

# Non-ecological speciation, niche conservatism and thermal adaptation: how are they connected?

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**Abstract** During the last decade, the ecological theory of adaptive radiation, and its corollary “ecological speciation”, has been a major research theme in evolutionary biology. Briefly, this theory states that speciation is mainly or largely the result of divergent selection, arising from niche differences between populations or incipient species. Reproductive isolation evolves either as a result of direct selection on mate preferences (e.g. reinforcement), or as a correlated response to divergent selection (“by-product speciation”). Although there are now many tentative examples of ecological speciation, I argue that ecology’s role in speciation might have been overemphasised and that non-ecological and non-adaptive alternatives should be considered more seriously. Specifically, populations and species of many organisms often show strong evidence of niche conservatism, yet are often highly reproductively isolated from each other. This challenges niche-based ecological speciation and reveals partial decoupling between ecology and reproductive isolation. Furthermore, reproductive isolation might often evolve in allopatry before ecological differentiation between taxa or possibly through learning and antagonistic sexual interactions, either in allopatry or sympatry. Here I discuss recent theoretical and empirical work in this area, with some emphasis on odonates (dragonflies and damselflies) and suggest some future avenues of research. A main message from this paper is that the ecology of species differences is not the same as ecological speciation, just like the genetics of species differences does not equate to the genetics of speciation.

**Keywords** Mike May Festschrift · Calopteryx · Learning · Learned mate preferences · Niche · Sexual conflict · By-product speciation · IR-camera · Thermal imaging · Ectotherms · Sexual isolation

## Introduction

Ecological speciation has been a central topic of study among ecologists and evolutionary biologists for more than a decade. A main starting point was the publication of Dolph Schluter’s highly influential volume *The Ecology of Adaptive Radiation* (Schluter 2000), as well as a number of other highly cited reviews and empirical studies (Bolnick and Doebeli 2003; Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000; Hawthorne and Via 2001; Hendry 2001; Hendry et al. 2007; Jiggins et al. 2001; Langerhans et al. 2007; Rundle et al. 2000; Rundle and Nosil 2005; Nosil et al. 2003; Ramsey et al. 2003). Without doubt, ecological speciation has been a highly successful research paradigm that has stimulated much investigation, and has seemingly provided a straightforward answer to the question of how biological diversity evolves: speciation is largely or mainly the result of divergent selection to different niches of organisms, and ecological interactions such as competition, predation or parasitism drives the evolution of reproductive isolation. These ecological factors lead to the accumulation of new species over time. Today, it is quite clear that ecology often plays some role in speciation, although its importance still remains to be clarified, particularly in evolutionary radiations on continents with complex faunas and floras, as opposed to radiations in the species-poor islands and postglacial lakes that have typically been the focus of study in this area (Schluter 2000).

Although the ecological theory of adaptive radiation has refreshed the field of speciation biology, which had for a

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very long time been dominated by systematists, it has been argued that all research paradigms, however successful they are at the outset, carry within them internal contradictions and inconsistencies, which are accepted initially, but which might emerge during scientific crises (Kuhn 1962). This certainly applies also to the ecological theory of adaptive radiation and ecological speciation. In this article, I will discuss some of the shortcomings and empirical inconsistencies of ecological (niche-based) speciation and suggest some viable alternatives.

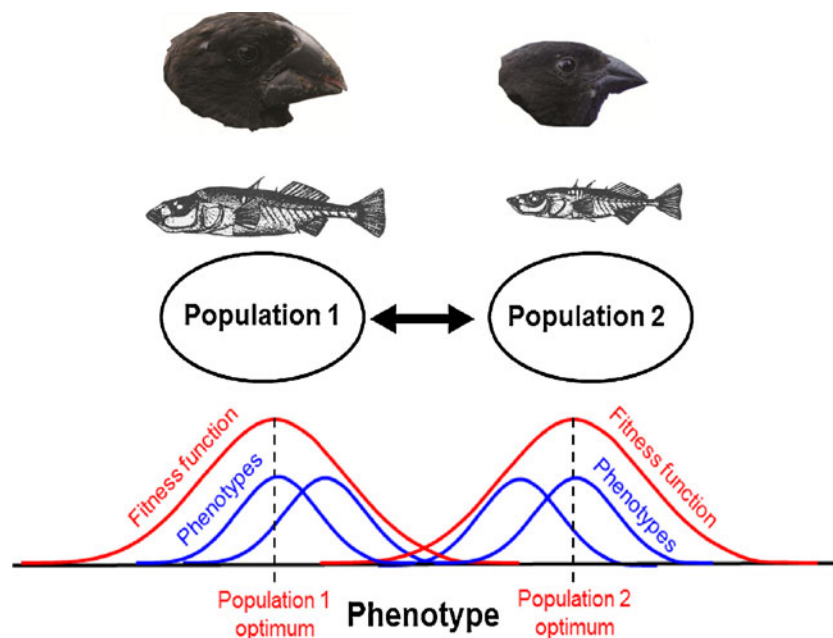
My starting point is that ecological speciation probably does occur and might certainly be important in some systems, but that its role and generality is likely to have been vastly exaggerated by some of its most enthusiastic supporters (Nosil et al. 2005; Nosil 2004, 2008, 2009; Nosil and Crespi 2004; Nosil and Sandoval 2008; Nosil et al. 2002, 2003, 2005, 2008). Many species in nature do certainly differ in ecological characteristics, but such slight or large niche differences are not sufficient evidence, in themselves, to prove ecological speciation or draw conclusions about its relative frequency. This does not mean, however, that we should abandon the study of ecological differences between species (far from it), or that ecology is not important (it is certainly important in many areas outside speciation). However, alternatives to ecological speciation need to be considered more seriously. Some of the criticisms of ecological speciation theory and some of

the points I raise in this article have also been discussed recently by other researchers (Wiens 2004; Wiens et al. 2010; Rundell and Price 2009; Price 2010; Sobel et al. 2010).

Since this special issue of *Organisms, Diversity & Evolution* is published to celebrate the work of Professor Mike May, I will refer frequently to speciation process in odonates (dragonflies and damselflies), given his research interests in this organismal group and his important contributions to our knowledge about their thermal adaptation (May 1976, 1977, 1979). I will also briefly discuss the role of thermal adaptations and niche divergence in odonates, its possible link to speciation (if any) and non-ecological mechanisms for the development of reproductive isolation in this insect group, in particular the potential role of learned mate preferences.

### A critical look at ecological speciation and its assumptions

Ecological speciation states that incipient species adapt to different niches, and that these niches are influenced by the ecological environment, such as resources, predators or abiotic factors. These niche differences in turn lead to ecological speciation and result in fitness trade-offs between environments, since the incipient species occupy different adaptive peaks (Fig. 1). Thus, niche differences lead to



**Fig. 1** Graphical framework for the classical process of ecological speciation resulting from divergent selection towards different adaptive peaks (modified from Schluter 2000 and A. P. Hendry, with permission). Two different fitness peaks (red lines) and a fitness valley in between them arise because of ecological differences, e.g. different food resources or habitats. These different fitness peaks in turn lead to divergent selection (double-headed arrow) in different directions, and

a bimodal phenotype distribution (blue lines), which evolve to match the two different fitness optima. Two classical and often cited examples of organisms that are thought to have evolved through this process above each fitness peak are shown: Darwin's finches (*Geospiza*; differ in bill size and bill shape) and benthic and limnetic sticklebacks (*Gasterosteus*; differ in gill raker number, dorsal spines and body size)

divergent natural selection, which pulls the two incipient species apart. Reproductive isolation in this scheme develops either as a correlated response to divergent selection, so-called “by-product speciation” (Rice and Hostert 1993), or as a result of selection on mate preferences themselves, due to poorly adapted hybrids with low fitness in intermediate environments, i.e. reinforcement (Servedio and Noor 2003). In contrast, ecological speciation differs from a more traditional view on speciation, promoted by the architects of the “Modern Synthesis” (primarily Ernst Mayr and Theodosius Dobzhansky), who emphasised intrinsic genetic incompatibilities caused by epistatic genetic interactions that were more or less unrelated to the external ecological environment (so-called “Dobzhansky-Muller incompatibilities”; Schluter 2000; Coyne and Orr 2004; Gavrillets 2004).

There are at least three critical assumptions that have to be fulfilled before we can claim that a particular taxon or organismal group evolved by means of ecological speciation. First, niche differences between incipient species have to exist, and these differences must be of sufficient magnitude to lead to divergent selection that can drive speciation. Second, these niche differences must persist for a sufficiently long time so that reproductive isolation has a reasonable chance to evolve. In animals, this usually requires dozens or hundreds of generations, when fast (Hendry et al. 2007), but might more often require a much longer time, such as 1–2 million generations (Coyne and Orr 2004). In plants, where various genetic mechanisms such as polyploidization and/or hybridization sometimes more or less instantaneously lead to reproductive isolation, the situation might be different (Schluter 2000). But for ecological speciation to have a chance, the adaptive peaks that separate two incipient species must be relatively stable over a long period of time. This seems somewhat difficult, given our knowledge of the dynamic nature of adaptive landscapes (Calsbeek et al. 2012; Hansen 2012) and the fact that selection might often fluctuate strongly between generations (Grant and Grant 2002; Siepielski et al. 2009). Third, ecological differentiation must evolve before or alongside reproductive isolation, and reproductive isolation is largely or entirely the result of ecological divergence (Nyman et al. 2010).

If not all of these three rather stringent criteria are fulfilled for a particular organismal group, one cannot conclude safely that ecological speciation has been involved in the diversification of that clade. Hence, it is crucial to test not only predictions of ecological speciation theory, but also its underlying assumptions before making any claim about the generality and frequency of ecological speciation in nature. I argue that these three assumptions are not always fulfilled and that ecological speciation might not be as important as has been claimed recently (see also Nyman et al. 2010). I discuss this view in the light of some empirical examples from various taxonomic groups, but with a focus on animals.

## A note on the geography of speciation and definition of the niche

This paper is not focused primarily on the geography of speciation, and the arguments I put forward are applicable to both allopatric, parapatric and sympatric speciation. It should be noted that ecological speciation is not the same as sympatric speciation, in spite of the fact that this connection has often been made implicitly by some researchers and in some volumes (Dieckmann et al. 2004). On the contrary, ecological speciation—a process that is independent of geographic setting—can take place both in allopatry (when isolated populations differ in ecology and are subject to divergent selection), in parapatry or in sympatry (e.g. when different feeding niches or resources are exploited; Schluter 2000). The critical issue addressed in this paper is thus not primarily the geographic setting where speciation takes place, but rather the role of ecology in the speciation process. Allopatric speciation could thus be entirely non-ecological (e.g. accumulation of Dobzhansky-Muller incompatibilities as discussed above), entirely ecological (e.g. when environments are radically different leading to strong divergent selection), or result from niche conservatism (Wiens 2004). Allopatric speciation could also be initiated by niche conservatism in its early stages and completed by ecological speciation processes in its later stages (J. J. Wiens, personal communication). Thus, niche conservatism and ecological divergence could both play a role, but at different stages in the speciation process.

In this paper, I will use a generalized and inclusive “Hutchinsonian” niche concept (Peterson et al. 2011). This niche concept includes both aspects of the “Grinnellian niche” (e.g. abiotic factors setting species ranges) and the “Eltonian niche” (e.g. different trophic resources used by sympatric species; Peterson et al. 2011). Other researchers might prefer a more fine-scaled niche concept, and I note that different aspects of the niche can have different roles in ecological speciation. Much past and current thinking in current ecological speciation is focused on trophic niches (Schluter 2000; Rundle and Nosil 2005), whereas the rapidly growing literature on niche conservatism is focused largely on abiotic factors (temperature and humidity) and climatic niches (Wiens 2004). Thus “ecological speciation” has focused largely on only a particular subset of ecology, namely competition over resources such as food, whereas other aspects of ecology have received less attention (but see Kozak and Wiens 2007).

## The challenge from niche conservatism

Here, I equate ecological speciation with speciation that is driven by divergent selection as populations and incipient

species adapt to different ecological niches—a definition that has also been used by other researchers (Nyman et al. 2010). The different niches set by the different environments result in different adaptive peaks, to which phenotypes evolve to match. This results in fitness valleys and trade-offs between adaptation to different environments (Fig. 1). The niches in ecological speciation theory are often assumed to be some food resource that occurs in different microenvironments or habitats, and the phenotypes that evolve are often thought of as feeding structures, such as bill size and bill shape in granivorous birds or gill rakers in postglacial fishes (Fig. 1).

Although this framework is conceptually straightforward, it becomes somewhat difficult to reconcile with recent findings that niches of closely related species are often very similar, i.e. niche conservatism (Wiens 2004; Kozak and Wiens 2006). The existence of strongly conserved ecological niches between closely related species indicates that these taxa have speciated through niche conservatism and its effects in causing population fragmentation and allopatry, rather than because of ecological differences between populations (Wiens 2004; Kozak and Wiens 2006). This seems to conflict with classical ecological speciation theory, where species are typically expected to adapt to radically different niches. There is an ongoing debate about the evolutionary significance of niche conservatism (Losos 2008a, b; Wiens 2008) but nobody denies that it is common for many traits in many different taxa. Therefore, when niche conservatism is strong, it poses somewhat of a challenge to proponents of ecological speciation, as ecological divergence is expected to erase niche conservatism over evolutionary time. The solution to this dilemma might be to focus on phenotypic traits, and to realize that, while some phenotypic traits are likely to be more conserved (e.g. those affecting climatic tolerance and hence geographic distribution), at the same time, other traits, such as those involved in biotic interactions and trophic structures related to feeding niches and diet, might evolve much faster (J. J. Wiens, personal communication, Keller and Seehausen 2012).

### Thermal adaptation in ectotherms and its role in speciation

In ectothermic animals, such as amphibians, reptiles and arthropods, important aspects of the niche can be attributed largely to organismal tolerance of various abiotic factors such as temperature and humidity (Wiens 2004). Temperature in particular is of fundamental importance to ectotherm fitness (Deutsch et al. 2008). Some limited but increasing evidence suggests that temperature is often important in explaining local adaptation between populations within a species, as well as differences between closely related species in thermal tolerance (Keller and Seehausen 2012).

Temperature has often been involved directly or indirectly in some of the Earth's most notable mass extinctions, such as the late Permian mass extinction about 250 million years ago (Huey and Ward 2005). If temperature is so important to ectotherm fitness and has been involved in causing mass extinctions, what then is its role in the more creative evolutionary process of speciation, particularly as a driver of reproductive isolation? Recent studies on biodiversity dynamics based on fossil series indicate a link between extinction rates and temperature change, but the link to speciation is less clear (Mayhew et al. 2008). Moreover, even when such patterns are found in the fossil record, they are, by necessity, correlative and might be attributed to temperature only indirectly, as are latitudinal gradients in extant species diversity (Erwin 2009).

Recently, Keller and Seehausen (2012) reviewed the limited evidence for a link between local adaptation to thermally divergent habitats and the development of reproductive isolation. They identified 16 putative cases among plants and animals where thermal adaptation was strongly implicated between pairs of closely related taxa, but concluded that the evidence that thermal adaptation had driven reproductive isolation as a by-product was very limited and hence that we cannot yet draw any general conclusion that temperature has played a major role in ecological speciation (Keller and Seehausen 2012). They also found that most of the cases reviewed were thermal adaptation along parapatric environmental gradients, rather than differences between taxa in allopatry or sympatry. In contrast, Struwe et al. (2011) recently quantified allopatric and sympatric niche divergence in relation to temperature and other abiotic factors in the plant family Gentianaceae in Brazil. They concluded that most thermal niche divergence was between allopatric taxa and nodes, compared to sympatric taxa and nodes (Struwe et al. 2011). In conclusion, there is clearly a need for quantitative studies of closely related taxa and thermal adaptation differences in both sympatry (between isolated species upon secondary contact), in allopatry and along parapatric thermal gradients. The importance to speciation of thermal gradients, such as elevational gradients, can also differ between tropic and temperate areas (Kozak and Wiens 2007). There is also some indication that temperature could play some role in affecting postzygotic interactions through genotype-by-sex-by-environment interactions, epistasis and the effects on thermal adaptation and performance in hybrids (Wade et al. 1999).

If temperature does play a major role in ecological speciation, we would expect closely related species to have different thermal niches, and a tight association between cladogenesis and divergence in thermal habitats in comparative studies. To my knowledge, few such systematic and phylogenetically explicit studies have been undertaken (but see Kozak and Wiens 2007). Comparative phylogenetic

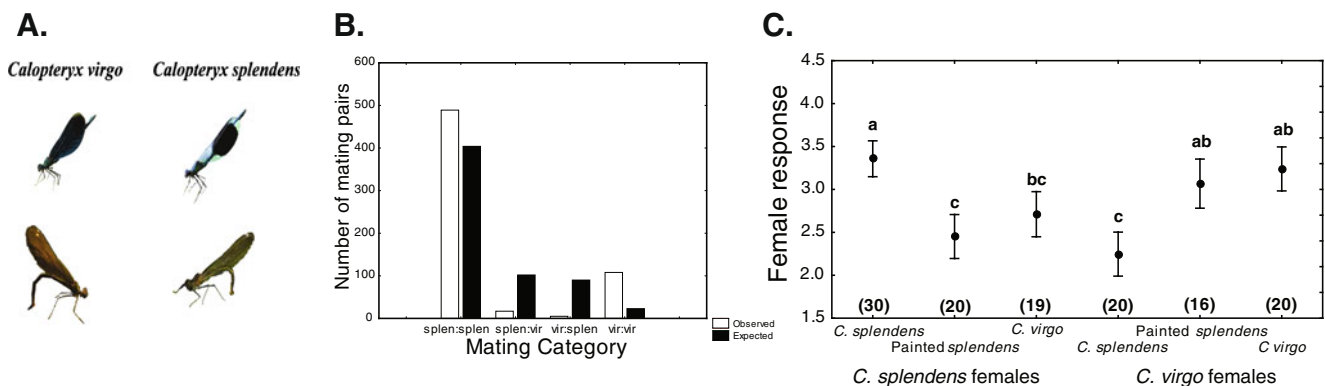


studies of niche conservatism in Hyliid frogs have revealed that speciation might be promoted by time (“time for speciation effect”), rather than by climate per se, as high species richness is found in those biogeographic regions where taxa invaded a long time ago and hence have had plenty of time to diversify and speciate (Wiens et al. 2011). In other studies of amphibians, however, species diversity seems to be linked to the rapid evolution of climatic niches, such as in tropical regions (Kozak and Wiens 2010a), whereas climatic niche conservatism might be more important in driving speciation in temperate regions (Kozak and Wiens 2006, 2007, 2010b). However, even if we accept some role for temperature in promoting speciation, it still seems difficult to view thermal niches in the same way as the foraging niches that have typically been the topic of study in ecological speciation (Fig. 1). Thermal niches might not be as easy to monopolise, and specialise on, as discrete food niches (Keller and Seehausen 2012), even though it has been shown recently that climatic niche evolution can also be influenced by biotic interactions (Kozak and Wiens 2010a).

In contrast, in some cases closely related and sympatric species might have very similar thermal niches. For instance, in calopterygid damselflies, two congeneric species (*C. splendens* and *C. virgo*) are strongly reproductively isolated from each other (Fig. 2), yet their thermal niches at sympatric sites are almost identical (Fig. 3). I have quantified the thermal niches in these and other odonate species using the relatively novel technique of thermal imaging (infrared, IR-camera) in the field (Fig. 3a,b; see Saastamoinen and Hanski 2008 for a general description of the method). These two damselfly species are quite old and shared a common ancestor about

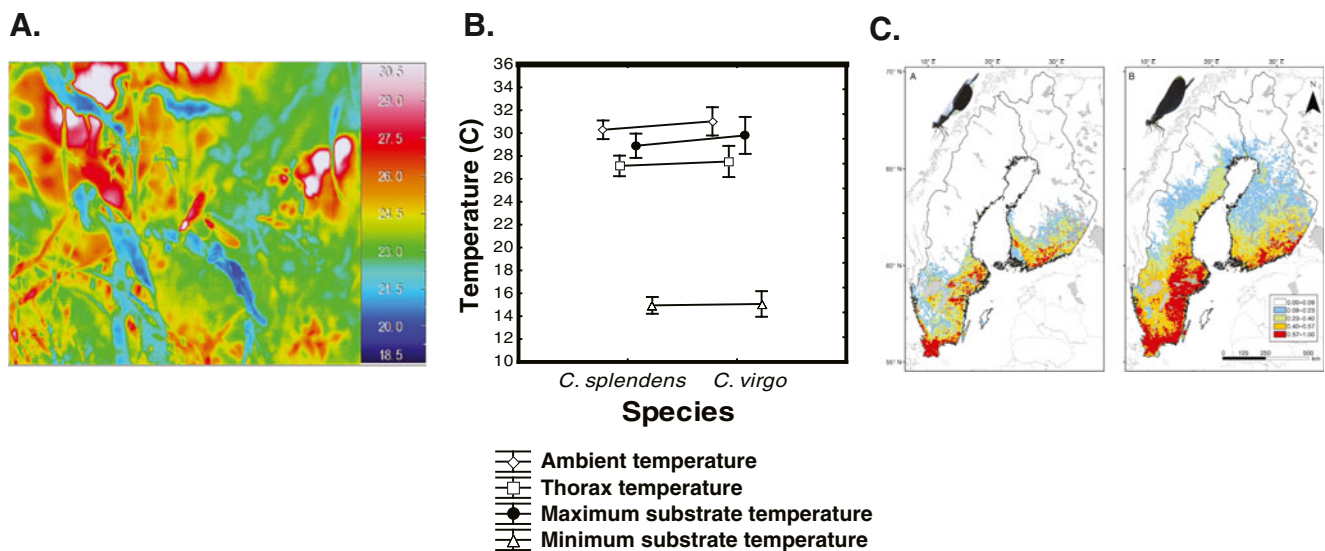
3.7 million years BP, although they are not sister species (Dumont et al. 2005). They have co-existed as reproductively isolated species in Europe for at least 1.6 million years, (Dumont et al. 2005). Given their old age, one would expect these two congeneric species to have had plenty of time to adapt to different thermal niches and to have evolved substantial phenotypic differences. However, both these species, as well as other members of the *Calopteryx* clade, are remarkably similar in morphology, with the exception of male secondary sexual traits, and are often subject to similar natural selection pressures on morphology due to predation (Svensson and Friberg 2007). Moreover, at the same sympatric site, where their thermal niches are almost identical and not significantly different from each other (Fig. 3), their flight season and daily activity pattern differ only slightly (E. I. Svensson, unpublished data). This modest ecological niche divergence suggests that their reproductive isolation was not driven by adaptation to different thermal niches. Both species have a very similar and shared realized thermal niche, which is probably related to their physiological tolerances to heat and cold (Fig. 3).

The conclusion from these mechanistic field studies at local sites is also largely supported by more formal niche modeling analysis, where we have used field observations and geo-referenced museum specimens obtained from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>) and the Swedish database The Species Portal (“Artportalen”: <http://www.artportalen.se/>) to model the distributions and habitat requirements of the two species (Fig. 3c; Wellenreuther et al. 2012). The beautiful Demoiselle (*C. virgo*) reaches further north than the more southern



**Fig. 2** a–c. Strong sexual isolation between two congeneric species of demoiselles (Odonata: *Calopteryx*) in Europe. **a** These two species differ mainly in the male’s secondary sexual character (amount of wing melanization), while females of both species are very similar. The banded demoiselle (*C. splendens*) has about 50 % of the wing covered with melanin, whereas the beautiful demoiselle (*C. virgo*) has almost the entire wing melanized. **b** At a sympatric locality in southern Sweden (“Klingavälsåns Naturreservat”) these two species are strongly sexually isolated from each other and mate assortatively, although a few heterospecific pairs are found. **c** Experimental manipulation of

wing colour to make *C. splendens* males resemble *C. virgo* males show that premating isolation between these species is determined almost entirely by this visual cue. The two female species responses to three male phenotypes (unmanipulated *C. splendens*, painted *C. splendens* and *C. virgo*) are shown. Different letters above each category show significant differences from Tukey’s post hoc tests, and sample sizes are shown below each category. Note that in both species, females are not able to distinguish between “real” *C. virgo* males and painted *C. splendens* males (i.e. *C. virgo*-like male phenotype). Modified from Svensson et al. (2007)



**Fig. 3** a–c. Weak interspecific thermal niche divergence between phenotypically and ecologically similar demoiselles (*C. splendens* and *C. virgo*). **a** Thermal images obtained from infrared (IR) photographs of demoiselles can be used to obtain accurate estimates of body temperatures, ambient temperatures and substrate temperatures. Here a copulating pair of *C. virgo* (pair in middle of figure). Note the white colour of the male, which reveals his substantially higher body temperature than the substrate (temperature scale on the right). **b** Interspecific niche divergence between *C. splendens* and *C. virgo* in minimum thorax temperature, substrate temperature, maximum substrate temperature and ambient temperature at a sympatric site (“Klingavälsåns Naturreservat” in southern Sweden). There is no

significant thermal niche difference between these two species (MANOVA with three different thermal response variables. Effects of species: Wilks Lambda=0.978;  $F(4,120)=0.542$ ,  $P=0.70$ ). **c** Geographic northern range limits in Fennoscandia for *C. splendens* and *C. virgo* and geographic variation in environmental suitability, obtained from GIS-based niche modeling, geo-referenced field observations and museum specimens (Wellenreuther et al. 2012). Red colour indicates suitable habitats based on Environmental Niche Modelling (ENM). Note that these two species have highly overlapping geographic ranges, except that *C. virgo* reaches further north. Also, note that *C. splendens* range (and niche) is “nested” within the range (and niche) of *C. virgo* in southern Fennoscandia

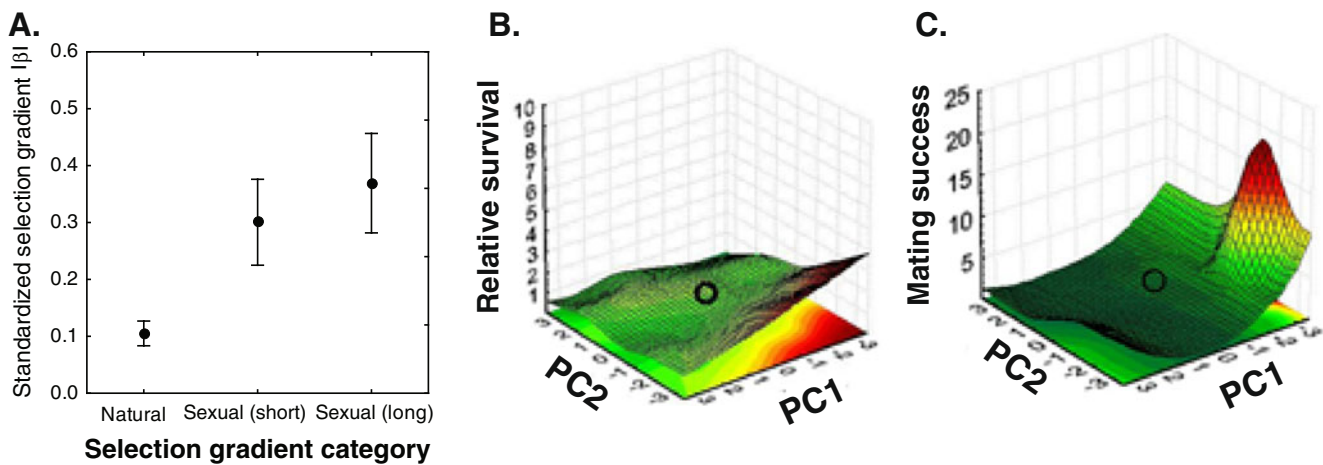
Banded Demoiselle (*C. splendens*), presumably because this species is more cold-tolerant than *C. splendens*. There are slight but significant environmental niche differences when analyzing occurrence data from the entire Fennoscandian range (Wellenreuther et al. 2012). However, these slight environmental niche differences disappear almost entirely when the analysis is restricted to the zone in sympatry in southern Fennoscandia, where their environmental niches are almost identical (Wellenreuther et al. 2012). More generally, other genera of odonates, such as *Enallagma* in North America, have extremely similar habitat requirements (McPeck and Brown 2000). As a consequence, at local ponds and lakes in eastern North America, there are often several sympatric and ecologically extremely similar species that differ only slightly, if at all, in their environmental niches (McPeck and Brown 2000). As a result of these species being close to ecologically equivalent, community dynamics in this insect assemblage is largely consistent with the so-called neutral theory of biodiversity (Hubbell 2001; Siepielski et al. 2010).

### Decoupling between reproductive isolation and ecological differentiation

Evidence is now accumulating from different radiations that suggests that, contrary to the prediction from ecological

speciation theory that they should be closely connected, reproductive isolation and ecological differentiation are often decoupled. For instance, strongly reproductively isolated but ecologically similar co-existing species are found in birds, snails, amphibians, fish and moths (Rundell and Price 2009; Arnegard et al. 2010; Imada et al. 2011) as well as in some insect groups such as odonates (McPeck et al. 2008).

Many congeneric odonate species are ecologically extremely similar and have largely overlapping niches (see previous section), yet they are strongly reproductively isolated from each other (Figs. 2 and 3). Their strong ecological similarity but well-developed reproductive isolation implies that reproductive isolation did not evolve as a result of niche-based divergent natural selection. Instead, structures involved in reproduction, such as morphological mating structures (McPeck et al. 2008) and visual colour signals involved in intra- and intersexual selection and sexual isolation (Svensson et al. 2007, 2010) vary substantially between species and/or populations in spite of extensive gene flow (Svensson et al. 2004). Field estimates of natural and sexual selection on morphological traits have revealed that divergent sexual selection is stronger on the same set of traits than divergent natural selection (Svensson et al. 2006). More formal analyses of selection gradients and fitness landscapes (Fig. 4) confirm the general picture that divergent sexual selection is more important than niche-based



**Fig. 4** a–c. Sexual and natural selection on 12 morphological traits in the banded demoiselle (*C. splendens*), based on field observations of mating success of marked individuals. **a** Sexual selection is stronger than natural selection across all traits, irrespective over which time scale sexual selection is measured (“short” vs “long”, referring to minutes and hours vs days). **b** Natural selection on the morphological

traits (the first two principal components, PC1 and PC2) reveals itself as a quite flat fitness landscape, as opposed to the more peaked landscape of sexual selection on the same traits (c). Divergent sexual selection is therefore a stronger force than natural selection in these damselflies. Modified from Svensson et al. (2006)

divergent natural selection in this group (Svensson et al. 2006). Antagonistic mating interactions (McPeck and Gavrilets 2006; Gosden and Svensson 2009) as well as sexual conflict and sexual selection (Gosden and Svensson 2008) are clearly important features of odonate ecology and mating system biology, and are likely to have been involved as drivers of speciation in this group.

Turning to other animal groups, some avian radiations have been put forward as prime examples of ecological speciation driven by niche-based divergent selection. The classical examples of ecological speciation in birds are found mainly in groups that are largely, although not entirely, granivorous, such as Darwin’s finches (Fig. 1) and conifer specialists like North American Crossbills (*Loxia*; Benkman 2003). However, the situation for insectivorous birds might be quite different (Price 2010), as insects are not as easy to partition into discrete niches as seeds (T.D. Price, personal communication). For instance, *Phylloscopus*-warblers in the Himalayas seem to have evolved reproductive isolation in allopatry and only secondarily become sympatric, whereafter they diverged in body size, colouration and song to avoid interspecific competition (Richman and Price 1992; Price 2010). Thus, today’s ecological differences between these species were not causally involved as drivers of reproductive isolation, as these niche differences evolved *after* the evolution of isolation had already been achieved in allopatry. The situation might be similar in *Ficedula*-flycatchers in Europe, which have most likely evolved reproductive isolation in allopatry (Saetre and Saether 2010), and have only recently come into contact where their diet overlap is still extensive (Wiley et al. 2007). These flycatchers are also ecologically extremely similar also in other respects, such as habitat choice, although slight

differences do exist (Vallin 2011). In summary, and to my knowledge, there is no insectivorous avian radiation that is a likely candidate for ecological niche-based speciation, unlike the situation for granivorous birds and fish (Fig. 1).

#### Learned mate preferences and their role in nonecological speciation

Speciation, at least in some organismal groups (see discussion above), cannot be explained convincingly and entirely as the role of ecological and niche-based divergent selection. How then could reproductive isolation develop in those cases when ecological differences between taxa are small or modest? Obviously, so-called “by-product speciation”, by which reproductive isolation develops as a correlated response to niche-based divergent selection as organisms adapt to different habitats (Rice and Hostert 1993), cannot operate when speciation is non-ecological or non-adaptive. In principle, divergent sexual selection could lead to reproductive isolation as a by-product [Lande 1981; Day classified as ecological speciation (Schluter 2000)]. However, one factor that could in principle generate reproductive isolation in the absence of environmental differences between populations is learning and learned mate preferences. Learning is gaining increased attention among evolutionary biologists (Lachlan and Servedio 2004; Verzijden et al. 2005; Servedio et al. 2009). Learning has previously been demonstrated experimentally mainly in animals with parental care, through the mechanism of parental imprinting, in many species of birds (Price 2008) and also in mouth-brooding cichlid fish (Verzijden and ten Cate 2007). More recently,

mate preference learning has also been demonstrated in animals that lack parental care, where it develops through male–female mating interactions during sexual ontogeny, e.g. in some species of fish (Magurran and Ramnarine 2004), fruit flies (Dukas 2004, 2005), spiders (Hebets 2003) and damselflies (Svensson et al. 2010).

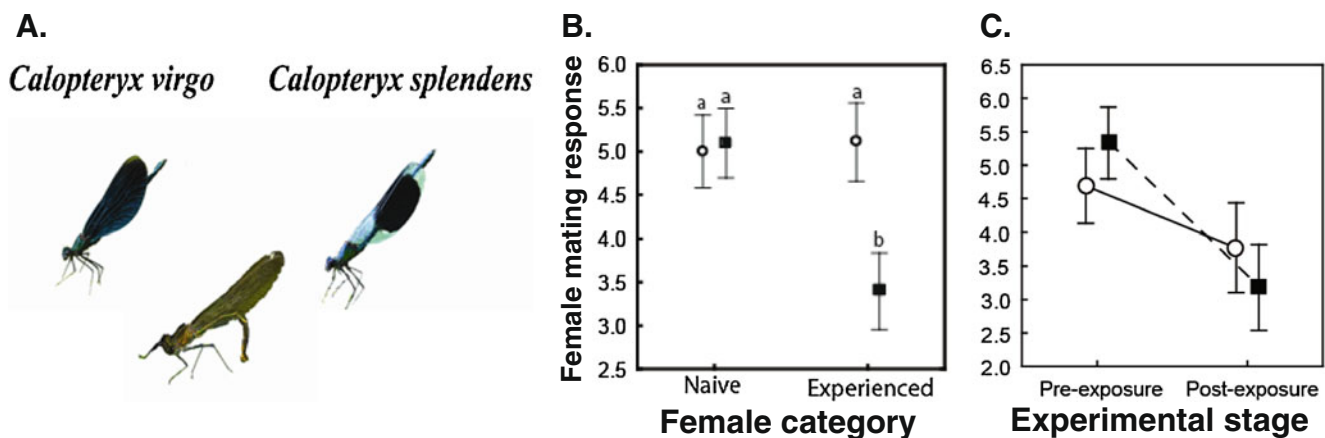
For instance, females of the banded demoiselle (*C. splendens*) do not discriminate between con- and hetero-specific males when sexually naïve, but species recognition instead develops gradually and after physical exposure to conspecific (*C. splendens*) or heterospecific (*C. virgo*) males (Fig. 5). However, it is important to stress that learning could play a role both when species are sympatric (through the development of discrimination learning) and when allopatric (through the development of association learning of local males; Wellenreuther et al. 2009). The significance of learned mate preferences to nonecological speciation is not only that learning could ensure faster and more efficient development of reproductive isolation compared to purely genetic mate preferences (Servedio et al. 2009), but also that mate preferences could potentially diverge also without the pronounced ecological or phenotypic divergence that is required by ecological speciation. For a possible example at the intraspecific level where association learning of local males might have been involved in developing discrimination against immigrants, see Svensson et al. (2006). The existence of sibling species, i.e. species that are phenotypically almost identical yet strongly reproductively isolated (Damm et al. 2010), is difficult to reconcile with ecological

speciation, but entirely consistent with nonecological speciation and possibly also with association learning for non-visual cues in local males.

### The ecology of species differences is not the same as ecological speciation

The major message from this article is not that ecological speciation is impossible or that it does not occur sometimes, but rather that more rigorous and stringent tests are required to infer its past signature as well as the ongoing operation of the process. It should hopefully be clear now that demonstrating ecological differences between reproductively isolated taxa that are currently sympatric is *not* enough to demonstrate ecological speciation. Yet such associations between ecology and reproductive isolation are often claimed as supporting ecological speciation (Wellenreuther et al. 2008). This inference is incorrect, because such ecological niche differences between reproductively isolated species could very well have evolved *after* the development of reproductive isolation was already achieved (Keller and Seehausen 2012), as has obviously been the case in some avian groups (Price 2010).

However, the opposite finding, i.e. that strongly reproductively isolated species show limited ecological niche divergence and high phenotypic similarity (Figs. 2, 3, and 4) *could* indicate that ecological speciation is unlikely to have driven the evolution of reproductive isolation, either



**Fig. 5** a–c. Mate preferences and species recognition is learned, rather than purely genetic among females of the banded demoiselle (*C. splendens*). **a** Female *C. splendens* discriminate between con- and hetero-specific males based on a visual cue: the amount of wing melanization (see also Fig. 2). Females (middle, below the two males) were allowed to choose and/or physically interact with either con- or hetero-specific males, and their mate responses were recorded (**b**, **c**). **b** Species discrimination is not present among sexually naïve *C. splendens* females that have been isolated since emergence from males of both species, but is present among sexually experienced females that have interacted with males in the field. Filled symbols Heterospecific

(*C. virgo*) males, open symbols conspecific (*C. splendens*) males. Not only do sexually experienced females discriminate against heterospecific males, sexually mature females show an equally strong response to males of either species. **c** Two hours of physical exposure in outdoor cages to either heterospecific males (black symbols) or conspecific males (white symbols) are sufficient to influence female mating responses. Note that female mating responses decline after exposure to both types of males, but the decline is steeper when females are exposed to heterospecific males than to conspecific males. Modified from Svensson et al. (2010)



directly or indirectly. This tentative conclusion would hold irrespective of whether speciation took place in allopatry, sympatry or parapatry. Therefore, and because of this asymmetry, it might be easier to argue against ecological speciation in many cases than to show convincingly that it has been important. A counter argument from proponents of ecological speciation might be that when observed niche differences are small or even non-existent (Fig. 3), some important aspect(s) of the niche might not have been measured or quantified. Although this argument could be valid in principle, it has the unfortunate effect that many cases of niche similarity might be dismissed on these grounds, thus discounting ecological speciation as an explanation, but it is impossible to discount completely, as it also almost impossible to guarantee in any study that all relevant aspects of the environment have been identified and correctly quantified. It is also important to emphasize that the existence of niche differences in themselves are not sufficient to make a case for ecological speciation, but these niche differences must have had (or have) the potential to cause reproductive isolation, either directly or indirectly.

To demonstrate the process of ecological speciation convincingly, one actually needs to show that ecological differences indeed preceded, or evolved jointly with, the evolution of reproductive isolation, i.e. that niche differences were causally involved as drivers of isolation. I suspect that experimental field studies alone will never provide convincing evidence for such a cause-and-effect relationship between ecological divergence and reproductive isolation. Instead we might have to also include comparative phylogenetic studies to demonstrate a link between cladogenesis and niche divergence. One such example comes from a recent study on 125 species of Hymenoptera, which found that, although niche shifts between larval diets on plants did occur, the frequency of such niche shifts was low compared to the actual number of speciation events (124; Nyman et al. 2010). The authors concluded that most speciation in this group was probably due to non-ecological speciation in allopatry, and they downscaled a previous estimate of speciation events caused by ecological niche shifts from 50–60 % to 20 % (Nyman et al. 2010).

Another possible avenue in evaluating ecological vs non-ecological speciation is to use experimental evolution to study if divergent selection does (Rice and Hostert 1993) or does not (Rundle 2003; Kwan and Rundle 2010) drive reproductive isolation between different environments. Interestingly, several studies on *Drosophila* have failed to demonstrate the emergence of reproductive isolation as a correlated response to divergent selection in different ecological environments (Rundle 2003; Kwan and Rundle 2010). These negative findings do partly support the arguments I have put forward in this paper that the importance of ecological speciation in nature might have been somewhat

overstated until quite recently (see also Nyman et al. 2010). One final approach to demonstrate ecological speciation that has been advocated in the past is detailed study of the genetic architecture of loci involved in ecological adaptation and loci involved in reproductive isolation. Close genetic linkage between ecological and isolating loci has often been taken as evidence for ecological speciation (Hawthorne and Via 2001; Funk et al. 2006). Yet, such associations at the genetic level do not necessarily prove causation more than associations in field studies as they are purely correlative and suggestive. The main message here is that finding ecological differences between reproductively isolated species does not prove ecological speciation, just as the genetics of species differences does not necessarily tell us much about the genetics of speciation (Coyne and Orr 2004).

## Conclusions

In this article, I have taken a critical look at ecological speciation. I have suggested that this process might have been overrated in importance and that non-ecological and non-adaptive speciation processes need to be considered more seriously. These criticisms are not entirely new, but have been made recently by several other researchers (Rundell and Price 2009; Sobel et al. 2010). Sobel and co-workers have argued that ecology is likely to have played some role in most speciation events, but that this does not necessarily make the term “ecological speciation” useful or informative (Sobel et al. 2010). Instead, they suggest that we should talk about the “biology of speciation”, as “ecological speciation” is too broad an umbrella and too vague to be informative. Schluter (2009) and Nosil and Flaxman (2011) have argued for “mutation-order speciation” as a true alternative to ecological speciation, as this process is entirely dependent on intrinsic factors (temporal order and timing of favourable mutations), with no role for the external environment or ecology. However, it seems that if the term ecological speciation is to be useful, it cannot be so broad that it includes all aspects of the external environment with all its diverse abiotic and biotic factors. I therefore suggest that the term ecological speciation should be restricted to speciation resulting from organisms becoming adapted to different niches through divergent natural selection (Nyman et al. 2010; Fig. 1). This narrower scope of ecological speciation would not include all aspects of the environment, such as male–female mating interactions, sexual selection, sexual conflict and learning, as these factors do not necessarily make organisms better adapted to their local environments and niches and hence their local adaptive peaks (Fig. 1).

Some evolutionary biologists may disagree with this more narrow definition, arguing that ecological speciation should require only divergent selection between environments, irrespective of its ecological cause (i.e. sexual or natural selection,

A. P. Hendry, personal communication). However, I would object strongly to such a broad, and overly inclusive, definition of ecological speciation, since it loses its meaning if other forms of speciation are so infrequent that they would require no environmental differences at all. Finally, if reproductive isolation precedes ecological divergence rather more than vice versa (as predicted by ecological speciation theory), some interesting new avenues of research open up, and reproductive isolation will remain at the centre stage of speciation biology. For instance, is reproductive isolation a prerequisite for sustained and accumulated evolutionary change, as argued by Futuyma and others (Futuyma 1987; Eldredge et al. 2005)? Thus, reproductive isolation might facilitate further morphological change, since it reduces gene flow between contemporary populations that would otherwise swamp phenotypic divergence (Uyeda et al. 2011). Uncoupling reproductive isolation from ecological divergence does not necessarily imply that ecology is not important or that we shall not study it further, but only that speciation is not always a result of niche-based divergent selection.

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