

The speed of ecological speciation

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Summary

1. Adaptation can occur on ecological time-scales (contemporary evolution) and adaptive divergence can cause reproductive isolation (ecological speciation). From the intersection of these two premises follows the prediction that reproductive isolation can evolve on ecological time-scales. We explore this possibility in theory and in nature. Finding few relevant studies, we examine each in some detail.

2. Theory: Several models have demonstrated that ecological differences can drive the evolution of partial reproductive barriers in dozens to hundreds of generations. Barriers likely to evolve quickly include dispersal rate, habitat preference and selection against migrants/hybrids.

3. Plants: Adjacent populations adapting to different fertilizer treatments or to mine tailings can develop reproductive barriers within at least 100 generations. These barriers include differences in flowering time and selection against migrants/hybrids.

4. Invertebrates: Populations on native and introduced host plants can manifest reproductive barriers in dozens to hundreds of generations. These barriers include local host preference and selection against migrants/hybrids.

5. Vertebrates: Salmon adapting to divergent breeding environments can show restricted gene flow within at least 14 generations. Birds evolving different migratory routes can mate assortatively within at least 10–20 generations. Hybrid sculpins can become isolated from their ancestral species within at least 20–200 generations.

6. Ecological speciation can commence within dozens of generations. How far it goes is an important question for future research.

Key-words: adaptive radiation, ecologically dependent isolation, mating isolation, microevolution, rapid evolution, reproductive isolation, temporal isolation

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Introduction

Our interest in the speed of ecological speciation has its origin in two basic premises. First, natural selection can drive adaptive divergence on ecological time-scales, a phenomenon often called ‘contemporary’ or ‘rapid’ evolution (Thompson 1998; Hendry & Kinnison 1999; Kinnison & Hendry 2001; Reznick & Ghalambor 2001; Stockwell, Hendry & Kinnison 2003; Hairston *et al.* 2005; Kinnison & Hairston 2007). Second, adaptive divergence can lead to reproductive isolation, a process now referred to as ‘ecological speciation’ (Schluter 2000; Coyne & Orr 2004; Gross & Rieseberg 2005; Rundle & Nosil 2005; Funk, Nosil & Etges 2006). From the intersection of these two premises follows the

prediction that adaptation to new ecological environments can cause the contemporary evolution of reproductive isolation. The present paper investigates this possibility by considering studies of reproductive isolation evolving on contemporary time-scales, here arbitrarily considered to be on the order of a hundred generations or less.

Our explicit focus on the intersection between contemporary evolution and ecological speciation led us to several strategic decisions. First, we do not explicitly consider several non-ecological mechanisms of rapid speciation, including cytoplasmic incompatibilities, changes in ploidy and parthenogenesis (Coyne & Orr 2004). Despite their exclusion here, these mechanisms can have an ecological component if the new species are adapted to different environments. Second, we do not dwell at length on experimental evolution in the laboratory (Rice & Hostert 1993) – because our interest is in natural populations. We do, however, review

theoretical studies, because these help organize a consideration of which specific reproductive barriers might evolve quickly in response to divergent selection. Third, we focus on the consequences of adaptation to divergent environments, rather than on competition within those environments, although the latter is certainly interesting (Schluter 2000; Coyne & Orr 2004; Dieckmann *et al.* 2004; Gavrillets 2004). Fourth, the reproductive isolation we discuss will rarely be absolute (i.e. zero gene flow), nor unconditional (i.e. intrinsic genetic incompatibilities). Instead, it will usually take the form of partial reductions in gene flow because of adaptation to different environments. The populations involved might ultimately become separated by absolute and unconditional barriers, but this will not necessarily be so. We therefore evaluate 'speciation' as a process, rather than an endpoint (Hendry *et al.* 2000a).

Despite many studies examining contemporary evolution or ecological speciation individually, it turns out that relatively few have examined their intersection. We therefore explore these few examples in some detail. We start by considering theoretical models of how divergent selection might contribute to the contemporary evolution of specific reproductive barriers. We then review studies of natural populations where recent ecological differentiation appears to have initiated reproductive isolation. We readily admit that many of the empirical studies we review would not hold up to the strictest criteria for confirming ecological speciation; but one must start somewhere.

In theory

Among the vast array of speciation models (Kirkpatrick & Ravigné 2002; Gavrillets 2003; Coyne & Orr 2004; Dieckmann *et al.* 2004; Gavrillets 2004), a relatively small subset is germane to our interest in ecological speciation on contemporary time-scales. As our main goal is simply to demonstrate that reproductive isolation can evolve on such time-scales, we focus on a subset of models that allow us to address this notion. We organize this work around specific reproductive barriers roughly in the order they might be expected to act when an individual adapted to one ecological environment moves to a different environment.

DISPERSAL AND HABITAT PREFERENCE

If different ecological environments are spatially discrete, reproductive isolation can arise when individuals typically reproduce within their native environment. Spatial discreteness of environments can take the form of alternative resources clustered at different locations (e.g. different host plants in different fields) or interspersed within the same general location (e.g. different host plants in the same field). In the first scenario, reduced gene flow between environments would result from an increased tendency by individuals to reproduce in their

natal *location* (i.e. reduced dispersal). In either scenario, reduced gene flow could arise if individuals tend to reproduce in their native *environment*, regardless of location (i.e. habitat preference). We therefore consider models of dispersal rate and then of habitat preference, while acknowledging that the two are not necessarily separable.

The evolution of dispersal rate has been examined in many theoretical models (Clobert *et al.* 2001), but these rarely focus on the importance of ecological differences. The few that do consider ecology, generally provide equilibrium solutions without exploring short-term dynamics. In fact, we are not aware of a single model that reports the *rate* at which dispersal can evolve after populations colonize and adapt to new ecological environments. One model, however, has shown that reduced dispersal can evolve in fewer than 100 generations following secondary contact between populations *already* adapted to different environments (Yukilevich & True 2006). Given that adaptation can be very rapid in new populations (see Introduction), this study hints that dispersal might evolve very quickly as well. We hope that future models will address this possibility.

Several models have examined how fast habitat preference can evolve. Rice (1984, 1987) envisioned a scenario where habitat preference has a quantitative genetic basis, the environment is patchily distributed into two habitat types, selection favours individuals who prefer a particular habitat (over those showing no preference), and mating probability decreases with increasing differences in habitat preference (because individuals would be less likely to encounter each other). Starting with a single population having habitat preferences in a quasi-normal distribution centred around no preference, almost perfect assortative mating evolved in less than 100 generations. The speed of this process seems to have been greatly accelerated by the fact that a single locus determined both adaptation and assortative mating. More generally, a variety of models have demonstrated that speciation will be easiest and fastest in these 'one-trait' or 'magic trait' scenarios, where selected loci have pleiotropic effects on reproductive isolation (Fry 2003; Coyne & Orr 2004; Gavrillets 2004).

The models of Rice (1984, 1987) assume a rather restrictive, and perhaps unrealistic, set of conditions. An alternative is to assume one or more loci at which opposing alleles are favoured in different environments, and one or more loci that determine preferences for those different environments (Diehl & Bush 1989; Fry 2003). Under these conditions, linkage disequilibrium can emerge between alleles conferring adaptation to a given host and alleles determining preference for that host. As this disequilibrium builds, the relative fitness of hybrids decreases because they select environments to which they are not adapted. Perfect assortative mating can arise in these models when the fitness of intermediate, generalist genotypes is less than one-half that of pure,

host specialist genotypes (Fry 2003). At the upper end of these fitness differences, the entire process can take less than 100 generations (Fry 2003). The evolution of habitat preference is thus a particularly plausible route to the contemporary evolution of reproductive isolation.

NATURAL SELECTION AGAINST MIGRANTS

Individuals that do move between ecological environments may die before reproducing, and therefore contribute little to gene flow (Nosil, Vines & Funk 2005). One theoretical model has examined how this selection against migrants (or 'immigrant inviability') might influence the rate of ecological speciation. Hendry (2004) explored deterministic single locus and quantitative genetic dynamics when a new 'island' population was founded from an established 'continent' population. Relative to the continent, the island environment favoured a different allele in the single locus model and a different mean phenotype in the quantitative genetic model. Hendry (2004) then tracked the fitness of migrants relative to residents on the island for 30 generations following the founding event. The critical result was that adaptation of the island population to its environment quickly and substantially reduces the relative fitness of an average migrant. For wide ranges of parameter values, migrants could have less than half the fitness of residents after less than 30 generations. This outcome is not too surprising given that selection against migrants is really just adaptation itself, which we already know can occur very quickly (see Introduction).

SEXUAL ISOLATION OF MIGRANTS: MATE CHOICE

Adaptation to different ecological environments can lead to assortative mating driven by sexual (mating) isolation. The dynamics of this process have been examined by Kondrashov & Kondrashov (1999). Their model assumes two discrete fitness peaks corresponding to particular phenotypes, with a low fitness valley between them (i.e. disruptive selection). An initially monomorphic population on one peak rapidly becomes polymorphic owing to frequency-dependent selection favouring individuals that can exploit the alternative peak. Continued selection against intermediates generates a bimodal distribution in less than 30 generations. Linkage disequilibrium then builds up between traits influencing adaptation and traits influencing mate choice – because hybrids have low fitness owing to their lack of adaptation to either parental environment. Almost perfect assortative mating can arise in a few hundred generations, even when natural selection, female choice and male attractiveness each depend on different quantitative traits. An extension of this model generates similar outcomes in less than 100 generations under certain conditions (Artzy-Randrup & Kondrashov 2006).

We should also mention two other contexts in which sexual isolation can evolve in less than 100 generations. One is 'adaptive speciation', where competition for limited resources causes evolutionary branching and assortative mating (Dieckmann *et al.* 2004). Another is 'reinforcement', where divergent populations coming into secondary contact evolve mating preferences that reduce maladaptive between-type matings (Yukilevich & True 2006). We have not considered these two contexts in detail owing to our focus on how *different* ecological environments drive *de novo* adaptive divergence and reproductive isolation.

INTRINSIC SELECTION AGAINST HYBRIDS

Many theoretical models examine the evolution of intrinsic genetic incompatibilities, where hybrid inferiority does *not* depend on ecological differences between the parental environments (Kirkpatrick & Ravigné 2002; Gavrillets 2003, 2004; Coyne & Orr 2004). Most of these models do not concern us here because they variously ignore selection, assume similar selection in all populations, or do not report short-term dynamics. Some initial insight, however, might be provided a consideration of speciation on 'holey' adaptive landscapes. These landscapes have multidimensional, almost 'flat', surfaces corresponding to genotype combinations of high fitness. These surfaces are then punctuated by large holes that correspond to genotype combinations of very low fitness (Gavrillets 2003, 2004). Different populations on these landscapes can evolve intrinsic genetic incompatibilities in hundreds to thousands of generations, with 'selection for local adaptation' dramatically decreasing the 'waiting time' to speciation (Gavrillets 2003, 2004). Thus, the evolution of intrinsic genetic incompatibilities here seems to require more than 100 generations, and we are not aware of any models showing otherwise. Empirical evidence is also sparse. In the only potential example, MacNair & Christie (1983) found complete genetic incompatibilities between plants that were or were not tolerant to mine tailings. The tolerant population had existed since only 1861, implying the rapid evolution of these incompatibilities, but ambiguity persists given that the tolerant and nontolerant populations in the study were not an ancestor-descendant pair. Based on the scarcity of theoretical and empirical support, we expect that intrinsic genetic incompatibilities are not particularly likely to evolve on ecological time-scales.

EXTRINSIC SELECTION AGAINST HYBRIDS

Ecologically divergent species generally occupy distinct fitness peaks on adaptive landscapes, with hybrids falling into the low fitness valleys (Schluter 2000; Rundle & Whitlock 2001). Although this extrinsic selection against hybrids is an important contributor to ecological speciation (Schluter 2000), no models have explicitly examined its short-term dynamics. We predict that these dynamics

will broadly parallel those for selection against migrants (see above), simply because local adaptation is the direct cause of reduced gene flow in both cases. One predicted difference, however, is that reductions in gene flow may be more sensitive to the fitness of migrants than to the fitness of hybrids. One reason is that hybrids are often phenotypically intermediate between parental species, and will therefore be less maladapted than are migrants. Another reason is that reproductive barriers acting earlier (on migrants before they reproduce) make a greater contribution to reductions in gene flow than do reproductive barriers acting later (on the hybrid offspring of migrants) (Coyne & Orr 2004; Nosil *et al.* 2005). These predicted differential effects of selection on migrants *vs* hybrids may depend on when migration takes place – individuals that migrate as adults may not experience much selection in the new environment. Another difference between migrants and hybrids is that selection against the latter may retard adaptation because it removes both adaptive and maladaptive alleles (both are found in hybrids), whereas selection against migrants removes only maladaptive alleles (Nosil *et al.* 2005). We eagerly await theoretical investigations of the relative importance of migrants and hybrids to the contemporary evolution of reproductive isolation.

ECOLOGICAL HYBRID SPECIATION

Hybrids may sometimes land on new adaptive peaks, rather than inevitably falling into the fitness valleys between peaks. This supposition is supported by a growing number of studies, including recent work on hybrid speciation in plants (Rieseberg *et al.* 2003), invertebrates (Schwarz *et al.* 2005), and vertebrates (Nolte *et al.* 2005). In such cases, hybrid populations may be partially isolated from parental species by dint of extrinsic selection owing to local adaptation (as well as other non-ecological reproductive barriers). Continued adaptation of the hybrid species to its new environment should then further reduce gene flow. The short-term dynamics of this process have not been modelled, but simulations have shown that occupancy of a new ecological environment can be very important in the formation of new homoploid hybrid species (Buerkle *et al.* 2000).

In nature

Theoretical models are helpful guides to the realm of possibility, but demonstrating the actual speed of ecological speciation requires real organisms. In this regard, laboratory studies have shown that strong disruptive selection can initiate reproductive isolation in only dozens of generations (reviews: Rice & Hostert 1993; Coyne & Orr 2004). A particularly interesting recent example is that of reproductive isolation linked to the evolution of insecticide resistance. Higginson *et al.* (2005) imposed selection on laboratory populations

of the pink bollworm *Pectinophora gossypiella* for increased resistance to an insecticidal protein of *Bacillus thuringiensis*. When tested with nonresistant females after 21–43 generations of selection, males from the resistant lines were competitively inferior to males from the nonresistant lines when producing offspring. What intrigues us most about this particular scenario is that similar patterns of selection may occur in nature, given the widespread use of this insecticide. In general though, selection in laboratory studies often differs from that in nature. In particular, laboratory studies often impose very strong selection that is abstracted from the ecological milieu in which natural populations evolve. Laboratory selection studies thus provide guidance as to how the genetics of organisms translate a particular type of selection into an evolutionary response, but they provide little information on how selection acts in natural populations.

The rest of our review therefore considers the speed of ecological speciation *in nature*. Here we have a number of excellent demonstrations of reproductive isolation evolving within thousands of generations (Schluter 2000; McKinnon & Rundle 2002; Barluenga *et al.* 2006) – but did the critical barriers evolve in just dozens of generations, or did they require the full measure of thousands? To answer this question, we focus on studies of conspecific plant, invertebrate, and vertebrate populations that shared a common ancestor within the previous hundred generations or so.

PLANTS

Plants can differentially adapt to alternative environments that abut each other on very small spatial scales, a property that enabled some excellent early work on the contemporary evolution of reproductive isolation. Here we first outline the classic studies of adaptation to fertilizer treatments and mine tailings, before then turning to recent demonstrations of hybrid ecological speciation.

The Park Grass Experiment has applied different fertilizer treatments to different plots in a contiguous field since 1856. Work in the 1960s showed that grass *Anthoxanthum odoratum* populations in the different treatments had diverged adaptively in a number of phenotypic traits (Snaydon & Davies 1976). These differences were apparently coupled to the emergence of several reproductive barriers. First, selection against migrants and hybrids seems likely given that seeds transplanted between treatments show reduced survival (Davies & Snaydon 1976). Second, assortative mating seems likely given the observed divergence in flowering time between treatments. This divergence is greatest near the boundary between treatments (Snaydon & Davies 1976; Silvertown *et al.* 2005), suggesting the action of selection to reduce maladaptive interbreeding (i.e. ‘reinforcement’). The ultimate signature of these reproductive barriers might be reduced gene flow between the treatments, which has indeed been

documented for microsatellite loci (Silvertown *et al.* 2005). These results are mostly based on single transects and would therefore benefit from replication.

Another set of classic studies is that of plants adapting to toxic mine tailings. The early work examined *Agrostis tenuis* and *Anthoxanthum odoratum* at the Drys-Y-Coed copper mine and the Trelogan zinc mine, both of which became active in the mid-1800s. Work in the 1960s showed that plants from the tailings were tolerant to the relevant metal, but that plants 5–10 m away on nontoxic pasture were not (Jain & Bradshaw 1966; Fig. 1). Selection against migrants and hybrids, at least in one direction, logically follows. Plants from the two environments also showed genetically based divergence in a host of other morphological characters (Antonovics & Bradshaw 1970). In particular, McNeilly & Antonovics (1968) showed that both species flowered earlier on the mine tailings than on the adjacent pasture (see also Antonovics & Bradshaw 1970; Fig. 1). They also showed that flowering time differences were greater at the boundary between environments than further away, again suggesting reinforcement. McNeilly & Antonovics (1968) came to the remarkably prescient conclusion that ‘divergence, directional change, colonization and speciation are inextricably linked’ and that the ‘time-scale of the evolution and colonization reported here is ... very short.

Ecological hybrid speciation may occur very quickly in plants, and the Oxford ragwort *Senecio squalidus* is

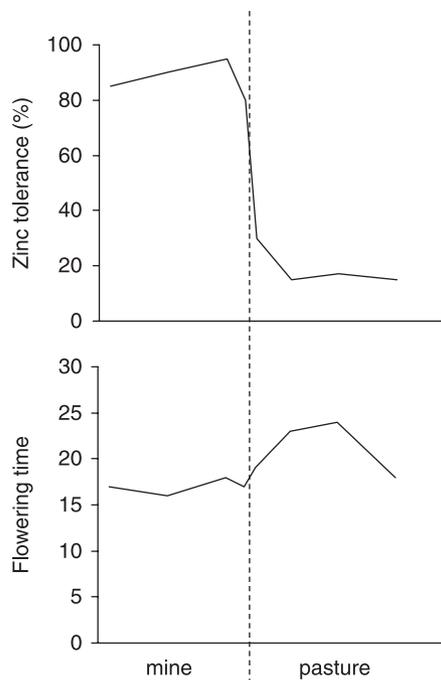


Fig. 1. *Anthoxanthum odoratum* shows higher zinc tolerance (top panel) and earlier flowering (bottom panel) on the tailings of a zinc mine than on the adjacent pasture (adapted from fig. 1 in Antonovics & Bradshaw 1970). These data are based on eight samples along a 100 m transect (x-axis) perpendicular to the transition between the mine and pasture. Flowering time represents stigma emergence in days after 9 June 1966.

a case in point (James & Abbott 2005). This species was originally brought from a hybrid zone between the two parental species on Mt Etna in Sicily to the Oxford Botanical Garden, England. Within 90 generations, it became invasive and is now widespread in the UK. Because the parental species had similar opportunities to spread in the UK but are not found in the wild, ecological novelty seems to have enabled success of the hybrid species. In another example, a hybrid sunflower species, *Helianthus anomalus*, appears to have arisen quickly and partly as a consequence of ecological divergence – in this case because of novel adaptation to sand dune habitats (Rieseberg *et al.* 2003; Ludwig *et al.* 2004). Although this species probably originated more than 100 000 years ago (Schwarzbach & Rieseberg 2002), analyses of genomic recombination reveal that the origin itself likely took place in less than 60 generations (Ungerer *et al.* 1998).

INVERTEBRATES

Insect host races are a fabulous system for examining how reproductive isolation evolves on ecological time-scales. They present such opportunities because native phytophagous insects have often colonized introduced exotic plants, with some examples including codling moths *Cydia pomonella* (Phillips & Barnes 1975), *Jadera* soapberry bugs (Carroll, Dingle & Klassen 1997; Carroll *et al.* 2005) and *Rhagoletis* flies (Feder, Chilcote & Bush 1988; Feder *et al.* 1994). In at least some cases, the new host races are now well adapted to the exotic plant and are reproductively isolated from the ancestral host race. Important ecological barriers in these cases include host preference (Singer, Thomas & Parmesan 1993; Feder *et al.* 1994) and trade-offs in fitness on the two hosts (Filchak, Roethele & Feder 2000). Most of these host races existed for hundreds of generations before reproductive isolation was examined – but how long did the process take in the first place? Perhaps not long, given evidence from more recently derived host races, including butterflies *Euphydryas editha* adapting to exotic weeds *Plantago lanceolata* (Singer *et al.* 1993), aquatic weevils *Euhrychiopsis sibiricum* adapting to exotic milfoil *Myriophyllum spicatum* (Sheldon & Jones 2001) and hybrid *Rhagoletis* adapting to exotic honeysuckle *Lonicera* spp. (Schwarz *et al.* 2005). We now further explore the last two of these examples.

Sheldon & Jones (2001) studied weevils from two North American lakes, one where exotic Eurasian watermilfoil invaded in 1983 and another where it had yet to invade. Several reproductive barriers were evident when the populations were compared approximately 33 weevil generations after the one lake was invaded. First, the exotic host race prefers to oviposit on the exotic milfoil over the native milfoil (Fig. 2). Although this preference may be the result of larval imprinting rather than evolutionary change (Solarz & Newman 2001), it may nevertheless help reduce gene flow to the point that other barriers can evolve. Second, selection against

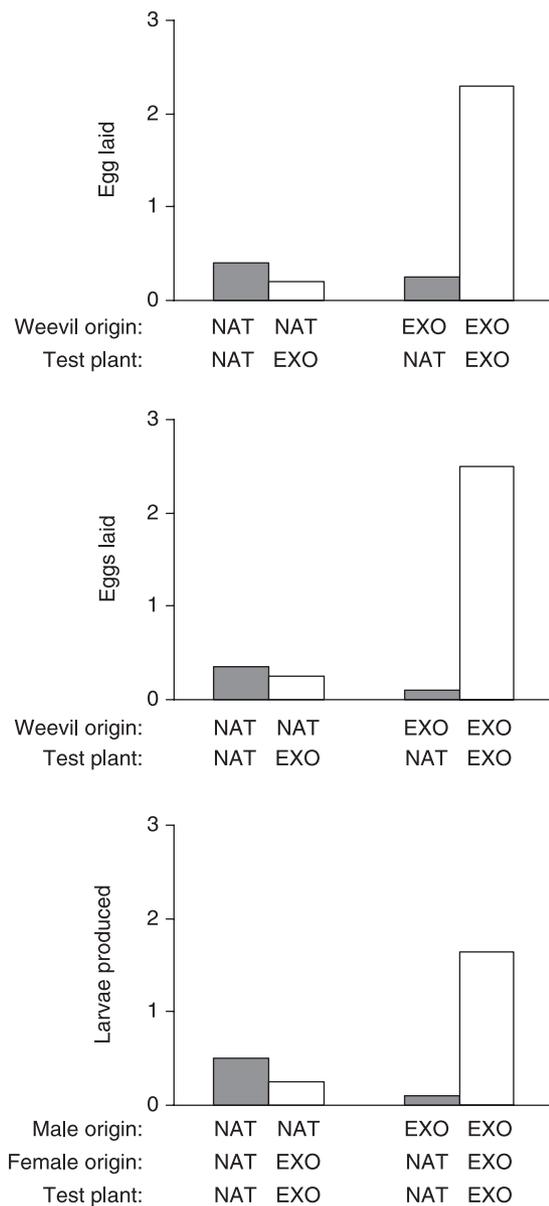


Fig. 2. Weevils collected from exotic milfoil (EXO) show a significant preference to oviposit on exotic milfoil rather than native milfoil (NAT) in no-choice trials (top panel; adapted from fig. 1 in Sheldon & Jones 2001) and in choice trials (middle panel; adapted from fig. 2 in Sheldon & Jones 2001). Moreover, females collected from exotic milfoil produce significantly more larvae when mated with males collected from exotic milfoil than with males collected from native milfoil (bottom panel; adapted from fig. 3 in Sheldon & Jones 2001). Weevils collected from native milfoil show no differences in preference or larval production on native vs. exotic milfoil.

migrants and hybrids seems likely because more larvae are produced on the *exotic* host plant by pure crosses within the exotic host race than by hybrid crosses between the native and exotic host races (Fig. 2). These reproductive barriers are asymmetric because larval production on the *native* host plant does not differ between pure and hybrid crosses (Fig. 2). Regardless, ecological divergence has initiated the evolution of reproductive isolation in a population adapting to a new environment.

Evidence for ecological hybrid speciation comes from North American *Rhagoletis* on exotic Japanese honeysuckle *Lonicera* sp. These new flies were first discovered in 1997, and genetic analyses show that they are most likely the result of hybridization between *Rhagoletis* flies from two other host plants (Schwarz *et al.* 2005). This new hybrid race is now reproductively isolated from the other host races. The specific reproductive barriers are not known, but they are likely similar to those isolating other *Rhagoletis* host races: host preference and selection against migrants and hybrids (Feder, Chilcote & Bush 1988; Feder *et al.* 1994). In another scenario, hybrid speciation might occur almost instantly when a hybrid phenotype directly induces mating isolation from the parental species, as appears to be the case for wing colours in some *Heliconius* butterflies (Mavárez *et al.* 2006). We initially hesitated to include this example because it is not certain that adaptation played a role in isolating the particular hybrid species studied by Mavárez *et al.* (2006). This does seem possible, however, given that the two parental species have colour patterns that mimic different model species and because they exhibit divergent mate preferences based upon these colour differences (Jiggins *et al.* 2001).

VERTEBRATES

Only a few studies have tested for reproductive isolation between conspecific vertebrate populations adapting to divergent environments on ecological time-scales. The first examined sockeye salmon *Oncorhynchus nerka* introduced into Lake Washington, Washington. When examined 14 generations later, derived river- and beach-spawning populations differed phenotypically in a number of traits likely reflecting local adaptation. Specifically, river females were larger than beach females, river males were shallower-bodied than beach males, and river embryos survived better than beach embryos at incubation temperatures typical in the river (Hendry *et al.* 2000b; Hendry 2001; Fig. 3). These differences paralleled those between river- and beach-spawning populations that have existed for thousands of generations in other watersheds (Hendry 2001). Hendry *et al.* (2000b) then showed that gene flow between the derived beach- and river-spawning populations (estimated from microsatellite analysis) was considerably lower than adult dispersal (estimated from environmentally induced natural ‘tags’) (Fig. 3). Reduced gene flow relative to dispersal indicates that some reproductive isolation had evolved over 14 generations, but the specific reproductive barriers remain unknown (Hendry 2001).

A second example is that of European blackcaps *Sylvia atricapilla* evolving a new migratory route. This species traditionally breeds in south-central Europe (Germany and Austria) and overwinters in southern Iberia and northern Africa. Since the 1960s, however, a new overwintering population has become established

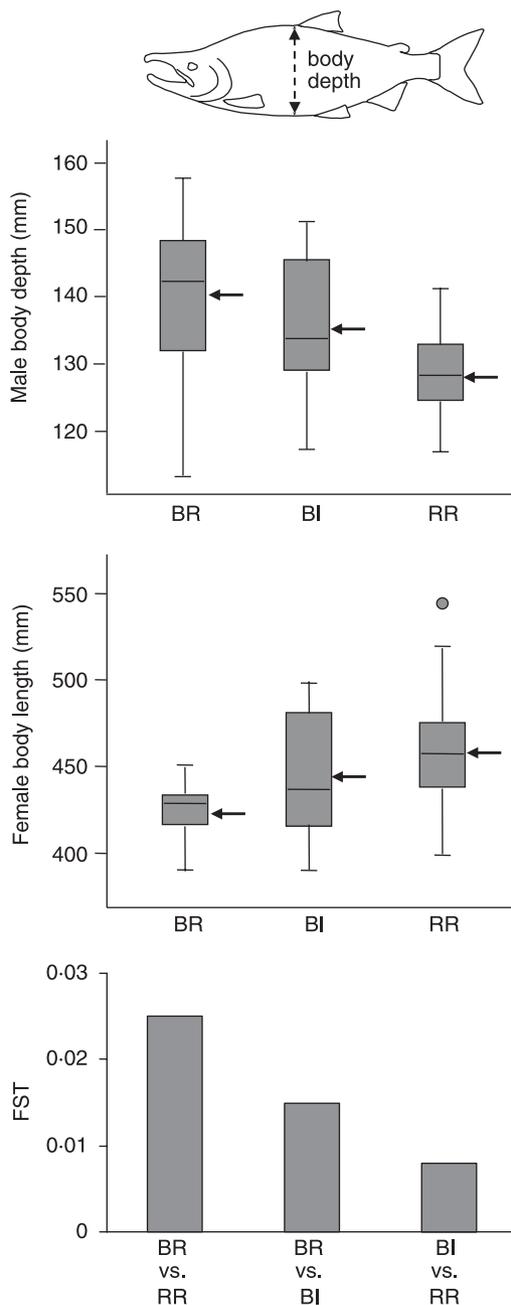


Fig. 3. Evidence for the contemporary evolution of reproductive isolation for introduced salmon populations adapting to river and beach breeding environments over the course of approximately 14 generations. The top panel shows that body depth (standardized to a common body length) is significantly greater for males hatched and breeding at the beach (beach residents; BR) than for males hatched and breeding at the river (river residents; RR). The middle panel shows that female body length (at a common age) is significantly less for beach residents than for river residents. For both traits, fish hatched in the river but breeding at the beach (beach immigrants, BI) are intermediate and not significantly different from either river or beach residents. In both panels, boxes contain 50% of the data and bars contain the remainder; horizontal lines indicate medians, arrows indicate means, and the circle indicates an outlier. The bottom panel shows that gene flow is limited between beach residents and river residents. Specifically, F_{ST} based on six microsatellite loci is significant between beach residents and both river residents and beach immigrants but not between river residents and beach immigrants.

in Britain and Ireland. Berthold *et al.* (1992) showed that the ancestral (southern) and derived (northern) overwintering populations showed genetically based adaptive differences in migratory orientation (i.e. compass directions). Bearhop *et al.* (2005) then showed that birds from the two overwintering populations (identified using stable isotopes) mate assortatively in sympatry on their shared breeding grounds. This assortative mating was the result of adaptive differences in migratory timing that led birds from the northern overwintering population to arrive on the breeding grounds earlier than birds from the southern overwintering population. Selection against hybrids is also expected because these would show an inappropriate intermediate migratory direction (Bearhop *et al.* 2005). Adaptive divergence in migratory orientation has thus led to the initiation of reproductive isolation in less than 50 years, which amounts to about 10–20 blackcap generations.

A third vertebrate example provides evidence for ecological hybrid speciation. Over the past 20 years (about 20 generations), a new form of sculpin *Cottus* sp. colonized and spread through the lower reaches of the Rhine River in Europe. Genetic analyses revealed that this invasive sculpin was the product of hybridization between two old sculpin lineages (Nolte *et al.* 2005). These lineages historically occupied separate drainages, only coming into contact after humans altered drainage patterns. This contact probably occurred sometime between 20 and 200 generations ago. The new hybrid lineage is morphologically distinct from its ancestral lineages and is found in an ecological environment that cannot be tolerated by the ancestral lineages: large stagnant water bodies. Where the invasive lineage and one of its ancestral lineages now come into contact, they form hybrid zones that are very abrupt, probably owing to selection against migrants and hybrids (Nolte, Freyhof & Tautz 2006). Hybridization thus allowed colonization of a new environment, which then contributed to reproductive isolation from the ancestors.

Conclusions and suggestions

We started our review with the prediction that substantial reproductive isolation should evolve quickly when populations colonize and adapt to different ecological environments. Theoretical work supports this assertion, but very few models have been specifically designed to examine the dynamics of ecological speciation. Moreover, most models examine only one or a few reproductive barriers, whereas ecological speciation may be a function of several. A profitable goal for future theoretical work would be to compare the relative speed with which different reproductive barriers can evolve during the early stages of ecological speciation. We predict that rapidly evolving barriers will include habitat preference (see also Feder & Forbes 2007) and selection against migrants/hybrids. Sexual isolation also may evolve quickly (see also Svensson & Gosden 2007) but we expect that intrinsic genetic compatibilities will come later.

Theoretical support is important but remains theoretical in the absence of confirmation from natural systems. This confirmation can be found in several studies of plants, invertebrates and vertebrates, although studies of reproductive isolation evolving on ecological time-scales are still quite rare. We suggest that investigators seek out cases of recent adaptive divergence and examine these for evidence of reproductive isolation. The opportunities for such work are manifold given the many demonstrations of adaptive divergence in contemporary time (see Introduction). Indeed, it may even be possible to use replicated, controlled introductions in nature to perform experimental studies of ecological speciation in action.

Signatures of contemporary ecological speciation might be revealed through several different approaches. One is to test whether individuals in new environments 'prefer' those new environments, a tendency that will reduce dispersal and therefore gene flow between populations in the new and ancestral environments. An important question here is whether preference divergence is genetically based or simply the result of environmental effects (e.g. imprinting). A second approach is to use reciprocal transplants among similar and different environments. Reduced survival or reproductive success for individuals moved *between* environments would suggest natural selection against migrants and hybrids (Nosil *et al.* 2005). A third approach is to examine the mate preferences of reproductively active males and females from similar and different environments. Greater mating probabilities for males and females from similar environments than for males and females from different environments would suggest sexual isolation of migrants and hybrids (Schluter 2000; Nosil, Crespi & Sandoval 2002; Schwartz & Hendry 2006). A fourth approach is to consider the integrated effect of multiple reproductive barriers by testing whether gene flow is lower between populations in different environments than between populations in similar environments (Rolán-Alvarez *et al.* 2004; Crispo *et al.* 2006; Grahame, Wilding & Butlin 2006).

In closing, it seems important to recognize that ecological differences may not always drive reproductive isolation. As an example, Crispo *et al.* (2006) showed that gene flow was not reduced between guppy populations in different predator environments, even though these environments impose very strong divergent selection (Endler 1980; Reznick, Bryga & Endler 1990). To explain this result, Crispo *et al.* (2006) argued that divergent selection can have a multiplicity of effects, some of which actually increase gene flow. The existence and speed of ecological speciation therefore remain open empirical questions in all but a few natural systems.

Generalizations about the speed of ecological speciation will require more studies like those reviewed above. Ultimately, however, we should begin to ask more quantitative questions about how the rate of ecological speciation is influenced by different factors, such as the strength of selection, the amount of dispersal, and the

nature of genetic architecture. It is also important to establish what determines how far ecological speciation ultimately proceeds. These questions seem pertinent given that some populations in different ecological environments show strong signatures of ecological speciation, whereas others do not. As the study of ecological speciation matures, we expect that more work will go beyond confirming its presence, and instead begin to focus more on quantifying its promoting and constraining forces (see also Garant, Forde & Hendry 2007).

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