gene flow or may alternate between periods of complete isolation and periods of contact and gene flow (Bennett, 1997; Bolnick & Fitzpatrick, 2007; Niemiller *et al.*, 2008). A task for theoreticians is to explore the parameter space between allopatry and sympatry with the goal of identifying general principles, for example Wright's rule that chance fixation of alternative alleles is likely when the average number of migrants per generation is less than $1/2$ (Wright, 1931) or that populations will diverge under selection when the selection coefficient is greater than the migration rate (Haldane, 1930; Bulmer, 1972). More recently, Gavrilets (2003) showed a similar result where sympatric groups will diverge under selection when the selection coefficient is greater than the probability of random mating $(1 -$ the strength of assortative mating). A task for empiricists is to estimate the distribution of population structures associated with divergence and the strengths of all relevant evolutionary forces (gene flow, selection, drift and mutation). The studies of Ramsey *et al.* (2003) and Bolnick & Nosil (2007) are exemplary in relating empirical parameter estimates to theory. These research endeavours will be far more profitable and influential than attempts to satisfy or reject criteria for sympatric speciation, however defined.

Acknowledgments

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