

SHORT COMMUNICATION

Pattern, process and geographic modes of speciation

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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, in 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.

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 is likely to be more common than generally assumed'. Coyne & Orr (2004) also favour the geographic classification (albeit with a different emphasis), claiming that the geographic mode of speciation can be identified and is useful because the relationship between geography and gene flow has clear implications for the nature and strength of the processes contributing to divergence. Here, we briefly review some major generalizations that can be drawn from decades of research on the geographic modes of speciation. Then we discuss arguments in favour of continuing to classify speciation as allopatric, parapatric, or sympatric. We end by arguing that the studies discussed by Mallet *et al.* might be better appreciated as detailed analyses of

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divergence with gene flow rather than as cases that pass or fail a set of criteria for 'sympatry' 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; Gavrillets & 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; Gavrillets, 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 (Gavrillets, 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 ($\geq 90\%$ 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 (Schliewen

et al., 2006; Stuessy, 2006). 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. 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 to the degree to which nonbiological causes must be introduced.’ In our opinion, the ‘allopatry vs. sympatry’ 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 ‘sympatry’ by Mallet *et al.* help illustrate this point.

Mallet *et al.* propose a ‘spatial population genetic definition of sympatry’ that attempts to extend the concept of sympatry to individual organisms in a continuous population. Following Poulton (1903), sympatry usually means ‘the state of being in the same place’. Sympatry 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, sympatry 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 $k\sigma_x$ 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 sympatry 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 ‘sympatry’ 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 more precise, but their criterion of ‘distance between populations $< k\sigma_x$ where k is a small number’ is patently less precise than $m = 0.5$ (Coyne & Orr, 2004) or ‘mating is random with respect to the birthplace of the mating partners’ (Gavrilets, 2003). We could be more precise by

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 Gavrillets (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 σ_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 preadaptation (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 (*Amphilophus zalius*) 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. zalius* 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. zalius*, a pattern consistent with hybridization between a second wave of *A. citrinellus* and the established endemic *A. zalius* (Schliewen *et al.*, 2006). Gavrillets *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. zalius*?

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 $k\sigma_x$ 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 separation. The prevalence of 'sympatric speciation' is a poor proxy for the relative importance of s and m . This is especially true if 'sympatric speciation' is defined to include cases where spatial structure severely limits gene flow in the first place. Many investigators (e.g. Mayr, 1942) have pointed out that ecology might be a critical driver of divergence between isolated populations, and mutation and drift alone can result in the emergence of reproductively isolated groups in a spatial continuum (Gavrilets *et al.*, 2000; Hoelzer *et al.*, 2008; de Aguiar *et al.*, 2009). There is not a simple relationship between pattern and process, and we maintain that progress in understanding the evolutionary origin and maintenance of biological diversity will come most efficiently from evaluating the spatial, ecological and genetic factors affecting divergence.

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References

- Agapow, P.-M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C. & Purvis, A. 2004. The impact of species concept on biodiversity studies. *Q. Rev. Biol.* **79**: 161–179.
- de Aguiar, M.A.M., Baranger, M., Baptestini, E.M., Kaufman, L. & Bar-Yam, Y. 2009. Global patterns of speciation and diversity. *Nature* **460**: 384–387.
- Barluenga, M., Stolting, K.N., Salzburger, W., Muschick, M. & Meyer, A. 2006. Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature* **439**: 719–723.
- Barracough, T.G. & Vogler, A.P. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *Am. Nat.* **155**: 419–434.
- Baylis, J.R. 1976. A quantitative study of long-term courtship: I. Ethological isolation between sympatric populations of the Midas cichlid, *Cichlasoma citrinellum*, and the arrow cichlid, *C. zalosium*. *Behaviour* **59**: 59–69.
- Berlacher, S.H. 1998. Can sympatric speciation be proven from phylogenetic and biogeographic evidence? In: *Endless Forms: Species and Speciation* (D.J. Howard & S.H. Berlacher, eds), pp. 99–113. Oxford University Press, London/New York.
- Berlacher, S.H. & Feder, J.L. 2002. Sympatric speciation in phytophagous insects: moving beyond controversy? *Annu. Rev. Entomol.* **47**: 773–815.
- Bolnick, D.I. & Fitzpatrick, B.M. 2007. Sympatric speciation: models and empirical evidence. *Annu. Rev. Ecol. Evol. Syst.* **38**: 459–487.
- Bush, G.L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* **23**: 237–251.
- Butlin, R., Galindo, J. & Grahame, J.W. 2008. Sympatric, parapatric or allopatric: the most important way to classify speciation? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **27**: 2997–3007.
- Coyne, J.A. & Orr, H.A. 2004. *Speciation*. Sinauer Association, Sunderland, MA.
- Coyne, J.A. & Price, T.D. 2000. Little evidence for sympatric speciation in island birds. *Evolution* **54**: 2166–2171.
- Dieckmann, U., Tautz, D., Doebeli, M. & Metz, J.A.J. 2004. Epilogue. In: *Adaptive Speciation* (U. Dieckmann, D. Tautz, M. Doebeli & J.A.J. Metz, eds), pp. 380–394. Cambridge University Press, Cambridge.
- Dobzhansky, T. 1937. *Genetics and the Origin of Species*. Columbia University Press, New York.
- Emelianov, I., Mallet, J. & Baltensweiler, W. 1995. Genetic differentiation in *Zeiraphera diniana* (Lepidoptera, Tortricidae, the larch budmoth): polymorphism, host races or sibling species. *Heredity* **75**: 416–424.
- Emelianov, I., Dres, M., Baltensweiler, W. & Mallet, J. 2001. Host-induced assortative mating in host races of the larch budmoth. *Evolution* **55**: 2002–2010.
- Emelianov, I., Simpson, F., Narang, P. & Mallet, J. 2003. Host choice promotes reproductive isolation between host races of the larch budmoth *Zeiraphera diniana*. *J. Evol. Biol.* **16**: 208–218.
- Emelianov, I., Marec, F. & Mallet, J. 2004. Genomic evidence for divergence with gene flow in host races of the larch budmoth. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: 97–105.
- Endler, J.A. 1977. *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton.

- Feder, J.L. (1998) The apple maggot fly, *Rhagoletis pomonella* flies in the face of conventional wisdom about speciation? In: *Endless Forms: Species and Speciation* (D.J. Howard & S.H. Berlocher, eds), pp. 130–144. Oxford University Press, New York.
- Feder, J.L., Berlocher, S.H., Roethele, J.B., Dambroski, H., Smith, J.J., Perry, W.L., Gavrilovic, V., Filchak, K.E., Rull, J. & Aluja, M. 2003. Allopatric origins for sympatric host-plant shifts and race formation in *Rhagoletis*. *Proc. Nat. Acad. Sci. USA* **100**: 10314–10319.
- Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals. *Evolution* **35**: 124–138.
- Fitzpatrick, B.M. 2002. Molecular correlates of reproductive isolation. *Evolution* **56**: 191–198.
- Fitzpatrick, B.M. & Turelli, M. 2006. The geography of mammalian speciation: mixed signals from phylogenies and range maps. *Evolution* **60**: 601–615.
- Fitzpatrick, B.M., Fordyce, J.A. & Gavrillets, S. 2008. What, if anything, is sympatric speciation? *J. Evol. Biol.* **21**: 1452–1459.
- Funk, D.J. 1998. Isolating a role for natural selection in speciation: host adaptation and sexual isolation in *Neochlamis bebbianae* leaf beetles. *Evolution* **52**: 1744–1759.
- Futuyma, D.J. & Mayer, G.C. 1980. Non-allopatric speciation in animals. *Syst. Zool.* **29**: 254–271.
- Gavrilets, S. 2003. Models of speciation: what have we learned in 40 years? *Evolution* **57**: 2197–2215.
- Gavrilets, S. 2004. *Fitness Landscapes and the Origin of Species*. Princeton University Press, Princeton.
- Gavrilets, S. 2005. “Adaptive speciation” – it is not that easy: a reply to Doebeli *et al.* *Evolution* **59**: 696–699.
- Gavrilets, S. & Vose, A. 2007. Case studies and mathematical models of ecological speciation. 2. Palms on an oceanic island. *Mol. Ecol.* **16**: 2910–2921.
- Gavrilets, S., Li, H. & Vose, M.D. 2000. Patterns of parapatric speciation. *Evolution* **54**: 1126–1134.
- Gavrilets, S., Vose, A., Barluenga, M., Salzburger, W. & Meyer, A. 2007. Case studies and mathematical models of ecological speciation. 1. Cichlids in a crater lake. *Mol. Ecol.* **16**: 2893–2909.
- Grant, P.R. & Grant, B.R. 1997. Hybridization, sexual imprinting, and mate choice. *Am. Nat.* **149**: 1–28.
- Hoelzer, G.A., Drewes, R., Meier, J. & Doursat, R. 2008. Isolation-by-distance and outbreeding depression are sufficient to drive parapatric speciation in the absence of environmental influences. *PLoS Comput. Biol.* **4**: e1000126.
- Isaac, N.J.B., Mallet, J. & Mace, G.M. 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends Ecol. Evol.* **19**: 464–469.
- Kirkpatrick, M. & Ravigné, V. 2002. Speciation by natural and sexual selection: models and experiments. *Am. Nat.* **159**: S22–S35.
- Lynch, J.D. (1989) The gauge of speciation: on the frequency of modes of speciation. In: *Speciation and its Consequences*, (D. Otte & J.A. Endler, eds), pp. 527–553. Sinauer Associates, Sunderland, MA.
- Mallet, J., Meyer, A., Nosil, P. & Feder, J.L. 2009. Space, sympatry and speciation. *Journal of Evolutionary Biology*, doi: 10.1111/j.1420-9101.2009.01816.x.
- Mayr, E. 1942. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. Columbia University Press, New York.
- Mayr, E. 1963. *Animal Species and Evolution*. Belknap, Cambridge.
- Muller, H.J. 1942. Isolating mechanisms, evolution and temperature. *Biol. Symp.* **6**: 71–125.
- Nosil, P. 2009. Adaptive population divergence in cryptic color-pattern following a reduction in gene flow. *Evolution* **63**: 1902–1912.
- Nosil, P. & Crespi, B.J. 2004. Does gene flow constrain divergence or vice versa? A test using ecomorphology and sexual isolation in *Timema cristinae* walking-sticks. *Evolution* **58**: 101–112.
- Poulton, E.B. 1903. What is a species? *Trans. Entomol. Soc. London* **1903**: 77–116.
- Rice, W.R. & Hostert, E.E. 1993. Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* **47**: 1637–1653.
- Schliwien, U., Kocher, T., McKaye, K.R., Seehausen, O. & Tautz, D. 2006. Evidence for sympatric speciation? *Nature* **444**: E12–E13.
- Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.* **16**: 372–380.
- Schluter, D. 2009. Evidence for ecological speciation and its alternative. *Science* **323**: 737–741.
- Slatkin, M. 1973. Gene flow and selection in a cline. *Genetics* **75**: 733–756.
- Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* **236**: 787–792.
- Stuessy, T.F. 2006. Evolutionary biology: sympatric plant speciation in islands? *Nature* **443**: E12.
- Turelli, M., Barton, N.H. & Coyne, J.A. 2001. Theory and speciation. *Trends Ecol. Evol.* **16**: 330–343.
- West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. *Ann. Rev. Ecol. Syst.* **20**: 249–278.
- Wright, S. 1943. Isolation by distance. *Genetics* **28**: 114–138.
- Wright, S. 1946. Isolation by distance under diverse systems of mating. *Genetics* **31**: 39–59.
- Wright, S. 1951. The genetical structure of populations. *Ann. Eugen.* **1**: 323–334.
- Xie, X.F., Rull, J., Michel, A.P., Velez, S., Forbes, A.A., Lobo, N.F., Aluja, M. & Feder, J.L. 2007. Hawthorn-infesting populations of *Rhagoletis pomonella* in Mexico and speciation mode plurality. *Evolution* **61**: 1091–1105.

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