

SHORT COMMUNICATION

Space, sympatry and speciation

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Abstract

Sympatric speciation remains controversial. ‘Sympatry’ originally meant ‘in the same geographical area’. Recently, evolutionists have redefined ‘sympatric speciation’ non-spatially to require panmixia ($m = 0.5$) between a pair of demes before onset of reproductive isolation. Although panmixia is a suitable starting point in models of speciation, it is not a useful definition of sympatry in natural populations, because it becomes virtually impossible to find or demonstrate sympatry in nature. The newer, non-spatial definition fails to address the classical debate about whether natural selection within a geographic overlap regularly causes speciation in nature, or whether complete geographic isolation is usually required. We therefore propose a more precise spatial definition by incorporating the population genetics of dispersal (or ‘cruising range’). Sympatric speciation is considerably more likely under this spatial definition than under the demic definition, because distance itself has a powerful structuring effect, even over small spatial scales comparable to dispersal. Ecological adaptation in two-dimensional space often acts as a ‘magic trait’ that causes pleiotropic reductions of gene flow. We provide examples from our own research.

Several biologists comment that different meanings of ‘sympatry’ can interfere with answering the question: ‘how common is sympatric speciation?’ (Berlocher & Feder, 2002; Gavrillets, 2003; Coyne & Orr, 2004; Mallet, 2005, 2008; Bolnick & Fitzpatrick, 2007; Butlin *et al.*, 2008). The current debate stems from earlier discussions of terminology (Mayr, 1947; Futuyma & Mayer, 1980; Kondrashov & Mina, 1986) that had become somewhat quiescent until today.

Fitzpatrick *et al.* (2008) have reviewed early and recent literature and provide an useful and detailed guide to the history of the term ‘sympatric speciation’ in sexual species. Their main emphasis is to contrast geographic with demic (or ‘population genetic’, in Fitzpatrick *et al.*’s terminology) definitions of sympatric speciation when assessing whether speciation is sympatric in nature.

While these authors suggest the demic definition is ‘more precise’, they also point out that based on this definition it would be almost impossible to demonstrate that speciation was sympatric (Fitzpatrick *et al.*, 2008). They concur that the geography of speciation remains interesting, but argue that it is of secondary importance. They therefore suggest that it is more meaningful to investigate actual gene flow and selection parameters, rather than to be too concerned about whether speciation was sympatric (in this newer, demic sense; see also Butlin *et al.*, 2008). We agree that quantifying gene flow and selection parameters is important for understanding speciation. However, the classical argument about whether sympatric speciation (in the original, spatial sense) is common in nature is inadequately addressed by this nonspatial, demic definition. Geographic and strictly demic definitions of sympatry are closely related, but are not the same.

We here develop a composite spatial and population genetic definition of sympatry. We believe this will be more useful and biologically more realistic than the recently adopted ‘demic’ view. We begin by discussing

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Table 1 Spatial and nonspatial definitions of sympatry, parapatry, and allopatry.

	Nonspatial, demic		Spatial population genetic	
	Verbal	Mathematical*	Verbal†	Mathematical‡
Sympatry	Panmixia	$m = 0.5$	Where individuals are physically capable of encountering one another with moderately high frequency. Populations may be sympatric if they are ecologically segregated, as long as a fairly high proportion of each population encounters the other along ecotones; and they may be sympatric, yet breed at different seasons	Distance between diverging populations $< k\sigma_x$ where k is a small number, say 2 or 3
Parapatry	Nonpanmictic	$0 < m < 0.5$	Where groups of populations occupy separate but adjoining geographic regions, such that only a small fraction of individuals in each encounters the other. Typically, populations in the abutment zone between two forms will be considered sympatric	As above, but only for populations at the abutment zone between geographic regions. Most other populations will have very low rates of gene flow
Allopatry	Zero gene flow	$m = 0$	Where groups of populations are separated by uninhabited space across which dispersal and gene flow occurs at very low frequency	Distance between regions and populations $\gg \sigma_x$

* m is the per generation fraction of individuals exchanged among demes.

†Modified from Futuyma & Mayer (1980).

‡ σ_x is the standard deviation in one dimension (x) of dispersal distances between sites of birth and breeding.

the history of the term sympatry and its development by Ernst Mayr in framing the ongoing debate about the geographic context of speciation. We then examine whether the original geographical/spatial definition of sympatry can be made precise enough to resolve Mayr's argument about the scarcity of sympatric speciation in nature. We advocate that a spatial meaning for sympatry is retained, albeit with some modification under a realistic spatial population genetic framework. Specifically, we argue that speciation is sympatric when it occurs over local distance scales not much greater than the width of the local population genetic 'neighbourhood' (Table 1), even though this has the potential to make modelling speciation trickier. Using this spatial definition, population genetics theory suggests that sympatric speciation is more likely than generally assumed.

The history and meaning of 'sympatry'

E.B. Poulton was fond of coining biological terms derived from Greek (*aposematism* for warning colour is one of his terms). In a discussion of the nature of species, he wrote: 'forms found together in certain geographical areas may be called *Sympatric* ($\sigma\nu\nu$, together; $\pi\alpha\tau\rho\alpha$, native country). The occurrence of forms together may be called *Sympatry*, and the discontinuous distribution of forms *Asympatry*' (Poulton, 1904). Mayr (1942) later accepted Poulton's term *sympatry*, but suggested *allopatry* as an alternative to *asympatry*: 'Two forms or species are *sympatric*, if they occur together, that is if their areas of distribution overlap or coincide. Two forms (or species) are *allopatric*, if they do not occur together, that is if they exclude each other geographically' (Mayr, 1942: 148–9). A third convenient term in common use today, *parapatry*, was invented later,

and 'was proposed for situations where ranges are in contact and genetic interchange is geographically possible even without sympatry' (Smith, 1965). Until recently, 'parapatry' was generally used in a large-scale geographic sense, for instance when subspecies or geographic races abut within species at contact zones or hybrid zones (e.g. Mayr, 1963; Rice & Hostert, 1993).

After considering the problem of gene flow more carefully, Mayr (1947: 269) revised his definition of sympatric speciation to 'the establishment of new populations in different ecological niches within the normal cruising range of individuals of the parental population'. However, such geographic realism is inconvenient for modelling the important parameters of gene flow and selection. As a result, sympatric speciation is often simplified for modelling purposes to the more tractable assumption that divergence is initiated within a single, randomly mating or panmictic population separated into two niches (or sub-populations) in which space is ignored. For example: 'we shall call speciation *sympatric* if in its course the probability of mating between two individuals depends on their genotypes only' (Kondrashov & Mina, 1986; see also e.g. Maynard Smith, 1966; Kirkpatrick & Ravigné, 2002). More recently, it has been argued that 'although intuitively appealing, [the geographic definition] is not precise enough for modelling purposes' (Gavrilets, 2003). Instead, modellers often mean by 'sympatric speciation' that initial gene exchange rate (m) between diverging demes is maximal, so that mating is random (i.e. $m = 0.5$; see Fig. 1). By contrast, Allopatry implies no gene exchange at all ($m = 0$), and all 'intermediate cases when migration between diverging (sub)populations is neither zero nor maximum' are considered parapatric (Fig. 1). 'Both this figure and biological intuition suggest that parapatric speciation is

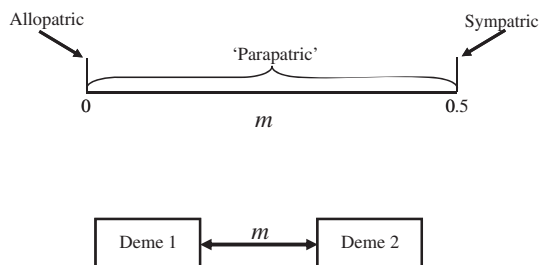


Fig. 1 Demic view of sympatry and allopatry in the Gavrillets (2003) formulation.

the most general (geographic) mode of speciation' (quotations are from Gavrillets, 2003: 2198), while sympatric and allopatric modes become extreme limits at the ends of the range of possibilities.

Although we criticize here the application of strictly demic assumptions to debates about the frequency of sympatric speciation in nature, the logic for employing these models of sympatric speciation is quite clear: if speciation can occur under initial panmixia, then it will occur even more readily under less stringent conditions in natural populations. While the demic definition is precise, it is questionable whether it usefully addresses the geographic, spatial issue originally posed by Mayr about speciation in nature. This issue remains of interest to generations of evolutionary biologists (Coyne & Orr, 2004; Bolnick & Fitzpatrick, 2007). The main problem, as we see it, is that demic models omit consideration of space, and therefore cannot deal with spatial population genetic aspects of speciation. While it is true that the terms sympatry, parapatry and allopatry break up a continuum into artificially discrete categories (Rice & Hostert, 1993; Fitzpatrick *et al.*, 2008), consideration of gene flow among demes alone has a tendency to prevent thinking about the spatial continuum at all. Yet appreciation of this spatial continuum is necessary to appreciate the potential role of geography in speciation in nature.

Geographic and genetic definitions of sympatry are, of course, not unrelated. For example, populations exchanging genes with $m = 0.5$ must be more or less sympatric in the spatial sense. But the demic definition does not map simply onto space. For example, reduction from $m = 0.5$ may only sometimes be because of geographic disjunction. Different ecological niches (sometimes called 'microallopatry', Mayr, 1947) or different times of emergence (allochryony) might also be sympatric in a spatial sense, but are not considered as such in the demic (population genetic) sense of Gavrillets (2003). Geography affects gene flow, which in turn affects the probability of speciation. But knowing about gene flow does not necessarily fix the geographic situation. A purely demic approach therefore makes inferences about geographic speciation in nature difficult.

In an early attempt to connect geography to gene flow, Mayr wrote: 'All degrees of geographic isolation are known, resulting in a complete interruption or only slight reduction of gene flow' (Mayr, 1947). The problem is especially severe in ecological speciation, where the two forms may begin to specialize on different resources or habitat parameters (Funk, 1998; Schluter, 2001, 2009; Barluenga *et al.*, 2006; Gavrillets *et al.*, 2007). Such populations will not be sympatric in the demic sense above (as in Fig. 2, 'pure sympatry') if resources are anything other than perfectly mixed. In nature, food and other resources are usually clumped and patchy, and dispersal limited. Thus, populations specializing on different resources locally within a defined geographic area will often have $m < 0.5$ (see Fig. 2, 'mosaic sympatry'). Modellers have concentrated on panmixia as the initial condition, but it does not follow that any actual individuals mate randomly in nature (Elmer *et al.*, 2009). As Fitzpatrick *et al.* (2008) point out, the more 'precise' demic definition of sympatric speciation is 'an infinitesimal end-point of a continuum'. Completely random mating is virtually impossible in nature, even though a useful null hypothesis in theoretical treatments. Thus, adopting a strict demic definition forces sympatric

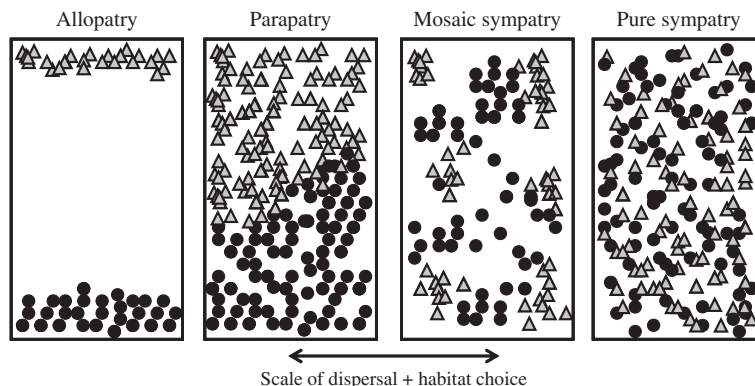


Fig. 2 The allopatry/sympatry spectrum, using spatial definitions (after Mallet, 2008).

speciation to be rare, as well as making it nearly impossible to demonstrate in nature.

Yet some authors have recently favoured the $m = 0.5$ criterion of sympatry when discussing speciation in nature (e.g. Coyne & Orr, 2004), and for this reason alone it is not surprising that they regard sympatric speciation as exceedingly rare (though they give other reasons). Bolnick & Fitzpatrick (2007) also state that sympatric speciation is probably rare, although they do not specify precisely what they mean by 'sympatric'. Fitzpatrick *et al.* (2008) argue that panmixia often acts a null hypothesis that is nearly impossible to demonstrate, but nonetheless favour a $m = 0.5$ criterion when proposing that 'a power analysis or goodness-of-fit approach... would be desirable to quantify the strength of support for panmixia'. If panmixia is a null hypothesis (inbreeding, $F = 0$), there really can be no empirical support for it; one can only have support for the alternative, a nonzero F . The adoption of a demic standard for sympatry in nature also has some other odd side effects. For example, geographically overlapping populations that speciate because of environmentally induced differences in time of mating will be considered allopatric with $m = 0$ under this definition, even if they exhibit fine spatial overlap, whereas if allochrony evolves as a result of genetic divergence, speciation is considered sympatric (Fitzpatrick *et al.*, 2008: 115). It seems more sensible to regard speciation under both scenarios as sympatric, in a spatial sense.

The recent demic definitions of sympatry obscure the reason for making the distinction in the first place, particularly the major thrust of the argument for the primacy of allopatric speciation made by Mayr (1942),¹ a view which persists today. For example: '... the evidence for sympatric speciation is scant. ... It is hard to see how the data at hand can justify the current wave of enthusiasm for sympatric speciation' (Coyne & Orr, 2004: 178). Despite difficulties caused by the definition of sympatry, Mayr felt that the distinction between speciation in sympatry and allopatry was an important advance that he himself had clarified, and one which

¹Late in life, Mayr himself became convinced by some cases of sympatric speciation, particularly by recent evidence on cichlids in crater lakes. He admitted he had been wrong to doubt its importance earlier (Mayr, 2001, 2002, 2004). He even felt that 'at the present time there is too little known about speciation in many of the phyla of animals in order to make a generalisation' about the relative abundance of sympatric and allopatric speciation. He states he hadn't realized how likely sympatric speciation could be when habitat choice had an indirect effect on assortative mating (Mayr, 2002: 967), which is more or less equivalent to our own spatial pleiotropy argument below. However, he still regarded most well studied cases of speciation to be allopatric, for instance in mammals, birds, butterflies, sea urchins etc. (Mayr, 2002: 967). He still saw sympatric speciation as 'unorthodox' and restricted to a few groups, such as 'cold-blooded vertebrates' (Mayr, 2004).

Darwin had not (Mayr, 1959; but see Darwin, 1859: 103–109). Making sympatric speciation an infinitesimal impossibility in nature ignores and devalues the original argument. Indeed, this precondition not only effectively eliminates sympatric speciation, but also relegates even allopatric speciation to a minor extreme: $m = 0$ is both unlikely and nearly impossible to demonstrate either as an initial starting condition or as an end-point, given the widespread occurrence of occasional hybridization between otherwise 'good' sympatric species (Coyne & Orr, 2004; Mallet, 2005, 2008). Appreciation of these points should temper enthusiasm for the abandonment of the original geographic distinction of Poulton and Mayr, even by those convinced of the primacy of allopatric speciation.

Part of the problem is that natural populations are poorly characterized by the island or demic models envisaged in theoretical treatments of speciation. Natural populations are typically spatially structured in two or even three dimensions, and organisms have more or less continuously declining dispersal (migration) distributions along these dimensions. As a result, no individual is truly in demic sympatry with its neighbour, nor, conversely, likely to be in complete demic allopatry either. It is often not realized how powerful is the effect of even very small distances on gene flow in continuous natural populations, and this we assume was chiefly responsible for the strongly pro-allopatric speciation views of Ernst Mayr. We therefore advocate revising the spatial definition to include specific spatial population genetic considerations.

Suggested resolution

A general interest of evolutionary biologists is whether Darwinian natural selection is a primary cause of speciation in the face of gene flow. The alternative view, strongly held by Mayr and others, is that even if selection is involved, events incidental to or in addition to biology are also required: specifically, complete geographic isolation. Such allopatric settings include, for example, the emergence of a desert between two forest populations, or long-distance colonization to a remote island where a founder event and 'genetic revolution' can take place (Mayr, 1963). We are interested in the allopatry vs. sympatry question because we would like to estimate the degree to which speciation depends only on natural selection and the biology of the organism in continuous natural populations, compared with the degree to which nonbiological causes must be introduced. For this reason, there will be continued interest in the geographic distinction of sympatry vs. allopatry if we wish to answer Mayr's classic question.

However, the absence of any population genetics at all in the definition of sympatry would make speciation difficult to interpret in the light of evolutionary theory. For example, typical gene flow distances among organisms can be so different that most of us will prefer

'sympatry' to reflect, to some extent, gene flow as well as geography. We therefore advocate a hybrid concept that blends geographic and population genetic ideas, where 'sympatry' implies being within the 'normal cruising range of individuals' (Mayr, 1947). A particularly useful verbal set of definitions with these spatial genetic ideas in mind is: 'Two populations are *sympatric* if individuals of each are physically capable of encountering one another with moderately high frequency. Populations may be sympatric if they are ecologically segregated, as long as a fairly high proportion of each population encounters the other along ecotones; and they may be sympatric, yet breed at different seasons' (Futuyma & Mayer, 1980). *Parapatry* would then refer, as in its original definition, to groups of populations occupying 'separate but adjoining regions, such that only a small fraction of individuals in each encounters the other' (Futuyma & Mayer, 1980; see also Rice & Hostert, 1993). '*Allopatric* populations are separated by uninhabited space (even if it is only a very short distance) across which migration (movement) occurs at very low frequency' (Futuyma & Mayer, 1980). A modified set of verbal definitions in this spatial sense is given in Table 1.

To make these ideas more precise, we might interpret 'cruising range' or 'encountering one another' in approximate terms *via* the spatial genetic 'neighbourhood' of Wright (1969); see also Slatkin & Barton (1989). Thus, sympatric populations are contained within areas, $4\pi\sigma_x^2 - 9\pi\sigma_x^2$, i.e. in areas having a radius not much greater than, say, 2–3 standard deviations, σ_x , of parent-offspring dispersal distance along a single dimension, x . Assuming a close-packed two-dimensional lattice of such neighbourhood areas considered as demes, the rate of exchange, m , between such areas is roughly equivalent to the probability of dispersing beyond a radius of $2\sigma_x$ or $3\sigma_x$. For two-dimensional Gaussian dispersal, this definition of sympatry is equivalent to $m = 0.089$ or $m = 0.005$ among local neighbourhoods respectively. The fraction moving more than just $4\sigma_x$ equivalent to just two Wrightian neighbourhoods apart, drops to only $m = 0.0001$ (all evaluations of the two-dimensional Gaussian integral courtesy of F. Úbeda de Torres, pers. comm.). It seems sensible to us that adjacent or nearly adjacent neighbourhoods in continuous population structures are always considered 'sympatric'. Typically, dispersal tends to be leptokurtic, but, unless leptokurtosis is extreme, its effects on the population genetic parameters of two-dimensional neighbourhoods do not strongly alter these conclusions (Wright, 1969: 303–307). Demic and spatial population genetic definitions are compared in Table 1.

Much sympatry under the above definition will be in a category we call 'mosaic sympatry' (Fig. 2), and, in the demic sense, will therefore have $m < 0.5$. It seems reasonable to us that genes that affect ecological divergence and cause a reduction from $m = 0.4$ to $m = 0.3$ (or even from $m = 0.04$ to $m = 0.03$) can sometimes be

considered both to contribute to and also perhaps initiate sympatric speciation, if this occurs under spatial conditions approximating local neighbourhoods. Sympatric speciation is then a *kind* of 'speciation with gene flow,' as is parapatric speciation, but 'speciation with gene flow' is not under this definition an exact *equivalent* of sympatric speciation. Similarly, as Futuyma & Mayer (1980) also argue, complete allopatry with $m = 0$ is also unlikely: if ancestors are to be geographically isolated and yet one population is a colonist from the other, we must allow some probability of gene flow during or directly after such colonization, and this leads to $m > 0$. As long as there is complete geographic separation, and migration is also low enough to allow differentiation because of genetic drift (i.e. that *any* selection can *always* overcome gene flow for population differentiation), then the mode should be considered allopatric.

Interpreting adaptive divergence in the face of gene flow in nature

Mayr (1947: 268) apparently based his original argument for the primacy of allopatric speciation on the grounds that 'it has never been determined how much gene flow strong selection pressure can neutralize'. Mayr apparently did not realize that the problem of the opposition of forces of natural selection, genetic drift, and gene flow had already been solved many years earlier by those that he called 'bean-bag geneticists'. For example, if gene flow is weak, approximately $m < \frac{1}{2N_e}$, where N_e is the locally effective population size, significant genetic drift at neutral loci becomes likely among separate populations or demes (Wright, 1931). Although N_e is often thought of as a large number, drift is nonetheless abundant in continuous populations in nature as evidenced by hundreds of studies showing appreciable gene frequency variation at marker loci (Morjan & Rieseberg, 2004). By contrast, strong selection will generally outweigh gene flow much more readily than drift, provided $m < s$, where s is the per locus divergent selection pressure (Haldane, 1932). Recent theory has shown that sympatric speciation is possible (Kondrashov & Kondrashov, 1999; Dieckmann & Doebeli, 1999; Bolnick, 2006), even when an $m = 0.5$ initial state is assumed, although it has also been argued to be rare in nature (Coyne & Orr, 2004; Bolnick & Fitzpatrick, 2007).

Strong selection in sympatry, as expected for ecological adaptation, should provide many opportunities for genetic divergence and reduction in gene flow, and hence, speciation (Schluter, 2001, 2009). And when one relaxes the strict $m = 0.5$ criterion for sympatry, sympatric speciation becomes even more likely, for example under realistic conditions of mosaic sympatry (Fig. 2). The reason is that ecological adaptations can often act as 'magic traits', (Gavrilets, 2004) which pleiotropically reduce gene flow between populations, because ecological resources are typically patchy on a scale comparable

to dispersal distance, σ_x . This spatial pleiotropy causing assortative mating acts in addition to situations where adaptations pleiotropically affect mating preference more directly. For example, divergence in colour patterns used in signalling to other species can also be important in mate choice in butterflies (Jiggins *et al.*, 2001), frogs (Reynolds & Fitzpatrick, 2007) and fish (Elmer *et al.*, 2009); body size similarly affects mate choice in fish (Nagel & Schluter, 1998). Modellers have often pointed out that pleiotropy would make sympatric speciation easy, but typically did not consider it very important, perhaps in part because they assume nonspatial demic population structures (e.g. Maynard Smith, 1966; Kirkpatrick & Ravigné, 2002; but see Rice & Hostert, 1993; Via, 2001; Gavrillets, 2004). Space, or local 'isolation by distance', may act as one of the most important pleiotropies of all.

However, we do not contend that all organisms necessarily possess such biology or suitable genetic variation for sympatric speciation to occur. Complete allopatry of course has its own built-in spatial pleiotropy causing complete assortative mating (Kirkpatrick & Ravigné, 2002) – in sympatry, this must probably evolve by ecological habitat choice or mating preference to facilitate sympatric divergence (Gavrillets *et al.*, 2007). These considerations mean that allopatry, or at least some degree of geographic isolation, will be necessary for speciation of organisms having natural histories not susceptible to evolution of preference-based assortative mating (for instance, lacking discrete niches).

Examples of divergence evolving and maintained in mosaic sympatry

We here cite examples from our own research to illustrate spatial effects on divergence and speciation. We do not argue that speciation was purely sympatric (in a spatial sense) in all these cases, but we do feel that these examples, as well as many others cited earlier (Berlocher & Feder, 2002; Drès & Mallet, 2002; Bolnick & Fitzpatrick, 2007) demonstrate a strong *likelihood* of sympatric speciation under the spatial definition of 'sympatry' of Table 1.

The apple maggot

Among the best-known examples of sympatric speciation are the apple and hawthorn host races of *Rhagoletis pomonella* flies. These races are broadly sympatric (in the spatial sense) across the northeastern and midwestern United States (Bush, 1966). Apples were introduced there approximately 400 years ago by European settlers. Sometime in the mid-nineteenth century a population of endemic hawthorn flies shifted to apple (Bush, 1966) and began to differentiate phenotypically and genetically (Feder *et al.*, 1988; McPherson *et al.*, 1988). The critical ecological adaptation affecting gene flow between ances-

tral hawthorn and derived apple host races is host plant choice. *Rhagoletis* flies mate almost exclusively on or near unabsconded fruit or nearby leaves of their host plants. Thus, host choice translates directly into mate choice, generating assortative mating and prezygotic isolation. Native hawthorns and feral apples most often occur in old fields or on the edges of woodlands. As such they represent a patchy resource, although interspersed clusters of hawthorn and apple trees are usually found close together (mosaic sympatry, Fig. 2). Not all adult flies migrate from their natal plant, the fruit of which they fed within as larvae. Thus, even in the absence of genetically determined host choice, inter-host $m < 0.5$ and the races, as well as individuals on different trees of the same species, might all be considered nonsympatric under the demic definition. Apple and hawthorns also fruit at different times of year (~3 week difference), further allochronically distancing the flies from sympatry in a strict demic sense (Feder *et al.*, 1993). Yet adult flies can travel reasonable distances ($\gg 2$ km) and mark-recapture studies have shown that many adult individuals move through a field and can frequent several different host plants in their lifetimes (Feder *et al.*, 1994). Thus, the apple and hawthorn host races are well within each others' individual cruising ranges. Overall inter-host migration is estimated to be $m = 0.04$ – 0.06 between apple and hawthorn host trees locally, despite host choice (Feder *et al.*, 1994). In this case, strong divergent selection in the form of diapause adaptation to host fruit phenology aids differentiation between the races (Filchak *et al.*, 2000).

It is likely that a series of chromosomal rearrangements evolved in allopatry which may have been important, particularly in the timing of emergence in *R. pomonella* host races (Feder *et al.*, 2003). The apple and hawthorn host races are members of a larger sibling species complex called the *R. pomonella* group (Bush, 1966; Berlocher, 2000). These taxa display more pronounced preferences for their respective native host plants and greater genetic differentiation than the apple and hawthorn host races (Feder & Bush, 1989; Xie *et al.*, 2008). Although some key innovations coupled with the chromosome rearrangements, which enabled speciation, may have evolved in allopatry (Feder *et al.*, 2003), it should be realized that not only the apple and hawthorn races of *R. pomonella*, but also several other species and races in the group (Berlocher, 2000) are also polymorphic for varying sets of these rearrangements. Clearly, all of these currently sympatric forms evolved in North America long after the inferred allopatric chromosomal rearrangement events. The initial host shifts to these plants almost certainly occurred under initial conditions that were not perfectly panmictic. Nevertheless, it is difficult to imagine that co-occurring hosts were not within the cruising range (i.e. that they were more than several σ_x apart) of one another for flies making the initial host shift. Hence, we consider it likely that most of these populations have

undergone sympatric divergence, in its original, spatial sense.

Cichlids in Nicaragua

Another recent example is given by crater lake cichlid fishes in Nicaragua. Until recently only three species (*Amphilophus citrinellus*, *Amphilophus labiatus* and *Amphilophus zalius*) were described from the two large lakes and several crater lakes in Nicaragua. *Amphilophus zalius*, the arrow cichlid, occurs in only one of the crater lakes (Lake Apoyo) and based on several lines of genetic evidence and ecological data such as stomach contents analyses and the quantification of morphological differences, it has been shown that this species originated sympatrically in this crater lake (Wilson *et al.*, 2000; Barluenga & Meyer, 2004; Barluenga *et al.*, 2006). It is ecologically distinct from the other endemic species now known exclusively from this lake. Furthermore, mitochondrial haplotypes of cichlids endemic to this lake are found nowhere else. Population genetic analysis based on microsatellites also supports an origin of all cichlid species in this lake from a single colonization. *Amphilophus zalius* prefers the open water to the benthos-associated environment occupied by other fish within this small crater lake (5 km diameter), and has a diet associated with open water and the surface rather than the benthic environments of the lake. There is no detectable genetic differentiation among conspecific populations sampled from around the perimeter of this ~2 km diameter crater lake, although complete panmixia ($m = 0.5$) seems very unlikely (Gavrilets *et al.*, 2007). In another crater lake, Lake Xiloá, incipient speciation has occurred through sexual selection based on a colour polymorphism and assortative mating (Elmer *et al.*, 2009). Apparently, mechanisms of ecological speciation as well as sexual selection can act together in sympatry to bring about new species in crater lakes.

Host specific *Timema* stick insects

Host ecotypes of *Timema cristinae* walking-stick insects living on *Ceanothus* vs. *Adenostoma* plants provide another example of adaptive divergence and ecological speciation maintained in the face of abundant and spatially varying gene flow (Nosil, 2007). In this system, patches of the two hosts are highly variable in size and exist in a geographic mosaic. Gene flow into a local population, from nearby populations using the alternative host, varies substantially among populations, with m potentially zero in some cases, $m = 0.04$ on average for directly adjacent patches, ranging up to 0.24 (inferred from DNA sequence data, see Sandoval, 1994; Nosil *et al.*, 2003). This gene flow often has a constraining effect, and can erode the adaptive divergence that drives ecological speciation in *Timema* (Nosil & Crespi, 2004; Bolnick & Nosil, 2007; Nosil, 2009). Nonetheless, numerous exper-

iments have demonstrated strong, divergent selection between hosts. This selection often counters gene flow to the extent that partial, sometimes relatively strong, reproductive isolation persists (Nosil & Crespi, 2006; Nosil, 2007).

The larch budmoth

A final example concerns the larch budmoth, *Zeiraphera diniana*. This species is distributed across the Palaearctic. Different forms are found on larch (*Larix*), pine (*Pinus*) and spruce (*Picea*). The larvae at times cause major defoliations and damage to these forest trees. In the Alps, defoliations on larch occur in 10- to 11-year cycles, and sweep across the Alps in waves accompanied by large mass migrations (Baltensweiler & Rubli, 1999; Bjørnstad *et al.*, 2002). Larch and pine host races differ in a number of characteristics, particularly host choice, colour pattern of larvae and female pheromone blends (Baltensweiler *et al.*, 1978; Emelianov *et al.*, 1995). However, none of these differences are absolute, and hybrids can be found in the wild at a frequency of 1–2% (Priesner & Baltensweiler, 1987; Emelianov *et al.*, 2004), despite strong host choice and pheromone-effected assortative mating. There are significant differences at around 10% of allozyme and AFLP loci between larch and pine forms, but marker loci rarely show completely fixed differences (Emelianov *et al.*, 1995, 2004).

Although assortative mating is primarily because of pheromonal communication, the host plant has a strong influence. Individual females calling from their host tree tend to attract males from within the same crown and from adjacent trees. Females choosing to settle on, or in the neighbourhood of the 'wrong' hosts are much more likely to attract the 'wrong' males, in spite of the structuring effect of pheromones. Larch and pine trees are clumped, even in areas of sympatry, so adjacent trees also tend to be of the same species (Emelianov *et al.*, 2001). Assuming absence of pheromonal communication, and that the realized choice of resting tree (86% 'correct' in females, and 82% in males) depends only on host choice and spatial distribution, one can estimate the probability of meeting in the wild: host choice should by itself lead to 73% assortative mating between the host races (Emelianov *et al.*, 2003).

Thus, although we do not know whether the original host shift in *Zeiraphera* was in geographic sympatry, the highly migratory population structure suggests it will not be easy to find geographically allopatric populations. Even so, the structuring effect of local host choice evolution alone, under conditions of greatest sympatry, would have immediately reduced gene flow to $m < 0.27$, so that further changes (e.g. pheromone-based assortative mating, host adaptation) should evolve provided selection on the first loci was at least $s \approx 0.27$. Any less perfect mixing of hosts would enhance this possibility. Today, and given all sources of assortative mating, any

divergent adaptation, such as those causing reproductive isolation, should readily evolve in sympatry under much smaller selection pressures, say $s > 0.02$ in sympatry.

Conclusions

The above examples illustrate that substantial gene flow is currently occurring in spatial overlap between divergent populations, and was likely to have performed so during initial stages of divergence in a number of species, even though in each case almost certainly $m < 0.5$ initially. It seems clear that ecological shifts important for speciation are neither expected nor found to be infrequent in geographic or spatial sympatry, in spite of the presence of gene flow.

A major difficulty with assessing the frequency of sympatric speciation may therefore not be the definition of sympatry, but in deciding when the crucial stage of speciation has been reached; when should an ecological race be considered an occasionally hybridizing species? A related issue is whether sympatric speciation will stall at ecologically divergent but insufficiently differentiated states to be accepted as species, requiring other factors to 'complete' the speciation process (Mayr, 1963; Matessi *et al.*, 2001; Berlocher & Feder, 2002; Gavrillets, 2003; Nosil *et al.*, 2009). In this regard, geographic modes of speciation may often be mixed, with important elements evolving during different time periods, partially in sympatry and partially during periods with a degree of geographic isolation (Feder *et al.*, 2003; Rundle & Schluter, 2004; Mallet, 2005). Work by Fry (2003) has also shown that selection coefficients facilitating later stages of sympatric speciation, e.g. strong assortative mating, can often be smaller than those required to initiate ecological differentiation in the face of gene flow. Similarly, deleterious hybrid sterility and inviability probably evolve as by-products of selection for something else, and provided their within-population selective advantage is higher than the value of m between habitats, then such barriers may also evolve in sympatry. If we have mosaic sympatry with $m \ll 0.5$, sympatric speciation may take place much more readily than generally appreciated (Mallet, 2005). We therefore argue that most of the objections raised by Mayr (1942, 1947, 1963) are today empirically as well as theoretically negated, and that sympatric processes, in Mayr's original sense of the term, are likely to be nontrivial contributors to the genesis of biodiversity and the tangled bank of life.

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