

Review Article

Habitat Choice and Speciation

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The role of habitat choice in reproductive isolation and ecological speciation has often been overlooked, despite acknowledgement of its ability to facilitate local adaptation. It can form part of the speciation process through various evolutionary mechanisms, yet where habitat choice has been included in models of ecological speciation little thought has been given to these underlying mechanisms. Here, we propose and describe three independent criteria underlying ten different evolutionary scenarios in which habitat choice may promote or maintain local adaptation. The scenarios are the result of all possible combinations of the independent criteria, providing a conceptual framework in which to discuss examples which illustrate each scenario. These examples show that the different roles of habitat choice in ecological speciation have rarely been effectively distinguished. Making such distinctions is an important challenge for the future, allowing better experimental design, stronger inferences and more meaningful comparisons among systems. We show some of the practical difficulties involved by reviewing the current evidence for the role of habitat choice in local adaptation and reproductive isolation in the intertidal gastropod *Littorina saxatilis*, a model system for the study of ecological speciation, assessing whether any of the proposed scenarios can be reliably distinguished, given current research.

1. Introduction

The role of divergent natural selection in speciation has been widely studied in recent years [1]. There is now broad acceptance that selection of this type can lead to the evolution of reproductive isolation, even in the face of gene flow [2]. Nevertheless, significant controversy remains. Is “ecological speciation” really distinct from other modes of speciation [3]? Why does reproductive isolation remain incomplete in some cases but not in others [4]? Do chromosomal rearrangements [5] or divergence hitchhiking [6] help to overcome the antagonism between selection and recombination? What is the role of the so-called “magic traits” [7]?

“Habitat isolation” is one part of the ecological barrier to gene exchange between species that includes effects due to local adaptation, competition, and choice [8]. In this paper, we will focus our attention on habitat choice, discussing the nature of its role in ecological speciation and the potential contribution towards reproductive isolation of various forms

of habitat choice. We define habitat choice as any behaviour that causes an individual to spend more time in one habitat type than another compared with the expectation based on random dispersal (see “habitat selection”, p. 184, [9]). On the basis of this definition, a simple reduction in dispersal distance would not constitute habitat choice. Examples of mechanisms that might underlie choice include active movement into a preferred habitat; reduced dispersal in the preferred habitat relative to a nonpreferred habitat; preferential settling of propagules after a dispersal phase or a change in the timing of dispersal that influences the probability of arriving in a different habitat. Habitats may be spatially separated on various scales, from abutting distributions to a fine-scale mosaic, even different parts of the same host plant [10]. They also need not be separated in space at all: temporal or seasonal separation is possible. In the case of seasonal separation, allochronic emergence or reproduction [11] effectively constitutes forms of habitat choice but will not be considered here.

Habitat heterogeneity can lead to ecological speciation in the presence of gene flow. It requires divergent selection, which results in the establishment of a multiple-niche polymorphism [1] (Figure 1). This might arise *in situ* or on secondary contact between previously allopatric populations. A mechanism for nonrandom mating must then become associated with this polymorphism [12]. As a result of this two-step process, habitat choice can influence the probability of speciation or the degree of reproductive isolation achieved in one of two ways; firstly, habitat choice may increase the range of parameters under which a stable polymorphism can be maintained by selection in a heterogeneous environment [13]. This effect can be independent of any effect on mating pattern if, for example, individuals feed in two contrasting environments but mate away from the food resources. Secondly, habitat choice may cause assortative mating if it results in partially independent mating pools. Habitat choice of this type may be favoured by selection against hybrids and so constitutes a form of reinforcement [14]. Choice of mating habitat may cause assortment without influencing local adaptation but, clearly, habitat choice may have both effects (i.e., on polymorphism and assortative mating) simultaneously in some systems, strongly influencing the likelihood and speed of speciation [15].

Additionally, the trait responsible for habitat choice and the locally adapted trait—responsible for adaptations to local conditions—must generally become associated, typically requiring the build-up of linkage disequilibrium but potentially facilitated by pleiotropy (see preference-performance correlations in [16]), as is the case for other components of reproductive isolation [2]. However, it is possible for habitat choice to be under direct selection and contribute to nonrandom mating, thus constituting a “magic trait” (*sensu* Gavrillets [17]). “Magic traits” are usually discussed in the context of locally adaptive traits that also contribute to assortative mating, such as signals and preferences, though the concept can clearly be applied to any trait that promotes reproductive isolation. A recent attempt at clarification of the “magic trait” definition suggested “a trait subject to divergent selection and a trait contributing to nonrandom mating that are pleiotropic expressions of the same gene(s)” [7] but this view unfortunately confounds two distinct ideas: the impact of a single trait on more than one component of reproductive isolation and the effect of a gene on more than one trait. Here, we follow the proposal by Smadja and Butlin [2] to distinguish “single-effect” and “multiple-effect” traits and avoid the use of the, now confusing, term “magic.”

Multiple-effect traits facilitate the evolution of reproductive isolation by reducing or removing the need for linkage disequilibrium and so avoiding the negative effects of recombination [2, 18]. Their contribution to speciation still depends on the magnitude of their effects [19]. A trait that contributes to reproductive isolation through habitat choice may also contribute to reproductive isolation in other ways, including but not exclusively through effects that lead to direct selection, and so may be a multiple-effect trait. Other things being equal, we expect such traits to increase the probability or speed of speciation.

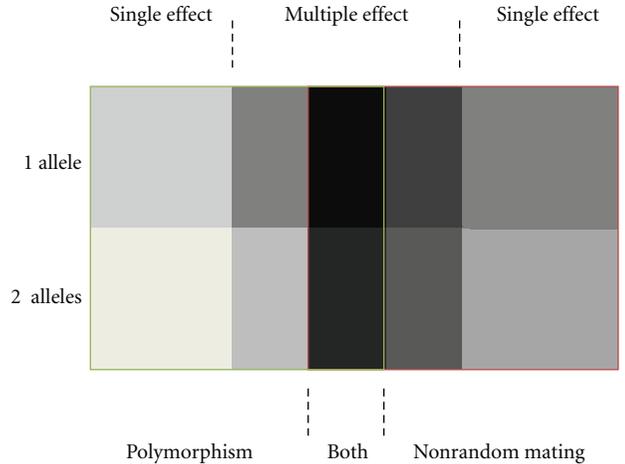


FIGURE 1: Habitat choice and the probability of speciation. Darker colours represent increased probability of speciation. See main text for further explanation.

Habitat choice may also evolve by either a “one-allele” or a “two-allele” mechanism [18], as in the “single-variation” and “double-variation” models of de Meeùs et al. [20]. A “one-allele” scenario might involve “habitat matching” (e.g., [21]), for example, causing an animal to move until it is cryptic against its background and then to remain stationary. Indirect selection would favour the spread of such an allele in an environment with two backgrounds where predation maintained a polymorphism for alternate cryptic colours, without the need for linkage disequilibrium because the matching allele is favoured in association with both colour morphs. Alternatively, a “two-allele” mechanism might involve one allele favouring upward movement and another favouring downward movement. Here, the evolution of habitat choice, and so reproductive isolation, relies on linkage disequilibrium between the upward movement allele and alleles conferring increased fitness in the high habitat and between the downward allele and the alternate alleles at the fitness loci. Note that the “one-allele” versus “two-allele” distinction still holds for polygenic traits and can be made without knowing the genetic basis of the trait—the primary issue is whether the trait has to change in the same direction (one-allele) or in different directions (two-allele) in the diverging populations. “One-allele” mechanisms increase the probability of speciation and can potentially be more effective in limiting gene flow between subpopulations than two-allele traits. As with multiple-effect traits, this is because they remove the need for linkage disequilibrium.

Habitat choice may be plastic, including the possibility of learning, and plasticity can be an important factor in speciation [22]. The extent of plastic response may vary, up to the point where no genetic difference needs to exist between individuals showing behavioural preferences for contrasting environments. However, plasticity itself has a genetic basis; evolution can act upon the degree of plasticity, both the ability to learn and biases in the way individuals learn can evolve. Evolution of plasticity or learning may be considered examples of a “one-allele” mechanism, where

the ability to modify the learning phenotype in a way that results in advantageous habitat choice is genetically determined and the same alleles, for effective learning, are beneficial everywhere.

These three different criteria for classifying traits responsible for habitat choice (whether habitat choice influences the maintenance of polymorphism or assortative mating; whether habitat choice traits are multiple or single effect; whether they follow a “one-allele” or “two-allele” inheritance mechanism) are largely independent. An exception arises because habitat choice may influence both the maintenance of polymorphism and assortative mating, and this is an example of a multiple-effect trait. If all possible combinations between the three criteria are considered, they may therefore lead, at least theoretically, to ten different habitat choice scenarios (Figure 1). Here we will discuss the implications of each one of these criteria for habitat choice and speciation, including examples of empirical studies and/or models. We will also review and discuss the current evidence for the role of habitat choice in local adaptation, including its possible effect on ecological speciation in an intertidal gastropod, the rough periwinkle *Littorina saxatilis*. We use this example to illustrate some of the practical difficulties involved in distinguishing among habitat choice scenarios empirically. This system also emphasises the generality of the distinctions by comparison with the more widely studied insect models in which host plants form the contrasting habitats.

2. Habitat Choice Scenarios

Figure 1 provides a conceptual classification of habitat choice scenarios, illustrating the likelihood of progression towards speciation under each scenario (a scenario consisting of a combination of criteria). It suggests that, at one extreme, habitat choice may contribute to the maintenance of polymorphism without directly contributing towards reproductive isolation (as indicated by the lightest area) whereas, at the other extreme, habitat choice evolution may be a primary driver of speciation (as indicated by the darkest, central areas). For simplicity we have erected a categorical system (our “criteria”). However, due to the dynamic nature of the evolutionary process, one or more habitat choice scenarios from our framework may contribute to speciation at different stages in the process. For example, stabilisation of multiple-niche polymorphism may often be an early stage of speciation whereas the evolution of divergent preferences for mating habitat could be a form of reinforcement at a late stage of the process. Below, we will discuss the relevance of each criterion of this classification with reference to illustrative examples. However, it will quickly become clear that there is often insufficient empirical information to be certain how individual case studies fit into our classification, partly because the role of habitat choice in speciation has not been addressed in a strong conceptual framework. Additionally, we were unable to identify good empirical examples that satisfactorily demonstrate some of our proposed scenarios—this highlights both the limited range of the studies that have been undertaken in this area and the difficulty in

identifying the mechanisms involved. We illustrate some of these difficulties in a final section dealing with one particular example, the periwinkle *Littorina saxatilis*.

2.1. Polymorphism or Nonrandom Mating. The first of our categories deals with the role of polymorphism and nonrandom mating in habitat choice scenarios: the establishment of polymorphism generated by divergent selection is a necessary step in ecological speciation.

Ecological speciation in the presence of gene flow requires divergent selection, which results in the establishment of polymorphism [1]. The maintenance of genetic variation within populations in heterogeneous environments has been widely discussed in the past, from theoretical models to experimental studies (reviewed in [23]). One of the first models, by Levene [24], showed that the maintenance of polymorphism in an environment with two habitats was possible. In this model there is random migration of individuals into the habitats, selection favours one of the genotypes in each habitat, each habitat contributes a constant number of individuals to the next generation, and there is random mating. The range of the parameters necessary to maintain polymorphism is rather restricted; nevertheless, this model was the basis for Maynard Smith’s [25] classic analysis of sympatric speciation. It is clear that under this model habitat choice is favoured by indirect selection (local adaptation to one of the habitats will secondarily promote preference for that habitat) and that habitat choice considerably expands the range of parameters under which the polymorphism is stable. Many subsequent models have shown that frequency- or density-dependent selection makes polymorphism more likely (e.g., [26, 27]) and so extends the range of situations in which an initial polymorphism will create conditions for the evolution of habitat choice, or where preexisting habitat choice will favour the establishment of multiple-niche polymorphism, reinforcing local adaptation (e.g., [20, 28]). The interplay between habitat choice and local adaptation has recently been reviewed by Ravigné et al. [13, 29]. From the point of view of speciation, the maintenance of local adaptation creates opportunities for the further evolution of reproductive isolation [25]. Therefore, if habitat choice helps to maintain polymorphism and if polymorphism reinforces local adaptation, it also increases the likelihood of speciation. This is true even if habitat choice has no influence on mating pattern. However, if habitat choice also generates assortative mating, its contribution to speciation will be greater (Figure 1). Habitat choice of this type is favoured by indirect selection when a polymorphism is established and this constitutes a form of reinforcement [14]. Finally, it is possible that habitat choice may apply only to the mating habitat and so influence mating patterns without being directly connected to a source of divergent selection. To understand the role of habitat choice in speciation, it is important to distinguish these categories and to determine the stage in the speciation process at which choice evolves.

Natural cases where both polymorphism and habitat choice are present in the population (but the choice does not influence mating pattern) are uncommon in the literature.

From the point of view of speciation, these examples should represent initial stages of speciation or divergence, but the outcome of this process is highly dependent on the reigning conditions (e.g., habitat distribution, habitat size, and selection coefficients) and there may actually be no progression towards greater isolation [4]. The most clear-cut examples are likely to come from species where mating occurs in a different habitat from the majority of the life-cycle, such as aquatic insects with a brief aerial mating phase. One interesting possible case concerns the aphid genus *Cryptomyzus* in which sibling species, which still occasionally hybridise in the field, utilise either dead nettle (*Lamium galeobdolon*) or hemp-nettle (*Galeopsis tetrahit*) as summer host. On these hosts they reproduce asexually, but their sexual generations occur on redcurrant (*Ribes rubrum*) regardless of the summer host [30]. Here, there is assortative mating but it is not due to the strong preference for distinct summer hosts. Rather, it seems to be mediated by differences in the diurnal cycle of pheromone release by females. This situation, where multiple races or species share the same primary host while utilising distinct summer hosts, seems to be common in aphids. The scenario where habitat choice can maintain a polymorphism but have no influence on nonrandom mating appears to be rare but may simply be under-represented in the literature. It is not likely to be favourable for progression to complete reproductive isolation.

The opposite situation, where habitat choice influences mating alone, is also not widely documented but is also most likely where mating occurs in a distinct habitat from the majority of the life cycle. A possible example may occur in the mosquito *Anopheles gambiae* whose larvae develop in small, often temporary water bodies but whose adults mate in aerial swarms. The M and S molecular forms of *A. gambiae* cooccur in many parts of Africa and show strong, but incomplete reproductive isolation. A major contributor to pre-zygotic isolation appears to be the choice of distinct habitats in which to form mating swarms [31]. This scenario is also unfavourable for speciation because there is no close connection between assortative mating and a source of divergent selection.

In the majority of cases habitat choice is likely to influence both maintenance of polymorphism and assortative mating, as mating usually takes place in the same habitat as the life-cycle phase in which selection occurs. A trait responsible for habitat choice of this type may be considered a multiple-effect trait because it has effects on reproductive isolation both through assortative mating and through enhancing local adaptation. This combination may generate a higher probability of progressing to complete reproductive isolation than cases where habitat choice influences only one component of isolation. The situation is typical of many phytophagous insects, which remain on their host to mate, and has been very widely studied in this context [32], including important early models (e.g., [28]) and classic research on the apple maggot fly, *Rhagoletis pomonella*.

Sympatric host races of the apple maggot fly in North America have evolved in the last 150 years, with a host shift occurring from hawthorn to apple around 1860 [33]. Life cycles in these two host races are very similar; mating

occurs on the plant and females oviposit in ripening fruit. Larvae complete their development in the ripe fallen fruits, pupate in the soil, and undergo a facultative diapause until spring. Adults congregate again on the host plant for mating. Host races are differentially adapted, primarily through their diapause characteristics which match the timing of the life-cycles to differences in phenology of their hosts [34, 35]. There are also host-associated differences in larval survival [36].

Host fidelity in *Rhagoletis* is partly a result of limited dispersal but there is clear evidence for active habitat choice involving fruit size and colour and, especially, volatile chemical signatures [37, 38]. Because there are clear fitness differences and mating occurs on the host fruit, host choice clearly contributes to both stabilisation of the coexistence of the races and to assortative mating between them.

The historical role of host choice is less easily determined. Feder [39] suggested that individuals with a genetic preference for apples, the derived host, may have gained an immediate selective advantage, perhaps involving the use of an empty niche or escape from parasitism (“apple race flies have less parasitoids than hawthorn race flies because parasitoids use plant cues when searching for their hosts,” [40]). In this case, habitat choice may have evolved first and facilitated subsequent host adaptation, rather than evolving in response to the fitness costs of oviposition on the wrong host. Habitat choice would then be a multiple-effect trait since it would be under direct selection, as well as contributing to assortative mating (see below). A further complication to this hypothesis is the association of some host-specific traits with chromosomal inversions. These inversions appear to predate the introduction of apples to North America and may have evolved during a period of allopatry [41]. Their presence in the population may also have facilitated the host shift, interacting with changes in preference.

2.2. Habitat Choice: “Multiple-Effect Trait” versus “Single-Effect Trait”. The *Rhagoletis* example nicely illustrates the distinction between multiple-effect and single-effect traits, as defined in Section 1. We can envisage two possible historical sequences. In the first, multiple-effect, scenario, an allele arose in the ancestral hawthorn population which increased the likelihood of females ovipositing on apple. This habitat choice allele was favoured by direct selection because larvae developing on apple had higher survival but at the same time contributed to isolation through its impact on assortative mating. This led to the establishment of a population on apple trees, which further adapted to the new habitat, including divergence in diapause timing. Johnson et al. [42] modelled a scenario of this type. An alternative, single-effect, scenario would begin with a proportion of females ovipositing on apple by chance. This favoured alleles for high survival on apple leading to the establishment of a multiple-niche polymorphism. Indirect selection could then have favoured habitat choice through its impact on assortative mating alone, requiring linkage disequilibrium between survival and choice alleles to be established in the face of gene flow and recombination (a form of reinforcement). Distinguishing such alternatives retrospectively is likely to be very difficult.

The importance of phenology in *Rhagoletis* suggests a further option. Apple and hawthorn fruit are temporally separated habitats. Therefore, any change in diapause timing early in the evolution of the apple race would have constituted a multiple-effect trait under direct selection, because of the benefits of matching timing to the host and also influencing habitat choice. Since the timing difference could have generated assortative mating, this trait would have made three distinct contributions to reproductive isolation.

Interestingly, disrupted host finding in *Rhagoletis* hybrids also contributes to postzygotic isolation [43], a neglected potential contribution of habitat choice to speciation. This constitutes a distinct pathway by which a habitat choice trait can have multiple effects on reproductive isolation, which is independent of the polymorphism versus nonrandom mating criterion. For this reason, we consider the single-effect/multiple-effect distinction separately, because the impact of a habitat choice trait on both polymorphism and nonrandom mating is not the only way in which it can act as a multiple-effect trait.

Another good example of a direct link between habitat choice and adaptation is the pea aphid, *Acyrtosiphon pisum*. In this phytophagous insect, feeding, mating, and oviposition occur only on the host plant. In the northeastern United States, host races of the subspecies *A. pisum pisum* live on alfalfa (*Medicago*) and clover (*Trifolium*), crops that are sometimes grown in adjacent fields, and some gene flow persists between the races [6]. The aphids acceptance of the host plant is one of the main reasons for assortative mating: pea aphids can distinguish between their preferred host and the alternate host by probing with their stylets. When they detect the alternate host they do not feed but will move in search of another plant in order to increase their probabilities of reproductive success [44]. Thus, habitat choice and habitat-associated fitness are aspects of the same underlying trait of host acceptance, which can be considered a multiple-effect trait. As with the apple maggot fly, host acceptance also influences assortative mating, and this situation greatly facilitates the evolution of reproductive isolation [2]. It is likely that the key genetic changes of host acceptance involve the aphids chemical senses, and the recent characterisation of chemosensory gene families in the pea aphid [45] opens the way to identification of the responsible genes.

Hawthorne and Via [46] showed that, for the traits they defined as host acceptance and host-associated performance, QTL mapped close together in the pea aphid genome. They suggest that there may be either close linkage between genes for the different traits or alleles with pleiotropic effects on the traits. Following Smadja and Butlin [2], we suggest that it is more instructive to view host acceptance as a multiple-effect trait with direct effects on fitness. Of course, there may be other traits that also adapt the aphids to different host environments, such as mechanisms for tackling host defensive compounds.

2.3. “One-Allele” versus “Two-Allele” Mechanisms. “One-allele” and “two-allele” mechanisms have been widely discussed in speciation research since the distinction was introduced by Felsenstein [18] and the distinction has been

considered one of the most useful ways to categorise speciation [47]. In principle, habitat choice may evolve by either mechanism [20] but making the distinction for empirical examples is not straightforward. Therefore, we begin with conceptual examples to illustrate the ways in which “one-allele” and “two-allele” mechanisms might apply to habitat choice before suggesting possible case studies.

In “one-allele” mechanisms, a single allele present in a population under divergent or disruptive selection generates habitat preference independently of the direction of selection. One possible way for this to work would be through natal habitat preference induction (reviewed in [48]), in which experience with a natal habitat shapes the preferences of individuals for that habitat. Experience with particular stimuli increases subsequent preference for a habitat that contains those same stimuli, which might help dispersing individuals to locate a suitable habitat quickly and efficiently. Because assessing habitat quality involves time, risk, and energy invested in sampling potential habitats, selection should favour mechanisms that help individuals to select and use habitats that best suit their phenotypes. Any allele that spreads in response to such selection would enhance divergent habitat choice in a population showing local adaptation to multiple niches. Habitat matching, for example in cryptically coloured species, would have a similar effect without the need to condition on the natal habitat (matching habitat choice, [21]), promoting local adaptation and even leading to speciation. On the other hand, in response to environmental change, adaptation could involve change or relaxation of habitat choice instead of adaptation to modified conditions, resulting in more variable habitat use [21], which could lead to breakdown of reproductive isolation. Under these conditions the “two-allele” mechanism would offer greater resistance to hybridisation than the “one-allele” mechanism, although “two-allele” habitat choice would be less likely to initiate the process of speciation.

“Two-allele” habitat choice is more likely to involve innate preferences for specific habitat features, such as substrate colour or odour or the presence of particular resources. Divergent or disruptive selection is required to establish such distinct preferences.

Differentiating between “one-allele” (e.g., habitat matching) and “two-allele” (distinct preferences in different subpopulations) scenarios is not an easy task, as previously mentioned. As an example, we consider colour morphs of another phytophagous insect, the walking stick *Timema cristinae* (see [49] for a review). Two host species with highly divergent leaf colour and shape, *Ceanothus spinosus* and *Adenostoma fasciculatum*, are utilised. Insects found on different hosts have different cryptic colour patterns because of selection due to predation. These wingless insects feed, mate, and reproduce on the same host individual and movement between plants is restricted (12 m per generation, [50]). They show host preference [51] and partial assortative mating [52]. Immigrant inviability (selection against ecotypes from the contrasting habitat: i.e., host plant) is also an important process maintaining the ecotype divergence [53]. It is clear that habitat choice contributes to the maintenance of *Timema* ecotypes but the mechanistic basis of this

preference has not yet been characterised. The preference could, for example, involve detection of different chemical compounds on the host plant surfaces that are unrelated to crypsis: a “two-allele” mechanism. Alternatively, the insects may match their own colouration to the background, a mechanism that could fall into the “one-allele” category. These possibilities could be distinguished experimentally, for example by allowing insects to choose between backgrounds of different colour/pattern in the absence of plant material.

Preferences for divergent chemical signals are likely to underlie host-plant preference in many phytophagous insects [54]. These are likely to involve “two-allele” mechanisms where different alleles for positive or negative responses [55] to particular stimuli have to be fixed in the diverging subpopulations and have to be associated, through linkage disequilibrium or pleiotropy, with traits that underlie local adaptation. Because this is less favourable to speciation than matching mechanisms, it is important to make the distinction in more case studies.

Particularly interesting possible cases of “one-allele” habitat choice involve learning, including imprinting. Such cases are sometimes described as “nongenetic” but clearly the ability to imprint or the strength of imprinting can have a genetic basis and the spread of a single allele can then cause divergent habitat preferences by promoting imprinting on different signals. Obligate brood parasitic birds represent potential examples of this process. In the continuum of divergence and/or speciation [4, 56, 57], different races or species pairs represent different stages in the process of ecological speciation, and this is also the case for brood parasitic birds. Indigobirds (genus *Vidua*) are obligate, host-specific brood parasites of firefinches (genus *Lagonosticta*) and other estrildid finches (family Estrildidae). Assortative mating is due to song learning and mimicry of the host song by the males [58, 59], and this allows a host switch to occur in a single generation. Females also learn the song of their foster parents and choose their mates and the nests they parasitise using song. Different degrees of divergence are found depending on the species under study, for example, some of them are morphologically indistinguishable [60, 61] and they lack genetic differentiation at neutral markers [62]. When host species of different indigobirds have overlapping distributions, hybridisation can occur due to egg-laying mistakes (e.g., a female lays an egg in a nest parasitised by another indigobird species). Individuals of different species would then learn the same song, through imprinting, and are likely to hybridise. However, in most of the cases, indigobird species have evolved several other polymorphisms, such as different male plumage colour and nestling mouth markings that match those of their respective hosts [63], thereby enabling young indigobirds to better compete for parental care in host nests. These polymorphisms represent different axes of divergence (greater “ecological niche dimensionality,” [64]) promoting increased divergence, despite the possibility of accidental hybridisation in regions where host ranges overlap. This suggests that, following colonisation of a new host, host fidelity due to imprinting can be sufficient for divergent natural and/or sexual selection on morphology, ecology, and/or behaviour to generate progress on the speciation

continuum. Imprinting causes habitat choice, through its influence on female choice of host nests, as well as mate choice and so is a multiple-effect as well as a “one-allele” trait [2, 7].

In these sections, we have selected empirical examples that illustrate each of our classifying criteria. Figure 1 shows the ways in which these criteria may combine to create conceptual scenarios with varying probabilities of progression to speciation. Working from the framework, how easily can these conceptual scenarios be applied to real-world systems? Our brief review of the literature suggests that habitat choice studies pertaining to ecological speciation are biased towards phytophagous insects. This is not surprising, because “host race” formation seems to be a common route to speciation, which has been widely studied. However, in an attempt to expand the scope of habitat choice studies in an ecological speciation context, we discuss below the evidence for habitat choice in the intertidal gastropod genus *Littorina*. We examine the current evidence for habitat choice, discussing which scenarios are likely to be involved and the difficulties in trying to distinguish them.

3. Habitat Choice in *Littorina*

Intertidal gastropods present ideal systems for studies of habitat choice: the littoral zone can create extreme environmental gradients and highly heterogeneous habitats within relatively short distances, and generally the animals are easy to locate and manipulate for both *in situ* and lab-based trials. Heterogeneous habitats of this type can lead to differential survival and generate divergent selection in polymorphic populations. Microhabitat use in this landscape has been identified as strongly influencing survival in intertidal gastropods [65–67], so habitat choice presents itself as a likely trait to respond to this selection.

Large-scale transplant experiments have indicated habitat preference behaviour in *Littorina* species, such as *L. keenae* [68], *L. angulifera* [69], and *L. unifasciata* [70]. All show that the snails tend to return to the approximate tidal height from which they were displaced, exhibiting directional movement towards the shore level of origin. However, these transplant experiments may also be influenced by effects of differential survival that are hard to separate from behavioural effects. We will examine this problem below.

Littorina saxatilis, the rough periwinkle, is a marine gastropod that is emerging as a model system for studying ecological speciation. It is widely distributed across rocky shorelines in the North Atlantic, extremely polymorphic (shell colour, shell shape, and behaviour), and prone to ecotype formation due to local adaptation because of its low average dispersal [71]. Pairs of phenotypically divergent ecotypes occupying different niches in the intertidal zone are found over scales of tens of metres or shorter across different shores along its distribution and are maintained through divergent natural selection [72]. These ecotypes of *L. saxatilis* have been studied in detail on shores from three geographical regions (Sweden, UK, and Spain), and a process of parallel ecological speciation between them has been suggested ([72], but see [73, 74]). However, despite displaying phenotypic

divergence, the ecotypes are not completely reproductively isolated, with gene flow still occurring (Sweden: [75], UK: [76], and Spain: [77]).

The ecotype pairs on each of these shores are separated on a microgeographic scale, exhibiting adaptations to the prevailing habitat. On Swedish shores, the habitat is composed of a mosaic of cliff habitat punctuated with boulder fields, whereas the UK and Spanish ecotype pairs are found on the same shores, but at different levels of the littoral zone. The ecotypes in the UK are known as H and M (high-shore and midshore), those in Sweden are termed E and S (exposed and sheltered), and the Spanish pair are termed RB and SU (ridged-banded and smooth-unbanded) (see [73]). The M, S, and RB ecotypes are morphologically congruent, exhibiting thick shells, relatively small shell apertures, and large body size. These features are considered to be adaptations to an important selection pressure: predation by crabs. The H, E, and SU ecotypes from these three shores also share similar morphological characters: smaller size, thinner shells, and a larger shell aperture. In avoiding the hazards of crab predation by their position on the shore (low in Spain, high in Britain and Sweden), these ecotypes are free to develop larger shell apertures, increasing foot area and thus grip on the substrate to minimise dislodgement. Nonrandom mating is also observed in each population of ecotype pairs [78–81], primarily due to assortative mating by size (see [72] for a review). *L. saxatilis* lacks a pelagic larval stage, instead exhibiting direct development where females retain their brood internally and release fully formed young [71]. Many other littorinid species (such as *L. littorea*) produce a pelagic larval stage, allowing dispersal over a wide range and maintaining gene flow between populations [71]. The low dispersal range of *L. saxatilis* (1–4 m, [82, 83]) limits gene flow, and this facilitates much greater local adaptation in this species than in many of its congeners [72].

Since selection drives differential adaptation to closely adjacent habitats, habitat choice mechanisms could easily be imagined to play a role in population divergence. Random dispersal combined with selection against less fit phenotypes may superficially look like habitat choice as the phenotypes are segregated into divergent habitats, as noted above. This is particularly true where dispersal distance is short allowing selection to produce sharp phenotypic transitions at habitat boundaries. Selection for reduced postnatal dispersal [84] may accentuate this effect. However, as there is no active behavioural mechanism, this does not constitute habitat choice as we define it.

A possible exception, where habitat choice can be inferred from phenotypic distributions, is where habitat heterogeneity is on a scale much smaller than the dispersal distance. It is then not possible for selection to maintain genetic differentiation between patches [85] independent from habitat choice, although phenotypic plasticity could still result in strong phenotype-habitat associations. Morphological and AFLP (amplified fragment length polymorphism, see [86] for a review) clines have been identified, which are too steep to have been generated by selection alone [87, 88]. In these cases, additional mechanisms such as habitat choice may contribute to the genesis and maintenance of

the gradient by strengthening barriers to gene flow. In the middle of the shore gradient in Spain, mussel and barnacle dominated patches are intermingled on a scale of a few centimetres and the RB and SU *L. saxatilis* ecotypes are associated with these patches [89]. This is strongly suggestive of active habitat choice [90]. The heterogeneous nature of this connecting habitat may be particularly important in the maintenance of the hybrid zone and the segregation of the ecotypes, as has been demonstrated with *Bombina* toads [91]. Nevertheless, in order to determine the role of habitat choice in maintaining divergent populations, in *L. saxatilis* and in other comparable systems, it is necessary to utilise manipulative experiments (e.g., using mark-recapture approaches).

Clear evidence for home-site advantages in littorinid species has been documented [83, 89, 92] along with evidence of selection on shell characters. In this context, we consider a home-site advantage to be where individuals are likely to have increased fitness in the habitat or microhabitat to which their ecotype may be presumed to be adapted. This advantage may vary at different stages of the life history. Is there also good evidence for habitat choice in the *L. saxatilis* ecotypes? Has *L. saxatilis* evolved habitat choice in response to divergent selection, or did nonrandom mating and adaptive polymorphism evolve in the presence of preexisting habitat choice? Habitat choice can be an adaptive behaviour, increasing fitness in the “home” habitat even when only a single habitat type is occupied [93] and so could have been present before ecotype differentiation began. Is habitat choice a multiple-effect trait in *Littorina* and is it based on “one-allele” or “two-allele” genetic variation? We discuss the evidence for the presence of habitat choice in *L. saxatilis* and consider whether it is possible to make any of these distinctions.

Work on Swedish populations indicates that morphological adaptation to the contrasting environment has a strong genetic basis but has an element of plasticity which can improve local adaptation [94, 95]. However, the E (exposed) ecotype displayed significantly lower levels of plasticity than the S (sheltered) ecotype, indicating differential plasticity within local populations. This leads to the question of the effect of plasticity on the role of habitat choice: it is feasible that lower phenotypic plasticity might favour the evolution of genetically based habitat choice, to increase occupation of the environment in which individuals are more fit. Increased plasticity may decrease selection for habitat choice, since individuals would be better able to adapt their phenotype to local conditions. This might be tested if the degree of morphological plasticity varies among regions, leading to a prediction of varying habitat choice.

Experimental evidence for nonrandom dispersal in *L. saxatilis* ecotype populations has been obtained in both Spain and Sweden [78, 82, 83]. In the Swedish populations, displaced snails exhibited greater average dispersal distances than nondisplaced ones and dispersal differed between E and S ecotypes, in addition to a tendency to recapture snails in their own habitat more often than expected from random dispersal [83]. However, this tendency to recapture snails in their own habitat may be a function of differential survival

in native and nonnative habitats. Additionally, although survival rates and migration distances were measured, direction of movement was not. Erlandsson et al. [82] expanded on this study to determine whether the dispersal was directional in the Spanish population. They detected random dispersal when snails were placed at their native shore level (with overall dispersal distances averaging less than 2 m), whereas when animals were transplanted to their nonnative shore level they moved further and more directionally, with the Spanish RB morph exhibiting the greatest directional response. Although this hinted at habitat choice in this ecotype, the recapture rate was low (<20%) and conclusions were drawn only from recaptured individuals (which are likely to be a strongly selected sample), therefore it is difficult to make any meaningful conclusions about habitat choice from these simpler experimental studies.

On the Galician shore in Spain, Cruz et al. [78] tried to separate survival and habitat preference in the two ecotypes of *L. saxatilis* using two reciprocal transplant experiments. In the first experiment, sample groups of each ecotype were transplanted both to their native and nonnative shore level at each of two sites. Snails were then recaptured and their movement recorded from two days after transplant. The study compared the recapture positions of the transplanted snails and the recapture positions of the corresponding control snails, to correct for movements that may be induced via prevailing climatic conditions. In addition to the confounding effect that such forced migration might have had on the snails survival, transplanted snails may have dispersed beyond the study area leading to reduced recapture. One way in which Cruz et al. [78] avoided these complications was to argue that only directional movement could result in more than 50% of the released snails in the treatment group being recaptured in the direction of their preferred habitat (up shore for RB, down shore for SU). With this stringent criterion, habitat choice was only observed in one site.

The second experiment involved collection of snails from five intertidal levels on each of two sites and reciprocal transplants across sites for release. This destroyed the correlation between shore level and snail phenotype (measured as the first axis of shell shape variation). Over a period of two weeks, they observed the reformation of the shell-shape cline and measured the relative contributions, for the cline reformation, of the snails migrating movements and survival. Using a clever comparison between the change in average positions of all snails recaptured and the change in position of those that were known to have survived, they separated the contributions of differential survival and habitat choice to the changing cline. Differential movement contributed between one-third and one-half of the change in cline at one site and hardly at all at the other site, leading to the conclusion that habitat choice was present but less important than differential viability in the maintenance of the phenotypic cline.

This important study illustrates the difficulties associated with demonstrating habitat choice in the field. Despite considerable effort and thoughtful design, the experiments were still hampered by low recapture rates (around 50%)

and could be criticised for releasing snails at high densities in potentially unnatural positions. The analyses do not provide quantitative estimates of survival, dispersal, or their ecotype-habitat interactions, the sort of variables that would be needed to model likely evolutionary scenarios. A recent theoretical model of ecotype formation in *Littorina saxatilis* [96] did not include habitat choice as a parameter. Due to the currently unknown contribution of habitat choice to reproductive isolation in this species, it would be interesting to see how the potential to evolve choice might influence model outcomes.

Cruz et al. [78] also discussed the possible behavioural basis of habitat choice. The observation that shell morphology provided the best predictor of habitat-specific viability but that sampling location best explained the pattern of movement led them to suggest that shell shape and habitat choice are genetically independent. Therefore, in the terms we use here, shell shape is not a multiple-effect trait in the sense that a change in shape alters the fitness profile but does not automatically alter habitat preference (as it might if snails had a pre-existing tendency to move to a habitat that was favourable for their shell shape). Note, however, that shell size does seem to be multiple-effect in that it influences both differential survival and assortative mating. A “two-allele” mechanism (or “double-variation”: [20, 78]) seems more likely than a “one-allele” mechanism for the same reason. Movement to the optimum habitat could be a “one-allele” mechanism but would result in a strong association between shell shape and differential movement, which may occur prior to local adaptation. An upward bias in RB and a downward bias in SU would most likely be a two-allele mechanism, dependent on linkage disequilibrium and so less tightly linked to shape. Under this assumption, habitat choice could evolve after local adaptation. Lack of preference in hybrids [90] tends to support this conclusion, suggesting that habitat choice evolved after local adaptation whereas a tendency toward matching position to optimal habitat preceded local adaptation. However, direct behavioural tests and genetic analysis are needed to confirm these speculations and will be difficult if habitat choice is as weak in other regions as it seems to be in Spain.

Other littorinid studies highlight the role of chemoreception in influencing the behaviour of individuals (such as trail following: [97, 98]). It has been determined that *L. saxatilis* E ecotype males (S males were not studied) are able to discriminate between mucous trails of the female of each ecotype [99] and show a clear preference for trails of females within the size range of the E ecotype females. In addition to its role in assortative mating, trail following could play a role in habitat choice. This has been studied to an extent in *L. littorea* [100]. When chemical cues were removed from the “home” boulder and substrate, *L. littorea* displayed a significantly impaired ability to navigate back to the boulder from which they had been displaced. In *L. saxatilis* it would be interesting to separate the role of assortative mating from habitat choice. Trail following could impact dispersal experiments by making individual movements nonindependent [78] and, if it forms the basis of philopatry, could represent a “one-allele” habitat choice

mechanism. More studies are needed to unveil the role of chemoreception in habitat choice in this species.

Did size-assortative mating evolve after ecological partitioning and evolution of habitat choice? Or did habitat choice facilitate ecotype formation after the development of assortative mating? The model by Sadedin et al. [96] suggested that assortative mating may be considered ancestral. However, although a number of ecological factors were modelled, habitat choice was not included as a parameter. Dispersal was included, but this was not directional. Dispersal was an important consideration though: frequent long-range random dispersal eliminated spatial genetic structure and did not lead to ecotype formation. Although the role and mechanism of habitat choice in *Littorina* have not yet been explicitly modelled, we may draw inferences from models developed for other organisms. Early models suggested that when fitness, mating, and habitat choice are all based on the same character, speciation with gene flow may result—the degree of reproductive isolation is determined by the strength of assortative mating and the strength of disruptive selection. For moderate selection, habitat-based nonrandom mating also facilitates reproductive isolation. However, in simulations, the size-related mate choice mechanism in *L. saxatilis* could not explain more than a small part of the sexual isolation between morphs [101]. This implies that size-related mate choice, although considered a multiple-effect trait, may only be important in a speciation context if it evolves in parallel with other ecological traits, including habitat choice.

These studies highlight the difficulties in connecting theoretical evolutionary scenarios with existing empirical data. However, if future habitat choice studies are carried out with an explicit conceptual framework in mind and across a wide range of study systems, they will contribute more effectively to our understanding of speciation.

4. Conclusion

The influence of habitat choice on ecological speciation clearly varies in both magnitude and mechanism, and in many cases we cannot be sure about the contribution it makes to reproductive isolation or at what stage it evolved. The empirical examples discussed for some of our projected scenarios provide an indication of which evolutionary scenarios have been observed in natural systems. We would expect those scenarios where habitat choice does not strongly favour progress towards speciation to be detected in studies of within-species polymorphism, whereas those promoting speciation may be more prevalent among studies of ecological speciation. A more exhaustive review is needed to test this prediction but may be premature since many case studies do not yet provide enough information to distinguish among scenarios for the evolution of habitat choice.

Although there have been some valuable habitat choice studies on *Littorina saxatilis*, there are still a lot of unanswered questions regarding its role in the maintenance of both the phenotypic and genetic clines. As a candidate system for ecological speciation, the understanding of the role of habitat choice prior to complete reproductive isolation in

L. saxatilis is an important facet in our overall understanding of the processes and mechanisms leading to species formation.

Describing the role of habitat choice within the conceptual framework that we propose represents an important step in understanding speciation. It shows how habitat choice can affect reproductive isolation in very different manners, influencing the likelihood of speciation and potentially leading to different stages along the continuum of speciation. Empirical studies of habitat choice in divergent populations or closely related species, representing different stages of speciation and different evolutionary scenarios, should form a focus for future research. When analysed within such a conceptual framework, we believe these studies will give more insight into the part that habitat choice plays in ecological speciation than if they are considered in isolation.

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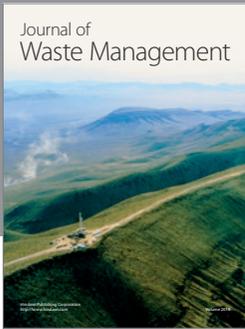
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