Inverting the null-hypothesis of speciation: a marine snail perspective

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Abstract Speciation is currently an intensely debated topic, much more so than 20–30 years ago when most biologists held the view that new species (at least of animals) were formed through the split of evolutionary lineages by the appearance of physical barriers to gene flow. Recent advances have, however, lent both theoretical and empirical support to speciation in the presence of gene flow. Nevertheless, the allopatric hypothesis of speciation is still the default model. The consequence of this is that to support sympatric and parapatric modes of speciation all allopatric alternatives must be rejected, while an allopatric explanation is usually accepted without rejecting possible non-allopatric alternatives. However, classical cases of allopatric speciation can be challenged by alternative non-allopatric explanations, and this begs for a more respectful view of how to deal with all models of speciation. An appealing approach is studying parallel evolution of reproductive barriers, which allows for comparative approaches to distinguish between allopatric and non-allopatric events, and explicit tests of a suitable null-hypothesis. Parallel evolution of reproductive isolation in a strongly polymorphic marine snail species serves as an illustrative example of such an approach. In conclusion, a more balanced debate on allopatric and non-allopatric speciation is needed and an urgent issue is to treat both allopatric and nonallopatric hypotheses critically, rather than using allopatry as the default model of speciation.

Keywords Sympatric speciation · Allopatric speciation · Parallel speciation · Incipient speciation · *Littorina saxatilis*

The allopatric: non-allopatric imbalance

Speciation is currently a headline topic in biology, but it has not always been so. Those among us that were trained in evolution during the 1960–1980s remember an era during

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which Ernst Mayr's verbal models of allopatric and founder-effect speciation (Mayr 1963) were considered robust and consequently a vivid debate on how new species were formed was absent. Despite John Maynard Smith's (1966) provocatively simple model of sympatric speciation, and White's (1978) strong rebuttal of Mayr's dogmatic statements, the view of allopatric speciation, remained more or less unchallenged until late during the last century (e.g. Felsenstein 1981; Rice and Salt 1990; Coyne 1994; Bush 1994; Via 2001). Indeed, with the exception of a general acknowledgement of instant sympatric speciation by polyploidy in plants, non-allopatric speciation is still presented as a highly controversial model by recent textbooks of evolution and speciation (Coyne and Orr 2004; Futuyma 2005), despite recent new and tractable models of sympatric and parapatric speciation (e.g., Dieckman and Doebeli 1999; Kondrashov and Kondrashov 1999; Doebeli and Dieckmann 2003). Moreover, publishing empirical data in support of a non-allopatric scenario of speciation, still provoke criticisms (e.g., Howard et al. 2001; Stuessy 2006; Schliewen et al. 2006), while the opposite—presenting data suggesting allopatric speciation—seldom raises opposition. Thus, although most evolutionary biologists today acknowledge non-allopatric speciation as possible, at least in theory, allopatric speciation remains the paradigm and non-allopatric speciation (with the exception of speciation through polyploidy) is thought to be rare.

This background opinion creates an imbalance between the hypotheses of allopatric and non-allopatric speciation, and an objective approach to studies of speciation is clearly missing. Indeed, we systematically use the allopatric speciation model as the null-hypothesis, and if arguing for non-allopatric speciation we first need to reject all possible allopatric alternatives, while the opposite—rejecting all sympatric alternatives to support allopatric speciation—is no issue. Perhaps not too surprising reflecting the knowledge of that time, Mayr (1963) wrote: "the burden of proof rests, however, on supporters of this alternative [sympatric] mode of speciation". What is notable is that in their book on speciation, Coyne and Orr (2004) still largely support this opinion by writing: "One can argue that allopatric speciation should be considered the "default" mode of speciation because it is supported by substantial evidence and occurs under a wider range of conditions than do other modes. In a given case, then, a strong support for parapatric or sympatric speciation requires excluding the possibility of allopatry." However, one can question if such a biased view of speciation is scientifically rewarding, or if research on speciation would not rather benefit from a more balanced perspective. We should perhaps, as suggested by Jiggins (2006) abandon allopatry as "The null-hypothesis" of speciation.

Inverting the null-hypothesis

A refreshing approach in studies of speciation mechanisms would simply be to put as much effort into rejecting non-allopatry in cases of presumed allopatric speciation, as we presently put effort into rejecting allopatry in cases of suggested non-allopatric speciation. Although, as will be further underlined below, there are certainly situations where we have to admit that distinguishing between allopatric and non-allopatric speciation might not be possible, and conclusions in favor of one or the other mechanism will simply be premature. However, before reaching such a conclusion, let us invert the classical approach by simply trying to reject alternative non-allopatric alternatives in cases of supposed allopatric speciation, as an illustrative exercise.

As already pointed out by Coyne (1994), a major concern assuming allopatric speciation as the dominating mode of speciation in any ecosystem is the challenge to provide solid

evidence for the extent and type of barriers that provided physical isolation during the number of speciation events required to explain at least the majority of all species. Taking a global perspective, and assuming that the described 1.5–1.8 million recent species (Wilson 2000) are actual accompanied by around 10 million more species (Wilson 2000; Novotny et al. 2002, bacteria not included), and adding to this all extinct species, amounting to 90% or more of all species ever evolved (Sepkoski 1998), we end up with a grand total of 100 million species reflecting as many speciation events. If we assume that allopatric speciation have been the overall dominating mechanism, where were all the barriers?

Perhaps, the question of finding relevant and functional barriers is most critical when it comes to marine species. As most marine organisms have effective means of pelagic dispersal during early developmental stages, physical barriers must be large and long lasting to provide support for allopatric speciation in the sea. Sea urchins, for example, have larval dispersal stages lasting for weeks and speciation among these require extensive barriers to larval flow. Nevertheless, Mayr (1954) concluded that the distribution of West Pacific sea urchins of the genus *Echinometra* was consistent with allopatric (vicariance) speciation, with deep or cold waters providing physical barriers to larval transport. Phylogeographic patterns based on molecular data have later been used to support allopatric speciation (Palumbi 1996; McCartney et al. 2000; Landry et al. 2003). However, an allopatric scenario requires the existence of ocean-wide barriers to gene flow that isolate incipient species. The existence of such barriers are somewhat at odds with the fact that while some species of sea urchins diverged, others remained more or less panmictic over the same geographic area (McCartney et al. 2000). To account for this, McCartney et al. (2000) refer to the barriers to larval transport acting as a "haphazard filter" that occasionally transmit larva that homogenized some populations but, in between, isolate others.

It seems obvious, that non-allopatric speciation is hard to reject in such a situation like with the sea urchins when no actual barrier has been observed, but the barriers are rather *post-hoc* explanations to an existing pattern. In particularly when closely related species have overlapping distributions, it would be hard to reject a non-allopatric null-hypothesis of speciation. In support of a non-allopatric alternative explanation, it has been shown that at least some broadcasting species have a capacity to retain pelagic larvae through behavioural adaptations, resulting in self-recruitment of local populations leading to genetic differentiation (Jones et al. 1999; Swearer et al. 1999; Taylor and Hellberg 2003). Moreover, studies of marine invertebrates and fishes show genetic partitions of populations of a species within a site being larger than between sites, indicating population divergence promoted by ecological differences rather than barriers to gene flow (Johannesson et al. 1993; Rocha et al. 2005). Among the most pronounced examples are tropical fish species in which host-shifts explain recent events of speciation (Munday et al. 2004; Wellenreuther et al. 2007). Indeed, genetic substructuring of marine species appears to be much more common than earlier thought even in species with broad-casting larvae (Karl and Avise 1992; Väinölä 2003; Baums et al 2005; Johannesson and André 2006; Andrade and Solferini 2007).

Speciation rate vary considerably over geological time and the variation is not at random; several of the mass extinctions are followed by periods of rebound speciation rates, in particularly the Permian extinction that eliminated about 96% of the marine species is followed by a 4–5-fold increase in speciation rate (Raup 1979; Sepkoski 1984, 1998). It seems unlikely that ocean-wide barriers to gene flow were major reasons behind the increased speciation intensity of marine lineages following mass-extinction events, while it seems more likely that speciation rate increased as a consequence of adaptive radiation in

seas with many empty niches following mass-extinctions. If so, the increased rate of speciation was promoted by ecological factors rather than by a dramatic increase in the number of barriers. (However, all ecological speciation is not necessarily non-allopatric, but ecological speciation does not *require* gene flow barriers.) Adaptive radiation promoting ecological speciation is observed among freshwater fishes of postglacial lakes (Schluter 1996; Bernatchez and Wilson 1998; Østbye et al. 2006), and among cichlids in African lakes (reviewed by Seehausen 2006), and in both these examples, it is likely that many of the speciation events have taken place without physical isolation of divergent species. Crater lakes provide particularly interesting data as physical barriers are unlikely in these types of lakes, and hence from such lakes we probably have the best examples of non-allopatric speciation (Schliewen et al 1994, 2001; Barluenga et al. 2006). Additional examples are coral reef and other subtidal fish communities in which high speciation rates are found in spite of no evidences what so ever of physical barriers to gene flow (Munday et al. 2004; Wellenreuther et al. 2007).

Although there are several good examples of speciation coupled to known physical barriers, but quite frequently pieces of information are missing that make a definite rejection of alternative non-allopatric scenarios impossible. For example, the speciation of alpheid shrimps on either side of the Isthmus of Panama (Knowlton et al. 1993) is, according to Coyne and Orr (2004), one of the best examples of speciation promoted by a physical barrier to gene flow. However, varying times of separation between species of the same genus (Knowlton and Weigt 1998) suggests that non-allopatric speciation events preceding the closure of the land-bridge can not be excluded, although allopatric speciation might still be the most likely scenario and the varying times of divergence explained by different depth distribution of species pairs.

Geographical coincidence of species borders or hybrid zones of several species pairs, so called suture zones (Remington 1968), are suggested supportive of earlier presence of physical barriers isolating diverging taxa (Hewitt 1996 and see Avise 2000 for a marine example). However, Swenson and Howard (2004) recently reviewed all potential suture zones of North America and concluded that the evidences for their existence were weak. Furthermore, it seems likely that genetic clines and hybrid zones evolved in the presence of gene flow might be trapped by strong environmental gradients, if loci or linked loci are under natural selection, as illustrated by the coinciding genetic clines in the presence of gene flow at the entrance of the Baltic Sea where a sharp salinity gradient was recently established less than 8000 years ago (Johannesson and André 2006).

Speciation events on island archipelagos are often considered good examples of allopatric speciation. The Darwin finches on the Galapagos Islands are classical examples. Here niche-separated species live in sympatry on the same islands and although it is possible to explain speciation from a series of between-island migration and isolation events (see Ricklefs and Bermingham 2007 for a review of these and similar island archipelago speciation events), the alternative possibility of within-island sympatric speciation and secondary migration, is hard to reject. Indeed, a recent study reveals an incipient reproductive barrier between sympatric morphs of small-beaked and large-beaked finches at the Galapagos islands (Huber et al. 2007).

A similar example is the endemic species of *Drosophila* in Hawaii, which is generally considered as having speciated by founder-induced mechanisms (peripatric speciation) including dispersal of small groups of individuals between islands (Carson 1987). However, from phylogeographic patterns of Hawaiian crickets (genus *Laupala*) a pattern of within-island speciation emerge (Shaw 1996) suggesting that occasional inter-island

migration and the corresponding barriers to dispersal between islands is not a necessary component of speciation in archipelago insect fauna.

Observations that many remote islands lack examples of closely related pairs of species of birds have been used to support the suggestion that sympatric speciation is unlikely (Coyne and Price 2000). However, a recent study shows a rather clear-cut example of when sympatric speciation actually occurred on a small and remote island (Savolainen et al. 2006). Moreover, it has been proposed that island speciation rates might be influenced by existing species diversity in the way that the more species, the higher the island speciation rate (Emerson and Kolm 2005a, b).

The main force generating evolution of reproductive isolation between incipient species (with or without physical isolation) is likely divergent natural selection (Schluter 2000; Mayhew 2007; Rieseberg and Willis 2007), but also sexual selection, or even sexual conflict, have been suggested as potentially important (e.g. Seehausen and van Alphen 1998; Arnqvist et al. 2000; Mayhew 2007). Moreover, it has been suggested that recombination will be impeded by chromosomal inversions, which will promote divergence also in the presence of gene flow (Rieseberg 2001; Kirkpatrick and Barton 2006). Indeed, with the exception of extreme examples such as speciation through fixation of reversed coiling in small populations of land-snails (Ueshima and Asami 2003), there is currently little evidence for the importance of genetic drift in speciation (Coyne and Orr 2004). If drift is not important, physical barriers will be optional rather than obligatory.

Thus, if there is no good direct or indirect evidence for the existence of a physical barrier it is premature to conclude that speciation must have been during a phase of allopatry, particularly if the species in question currently have sympatric or parapatric distributions. A scientifically more productive approach will be to try to reject either allopatric or non-allopatric scenarios of speciation, and if none can be rejected, acknowledge that the question remains unresolved.

Comparative studies of speciation mechanisms

Comparative tests of the mechanisms of evolution of reproductive barriers are possible under situations of parallel evolution, and using a comparative approach provides opportunities to test alternative models of speciation. Parallel speciation (Schluter and Nagel 1994; Rundle et al. 2000) in the first place presents a straightforward support for a major role of natural selection in speciation; if independently, populations of a species evolve similarly diverging morphs/ecotypes upon invading a heterogeneous environment, and if these ecotypes become reproductively isolated while maintaining reproductive compatibility with ecologically similar morphs at other locations, it is highly unlikely that anything but natural selection has produced the reproductive barriers. Furthermore, it is often possible to investigate the direct factors influencing the barrier under scenarios of parallel evolution of reproductive barriers. For example, divergence in size, as a consequence of ecological specialization to different niches, has been identified as the proximate factor of assortative mating leading to an impeded gene flow in both species of fish and snails (Nagel and Schluter 1998; Schliewen et al. 2001; Hollander et al. 2005). The number of examples of parallel evolution of reproductive barriers is steady increasing (e.g. ground beetles—Su et al. 1996, sticklebacks—Rundle et al. 2000; Boughman et al. 2005, walking-sticks—Nosil et al. 2002, whitefish—Lu et al. 2001; Østbye et al. 2006, marine snails—Rolán-Alvarez et al. 2004; Grahame et al. 2006), and we may expect to learn much more from the mechanisms of speciation using these and similar model systems. Indeed, adding

information from the molecular level of parallel evolution has already contributed with exciting findings, for example, showing independent and repeated evolution of ecologically important traits (Foster and Baker 2004; Colosimo et al. 2005; Rogers and Bernatchez 2005; Wood et al. 2005; Derome et al. 2006).

In parallel evolution of reproductive isolation natural selection is the main factor driving speciation, but there still remains critical tests to distinguish between an allopatric and a non-allopatric scenario. In fact, an earlier phase of allopatric separation of lineages might have contributed genetic differentiation critical for the separation in sympatry to be completed, and examples of when this have happened include incipient species of stickleback (McKinnon and Rundle 2002). Even if phylogenetic data showing monophyly of local ecotypes and paraphyly of reproductively compatible populations from different areas suggests a non-allopatric origin of the taxa, an unequivocal support for a non-allopatric explanation requires the rejection of the alternative allopatric scenario. The alternative is that an allopatric origin of the taxa was followed by secondary overlap in distribution and local hybridization producing an apparent local monophyly of ecotypes (Grahame et al. 2006). Two recent studies of the evolution of reproductive isolation among ecotypes of *Littorina saxatilis* have used a rather simple approach to separate the two competing explanations, the non-allopatric and the allopatric followed by secondary overlap and hybridization (Rolán-Alvarez et al. 2004; Panova et al. 2006), and I will review this model system and refer to these two studies as they provide an interesting example of a test of a speciation null-hypothesis.

Rejecting a speciation null-hypothesis: a snail example

Littorina saxatilis is a strongly polymorphic species with ecotypes of different size, shape and color developing in discrete rocky shore habitats such as boulders, bare cliffs, barnacle belts and mussel zones (Reid 1996). Ecotypes have been analyzed in detail in Spain, Sweden and UK, showing that differences in quantitative traits such as size, shell shape and behavior are largely inherited (Johannesson et al. 1993; Hull et al. 1996; Johannesson and Johannesson 1996), although a minor component of plasticity adds further adaptive differences (Hollander et al. 2006). Ecotype differences are strongly correlated to habitat type and maintained in spite of a gene flow through strong directional selection (Janson 1983; Johannesson et al. 1995; Rolán-Alvarez et al. 1997) (Fig. 1). A scientific challenge has been to understand how distinct ecotypes evolve. Two alternative models have been proposed; (i) allopatric separation followed by secondary overlap and introgression, and (ii) primary separation over each habitat cline, which means parallel and microparapatric separation (Johannesson 2001; Grahame et al. 2006).

From studies of mate choice in both field and laboratory, it is shown that non-allopatric (microparapatric) ecotypes are strongly reproductively isolated. On a scale from 0 to 1, with 0 being random mating and 1 being complete reproductive isolation, isolation is 0.5–1.0 in different Spanish populations (Johannesson et al. 1995; Rolán-Alvarez et al. 1999), 0.6 in a Swedish population (Hollander et al. 2005; Panova et al. 2006) and 0.9–1 in UK (Pickles and Grahame 1999). In comparison, pairs of overlapping *Drosophila* species between which reproductive isolation is 0.5 or more have almost no genetic exchange, and with an index of above 0.9 fusion of sympatric species are no longer expected (Coyne and Orr 2004). Notably, the reproductive barriers between *L. saxatilis* ecotypes are prezygotic, and hybrids between ecotypes have high fecundity and their survival in the transition zones is at least similar to those of parental ecotypes (Janson 1983; Johannesson et al. 2000;
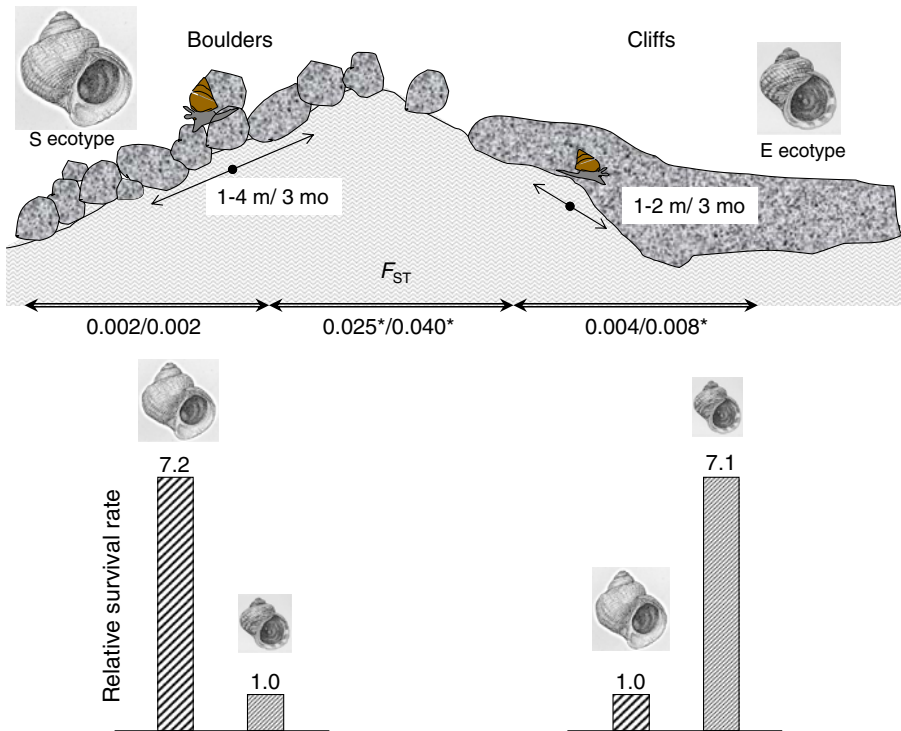
Fig. 1 Appearance, relative survival rate and average migration distance (from Janson 1983) of S ecotype (boulder shores) and E ecotype (rocky cliffs) *Littorina saxatilis*. Pairwise F_{ST} values over 18 m distances within and between S and E subpopulations are indicated for two different islands (from Panova et al. 2006), and these indicate that gene flow between ecotype subpopulations is impeded compared to gene flow within ecotype at similar distances

Rolán-Alvarez et al. 1997, although see Cruz and Garcia 2001 for a somewhat conflicting result).

Analyzes of the genetic structure of two Swedish island populations showed local monophyly of contrasting ecotypes within each area and paraphyly of populations of similar ecotype (Fig. 2) (Panova et al. 2006). A more general approach using an orthogonal analysis of genetic variance based on both neutral allozyme and microsatellite loci at a number of islands applied by Johannesson and Tatarenkov (1997) and later by Mäkinen et al. (2007) showed essentially the same result; genetic differentiation among islands being larger than differentiation between local habitats within islands. Similarly, in Spain, genetic differentiation between ecotypes within localities is established through reproductive barriers, but even so this differentiation is always less than differentiation between populations of similar ecotype at geographic distances (Johannesson et al. 1993; Rolán-Alvarez et al. 2004), hence the Spanish system was very similar to the Swedish still mainland populations were compared instead of island populations.

To separate between in situ non-allopatric evolution of reproductive isolation in each site (island), and allopatric evolution followed by secondary overlap and introgression (Fig. 3), Rolán-Alvarez et al. (2004) analyzed the detailed genetic relationship between and among ecotypes of the separate Spanish areas using F_{ST} statistics. They showed that

Fig. 2 Local monophyly; ecotypes of the same site (island) are more closely related than populations of the same ecotype from different sites. Local monophyly can be explained by parallel evolution driven by diversifying selection within each site
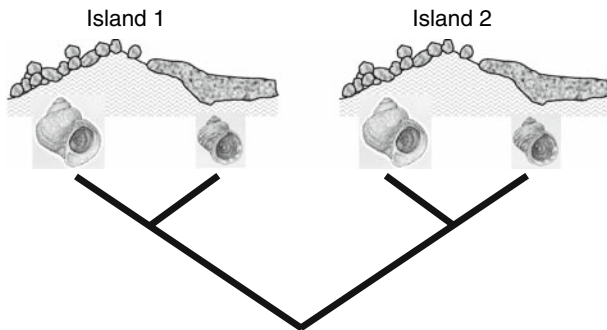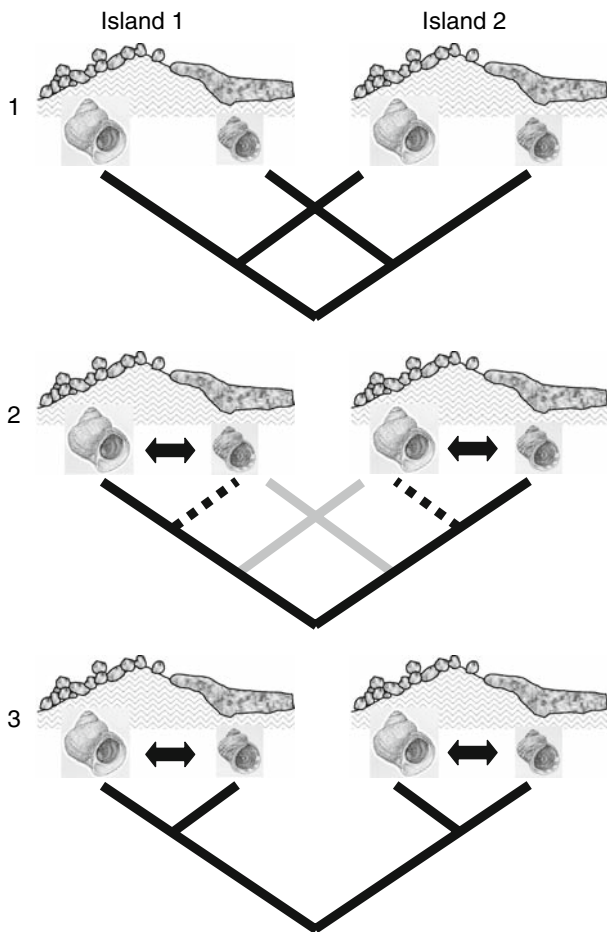

Fig. 3 The alternative explanation for a seemingly local monophyly is allopatric evolution of ecotypes, followed by secondary overlap (1) and hybridization (2–3)

while there was no overall genetic difference between ecotypes, there was indeed significant local differentiation. The reason that the local differences did not add up to an overall difference between ecotypes was that these differences were not systematic but rather

haphazardly distributed with respect to both magnitude and direction, as predicted from parallel and in situ origin of each reproductive barrier.

An even simpler approach was used when analysing the Swedish populations. Here a principal component analysis was applied on microsatellite data and showed that each island had a unique set of loci that were responsible of the genetic separation between the particular ecotypes in that island; a result incompatibility with a common allopatric origin of all populations of the same ecotype (Panova et al. 2006). In both these studies it was possible to critically test and reject the null-hypothesis of an allopatric origin of the reproductive barrier between ecotypes of *Littorina saxatilis* in both Spain and Sweden. A recent study of the Spanish *L. saxatilis* ecotypes (Quesada et al. 2007) used a somewhat different approach; building on predicted patterns of mtDNA trees they reached the same conclusion that ecotypes evolve in situ.

Hence, finding site-specific differences in neutral markers between incipient species (ecotypes or morphs) evolved by parallel evolution will indicate that these differences evolved in situ as a consequence of a local reproductive barrier. If, on the other hand, the local differences found between ecotypes are copies of general differences appearing through out the distribution of the ecotypes, these differences are likely the remaining of a common ancestry of each morph. In general, studying incipient speciation is a promising approach to understand the mechanisms of speciation, and parallel evolution of reproductive isolation is particularly rewarding by the application of comparative analysis. The test of allopatric versus non-allopatric models of reproductive isolation in *Littorina saxatilis* provides an example of such an approach.

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