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Speciation by selection: A framework for understanding ecology's role in speciation

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Abstract Speciation research during the last several decades has confirmed that natural selection frequently drives the generation of new species. But how does this process generally unfold in nature? We argue that answering this question requires a clearer conceptual framework for understanding selection's role in speciation. We present a unified framework of speciation, providing mechanistic descriptions of fundamentally distinct routes to speciation, and how these may interact during lineage splitting. Two major categories are recognized: reproductive isolation resulting from (1) responses to selection, "speciation by selection," or (2) non-selective processes, "speciation without selection." Speciation by selection can occur via three mechanisms: (1) similar selection, (2) divergent selection, and (3) reinforcement selection. Understanding ecology's role in speciation requires uncovering how these three mechanisms contribute to reproductive isolation, and their relative importance compared to non-selective processes, because all three mechanisms can occur side-by-side during speciation. To accomplish this, we highlight examination of groups of organisms inhabiting replicated environmental gradients. This scenario is common in nature, and a large literature illustrates that both parallel and non-parallel responses to similar environments are widespread, and each can result in speciation. This recognition reveals four general pathways of speciation by similar or divergent selection—parallel and nonparallel responses to similar and divergent selection. Altogether, we present a more precise framework for speciation research, draw attention to some under-recognized features of speciation, emphasize the multidimensionality of speciation, reveal limitations of some previous tests and descriptions of speciation mechanisms, and point to a number of directions for future investigation [*Current Zoology* 59 (1): 31–52, 2013].

Keywords Speciation, Ecological speciation, Mutation order, Reinforcement, One-allele mechanism, Reproductive isolation

1 Background

Evidence accumulated since *On the Origin of Species* (Darwin, 1859) leads to the conclusion that natural selection often plays an important role in the speciation process (e.g., Coyne and Orr, 2004; Grant and Grant, 2008; Price, 2008; Schluter, 2009; Nosil, 2012). Thus, to a large extent, Darwin (1859) was right when he posited in his long argument that adaptation by natural selection often provides the ultimate cause of the origin of new species. While today we recognize the central importance of reproductive isolation in the speciation process, and are gaining an understanding of genetic complexities involved in adaptation and speciation that would probably astound Darwin, support for his assertion regarding the importance of natural selection in speciation has only gained in strength over the years (Coyne and Orr, 2004; Reznick, 2009; Schluter, 2009).

In a recent review and synthesis, Schluter (2009) pointed out that the question of the day is no longer whether selection plays an important role in the origin of species, but rather how selection leads to speciation. We need to know what types of selection, what kinds of selective agents, what types of traits, what sorts of genes, and what kinds of isolating barriers are involved in the generation of new species. We additionally need to understand the relative importance of alternative pathways to reproductive isolation during speciation—both those involving selection and those not involving selection—as multiple mechanisms may contribute to reproductive isolation during the speciation process (even simultaneously). To this end, a clear conceptual framework for understanding selection's role in speciation is paramount, because speciation research requires a framework that provides mechanistic descriptions of alternative routes to speciation and coherently organizes fundamentally distinct mechanisms of speciation. While a vast literature evinces the considerable attention speciation research has received so far, we believe that an improved framework that is both thorough and lucid

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will prove critical in advancing our understanding of the speciation process. We attempt to present such a framework here, which should further aid in directing future research, as it highlights some under-recognized features of speciation, emphasizes the multidimensionality of speciation, and reveals shortcomings and imprecisions of some previous tests and descriptions of speciation mechanisms.

We begin by illustrating that speciation can be conceptualized as a three-step process (Box 1), beginning with an evolutionary mechanism driving evolutionary change, subsequently leading to increased levels of reproductive isolation among populations, and eventually speciation. Under this conceptualization, the first component of speciation—an evolutionary mechanism—can be broken down into two categories: (1) mechanisms by which speciation results from selection, "speciation by selection," and (2) mechanisms that do not involve selection, "speciation without selection." The focus of this study is on the former, but because the explicit description of these two categories is novel to this paper, we elucidate both below. We then spend the remainder of the paper investigating the varied ways that speciation by selection may occur, and how future research can gain critical insights into the process.

2 Speciation by Selection and Speciation without Selection: Clarifying Ecology's Role in Speciation

We are most interested here in the ways that selection can drive reproductive isolation, i.e., the role of ecology in speciation. We use *ecology* in a broad sense, including any interactions among organisms and their environments that result in selection (nonrandom association between phenotype/genotype and fitness). This includes interactions among sexes and genetic elements, and thus encompasses natural and sexual selection, as well as social selection more broadly (sensu West-Eberhard, 1983). For ecology to facilitate speciation, it must elicit a response to selection that results in increased levels of reproductive isolation among populations. This can occur either directly, when selection on some trait/gene pleiotropically influences reproductive isolation or when selection favors reproductive isolation per se, or indirectly, when selection acts on some trait/gene that is in linkage disequilibrium with a trait/gene that influences reproductive isolation. We refer to this process, in which reproductive isolation evolves as a result of evolutionary responses to selection as "speciation by selection." This link between ecology and reproductive isolation distinguishes speciation by selection from other causes of speciation like genetic drift, here termed "speciation without selection." This renders "the role of ecology in speciation" synonymous with "speciation by selection." We believe this latter result will be intuitive for many researchers in the field and can help clarify current terminology and settle debates regarding when ecology is said to have played a role in speciation.

Under this perspective, ecology is involved in speciation if and only if responses to selection result in increased reproductive isolation. As a consequence, many ecological interactions important to the survival and reproduction of organisms during the speciation process will not result in increased reproductive isolation, and thus do not engender speciation by selection. For instance, ecological processes affecting geographical separation of populations or population persistence may facilitate the conditions under which speciation may occur, but these do not elicit responses to selection that increase reproductive isolation (Rundell and Price, 2009; Nosil, 2012). If selection did not prompt the evolution of the states of traits or genes that ultimately cause reproductive isolation (even if only indirectly through linkage disequilibrium), then the source of reproductive isolation is not ecological in nature; it is rather a speciation without selection process.

It is important to briefly consider the two major categories of speciation described here in relation to previous uses of these phrases, as well as another commonly used phrase, "nonecological speciation." First, speciation by selection has sometimes been used to refer specifically to ecological speciation (e.g., Kirkpatrick and Ravigne, 2002; Allender et al., 2003; Rosenblum and Harmon, 2011), which we view instead as a subset of speciation by selection processes (see below); but it has also sometimes been used in virtually the same context as that used here (e.g., Schluter, 2009). However, speciation by selection has never previously been offered as a precisely defined category of speciation. Second, the term speciation without selection has rarely been used in the literature; however, Nosil (2012) uses the term to categorize speciation mechanisms in the same way as described here. Thus, some precedence for this terminology already exists, and precisely defining the terms here should enhance clarity and aid in communication amongst speciation researchers in the future. Finally, the term nonecological speciation has been previously used to refer to various categories of speciation,

Box 1. What is speciation?

Following the Biological Species Concept (Mayr, 1942), speciation can be envisioned as a three-step process (Fig. I). First, one or more evolutionary mechanisms act on existing variation, resulting in evolutionary change (including cultural evolution). Typically, this comprises differentiation of genes or traits within or between populations, but can also result in uniformity across populations (so called "one-allele" mechanisms; Felsenstein, 1981). Second, these genes or traits subsequently result in increased reproductive isolation between populations. Third, when total reproductive isolation appears complete, speciation is said to have occurred. This three-step conceptualization highlights that understanding the speciation process requires us to understand three key things: **evolutionary mechanisms** responsible for causing changes in **genes and traits** that subsequently increase reproductive isolation among populations through a range of possible **reproductive isolating barriers**.

While each arrow in Fig. I points in the direction of "progress" toward speciation, a range of factors can influence the strength and directionality of each step. For instance, step 1 can be influenced by changes in selection, gene flow, bottleneck events, or hybridization, as well as feedback loops where changes in genes or traits modify subsequent selection. Step 2 can be modified by the nature of associations between characters and reproductive isolation (e.g., pleiotropy, linkage disequilibrium), types of isolating barriers involved (e.g., see Table 1.2 in Coyne and Orr, 2004), context dependence of links between traits and reproductive isolation, and changes in genes and traits resulting from changes in step 1. Finally, while step 3 is somewhat subjective (when divergent groups truly become "good" species can be unclear), even groups with apparently "complete" reproductive isolation can collapse back into interbreeding, or even panmictic populations, depending on the types and number of isolating barriers involved, and changes in steps 1 or 2 (e.g., Seehausen et al., 2008, Behm et al., 2010).

Importantly, this conceptual description of speciation does not refer to the geographic arrangement of populations. Despite an historical emphasis on the geography of speciation (e.g., Jordon, 1905; Allen, 1907; Mayr, 1963; Bush, 1975; Futuyma and Mayer, 1980), this factor largely influences the likelihood of speciation rather than playing a mechanistic role in the process per se (Dieckmann et al., 2004; Nosil, 2008). Thus, speciation can occur via this three-step process in any geographic context.

As is often the case in science, it is useful to categorize the speciation process into broad types of speciation so that we can more appropriately investigate the various causes and pathways of the process. Rather than categorize speciation based on geography, types of genes or traits involved, or isolating barriers, a fruitful approach to categorization is to focus on the evolutionary mechanism responsible, yielding two general categories: (1) **Speciation by Selection** and (2) **Speciation without Selection** (see Fig. I). Speciation by selection describes the evolution of reproductive isolation resulting from responses to selection, while speciation without selection describes the evolution of reproductive isolation as a result of non-selective processes (see text for details). While the two categories are conceptually distinct, both processes may contribute to speciation during population divergence.

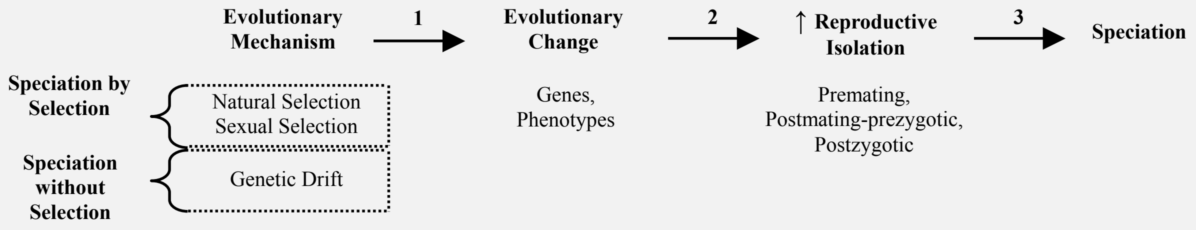


Fig. I Conceptual illustration of the three-step process of speciation

often in vague terms, and encompassing either all speciation mechanisms other than ecological speciation (e.g., Price, 2008; Rundell and Price, 2009; Nyman et al., 2010; a category which would actually include other speciation by selection processes) or strictly genetic drift (Sobel et al., 2010). We feel this term has fostered confusion in the past, and suggest researchers henceforth avoid its use and instead follow the terminology and definitions for the two categories of speciation described here.

We now briefly examine some scenarios where selection's role in speciation has previously been controversial to help solidify distinctions and utility of these two categories of speciation. First, some ecological interactions might lead to geographic isolation, for instance niche conservatism followed by climatic or geologic processes that effectively isolate populations by uninhabitable intervening habitat (Ramsey et al., 2003; Wiens, 2004; Sobel et al., 2010). However, the reduction in gene flow in this scenario results from environmental change, not any response to selection—nonetheless, there may be factors that additionally contribute to reproductive isolation under these circumstances (especially in the case of secondary contact), and they may or may not involve selection. Only if selection drives differentiation in traits leading to spatial or temporal isolation (e.g., habitat or host preference, dispersal, divergent adaptations, timing of breeding) does such separation result from speciation by selection processes. Thus, "ecogeographic isolation" as described by Sobel et al. (2010) only comprises a speciation by selection process if the genetic differences between populations that cause geographic isolation are the products of selection.

Second, evolution of traits leading to enhanced population persistence, such as local adaptation, may allow large population sizes that can better avoid extinction over long time periods. This situation promotes speciation by simply allowing enough time for reproductive isolation to evolve by some mechanism—population persistence per se does not cause reproductive isolation. Thus, traits that merely prolong the existence of populations without affecting reproductive isolation are not involved in speciation by selection.

Polyploid speciation represents a phenomenon that could, but does not necessarily, involve speciation by selection. Polyploidy is common in plants and can result in immediate reproductive isolation in the absence of any selection for polyploidy (Grant, 1981; Ramsey and Schemske, 1998; Mallet, 2007; Wood et al., 2009). While selection is not required, it may nevertheless be common during polyploid speciation. Sobel et al. (2010) argue that ecology is involved in polyploid speciation if neopolyploids have distinct ecological characters which contribute to their persistence. We contend that such circumstances only comprise speciation by selection if selection favors polyploidy—that is, if trait values conferred by polyploidization actually result in enhanced fitness, favoring their proliferation. This may occur if neopolyploids reside near a novel fitness peak (see Mallet, 2007; Sobel et al., 2010), and one putative example is found in wild yarrow, where neopolyploids appear to experience a strong fitness advantage in a novel environment (Ramsey 2011). So, neopolyploids can initiate a new, reproductively isolated population either with or without selection (Rodriguez, 1996; Ramsey and Schemske, 2002; Sobel et al., 2010), and while the action of selection seems much more likely to result in speciation under most circumstances (perhaps less so in parapatry or allopatry), further research is needed to uncover the relative frequency and strength of selection in polyploid speciation.

Homoploid hybrid speciation is another phenomenon that could, but does not necessarily, involve speciation by selection. In cases where chromosomal combinations resulting from hybridization directly increase reproductive isolation, the event resembles allopolyploidy and thus follows the description above regarding the possible involvement of selection (see Gross and Rieseberg, 2005). If hybridization does not result in any intrinsic isolation, then the distinctiveness of this phenomenon regarding its route to speciation disappears, as its uniqueness derives only from its hybrid source of genetic/phenotypic variance and not its source of reproductive isolation. In this latter scenario, any mechanism of speciation described in this paper could play an important role, whether involving selection or not.

Of the two broad categories of speciation, previous theoretical and empirical research clearly implicates speciation by selection as the category of greater importance in generating biodiversity. This is because of the wide array of conditions that allow and facilitate speciation in the presence of selection compared to the much more restrictive conditions of speciation without selection processes (e.g., Coyne and Orr, 2004; Dieckmann et al., 2004; Gavrilets, 2004; Grant and Grant, 2008; Price, 2008; Nosil, 2012). So, how can selection drive speciation and how can we test these mechanisms?

3 The Mechanisms of Speciation by Selection

We argue that there are three general mechanisms of speciation by selection, distinguished by differences in how selection acts within or between populations during speciation (Box 2). All three mechanisms of speciation by selection can occur side-by-side, or at different time-points along the continuum of speciation, or interact with each other during a given speciation event. In other words, speciation may be multidimensional, with reproductive isolation evolving via several alternative mechanisms, involving multiple traits and genes, and affecting multiple reproductively isolating barriers. Below we describe each mechanism, the ways they can operate during population divergence, and briefly assess their putative importance in speciation by selection. Then in the next section, we evaluate how multiple mechanisms may act together during speciation.

3.1 Speciation by similar selection

Similar selection pressures can elicit evolutionary responses that result in increased reproductive isolation between populations. Speciation by similar selection includes two processes: (1) mutation-order speciation and (2) one-allele mechanisms by which reproductive isolation evolves as a response to similar selection pressures across populations. Thus, there are two major ways that speciation by similar selection can occur, either through responses to similar selection pressures that are different or the same across populations.

Under one scenario, populations experiencing similar selection pressures evolve reproductive isolation by fixation of different advantageous mutations, i.e. mutation-order speciation (e.g., Mani and Clarke, 1990; Schluter, 2009; Schluter and Conte, 2009; Nosil and Flaxman, 2011). In other words, different populations essentially find different solutions to the same selective problem, which results in reproductive isolation. Although the response to selection observed in either population (i.e., fixation of mutation) would have had similar fitness in all populations (implying multiple adaptive peaks of similar height), different responses—or genetically correlated changes—are incompatible with one another, and thus populations exhibiting these equally-fit alternative responses become reproductively isolated from one another. This can occur for example, by intragenomic conflict (e.g., cytoplasmic male sterility, meiotic drive), sexual conflict, sexual (or social) selection for arbitrary traits, and alternative adaptive solutions to selection via competition, predation, parasitism, etc. (e.g., morphology, physiology) (Price, 2008; Schluter, 2009; Martin and Mendelson, 2012). Although called mutation-order speciation, referring to differences in the order of fixation of alternative mutations, this process does not require any differences in the order of appearance of mutations, and can even occur while acting only on standing genetic variation. A number of putative examples of mutation-order speciation exist (Box 2), although most examples from the wild so far center on cytoplasmic male sterility in plants or meiotic drive (e.g., Fishman and Willis, 2006; Case and Willis, 2008). The role of alternative factors in driving this process is largely unknown, as is its general importance in speciation owing to the comparatively little attention it has received to date. While not often discussed in the context of mutation-order speciation, sexual selection via Fisher's runaway sexual selection, multiple arbitrary sexual signals, or sexual conflict may often play important roles in speciation via this process (Lande, 1981; Schluter and Price, 1993; Rice, 1998; Gavrilets, 2000; Chapman et al., 2003; Rice et al., 2005). For three reasons, we believe this mechanism's importance in speciation may have been greatly underestimated so far: (1) unique responses to seemingly similar selection pressures are ubiquitous (see section 5.2 below), (2) some of the understudied factors that can lead to mutation-order speciation, like divergent preferences for arbitrary traits, sexual conflict, and many-to-one mapping of morphology to performance, are widespread, and (3) geographic separation of populations is quite common in most taxa (a great facilitator of mutation-order speciation, as gene flow could otherwise cause the spread of equally beneficial mutations across all populations). Thus, additional research into this process is greatly warranted.

Under an alternative scenario of speciation by similar selection, populations experiencing similar selection evolve reproductive isolation due to the fixation of the same allele, comprising certain cases of the so-called "one-allele mechanism" of speciation. Felsenstein (1981), and many subsequent papers (e.g., see Kirkpatrick and Ravigne, 2002; Servedio and Noor, 2003; Ortiz-Barrientos and Noor, 2005; Servedio, 2009) have discussed the intriguing possibility that assortative mating can evolve via the substitution of a single allele across multiple populations. Reproductive isolation under this scenario is theoretically much easier to evolve than in a two-allele system where recombination can inhibit linkage disequilibrium required for reproductive isolation. Most previous discussions of one-allele

Box 2. A three-mechanism framework for speciation by selection

Selection can drive speciation in three general ways: similar selection, divergent selection, and reinforcement selection (Table I). The three mechanisms are distinguished by the way selection acts during speciation. Below we discuss two key factors in understanding the likelihood and pathways of these three mechanisms, and the evidence to date for each.

Table I The three mechanisms of speciation by selection

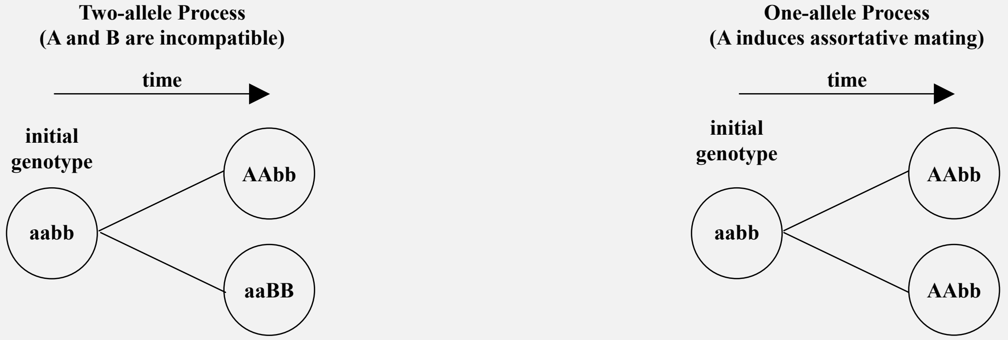
Speciation by Selection Mechanism	Common Name Used in Literature	Description
Similar Selection	Mutation Order (certain cases of) One-allele Mechanism	reproductive isolation between populations results from evolutionary responses to similar selection pressures
Divergent Selection	Ecological Speciation	reproductive isolation between populations results from evolutionary responses to divergent selection pressures
Reinforcement Selection	Reinforcement (broad sense)	reproductive isolation between populations results from selection against inter-population matings, driving prezygotic isolation

Geography of speciation by selection: One of the most important factors influencing the likelihood of speciation is geographic context, as extrinsic factors like geographic isolation among populations can greatly facilitate the evolution of reproductive isolation under many mechanisms of speciation. Speciation by similar selection may typically require allopatry, or at least considerably low levels of gene flow (for mutation-order speciation) or spatial or temporal isolation during breeding (for one-allele mechanism). Speciation by divergent selection can occur in any geographic context, although geographic separation facilitates the evolution of reproductive isolation under most circumstances. Speciation by reinforcement selection requires interaction among diverging populations, and thus can only occur in sympatry or parapatry.

Genetics of speciation by selection: The three mechanisms of speciation by selection comprise two broad pathways to speciation from a genetics perspective. That is, selection either drives (1) genetic divergence, which results in reproductive isolation, or (2) genetic uniformity, which results in reproductive isolation (Fig. I). This dichotomy captures the critical distinction between one-allele and two-allele mechanisms of speciation (Felsenstein, 1981). Just as the three selection mechanisms may occur together during a speciation event, so may the two genetic pathways; in fact, some one-allele mechanisms (e.g., assortative mating for trait A) may depend on other two-allele mechanisms (e.g., divergence in trait A) to drive reproductive isolation (Servedio, 2009).

Examples of speciation by selection: Speciation by similar selection has been demonstrated in laboratory settings, e.g., in *Escherichia coli* (Travisano et al., 1995) and *Drosophila* (Cohan and Hoffmann, 1989), but has been difficult to unequivocally demonstrate in natural populations so far (reviewed in Schluter, 2009; Nosil and Flaxman, 2011). Considerable empirical evidence exists for speciation by divergent selection (i.e., ecological speciation), including *Gasterosteus* sticklebacks (e.g., McKinnon and Rundle, 2002; Rundle and Schluter, 2004), *Timema* walking-stick insects (e.g., Nosil et al., 2002), *Littorina* snails (e.g., Johannesson et al., 2010), *Geospiza* Darwin's finches (e.g., Grant and Grant, 2008), *Anolis* lizards (e.g., Losos, 2004), *Gambusia* and *Poecilia* fishes (e.g., Langerhans et al., 2007; Tobler and Plath, 2011), among many others (reviewed in Nosil, 2012). Although considered quite controversial for some time, examples of a role for reinforcement selection in speciation (e.g., Butlin, 1987; Servedio and Noor, 2003) exists in many cases now, such as *Timema* walking-stick insects (Nosil et al., 2003), the guppy *Poecilia reticulata* (Schwartz et al., 2010), and *Spea* spadefoot toads (Pfennig, 2003).

Box 2. continued



Example Mechanisms:

- **Speciation by Similar Selection (divergent adaptations to same environment)**
- **Speciation by Divergent Selection (divergent adaptations to different environments)**
- **Speciation by Reinforcement Selection (divergent mating preferences or gamete recognition)**

Example Mechanisms:

- **Speciation by Similar Selection (reduced migration)**
- **Speciation by Divergent Selection (culturally transmitted signaling behavior)**
- **Speciation by Reinforcement Selection (self-pollination)**

Fig. I Conceptual depiction of the genetics of speciation by selection
Left panel: populations evolve reproductive isolation by fixing alternative, incompatible alleles favored by selection. Right panel: populations evolve reproductive isolation by fixing the same allele favored by selection.

mechanisms have focused on their possible role in reinforcement (which may indeed be more prevalent, see below), but a one-allele mechanism can additionally drive speciation by similar selection in the absence of reinforcement. For instance, selection could favor natal philopatry (or reduced migration/dispersal) in multiple populations for reasons such as reduced fitness of adults or offspring in surrounding habitat (but not selection against inter-population matings, which is speciation by reinforcement, see below). A single allele could cause natal philopatry, and reach fixation in all populations. Because of spatial separation of populations, strengthened by this shared response to similar selection, fixation of the same allele results in reproductive isolation between populations. Potentially common means of speciation through this process involve learning and culture, if populations exhibit differences in learned behaviors or cultural traditions that can enhance reproductive isolation without any underlying genetic change. For instance, the learned songs of birds and acoustic signals of whales and dolphins can diverge among populations even though the different dialects would have originally had equal fitness in all populations, and these differences can increase reproductive isolation (Price 2008; Danchin and Wagner, 2010; Riesch et al., 2013). While it is currently unknown how important this process may be for speciation, if future work could rule out the role of divergent selection or reinforcement in particular instances where learned behaviors affect reproductive isolation, then we could gain a better understanding of the strength and frequency of this mechanism.

3.2 Speciation by divergent selection

Divergent selection pressures can drive evolutionary responses that result in increased reproductive isolation between populations. Speciation by divergent selection represents the topic widely termed ecological speciation and has received a wealth of attention in recent years (e.g., Schluter, 2000, 2001; Rundle and Nosil, 2005; Nosil, 2012). Our definition here could be viewed as somewhat broader than what many consider ecological speciation because we are not as restrictive about what constitutes "ecologically-based" divergent selection. We view that as a somewhat subjective and tangential issue—the crux of the matter is that *divergent* selection is the ultimate cause of reproductive isolation in this process. In this case, selection favors different traits across environments, and because these traits (or genetically correlated ones) incidentally cause reproductive isolation, populations accumulate reproductive isolation as they adapt to different conditions. This is largely in line with Darwin's original conception of the origin of species: new species originated as populations acquired differential adaptations to alternative environments (Darwin, 1859). Thus, ecological speciation essentially describes the formal link between divergent selection, divergent adaptation, and reproductive isolation. Speciation by divergent selection appears to represent a common route to speciation in nature, and numerous empirical examples are known (Box 2; Nosil, 2012).

There are two general ways that divergent selection can arise: natural selection and sexual selection (Note that while previous treatments of ecological speciation typically referred to three sources of divergent selection [e.g., Schluter, 2000, 2001; Rundle and Nosil 2005; Nosil 2012], we believe only two conceptually distinct sources exist, and that reinforcement represents a mechanism distinct from divergent selection.). First, divergent *natural* selection can arise from environmental differences or inter-population interactions (excluding reinforcement). For instance, populations may adapt to different ecological conditions or respond to negative interactions with one another such as competitive or predator-prey interactions (e.g., character displacement). Second, divergent *sexual* selection can arise via sensory drive, natural selection against conspicuous sexual signals, or indicator traits. For instance, preferences and signals may diverge between different background environments to enhance signal transmission, between different predator or prey regimes in response to selection for more cryptic or conspicuous signals, or between ecological environments where condition-dependence of indicator traits differs. Either source of divergent selection can drive trait differences that result in elevated reproductive isolation among populations. Although the role of natural selection has received more attention and support to date, accumulating evidence suggests that both sources are widely important (Boughman, 2002; Rundle and Nosil, 2005; Nosil, 2012).

Speciation by divergent selection probably occurs via genetic divergence in most cases, but can also proceed via a one-allele mechanism (Box 2). For example, learned behaviors or cultural traditions can diverge between populations because of environmental differences, and these can incidentally increase reproductive isolation. Sensory drive comprises one potentially common way this can occur—learned behaviors can enhance signal transmission in different background environments, such as divergent learned songbird dialects (Boncoraglio and Saino, 2007; Price, 2008).

3.3 Speciation by reinforcement selection

Selection against inter-population matings can drive evolutionary responses that result in increased reproductive isolation (prezygotic isolation) between populations: "speciation by reinforcement selection." Only under this mechanism does selection favor reproductive isolation per se (i.e., under the other two mechanisms of speciation by selection, reproductive isolation evolves incidentally as a by-product of selection on other traits). Here we take a broad view of reinforcement (Servedio and Noor, 2003) that includes both selection for assortative mating to prevent hybridization following secondary contact (after some degree of postzygotic isolation has already evolved), as well as selection for assortative mating arising from frequency-dependent ecological interactions among diverging populations in the absence of initial allopatric divergence and secondary contact (i.e., adaptive speciation, Dieckmann et al., 2004). Selection against inter-population matings may either result from direct fitness costs to the individuals involved (e.g., injury, reduced fertility) or indirect fitness costs due to reduced fitness of hybrid offspring (i.e., reduced viability, fecundity, or ability to acquire mates). Direct costs of inter-population matings are superficially similar to other forms of antagonistic interactions among populations, but are distinct in that they arise specifically from mating and result in selection directly against hybridization. While both means of reinforcement can occur in natural systems (Nosil et al., 2007), most research has focused on indirect costs, which are generally viewed as more common. Overall, considerable evidence for speciation by reinforcement selection exists (Servedio and Noor, 2003), although we do not yet know its relative frequency and importance compared to other mechanisms.

Reinforcement has been a historically difficult-to-categorize process, as it can so obviously play a role in speciation initiated by any other process—although, as we emphasize below, this is actually true of most speciation mechanisms—and because selection can either be uniform or divergent across populations and still result in speciation by reinforcement selection. We argue that this process deserves a place as a third mechanism of speciation by selection, with the distinction here resting on the specific target of selection: selection against inter-population mating. Selection favoring assortative mating is uniform across populations in the case of a one-allele mechanism, where a single allele fixes in all populations, enhancing assortative mating by means such as adaptive habitat selection, reduced migration, self-pollination, sexual imprinting (including xenophobia), mate-choice copying, or self-referent phenotype matching (some of these will often require a two-allele mechanism via another mechanism of speciation). Perhaps more commonly, selection favoring assortative mating is divergent between populations, favoring different alleles contributing to assortative mating by means such as alternative mating preferences, host or habitat preferences, or flowering or breeding time.

It is important to point out circumstances in which speciation by reinforcement selection is not occurring despite evidence that may seem contradictory. For instance, the presence of divergent selection on mating preferences or assortment traits across populations does not imply that reinforcement selection is occurring. Reinforcement selection describes selection against inter-population matings, and so if selection favors divergent mating preferences or assortment traits for other reasons (e.g., sensory drive, direct fitness benefits of traits also used as assortment traits), then reinforcement selection is not relevant. Such a phenomenon may be common in the so-called cases of “magic traits” in speciation (reviewed in Servedio et al., 2011; Servedio and Kopp, 2012). Reinforcement selection additionally does not apply to cases where similar selection pressures drive reproductive isolation via a one-allele mechanism such as natal philopatry or reduced migration (see above), if selection did not actually act against inter-population matings per se. Further, speciation by reinforcement selection may not only increase reproductive isolation among the two focal diverging populations, but incidentally result in increased reproductive isolation between other populations in a “cascade effect” (Hoskin et al., 2005; Ortiz-Barrientos et al., 2009). This may occur, for instance, when females evolve mating preferences to reduce inter-population matings that are based on a population-specific trait that also happens to enhance sexual isolation with other populations. Under this reinforcement cascade scenario, only the reproductive isolation accumulating due to selection against inter-population matings is caused by the speciation by reinforcement selection mechanism; reproductive isolation accumulating, for instance, between one of the focal populations and other populations as a cascade effect will typically comprise a speciation by divergent selection mechanism.

4 Interplay of Speciation by Similar and Divergent Selection

While reinforcement has been widely recognized as a process that can interact with other speciation processes, mainly to facilitate the completion of speciation after it has already begun (or in conjunction with others during sympatric speciation), the other two speciation by selection mechanisms have often been discussed largely as mutually exclusive categories or as operating in an “either or” fashion. That is, researchers have sometimes attempted to determine whether similar selection or divergent selection has ultimately driven a given speciation event, when in reality this question is flawed because both mechanisms may occur together. Because of this confusion, it is worthwhile to consider similarities and dissimilarities of the two mechanisms, means of testing their importance, and evaluating how they may interact during speciation.

4.1 Conceptual distinction between speciation by similar and divergent selection

Although similar-selection and divergent-selection mechanisms of speciation are conceptually distinct, their distinction is not as straightforward as the difference between speciation by selection and speciation without selection, which is qualitative in nature. The distinction between these two mechanisms is comparatively more fuzzy for two reasons: (1) selection on a given trait may rarely be perfectly uniform or strongly divergent between environments, and can vary continuously along this gradient, and (2) selection may be similar for some traits and divergent for others, and evolutionary responses to both types of selection can contribute to reproductive isolation during a given speciation event (Box 3).

First, if only small differences in selection exist across populations, it can be relatively subjective to define them as either similar or divergent. While this may seem trivial at first glance, small differences in selection can drive strong divergence under certain scenarios, depending on factors such as phenotypic differences in optima, effective population size, genetic architecture, and time since divergence. In our view, if differences in selection lead to divergence and subsequently reproductive isolation, then this describes speciation by divergent selection. Difficulty in distinguishing similar from divergent selection may also arise in cases we view as mutation-order speciation via sexual or genetic conflict. For instance, once an allele that would have equal fitness across environments arises in one population, but not the other (e.g., segregation distorter), and elicits selection for a counter allele (e.g., segregation restorer), is selection now divergent rather than similar across populations? We argue no, selection is still similar across these populations because the fitness of both alleles would be similar (or even identical) in either population; simply by chance, mutations of equivalent fitness were fixed in a different order across populations.

Difficulty in characterizing selection as either similar or divergent can also arise due to methodological issues related to our ability to accurately measure selective regimes, but these problems are logistical not conceptual. For instance, inherent difficulties in detecting selection in the wild due to statistical power, organismal characteristics, temporal variation in selection, etc. (e.g., Lande and Arnold, 1983; Kingsolver and Pfennig, 2007) can reduce our accuracy of estimating selection. However, field studies overall have been quite successful in measuring selection (e.g., Kingsolver et al. 2001; Kingsolver and Pfennig, 2007), and experimental studies employing artificial selection in the field or laboratory can alleviate most of these concerns.

Finally, the fact that multiple traits experiencing either similar or divergent selection can all contribute to reproductive isolation during speciation forces a multivariate view of speciation upon us (Box 3). Thus, we must strip the notion of atomized, univariate pathways to speciation from the field of speciation research, and instead conceptualize speciation as potentially a culmination or interaction of multiple mechanisms and pathways. Recognizing that speciation by both similar and divergent selection can occur simultaneously leads to some insights into how we discuss the operation of these mechanisms, how we distinguish between them, and how we conduct tests to uncover their operation and relative importance.

4.2 Sources and contributions of similar and divergent selection to speciation

Some have suggested that these two mechanisms may typically occur via different selective agents, and thus the agent of selection may inform us of the likelihood of speciation by similar or divergent selection. For instance, Nosil (2012) suggested that speciation by similar selection may often involve intrinsic agents of selection (e.g., internal genetic environment), while speciation by divergent selection will involve extrinsic agents (e.g., climate, competition, predation). However, as described in Section 3.1, speciation by similar selection may often result from various extrinsic selective agents as well. Nevertheless, speciation by divergent selection probably rarely involves intrinsic agents. Thus, inferring mechanism from type of selective agent may only prove useful in cases where intrinsic selective agents are identified—and most studies center on extrinsic agents.

Do these mechanisms usually occur in isolation or together? If together, do they typically occur during different stages of speciation or simultaneously, and do they often contribute additively to reproductive isolation or interact in complex ways? Today, we have little data at our disposal to answer these questions. Because the occurrence of multiple speciation mechanisms is more likely to complete speciation under most circumstances, we might expect to find multiple mechanisms operating in most cases (beyond the very initial stages). If correct, should we then expect to find multiple types of mechanisms (e.g., a form of divergent selection and a form of similar selection), multiple forms of the same mechanism (e.g., divergent natural and sexual selection), or both? The most obvious predictions are that speciation by similar selection should be more probable in cases of allopatric populations experiencing highly similar ecological conditions, while speciation by divergent selection is more likely across ecologically dissimilar environments; of course, it may be that most natural situations fall in between these two endpoints, where we might expect both. Moreover, it may be commonplace for populations to experience similar selection on some traits and divergent selection on others, potentially leading to their simultaneous action. Gene flow generally reduces the likelihood of speciation by similar selection, but has much less impact on speciation by divergent selection (Feder et al., 2012). As a corollary, speciation initiated by divergent selection could enhance the subsequent likelihood of speciation by similar selection through initial reduction of gene flow. To address this question, researchers could examine the links between reproductive isolation and traits that have either diverged due to similar or divergent selection, across multiple stages of speciation.

Given the occurrence of a particular mechanism, are some combinations of pathways more likely than others? For instance, divergent sexual selection via indicator traits may often be combined with divergent natural selection on those traits, and can form a potent means of speciation by divergent selection. Here, natural selection could favor different body shapes across environments,

Box 3. A multivariate view of speciation by similar and divergent selection

A continuum exists regarding the similarity and dissimilarity of selection between two populations (Fig. I). At either end of the spectrum, it is clear whether a given trait experiences similar or divergent selection pressures, but a gray area exists where differences in selective regimes are relatively weak. Whether traits experiencing only moderate differences in selection contribute to speciation by similar or divergent selection depends on whether divergence in the trait is caused by chance fixation of relatively similarly fit mutations (speciation by similar selection via mutation-order process), fixation of a single allele experiencing only somewhat different fitness across populations (speciation by similar selection via one-allele process), or differences in selection pulling trait values in different directions (speciation by divergent selection). For traits in this gray area, divergent selection is probably more likely due to the more restrictive conditions for speciation by similar selection and because even small differences in selection can lead to divergence.

Selection experienced by organisms rarely (if ever) is concentrated solely on a single trait. Moreover, multiple traits may influence reproductive isolation, and thus our view of speciation by selection should encapsulate this complexity, acknowledging that multiple traits may respond to different forms of selection, and all contribute to speciation (Nosil et al., 2009). In Fig. I, three traits are diverging between populations, and all three influence reproductive isolation. Trait 1 contributes to speciation by similar selection, while traits 2 and 3 contribute to speciation by divergent selection. Trait 1 has two alternative states or values of equal fitness in both populations, and diverges between populations as a result of the same underlying selection surfaces. Traits 2 and 3 experience different levels of fitness between populations, and diverge because of differences in the underlying selection surfaces. Although trait 2 experiences only moderate divergent selection, its divergence is caused by differences in selection, and its role in speciation may not be weak, as this additionally depends on factors such as genetic architecture and the nature and magnitude of its link to reproductive isolation.

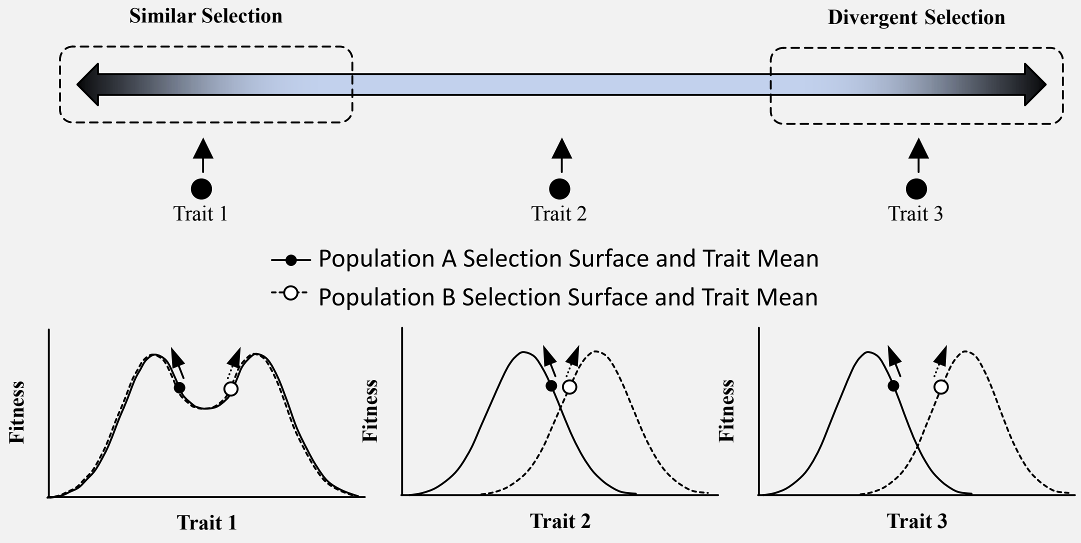


Fig. I Illustration of the continuous and multivariate nature of selection similarity between two populations, and its role in speciation

and body shape could serve as an indicator trait reflecting good genes in different ways across environments (e.g., short, round body could reflect high fitness or condition in one environment, but a long, elongate body could do so in another), leading to divergent mating preferences that then lead to increased reproductive isolation, and then to even greater body-shape divergence.

How might the dimensionality or strength of selection influence the likelihood of these two mechanisms (Nosil et al., 2009)? Although usually discussed in relation to divergent selection, this question applies equally to similar selection. Populations experiencing similar forms of strong selection on multiple traits should be more likely to exhibit some unique responses to similar selection that incidentally increase reproductive isolation. Thus, greater dimensionality and stronger selection should generally enhance progress toward speciation by any combination of these two mechanisms. Furthermore, in all scenarios discussed, reinforcement selection can facilitate completion of speciation in sympatry or parapatry.

4.3 Testing for speciation by similar or divergent selection

A range of approaches have been employed for testing mechanisms of speciation. In particular, tests for ecological speciation (≈ speciation by divergent selection) have become well developed in recent years with many empirical tests being conducted. In all cases, the best tests of the operation of these two mechanisms will involve measuring selection on the trait(s) or gene(s) in question across populations and determining its link to reproductive isolation. However, uncovering such traits and genes has proven difficult (Nosil and Schluter, 2011; Shaw and Mullen, 2011), as can be measuring selection across multiple populations, and thus many indirect approaches exist. There are some things to keep in mind when considering how to determine whether one or both of these mechanisms is operating in the wild, and some underappreciated limitations to commonly-employed tests.

First, finding reproductive isolation between populations in different environments does not unequivocally implicate speciation by divergent selection, just as finding reproductive isolation between populations in similar environments does not implicate speciation by similar selection. In both of these cases, other mechanisms could have produced observed patterns of reproductive isolation. Fortunately, such approaches to testing these mechanisms are rarely taken, as they would suffer from inflated type I error (concluding presence of mechanism when absent).

Two commonly-employed tests of ecological speciation suffer inflated type II error (i.e., failing to detect mechanism when present), causing the tests to be overly stringent for the detection of speciation by divergent selection. In one test, reproductive isolation is tested for a positive association with ecological differences, controlling for time (“ERG” tests of Nosil, 2012). In another test, speciation events identified on a phylogeny are tested for associations with ecological shifts (e.g., Winkler and Mitter, 2008; Nyman et al., 2010). Their limitations can be understood when considering their null hypotheses, which is not one of no effect of speciation by divergent selection on reproductive isolation, but rather that equivalent levels of reproductive isolation occur (or speciation events are equally likely) regardless of whether speciation by divergent selection is predicted to be present or absent. That is, the tests do not actually test for the presence of ecological speciation, but instead test for a stronger signal of ecological speciation compared to that of other mechanisms potentially driving speciation among relatively similar environments. When viewed mechanistically—that is, from a perspective targeted toward elucidating whether similar selection or divergent selection contributed to speciation—it is obvious that the evolution of reproductive isolation between similar environments has no bearing whatsoever on whether divergent selection drove reproductive isolation between populations experiencing different environments. If speciation by similar selection drives reproductive isolation among similar environments at a comparable rate as speciation by divergent selection across different environments, then these tests will fail to detect speciation by divergent selection even though it is important. On the other hand, rejecting the null hypothesis in these tests does lend credence to the important role of divergent selection in speciation.

One may argue that these tests are still adequate for detecting ecological speciation considering its operation may be considerably more rapid than most alternative mechanisms, and thus type II errors may rarely occur in nature. This may or may not be true: (1) if tests are applied to “old” systems, even “slow” mechanisms may have had time to catch up and produce similarly strong signals of speciation, or (2) speciation by similar selection could be rapid in some cases (e.g., sexual selection, including social selection, for arbitrary traits), resulting in a similarly strong role in speciation as compared to divergent selection even in “young” systems (perhaps especially in conjunction with allopatry). We are thus not advocating that these tests should not be used, in fact, these tests are still useful; however we simply encourage researchers to acknowledge such limitations to detecting speciation by divergent selection with these methods.

A gene flow approach to testing ecological speciation ("isolation by adaptation," sensu Nosil et al., 2008) also suffers several limitations. First, if low levels of adaptive divergence can result in strong reproductive isolation (reduced gene flow), the power to detect speciation by divergent selection will be reduced. Moreover, ability to detect such a pattern given the presence of ecological speciation will depend on several factors, including that "adaptive" divergence is measured properly (e.g., traits actually under divergent selection, or selection itself is measured), that the converse causation can be ruled out (i.e., gene flow actually constraining adaptive divergence rather than adaptive divergence actually reducing gene flow), that geographic distance is controlled for, and that the populations examined reside in a parameter space conducive for detecting the signal, such as intermediate migration and strong divergent selection (Räsänen and Hendry, 2008; Feder and Nosil, 2010; Thibert-Plante and Hendry, 2010).

Fortunately, alternative approaches for detecting ecological speciation exist that do not suffer from such limitations. Specifically, trait-based and fitness-based approaches directly asses the role of divergent selection in speciation (e.g., Rundle and Whitlock, 2001; Schluter, 2001; Nosil et al., 2005; Servedio et al., 2011). In these cases, positive findings comprise either uncovering traits experiencing divergent selection that also increase reproductive isolation among conspecific populations (trait-based approach), or finding that divergent selection results in reduced fitness of immigrants or hybrids relative to parental forms (fitness-based approach). These approaches provide especially powerful tests as they directly link selection and reproductive isolation, unequivocally revealing the role of speciation by divergent selection in speciation.

One recently suggested approach to testing for speciation by similar selection via the mutation-order process is to test for a positive association between trait differences between populations (or species) and time since divergence (typically estimated as genetic distance) (Martin and Mendelson, 2012). However, this general association may result even in the presence of divergent selection on the traits in question, and mutation-order speciation does not necessarily predict such a pattern. Remember, mutation-order speciation simply describes non-parallel evolutionary responses to similar selection pressures that result in reproductive isolation, and these divergent responses can be influenced by the strength of selection, variation in standing genetic variation, genetic (co)variances of traits, effective population size, as well as the order of appearance and fixation of alternative mutations—not simply on time since divergence. For instance, it is possible for more recently diverged populations to happen to fix alternative incompatible alleles while more anciently diverged populations happen to evolve similar solutions to their shared selection pressures (and thus may not be reproductively isolated); this would result in the opposite pattern, where trait differences are negatively associated with time since divergence. Moreover, processes such as genetic drift can produce positive associations between trait differences and time since divergence, making this approach less than ideal for revealing much about mechanisms of speciation.

Given these limitations, it is obvious that the most reliable and insightful tests for speciation by similar or divergent selection require elucidation of the traits or genes responsible for speciation—only by examining both the nature of selection experienced by these characters across populations (i.e., similar or divergent) and how these traits or genes influence reproductive isolation, may we truly gain a clear appreciation of the frequency and structure of similar-selection and divergent-selection processes in speciation. We believe this recognition points to the types of biological systems where we may gain the greatest insights into selection's role in speciation: closely related groups of organisms inhabiting replicated environmental gradients. Below we use these systems to highlight the varied ways that similar and divergent selection might lead to speciation, and how existing data from such systems suggests that all pathways may play some role in speciation.

5 Young Systems, Replicated Environmental Gradients, and Parallel and Nonparallel Paths to Speciation by Selection

5.1 Utility of investigating recent inhabitants of replicated environments

An ideal scenario for disentangling the roles of similar and divergent selection in speciation involves young systems where speciation is either incomplete or only very recently completed, and in which populations (or species) inhabit replicated environmental gradients. In this situation, researchers can examine replicate groups of closely related organisms (ideally, still undergoing speciation) wherein some replicates (i.e., populations/ species) experience broadly similar selection pressures, while others experience broadly divergent selection pressures (of course, some may experience both similar and divergent selection across various traits). Better still, these systems would include variation in the degree of reproductive isolation among population pairs, ranging from minimal to (essentially) complete isolation.

The investigation of ongoing speciation, or young species has many advantages that have been well described previously (e.g., Schluter, 2000; Coyne and Orr, 2004; Hendry, 2009; Nosil et al., 2009). Briefly, such systems represent the most direct way of evaluating mechanisms actually driving speciation, as "older" species can display a number of isolating barriers that may have evolved after, and not during, speciation. Second, young systems offer greater confidence in assessing *causation*, because the short time since population divergence implies reduced likelihood of the evolution of many confounding factors. Third, with populations experiencing varying levels of reproductive isolation, temporal stages of speciation can be more directly examined. Finally, the possibility of hybridization opens the door for a number of experimental approaches for assessing the causes of speciation. Nonetheless, there are also some limitations with young systems, such as uncertainty regarding the actual completion of speciation, dynamic populations not residing on fitness peaks, and the possible lack of adequate representative systems for particular taxa. Yet overall, young systems offer critical advantages, and it is simply much more difficult to uncover true causes of speciation the more generations removed from speciation one becomes.

The comparative approach represents one of the great stalwart methods of evolutionary biology, e.g., serving as a primary tool for uncovering patterns of convergent evolution (e.g., Brooks and McLennan, 1991; Harvey and Pagel, 1991; Roff, 1992; Schluter, 2000; Losos, 2011). Considering that speciation usually comprises a singular event from a historical perspective, it is quite remarkable to have the opportunity to catch speciation in the act, with multiple populations (across replicated environments) at different stages along the continuum of speciation (Hendry, 2009; Nosil et al., 2009). As it turns out, the phenomenon of multiple populations (or closely related species) experiencing replicated environmental gradients is common in nature (Table 1). Thus, we have many opportunities to peer into the speciation process, and extract as much as we can about how new species form. It is without coincidence that many classic systems for studying speciation represent examples of such systems, such as threespine stickleback fishes, *Timema* walking-stick insects, *Mimulus* monkeyflowers, and Darwin's finches.

5.2 Ubiquity of parallel and non-parallel evolutionary responses to shared environmental gradients

While the focus of the described framework is centered on the initiators of speciation, there can be no evolution of reproductive isolation without evolutionary responses to these evolutionary mechanisms (see Box 1). Thus, to learn how selection drives speciation, one cannot simply study selection and reproductive isolation alone, but instead must include detailed investigation of evolutionary responses to selection.

When multiple groups of organisms experience similar environmental gradients, their patterns of differentiation might exhibit both shared and unique features (e.g., Travisano et al., 1995; Langerhans and DeWitt, 2004; Langerhans et al., 2006; Ozgo and Kinnison, 2008; Langerhans and Makowicz, 2009; Riesch et al., 2010a). While parallel evolutionary responses have historically provided strong evidence for a deterministic role of natural selection in driving evolutionary patterns (see Losos, 2011), non-parallel responses to similar selection pressures can arise for a variety of reasons, including those discussed above in section 3.1, as well as genetic (co)variances of traits, gene flow, and effective population size (in empirical data, trait differences across "similar" environments can also reflect cryptic differences in selection or genetic drift). Either type of response to selection might result in increased reproductive isolation among populations.

A great number of studies investigating these sorts of systems now exist, and both parallel and non-parallel responses to common environmental gradients are widespread across systems (Table 1). A common scenario observed in the wild is populations exhibiting some degree of parallel divergence between environments for one or more traits experiencing divergent selection, as well as nonparallel aspects of divergence for either these same traits or alternative traits. That is, even though patterns of convergence typically exist, not all populations within each environment are identical. By far, most studies center on parallel patterns of divergence and the role of divergent selection between environments in driving speciation. In these cases, evidence for speciation by divergent selection is commonplace,

Table 1 A non-exhaustive summary of taxa experiencing replicated environmental gradients, and whether they are known to exhibit parallel or non-parallel phenotypic responses, as well as evidence for ecological speciation (≈ speciation by divergent selection) and reproductive isolation (RI) between populations inhabiting the same type of environment; NA = relevant data not available.

Taxa	Replicated Environmental Gradient	Primary Trait(s)	Parallel Response	Non-parallel Response	Ecological Speciation	RI within Environments	References
Threespine stickleback *Gasterosteus aculeatus*	benthic vs. limnetic	morphology, diet, color, behaviors, life history	Yes	Yes	Yes	No	Rundle et al., 2000; Taylor, 2000; McKinnon and Rundle, 2002; Rundle and Schluter, 2004.
	anadromous vs. freshwater	morphology, diet, color, behaviors	Yes	Yes	Yes	No	Ziuganov, 1995; McKinnon and Rundle, 2002; Rundle and Schluter, 2004; Chan et al., 2010.
	lake vs. stream	morphology, color	Yes	Yes	Yes	NA	McKinnon and Rundle, 2002; Kaeuffer et al., 2011.
	lava vs. nitella/mud	morphology, shoaling behavior	Yes	Yes	Likely	NA	Kristjánsson et al., 2002; Ólafsdóttir et al., 2007; Ólafsdóttir and Snorrason, 2009.
Arctic charr *Salvelinus alpinus*	benthic vs. limnetic vs. piscivore	diet, morphology, color, life history, behavior, spawning time/place	Yes	Yes	Yes	NA	Gíslason et al. 1999; Jonsson and Jonsson, 2001; Knudsen et al., 2010.
Whitefish *Coregonus spp*.	benthic vs. limnetic	body size, diet, energy metabolism, life history, swimming behavior, morphology	Yes	Yes	Yes	NA	Østbye et al., 2006; Derome et al., 2006; Bernatchez et al., 2010.
Sockeye salmon *Oncorhynchus nerka*	anadromous vs. freshwater	behavior, life history, morphology, swimming performance	Yes	NA	Yes	NA	Taylor et al., 1996; Taylor, 2000.
	beach vs. river spawning	life history, morphology	Yes	NA	Yes	NA	Hendry et al., 2000; Pavey et al., 2010.
Bahamas mosquitofish *Gambusia hubbsi*	presence/absence of predatory fish	body shape, male genitalia, male coloration, life histories, behaviors, swimming abilities	Yes	Yes	Yes	Yes	Langerhans et al. 2007; Langerhans, 2009; Langerhans, 2010; Riesch et al., in press; Heinen and Langerhans, submitted.
Mormyrid electric fish	resource polymorphism: electrolocation and diet specializations	electric discharges	Yes	Yes	Yes	NA	Arnegard et al., 2005; Feulner et al., 2009.
Killifish *Fundulus spp.*	toxic vs. nontoxic	osmoregulation, physiology	Yes	Yes	Likely	NA	Whitehead et al., 2011a; 2012.
	marine vs. freshwater	life history, osmoregulation	Yes	NA	Yes	NA	Fuller et al., 2007; Whitehead et al., 2011a, b.
Smelt *Osmerus spp.*	anadromous vs. lacustrine	diet, life history, morphology	Yes	Yes	Yes	NA	Copeman, 1977; Taylor and Bentzen, 1993.
	dwarf lacustrine vs. normal-sized lacustrine	diet, life history, morphology	Yes	Yes	Yes	NA	Copeman, 1977; Taylor and Bentzen, 1993.
Extremophile poeciliids (*Gambusia* and *Poecilia spp.*)	toxic vs. nontoxic	behavior, diet, life history, morphology	Yes	Yes	Yes	NA	Tobler et al., 2011; Riesch et al., 2010a; Tobler and Plath, 2011.
Cave mollies *Poecilia mexicana*	cave vs. surface	behavior, diet, life history, morphology, pigmentation	Yes	Yes	Yes	NA	Riesch et al., 2010b; Tobler et al., 2008; Tobler and Plath, 2011.
Astyanax cavefishes	cave vs. surface	eye development, morphology, pigmentation	Yes	Yes	Yes	NA	Jeffery, 2009; Strecker et al., 2011.
Galaxiids *Galaxias spp*.	diadromous vs. freshwater	life history, morphology	Yes	Yes	Likely	Yes	Waters and Wallis, 2001.
Alewife *Alosa pseudoharengus*	anadromous vs. freshwater	life history, morphology	Yes	NA	Likely	NA	Palkovacs et al., 2008.
New Zealand eleotrids *Gobiomorphus spp.*	amphidromous vs. freshwater	life history, morphology	Yes	NA	Likely	NA	Michel et al., 2008.
Lampreys	freshwater vs. anadromous	parasitic vs. nonparasitic life style, life history	Yes	NA	Likely	NA	Zanandrea, 1959; Espanhol et al., 2007.

Continued Table 1

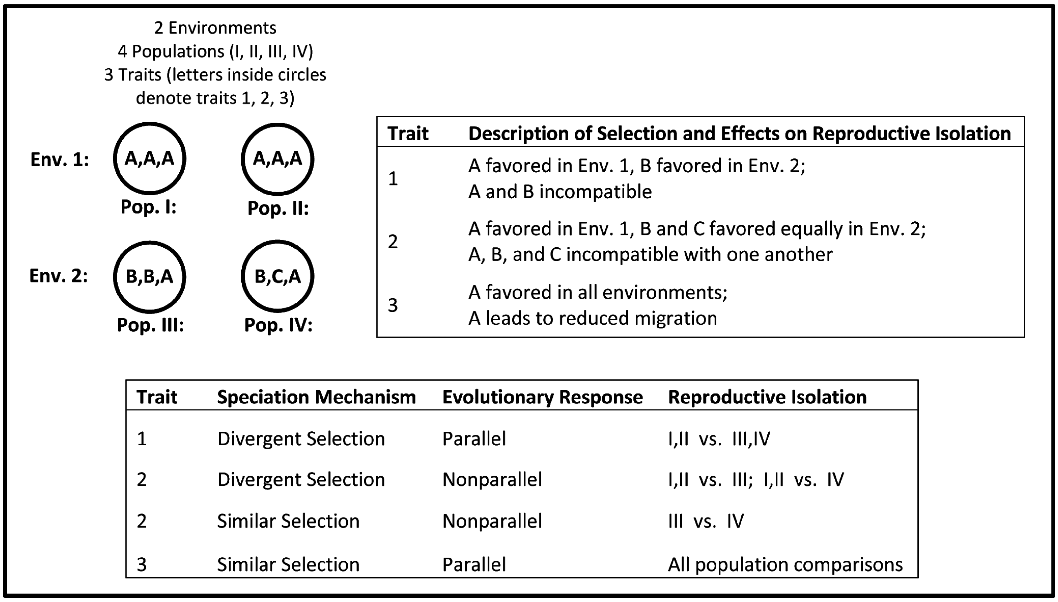
Taxa	Replicated Environmental Gradient	Primary Trait(s)	Parallel Response	Non-parallel Response	Ecological Speciation	RI within Environments	References
Crossbills *Loxia* spp.	different pine trees	call types, bill size and shape	Yes	Yes	Yes	NA	Benkman, 1993; Snowberg and Benkman, 2009; Edelbaar et al., 2012.
Darwin's finches *Geospiza spp.*	different-sized seeds	call types, bill size and shape	Yes	likely	Yes	Yes	Podos, 2001; Huber et al., 2007.
Tristan finches *Nesospiza spp.*	resource use: diet specialization	morphology	Yes	Yes	Yes	NA	Ryan et al., 1994, 2007.
Various birds	different habitats (e.g., urban vs. grassland vs. forest)	acoustical signal properties	Yes	Yes	NA	NA	Morton, 1975; Derryberry, 2009; Ripmeester et al., 2010.
Timema walking-stick insects; emphasis on *T. cristinae*	host plant specialization	behavior, body size, color patterns, host preference, morphology	Yes	Yes	Yes	No	Crespi & Sandoval, 2000; Nosil et al., 2002; Nosil & Crespi, 2004.
Heliconius butterflies	different mimetic forms	color pattern	Yes	Yes	Yes	NA	Jiggins et al., 2001; Jiggins, 2008; Merrill et al., 2011.
Leaf beetles *Neochlamisus bebbianae*	host plant specialization	life history, feeding response, larval fidelity, morphology	Yes	Yes	Yes	No	Adams and Funk, 1997; Egan and Funk, 2009; Funk, 2010.
Enallagma damselflies	fish vs. dragonfly predation regimes	morphology, behavior, life history	Yes	NA	Yes	NA	Stoks et al., 2005.
Hyalella species complex	small vs. large ecotypes	body size	Yes	Yes	Yes	Yes	McPeek and Wellborn, 1998; Wellborn and Cothran, 2004; Wellborn et al., 2005.
Asellus aquaticus	vegetation cover: *Chara* spp. vs. *Phragmites australis*	morphology, color, behavior	Yes	Yes	Yes	No	Eroukhmanoff et al., 2009, 2011; Karlsson et al., 2010.
	cave vs. surface	eye development, morphology, pigmentation	Yes	Yes	Yes	NA	Turk et al., 1996; Protas et al., 2011.
Gammarus minus	cave vs. surface	eye development, life history, morphology, pigmentation	Yes	Yes	Yes	NA	Culver, 1987; Jones et al., 1992; Carlini et al., 2009.
Littorina snails	upper vs. lower intertidal zones	behavior, size, shell texture, shell color, foot size, aperture size	Yes	Yes	Yes	No	Johannesson et al., 2010; Cruz et al., 2004; Rolán-Alvarez, 2007.
Satsuma snails	presence/absence of snake predation	shell chirality, aperture modifications	Yes	NA	Likely	NA	Hoso et al., 2010.
North American scincid lizards	lower vs higher elevation	body size, coloration	Yes	Yes	Yes	NA	Richmond and Reeder, 2002; Richmond et al., 2011.
Anolis lizards	microhabitat (e.g. trunk-crown vs. trunk-ground); macro-habitat (e.g., xeric vs. mesic)	body size, morphology, color	Yes	Yes	Yes	Yes	Irschick et al., 1997; Losos et al., 1998; Ogden and Thorpe, 2002; Glor et al. 2003; Losos, 2004; Thorpe et al., 2005; Langerhans et al., 2006; Losos, 2009.
Lizards in White Sands, NM	white sand vs. dark soil habitats	coloration, morphology	Yes	Yes	Yes	NA	Rosenblum, 2006; Rosenblum and Harmon, 2010.
Horseshoe bats	resource use: diet specialization	echolocation	Yes	NA	Yes	NA	Kingston and Rossiter, 2004.
Killer whales	resource use: diet specialization	foraging behaviors, acoustic communication	Yes	Yes	Yes	Yes	Riesch et al., 2012.
Lasthenia californica	heavy metal contaminated soils	edaphic tolerance, flavonoid profiles	Yes	NA	Yes	NA	Rajakaruna et al., 2003; Ostevik et al., 2012.
Mimulus guttatus	interior vs. coastal	size, flowering time, morphology, salt tolerance	Yes	NA	Yes	NA	Clausen and Hiesey, 1958; Lowry et al., 2008.
Eucalyptus globulus	interior vs. coastal: dwarf vs. normal phenotype	size, morphology	Yes	NA	Likely	NA	Foster et al., 2007.

however, details regarding nonparallel features of divergence, and the presence of reproductive isolation between populations inhabiting similar environments is often lacking (Table 1).

This highlights the need for future work to focus on (1) nonparallel evolutionary responses and (2) populations inhabiting similar environments. Lack of knowledge in these areas is notable, as this encapsulates three of the four possible pathways to speciation by similar and divergent selection (Fig. 1). That is, for a group of populations or closely related species inhabiting replicated environmental gradients, speciation may proceed via parallel or non-parallel responses for either similar or divergent selection. Nonparallel responses are ubiquitous, and yet their underlying causes and potential links to reproductive isolation are largely unknown. While evidence for ecological speciation is well documented (reviewed by Nosil, 2012), we currently have little knowledge regarding the frequency with which populations in divergent environments have evolved reproductive isolation via parallel or nonparallel responses (e.g., Kaeuffer et al., 2011; Ostevik et al., 2012). The commonality of unique responses to replicated environmental gradients further suggests that similar selection may drive speciation in some of these systems. A caveat, however, is that selection per se has very rarely been directly measured in these systems. Rather, environmental variation usually serves as a surrogate for variation in selection. Thus, nonparallel responses could actually reflect the work of divergent selection (via relatively cryptic selective agents), not similar selection. But this fact only underlines the need for further investigation so that we can gain a fuller understanding of the ways selection drives speciation. Moreover, most studies have examined only a few traits predicted a priori to respond to divergent selection between environments, likely failing to measure traits with the greatest probabilities of exhibiting unique responses to similar selection pressures, such as those involved in sexual conflict or signal traits that may be experiencing sexual selection in arbitrary directions (see above). This suggests that the frequency and strength of nonparallel responses in these systems may have been underestimated so far.

6 Conclusions

Although speciation research represents a major focus of evolutionary biology, and has comprised a thriving research arena for decades, we argue that a clearer conceptual framework for understanding selection's role in speciation is needed to elucidate a fuller understanding of how selection actually generates new species. Without a clear framework, progress can be inhibited by miscommunication and failure to recognize critical areas in need of investigation. With the framework described here, speciation by selection forms an overarching umbrella for the study of how selection drives speciation, providing the canvas on which researchers can then investigate the influence of various types of selection (natural, sexual, social), selective agents, forms of selection (similar, divergent, reinforcement), types of traits and genes, nature of evolutionary responses to



Trait	Description of Selection and Effects on Reproductive Isolation
1	A favored in Env. 1, B favored in Env. 2; A and B incompatible
2	A favored in Env. 1, B and C favored equally in Env. 2; A, B, and C incompatible with one another
3	A favored in all environments; A leads to reduced migration

Trait	Speciation Mechanism	Evolutionary Response	Reproductive Isolation
1	Divergent Selection	Parallel	I,II vs. III,IV
2	Divergent Selection	Nonparallel	I,II vs. III; I,II vs. IV
2	Similar Selection	Nonparallel	III vs. IV
3	Similar Selection	Parallel	All population comparisons

Fig. 1 Four pathways of speciation by similar or divergent selection

selection (parallel, non-parallel), links between responses to selection and reproductive isolation, and isolating barriers involved in the speciation process, as well as mitigating factors like the geographic structure of populations during speciation, gene flow, genetic (co)variances of traits, etc. We emphasize the utility of investigating young systems inhabiting replicated environmental gradients to gain the greatest insights into mechanisms of speciation, and highlight that future research is needed on the traits and genes underlying reproductive isolation. By centering our conceptualization of speciation around the evolutionary mechanism(s) driving the process (similar, divergent, and reinforcement selection) and the types of evolutionary responses that cause reproductive isolation (parallel and nonparallel), we can strengthen our understanding of questions like what selective agents often drive speciation via alternative mechanisms, what types of traits or genes are typically involved in speciation by similar selection, and whether parallel or non-parallel responses might be more important for speciation by similar or divergent selection. Looking to the future, we hope that the framework described in this paper will aid in answering Schluter's (2009) pressing question of today, "how does selection lead to speciation?"

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