

INVITED REVIEW

Thermal adaptation and ecological speciation

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Abstract

Ecological speciation is defined as the emergence of reproductive isolation as a direct or indirect consequence of divergent ecological adaptation. Several empirical examples of ecological speciation have been reported in the literature which very often involve adaptation to biotic resources. In this review, we investigate whether adaptation to different thermal habitats could also promote speciation and try to assess the importance of such processes in nature. Our survey of the literature identified 16 animal and plant systems where divergent thermal adaptation may underlie (partial) reproductive isolation between populations or may allow the stable coexistence of sibling taxa. In many of the systems, the differentially adapted populations have a parapatric distribution along an environmental gradient. Isolation often involves extrinsic selection against locally maladapted parental or hybrid genotypes, and additional pre- or postzygotic barriers may be important. Together, the identified examples strongly suggest that divergent selection between thermal environments is often strong enough to maintain a bimodal genotype distribution upon secondary contact. What is less clear from the available data is whether it can also be strong enough to allow ecological speciation in the face of gene flow through reinforcement-like processes. It is possible that intrinsic features of thermal gradients or the genetic basis of thermal adaptation make such reinforcement-like processes unlikely but it is equally possible that pertinent systems are understudied. Overall, our literature survey highlights (once again) the dearth of studies that investigate similar incipient species along the continuum from initial divergence to full reproductive isolation and studies that investigate all possible reproductive barriers in a given system.

Keywords: adaptation, climate change, temperature, speciation

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Ecological speciation

Virtually all environments are spatially heterogeneous. Environmental variation can be observed even within bacterial culture vials in the laboratory (e.g. Rainey & Travisano 1998) and is certainly much more pronounced in nature. Under such circumstances, we often observe that divergent selection leads to the evolution of locally adapted forms where, in a given environment, local

individuals outperform nonlocal ones (Kawecki & Ebert 2004). Ecological speciation may result if this adaptive divergence causes some form of reproductive isolation (e.g. Schluter 2000, 2009; Rundle & Nosil 2005; Hendry *et al.* 2007). Specifically, ecological speciation requires 'an ecological source of divergent selection, a form of reproductive isolation, and a genetic mechanism linking the two' (Rundle & Nosil 2005). Such a relationship is possible for different types of reproductive barriers, including both pre- and postzygotic mechanisms.

Empirical examples of (incipient) ecological speciation exist from a range of animals and plants. Very often

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adaptive divergence involves biotic interactions like the use of different food resources or, in the case of outcrossing plants, different pollinators (see e.g. examples in Nosil *et al.* 2005; Lowry *et al.* 2008). However, abiotic environmental variables may also be relevant and may underlie adaptive divergence, for example, between populations from clearly distinct habitats like high vs. low altitude (Hall 2005) or dry vs. wet microhabitats (Rieseberg *et al.* 1999). In this review, we investigate whether differences in the thermal environment can be expected to drive ecological speciation and whether pertinent empirical examples exist in the literature.

Local adaptation to thermal environments

Ambient temperature is expected to have pervasive effects in nature. First and foremost, it directly affects biochemical reaction rates (e.g. Kingsolver 2009), which has potentially important physiological consequences especially in organisms that do not maintain a stable internal temperature (e.g. plants and poikilothermic animals). Temperature effects extend from the molecular level to the whole organism and include, e.g. growth, development, reproductive timing and the speed of locomotion (Angilletta 2009). Finally, the thermal environment is expected to have indirect effects by influencing the biological interactions experienced by an organism. Species richness and individual abundance tend to decrease with altitude and latitude (Rahbek 1995; Hawkins *et al.* 2003), which means that individuals from cooler environments are, on average, exposed to fewer and fewer kinds of competitors, predators and parasites. Furthermore, some parasites and pathogens have been found to be less virulent at lower temperatures (e.g. Marcogliese 2008). On the other hand, resources are generally scarcer at lower temperatures (Krug *et al.* 2009).

With the exception of very few 'habitats' like, e.g. hot springs or the bodies of homeothermic animals, the thermal environment at a given location is typically not stable in time. In many regions of the world, temperature differences are particularly pronounced between seasons and many organisms avoid particularly unsuitable conditions, for example, through migration, dormancy or hibernation (Marchand 1996). Fluctuations on shorter timescales, including diurnal variation, may be more difficult to avoid and may impose 'obligations that only generalists can meet' (Kawecki & Ebert 2004; Bell 2008, p. 300). Indeed, it has been proposed that the increased thermal stability of tropical environments (especially across seasons) may facilitate thermal specialization and may thus contribute to the higher species diversity observed in the tropics (Janzen 1967; Ghalambor *et al.* 2006).

Different models predict somewhat different effects of environmental variation on optimal performance breadth (i.e. the extent of specialization). In particular, depending on the exact model assumptions, performance breadth was found to be more strongly influenced by how stable the thermal environment was within generations or between generations, respectively (Lynch & Gabriel 1987; Gilchrist 1995 summarized in Angilletta 2009). However, both models agree that the performance of an organism should be maximal at the temperature it experiences most often (Angilletta 2009). Consequently, we would expect to observe local adaptation where organisms from cold and warm environments should have different thermal optima, i.e. their performance would peak at lower and higher temperatures, respectively.

Local adaptation to different thermal habitats has indeed been demonstrated by a number of studies of conspecific populations (e.g. Dahlhoff & Rank 2000; Hoffmann *et al.* 2002; Kavanagh *et al.* 2010). Also, organisms often actively seek out ambient temperatures that match the conditions experienced in their natural habitat (Korol *et al.* 2006; Vinsálková & Gvozdík 2007; Matute *et al.* 2009). In fact, it is often found that, in the absence of ecological constraints, conspecific individuals prefer very similar thermal environments (e.g. Angilletta 2009), i.e. that there is a final thermal preferendum which is fairly independent of an individual's previous experience (Fry 1947). Finally, in several plants and animals, the frequency of particular genetic variants shows patterns that are consistent with the action of divergent selection between thermal habitats (e.g. McAllister *et al.* 2008; Cheviron & Brumfield 2009; Manel *et al.* 2010; Poncet *et al.* 2010). However, in most cases, local adaptation does not lead to speciation (Nosil *et al.* 2009) and hence one cannot predict speciation from the observation of local adaptation alone.

At the other end of the 'speciation transect', after speciation is completed, species typically differ in many ecological, phenotypic and genetic dimensions (Seehausen 2009). This makes inferring causality from observing current species differences difficult if not impossible. For example, the physiological tolerance of congeneric species often corresponds to the thermal environment they typically experience in nature (e.g. Hilbish *et al.* 1994; Somero 2002; Hilton *et al.* 2008; Ohlberger *et al.* 2008) but these differences may have evolved after the establishment of reproductive isolation because of other ecological or nonecological factors. While these examples show that different conspecific populations or closely related species often are adapted to different thermal habitats, it is less clear whether such thermal adaptation is an important driver of speciation in nature.

Reproductive isolation driven by thermal adaptation

The evidence for such a mechanism from experimental evolution studies is mixed. In several experiments, *Drosophila* spp. were kept under different thermal conditions and, after many generations, the flies from these different environments were tested for evidence of reproductive isolation. While Kiliias *et al.* (1980) found that flies tended to mate assortatively with individuals from the same environment (same temperature-humidity-light conditions), Ehrman (1964, 1969) did not find evidence of prezygotic isolation as a by-product of divergent adaptation. The traits underlying assortative mating in the experiment of Kiliias *et al.* (1980) are unknown but prezygotic isolation was independent of the environment in which it was assessed. Along somewhat different lines, Dolgin *et al.* (2006; but not Correia *et al.* 2010) found that the mating success of *D. melanogaster* males was higher in the temperature environment they were adapted to, probably as a result of overall better condition.

These studies suggest that, sometimes, reproductive isolation may evolve as a by-product of divergent adaptation, in this case to different thermal environments. Under such **by-product speciation**, divergent adaptation is thought to come first, and some form of premating isolation emerges only as a consequence (not as a driver or facilitator) of divergence (Schluter 2001; Coyne & Orr 2004). If mate choice is based on a trait under divergent ecological selection, assortative mating can follow 'magically' (i.e. pleiotropically; e.g. Servedio *et al.* 2011) from thermal adaptation, although reproductive isolation still requires the build-up of linkage disequilibria between these mating signals and female preferences for them. A by-product mechanism can involve the accumulation of both pre- and postzygotic barriers to reproduction. It is the only possible route to ecological speciation in allopatry, but it may also occur in parapatry under certain conditions (see e.g. Schluter 2001). Upon secondary contact between two diverging lineages, prezygotic barriers may be strengthened through reinforcement to prevent the formation of (intrinsically or extrinsically) unfit hybrids (Schluter 2001; Servedio & Noor 2003).

Alternatively, theoretical models propose that disruptive selection against a niche generalist may drive the evolution of distinct groups of genotypes and, ultimately, speciation in parapatry or sympatry through a **reinforcement-like process** (e.g. Coyne & Orr 2004). This probably requires competition-mediated specialist-generalist trade-offs, and in contrast to a by-product mechanism, reproductive isolation is directly favoured by selection against the production of intermediate genotypes (e.g. Schluter 2001). In fact, assortative

mating may provide the impetus for sympatric divergence in response to disruptive selection, and ecological differentiation and premating isolation may then increase in concert (e.g. Coyne & Orr 2004). Such a mechanism is different from classical reinforcement in that the fitness of intermediates is reduced from the start by direct ecological selection while, under classical reinforcement, there is thought to be an initial accumulation of incompatibilities, typically in allopatry (Schluter 2001).

At first glance, competition-mediated disruptive selection may seem unlikely in the context of thermal adaptation because temperature, like many other physical factors, is not a depletable resource. This means that the evolutionary change within a population in response to temperature-mediated selection will not affect the intensity or the direction of the selection pressures (e.g. Bell 2008, p. 332). What can be used up, however, is space or resources in a preferred thermal microhabitat, which could lead to strong competitive interactions between (conspecific or heterospecific) individuals. Such competition may indeed be prevalent in nature as suggested, for example, by the observation that the thermal niches of species may shift in the presence of interspecific competitors (Magnuson *et al.* 1979), i.e. that there is character displacement in the thermal niche. Along similar lines, Bertolo *et al.* (2011) found that brook charrs from a single lake exhibit different thermal tactics which potentially reduces niche overlap between conspecifics.

In the following, we first discuss the different possibilities for ecology-based barriers to reproduction between populations adapted to different thermal regimes. This discussion is structured by the temporal order in which specific barriers act. We then perform a literature survey where we investigate whether examples of particular barriers have indeed been documented in nature.

Differentially adapted individuals do not meet in nature

Reproductive isolation automatically follows if ecologically diverging populations do not normally come into contact. Such isolation may result if (i) two taxa have an allopatric distribution, (ii) populations evolve reduced dispersal, (iii) individuals preferentially move between similar environments (Edelaar *et al.* 2008), or (iv) immigrants are maladapted and many of them die before they are able to reproduce (Nosil *et al.* 2005). Such immigrant inviability could potentially be accentuated between thermal environments because many factors co-vary with temperature (see above) and, consequently, divergent selection may act on a range of

different traits. All of these barriers can evolve as a by-product of ecological divergence and, because differentially adapted individuals do not come into contact, reinforcement-like processes are not possible.

Differentially adapted individuals meet but do not mate

Speciation can also result if (i) behavioural or (ii) temporal barriers prevent mating between differentially adapted populations. In the following discussion, we focus on traits with a pleiotropic role in thermal adaptation and mate choice. While such a link is thought to facilitate the evolution of prezygotic barriers, it is not a prerequisite.

It may, at first, seem unlikely that divergent thermal adaptation could pleiotropically change traits underlying behavioural mate choice. Temperature adaptation probably often relies on physiological changes involving, for example, the composition of cell membranes or the thermal stability of enzymes (e.g. Angilletta 2009). It is hard to see how such differences could be important for mate choice, where phenotypic divergence is likely to play a greater role than cryptic genetic differences (Stelkens & Seehausen 2009). One possibility is that mate choice is based on an indicator trait that is affected by overall body condition which indicates how well an individual is adapted to a given environment (van Doorn *et al.* 2009).

Sometimes, thermal adaptation also does produce visible phenotypic differences. One of the most prominent examples may be that of melanism. In some ectotherms, particularly insects, individuals from high altitudes/latitudes are darker than individuals from warmer climates (Clusella Trullas *et al.* 2007). Altitudinal or latitudinal clines are also often observed for body size (Bergmann's rule states that body size in cold climates usually exceeds that in warmer climates), and in some groups, most prominently *Drosophila* spp, it has been demonstrated that these patterns have a genetic basis (reviewed e.g. in Partridge & Coyne 1997). Divergent selection on body size between populations could promote reproductive isolation if individuals preferentially mate with similarly sized partners (size assortative mating; e.g. McKinnon *et al.* 2004). However, the role of body size differences may not be straightforward and, sometimes, natural and sexual selection may even act in opposite directions. This pattern is illustrated, for example, by the *Drosophila* selection experiment of Dolgin *et al.* (2006): Overall, in a given environment, locally adapted males enjoyed greater mating success than nonadapted males. However, female preference for large males reduced the advantage of smaller warm-adapted males over larger cold-adapted males at high

temperature. Insect cuticular hydrocarbons (CHC) provide a final example of a (olfactory) trait for which a pleiotropic role in temperature adaptation and mate choice has been suggested (Greenberg *et al.* 2003; but see also Coyne & Elwyn 2006; Greenberg *et al.* 2006).

Clinal variation (typically with altitude or latitude) may also be observed for phenological traits. Several insect species, for example, have two generations per year in warm environments and only one in colder climates (e.g. Sauer *et al.* 2003; Scriber & Ordning 2005), and temporal divergence of the reproductive period can directly lead to reproductive isolation between populations (e.g. Ordning *et al.* 2010). In principle, such differences would not need to be genetically based but could be down to purely environmental effects (see also Coyne & Orr 2004, pp. 202–203). Instant temporal isolation could result, for example, if two populations live in different thermal environments but require the same number of degree-days to complete larval development or if the same thermal thresholds trigger specific life-history events. It is unclear how common such scenarios are in nature. More typically, phenological traits may evolve in response to local (thermal) environments (e.g. Berner *et al.* 2004; Dambroski & Feder 2007; Ragland & Kingsolver 2007).

Finally, we could envisage an indirect effect of the thermal environment on mate choice. As mentioned above, we often observe an association between the diversity and/or virulence of parasites and pathogens and ambient temperature (Marcogliese 2008). This means that the selection pressures acting on the immune system of an organism may be quite different in cold and warm environments. In vertebrates, a central role in immune defence is played by the major histocompatibility complex (MHC), and we could expect adaptive divergence between environments with different pathogen/parasite communities if particular MHC alleles exhibit at least some specificity against particular challenges. In fact, such examples exist (Palti *et al.* 2001; Miller *et al.* 2004), and the MHC has been implicated in local adaptation in a range of species (Bernatchez & Landry 2003). At the same time, the MHC can play an important role in mate choice (reviewed e.g. in Pieltney & Oliver 2006). This pleiotropic effect could promote assortative mating between populations experiencing parasite-mediated divergent selection between (thermal) environments (Summers *et al.* 2003; Eizaguirre *et al.* 2009).

Individuals mate but produce inviable or infertile offspring

Finally, reproductive barriers may act after the formation of the zygote through (i) environment-mediated

(i.e. extrinsic) selection against intermediate genotypes or (ii) intrinsic genetic incompatibilities between the two parental genomes. In the case of extrinsic postzygotic isolation, a role of thermal adaptation can be expected whenever intermediate genotypes suffer from reduced fitness because they are maladapted to both parental environments.

Intrinsic postzygotic barriers, on the other hand, are typically thought to be independent of the environment (but see e.g. Wade *et al.* 1999; Demuth & Wade 2007 for examples of environment-dependent expression of intrinsic incompatibilities). Their evolution is generally considered under the classical Bateson-Dobzhansky-Muller (BDM) model (Orr 1996) which explains how two isolated populations accumulate a series of genetic changes some of which will be incompatible if ever brought together in hybrids between the two diverging lineages (e.g. Coyne & Orr 2004). The BDM model strongly emphasizes the role of epistasis, i.e. incompatibilities of alleles at different loci. Such epistatic effects may involve different nuclear loci but also, and perhaps more importantly, interactions between nuclear and cytoplasmic genes (i.e. chloroplast and mitochondrial genomes). The nuclear and the mitochondrial genomes are highly interdependent. Mitochondrial transcription and replication, for example, rely on machinery encoded entirely by nuclear genes, and ATP production through oxidative phosphorylation involves both nuclear and mitochondrial genes (e.g. Gershoni *et al.* 2009).

This interdependence may cause strong coevolutionary dynamics because changes in one gene may entail compensatory changes in another. As a result, strong BDM effects could be observed in hybrids where nuclear and mitochondrial components from different populations are incompatible and mitochondrial function is compromised. This divergence is typically thought to be driven by the mitochondrial genome. First, mutation rates are considerably higher in mitochondrial than nuclear genes. Secondly, unless the mating system is highly skewed, the mitochondrion has a smaller effective population size and, as a result, is more strongly affected by random genetic drift (Ballard & Whitlock 2004). Evidence for mitochondrial-nuclear co-adaptation is available from a range of plants and animals (reviewed in Dowling *et al.* 2008), and it has even been postulated that mitochondrial divergence and the associated changes in the nuclear genome could act as an 'engine for speciation' (Dowling *et al.* 2008).

Interestingly, several authors have also proposed that mitochondrial variation may be directly involved in adaptation to thermal environments (see Dowling *et al.* 2008, and references therein). The postulated mechanistic link is through the general effect of temperature on

enzyme function, which of course encompasses the respiratory enzymes partly encoded by mitochondrial genes. Specifically, the optimal conformational stability of an enzyme is expected to vary with temperature (Somero 1995). An additional link between ambient temperature and the mitochondria is postulated by the oxygen and capacity limited thermal tolerance hypothesis (Pörtner 2001) which states that the thermal limits of an organism will be determined by the (minimum and maximum) temperatures at which aerobic respiration fails to meet the energy demands of the organism (e.g. Angilletta 2009). Against this background, we can easily envisage a scenario where the thermal environment drives adaptive changes in the mitochondrial genome (and associated nuclear genes) and where these differences then underlie BDM incompatibilities in interpopulation hybrids.

Literature survey

Methodology

Ecological speciation is a continual process initiated by divergent natural or divergent ecology-based sexual selection between conspecific populations (Rundle & Nosil 2005; Maan & Seehausen 2011), followed by the accumulation of differences, typically in many ecological, phenotypic and genetic dimensions, then complete and finally irreversible reproductive isolation (Hendry *et al.* 2009; Seehausen 2009). Ideally, we would study the complete series from the beginning of adaptive divergence to the completion of speciation in the same taxon, referred to as a speciation transect (Seehausen 2009) or speciation continuum (Hendry *et al.* 2009). However, such continua have been studied in less than half a dozen taxa (Nosil *et al.* 2009), and we did not find a single case related to thermal adaptation. Therefore, we structured our literature search so as to combine evidence for the microevolutionary process of temperature-mediated divergent adaptation and the emergence of (partial) reproductive isolation with evidence for macroevolutionary patterns of temperature-mediated coexistence of closely related species.

First, we performed a literature survey to identify taxa where adaptation to divergent thermal regimes may have led to the evolution of (partial) reproductive isolation between populations. Closely following the approach of Nosil *et al.* (2005), we used ISI Web of Knowledge to conduct a search for papers on 'local* adapt*'. The journals included in the survey of Nosil *et al.* (2005) were searched only for articles published after 2003, and additional journals were searched across all years to cover 33 journals deemed to be particularly relevant for our purpose: American Naturalist, Biologi-

cal Journal of the Linnean Society, Biology Letters, BMC Biology, BMC Ecology, BMC Evolutionary Biology, BMC Genetics, BMC Plant Biology, Current Biology, Ecology, Ecology Letters, Evolution, Evolutionary Ecology, Evolutionary Ecology Research, Genetica, Genetics, Heredity, Journal of Biogeography, Journal of Ecology, Journal of Evolutionary Biology, Journal of Plant Sciences, Molecular Ecology, Nature, New Phytologist, Oecologia, Oikos, Philosophical Transactions of the Royal Society B Biological Sciences, PLoS Biology, PLoS Genetics, PLoS One, Proceedings of the National Academy of Sciences of the United States of America, Proceedings of the Royal Society B Biological Sciences, Science. This search produced a list of 907 articles. Based on the abstracts, we retained only studies on closely related (i.e. congeneric), outcrossing species of plants or animals for which some component of fitness (i.e. viability, fecundity) had been assessed in different environments, and where the environmental differences potentially included temperature. This typically involved either common garden or reciprocal transplant experiments. For all taxa in this reduced list, we performed a second literature search for (species name) AND (isolation OR barrier* OR gene flow OR speciat*) and retained only systems for which at least one reproductive barrier was reported in addition to geographic isolation or immigrant inviability. The results from our own search were combined with the systems identified by Nosil *et al.* (2005), for which a significant role of temperature in ecological divergence seemed possible or likely. The information from Nosil *et al.* (2005) was updated based on Lowry *et al.* (2008) and our own literature search to find more recent articles on these taxa. Additional relevant study systems were identified based on Schwartz & Hendry (2006) and Sobel *et al.* (2010) and our own knowledge of the literature.

Second, to recover additional papers dealing with patterns of species differences and isolation, we conducted a search for papers on 'speciation AND temperature', 'speciation AND thermal adaptation' and 'speciation AND thermal niche' in the same 33 journals. We did not limit these searches to recent years because this literature may not have been fully covered by Nosil *et al.* (2005) or Lowry *et al.* (2008). These searches produced 186 hits, 37 of which were retained based on the abstracts.

Results of literature survey

Based on our first literature survey, we identified 26 systems (15 plants, 11 animals) for which local adaptation to different climatic conditions has been suggested. Eight of these showed both evidence of divergent thermal adaptation and (partial) reproductive isolation (taxon name in bold in Table 1a,b). In these cases, fur-

ther evidence suggests that at least some of the morphological or physiological differences between the populations play a role in thermal adaptation. In an additional three systems, temperature is one of several environmental variables differing between habitats (*Gilia capitata*, *Mimulus guttatus*, *Littorina saxatilis*; Table 1a,b). Local adaptation is mostly evidenced as reduced survival of individuals when exposed to an unfamiliar environment either in the field (indicated as immigrant inviability in Table 1) or in the lab (*Lucania* spp., *Tigriopus californicus*). An exception are the *Colias* butterflies where adaptation to different thermal conditions has been suggested for a trait with a less direct link with fitness (flight activity; Ellers & Boggs 2004).

In most cases, the differentially adapted populations are allo- or parapatric because the different (thermal) environments are spatially segregated. Very often, the environment changes in a clinal manner along a gradient, e.g., in altitude (*Colias*, *Ipomopsis*, *Mimulus lewisii*, *Mimulus cardinalis*, *Polemonium*), salinity (*Lucania*), solar radiation (*Drosophila*), or exposure (*Littorina*). In all of these cases, the environmental transition is steep enough to allow some dispersal between environments, and very often, a zone of increased hybridization is observed at some intermediate position in the gradient. In some cases, such as periwinkles (*Littorina*), the environmental transition is geographically sympatric, though by definition not syntopic. Similarly, the habitats of the two fire-bellied toads (*Bombina* spp.) are in some parts of Europe distributed in a patchy and geographically sympatric manner, referred to as mosaic sympatry (Mallet *et al.* 2009), where dispersal between habitats is easily possible (MacCallum *et al.* 1998; Vines *et al.* 2003). In such a mosaic hybrid zone, any component of reproductive isolation because of divergent temperature adaptation would have to be associated with microclimatic rather than latitudinal or altitudinal variation. Only three of the systems are characterized by more or less complete geographic isolation (*Tigriopus*, *Gilia*, *M. guttatus*; Table 1a,b).

Even when dispersal between environments does occur, the actual rate of gene flow is often reduced because of exogenous selection against immigrant genotypes and their hybrid offspring (Table 1a,b). Together, these results suggest that, at least sometimes, the traits involved in local adaptation also directly confer (some) reproductive isolation. Such traits are often considered 'magic' because the evolution of reproductive isolation does not rely on the build-up of linkage disequilibrium between the trait under divergent selection and the trait underlying nonrandom mating (e.g. Maan & Seehausen 2011; Servedio *et al.* 2011).

Do these results suggest that natural selection against maladapted genotypes is the main basis of isolation between populations adapted to contrasting thermal

Table 1 Empirical examples identified in our literature survey. Search 1 (microevolutionary process) identified systems with evidence for both adaptive divergence and (partial) reproductive isolation. (a) plants, (b) animals. Bold type highlights cases where a direct link between adaptive divergence and temperature has been suggested. Search 2 (macroevolutionary process) identified systems where divergent thermal adaptation may underlie the current coexistence of taxa (c). The different barriers are arranged according to the temporal sequence in which they act. The leaf indicates ecology-based barriers.





Organism	Common name	State in speciation continuum	Geography of divergence	Environmental context	Evidence of thermal adaptation 	Immigrant inviability 		Sexual isolation* 	Pollen competition	Intrinsic genetic incompatibilities		Extrinsic postzygotic isolation 	References
						Yes	NA			Yes	Yes		
						General	Cytosuclear						
(a) Plant taxa from search 1													
<i>Gilia capitata</i>	Herbaceous plant	Distinct species	Probably allopatric	Inland vs. coastal habitat	T is one of many variables differing between habitats	Yes	NA	NA	Yes	Yes	NA	NA	Nosil <i>et al.</i> (2005); Lowry <i>et al.</i> (2008)
<i>Ipomopsis aggregata/ tenuituba</i>	Phlox	Incipient species or ecotypes	Unclear (parapatric or secondary contact)	Altitudinal gradient	Different thermal optima for photosynthesis	Yes	Pollinator	Yes	Yes	No (FI)	NA	Yes/HA ⁺	Nosil <i>et al.</i> (2005); Lowry <i>et al.</i> (2008); Wolf <i>et al.</i> (1997); Wu & Campbell (2006); Aldridge & Campbell (2007); Campbell & Waser (2007)
<i>Mimulus guttatus</i>	Monkeyflower	Distinct species	Unclear	Inland vs. coastal habitat	T is one of many variables differing between habitats (moisture, salt spray are considered more important)	Yes	Time	NA	NA	No	NA	Yes/HA ⁺	Hall & Willis (2006); Lowry <i>et al.</i> (2008b)
<i>Mimulus lewisii/ cardinalis</i>	Monkeyflower	Distinct species	Secondary contact	Altitudinal gradient	High altitude form (<i>lewisii</i>) sensitive to heat stress	Yes	Pollinator	Yes	Yes	Yes	NA	NA	Nosil <i>et al.</i> (2005); Lowry <i>et al.</i> (2008); Beardsley <i>et al.</i> (2003)
<i>Polemonium viscosum</i>	Alpine flower	Incipient species or ecotypes	Probably parapatric	Altitudinal gradient	Differences e.g. in leaf morphology which are likely adaptive in different T environments	Yes	Pollinator	NA	NA	NA	NA	NA	Nosil <i>et al.</i> (2005)

Table 1 Continued

Organism	Common name	State in speciation continuum	Geography of divergence	Environmental context	Evidence of thermal adaptation	Habitat preference	Immigrant viability	Sexual isolation*	Sexual isolation [§]	Intrinsic genetic incompatibilities	Extrinsic postzygotic isolation	References	
(b) Animal systems from search 1													
<i>Bombina</i>	Toad	Distinct species	Secondary contact	Ponds vs. puddles	Optimal temperature for larval development differs	Yes	Yes	No	No	Yes	Maybe	NA	Nosil <i>et al.</i> (2005) and Szymura (1993);
<i>Bombina</i>													Szymura (1993);
<i>variegata</i>													Nürnberg <i>et al.</i> (2004); Yanchukov <i>et al.</i> (2006); Hofman & Szymura (2007)
<i>Colias philodice eriphyle</i>	Butterfly	Conspecific population cline	Probably parapatric	Altitudinal gradient	Phenotypic cline (darker individuals at higher altitudes)	NA	Maybe [†]	No (colour)	NA	NA	NA	NA	Ellers & Boggs (2002,2003,2004)
<i>Drosophila melanogaster</i>	Fruitfly	Conspecific populations	Probably parapatric	North-facing vs. south-facing slope ('Evolution canyon' Israel)	Flies from hotter slope are more heat tolerant	Yes	Probably	**	**	NA	NA	NA	Nevo <i>et al.</i> (1998); Korol <i>et al.</i> (2000); Michalak <i>et al.</i> (2001); Schlötterer & Agis (2002); Korol <i>et al.</i> (2006); Rashkovetsky <i>et al.</i> (2006); Pavlicek <i>et al.</i> (2008)

Table 1 Continued











Organism	Common name	State in speciation continuum	Geography of divergence	Environmental context	Evidence of thermal adaptation 	Habitat preference 	Immigrant inviability 	Sexual isolation* 	Sexual isolation [§]	Intrinsic genetic incompatibilities		Extrinsic postzygotic isolation 	References
										General	Cytonuclear		
<i>Littorina saxatilis</i>	Periwinkle	Incipient species or ecotypes	Geographically sympatric, ecologically parapatric	Upper vs. lower shore (Galicia, Spain)	Upper shore ecotype survives better than lower shore ecotype when exposed to sun (main factors probably predation and wave action)	Yes	Yes	Size assortative mating	NA	No	NA	Maybe	Nosil <i>et al.</i> (2005); Cruz & Garcia (2001); Cruz <i>et al.</i> (2004a,b); Rolan-Alvarez <i>et al.</i> (2004); Rolan-Alvarez (2007); Butlin <i>et al.</i> (2008)
<i>Lucania goodei/parva</i>	Killifish	Distinct species	Probably secondary contact	Saltwater/freshwater gradient and latitude	Tentative evidence that local adaptation is driven by salinity x T interaction	NA	NA	**	**	Yes	NA	Yes	Fuller <i>et al.</i> (2007); Fuller (2008); Fuller & Noa (2008)
<i>Tigriopus californicus</i>	Copepod	Conspecific populations	Allopatric	Latitudinal gradient	Thermal stress tolerance depends on latitudinal origin	NA	NA	No	No	Yes	Yes	Yes	Palmer & Edmands (2000); Willett & Burton (2003); Burton <i>et al.</i> (2006); Willett (2010)

Table 1 Continued

Organism	Common name	State in speciation continuum	Geography of divergence	Environmental context	Evidence of thermal adaptation 	Habitat preference 	Immigrant inviability 	Sexual isolation* 	Sexual isolation ^s	Postzygotic isolation [†] 	References
(c) Systems from search 2											
<i>Callipepla californica/gambelii</i>	Quail	Distinct species	Probably secondary contact	Mesic coastal vs. xeric inland habitat	Hybrid zone coincides with climatic (T, precipitation) transition	NA	NA	NA	No	Weak (?)	Gee (2003, 2004, 2005)
<i>Colaptes auratus</i> spp.	Northern flicker	Distinct species	Probably secondary contact	Different climatic regions	Hybrid zone coincides with Great Plains-Rocky Mountains ecotone	NA	NA	NA	Sometimes [#]	No	Moore & Koenig (1986); Moore (1987); Wiebe (2000); Wiebe & Bortolotti (2001); Swenson (2006); Flockhart & Wiebe (2009)
<i>Icterus galbula/bullockii</i>	Oriole	Distinct species	Secondary contact	Different climatic regions	Hybrid zone coincides with Great Plains-Rocky Mountains ecotone; species differ in T tolerance	NA	NA	NA	No	NA	Rising (1969, 1983); Swenson (2006); Carling <i>et al.</i> (2011)
<i>Passerina amoena/cyanea</i>	Bunting	Distinct species	Probably secondary contact	Different climatic regions	Hybrid zone coincides with Great Plains-Rocky Mountains ecotone	NA	NA	NA	Yes	Maybe	Baker (1996); Baker & Boylan (1999); Swenson (2006); Carling & Zuckenberg (2011)
<i>Plethodon shermani/teyahualec</i>	Salamander	Distinct species	Probably secondary contact	Altitudinal gradient	Centre of hybrid zone has shifted upward, potentially as a result of T increase	NA	NA	NA	NA	NA	Wiens <i>et al.</i> (2006); Walls (2009)

HA, hybrid advantage.

*Sexual isolation driven by divergent adaptation (e.g. different pollinators, different reproductive timing or assortative mating based on traits involved in adaptation).

[†]Depending on direction of cross.

[‡]Reduced hybrid fitness in inland and HA in coastal habitat.

[§]Sexual isolation based on trait not involved in adaptation.

*Some evidence that flight activity is higher in local individuals than non-local.

^{††}There is evidence of premating isolation but the traits conferring it are unclear.

^{‡‡}Assessed under field conditions.

^{‡‡‡}Colour-based assortative mating in some hybrid zone populations but not in others.

environments? Or are there additional barriers which act earlier and prevent an individual from migrating to the wrong thermal habitat or mating with individuals adapted to different thermal regimes?

In plants, pollen competition may often lead to an overrepresentation of nonhybrid offspring when a flower is pollinated by several males (Table 1a). More interestingly for our present discussion, the crossing between plant individuals from different thermal environments may quite often also be prevented by ecological barriers (Table 1a). The differentially adapted populations may differ in flowering time (*M. guttatus*) or, more commonly, in their pollinators (*Ipomopsis*, *Mimulus lewisii*, *M. cardinalis*, *Polemonium*). In the latter case, populations have typically diverged with respect to some floral trait and are adapted to pollinators common in a particular habitat.

In animals, different ecological barriers may prevent hybridization between divergently adapted populations. First, evidence for habitat preference was found in all three studies where it was investigated (Table 1b). Individuals preferentially moved to habitats similar to their home site (toads: MacCallum *et al.* 1998; Vines *et al.* 2003; periwinkles: Cruz *et al.* 2004b), or their temperature preferences coincided with the conditions they would typically experience in the field (fruitflies: Nevo *et al.* 1998).

Secondly, the production of hybrid offspring can be prevented if individuals mate assortatively based on a trait which is directly involved in thermal adaptation or in linkage disequilibrium with such a trait. Evidence of assortative mating was found in three out of five systems where it had been investigated (Table 1b). In two cases, the cue underlying mate choice is not entirely clear (*Lucania*, *Drosophila*), while periwinkles mate assortatively based on size, a trait thought to be under divergent selection (Cruz *et al.* 2004a) but probably not in response to temperature. *Colias* butterflies provide the only example where mate choice is based on a morphological trait involved in thermal adaptation, namely wing melanisation. However, sexual selection opposes the effects of natural selection. While dark wings are advantageous at high altitudes, males prefer light coloured females at all altitudes (Ellers *et al.* 2003).

Empirical evidence for a role of mitochondrial sequence variation in thermal adaptation and, subsequently, in intrinsic genetic incompatibilities is provided by the copepod *T. californicus* (Box; Table 1). Hofman & Szymura (2007) report a second possible example from the hybrid zone between yellow-bellied and fire-bellied toads where mtDNA clines were found to be steeper than allozyme clines. It is currently unclear whether this pattern is indeed caused by (exogenous and/or endogenous) selection (e.g. Kruuk *et al.*

1999) or by neutral processes (Hofman & Szymura 2007).

Our second literature search with a focus on macroevolutionary patterns yielded five vertebrate systems where temperature-related adaptation may be involved in the current coexistence of distinct (sub)species (Table 1c). In all cases, two taxa meet and hybridize along a hybrid zone whose position coincides closely with a climatic transition, suggesting a role for exogenous selection against locally maladapted genotypes. The initial divergence between the taxa most likely occurred in allopatry. Specifically, different populations are thought to have persisted in separate glacial refugia where they may have adapted to different climatic conditions (Swenson 2006).

Upon secondary contact, reproductive isolation between the two taxa could potentially be strengthened through reinforcement. In these systems, there is little evidence for such a process, except maybe in *Passerina* buntings. The hybrid zone between Lazuli and Indigo buntings has narrowed over the last four decades which could be consistent with a reduction in the hybridization rate because of reinforcement although alternative explanations cannot be excluded (Carling & Zuckerberg 2011).

Discussion and conclusions

Based on our first literature survey, we were able to identify several natural systems where thermal differences possibly underlie adaptive divergence and the evolution of (partial) reproductive isolation between populations. While the total number of such examples may appear limited (Table 1a,b), it has to be kept in mind that, overall, relatively few systems have been explored in sufficient detail to meet our demanding selection criteria, which required the availability of data relating to local adaptation as well as additional reproductive barriers. Using the same criteria, Nosil *et al.* (2005) identified only 20 such cases in a search that was not limited to particular selective agents. In many of these 20 examples, adaptive divergence was associated with biotic interactions, e.g. phytophagous insects utilizing different host plants (eight cases) or diverging taxa with different dietary specialization or predation regimes (three cases). Still, a role of abiotic factors was suspected in several cases and, in as many as six (30%) of the systems identified by Nosil *et al.* (2005), temperature differences may be important (see our Table 1a,b).

Our second search employed less stringent criteria and was targeted at the section of the speciation continuum where the incipient species are already strongly isolated. This search yielded another five examples where adaptation to different thermal environments

may have been involved in the divergence between taxa (Table 1c). If we move even further along the speciation continuum, we often find that the current distribution of closely related but reproductively fully isolated species is consistent with adaptation to different thermal conditions. For example, closely related species often replace one another along latitudinal (e.g. Graves 1991) or altitudinal gradients (e.g. Kozak & Wiens 2007; McCain 2009; Cadena *et al.* 2011).

While, in these cases, it is no longer possible to infer whether thermal adaptation was important during the early stages of speciation, these patterns at least suggest that differential adaptation may allow current coexistence. Similarly, in many of the systems in Table 1, the initial divergence may have occurred in allopatry, but upon secondary contact, both taxa are able to coexist stably. While hybridization often does occur, the combined effect of all pre- and postzygotic barriers is strong enough to prevent the complete mixing of the two gene pools. These examples strongly suggest that divergent selection between environments is often strong enough to maintain thermal niche partitioning upon secondary contact.

What is less clear is whether such divergent selection can sometimes also be strong enough to allow divergence with gene flow through reinforcement-like processes. While prezygotic barriers are observed in several animal and plant systems, it remains largely unclear whether assortative mating followed as a by-product of thermal adaptation or whether it allowed the ecological divergence in the first place.

In the plant systems, a by-product mechanism may in fact be more likely. In three of the identified cases, prezygotic isolation is mediated by differences in the pollinator species that visit a given plant. Sometimes, this premating isolation is strong enough to allow the maintenance of a bimodal genotype distribution even in sympatry (Ramsey *et al.* 2003; Aldridge & Campbell 2006, 2007, 2009). The initial emergence of the barrier, however, is almost certainly a by-product of allopatric divergence as pollinator shifts are virtually impossible to evolve in sympatry (Coyne & Orr 2004, p. 200).

The local spectrum of pollinators will be strongly influenced by environmental factors including temperature, and flowers may evolve in response to such locally abundant pollinators. In all three cases of pollinator isolation identified here, the plant taxon occurring at higher altitudes is pollinated by insects able to fly at low ambient temperatures, hawkmoths or bumblebees respectively. These insects are characterized by large and well-insulated bodies and are able to elevate the temperature in their flight muscle well above ambient levels (Heinrich 1974). The plant taxa occurring at lower altitude, in contrast, are pollinated by hummingbirds (*Ipomopsis*, *Mimulus cardinalis*) or flies (*Polemonium*). A

very direct link between temperature and pollinator preferences was suggested in *Ipomopsis*, where the selectivity of hawkmoths and hummingbirds depended on the local thermal conditions (Aldridge & Campbell 2007; see Box for details).

While five out of eleven animal systems show some evidence of assortative mating (Table 1b,c), the traits involved in mate choice and their adaptive significance (if any) are mostly unclear. It is possible that assortative mating is generally not very common in animal populations from different thermal environments, maybe because local adaptation does not involve pronounced phenotypic change. However, it is just as possible that assortative mating is often not investigated, potentially for the same reason.

A conspicuous characteristic of many of the systems identified here (Table 1) is that they involve environmental gradients. Theoretical models disagree on whether speciation through reinforcement-like processes is a likely outcome under such conditions (Doebeli & Dieckmann 2003; Polechová & Barton 2005). Empirical examples show that speciation along environmental gradients is sometimes possible (e.g. along light gradient: Seehausen *et al.* 2008; depth gradient: Ingram 2010) but the likelihood may depend on the characteristics of both the gradient (e.g. its steepness; Seehausen *et al.* 2008) and the organism involved (e.g. its population structure, dispersal ability) and the genetic architecture of the trait underlying adaptation.

Two features of thermal gradients could potentially weaken the potential for reinforcement-like processes. First, many thermal gradients may not be stable across time. In fact, it has been suggested that speciation along altitudinal gradients may be more likely in the tropics, precisely because the thermal environment at a given location typically fluctuates less than in temperate regions (Janzen 1967; Ghalambor *et al.* 2006; Kozak & Wiens 2010). So perhaps then, stable thermal gradients may be the most promising system to look for ongoing ecological speciation driven by thermal adaptation. In addition to tropical mountain ranges, such gradients could probably be found in aquatic environments where temperature fluctuations may be less pronounced than in terrestrial habitats because of the high specific heat of water. Secondly, it is currently difficult to assess whether disruptive selection is typically operating along thermal gradients. In particular, exogenous selection against hybrids may be weak if the environment changes gradually. In fact, hybrids could then even be superior to parental genotypes in an intermediate habitat (bounded hybrid superiority model; Moore 1977).

Overall, our literature survey has shown a pronounced lack of (i) parallel investigations of similar incipient species at different stages of the speciation

Box: Selected empirical examples*Tigriopus californicus*

These copepods living in splash pools along the western coast of North America probably provide one of the best documented examples of cytonuclear coadaptation. The genetic differences between populations are often quite large (Burton 1997), and common garden experiments have demonstrated local adaptation to different thermal conditions (Willett 2010). Interpopulation hybrids show evidence of intrinsic incompatibilities because of epistatic interactions between nuclear and mitochondrial components of the electron transport chain (reviewed in Burton *et al.* 2006; Ellison & Burton 2006, 2008). This cytonuclear coevolution is probably driven by the fast evolving mitochondrial genome but there is currently no evidence to suggest that divergent natural selection has promoted mtDNA differentiation between populations (Willett & Burton 2004).

Ipomopsis aggregata and *Ipomopsis tenuituba*

This system provides an example of how indirect thermal effects could potentially promote reproductive isolation. These two self-incompatible herbs are common in the western United States, and *I. tenuituba* is locally adapted to higher altitudes than *I. aggregata* (Campbell & Waser 2007). The two species differ in flower colour and morphology probably as an adaptation to different pollinators—hummingbirds in *I. aggregata* and hawkmoths in *I. tenuituba*. Still, the two forms are not fully isolated, and hybrids are formed where their distributions overlap. The rate of hybridization, however, varies between sites and these differences may, at least partly, be caused by differences in pollinator behaviour (Aldridge & Campbell 2009). Hawkmoths and hummingbirds were found to exhibit stronger preferences for a certain flower type at a warmer site where the frequency of hybrids is indeed lower (Aldridge & Campbell 2007). Aldridge and Campbell propose that the warmer conditions may allow the hawkmoths to forage at night when the white flowers of *I. tenuituba* are more visible. As a result of this night-time activity, *I. tenuituba* flowers are empty in the morning when hummingbirds start foraging which, in turn, may cause them to more strongly prefer *I. aggregata* (Aldridge & Campbell 2007).

Callipepla californica and *Callipepla gambelii*

These birds provide an example where differential thermal adaptation potentially allows the persistence of two closely related species. The distribution ranges of the two quails are largely allopatric, with California quails occurring in more mesic chaparral habitats and Gambel's quails in the deserts of the American Southwest (e.g. Fig. 1 of Gee 2004). The two species show physiological differences that are consistent with adaptation to local climates (Bartholomew & Dawson 1958; Carey & Morton 1971). The quails interbreed along a hybrid zone, where they show no evidence of assortative mating (Gee 2003, 2005) or strong genetic incompatibilities (Gee 2003). However, the observed genetic and phenotypic clines coincide closely with temperature and precipitation gradients (Gee 2004). Also, temporal changes in the composition of a mixed-species flock suggest that the relative reproductive success of the two species may depend on the climate in a given year (Gee 2004). Together, these observations indicate that the hybrid zone is probably maintained by climate-mediated exogenous selection.

continuum and (ii) speciation studies that investigate the full range of possible sources of divergent selection and reproductive barriers. Such studies would be particularly timely in the context of thermal adaptation. The ongoing and anticipated changes in global temperature regimes may lead to shifts in the distribution of many animals and plants. Not only may currently allopatric populations come into secondary contact (Mooney & Cleland 2001), but the unavoidable changes in the balance between divergent selection and gene flow could render young species in the process of parapatric speciation along thermal gradients vulnerable to genetic

collapse. Against this background, it is particularly relevant to understand whether, as tentatively suggested by our results, divergent selection along thermal gradients is indeed often strong enough to maintain differentially adapted (sub)species upon secondary contact but not strong enough to allow their *in situ* evolution in the face of gene flow.

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References

- Aldridge G, Campbell DR (2006) Asymmetrical pollen success in *Ipomopsis* (Polemoniaceae) contact sites. *American Journal of Botany*, **93**, 903–909.
- Aldridge G, Campbell DR (2007) Variation in pollinator preference between two *Ipomopsis* contact sites that differ in hybridization rate. *Evolution*, **61**, 99–110.
- Aldridge G, Campbell DR (2009) Genetic and morphological patterns show variation in frequency of hybrids between *Ipomopsis* (Polemoniaceae) zones of sympatry. *Heredity*, **102**, 257–265.
- Angilletta MJ (2009) *Thermal Adaptation – A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Baker MC (1996) Female buntings from hybridizing populations prefer conspecific males. *Wilson Bulletin*, **108**, 771.
- Baker MC, Boylan JT (1999) Singing behavior, mating associations and reproductive success in a population of hybridizing Lazuli and Indigo Buntings. *Condor*, **101**, 493.
- Ballard JWO, Whitlock MC (2004) The incomplete natural history of mitochondria. *Molecular Ecology*, **13**, 729–744.
- Bartholomew GA, Dawson WR (1958) Body temperatures in California and Gambel's quails. *Auk*, **75**, 150–156.
- Beardsley PM, Yen A, Olmstead RG (2003) AFLP phylogeny of *Mimulus* section *Erythranthe* and the evolution of hummingbird pollination. *Evolution*, **57**, 1397.
- Bell G (2008) *Selection – the Mechanism of Evolution*, 2nd edn. Oxford University Press, Oxford.
- Bernatchez L, Landry C (2003) MHC studies in nonmodel vertebrates: what have we learned about natural selection in 15 years? *Journal of Evolutionary Biology*, **16**, 363–377.
- Berner D, Körner C, Blanckenhorn WU (2004) Grasshopper populations across 2000m of altitude: is there life history adaptation. *Ecography*, **27**, 733–740.
- Bertolo A, Pépino M, Adams J, Magnan P (2011) Behavioural thermoregulatory tactics in lacustrine brook charr, *Salvelinus fontinalis*. *PLoS ONE*, **6**, e18603.
- Burton RS (1997) Genetic evidence for long term persistence of marine invertebrate populations in an ephemeral environment. *Evolution*, **51**, 993–998.
- Burton RS, Ellison CK, Harrison JS (2006) The sorry state of F2 hybrids: consequences of rapid mitochondrial DNA evolution in allopatric populations. *The American Naturalist*, **168**, S14–S24.
- Butlin RK, Galindo J, Grahame JW (2008) Sympatric, parapatric or allopatric: the most important way to classify speciation? *Philosophical Transactions of the Royal Society of London. Series B*, **363**, 2997.
- Cadena CD, Kozak KH, Gómez JP *et al.* (2012) Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 194–201.
- Campbell DR, Waser NM (2007) Evolutionary dynamics of an *Ipomopsis* hybrid zone: confronting models with lifetime fitness data. *American Naturalist*, **169**, 298–310.
- Carey C, Morton ML (1971) A comparison of salt and water regulation in California quail (*Lophortyx californicus*) and Gambel's quail (*Lophortyx gambelii*). *Comparative Biochemistry and Physiology Part A: Physiology*, **39**, 75–101.
- Carling MD, Zuckerberg B (2011) Spatio-temporal changes in the genetic structure of the *Passerina* bunting hybrid zone. *Molecular Ecology*, **20**, 1166–1175.
- Carling MD, Serene LG, Lovette IJ (2011) Using historical DNA to characterize hybridization between Baltimore Orioles (*Icterus galbula*) and Bullock's Orioles (*I. bullockii*). *Auk*, **128**, 61.
- Cheviron ZA, Brumfield RT (2009) Migration-selection balance and local adaptation of mitochondrial haplotypes in rufous-collared sparrows (*Zonotrichia capensis*) along an elevational gradient. *Evolution*, **63**, 1593–1605.
- Clusella Trullas S, van Wyk JH, Spotila JR (2007) Thermal melanism in ectotherms. *Journal of Thermal Biology*, **32**, 235–245.
- Correia L, Yeaman S, Whitlock MC (2010) Local adaptation does not always predict high mating success. *Journal of Evolutionary Biology*, **23**, 875–878.
- Coyne JA, Elwyn S (2006) Does the desaturase-2 locus in *Drosophila melanogaster* cause adaptation and sexual isolation? *Evolution*, **60**, 279–291.
- Coyne JA, Orr HA (2004) *Speciation*. Sinauer Associates, Sunderland, Massachusetts.
- Cruz R, García C (2001) Disruptive selection on female reproductive characters in a hybrid zone of *Littorina saxatilis*. *Evolutionary Ecology*, **15**, 167.
- Cruz R, Carballo M, Conde-Padín P, Rolán-Alvarez E (2004a) Testing alternative models for sexual isolation in natural populations of *Littorina saxatilis*: indirect support for by-product ecological speciation? *Journal of Evolutionary Biology*, **17**, 288–293.
- Cruz R, Vilas C, Mosquera J, García C (2004b) Relative contribution of dispersal and natural selection to the maintenance of a hybrid zone in *Littorina*. *Evolution*, **58**, 2734–2746.
- Dahlhoff EP, Rank NE (2000) Functional and physiological consequences of genetic variation at phosphoglucose isomerase: heat shock protein expression is related to enzyme genotype in a montane beetle. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 10056–10061.
- Dambroski HR, Feder JL (2007) Host plant and latitude-related diapause variation in *Rhagoletis pomonella*: a test for multifaceted life history adaptation on different stages of diapause development. *Journal of Evolutionary Biology*, **20**, 2101–2112.
- Demuth JP, Wade MJ (2007) Population differentiation in the beetle *Tribolium castaneum*. II. Haldane's rule and incipient speciation. *Evolution*, **61**, 694–699.
- Doebeli M, Dieckmann U (2003) Speciation along environmental gradients. *Nature*, **421**, 259–264.
- Dolgin ES, Whitlock MC, Agrawal AF (2006) Male *Drosophila melanogaster* have higher mating success when adapted to their thermal environment. *Journal of Evolutionary Biology*, **19**, 1894–1900.
- Dowling DK, Friberg U, Lindell J (2008) Evolutionary implications of non-neutral mitochondrial genetic variation. *Trends in Ecology & Evolution*, **23**, 546–554.
- Edelaar P, Siepielski AM, Clobert J, Rausher M (2008) Matching habitat choice causes directed gene flow: a

- neglected dimension in evolution and ecology. *Evolution*, **62**, 2462–2472.
- Ehrman L (1964) Genetic divergence in *M. Vetukhiv's* experimental populations of *Drosophila pseudoobscura* 1. Rudiments of sexual isolation. *Genetical Research*, **5**, 150–157.
- Ehrman L (1969) Genetic divergence in *M. Vetukhiv's* experimental populations of *Drosophila pseudoobscura* 5. A further study of rudiments of sexual isolation. *American Midland Naturalist*, **82**, 272–276.
- Eizaguirre C, Lenz TL, Traulsen A, Milinski M (2009) Speciation accelerated and stabilized by pleiotropic major histocompatibility complex immunogenes. *Ecology Letters*, **12**, 5–12.
- Ellers J, Boggs CL (2002) The evolution of wing color in *Colias* butterflies: Heritability, sex linkage, and population divergence. *Evolution*, **56**, 836.
- Ellers J, Boggs CL (2004) Functional ecological implications of intraspecific differences in wing melanization in *Colias* butterflies. *Biological Journal of the Linnean Society*, **82**, 79–87.
- Ellers J, Boggs CL (2003) The evolution of wing color: male mate choice opposes adaptive wing color divergence in *Colias* butterflies. *Evolution*, **57**, 1100–1106.
- Ellison CK, Burton RS (2006) Disruption of mitochondrial function in interpopulation hybrids of *Tigriopus californicus*. *Evolution*, **60**, 1382–1391.
- Ellison CK, Burton RS (2008) Interpopulation hybrid breakdown maps to the mitochondrial genome. *Evolution*, **62**, 631–638.
- Flockhart DTT, Wiebe KL (2009) Absence of reproductive consequences of hybridization in the Northern flicker (*Colaptes auratus*) hybrid zone. *Auk*, **126**, 351.
- Fry FEJ (1947) Effects of the environment on animal activity. University of Toronto studies. Biological series, no. 55. Publications of the Ontario Fisheries Research Laboratory 68: 1–62.
- Fuller RC (2008) Genetic incompatibilities in killifish and the role of environment. *Evolution*, **62**, 3056.
- Fuller RC, Noa LA (2008) Distribution and stability of sympatric populations of *Lucania goodei* and *L. parva* across Florida. *Copeia*, **2008**, 699.
- Fuller RC, McGhee KE, Schrader M (2007) Speciation in killifish and the role of salt tolerance. *Journal of Evolutionary Biology*, **20**, 1962.
- Gee JM (2003) How a hybrid zone is maintained: behavioral mechanisms of interbreeding between California and Gambel's quail (*Callipepla californica* and *C. gambelii*). *Evolution*, **57**, 2407–2415.
- Gee JM (2004) Gene flow across a climatic barrier between hybridizing avian species, California and Gambel's quail (*Callipepla californica* and *C. gambelii*). *Evolution*, **58**, 1108–1121.
- Gee JM (2005) No species barrier by call in an avian hybrid zone between California and Gambel's quail (*Callipepla californica* and *C. gambelii*). *Biological Journal of the Linnean Society*, **86**, 253–264.
- Gershoni M, Templeton AR, Mishmar D (2009) Mitochondrial bioenergetics as a major motive force of speciation. *Bioessays*, **31**, 642–650.
- Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, **46**, 5–17.
- Gilchrist GW (1995) Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *The American Naturalist*, **146**, 252–270.
- Graves GR (1991) Bergmann rule near the equator – latitudinal clines in body size of an Andean passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, **88**, 2322–2325.
- Greenberg AJ, Moran JR, Coyne JA, Wu CI (2003) Ecological adaptation during incipient speciation revealed by precise gene replacement. *Science*, **302**, 1754–1757.
- Greenberg AJ, Moran JR, Wu C-I (2006) Proper control of genetic background with precise allele substitution: a comment on Coyne and Elwyn. *Evolution*, **60**, 623–625.
- Hall JPW (2005) Montane speciation patterns in *Ithomiola* butterflies (Lepidoptera: Riodinidae): are they consistently moving up in the world? *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2457–2466.
- Hall MC, Willis JH (2006) Divergent selection on flowering time contributes to local adaptation in *Mimulus guttatus* populations. *Evolution*, **60**, 2466.
- Hawkins BA, Field R, Cornell HV *et al.* (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Heinrich B (1974) Thermoregulation in endothermic insects. *Science*, **185**, 747–756.
- Hendry AP, Nosil P, Rieseberg LH (2007) The speed of ecological speciation. *Functional Ecology*, **21**, 455–464.
- Hendry AP, Bolnick DI, Berner D, Peichel CL (2009) Along the speciation continuum in sticklebacks. *Journal of Fish Biology*, **75**, 2000–2036.
- Hilbish TJ, Bayne BL, Day A (1994) Genetics of physiological differentiation within the marine mussel genus *Mytilus*. *Evolution*, **48**, 267–286.
- Hilton Z, Wellenreuther M, Clements KD (2008) Physiology underpins habitat partitioning in a sympatric sister-species pair of intertidal fishes. *Functional Ecology*, **22**, 1108–1117.
- Hoffmann AA, Anderson A, Hallas R (2002) Opposing clines for high and low temperature resistance in *Drosophila melanogaster*. *Ecology Letters*, **5**, 614–618.
- Hofman S, Szymura JM (2007) Limited mitochondrial DNA introgression in a *Bombina* hybrid zone. *Biological Journal of the Linnean Society*, **91**, 295–306.
- Ingram T (2010) Speciation along a depth gradient in a marine adaptive radiation. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 613–618.
- Janzen DH (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101**, 233–249.
- Kavanagh KD, Haugen TO, Gregersen F, Jernvall J, Vollestad LA (2010) Contemporary temperature-driven divergence in a Nordic freshwater fish under conditions commonly thought to hinder adaptation. *BMC Evolutionary Biology*, **10**, 350.
- Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecology Letters*, **7**, 1225–1241.
- Kilias G, Alahiotis SN, Pelecanos M (1980) A multifactorial genetic investigation of speciation theory using *Drosophila melanogaster*. *Evolution*, **34**, 730–737.
- Kingsolver JG (2009) The well-temperated biologist. *American Naturalist*, **174**, 755–768.
- Korol A, Rashkovetsky E, Iliadi K, Michalak P, Ronin Y, Nevo E (2000) Nonrandom mating in *Drosophila melanogaster* laboratory populations derived from closely adjacent

- ecologically contrasting slopes at "Evolution Canyon". *PNAS*, **97**, 12637.
- Korol A, Rashkovetsky E, Iliadi K, Nevo E (2006) *Drosophila* flies in "Evolution Canyon" as a model for incipient sympatric speciation. *Proceedings of the National Academy of Sciences*, **103**, 18184–18189.
- Kozak KH, Wiens JJ (2007) Climatic zonation drives latitudinal variation in speciation mechanisms. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2995–3003.
- Kozak KH, Wiens JJ (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.
- Krug AZ, Jablonski D, Valentine JW, Roy K (2009) Generation of Earth's first-order biodiversity pattern. *Astrobiology*, **9**, 113–124.
- Kruuk LEB, Baird SJE, Gale KS, Barton NH (1999) A comparison of multilocus clines maintained by environmental adaptation or by selection against hybrids. *Genetics*, **153**, 1959–1971.
- Lowry DB, Modliszewski JL, Wright KM, Wu CA, Willis JH (2008a) The strength and genetic basis of reproductive isolating barriers in flowering plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 3009–3021.
- Lowry DB, Rockwood RC, Willis JH (2008b) Ecological reproductive isolation of coast and inland races of *Mimulus guttatus*. *Evolution*, **62**, 2196.
- Lynch M, Gabriel W (1987) Environmental tolerance. *The American Naturalist*, **129**, 283–303.
- Maan ME, Seehausen O (2011) Ecology, sexual selection and speciation. *Ecology Letters*, **14**, 591–602.
- MacCallum CJ, Nürnberger B, Barton NH, Szymura JM (1998) Habitat preference in the *Bombina* hybrid zone in Croatia. *Evolution*, **52**, 227–239.
- Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *American Zoologist*, **19**, 331–343.
- Mallet J, Meyer A, Nosil P, Feder JL (2009) Space, sympatry and speciation. *Journal of Evolutionary Biology*, **22**, 2332–2341.
- Manel S, Poncet BN, Legendre P, Gugerli F, Holderegger R (2010) Common factors drive adaptive genetic variation at different spatial scales in *Arabidopsis thaliana*. *Molecular Ecology*, **19**, 3824–3835.
- Marchand PJ (1996) *Life in the Cold*, 3 edn. University Press of New England, Hanover and London.
- Marcogliese DJ (2008) The impact of climate change on the parasites and infectious diseases of aquatic animals. *Revue Scientifique et Technique/Office International des Epizooties*, **27**, 467–484.
- Matute DR, Novak CJ, Coyne JA (2009) Temperature-based extrinsic reproductive isolation in two species of *Drosophila*. *Evolution*, **63**, 595–612.
- McAllister BF, Sheeley SL, Mena PA, Evans AL, Schlotterer C (2008) Clinal distribution of a chromosomal rearrangement: a precursor to chromosomal speciation? *Evolution*, **62**, 1852–1865.
- McCain CM (2009) Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecology Letters*, **12**, 550–560.
- McKinnon JS, Mori S, Blackman BK *et al.* (2004) Evidence for ecology's role in speciation. *Nature*, **429**, 294–298.
- Michalak P, Minkov I, Helin A, Lerman DN, Bettencourt BR, Feder ME, Korol AB, Nevo E (2001) Genetic evidence for adaptation-driven incipient speciation of *Drosophila melanogaster* along a microclimatic contrast in "Evolution Canyon," Israel. *PNAS*, **98**, 13195.
- Miller K, Winton J, Schulze A, Purcell M, Ming T (2004) Major histocompatibility complex loci are associated with susceptibility of Atlantic salmon to infectious hematopoietic necrosis virus. *Environmental Biology of Fishes*, **69**, 307–316.
- Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 5446–5451.
- Moore WS (1977) An evaluation of narrow hybrid zones in vertebrates. *Quarterly Review of Biology*, **52**, 263–277.
- Moore WS (1987) Random mating in the northern flicker hybrid zone: implications for the evolution of bright and contrasting plumage patterns in birds. *Evolution*, **41**, 539.
- Moore WS, Koenig WD (1986) Comparative reproductive success of yellow-shafted, red-shafted, and hybrid flickers across a Hybrid Zone. *Auk*, **103**, 42.
- Nevo E, Rashkovetsky E, Pavlicek T, Korol A (1998) A complex adaptive syndrome in *Drosophila* caused by microclimatic contrasts. *Heredity*, **80**, 9–16.
- Nosil P, Vines TH, Funk DJ (2005) Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution*, **59**, 705–719.
- Nosil P, Harmon LJ, Seehausen O (2009) Ecological explanations for (incomplete) speciation. *Trends in Ecology & Evolution*, **24**, 145–156.
- Nürnberger B, Barton NH, Kruuk LEB, Vines TH (2004) Mating patterns in a hybrid zone of fire-bellied toads (*Bombina*): inferences from adult and full-sib genotypes. *Heredity*, **94**, 247.
- Ohlberger J, Staaks G, Petzoldt T, Mehner T, Hoelker F (2008) Physiological specialization by thermal adaptation drives ecological divergence in a sympatric fish species pair. *Evolutionary Ecology Research*, **10**, 1173–1185.
- Ording GJ, Mercader RJ, Aardema ML, Scriber JM (2010) Allochronic isolation and incipient hybrid speciation in tiger swallowtail butterflies. *Oecologia*, **162**, 523–531.
- Orr HA (1996) Dobzhansky, Bateson, and the genetics of speciation. *Genetics*, **144**, 1331–1335.
- Palmer CA, Edmands S (2000) Mate choice in the face of both inbreeding and outbreeding depression in the intertidal copepod *Tigriopus californicus*. *Marine Biology*, **136**, 693.
- Palti Y, Nichols KM, Waller KI, Parsons JE, Thorgaard GH (2001) Association between DNA polymorphisms tightly linked to MHC class II genes and IHN virus resistance in backcrosses of rainbow and cutthroat trout. *Aquaculture*, **194**, 283–289.
- Partridge L, Coyne JA (1997) Bergmann's rule in ectotherms: is it adaptive. *Evolution*, **51**, 632–635.
- Pavliček T, Frenkel Z, Korol AB, Beiles A, Nevo E (2008) *Drosophila* at the "Evolution Canyon" Microsite, MT. Carmel, Israel: Selection Overrides Migration. *Israel Journal of Ecology and Evolution*, **54**, 165.
- Piertney SB, Oliver MK (2006) The evolutionary ecology of the major histocompatibility complex. *Heredity*, **96**, 7–21.
- Polechová J, Barton NH (2005) Speciation through competition: a critical review. *Evolution*, **59**, 1194–1210.

- Poncet BN, Herrmann D, Gugerli F *et al.* (2010) Tracking genes of ecological relevance using a genome scan in two independent regional population samples of *Arabis alpina*. *Molecular Ecology*, **19**, 2896–2907.
- Pörtner HO (2001) Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, **88**, 137–146.
- Ragland GJ, Kingsolver JG (2007) Influence of seasonal timing on thermal ecology and thermal reaction norm evolution in *Wyomyia smithii*. *Journal of Evolutionary Biology*, **20**, 2144–2153.
- Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200–205.
- Rainey PB, Travisano M (1998) Adaptive radiation in a heterogeneous environment. *Nature*, **394**, 69–72.
- Ramsey J, Bradshaw HD, Schemske DW (2003) Components of reproductive isolation between the monkeyflowers *Mimulus lewisii* and *M. cardinalis* (Phrymaceae). *Evolution*, **57**, 1520–1534.
- Rashkovetsky E, Iliadi K, Michalak P, Lupu A, Nevo E, Feder ME, Korol A (2006) Adaptive differentiation of thermotolerance in *Drosophila* along a microclimatic gradient. *Heredity*, **96**, 353.
- Rieseberg LH, Whitton J, Gardner K (1999) Hybrid zones and the genetic architecture of a barrier to gene flow between two sunflower species. *Genetics*, **152**, 713–727.
- Rising JD (1969) A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. *Comparative Biochemistry and Physiology*, **31**, 915.
- Rising JD (1983) The progress of oriole hybridization in Kansas. *Auk*, **100**, 885.
- Rolán-Alvarez E (2007) Sympatric speciation as a by-product of ecological adaptation in the Galician *Littorina saxatilis* hybrid zone. *Journal of Molluscan Studies*, **73**, 1.
- Rolán-Alvarez E, Carballo M, Galindo J and 6 coauthors (2004) Nonallopatric and parallel origin of local reproductive barriers between two snail ecotypes. *Molecular Ecology*, **13**, 3415.
- Rundle HD, Nosil P (2005) Ecological speciation. *Ecology Letters*, **8**, 336–352.
- Sauer KP, Vermeulen A, Aumann N (2003) Temperature-dependent competition hierarchy: a mechanism stabilizing the phenological strategy in the scorpionfly *Panorpa communis* L. *Journal of Zoological Systematics and Evolutionary Research*, **41**, 109–117.
- Schlötterer C, Agis M (2002) Microsatellite analysis of *Drosophila melanogaster* populations along a microclimatic contrast at Lower Nahel Oren Canyon, Mount Carmel, Israel. *Molecular Biology and Evolution*, **19**, 563.
- Schluter D (2000) *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- Schluter D (2001) Ecology and the origin of species. *Trends in Ecology and Evolution*, **16**, 372–380.
- Schluter D (2009) Evidence for ecological speciation and its alternative. *Science*, **323**, 737–741.
- Schwartz AK, Hendry AP (2006) Sexual selection and the detection of ecological speciation. *Evolutionary Ecology Research*, **8**, 399–413.
- Scriber JM, Ording GJ (2005) Ecological speciation without host plant specialization; possible origins of a recently described cryptic *Papilio* species. *Entomologia Experimentalis et Applicata*, **115**, 247–263.
- Seehausen O (2009) Progressive levels of trait divergence along a ‘speciation transect’ in the Lake Victoria cichlid fish *Pundamilia*. In: *Speciation and Patterns of Diversity* (eds Butlin R, Bridle J, Schluter D), p. 346. Cambridge University Press, Cambridge.
- Seehausen O, Terai Y, Magalhaes IS *et al.* (2008) Speciation through sensory drive in cichlid fish. *Nature*, **455**, 620–626.
- Servedio MR, Noor MAF (2003) The role of reinforcement in speciation: data and theory. *Annual Review of Ecology and Systematics*, **34**, 339–364.
- Servedio MR, Doorn GSV, Kopp M, Frame AM, Nosil P (2011) Magic traits in speciation: ‘magic’ but not rare? *Trends in Ecology & Evolution*, **26**, 389–397.
- Sobel JM, Chen GF, Watt LR, Schemske DW (2010) The biology of speciation. *Evolution*, **64**, 295–315.
- Somero GN (1995) Proteins and temperature. *Annual Review of Physiology*, **57**, 43–68.
- Somero GN (2002) Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integrative and Comparative Biology*, **42**, 780–789.
- Stelkens RB, Seehausen O (2009) Phenotypic divergence but not genetic distance predicts assortative mating among species of a cichlid fish radiation. *Journal of Evolutionary Biology*, **22**, 1679–1694.
- Summers K, McKeon SEA, Sellars JON *et al.* (2003) Parasitic exploitation as an engine of diversity. *Biological Reviews*, **78**, 639–675.
- Swenson NG (2006) GIS-based niche models reveal unifying climatic mechanisms that maintain the location of avian hybrid zones in a North American suture zone. *Journal of Evolutionary Biology*, **19**, 717–725.
- Szymura JM (1993) Analysis of hybrid zones with *Bombina*. In: *Hybrid zones and the evolutionary process* (ed. Harrison R), p. 261–289. Oxford University Press, New York, NY.
- van Doorn GS, Edelaar P, Weissing FJ (2009) On the origin of species by natural and sexual selection. *Science*, **326**, 1704–1707.
- Vines TH, Kohler SC, Thiel M *et al.* (2003) The maintenance of reproductive isolation in a mosaic hybrid zone between the fire-bellied toads *Bombina bombina* and *B. variegata*. *Evolution*, **57**, 1876–1888.
- Vinsáková T, Gvozdík L (2007) Mismatch between temperature preferences and morphology in F1 hybrid newts (*Triturus carnifex* × *T. dobrogicus*). *Journal of Thermal Biology*, **32**, 433–439.
- Wade MJ, Johnson NA, Toquenaga Y (1999) Temperature effects and genotype-by-environment interactions in hybrids: Haldane’s rule in flour beetles. *Evolution*, **53**, 855–865.
- Walls SC (2009) The role of climate in the dynamics of a hybrid zone in Appalachian salamanders. *Global Change Biology*, **15**, 1903.
- Wiebe KL (2000) Assortative Mating by color in a population of hybrid northern flickers. *Auk*, **117**, 525.
- Wiebe KL, Bortolotti GR (2001) Variation in colour within a population of northern flickers: a new perspective on an old hybrid zone. *Canadian Journal of Zoology*, **79**, 1046.
- Wiens JJ, Engstrom TN, Chippindale PT (2006) Rapid diversification, incomplete isolation, and the ‘‘speciation clock’’ in North American salamanders (genus *Plethodon*):

- testing the hybrid swarm hypothesis of rapid radiation. *Evolution*, **60**, 2585.
- Willett CS (2010) Potential fitness trade-offs for thermal tolerance in the intertidal copepod *Tigriopus californicus*. *Evolution*, **64**, 2521–2534.
- Willett CS, Burton RS (2003) Environmental influences on epistatic interactions: Viabilities of cytochrome c genotypes in interpopulation crosses. *Evolution*, **57**, 2286.
- Willett CS, Burton RS (2004) Evolution of interacting proteins in the mitochondrial electron transport system in a marine copepod. *Molecular Biology and Evolution*, **21**, 443–453.
- Wolf PG, Murray RA, Sipes SD (1997) Species-independent, geographical structuring of chloroplast DNA haplotypes in a montane herb *Ipomopsis* (Polemoniaceae). *Molecular Ecology*, **6**, 283.
- Wu C, Campbell D (2006) Environmental stressors differentially affect leaf ecophysiological responses in two *Ipomopsis* species and their hybrids. *Oecologia*, **148**, 202.
- Yanchukov A, Hofman S, Szymura JM, Mezhzherin SV, Morozov-Leonov SY, Barton NH, Nürnberger B (2006) Hybridization of *Bombina bombina* and *B. variegata* (Anura, Discoglossidae) at a sharp ecotone in western Ukraine: comparisons across transects and over time. *Evolution*, **60**, 583.

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