SHORT COMMUNICATION

Pattern, process and geographic modes of speciation

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Introduction

Sympatric speciation has been fascinating and controversial because the evolution of two distinct gene pools is hampered by sexual reproduction, which tends to homogenize genetic variation among individuals. However, there is not a simple mapping between the spatial pattern of sympatry (literally, being in the same place) and the processes of gene flow and recombination. As a consequence, investigators using a biogeographic definition of sympatric speciation might appear to come to different conclusions than those using population genetic processes to define sympatric speciation. In addition, it has become increasingly clear that the classification of speciation as allopatric, parapatric or sympatric is an artificial subdivision of a continuum and misses many potentially important nuances (Endler, 1977; Rice & Hostert, 1993; Schluter, 2001; Gavrilets, 2003; Coyne & Orr, 2004; Xie et al., 2007). In recognition of this, and to avoid further confusion arising from different usage of the terms, we and others have advocated research that emphasizes modelling and estimating important parameters for describing the process of divergence, rather than evaluating criteria for classifying geographic patterns (Kirkpatrick & Ravigné, 2002; Dieckmann et al., 2004; Bolnick & Fitzpatrick, 2007; Butlin et al., 2008; Fitzpatrick et al., 2008).

Mallet et al. (2009) promote a different view. Although they agree that the traditional taxonomy depends on ‘artificially discrete categories’ and the most precise definitions often imply absurd empirical standards, they advocate retaining a geographic framework chosen such that ‘sympatric speciation’ more or less common does not constitute scientific progress. Advances in the study of speciation have come from studies of the processes that constrain or promote divergence, and how they are affected by geography.

Keywords:
allopatry;
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ecological speciation;
gene flow;
migration rate;
parapary;
selection;
sympatry.

Abstract

The tradition of classifying cases of speciation into discrete geographic categories (allopatric, parapatric and sympatric) fuelled decades of fruitful research and debate. Not surprisingly, as the science has become more sophisticated, this simplistic taxonomy has become increasingly obsolete. Geographic patterns are now reasonably well understood. Sister species are rarely sympatric, implying that sympatric speciation, its most general sense, is rare. However, sympatric speciation, even in its most restricted population genetic sense, is possible. Several case studies have demonstrated that divergence has occurred in nature without geographic barriers to gene flow. Obviously, different sets of criteria for sympatric speciation will lead to different numbers of qualifying cases. But changing the rules of nomenclature to make ‘sympatric speciation’ more or less common does not constitute scientific progress. Advances in the study of speciation have come from studies of the processes that constrain or promote divergence, and how they are affected by geography.

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divergence with gene flow rather than as cases that pass or fail a set of criteria for ‘sympathy’ or ‘sympatric speciation’.

**What have we learned in 60 years?**

The main reason sympatric speciation was controversial for so long is not geography. It was controversial on theoretical and experimental grounds because gene flow tends to constrain divergence (Dobzhansky, 1937; Wright, 1951; Felsenstein, 1981; Slatkin, 1987; Rice & Hostert, 1993) and most evolutionary biologists were convinced by Mayr and others (Dobzhansky, 1937; Mayr, 1942, 1963; Muller, 1942; Futuyma & Mayer, 1980; Felsenstein, 1981; Slatkin, 1987; Rice & Hostert, 1993; Coyne & Orr, 2004) that intrinsic barriers to hybridization were unlikely to evolve without the help of extrinsic barriers – most notably physical geographic barriers to dispersal. It has been noted many times that environmental induction can have the same effect as a physical barrier, if for example plants on different soil types flower at different times (West-Eberhard, 1989; Kirkpatrick & Ravigné, 2002; Coyne & Orr, 2004; Gavrilets & Vose, 2007). Examples of genetic isolation owing to environmental induction would contradict the assertion that geographic barriers to dispersal are necessary for speciation, but they do not contradict the idea that gene flow prevents divergence and that speciation might generally require extrinsic constraints on gene flow. Although it makes no geographic sense to categorize such examples as ‘allopatric speciation’, it is important to recognize that environmentally induced barriers to interbreeding and physical barriers to dispersal can have equivalent effects on gene flow. So too, it makes no sense to use such examples to contradict the classic argument against sympatric speciation. The controversy over the feasibility or likelihood of sympatric speciation has been centred on the processes of gene flow and selection, not on geographic pattern (range overlap or distance) per se.

Mathematical analyses debunked the simple idea that divergence with gene flow is impossible by confronting the central argument that interbreeding constrains divergence to such an extent that intrinsic isolating mechanisms are unlikely to evolve. The most powerful way to make the argument that divergence with gene flow is possible is to model speciation from a panmictic ancestral population, because this gives gene flow the maximum possible leverage. The theoretical question is now settled: natural selection can overcome the homogenizing processes of gene flow and recombination, and produce distinct, isolated gene pools without the intervention of extrinsic barriers (Turelli et al., 2001; Gavrilets, 2003, 2004; Coyne & Orr, 2004). The conditions for sympatric speciation identified from theoretical research are: (1) strong combined effects of disruptive selection and nonrandom mating, (2) strong association between genes affecting fitness and genes affecting nonrandom mating, (3) high levels of genetic variation and (4) minimal costs of being choosy (Gavrilets, 2005). How commonly these conditions exist in nature is an empirical issue.

Bolnick & Fitzpatrick (2007) considered alternatives for assessing the prevalence of sympatric speciation. Counting published examples was unworkable because of an obvious publication bias and ambiguity about which examples should count owing to variation in definitions, criteria and credibility. Age-range correlation (Berlocher, 1998; Barraclough & Vogler, 2000; Berlocher & Feder, 2002) was also determined to be frustratingly inconclusive (Fitzpatrick & Turelli, 2006). The best evidence comes from the geographic relationships of sister species: Sympatric speciation, by any concept or criterion, should generate sympatric sister species. Of 309 sister species (mostly vertebrate animals) considered in the speciation literature (Lynch, 1989; Berlocher, 1998; Barraclough & Vogler, 2000; Coyne & Price, 2000; Fitzpatrick & Turelli, 2006), less than 10% were highly sympatric (≥90% range overlap) and over 70% were entirely allopatric (zero range overlap). On this basis, Bolnick & Fitzpatrick (2007) cautiously concluded that sympatric speciation is probably rare. Bolnick & Fitzpatrick (2007) noted that studies of range overlap have not been conducted in the two groups thought most likely to undergo sympatric speciation, phytophagous insects and lacustrine fishes. If the trend holds true in these groups, it is hard to imagine any way to redefine sympatric speciation that will make it commonplace.

**Arguments for retaining a geographic classification**

Coyne & Orr (2004) favour the geographic classification for three reasons (p. 85). First, biogeography can limit the range of evolutionary forces relevant to divergence. When populations are allopatric, gene flow is largely irrelevant and any process that causes divergence can result in distinctive forms meeting any criteria for species classification given enough time. On the contrary, sympatric and parapatric speciation usually require divergent forces to overcome recombination and gene flow. Second, they say that alternative classification schemes require consideration of biogeography (again, because of its association with gene flow). Finally, they find it easier to ascertain the geographic mode of speciation than to elucidate the genetic basis or evolutionary forces promoting divergence.

Coyne & Orr (2004) did more to promote research on sympatric speciation than anyone else in recent years. By proposing allopatric speciation as a null hypothesis and writing down a set of criteria for classifying a case study as sympatric speciation, they issued a challenge that has been answered (to one degree or another) by several research groups, although whether or not each criterion is satisfied in each case can still be contested (Schlieven
Empirical examples documenting the likely occurrence of divergence with gene flow now abound in the literature (Bolnick & Fitzpatrick, 2007). But if the important question is ‘what is the frequency of sympatric speciation?’, each new example adds little to our knowledge, especially if we refuse to agree on what constitutes a credible example (and we recognize that no one bothers to publish another example of allopatric speciation). Empirical research focused on specific study systems has advanced our understanding of evolution and biodiversity, not by falling neatly into allopatric, parapatric and sympatric bins, but by exposing the rich variety of genetic, ecological and geological processes that interact to cause and constrain divergence.

Butlin et al. (2008) made similar arguments against the geographic classification, pointing out that it artificially divides a continuum, draws too much focus towards the extremes (sympatric and allopatric) and distracts attention from other important questions. They recognized that the timescale of speciation often makes it impossible to determine whether Coyne & Orr’s (2004) criteria are TRUE. Instead, Butlin et al. (2008) recommended asking three questions about any temporal snapshot of a speciation process: (1) What is the spatial context? (2) What is causing divergence? (3) What is the genetic basis of biological barriers to gene flow? We are somewhat more optimistic than Butlin et al. (2008) regarding the value of trying to understand how divergence might have initiated in the past and how it might progress in the future, at least in theory (Gavrilets & Vose, 2007; Gavrilets et al., 2007).

Mallet et al. state that they ‘are interested in the allopatry vs. sympathy question because we would like to estimate the degree to which speciation depends on natural selection and the biology of the organism in continuous natural populations, compared to the degree to which nonbiological causes must be introduced.’ In our opinion, the ‘allopatry vs. sympathy’ question is a distraction that could be positively misleading if the real goal is to understand the influence of natural selection on divergence. If sympatric speciation is rare, it does not follow that natural selection rarely promotes divergence; selection can be a critical cause of divergence and reproductive isolation even when gene flow is negligible (Funk, 1998; Schluter, 2001, 2009; Fitzpatrick, 2002). Conversely, if sympatric speciation is defined broadly to include cases in which environmental induction reduced gene flow, then divergent selection is not necessary to explain all cases of sympatric speciation.

We argued (Fitzpatrick et al., 2008) that the allopatric–parapatric–sympatric classification of speciation is useful in its representation of biogeographic pattern, but not evolutionary process. Turning Coyne & Orr’s (2004) statement around, a biogeographic classification scheme still requires consideration of the actual evolutionary forces and genetics causing divergence. In addition, we suggested 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.’ The discussion of the relationship between spatial population genetics and the geographic pattern ‘sympathy’ by Mallet et al. help illustrate this point.

Mallet et al. propose a ‘spatial population genetic definition of sympathy’ that attempts to extend the concept of sympathy to individual organisms in a continuous population. Following Poulton (1903), sympathy usually means ‘the state of being in the same place’. Sympathy describes the geographic relationship of two or more things and is usually used in reference to groups such as populations or taxonomic species (Butlin et al., 2008). Humans, House Sparrows and Taraxacum erythrospermum are sympatric regardless of how rarely they interbreed. That is, sympathy is a spatial pattern that includes no assumptions about the process of gene flow (Fitzpatrick et al., 2008). Mallet et al. propose that individuals in a population be considered sympatric (‘in the same place’) if they are within a radius of $kr$, with $k$ small enough that mating between individuals born that far apart is not too unlikely. Although we question the value of a definition that requires an arbitrary criterion ($k$), we think further refinement of these ideas might be a valuable way to relate the concepts of grain, dispersal, and gene flow (e.g. Slatkin, 1973).

Wright (1943, 1946) invented the concept of the genetic neighbourhood of an individual to approximate the group from which its ‘parents may be considered as if drawn at random’ (Wright, 1943: p. 117). Thus, it includes both distance and the assumption of genetic compatibility. A horse and rider are not in each other’s genetic neighbourhoods although they are spatially inseparable; likewise, environmentally induced differences – e.g. learning a different courtship song (Grant & Grant, 1997) – can place spatially proximate individuals in different genetic neighbourhoods. Therefore, the relationships between dispersal, the grain of ecological variation and the probability of interbreeding still need to be clarified in order to understand the significance of geographic structure for evolutionary divergence.

Mallet et al. contrast their definition of sympathy with what they call a ‘demic definition’, but we find this misleading for three reasons. First, what they are really objecting to (we think) is not a definition of ‘sympathy’ but a set of definitions of ‘sympatric speciation’ that specify random mating within an ancestral population as an initial condition [only one of the population genetic definitions quoted by Fitzpatrick et al. (2008) used the imagery of demes]. Second, they portray their view as inseparable; likewise, environmentally induced differences – e.g. learning a different courtship song (Grant & Grant, 1997) – can place spatially proximate individuals in different genetic neighbourhoods. Therefore, the relationships between dispersal, the grain of ecological variation and the probability of interbreeding still need to be clarified in order to understand the significance of geographic structure for evolutionary divergence.

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setting \( k = 2 \), but this generates the same kind of empirical stalemate as other criteria that demand precise knowledge of initial conditions. Finally, the definition of Gavrilets (2003) is applicable to both demic and continuous population structures, so labelling it as ‘demic’ is not justified. In contrast, the language used by Mallet et al. in their Table 1 – ‘distance between populations’ – is itself ‘demic’ without being explicitly genetic.

Defining sympatry is not the same as defining ‘sympatric speciation’ or setting criteria for empirical evidence of it. Sympatry is a pattern; sympatric speciation is a process (or class of processes). If we interpret Mallet et al. correctly, their preference is that the initial conditions for ‘sympatric speciation’ be more inclusive than the extreme requirement of panmixia. However, (as explained above) even the extremely inclusive view of sympatric speciation as ‘any process that gives rise to sympatric sister species’ leads to the conclusion that sympatric speciation is rare in nature.

**Why is it preferable to focus on process?**

Mayr has been answered. Sympatric speciation, in its most restrictive population genetic sense, is theoretically possible. Evidence of divergence with gene flow is common enough to support a steady stream of papers celebrating the refutation of the now thoroughly discredited view that geographic isolation is necessary for speciation. Little new can be gained by assigning category labels to case studies, but we are enriched by detailed analyses of spatial, genetic and ecological variables affecting the evolution and maintenance of distinct forms.

In reviewing their own research, Mallet et al. do not make strong claims for classifying each case as sympatric speciation, nor do they illustrate how their ‘spatial population genetic definition of sympatry’ should be implemented (no estimates of \( \sigma_x \) or genetic neighbourhood size are provided). Instead, they directly pursue questions about the causes and strengths of selection, magnitude of gene flow (several estimates of the demic gene flow parameter \( m \) are given) and intervention of historical biogeographic changes.

**Apple maggots and speciation mode plurality**

For decades, *Rhagoletis pomonella* has been the premier example of sympatric speciation (Bush, 1969; Feder, 1998; Coyne & Orr, 2004). But some of the most interesting recent research on the group has revealed a more complex scenario with a potentially crucial predation (diapause phenology appropriate for apple infestation) arising in a disjunct population in Mexico 1–2 million years ago (Feder et al., 2003; Xie et al., 2007). Thus, by Coyne & Orr’s (2004) criterion 4, this example is demonstrably not sympatric speciation. Does this mean decades of research on speciation in *Rhagoletis* is without merit? Do we need a new label (‘allo-sympatric speciation’) or a new set of criteria to keep this body of research interesting? We think *Rhagoletis* remains a very important study system for helping to understand the influence of historical biogeography, contemporary spatial structure, natural selection, and gene flow on the origin and maintenance of biological diversity. How we choose to label it does not change the facts or their biological significance.

**Sympatric cichlids in a crater lake**

Barluenga et al. (2006) described ecological and genetic differentiation between the endemic Arrow cichlid (*Amphilephus zaliosus*) and the widespread Midas cichlid (*A. citrinellus*) in Lago Apoyo, Nicaragua. The taxa are sympatric (found together at the same sampling localities throughout the lake) and mate assortatively (Baylis, 1976). Analyses of mtDNA data were consistent with a single invasion by *A. citrinellus* and later evolution of *A. zaliosus* within Lago Apoyo (Barluenga et al., 2006), although microsatellite analysis indicated that Lago Apoyo *A. citrinellus* were intermediate between Lago Nicaragua *A. citrinellus* and *A. zaliosus*, a pattern consistent with hybridization between a second wave of *A. citrinellus* and the established endemic *A. zaliosus* (Schliewen et al., 2006). Gavrilets et al. (2007) showed that spatial structure within the lake could have been important in promoting speciation, even with levels of dispersal high enough to prevent significant differentiation at neutral loci. Mallet et al. remarked that, in this case, ‘complete panmixia (\( m = 0.5 \)) seems very unlikely’. If we choose to label the case as ‘sympatric speciation’ the question remains how important were divergent selection, gene flow, and mating behaviour (and their underlying genetics) in the origin of *A. zaliosus*?

**Walking-stick insects in a geographic mosaic**

Divergence between host ecotypes of *Timema cristinae* is highlighted as an example of research on the tension between gene flow and divergent selection. Gene flow between populations living on *Ceanothus* and on *Adenostoma* host plants varies over an order of magnitude and has been clearly documented as constraining adaptive divergence and preventing speciation (Nosil & Crespi, 2004; Nosil, 2009). Nosil’s research is exemplary for its integrated studies of ecology, selection and gene flow. However, it has not been widely discussed as a possible example of ‘sympatric speciation’, and it is not clear that the ecotypes would be classified as sympatric under the \( k_x \) criterion.

**Larch budmoths**

Host races of *Zeiraphera diniana* using larch, pine and spruce trees are unambiguously sympatric: their geo-
graphic ranges overlap, specimens can be found together on the same tree and hybrids are produced in nature (Emelianov et al., 1995, 2001, 2004). The forms are widespread and migratory, making both panmixia and geographic isolation extremely unlikely; Mallet et al. portray the case as inconclusive with respect to classification as ‘sympatric speciation’ or not. To leave it as an inconclusive case misses the great value of the work. Emelianov and coworkers have estimated how much the evolution (or induction) of host choice is likely to affect local gene flow (Emelianov et al., 2003), making this an excellent example of a ‘magic trait’ that simultaneously promotes ecological performance and reproductive isolation (Gavrilets, 2004).

In three of the cases discussed (Rhagoletis, Timema and Zeiraphera), the divergent clusters of organisms under study have not been classified as separate taxonomic species, leading Mallet et al. to point out another major problem for assessing the prevalence of modes of speciation. Even if sympatric speciation is defined only by the result of sympatric sister species, different taxonomic criteria might lead different investigators to different conclusions (Agapow et al., 2004; Isaac et al., 2004). Here again, we find support for the recommendation to emphasize the study of process rather than classification of pattern.

Conclusion
We now have both a solid mathematical theory of speciation (Gavrilets, 2004) and a wealth of empirical data (Coyne & Orr, 2004; Bolnick & Fitzpatrick, 2007). As a result, geographic patterns of speciation are well-understood. Speciation occurs across the range of spatial contexts summarized by the allopatric to sympatric continuum, but most speciation is associated with geographic isolation. Speciation occurs across the range of spatial contexts summarized by the allopatric to sympatric continuum, but most speciation is associated with geographic isolation. Speciation (Gavrilets, 2004) and a wealth of empirical models and empirical evidence. Speciation becomes the most important way to classify speciation? Philos. Trans. R. Soc. Lond. B Biol. Sci. 27: 2997–3007.


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