

Evolutionary Implications of Habitat Choice

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There is a growing realisation that habitat choice can have profound consequences for the processes of adaptation and speciation. Habitat choice may be a rapid and effective route by which individual and population fitness are increased, potentially playing a major role in adaptive evolution that has historically been solely attributed to natural selection. Recent research indicates that there may be complex interactions between habitat selection and other processes (i.e. natural selection, phenotypic plasticity) during adaptive evolution. Likewise, the use of alternative habitats by diverging lineages appears to be a major barrier to gene flow in nature, suggesting that habitat choice also plays a major role in the diversification of life. Although the available evidence is tantalising, much remains to be known about the true extent of habitat choice's role in the evolutionary process and the mechanisms underlying its evolutionary consequences.

Introduction

The two central goals of evolutionary biology are to explain the fit of organisms to their environment (i.e. *adaptation*) and the diversity of life (i.e. *speciation*). In recent decades, there have been growing efforts to integrate ecological and evolutionary perspectives and approaches to study the mechanisms underlying these processes (Endler, 1986; Schluter, 2000; Nosil, 2012). One of the consequences of this integration has been increasing interest in the role of *habitat choice* in adaptation and speciation. Although the empirical study of habitat choice and its evolutionary implications is still somewhat in its infancy, there is tantalising evidence that habitat choice can play a major role in adaptation

and speciation. Here, we provide an overview of the literature on habitat choice's role in adaptation and speciation, focusing primarily on the available empirical research. We also suggest potentially fruitful directions for future research in each area. Perhaps the most important topic for future research is to empirically explore how variation in the mechanisms underlying habitat choice (i.e. how individuals make dispersal and settlement decisions) affects evolutionary outcomes.

Habitat Choice and Adaptation

Organisms face numerous challenges to survive and reproduce successfully, and adaptation is the evolutionary process by which organisms increase their success at surviving and reproducing (i.e. fitness). It is widely accepted that the primary cause of adaptive evolution within natural populations is *natural selection*: the nonrandom differential survival or reproduction of phenotypically different individuals (Rose and Lauder, 1996). Indeed, there are now hundreds of demonstrations of natural selection in natural populations (Endler, 1986; Kingsolver *et al.*, 2001). Consequently, biologists often attribute evidence of adaptation in nature to natural selection (Hereford, 2009). However, it is increasingly recognised that other processes can also lead to adaptive evolution (Edelaar and Bolnick, 2019). **See also: [Adaptation and Natural Selection: Overview](#)**

Although habitat choice has long been recognised to be a consequence of adaptation (Lack, 1933; Wecker, 1963), it can also be a cause of adaptation by providing a means by which organisms can increase their own adaptive fit and thus fitness (Edelaar *et al.*, 2008). When individuals avoid habitats in which they have low fitness and settle in habitats where they experience higher fitness, a pattern of local adaptation can emerge if there is a phenotype x environment interaction in fitness (i.e. individuals with similar phenotypes and genotypes occurring in similar environments more than random expectation; Kawecki and Ebert, 2004; Edelaar *et al.*, 2008). Because individual movement drives increases in fitness, adaptation via habitat choice can occur much more rapidly (e.g. within generations) compared to natural selection, which often requires several generations to produce similar patterns. Indeed, a few studies have now suggested that habitat choice can be a powerful driver of local adaptation (Edelaar *et al.*, 2008; Bolnick *et al.*, 2009; Bolnick and Otto, 2013), facilitate the evolution of adaptive polymorphisms (Maynard Smith, 1966; de

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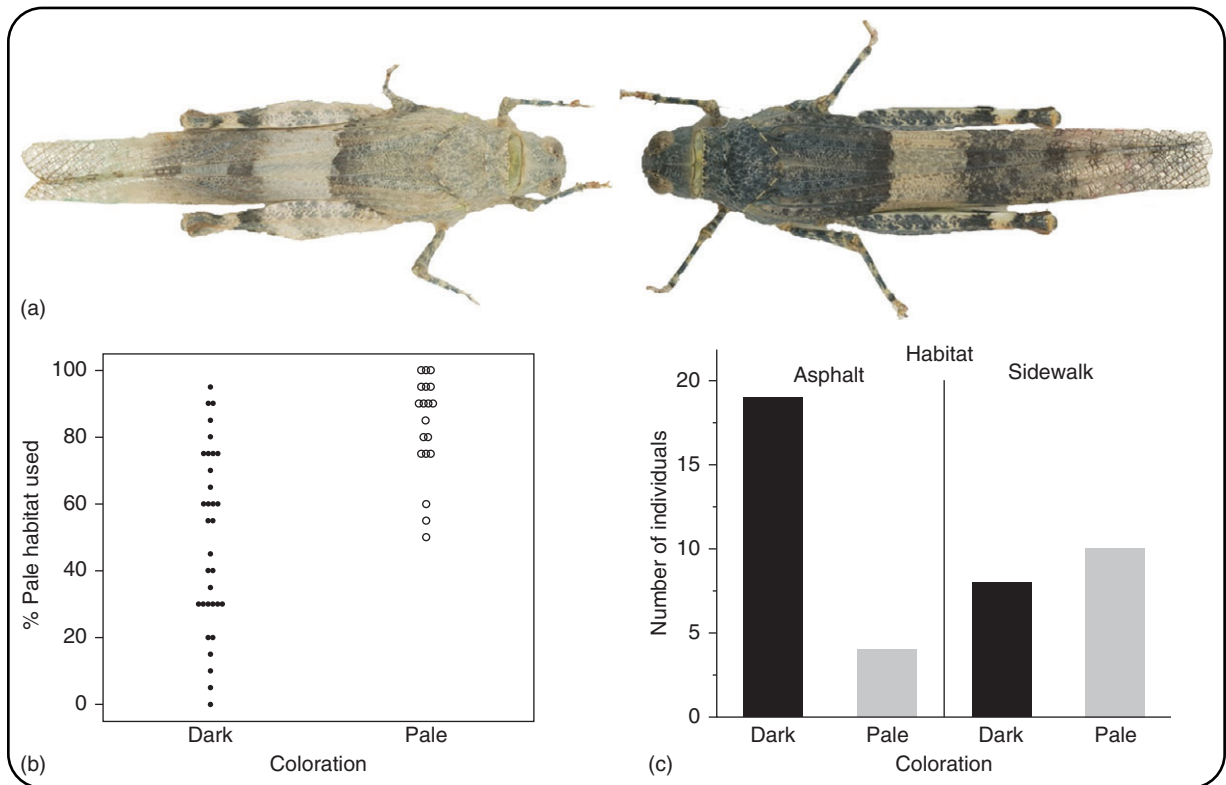


Figure 1 Habitat choice is the main driver of local crypsis in the azure sand grasshopper, *Sphingonotus azureus*, in an urban habitat, a deserted housing development site consisting of asphalt roads, sidewalks, parking spaces and bike paths. Colour variation in *S. azureus* is continuous and can range from bluish-grey (a, left) to darker greyish-brown (a, right). (a) Photos reproduced with permission from Pim Edelaar. © Pim Edelaar In the laboratory, grasshoppers painted dark (b, dark dots, left) used available dark habitat much more than grasshoppers painted pale (b, pale dots, right). Additionally, in the field, artificially darkened grasshoppers (c) were recaptured more frequently on dark asphalt, whereas pale individuals were recaptured more frequently on paler surfaces, such as sidewalks and parking spaces. (b,c) From Edelaar P, Baños-Villalba A, Quevedo DP, Escudero G, Bolnick DI, and Jordán-Andrade A (2019) Biased movement drives local cryptic coloration on distinct urban pavements. *Proceedings of the Royal Society B: Biological Sciences* 286: 20191343.

Meeûs *et al.*, 1993; Ravigné *et al.*, 2004; Ravigné *et al.*, 2009), and, in many cases, provides the only explanation for unexpectedly abrupt genetic and phenotypic clines in highly mobile organisms (Bolnick *et al.*, 2009; Urban, 2010; Richter-Boix *et al.*, 2013; Richardson *et al.*, 2014).

As habitat choice provides a means by which organisms can increase their individual fitness, the evolution of habitat choice by natural selection should reduce the scope for other adaptive processes to increase both individual fitness (via adaptive *phenotypic plasticity* or niche construction) and population fitness (via natural selection) (Edelaar and Bolnick, 2019). Generally, previous work has confirmed this (Scheiner, 2016; Nicolaus and Edelaar, 2018; Clark *et al.*, 2020), although specific habitat choice mechanisms likely vary in their effects (Berner and Thibert-Plante, 2015; Akcali and Porter, 2017). The few empirical studies that have characterised the relative contributions of multiple processes in natural populations suggest that habitat choice can sometimes have significant effects on the strength of other adaptive processes.

One of the most robust case studies to date is that of the evolution of crypsis in azure sand grasshoppers (*Sphingonotus azureus*) (Edelaar *et al.*, 2017; Peralta-Rincon *et al.*, 2017;

Baños-Villalba *et al.*, 2018; Edelaar *et al.*, 2019). These sand grasshoppers are a ground-dwelling species that typically inhabit xeric scrublands and grasslands but can also be found in adjacent urban habitats (Peralta-Rincon *et al.*, 2017) (Figure 1a). Even though both urban and natural habitats are within the dispersal kernels of individual grasshoppers, individuals tend to match their local substrates, and perceived predation risk affects the degree of local crypsis (Edelaar *et al.*, 2017). However, differences in grasshopper colouration between urban and natural habitats cannot be explained by natural selection, as there is no differential mortality (Edelaar *et al.*, 2019). Phenotypic plasticity cannot explain such a pattern either given that plasticity in colour is weak and unidirectional (Peralta-Rincon *et al.*, 2017; Edelaar *et al.*, 2019). Habitat choice appears to be the most important process contributing to local crypsis given that individuals use positioning behaviour to increase their camouflage (Baños-Villalba *et al.*, 2018) and that experimental manipulation of body colouration alters the substrate use of individuals (Edelaar *et al.*, 2019) (Figure 1b,c). Habitat choice has also been suggested to be a dominant process in adaptation in a few other systems, including bill morphology in ecotypes of the red crossbill (*Loxia curvirostris*) complex (Benkman, 2017; Gómez-Blanco *et al.*, 2019) and

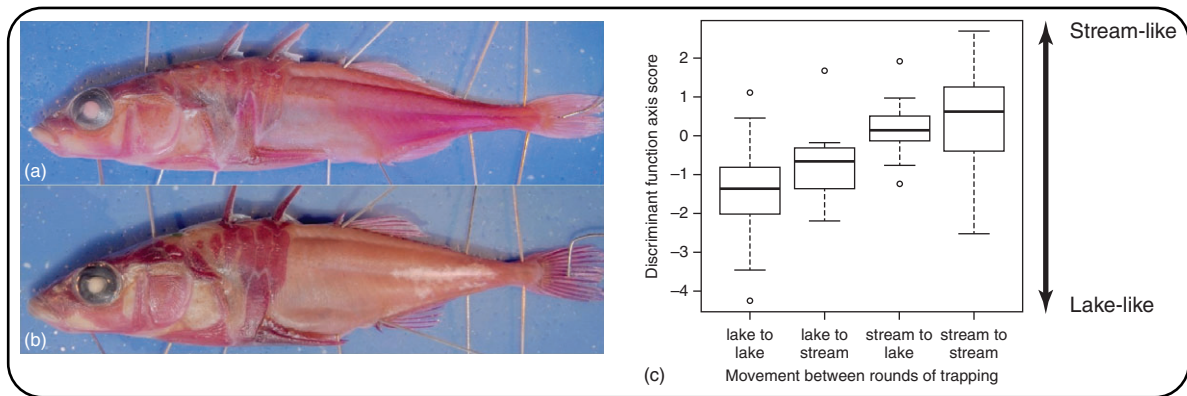


Figure 2 Habitat choice contributes to local adaptation in the morphology of three-spined stickleback (*Gasterosteus aculeatus*) between lake and stream environments. Morphological variation is continuous in stickleback: (a) lake fish tend to have a more streamlined body shape and longer tail compared to (b) stream fish to facilitate the use of open water (limnetic) habitats. (a,b) Photos reproduced with permission from Marius Roesti. © Marius Roesti. (c) Following transplantation of lake and stream fish to the intersection of lake and stream habitats, lake individuals were more likely to be recaptured in the lake (lake to lake) and stream fish in the stream (stream to stream). Interestingly, lake fish that were recaptured in the stream (lake to stream) were more stream-like in their morphology among lake fish. Likewise, stream fish that were recaptured in the lake (stream to lake) were more lake-like in their morphology among stream fish. (c) From Bolnick DI, Snowberg LK, Patenia C, Stutz WE, Ingram T, and Lau OL (2009) Phenotypic-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution* 63: 2004–2016.

morphology, sensory biology and behaviour in three-spined stickleback (*Gasterosteus aculeatus*; Bolnick *et al.*, 2009; Jiang *et al.*, 2015; Jiang *et al.*, 2017) (**Figure 2**).

Another interesting case study where habitat choice appears to play more of a synergistic rather than dominating role is that of local adaptation in spring salamanders (*Gyrinophilus porphyriticus*) (**Figure 3a,b**). Spring salamanders occupy both shallow, fast-moving riffles and deep, slow-moving pools within headwater streams. Individuals found in riffles have shorter limbs than those found in pools (Lowe *et al.*, 2018), presumably to reduce hydrodynamic drag during swimming (Addis *et al.*, 2019). Survival is positively correlated with dispersal distance, suggesting that fitness increases as individuals sample more habitats (Lowe, 2010; Lowe and McPeck, 2012). Furthermore, individuals are more likely to switch between riffle and pool habitats if their initial limb lengths match their destination habitats better than their original native habitats (Lowe and Addis, 2019) (**Figure 3c**). However, there is also phenotypic plasticity in limb length, as the limb length of individuals that switch between habitats changes to better match their destination habitats (Lowe and Addis, 2019) (**Figure 3d**). Interestingly, plasticity in limb length is negligible among individuals that remain in the same habitat, suggesting that habitat choice and phenotypic plasticity act in conjunction and thus have perhaps jointly evolved (Lowe and Addis, 2019).

The case of spring salamanders demonstrates the importance of assessing multiple adaptive processes given the observation that phenotypic plasticity has a noticeable effect on local adaptation only when individuals exert habitat choice. A similar dynamic might also be taking place for adaptation in the cryptic colouration of ambush bugs (*Phymata americana*), as laboratory tests indicate that the degree to which individuals match their background predicts choice of background substrate and the degree of change in body colouration via plasticity (Boyle and Start, 2020). However, additional work is needed to confirm that the

movements of individuals in natural populations are indicative of habitat choice. Theory has suggested that, when habitat choice and phenotypic plasticity act synergistically, adaptation can be achieved particularly rapidly (Nonaka *et al.*, 2015).

Future work

Although additional empirical demonstrations that habitat choice can contribute to adaptation would be beneficial given the general dearth of such studies, the focus of future work should not be whether habitat choice can facilitate adaptation but rather on its relative importance against alternative routes to increased fitness. Specifically, what features of species and what environmental conditions might we expect to cause habitat choice to figure more prominently in the adaptive process compared to other adaptive mechanisms? Does habitat choice often interact with other mechanisms of adaptation? If so, how and to what extent? These questions call for more empirical work, especially in natural populations in the field.

Another focus of future work should be on characterising the ability of habitat choice to facilitate adaptation in a wider variety of traits. Most studies of habitat choice have focused on assessing the role of habitat choice to adaptation in ecological trait axes (e.g. crypsis, feeding morphology, etc.). However, the need to acquire mates should often demand more precise use of habitat compared to the need to survive, given that variation in fecundity often has a greater impact on fitness variation than variation in survival (Kingsolver *et al.*, 2001; Hereford *et al.*, 2004; Porter and Benkman, 2017). Can habitat choice facilitate adaptation in mating signals and preferences (Porter and Akcali, 2018)? How might the sometimes-opposing demands to survive and reproduce impede the efficacy of habitat choice to promote adaptation? Little work has been conducted to address these questions; thus, theoretical approaches, as well as empirical work in both the

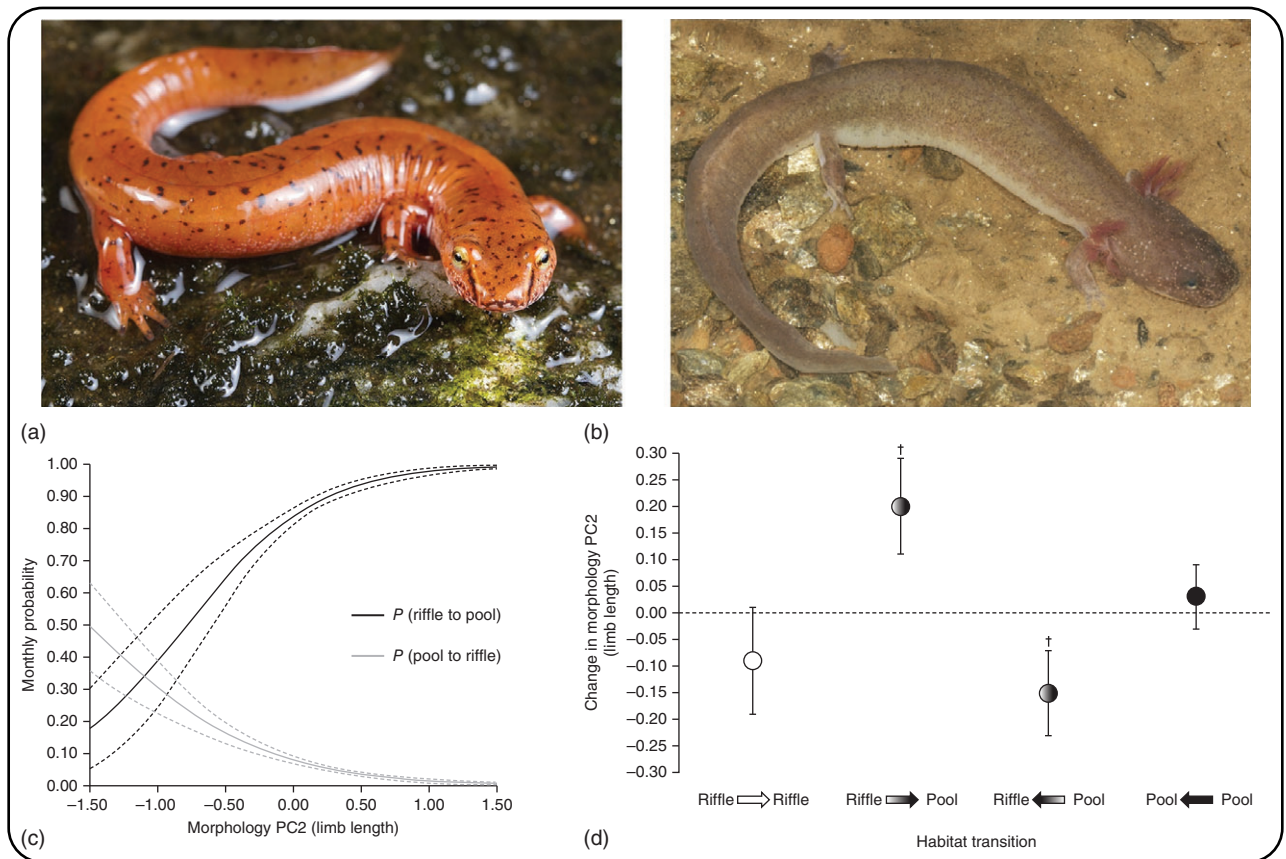


Figure 3 Phenotypic plasticity and habitat choice contribute to local adaptation in limb length in the spring salamander, *Gyrionophilus porphyriticus*, between fast-flowing riffles and slow-flowing pools in headwater streams. Whereas (a) adults are mainly aquatic and sometimes make terrestrial movements at night, (b) larvae are exclusively aquatic. (a,b) Photos reproduced with permission from Todd W. Pierson. © Todd W. Pierson. (c) Habitat choice contributed to adaptation in limb length, as the probability of individuals moving between habitats and the directionality of their movement between habitats depends on limb length. Specifically, long-limbed individuals were more likely to move from riffles to pools, whereas short-limbed individuals were more likely to move from pools to riffles. (d) However, salamanders also showed phenotypic plasticity in limb length: the limb lengths of salamanders that moved between habitats changed to become better adapted to their destination habitats, while the limb lengths of salamanders that did not move between habitats did not change. (c,d) From Lowe WH, and Addis BR (2019) Matching habitat choice and plasticity contribute to phenotypeenvironment covariation in a stream salamander. *Ecology* 100: e02661.

laboratory and the field, would be most welcome. We encourage future empirical studies to ensure that habitat-associated fitness benefits are quantified or, in the case of laboratory experiments, provided, as variation in fitness benefits among habitats is often a critical precondition for habitat choice to occur.

Lastly, given the rapidity with which habitat choice can promote adaptation, it should have the potential to facilitate the ability of organisms to adapt to rapid, human-induced environmental change. Nevertheless, few studies have examined the capacity of habitat choice to promote adaptation in the face of rapid environmental change (but see Edelaar *et al.*, 2019). How important might habitat choice be as a mechanism to adapt to rapid environmental change relative to other more well-studied mechanisms, such as phenotypic plasticity or natural selection? How might its relative importance depend on the severity of environmental changes? For example, might severe habitat change, such as urbanisation, increase the importance of habitat choice relative

to less severe forms, such as alterations of habitat structure? The myriad forms of anthropogenic disturbance that natural populations face today provide ample material for additional empirical study. **See also: Natural Selection: Responses to Current (Anthropogenic) Environmental Changes**

Habitat Choice and Speciation

A key event in the evolutionary process occurs when lineages evolve different phenotypes that lead to reductions in gene flow between them (i.e. reproductive isolation; Mayr, 1963). Once lineages start to evolve *reproductive isolating barriers*, they become less constrained in their capacity to explore independent evolutionary trajectories because the homogenising effect of gene flow is reduced (Futuyma, 1987). Eventually, if reproductive isolating barriers evolve to restrict most gene flow between lineages,

speciation may occur. Speciation may not always occur once reproductive isolation starts to evolve, as many systems appear to be at equilibrium despite having evolved only partial reproductive isolation (e.g. Bolnick, 2011) consistent with theoretical expectations (Rueffler *et al.*, 2006; Nosil *et al.*, 2009). Reproductive isolating barriers are still important in such systems, as they can allow certain phenotypes and associated genomic regions to diverge between lineages in response to divergent natural selection (Nosil and Crespi, 2004; Via, 2009). Thus, reproductive isolating barriers are thought to be a fundamental contributor to the origin and maintenance of biodiversity at multiple scales (Mayr, 1963; Futuyma, 1987). **See also: Isolating Mechanisms**

Since Theodosius Dobzhansky and Ernst Mayr emphasised the study of reproductive isolating barriers, the role that habitat choice might play in speciation and diversification has been apparent: if lineages evolve divergent habitat preferences (especially habitats in which mating occurs), individuals from different lineages are less likely to encounter each other as potential mates, thus reducing gene flow between them (Dobzhansky, 1937). Therefore, differences in habitat use between lineages can be considered a type of reproductive isolating barrier, usually termed habitat isolation. Even if individuals have no preference to mate with others from their own lineage, habitat isolation will still lead to assortative mating, thus reducing gene flow and promoting diversification (Via, 1999; Linn Jr *et al.*, 2003). While the role of habitat choice in speciation is often conceptualised on a local scale (e.g. preference for one forest type over another within a region), some have suggested that preferences for different habitats could manifest over much larger scales, leading to observed differences in geographic distributions of some closely related pairs of taxa (Sobel *et al.*, 2010; Sobel, 2014). The scope for habitat choice's role in speciation and diversification is thus potentially massive.

Inspired by the observation that closely related species often differ in habitat use, biologists have long thought that habitat isolation might be a particularly important reproductive isolating barrier (Dobzhansky, 1937; Mayr, 1942, 1947, 1963). Recently, there has been a major push by biologists to quantitatively estimate the degree to which various reproductive isolating barriers reduce gene flow between diverging lineages in nature (Coyne and Orr, 1989; Ramsey *et al.*, 2003; Coyne and Orr, 2004). The results of this work thus far indicate that habitat isolation is often one of the strongest barriers to gene flow in nature (**Figure 4**; Nosil *et al.*, 2005; Schemske, 2010; Lackey and Boughman, 2017). Furthermore, habitat isolation appears to be one of the strongest reproductive isolating barriers in the critical early stages of speciation, suggesting that it plays a key role in initiating diversification. These latter results are consistent with a handful of studies that have documented the rapid evolution of strong habitat isolation between lineages over just a few decades (Via, 1999; Hendry *et al.*, 2000; Linn Jr *et al.*, 2003), leading to substantial phenotypic and genetic divergence. Collectively, the available evidence supports the longstanding view of many biologists that habitat isolation plays a major role in generating biodiversity.

Indeed, habitat isolation appears to have been a key driver of diversification in one of Earth's most biodiverse groups: herbivorous insects. Almost half of all species described on our planet are

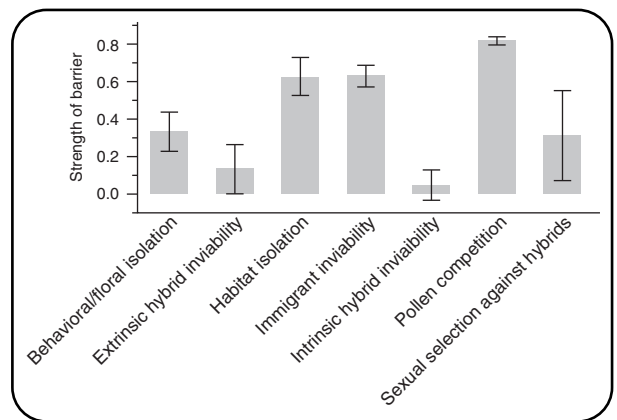


Figure 4 The mean strength (individual contribution to total isolation) of multiple reproductive isolating barriers (\pm SE) across several systems. Data from Nosil P, Vines T, and Funk DJ (2005) Perspective: Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution* 59: 705–719.

insects, and half of those are herbivorous (Grimaldi and Engel, 2005). The extraordinary diversity of herbivorous insects may be tied to the myriad and intimate links between host plant use and the evolution of reproductive isolating barriers (Berlocher and Feder, 2002; Matsubayashi *et al.*, 2010). Reproductive isolating barriers have been especially well studied in recently diverged host races that specialise in alternative plant species. In virtually every host race system studied to date, habitat isolation is one of, if not the, strongest barriers to gene flow (Bierbaum and Bush, 1990; Funk, 1998; Nokkala and Nokkala, 1998; Via, 1999; Craig *et al.*, 2001; Pappers *et al.*, 2002; Linn Jr *et al.*, 2003; Forister, 2004; Egan *et al.*, 2012). Habitat isolation and reproductive isolating barriers directly related to the use of alternative host plants are often the only barriers to gene flow in such host race systems (e.g. Hawthorne and Via, 2001), yet have led to the evolution of complete or nearly complete reproductive isolation in some cases (Via, 1999; Caillaud and Via, 2000; Via *et al.*, 2000). The effectiveness with which habitat isolation can restrict gene flow in such host race systems is thought to be the main reason that the evidence for sympatric speciation is stronger in herbivorous insects than any other group (Bolnick and Fitzpatrick, 2007). While habitat isolation has been implicated as a major factor in speciation in a wide range of groups (Schemske, 2010; Smith and Benkman, 2012; Lackey and Boughman, 2017), the diversifying potential of this reproductive isolating barrier in herbivorous insects is striking.

Future work

Clearly, habitat choice can act as an effective reproductive isolating barrier between co-occurring lineages within a region. But to what extent might habitat choice (as opposed to random, historical contingencies) be responsible for large-scale differences in the geographic distributions of closely related lineages? If habitat choice plays a role in maintaining distinct geographic ranges of diverging lineages, this suggests that geographic range

differences themselves might constitute a legitimate reproductive isolating barrier, as recently suggested by some authors (e.g. Sobel *et al.*, 2010). It is worth noting that these authors primarily work on plants: a system in which habitat choice might be important but is rarely considered (Bazzaz, 1991). Indeed, some authors have suggested that habitat isolation may play a role in plant speciation (Donohue, 2003), but little work on this exists to date. Both of these research topics could greatly increase the scope for habitat choice's role in speciation and diversification.

The available evidence indicates that habitat isolation can evolve early and rapidly during divergence. Once diverging lineages begin to use different habitats, they may be exposed to a variety of different environmental conditions that further reduce gene flow between them. For example, different habitats may have different resource phenologies, leading to divergent selection on the timing of breeding and, ultimately, temporal isolation between diverging lineages. Likewise, individuals that use different habitats have been found to preferentially associate with each other based on different habitat-related cues (Webster *et al.*, 2007), potentially resulting in behavioural isolation. To what extent can the evolution of habitat isolation 'trigger' the evolution of these and other reproductive isolating barriers in the initial stages of diversification?

Conversely, in later stages of divergence, once postzygotic barriers like hybrid inviability evolve, there may be selection for the evolution of prezygotic barriers that reduce the frequency of maladapted hybridisation (i.e. reinforcement; Servedio and Noor, 2003). Most research to date has focused on how reinforcement leads to the evolution of increased behavioural isolation between diverging lineages (Servedio and Noor, 2003), but it may promote the evolution of any prezygotic barrier that reduces the frequency of hybridisation, including habitat isolation. How often and under what conditions might habitat isolation evolve as an adaptive response to such maladaptive hybridisation? Given the well-known difficulties associated with evolving assortative mate choice behaviour (Kopp *et al.*, 2018), might habitat isolation be a more common route to speciation by reinforcement? Could selection against hybrids in the later stages of divergence be a more common driver of habitat isolation than the adaptive differentiation in the early stages of divergence that is so well documented? **See also:** [Reinforcement](#)

Habitat Choice Mechanisms

So far in this article, our discussion of habitat choice has been restricted to its evolutionary consequences in a general sense. However, the ultimate evolutionary consequences of habitat choice critically depend on its underlying mechanism: that is, how individuals make dispersal and settlement decisions. Below, we introduce the primary mechanisms of habitat choice and provide a brief discussion of the varying evolutionary implications they might have.

Generally, there are three main types of habitat choice (Akcali and Porter, 2017): *plastic habitat choice* (i.e. imprinting or learned habitat choice), *direct genetic habitat choice* and *matching habitat choice*. Plastic habitat choice occurs when individuals prefer habitats as a consequence of an environmental cue

experienced during ontogeny; direct genetic habitat choice occurs if individuals prefer habitats due to alleles that directly induce preference; and matching habitat choice occurs when individuals prefer habitats as a consequence of local performance assessment.

All three of these habitat choice mechanisms can result in the spatial or temporal isolation of individuals within a species and thus can contribute to the evolution of reproductive isolation. Plastic habitat choice and matching habitat choice are likely most important during early stages of divergence given that they can produce the immediate separation of individuals based on either exposure to an environmental cue (for plastic habitat choice) or via phenotype \times environment interactions in performance (for matching habitat choice). In contrast, the importance of direct genetic habitat choice is most likely greatest at later stages of divergence given that genetic associations are vulnerable to being disrupted by gene flow and subsequent recombination between populations (Felsenstein, 1981). However, their specific evolutionary consequences ultimately depend on knowing more details, such as the reversibility of plasticity in habitat choice, the genetic architecture underlying habitat preference, and the traits mediating variation in performance among habitats.

Additionally, all three of these mechanisms can promote increases in fitness and thus contribute to adaptation. Matching habitat choice is likely the most potent mechanism for promoting adaptation relative to plastic habitat choice and direct genetic habitat choice, as it permits individuals to rapidly match their phenotypes to changing environmental conditions. A corollary to this prediction is that the ability of matching habitat choice to reduce the scope for other adaptive mechanisms should be stronger relative to plastic habitat choice and direct genetic habitat choice. Overall, much remains to be learned about the relative efficacy of different habitat choice mechanisms to contribute to speciation and adaptive evolution.

Proximate Basis of Habitat Choice

Any one of the three main habitat choice mechanisms outlined above could be underlain by a variety of proximate factors that lead to individuals choosing certain habitats over others. While little is known about the proximate underpinnings of these habitat choice mechanisms, there has been some progress made in several systems illustrating the diversity of potential proximate factors contributing to a given habitat choice mechanism. For example, the outward, protruding eyes of grasshoppers might allow individuals to assess the degree of matching between their own colouration and the surrounding substrate. If individuals use this information to choose habitats where substrate-body colouration mismatch is minimal, this could produce the results found in Edelaar *et al.* (2019). Consistent with this hypothesis, experimentally manipulating the ability of individuals to visually assess their substrate-body colouration mismatch in another ground-dwelling grasshopper species (*Circotettix rabula*) alters patterns of habitat use to promote increased crypsis (Gillis, 1982).

By contrast, crossbills appear to directly assess their own performance in different habitats, not the degree of fit between their phenotype and environment as in grasshoppers. Specifically, crossbill habitat selection is extremely sensitive to variation

in feeding rates, with individuals preferring to feed on conifer trees that maximise their energetic intake rates (Benkman, 1987; Smith *et al.*, 1999). Because bill size predicts the feeding rates of crossbills on conifers with different cone and seed structures (Benkman, 1993), this direct assessment of individual feeding rate results in a correlation between bill size and conifer use. Similarly, stickleback seems to use microhabitats that minimise the energetic costs of swimming, with the result that parapatric lake and stream populations have diverged in their propensity to move up- or down-stream (i.e. their rheotactic response; Jiang *et al.*, 2015). This behavioural difference appears to be based on divergence in sensory systems (specifically, superficial neuromast lines; Jiang *et al.*, 2017). Given the diversity of proximate factors underlying one main mechanism of habitat choice (matching habitat choice) in just these three examples, it seems likely that there is tremendous variation in the proximate basis of habitat choice in nature, most of which has yet to be described.

Final Remarks

Although habitat choice has long been recognised as a potential evolutionary force by biologists, a detailed understanding of its actual evolutionary consequences in natural populations is still in its infancy. It is now clear that habitat choice can sometimes figure prominently in adaptation relative to natural selection and phenotypic plasticity and in speciation relative to other reproductive isolating barriers. However, there is a need for more empirical work in natural populations in more systems to more precisely characterise the various roles that habitat choice could play in these evolutionary processes. The study of habitat choice mechanisms in particular needs increased attention. Some recent exhaustive studies in diverse systems, including azure sand grasshoppers (Edelaar *et al.*, 2019), three-spined stickleback (Bolnick *et al.*, 2009; Jiang *et al.*, 2015; Jiang *et al.*, 2017) and salamanders (Lowe, 2010; Lowe and McPeck, 2012; Lowe *et al.*, 2018; Lowe and Addis, 2019) provide demonstrations of some fruitful approaches that could be used to further elucidate the diverse implications that habitat choice can have on the evolution of species and their traits.

Glossary

- Adaptation** The process by which organisms within a population become better at using their environments. Also, the state achieved by a population during the adaptive process.
- Direct genetic habitat choice** A form of habitat choice wherein individuals select habitats via alleles that directly induce preference.
- Habitat choice** The process by which individuals choose a habitat in which to perform their activities.
- Matching habitat choice** A form of habitat choice wherein individuals select habitats based on assessments of their local performance.
- Natural selection** The process by which individuals are differentially eliminated from breeding within a population.

Phenotypic plasticity The ability of an organism to alter its phenotype in response to changes in environmental conditions.

Plastic habitat choice A form of habitat choice wherein individuals select habitats based on an environmental cue experienced during ontogeny.

Reproductive isolating barrier Intrinsic organismal features that reduce gene flow between members of different populations, ecotypes, species, etc. Can be classified as acting before zygote formation (prezygotic) or after zygote formation (postzygotic).

Speciation The process by which new species are formed.

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