Ecological speciation! Or the lack thereof?[1]

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Abstract: Ecological speciation occurs when adaptation to different environments or resources causes the evolution of reproductive isolation. This process is now thought to be very important in the evolution of biological diversity. Indeed, support for ecological speciation is so often asserted in the literature that one can get the impression of ubiquity. Eager to ride on the coattails of this exciting work, my own research has investigated ecological speciation in guppies, sticklebacks, and Darwin's finches. Much to my initial dismay, I failed to find simple and strong signatures of ecological speciation in the first two of these systems. Setting aside the possibility of personal incompetence, my apparent deviation from ubiquity might simply reflect an existing literature bias. This bias seems obvious in retrospect given that essentially all published studies of ecological speciation purport to be confirmatory, whereas many cases of divergent selection and adaptive divergence are associated with only weak to modest levels of reproductive isolation. In short, different populations can be arrayed along a continuum from panmixia to complete reproductive isolation. Variation along this continuum might profitably be used for studying factors, outlined herein, that can promote or constrain "progress" toward ecological speciation.

Résumé : La spéciation écologique se produit lorsqu'une adaptation à des ressources ou des milieux différents entraîne l'évolution d'un isolement reproductif. On croit actuellement que ce processus est très important dans l'évolution de la diversité biologique. En fait, la spéciation écologique est si souvent invoquée dans la littérature qu'on a l'impression qu'elle est ubiquiste. Dans la foulée de cette recherche intéressante, mes travaux personnels ont examiné la spéciation écologique chez les guppys, les épinoches et les pinsons de Darwin. Au départ, il m'a été impossible, à mon désarroi, de trouver des signatures simples et prononcées de spéciation écologique dans les deux premiers de ces systèmes. Excluant la possibilité de mon incompétence personnelle, mon incapacité à trouver l'ubiquité du phénomène peut être due à une distorsion de la littérature actuelle. Rétrospectivement, cette distorsion paraît évidente parce qu'essentiellement toutes les études publiées sur la spéciation écologique prétendent avoir un caractère confirmatif, alors que plusieurs cas de sélection divergente et de divergence adaptative sont associés avec seulement des niveaux faibles à modestes d'isolement reproductif. Bref, les différentes populations peuvent être placées sur un continuum qui va de la panmixie à l'isolement reproductif complet. La variation le long de ce gradient peut être utilisée avec profit pour étudier facteurs, énumérés ici, qui peuvent favoriser ou restreindre la « progression » vers la spéciation écologique.

[Traduit par la Rédaction]

Introduction

Ecological speciation can perhaps be best illustrated by reference to a clear example from nature. For this, I will use the threespine stickleback (*Gasterosteus aculeatus*) populations in a few small lakes (Paxton, Priest, Enos, Emily) in southern British Columbia, Canada (reviews: McPhail 1994; McKinnon and Rundle 2002; Boughman 2006). Within each of these lakes, two reasonably distinct ecotypes are evident. One is adapted to a limnetic feeding mode and has a shallow body and numerous, long gill rakers. The other is adapted to a benthic feeding mode and has a deep body and few, short gill rakers. The two types are independently derived within

each lake and now exchange very few genes. In essence, each lake harbors two reproductively isolated stickleback species that have evolved since the last glaciation. Within each lake, reproductive isolation has arisen specifically because of adaptive divergence into the different environments (limnetic or benthic). First, ecological selection against "migrants" occurs because individuals adapted to one environment show higher survival and growth in that environment than do individuals adapted to the other environment. Second, ecological selection against hybrids occurs because they show low growth and survival relative to locally adapted pure types within each environment — but not under benign conditions. Third, ecologically driven, positive

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Table 1. Some major contexts for ecological speciation.

Context	Some examples and some key references
1. Phytophagous insects on different host plants	Pea aphids (Via 1999; Via et al. 2000; Ferrari et al. 2006)
	Rhagoletis (Filchak et al. 2000; Feder et al. 2005; Xie et al. 2007)
	Timema walking sticks (Nosil 2007; Nosil and Sandoval 2008)
	Other groups (Drès and Mallet 2002)
2. Mimicry rings in butterflies	*Heliconius* (Jiggins 2008)
3. Plants on different soils	Mine tailings (McNeilly and Antonovics 1968; Antonovics and Bradshaw 1970)
	Fertilizer treatments (Snaydon and Davies 1976; Silvertown et al. 2005)
4. Plants in different climates	Interior vs. coastal (Hall and Willis 2006)
5. Birds feeding on different seed types	Darwin's finches (Huber et al. 2007; Hendry et al. 2009*a*)
	Tristan finches (Ryan et al. 2007)
6. Lizards in different habitats	*Anolis* lizards (Ogden and Thorpe 2002; Thorpe et al. 2005)
7. Snails at different tidal elevations	*Littorina saxatilis* (Pérez-Figueroa et al. 2005; Quesada et al. 2007)

Note: Fishes are excluded here, as they are covered in more detail in Table 2.

assortative mating is present because individuals of each type prefer to mate with their own type even across the different lakes. In short, adaptation to limnetic versus benthic environments has caused the evolution of reproductive barriers that have substantially reduced gene flow (reviews: McPhail 1994; McKinnon and Rundle 2002; Boughman 2006).

Ecological speciation thus occurs when reproductive isolation evolves as a consequence of adaptation to different environments–resources–habitats (Schluter 2000). (I will use these three terms interchangeably in a broad sense — i.e., different ecological conditions — but I will often vary them among specific contexts to match their connotations and typical use in the literature.) Ecological speciation appears to be quite general, having been documented in a variety of taxa and ecological–geographical contexts (Rundle and Nosil 2005; Funk et al. 2006; Schluter 2009; Table 1). Moreover, research on ecological speciation is quickly coming to dominate that on other speciation mechanisms (Fig. 1).

My own interest in ecological speciation began during my postdoctoral fellowship at The University of British Columbia, Canada, one of the major centres of research in this area. Working there, it was natural to see implications for my own studies of sockeye salmon (*Oncorhychus nerka*) adapting to different breeding environments (lake beaches vs. streams). Motivated by the swell of enthusiasm for ecological speciation, I soon published a paper arguing for rapid progress toward ecological speciation in these salmon (Hendry et al. 2000; see also Hendry 2001). Encouraged by my own positive results, published in a flashy journal, and reinforced by the explosion of work on ecological speciation (Fig. 1), I decided to make this topic a major focus of my future work. On starting my faculty position at McGill University in Montréal, I therefore initiated a series of studies on possible ecological speciation in (*i*) stickleback (*G. aculeatus*) adapted to lakes versus streams, (*ii*) Trinidadian guppies (*Poecilia reticulata*) adapted to high-predation versus low-predation environments, and (*iii*) Darwin's finches (*Geospiza* spp.) adapted to different seed types. Some of this work failed to show the strong signatures of ecological speciation that I had come to expect based on the existing literature — much to my initial surprise and disappointment.

The increasingly ambiguous evidence for ecological speciation in my own work has led me to re-evaluate the power

Fig. 1. Citation rates according to the Institute for Scientific Information (ISI) Web of Science for all papers including "ecological speciation" as a keyword (solid line), in relation to papers using other speciation keywords: hybrid speciation (medium-dashed line), genetic incompatibility (short-dashed line), and chromosomal speciation (long-dashed line). Panel (*a*) shows the total number of citations each year. Panel (*b*) shows the numbers in panel (*a*) as a proportion of the total number of citations for papers with both "speciation" and "evolution" as keywords. A key to interpreting these graphs is that they only include citations between 1995 and 2008 to papers published between 1995 and 2008, which is why the citation rates start at zero in 1995 (panel *a*).
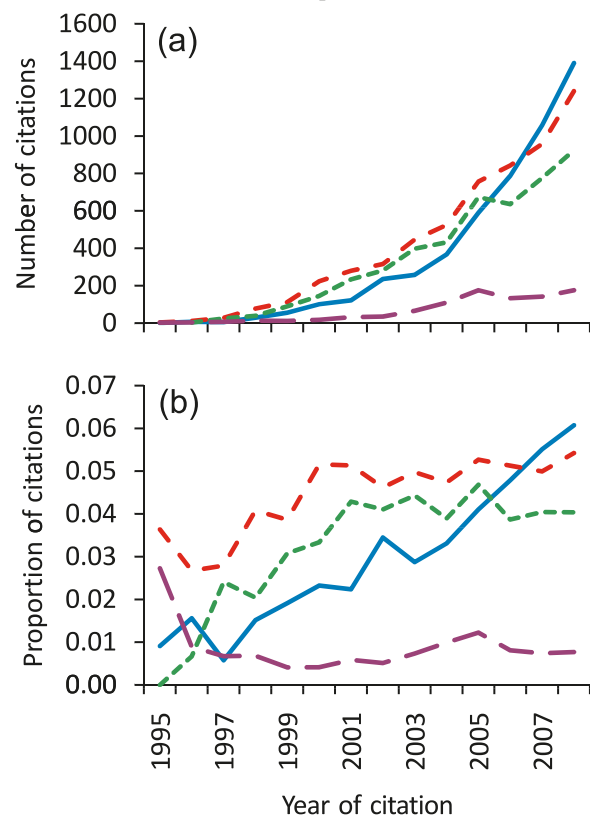
and prevalence of this mechanism in nature, as well as the evidence required to support it. The present review and perspective comprises my initial attempts at this re-evaluation. I

will here consider the nature of evidence that can be used to infer ecological speciation, and I will then review published work in light of these standards of evidence. Although most published studies make positive assertions about the importance of ecological speciation in their natural system, I will argue that only a subset of these studies provide robust evidence to confidently make such an assertion. In addition, I find a growing number of studies that fail to find support for ecological speciation. I conclude that the process of ecological speciation can have different possible outcomes that range from essentially no divergence all the way to complete and irreversible reproductive isolation. Although this conclusion seems obvious in retrospect, it highlights the need for more published work on the conditions that promote and constrain progress toward (or away from) ecological speciation.

How is ecological speciation inferred?

When considering support for ecological speciation, we must first consider the types of evidence required to make robust inferences. Therefore, I here outline common methods for inferring ecological speciation while also highlighting some of their strengths and weaknesses. In doing so, it helps to remember the likely sequence of events during ecological speciation (Räsänen and Hendry 2008). First, populations should experience some sort of ecological contrast, such as different environments or resources. Second, this ecological contrast should impose divergent or disruptive selection on particular genes or traits. Third, this divergent or disruptive selection should cause adaptive divergence between groups using the different environments or resources. Fourth, adaptive divergence should cause the evolution of reproductive isolation. Thus, one might infer ecological speciation by looking for correlations between reproductive isolation (integrated signatures or particular reproductive barriers — see below) and either ecological differences, divergent selection, or adaptive divergence. A key, however, is that adaptive divergence must be present for ecological speciation to proceed. Thus, an ecological contrast and the resulting divergent selection will not cause ecological speciation unless they first cause adaptive divergence (Räsänen and Hendry 2008). The ultimate confirmation of ecological speciation comes from evidence that reductions in gene flow were the result of adaptation to different environments–resources–habitats. This requirement of causation, rather than just correlation, has led to two major design elements often seen in studies of ecological speciation.

The first design element is a focus on the very early stages of speciation, such as between conspecific populations that show only partial reproductive isolation. This focus is intended to reveal the processes that caused speciation in the first place, rather than simply occurring after the fact. As an example of why this is important, intrinsic genetic incompatibilities might arise long after two groups stopped interbreeding for some other reason. Such incompatibilities would certainly correlate with current reproductive isolation, but they might not have been the reason for speciation in the first place. This design element is one of the reasons that postglacial fishes have figured so prominently in the study of ecological speciation (Table 2).

Focusing on young taxa, however, generates its own caveats. One limitation is that any existing partial isolation may never accumulate to the point of full speciation, raising the question of whether processes acting within species are the same as those acting to sunder species. Another limitation is that this design element can ignore ecological speciation that happened further in the past. That is, species that formed long ago may have arisen through ecological speciation — but the obvious signatures of this process may have been eroded owing to evolution after speciation. In short, it is difficult to provide direct evidence for ecological speciation (or for any other speciation mechanism) in older taxa. In some cases, this problem can be circumvented by comparing divergence and isolation between established species with that between populations within those species (e.g., Langerhans et al. 2007; Nosil and Sandoval 2008; Hendry et al. 2009b).

The second design element is based on the idea that biologically relevant reproductive isolation (as opposed to just a geographical barrier) can really only be confirmed if the different groups interact in nature. Partly for this reason, many studies of ecological speciation have focused on sympatric or parapatric groups — because reproductive isolation here is the result of factors intrinsic to the organism (perhaps through an interaction with their environment). Reproductive barriers between allopatric groups can also be considered by bringing them into contact in the laboratory or in the wild (e.g., Funk 1998; Vines and Schluter 2006; Langerhans et al. 2007). Limitations here can include logistics, ethics, and the fact that artificial secondary contact, particularly in the laboratory, may not accurately mimic natural secondary contact. When choosing a particular geographical context for study, it is important to remember that some current reproductive barriers may have originated in a different geographical context (Losos and Glor 2003; Feder et al. 2005; Xie et al. 2007). Moreover, the traditionally recognized categories of allopatry, sympatry, and parapatry are ambiguous and potentially misleading (Butlin et al. 2008; Fitzpatrick et al. 2008).

In light of these two design elements, I now evaluate the types of evidence typically provided in support of ecological speciation. I first mention types of evidence that are supportive and valuable, but not sufficiently robust to be definitive. First, ecological speciation is sometimes inferred simply when different populations or species show adaptive divergence. A major limitation here is that one must also demonstrate that this adaptive divergence has contributed to the evolution of reproductive isolation. Second, ecological speciation is sometimes inferred simply when different species reside in different ecological environments. A major limitation here is that the ecological divergence may have occurred after speciation. Third, ecological speciation is sometimes inferred when two ecologically or adaptively differentiated species do not interbreed in natural or artificial secondary contact. A major limitation here is that it must be shown that adaptive divergence is the reason for the reduced interbreeding. In short, the above methods do not by themselves allow robust inferences about ecological speciation.

Two additional analytical approaches can be used to provide more definitive evidence of ecological speciation. One approach is based on integrated signatures of reproductive

Table 2. Arguments for ecological speciation in fishes, with selected papers reporting evidence for particular signatures expected under ecological speciation.

	Parallel evolution	Reduced gene flow	Selection against migrant	Selection against hybrids	Temporal isolation	Assortative mate choice	Key references
1. Benthic–limnetic stickleback	Yes	Yes	Yes	Yes	?	Yes	Schluter 1995; Rundle et al. 2000; Taylor and McPhail 2000; Rundle 2002; Taylor et al. 2006; Gow et al. 2007
2. Anadromous–freshwater stickleback	Yes	Yes	?	Probably	Sometimes	Sometimes	Hagen 1967; McKinnon et al. 2004; Mäkinen et al. 2006; Jones et al. 2006, 2008
3. Lake–stream stickleback	Yes	Perhaps	Sometimes	?	Sometimes	No	Thompson et al. 1997; Hendry et al. 2002; Hendry and Taylor 2004; Berner et al. 2009; K. Räsänen and A. Hendry, unpublished data
4. Lava–mud stickleback	Probably	Yes	?	?	No	Yes	Kristjánsson et al. 2002; Ólafsdóttir et al. 2006, 2007
5. Arctic char morphs	Yes	Sometimes	Probably	?	Sometimes	Probably	Gíslason et al. 1999; Jonsson and Jonsson 2001
6. Dwarf–normal lake whitefish	Yes	Yes	Probably	Probably	?	?	Pigeon et al. 1997; Lu and Bernatchez 1998, 1999; Campbell and Bernatchez 2004; Østbye et al. 2006; Derome et al. 2006; Rogers and Bernatchez 2006, 2007
7. Hamlets	Perhaps	Sometimes	Probably	?	?	Yes	McCartney et al. 2003; Puebla et al. 2007, 2008
8. Sockeye–kokanee	Yes	Yes	Probably	Probably	Yes	Yes	Foote and Larkin 1988; Taylor et al. 1996; Wood and Foote 1996; Craig et al. 2005
9. High–low predation mosquitofish	Yes	?	Yes	?	No	Yes	Langerhans et al. 2007; R.B. Langerhans, University of Oklahoma Biological Station, HC 71, Box 205, Kingston, OK 73439, USA, unpublished data
10. High–low salinity killifish	?	?	Yes	Sometimes	No	Yes	Fuller et al. 2007; Fuller 2008
11. Dwarf–large freshwater smelt	Yes	Yes	Probably	?	Yes	Probably	Taylor and Bentzen 1993a, 1993b; Saint Laurent et al. 2003; Curry et al. 2004

Note: "Yes" refers to positive evidence. "No" refers to negative evidence. "Probably" refers to circumstantial, but reasonably strong, evidence. "Sometimes" refers to variable evidence within a study or between studies. "?" refers to a lack of studies addressing the problem.

isolation, such as measures of genetic differentiation or estimates of gene flow. More details on this approach are provided below in the section on "Testing for integrated signatures of ecological speciation". Another approach is to test whether particular reproductive barriers are associated with ecological differences, divergent selection, or adaptive divergence. More details on this approach are provided below in the section on "Examining the ecological basis for particular reproductive barriers".

Testing for integrated signatures of ecological speciation

The ultimate signature of speciation is a reduction in gene flow between potentially interbreeding populations (Dobzhansky 1937; Mayr 1963; Coyne and Orr 2004). Several different methods have therefore been advanced for inferring ecological speciation from patterns of genetic differentiation or gene flow. I first briefly introduce each method. I then discuss a variety of methodological considerations in their application.

(1) Gene flow should be lower than dispersal. Ecological speciation is expected to follow from adaptive divergence between populations in different environments. The reason is that fitness in a given environment should be higher for individuals adapted to that environment than for individuals adapted to different environments (Schluter 2000; Nosil et al. 2005; Hereford 2009). One expected signature of this adaptive divergence is that the rate of physical dispersal between environments (movement of individuals or gametes or zygotes) should be higher than the resulting rate of gene flow (because immigrants should perform poorly relative to residents). This prediction can be tested by comparing the rate of physical dispersal between populations, as estimated from natural or artificial marks–tags, with the rate of gene flow as estimated from neutral genetic markers (e.g., Hendry et al. 2000). An extension of this method is to show that gene flow is low when dispersal (even if not actually quantified) must be very high — such as when the groups occur in full sympatry.

(2) Greater environmental differences should lead to lower gene flow. The idea here is to examine patterns of genetic divergence or gene flow in relation to environmental differences. The expectation is that populations experiencing greater environmental differences should be subject to greater divergent selection, which should cause greater adaptive divergence and therefore lower gene flow (Räsänen and Hendry 2008). Motivated by this expectation, a number of studies have tested whether genetic divergence is higher (or gene flow is lower) between populations in different environments than between populations in similar environments (e.g., Ogden and Thorpe 2002; Crispo et al. 2006; Nosil et al. 2008).

(3) Greater adaptive differences should lead to lower gene flow. This approach is an extension of the one above because it tests for an intermediate (and necessary) step in the pathway from ecological differences to gene flow. That is, populations must be adaptively divergent if they are to show reduced gene flow owing to divergent selection (Räsänen and Hendry 2008). Here, a number of studies have tested whether populations showing greater phenotypic differences in presumed adaptive traits also show greater genetic divergence or lower gene flow (e.g., Gíslason et al.

1999; Lu and Bernatchez 1999). Recent studies applying genome scans to this hypothesis have dubbed the expectation "isolation-by-adaptation" (Nosil et al. 2008, 2009a).

A key to inferring ecological speciation from the above three methods is to confirm that adaptation is the reason for reduced gene flow. I now describe common ways of doing so for each method — but all of these ideas could be relevant to all three methods. In the first method (dispersal > gene flow), common routes to confirm a role for adaptive divergence are (i) demonstrating similar patterns in multiple independent replicates (i.e., parallel evolution), (ii) showing that dispersers have traits expected to be maladaptive in the new environment, and (iii) examining particular reproductive barriers tied to adaptation (see below). In the second method (environmental differences negatively correlate with gene flow), it is important to statistically control for nonecological factors (e.g., barriers, distance, distinct lineages) that might correlate with environmental differences (e.g., Ogden and Thorpe 2002; Crispo et al. 2006). In the third method (adaptive differences negatively correlate with gene flow), it is important to rule out the possibility of the opposite casual pathway (i.e., increasing gene flow can reduce adaptive divergence; Räsänen and Hendry 2008).

These genetically based methods have the benefit of looking at overall reproductive isolation in nature. They thereby circumvent concerns about whether or not specific reproductive barriers accurately predict overall reproductive isolation and whether or not experimental assays of reproductive barriers are realistic (see below). But other concerns are nevertheless present. First, estimates of gene flow and dispersal are often imprecise and biased (Whitlock and McCauley 1999; Abdo et al. 2004; Faubet et al. 2007). Second, the relative success of dispersers between environments can be influenced by factors other than adaptive differences, such as inbreeding (Ingvarsson and Whitlock 2000; Ebert et al. 2002). Third, regions of the genome that are not under divergent selection (the very regions targeted when examining "neutral genetic markers") might flow relatively freely between populations. For example, Nosil et al. (2008) found that only about 10% of amplified fragment length polymorphism (AFLP) loci had diverged between populations of insects that were clearly adapted to different host plants. Alternatively, divergent selection on parts of the genome might cause a generalized barrier to gene flow across the rest of the genome (Grahame et al. 2006), although the strength and consistency of this barrier are uncertain (Gavrilets and Vose 2005; Thibert-Plante and Hendry 2009; Nosil et al. 2009a). These and other complications mean that it can be tricky to infer ecological speciation from neutral genetic markers — an issue that we are actively investigating (X. Thibert-Plante and A. Hendry, unpublished data).

I close this section by addressing the apparent paradox that some authors infer ecological speciation is likely when gene flow is *high* between populations adapted to different environments (e.g., Dudycha 2004; Smith et al. 2005; Calsbeek et al. 2007). This argument initially seems to be opposite to the one presented above — that adaptive divergence should reduce gene flow — but the idea here is that divergent selection must be very important if adaptive divergence is present despite high gene flow. In truth, these two opposing predictions represent two expected phases of ecological

speciation: first comes adaptive divergence and then reproductive isolation (although the two can feedback throughout the sequence; Räsänen and Hendry 2008). It nevertheless remains true that demonstrating ecological speciation requires the demonstration that adaptive divergence ultimately reduces gene flow.

Examining the ecological basis for particular reproductive barriers

One problem encountered when interpreting the above integrated measures of reproductive isolation is uncertainty regarding whether adaptive divergence is the ultimate cause. This inference can be aided by examining particular reproductive barriers expected to follow from adaptive divergence. Many such barriers are possible (Schluter 2000; Coyne and Orr 2004; Rundle and Nosil 2005), but only a few are frequently examined. I here summarize methods for assessing some of these more commonly studied barriers. Afterward, I discuss a variety of methodological considerations in using these methods to infer ecological speciation.

(1) Habitat preference: Individuals adapted to one habitat type should evolve increased preference for that habitat type over alternative habitat types (Rice and Hostert 1993; Fry 2003). This evolution of habitat preference should reduce the chance that individuals from different habitats (or their gametes) will encounter each other during reproduction. Many studies, particularly in phytophagous insects, have therefore tested the habitat preference of individuals from populations adapted to different habitats. This has been done by testing for nonrandom associations between morphological types and habitat types in nature (e.g., Via 1999) or by presenting individuals with different habitats (e.g., host plants) in the laboratory (e.g., Ferrari et al. 2006).

(2) Natural selection against migrants: When adaptive divergence is present, individuals moving between environments might have reduced survival (i.e., immigrant inviability; Nosil et al. 2005) or fecundity (i.e., immigrant infecundity; Smith and Benkman 2007) relative to residents. Indeed, many studies have examined whether performance (e.g., foraging, growth, survival, offspring production) in a given environment (or when using a given resource) is higher for individuals from that environment than for individuals from other environments (Schluter 2000; Kawecki and Ebert 2004; Hereford 2009). In the specific context of ecological speciation, these predictions have been tested in the laboratory (e.g., Schluter 1993), in field enclosures (e.g., Schluter 1995), and in natural populations (e.g., Via et al. 2000; Lin et al. 2008).

(3) Natural selection against hybrids: If hybrids are phenotypically different from parental types, they might be poorly adapted for either parental environment. A number of studies have therefore tested whether hybrids do not perform as well as locally adapted parental types in the parental environments. Studies of this sort have used artificially generated hybrids in laboratory treatments (e.g., Schluter 1993) or field enclosures (e.g., Schluter 1995) and have monitored the success of naturally produced hybrids in the wild (e.g., Grant and Grant 1996; Gow et al. 2007).

(4) Temporal isolation: The abiotic and biotic features of different environments often have different phenologies. Examples including the timing of the spring plankton bloom,

bud break, flowering, wet or dry seasons, and freshets or droughts. Organisms that depend on these features can then experience divergent selection on their reproductive timing. When reproductive timing is heritable, isolation-by-time results, and organisms can then begin to adapt to their reproductive times (adaptation-by-time; Hendry and Day 2005). Divergence in reproductive timing and adaptation to those times can then jointly reduce gene flow. Studies of temporal isolation have inferred contributions to ecological speciation based on correlations between the timing of a focal species and the timing of its resources (e.g., Thomas et al. 2003) and natural selection on timing in the different environments (e.g., Filchak et al. 2000).

(5) Mate choice: If the traits undergoing adaptive divergence also influence mate choice, then individuals adapted to different environments may prefer to mate with their own type (Schluter 2000). A number of studies have therefore tested whether individuals (usually females) are more willing to mate with individuals (usually males) from similar environments than with individuals from different environments. These experiments have been conducted in controlled trials in the laboratory (e.g., Funk 1998; Rundle et al. 2000; Nosil et al. 2002) or by examining mating patterns in nature (e.g., Huber et al. 2007; Puebla et al. 2007).

One important decision when implementing the above methods is the choice of experimental material. When wild-caught individuals are used, the resulting patterns can reflect some combination of genetic differences and plasticity (e.g., prior experience, imprinting). The distinction is relevant because although both might be important to reproductive isolation in nature, plasticity can potentially make its contribution without any evolutionary differences between groups (see below). More studies should therefore quantify reproductive barriers in the presence and absence of possible plasticity. For example, habitat preference might be examined for individuals of each population type raised in each habitat type (e.g., Nosil et al. 2006), and mate choice could be examined by using both wild-caught and lab-reared individuals.

In all cases, it is important to confirm that the observed reproductive barriers are the result of adaptive divergence. One route to this end is to perform the above tests across multiple independent lineages, each with populations in replicate environments (i.e., a test for the parallel evolution of reproductive barriers). For example, investigators have tested whether benthic female stickleback prefer benthic male stickleback (and limnetic females prefer limnetic males) when the males and females in a trial come from similar or different lakes (Rundle et al. 2000). If benthic females from all lakes prefer benthic males from all lakes over limnetic males from all lakes, then adaptation to these two environments per se has probably contributed to the reproductive isolation seen in nature. Similar experimental designs have been applied to freshwater resident versus anadromous stickleback (McKinnon et al. 2004) and *Timema* walking sticks from different host plants (Nosil et al. 2002). In my opinion, a similar design could be applied (ethics and permits allowing) to testing all of the above reproductive barriers. For example, benthic stickleback from all lakes should perform better while feeding in benthic environments in all lakes than should limnetic stickleback from all lakes.

Testing for parallel reproductive barriers (as above) can be prohibitively difficult or even impossible to implement for some taxa. An alternative (or complement) is to confirm that the specific reproductive barriers are indeed caused by the specific traits that have undergone adaptive divergence. For example, body size is clearly under divergent selection between benthic and limnetic stickleback, and female stickleback often prefer to mate with male stickleback closest to their own size (Nagel and Schluter 1998; Boughman et al. 2005). In addition, beak size is under divergent selection in Darwin's finches, and beak size (along with its pleiotropic effects on song; Podos 2001) influences reproductive isolation (Ratcliffe and Grant 1983; Huber et al. 2007). Other examples included colour patterns in mimetic butterflies (Jiggins 2008) and hamlet fishes (*Hypoplectrus* spp.; Puebla et al. 2007, 2008).

Additional methods have been proposed for confirming that selection against hybrids is the result of adaptive divergence, as opposed to ecologically independent genetic incompatibilities. This verification often takes the form of evidence that hybrids do not have problems in benign laboratory conditions, but it has also been argued that some genetic incompatibilities might only be manifest under stressful natural conditions (Coyne and Orr 2004). Several solutions to this potential problem have been suggested (Rundle and Whitlock 2001; Rundle 2002; Craig et al. 2007); and of course, it remains possible that intrinsic genetic incompatibilities are themselves the result of adaptive divergence. This is harder to demonstrate, but it has been argued from evidence that genes underlying hybrid incompatibilities have been under positive selection (Orr et al. 2004; Presgraves and Stephan 2007; Rogers and Bernatchez 2007).

Even when a reproductive barrier can be confirmed to result from adaptive divergence, inferences about ecological speciation as a whole can still be tricky. One issue is that reproductive isolation is a combination of all potential reproductive barriers, and so the failure to find one barrier does not mean that ecological speciation has not proceeded through some other barrier. On the flip side, demonstrating the presence of one partial reproductive barrier does not mean that ecological speciation has proceeded very far — for several reasons. First, other barriers may be absent. Second, gene flow may be increased through an offsetting reproductive "enhancer" (my term — established antonyms for "barrier" are lacking). For example, colourful low-predation male guppies moving downstream over waterfalls into high-predation sites, where resident males are drab, might have lower survival (because higher colour may increase susceptibility to predators) but higher mating success (because female guppies often prefer more colourful males). Third, specific reproductive barriers are often assessed in artificial situations and may not be similar in other situations, including in nature. For example, assortative mating is seen for freshwater versus anadromous stickleback in some tests (McKinnon et al. 2004) but not in others (Jones et al. 2006, 2008). Fourth, reproductive barriers or enhancers are often asymmetric, constraining gene flow from one group to another while sometimes enhancing it in the reverse direction (e.g., Ellers and Boggs 2003; Forister 2004).

For all of the above reasons, the best studies employing

the reproductive barrier approach examine multiple potential barriers in multiple populations in multiple ecological and geographical contexts (for examples see McKinnon and Rundle 2002; Nosil 2007; Jiggins 2008). It nevertheless remains true that additional potential reproductive barriers and contexts could be examined in all natural systems studied thus far.

The literature

Considering the above methods for generating reasonably robust evidence for or against ecological speciation, I surveyed the literature to address two basic questions. First, how often do published studies assert positive evidence for ecological speciation? This question stems from my own perception that the published literature overwhelmingly argues in support of ecological speciation. Second, what is the strength of evidence for ecological speciation provided by each study? This question considers how often authors have applied the best methods described above and how often those methods have provided support for ecological speciation. The intersection of these two questions informs the possibility that we are currently laboring under an exaggerated view of the ubiquity of ecological speciation. Note that I am not here addressing typical publication bias (e.g., failure to publish conflicting results), although such a bias is certainly present in many aspects of ecology and evolution (Jennions and Møller 2002). Here, however, I am specifically concerned with what one might call "interpretation bias" within those papers that are actually published.

I began by using the key word "ecological speciation" in a topic search in the Institute for Scientific Information (ISI) Web of Science. This search criterion did not recover a complete listing of papers on ecological speciation, particularly those published before the specific term became popular. Thus, my formal literature survey does not include some of the important papers on, for example, leaf beetles (e.g., Funk 1998), *Rhagoletis* (e.g., Filchak et al. 2000), stickleback (Hagen 1967; Schluter 1993, 1995; Rundle et al. 2000), pea aphids (e.g., Via 1999), and walking sticks (e.g., Nosil et al. 2002). However, use of ecological speciation as a keyword should nevertheless be a reasonably objective way to gauge the body of work currently falling under that rubric.

My search revealed 219 records through 22 September 2008, of which 207 were both valid and accessible. Ten of these papers were mathematical models, all of which show that ecological speciation can occur under some, but not all, conditions. Of the remaining 197 papers, 160 ventured a statement in the abstract or discussion as to whether or not their study provided support for the theory of ecological speciation. (The 37 other papers typically had "ecological speciation" as a keyword but did not directly consider the process.) Of these 160 papers, 131 (81.9%) asserted positive evidence for ecological speciation, 17 (11.9%) asserted equivocal or mixed evidence, and 10 (6.2%) asserted negative evidence. Considering only the 132 primary research papers (i.e., excluding reviews, meta-analyses, and laboratory experimental evolution studies), the corresponding values are 82.6% for positive evidence, 9.9% for mixed evidence, and 7.6% for negative evidence.

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In addition to a majority of primary research papers asserting positive evidence for ecological speciation, these papers are often the highest cited. From 1998 to 2005, for example, the nine most cited papers assert positive evidence (Fig. 2). Some additional observations are interesting, provided here with citations updated through 8 April 2009. First, the few highly cited negative papers tended to be cited for other reasons. For example, Seehausen et al. (1999; 55 citations) is frequently cited in reference to speciation by sexual selection, and Hendry and Taylor (2004; 62 citations) is almost always cited in reference to the role of gene flow in constraining adaptation. (To be fair, the most cited paper reporting positive evidence (Hendry et al. 2000; 178 citations) is also often cited for other reasons: rapid adaptation in salmon.) Second, many of the classic ecological speciation papers that did not show up in my keyword search also have very high citations rates: e.g., Hagen (1967; 192 citations); Funk (1998; 83 citations); Via (1999; 142 citations); Rundle et al. (2000; 197 citations); and Nosil et al. (2002; 83 citations). Overall, I conclude that the answer to my first question is that published studies almost always assert positive support for ecological speciation.

I next made my own evaluation of the evidence for ecological speciation in each of the above studies. (In considering the results of this assessment, remember that I do personally think ecological speciation is important.) Of the 132 primary research papers, the taxa most commonly represented were fish (30.3%), insects (28.8%), plants (9.8%), birds (9.8%), gastropods (6.8%), and reptiles–amphibians (6.8%). The large majority (82.6%) of these studies state that their results support ecological speciation, but my own assessment was that studies providing robust support were actually much less common (36.4%) (Fig. 3). Similarly, I felt that some of the studies reporting mixed evidence actually had insufficient evidence to make such a statement. I did, however, agree with all 10 studies reporting mostly negative evidence. I do not provide my detailed assessment of each individual paper, because I feel this would detract from my attempt at generalization and would diffuse criticisms toward specific details rather than generalizations.

My reasons for disagreeing with the assertions of many published papers were several. Most frequently, I felt that studies did not employ methods that allow robust inferences about ecological speciation (i.e., the methods outline above). Instead, they often used methods that, while informative, leave the fundamental questions unanswered. First, many studies concluded ecological speciation simply when different species occupied different environments or used different resources (i.e., they did not provide any direct evidence that the species originated for this reason). Second, some studies demonstrated reduced fitness in hybrids — but did not provide any direct evidence that maladaptation was the reason. Third, some studies found asymmetric reproductive barriers and chose to emphasize the limitations on gene flow in one direction while de-emphasizing the enhancements to gene flow in the other direction. Fourth, some studies showed the parallel evolution of adaptive traits, but did not formally evaluate their contribution to reproductive isolation. Overall, then, many studies seem to be taking "some data consistent with ecological speciation" to mean "our study provides evidence of ecological speciation."

Fig. 2. Total numbers of citations according to ISI Web of Science for individual primary research papers using "ecological speciation" as a keyword, coded by assertions in those papers as to whether their results provided positive (open circles), negative (solid circles), or mixed (triangles) evidence for ecological speciation. I show citations through 22 September 2008, when my literature search stopped, for papers published between 1998 (few used the keyword "ecological speciation" before that year) and 22 September 2008.
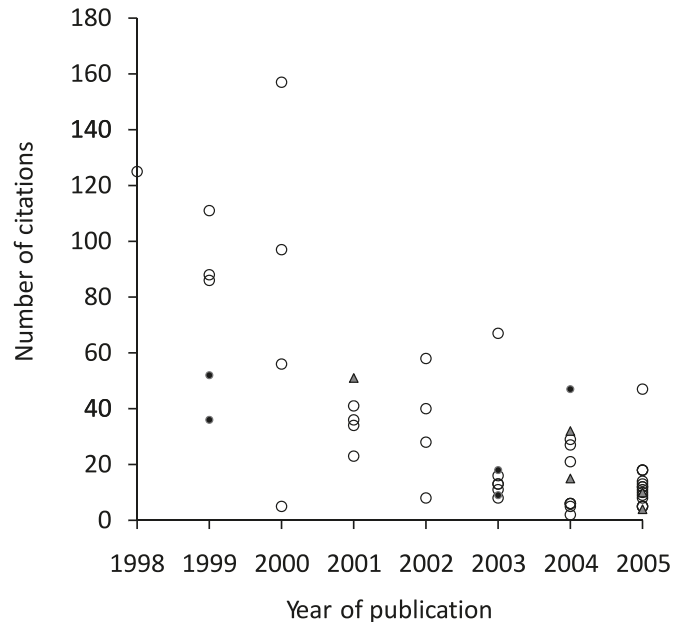
Fig. 3. A comparison of the manner in which the evidence for ecological speciation in primary research papers is interpreted by the original authors (i.e., their assessment) and by myself (i.e., my assessment). The various categories include positive, negative, mixed, and insufficient to make robust inferences.
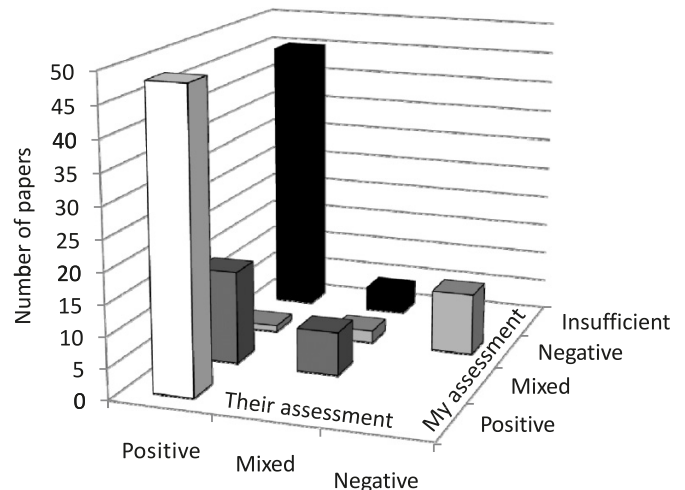
But perhaps I should be more charitable. First, it is difficult to confirm ecological speciation when species can no longer interbreed (see above), and so studies conducted at this taxonomic level are inherently handcuffed. At present, I am not aware of an obvious way around this inferential hurdle. Second, some of the studies did not by themselves provide robust evidence of ecological speciation, but instead

contributed various types of information (e.g., the genetic basis for adaptive traits) to a study system where ecological speciation had been addressed in other papers. It would thus be useful to also do an analysis of the support for ecological speciation within different systems — but my focus in the present paper is different (i.e., how authors interpret evidence rather than the actual frequency of ecological speciation). In this sense, it remains true that these individual studies did not by themselves provide evidence for ecological speciation despite frequent allusion to having done so. Third, the propagation of any new idea will initially be based on positive affirmation that it does actually occur in at least some instances. Once this is established, it then becomes worthwhile to challenge its ubiquity — and the present paper is a part of that effort.

In closing this brief evaluation of the literature, I would like to focus attention on a few papers that did emphasize how ecological speciation is not inevitable and may even be rare in some taxa. First, some authors have not found negative associations between ecological divergence and signatures of speciation (Seehausen et al. 1999; Turgeon et al. 1999; Kozak and Wiens 2006), such as no correlation between genetic and ecological differences (Hendry and Taylor 2004; Crispo et al. 2006). Second, similar ecological contrasts (e.g., benthic vs. limnetic environments) that recur in many different locations only drive ecological speciation in some of these locations (Taylor and McPhail 2000; Lu et al. 2001; Berner et al. 2009). Third, laboratory experiments imposing strong divergent selection only sometimes generate premating isolation (Rice and Hostert 1993; Rundle 2003). Fourth, hybrids between ecologically divergent species can sometimes have a survival or mating advantage (Grant and Grant 1996; Campbell 2003; Pfennig et al. 2007). These studies suggest that the interesting question in ecological speciation is not its contribution in one particular group of populations, but rather in when and why it does and does not proceed to a given extent in different groups. I now turn to a consideration of factors that might influence such progress.

Factors influencing progress toward ecological speciation

I can envision several factors that might influence the extent to which ecological speciation proceeds in a given situation. Studies formally examining these factors in natural populations are rare, and so this section amounts to an outline of alternative hypotheses that will require empirical testing.

Natural selection

The specifics of natural selection might be important in several ways. First, stronger divergent selection is presumably more conducive to adaptive divergence, and therefore to ecological speciation (Schluter 2000; Nosil et al. 2009b), and yet divergent selection that is too strong may prevent colonization of new environments and hence limit the generation of new species (Thibert-Plante and Hendry 2009). Second, increasing the number of trait dimensions (e.g., colour, morphology, physiology, behavior) on which selection acts might increase the potential for reproductive isolation

(Rice and Hostert 1993; Nosil and Sandoval 2008; Nosil et al. 2009b). Alternatively, ecological speciation might be more likely when selection acts on a few key traits, such as beak size in finches (Huber et al. 2007; Ryan et al. 2007; Grant and Grant 2008) and colour in hamlet fishes (Puebla et al. 2007, 2008) and butterflies (Jiggins 2008). Third, even if selection acts against intermediate forms, other nuances of the adaptive landscape may prevent substantial divergence (Hendry et al. 2009a).

Genetics

The ability of adaptive divergence to become coupled to mating isolation probably depends on several genetic properties. First, speciation should proceed most easily when both adaptation and mating isolation involve the same (or closely linked) traits or genes, such as in "magic trait" models (Fry 2003; Gavrilets 2004). These strong genetic associations do seem to attend at least some examples of ecological speciation (e.g., Hawthorne and Via 2001). At the same time, however, many models have shown that ecological speciation can sometimes proceed even when such linkage is absent (Fry 2003; Gavrilets 2004; Thibert-Plante and Hendry 2009). Second, speciation should proceed most easily when reproductive isolation involves the fixation of the same allele (e.g., mate with your own type) in different populations rather than the fixation of different alleles in different populations (e.g., mate with blue in environment one but mate with red in environment two). Yet, models have also shown that speciation can sometimes occur even in the later situation (Fry 2003). Given the wide range of theoretical possibilities, more comparative studies of real organisms are needed.

Geography

Physical separation (i.e., allopatry) has traditionally been thought of as a prerequisite for speciation, because it prevents recombination between diverging gene pools (Mayr 1963; Felsenstein 1981). More recently, however, a number of studies have emphasized how interactions in sympatry or parapatry can enhance divergence and thus initiate, accelerate, or complete ecological speciation. First, competition for shared resources can cause divergent–disruptive selection (Schluter 2000; Rueffler et al. 2006; Doebeli et al. 2007). Second, reduced hybrid fitness due to maladaptation can cause direct selection for positive assortative mating (e.g., reinforcement; Servedio and Noor 2003). Third, genetic exchange between populations can, under some conditions, enhance adaptive potential (see review by Garant et al. 2007) and therefore also ecological speciation (Thibert-Plante and Hendry 2009). For all of the above reasons, some authors now suggest that an intermediate level of dispersal is optimal for adaptive divergence (see review by Garant et al. 2007) and the evolution of reproductive isolation (Nosil et al. 2003). This optimal level may vary through time. For example, a two-phase sequence (allopatry followed by sympatry or parapatry) might be particularly conducive to ecological speciation (Lack 1947; Rundle and Nosil 2005; Grant and Grant 2008); or perhaps different geographical contexts might alternate and reinforce each other multiple times during the course of ecological speciation (Feder et al. 2005).

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Plasticity

Ecological speciation is typically envisioned as resulting from genetically based adaptive divergence, but phenotypic plasticity might also be important (Crispo 2008). On the one hand, some aspects of adaptive plasticity might limit progress toward ecological speciation. First, selection against migrants or hybrids may not occur if plasticity is relatively rapid and cheap. Second, increasing adaptive plasticity can sometimes reduce the potential for adaptive genetic divergence (Sultan and Spencer 2002). Third, adaptive plasticity might reduce selection against dispersal or for local habitat preference (Price et al. 2003; Ghalambor et al. 2007). On the other hand, some aspects of adaptive plasticity may enhance ecological speciation. First, plasticity in one trait that enables the colonization of new environments might increase divergent selection between those environments for other traits. Second, selection against migrants and hybrids might be increased by plasticity that improves the fit of organisms for local environments, if these changes cannot be altered following subsequent colonization of new environments. These different outcomes will depend in part on the costs and developmental limitations to plasticity when organisms disperse at different points in their life cycle.

Mate choice

Mate choice can enhance ecological speciation if it acts in parallel to adaptive divergence. For example, adaptive divergence and mate choice are closely coupled in at least some stickleback populations in different environments (Nagel and Schluter 1998; Rundle et al. 2000; McKinnon et al. 2004). An alternative, however, is that mate choice does not act in parallel to adaptive divergence and therefore constrains progress toward ecological speciation. This might occur when similar patterns of mate choice are favored by selection even in different ecological environments (Schwartz and Hendry 2006). As one example, melanic pigment has diverged adaptively between elevations in the butterfly *Colias philodice eriphyle*, but males prefer less melanic females at all elevations, perhaps owing to sensory bias or species recognition (Ellers and Boggs 2003). As another example, particular male traits (e.g., orange colour) may reliably signal male quality, such as parasite resistance or foraging ability, in multiple environments. Under these circumstances, some aspects of mate choice might be conserved among environments and thus limit ecological speciation despite adaptive divergence.

Mating system

Other aspects of the mating system can also influence progress toward ecological speciation. In particular, mating systems with frequent coercion by males might break the critical link between adaptive divergence and mating isolation. Magurran (1998) has suggested this scenario for Trinidadian guppies because males often employ "sneaky" copulations over which females do not have complete control.

Ecological speciation as a continuum

My main conclusion after reviewing the literature is that progress toward (or away from) ecological speciation is highly variable and is contingent on many factors that need further study. I suggest there is value in considering the position of different populations and species along a speciation continuum ranging between adaptive variation within panmictic populations to complete and permanent reproductive isolation between distinct species (see also Nosil et al. 2009b). One might then define several states along this continuum to discuss important transitions. In such a consideration, it is important to recognize that state transitions are not inevitable (some populations can get stuck in one state) nor always unidirectional (populations can also move from a "higher" state to a "lower" state), and populations can sometimes achieve a higher state without necessarily passing through the lower states. I now explain these states in more detail with some putative examples from north temperate freshwater fishes (Table 2; Fig. 4), supplemented by other taxa.

State 1 is continuous variation without reproductive isolation. Many species show continuous (often unimodal) adaptive variation within populations, with individuals at the extremes specializing on different environments or resources. This state probably characterizes most north temperate fish populations, with some examples coming from variation along the limnetic–benthic foraging axis in lacustrine stickleback (*G. aculeatus*) (e.g., Bolnick and Lau 2008), yellow perch (*Perca flavescens*) and roach (*Rutilus rutilus*) (e.g., Svanbäck et al. 2008), pumpkinseed (*Lepomis gibbosus*) (e.g., Jastrebski and Robinson 2004), and brook trout (*Salvelinus fontinalis*) (Bertrand et al. 2008). A distinguishing feature of this state, as opposed to the next, is that evidence is here lacking for somewhat discrete phenotypic clusters.

State 2 is discontinuous adaptive variation with minor reproductive isolation. Some groups show discontinuous (e.g., bimodal) adaptive variation, with individuals in the different modes specializing on different environments–resources but still showing relatively high gene flow. Potential examples from north temperate fishes include beach–stream sockeye salmon pairs (Hendry et al. 2000; Hendry 2001; Lin et al. 2008), lake–stream stickleback pairs (Hendry and Taylor 2004; Berner et al. 2009), and Arctic char (*Salvelinus alpinus*) morphs in some lakes (Gíslason et al. 1999; Jonsson and Jonsson 2001). A similar situation also may be present for high- versus low-predation guppy populations in Trinidad (Magurran 1998; Crispo et al. 2006; Schwartz and Hendry 2007). A distinguishing feature of this state, as opposed to the next, is that evidence is here lacking for strong reproductive isolation between the phenotypic clusters.

State 3 is discontinuous variation with strong, but reversible, reproductive isolation. Some species show strongly discontinuous adaptive variation (e.g., discrete phenotypic clusters) that is associated with reproductive isolation. Potential examples from north temperate fishes in lakes include sockeye versus kokanee (i.e., landlocked *O. nerka*) (Taylor et al. 1996; Wood and Foote 1996), Arctic char morphs (Gíslason et al. 1999; Jonsson and Jonsson 2001), dwarf versus large freshwater rainbow smelt (*Osmerus mordax*) (Taylor and Bentzen 1993a, 1993b), and benthic versus limnetic stickleback (McKinnon and Rundle 2002; Hendry et al. 2009b). A distinguishing feature of this state, as opposed to the next, is that the reproductive barriers can be reversible,

Fig. 4. Ecological speciation can be conceived as a continuum with several alternative (but overlapping) states as described in the text. Different empirical systems fall in different places along this continuum. Shown are some of the fish species (top to bottom, moving left to right) that may often fall into these different states. Continuous adaptive variation without reproductive isolation has been documented in some populations of roach (*Rutilus rutilus*) (photo: www.sfca.co.uk), pumpkinseed (*Lepomis gibbosus*) (photo: Inspired By Nature, Inc., www.ibnature.com), yellow perch (*Perca flavescens*) (photo: pond.dnr.cornell.edu/), and brook trout (*Salvelinus fontinalis*) (photo: pond.dnr. cornell.edu/). Discontinuous adaptive variation with relatively little reproductive isolation has been seen in some lake–stream stickleback (*Gasterosteus aculeatus*) pairs and beach versus stream spawning sockeye salmon (*Oncorhynchus nerka*) (photos by Andrew Hendry). Adaptive differences with reversible reproductive isolation are perhaps best illustrated by benthic–limnetic species pairs of stickleback (image by Elizabeth Carefoot, Surrey, British Columbia) and different Arctic char (*Salvelinus alpinus*) morphs in some lakes, such as Thingvallavatn (image from Johnston et al. 2004). Adaptive differences with irreversible reproductive isolation are perhaps typified by some dwarf–normal pairs of lake whitefish (*Coregonus clupeaformis*) (image by Steve Johnson, University of Massachusetts). All images are used with permission.

State 1: Continuous adaptive variation without reproductive isolation

State 2: Discontinuous adaptive variation with minor reproductive isolation

State 3: Adaptive differences with reversible reproductive isolation

State 4: Adaptive differences with irreversible reproductive isolation
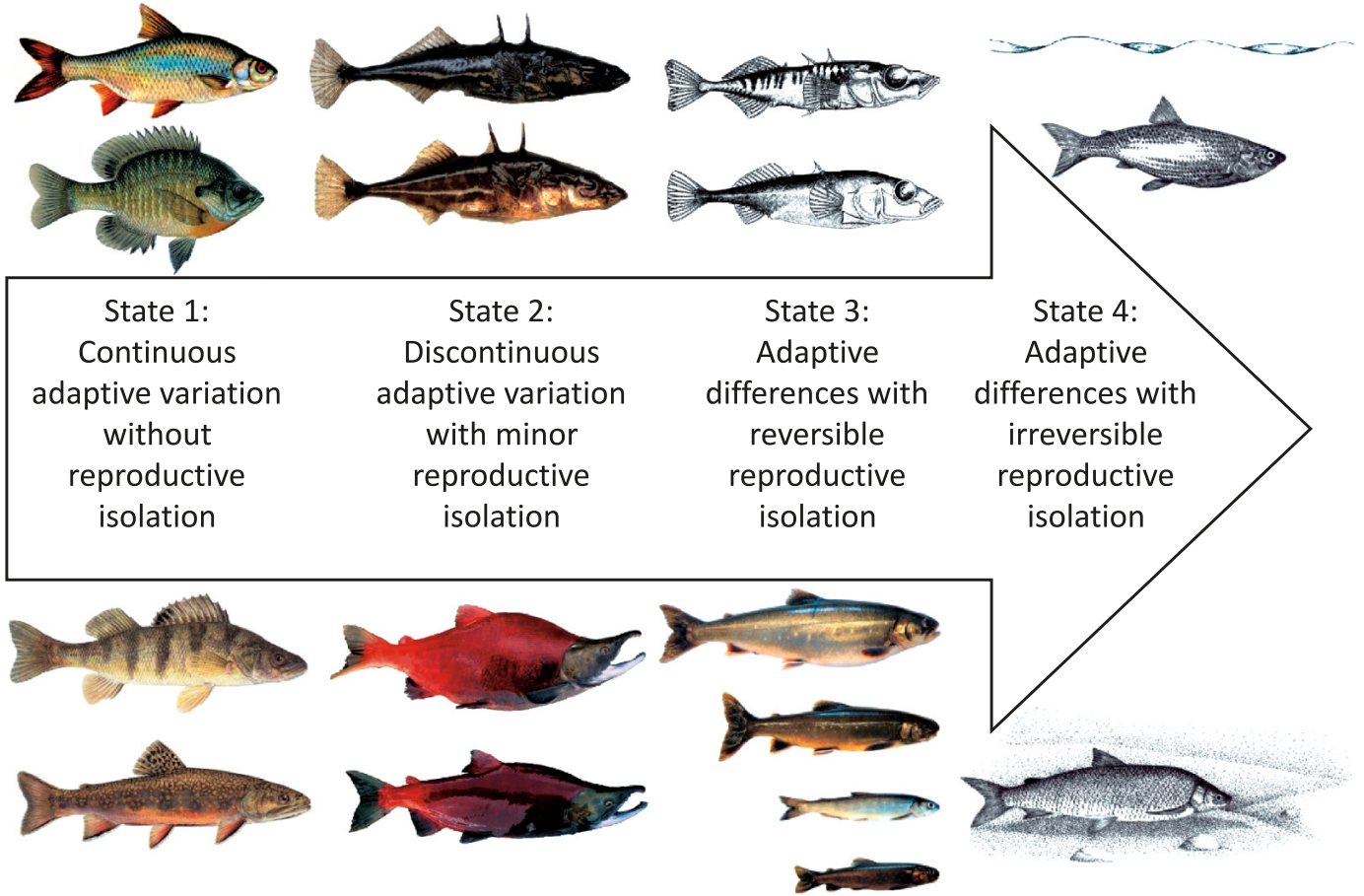
such that a change in ecological conditions could precipitate a collapse back into state 2 or state 1 (Seehausen et al. 2008*a*). Potential examples of such collapses include Lake Victoria cichlids (*Neochromis* spp.) following eutrophication (Seehausen et al. 1999), Darwin's finches following a change in food resources (Grant and Grant 1996; Grant et al. 2004; Hendry et al. 2006), and one of the sympatric benthic–limnetic stickleback pairs following the introduction of signal crayfish (*Pacifastacus leniusculus*) (Taylor et al. 2006).

State 4 is complete and irreversible reproductive isolation. At some point, adaptively divergent groups may accumulate irreversible reproductive barriers, such as genetic incompatibilities. In the context of ecological speciation, these incompatibilities might be the result of divergent selection or they might have arisen for other reasons after gene flow was first reduced owing to divergent selection. In this state, the two

species will probably never fuse again — although one or the other could certainly go extinct. A potential example from North temperate fishes comes from some of the dwarf–normal lake whitefish pairs (Lu et al. 2001; Rogers and Bernatchez 2006, 2007).

The transition from stage 1 to stage 2 thus involves some sort of cluster-generating mechanism, perhaps microhabitat segregation, strong disruptive–divergent selection, or assortative mating. The transition from stage 2 to stage 3 requires the evolution of ecologically based reproductive barriers that remain strong in sympatry–parapatry, such as strong assortative mating and strong selection against migrants and hybrids. The transition from stage 3 to stage 4 requires the evolution of reproductive barriers that are not just ecologically based and so will not depend on the maintenance of specific environmental conditions.

I believe that the way forward in the study of ecological

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speciation is to identify different groups across this continuum within a particular taxon and then study how various factors, including those described above, influence progress along the continuum, as well as transitions between the states. Many taxa might be suitable for such investigations, with some possibilities including walking sticks (Nosil 2007; Nosil and Sandoval 2008), *Neochlamisus* leaf beetles (Funk 1998), some African cichlids (Seehausen et al. 2008*b*), lake–stream stickleback (Berner et al. 2009), dwarf–normal lake whitefish (Lu et al. 2001), and Arctic char (Gíslason et al. 1999; Jonsson and Jonsson 2001).

Conclusion

Ecological speciation has undoubtedly been important in the evolution of biological diversity — and we can now point to a number of concrete examples. Moreover, the existing literature asserts positive support so overwhelmingly that ecological speciation can seem almost inevitable. My examination of the literature, however, reveals that many studies of ecological speciation do not employ methods that allow robust inferences, and those studies that do use such methods often find exceptions and nuances to the standard predictions. In short, although the mechanisms of ecological speciation may be typically initiated by adaptive divergence, the accumulation of reproductive isolation is highly variable. This conclusion is obvious in retrospect given the many instances of divergent selection and adaptive divergence that have not generated new species. I suggest that progress toward (or away from) ecological speciation can be examined along a continuum ranging from continuous variation within panmictic populations all the way to discontinuous variation coupled to complete reproductive isolation. The key now is to explicitly study factors influencing progress back and forth along this continuum.

Acknowledgements

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