

The multifarious effects of dispersal and gene flow on contemporary adaptation

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Summary

1. Dispersal and gene flow can have a variety of interacting effects on evolution. These effects can either promote or constrain adaptive divergence through either genetic or demographic routes. The relative importance of these effects is unknown because few attempts have been made to conceptually integrate and test them.

2. We draw a broad distinction between situations *with* vs. *without* strong coevolutionary dynamics. This distinction is important because the adaptive peak for a given population is more mobile in the former than in the latter. This difference makes ongoing evolutionary potential more important in the presence of strong coevolutionary dynamics than in their absence.

3. We advance a conceptual integration of the various effects of gene flow and dispersal on adaptive divergence. In line with other authors, but not necessarily for the same reasons, we suggest that an intermediate level of gene flow will allow the greatest adaptive divergence.

4. When dispersal is quite low, we predict that an increase will have positive effects on adaptive divergence, owing to genetic/demographic rescue and ‘reinforcement.’ The rescue effect may be more important in small populations and in homogeneous environments. The reinforcement effect may be more common in large populations and in heterogeneous environments.

5. Once a certain level of dispersal is reached, we predict that a further increase may have negative effects on adaptive divergence. These effects may arise if carrying capacity is exceeded or maladaptive genes are introduced.

6. Many additional effects remain to be integrated into this framework, and doing so may yield novel insights into the factors influencing evolution on ecological time-scales.

Key-words: adaptive divergence, coevolution, demography, ecological speciation, genetics.

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Introduction

Evolution on ecological time-scales, also called ‘rapid’ or ‘contemporary’ evolution, may be influenced in a multitude of ways by dispersal (the movement of individuals) and gene flow (the movement of genes). Our goal in the present paper is to review these influences and advance their conceptual integration. This attempt is timely because a growing number of studies have revealed new and complicated ways in which dispersal and gene flow can influence evolution. Even though these various effects can occur simultaneously, most studies usually consider only one or a few. Our goal is to illustrate

the importance of integrating these multiple influences into a common conceptual framework. We begin by introducing dispersal and gene flow, before then turning to a consideration of their influences.

Why should organisms disperse in the first place? One possibility is that dispersal is unavoidable even when individuals would ‘prefer’ *not* to disperse. Alternatively, dispersal may reflect adaptive evolution, which seems possible given its genetic basis and fitness consequences (Clobert *et al.* 2001; Hansson, Bensch & Hasselquist 2003; Pasinelli, Schiegg & Walters 2004). The potential selective forces acting on dispersal are many (Johnson & Gaines 1990; Clobert *et al.* 2001; Holt, Barfield & Gomulkiewicz 2005), and we will review only a small sampling. The reason is that our primary concern is with the consequences of dispersal, rather than its causes.

Dispersal can have several benefits. First, it can sometimes increase average fitness when environmental quality varies in time and space – because dispersers can avoid poor conditions at local sites (Olivieri, Michalakis & Gouyon 1995). Second, dispersal can reduce kin competition and thereby increase inclusive fitness (Hamilton & May 1977). Third, dispersal can reduce inbreeding and its associated costs (Greenwood, Harvey & Perrins 1978; Waser, Austad & Keane 1986). Each of these conditions may thus select for increased dispersal.

Dispersal can also have substantial costs. First, dispersers may suffer greater en route mortality owing to increased energetic expenditure or predation risk (Alberts & Altmann 1995; Hanski, Alho & Moilanen 2000). Second, dispersers may suffer reduced survival or reproductive success owing to unfamiliarity with, or maladaptation to, the new environment (Bensch *et al.* 1998; Hendry 2004; Nosil, Vines & Funk 2005). Third, dispersal from high-quality source environments to low-quality sink environments may increase population density above carrying capacity in the sinks but reduce it in the sources. These dynamics can increase average fitness because most of the individuals in a metapopulation are found in sources, where the reduced density leads to higher fitness (McPeck & Holt 1992; but see Holt 1997). Each of these conditions may thus select for reduced dispersal.

The optimal level of dispersal in any given system should reflect a balance among the various costs and benefits (Gandon & Michalakis 2001; Lenormand 2002). But what are the consequences of dispersal for gene flow? The two phenomena are obviously related but several factors can cause discrepancies between them. For instance, dispersal may be *higher* than gene flow if dispersers have reduced survival or reproductive success in the new location (Bensch *et al.* 1998; Hendry 2004; Nosil *et al.* 2005). In contrast, dispersal may be *lower* than gene flow if populations are inbred – because heterosis can increase the fitness of immigrants relative to residents (Ingvarsson & Whitlock 2000; Ebert *et al.* 2002). In addition, gene flow can exceed dispersal in the case of pollen flow in plants (e.g. Latta *et al.* 1998), and in polygamous mating systems where many members of one sex are excluded from mating. In any case, gene flow is certainly a prominent feature of many species (Slatkin 1987; Clobert *et al.* 2001), justifying careful meditation on its evolutionary implications.

The rest of this paper proceeds in three steps. First, we review possible interactions between gene flow and adaptive divergence. In doing so, we make a broad distinction between situations *with* vs. *without* strong coevolutionary dynamics. This distinction is important because, for example, antagonistic coevolution causes adaptive peaks to continually shift away from populations metaphorically attempting to occupy them (i.e. the Red Queen process). Although we dichotomize these two contexts for the sake of illustration, adaptation in most natural populations will have both coevolutionary and noncoevolutionary components. Second, we con-

sider the demographic effects of dispersal, and how these can feed back onto evolutionary dynamics. Third, we close by illustrating how the various effects of dispersal and gene flow might be integrated into a general conceptual framework.

Without strong coevolutionary dynamics

The principal effects of gene flow are to decrease genetic variation *among* populations and to increase it *within* populations. Both of these effects can have positive and negative impacts on adaptive divergence between populations and on overall adaptation across the range of species. We first consider the factors that constrain adaptation and then those that facilitate it. We then turn to a consideration of additional nuances.

GENE FLOW CONSTRAINS ADAPTIVE DIVERGENCE

Theory predicts that adaptive divergence between populations within a species will often reflect a balance between the diversifying effects of local selection and the homogenizing effects of gene flow (Slatkin 1987; Garcia-Ramos & Kirkpatrick 1997; Hendry, Day & Taylor 2001; Lenormand 2002). Consistent with this prediction, inverse relationships between gene flow and adaptive divergence have been documented in many taxa, including birds (Smith *et al.* 1997; Blondel *et al.* 2006), fish (Lu & Bernatchez 1999; Hendry & Taylor 2004), insects (Ross & Keller 1995; Nosil & Crespi 2004), mammals (Hoekstra, Krenz & Nachman 2005), spiders (Riechert 1993), reptiles (King & Lawson 1995; Calsbeek & Smith 2003) and plants (Stanton & Galen 1997; Sambatti & Rice 2006). Many studies have thus argued for a constraining role of gene flow, and we do not attempt to review this body of work. Instead, we simply provide a couple of recent examples that are selected to illustrate how such studies typically proceed, and for their use in illustrating subsequent points.

One example comes from walking-sticks *Timema cristinae*, a phytophagous insect occurring on several different host plant species. Nosil & Crespi (2004) found strong morphological differences between walking-sticks when host plants species were isolated from each other (allopatry), but weaker differences when they were in contact (parapatry). Morphological differentiation in walking-sticks thus appears to reflect a balance between divergent selection owing to different host plants and the extent of gene flow between them. Another example comes from threespine sticklebacks *Gasterosteus aculeatus* in lakes and streams. Divergent selection should favour adaptive divergence between these environments, but Hendry & Taylor (2004) found that parapatric lake–stream pairs experiencing higher gene flow differed less in morphological traits (Fig. 1a). Moore & Hendry (2005) then showed that the morphological divergence of stream fish from lake fish increased with increasing distance from the lake. This

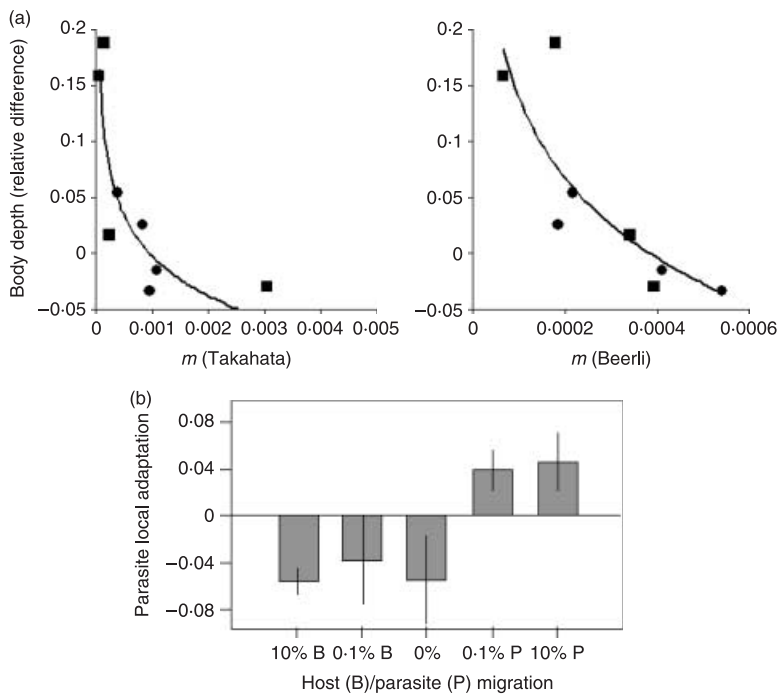


Fig. 1. Empirical results exemplifying some effects of gene flow and dispersal on adaptation. (a) Without strong coevolutionary dynamics: The negative correlation between adaptive divergence (body depth) and gene flow (based on microsatellites) in evolutionarily independent lake–stream stickleback pairs. Each point is a different lake–stream pair, with lake–outlet pairs shown in squares and lake–inlet pairs in circles. The two panels show different methods for estimating gene flow, as described by Hendry & Taylor (2004). (b) With strong coevolutionary dynamics: local adaptation by parasites to their hosts increases with increasing parasite dispersal (P) but is not influenced by increasing host dispersal (B). [Adapted by permission from Macmillan Publishers Ltd: *Nature* (Morgan *et al.* 2005) © 2005].

observation is consistent with the expectation that gene flow from the lake, and therefore its constraining effect, decreases with increasing distance from the lake.

Most of the evidence that gene flow constrains adaptive divergence in nature comes from correlational studies, i.e. morphological divergence vs. gene flow. A major potential problem with this approach is spatial covariance between divergent selection and gene flow. For example, spurious correlations may arise between adaptive divergence and gene flow if more distant sites may experience both lower gene flow and stronger divergent selection. Indeed, this seems to at least partly explain the morphological trends observed by Moore & Hendry (2005). Another potential problem is ambiguity regarding cause and effect: gene flow could be influencing adaptive divergence (as above) or adaptive divergence could be influencing gene flow (see below). Perhaps we can be reassured, however, in that the few correlative studies attempting to discriminate between alternative causal pathways have concluded that an arrow of causality does indeed fly from gene flow to adaptive divergence (Hendry & Taylor 2004; Nosil & Crespi 2004). The few experimental manipulations of dispersal in nature further support this interpretation (Riechert 1993).

GENE FLOW PROMOTES ADAPTIVE DIVERGENCE

Among the potential positive effects of gene flow is its ability to counteract inbreeding depression in small populations (Ingvarsson & Whitlock 2000). One suggestive example comes from a natural *Daphnia* metapopulation, where the residents of isolated pools are often inbred and have low fitness (Ebert *et al.* 2002). Migrants between pools, however, have higher fitness than residents because of heterosis. These migrants thus produced offspring with higher fitness, which should then increase population persistence. Another example is that of endangered Florida panthers *Felis concolor*, which had very low levels of genetic variation and manifested conspicuous maladaptive traits, such as undescended testicles and very poor sperm quality (Hedrick 1995). Controlled introductions of a related subspecies then reduced inbreeding and the prevalence of these maladaptive traits (Hedrick 2004; but see Gross 2005). Reductions in inbreeding depression due to gene flow may then aid population persistence and thus increase the chance of adaptation to changing conditions.

Another potential positive effect of gene flow is that the resulting increase in genetic variation can increase adaptive potential. To test this prediction, Swindell & Bouzat (2006) isolated replicate lines of *Drosophila* at small population sizes for 37 generations, which reduced genetic variation. They then imposed three generations of 5% dispersal between a subset of these populations, a manipulation that increased genetic variation. They then selected all of the lines for increased bristle number. Consistent with the above prediction, the lines that experienced gene flow showed a 30–40% increase in evolutionary response over the lines that did not experience gene flow. Bristle number is a neutral trait in *Drosophila*, and so the relevance of these results to adaptation in natural populations is uncertain. We encourage similar experiments on traits already under selection.

Several other positive effects of gene flow are possible. For example, gene flow can facilitate the spread of beneficial mutations among populations (Peck, Ellner & Gould 1998). Gene flow can also dampen stochastic variation that reduces fitness (Alleaume-Benharira, Pen & Ronce 2006). That is, genetic drift in small populations can cause deviations of mean phenotype from the local optimum, which can then decrease mean fitness across the entire range of a species. Gene flow dampens this variation, and may thereby facilitate population persistence and the potential for future adaptation.

The positive effects of gene flow described in this section are most likely in small populations and when selection varies in time – because genetic variation for future adaptation is then particularly important. An extreme case of temporally varying selection is coevolutionary dynamics, where adaptation by one species may require counter-adaptation by another species, ad infinitum. We will later consider coevolutionary dynamics in detail.

ADAPTIVE DIVERGENCE CONSTRAINS GENE
FLOW

We have thus far emphasized the effects of gene flow on adaptive divergence, but the reverse causal pathway is also possible. That is, adaptive divergence may decrease gene flow when individuals that move between environments have low fitness owing to maladaptation in the new environment. This is the logic of ecological speciation (Schluter 2000; Rundle & Nosil 2005; Hendry, Nosil & Rieseberg 2007), and it leads to several predictions regarding gene flow in nature.

First, the rate of gene flow should be lower than the rate of dispersal, which is indeed the case in at least some taxa. In a particularly striking example, pea aphid *Acyrtosiphon pisum* host races show lower gene flow than dispersal. In this case, the difference is clearly because of selection against maladapted migrants and hybrids that move between different host plants (Via, Bouck & Skillman 2000). Gene flow is also lower than dispersal in sockeye salmon *Oncorhynchus nerka* adapting to beach and river spawning environments (Hendry *et al.* 2000). Of particular interest in this example is the rate at which the difference arose – the two salmon populations diverged from a common ancestor only 14 generations previously. Other examples of adaptive divergence reducing gene flow on short time-scales are reviewed by Hendry *et al.* (2007).

Second, greater divergent selection should lead to greater adaptive divergence and hence lower gene flow. In accord with this prediction, several studies of natural populations have found that measures of divergent selection or adaptive divergence are negatively correlated with measures of gene flow (e.g. Lu & Bernatchez 1999; Ogden & Thorpe 2002). Yet this relationship is not always evident (Hendry & Taylor 2004; Jordan *et al.* 2005; Crispo *et al.* 2006), raising uncertainty as to its necessary conditions. One potential complication is that gene flow at a particular locus will be heavily influenced by its degree of physical linkage to loci under selection. As a result, linked loci may show very low gene flow between selective environments, whereas unlinked loci may flow *almost* freely (Emelianov, Marec & Mallet 2004); however, not entirely freely, because a generalized barrier to gene flow (Gavrilets 2004, pp. 147–148) will still leave signatures of ecological speciation even for unlinked neutral genetic markers (e.g. Grahame, Wilding & Butlin 2006). This generalized barrier may arise because neutral loci can be in linkage disequilibrium with selected loci in migrants and hybrids, where recombination between genomes has not yet occurred.

NONRANDOM GENE FLOW

Gene flow is usually considered to be random with respect to phenotype and habitat (but see Aars & Ims 2000; Armsworth & Roughgarden 2005). Recent studies, however, have found that nonrandom dispersal is common (e.g. Conradt *et al.* 2000; Fraser, Lippe & Bernatchez

2004), and can have important consequences for phenotypic divergence. In an example from great tits *Parus major*, Garant *et al.* (2005) showed that differentiation in fledgling body mass between the north and east areas of Wytham wood (Oxfordshire, UK) was driven by density-related differences in habitat quality. Specifically, the north was a better habitat and produced larger fledglings than the east. The north also attracted larger immigrants, which thus contributed to the evolution of larger fledglings at this site (Garant *et al.* 2005). In the Netherlands, Postma & van Noordwijk (2005) examined two island populations in similar environments that received different proportions of immigrants from the mainland. Low immigration into one population allowed local adaptation, whereas high immigration into the other population hampered local adaptation. Different rates of gene flow thus drove phenotypic divergence between the two island populations, despite their similar selective environments.

Nonrandom dispersal in both of these studies thus caused *increased* phenotypic divergence between some populations. Moore & Hendry (2005) pointed out that this diversifying effect of gene flow can be part and parcel of its established constraining effect. As an example, natural selection should favour different phenotypes in stickleback from lakes vs. streams, but similar phenotypes in stickleback from different streams connected to the same lake (i.e. inlet and outlet). Gene flow from the lake, however, can be highly nonrandom, perhaps occurring at a higher rate into the outlet than into the inlet, a difference strongly manifest in the Misty Lake system (Hendry, Taylor & McPhail 2002). This difference in gene flow then *reduced* divergence between lake and outlet stickleback (constraining effect) but *increased* divergence between outlet and inlet stickleback (diversifying effect) (Moore & Hendry 2005).

GENE FLOW, SPECIATION AND
REINFORCEMENT

Gene flow generally retards speciation by reducing divergence among populations, and by breaking associations between genes for adaptation and genes for reproductive isolation (Coyne & Orr 2004). Some studies, however, have shown that speciation can occur readily in the face of substantial gene flow, particularly when divergent selection is very strong (Endler 1973; Rice & Hostert 1993; Kondrashov & Kondrashov 1999). Indeed, dispersal may sometimes even *enhance* speciation through the process of 'reinforcement' (Dobzhansky 1940; Kirkpatrick 2001). Reinforcement can occur when individuals from different populations (or species) are under direct selection to avoid mating with individuals from the other population. This sort of selection can arise when populations are adapted to different environments, because here the offspring of between-type matings often have lower fitness (Schluter 2000; Rundle & Nosil 2005). Direct selection against between-type matings can only occur when some dispersal is possible,

and so an increase in dispersal can potentially 'reinforce' reproductive barriers (Nosil, Crespi & Sandoval 2003).

With strong coevolutionary dynamics

Many of the above effects can also apply here, and yet coevolutionary dynamics deserve special consideration because ongoing evolutionary potential becomes more important. This potential may be particularly important in the case of antagonistic coevolution, where populations are 'chasing' adaptive peaks that are actively 'retreating.' Examples include evolutionary arms races between competitors, between predators and prey, and between hosts and parasites. Studies of coevolution often consider a set of spatially discrete locations, each potentially occupied by local populations of two interacting species (Thompson 2005). Dispersal might then influence local adaptation of each species to the other. As above, high rates of gene flow are expected to reduce adaptation and yet some gene flow might aid adaptation by replenishing the genetic variation on which ongoing evolution depends.

Theoretical work on host–parasite systems confirms that high gene flow can reduce local adaptation (Gandon *et al.* 1996; Gomulkiewicz *et al.* 2000; Nuismer, Thompson & Gomulkiewicz 2000). This work also highlights several consequences of differences in gene flow for hosts vs. parasites (Gandon & Michalakis 2001, 2002; Holt & Hochberg 2002). First, when parasites disperse at greater rates than the host, parasites are expected to show improved local adaptation (as long as gene flow is not too high, of course). Under these conditions, the increase in genetic variation owing to gene flow gives the more mobile species an advantage in its ability to adapt to the more sedentary species. Second, if hosts and parasites show similar levels of gene flow, similar increases or decreases for both may have no effect on their differential adaptation. Third, if gene flow couples source and sink habitats, whichever species locally experiences sink conditions will have lower genetic variation, and may therefore benefit more strongly from gene flow.

Studies of natural coevolutionary interactions have yielded variable results, as the following examples illustrate. Some studies of host–parasite interactions have found evidence of local adaptation (Mopper *et al.* 2000; McCoy *et al.* 2002; Thrall, Burdon & Bever 2002) whereas others have not (Kaltz *et al.* 1999; Oppliger, Vernet & Baez 1999; Altizer 2001). In a plant–herbivore interaction, gene flow reduced adaptation between parsnips and webworms (Zangerl & Berenbaum 2003). In a predator–prey interaction, there was no evidence of reduced adaptation between garter snakes and newts, despite potentially high levels of gene flow among the predator populations (Brodie, Ridenhour & Brodie 2002). This diversity of results may reflect the multitude of effects that gene flow can have in these systems. Additional research will be required to determine the specific conditions that tip the balance between constraining and facilitating effects of gene flow in coevolutionary interactions.

Laboratory microcosms of bacteriophage and bacteria may help reveal these conditions. For example, Brockhurst *et al.* (2003) demonstrated that an increase in dispersal of both the bacterium *Pseudomonas fluorescens* and its parasitic bacteriophage increased the rate of antagonistic coevolution. In addition, Forde, Thompson & Bohannan (2004) showed that some gene flow by parasitoids (bacteriophage T7) increased adaptation to their hosts (*Escherichia coli*), and that patterns of adaptation can fluctuate in both space and time. Other research has shown that parasite populations lacking dispersal are not well adapted to their hosts (Morgan, Gandon & Buckling 2005; see Fig. 1b). The spatio-temporal variation frequently observed in these experimental studies suggests that the variable results in field studies may be partly due to their more limited time span.

The above work primarily examines adaptation when dispersal is equally probable among all spatially discrete populations. And yet dispersal will often be spatially structured. Isolation-by-distance, for example, can lead to higher gene flow among nearby populations than among distant populations. To the extent that gene flow is beneficial for adaptation, this pattern predicts a negative relationship between adaptation and geographical distance, i.e. parasites should be more locally adapted to nearby hosts than to more distant hosts (Ebert 1994; Kaltz *et al.* 1999). Empirical tests of this hypothesis have yielded variable results. Ebert (1994) showed that parasite (*Pleistophora*) populations were more virulent in nearby host (*Daphnia*) populations than in distant host populations. Kaltz *et al.* (1999) found a humped relationship for infection success with distance in a fungus/plant interaction. That is, success of the fungus at infecting the plant increased with distance at relatively short distances but decreased with distance at relatively large distances. The authors suggest that this pattern illustrates the potentially unpredictable spatial patterns of host–parasite coevolution. In contrast, adaptation and distance were not associated in another plant–pathogen interaction (Thrall *et al.* 2002), nor in a snail–trematode interaction (Lively *et al.* 2004). As noted above, these variable results might again be due to the limited time period for each study.

In sum, research on coevolutionary interactions indicates that the effects of dispersal and gene flow on adaptation to coevolutionary partners can be positive, negative or nonexistent. These qualitatively different outcomes may arise because coevolutionary interactions are influenced by variation in the strength of selection in space and time, and by gene flow differences between species. Disentangling these interactive effects will require more empirical work, particularly in light of the dynamic nature of coevolutionary interactions. Another profitable direction for future work could be the interplay between population dynamics and evolutionary dynamics in coevolutionary systems. For example, if strong antagonistic interactions result in population cycles, the relative effect of gene flow on adaptation to coevolutionary

partners will constantly shift (R.D. Holt, personal communication).

Dispersal, demography and adaptation

Most empirical studies of gene flow ignore the effects of dispersal on demography, and yet theoretical work suggests that we do so at our peril. Here we briefly outline how the demographic effects of dispersal might constrain or facilitate adaptation.

DISPERSAL MAINTAINS POPULATION SIZE

Some populations may be demographic sinks, unable to persist without repeated immigration. Dispersal from sources can sometimes maintain these sinks long enough that they can eventually adapt and themselves become sources (Kawecki 1995; Holt & Gomulkiewicz 1997). Potential reasons are that immigration can: (1) maintain populations long enough for beneficial mutations to occur, and (2) improve the chances that alleles of modest effect are captured by selection (Nagylaki 1978; Holt, Gomulkiewicz & Barfield 2003; Holt, Knight & Barfield 2004). Some aspects of dispersal may thus facilitate adaptation to marginal conditions. It is important to remember, however, that this effect will not be universal, particularly in heterogeneous environments where local adaptations are important. Indeed, some theoretical studies have shown that marginal populations are *more* likely to become extinct when they receive more maladapted immigrants (Kirkpatrick & Barton 1997; Case & Taper 2000; Boulding & Hay 2001).

DISPERSAL EXCEEDS CARRYING CAPACITY

Immigration may sometimes elevate local densities above carrying capacity, thus reducing fitness and disrupting local adaptation (Holt 1983; Holt & Gomulkiewicz 1997; Gomulkiewicz, Holt & Barfield 1999). This effect is more likely in environments with low carrying capacity, where a given number of immigrants will have a greater proportional effect. Similar effects can occur owing to directionally biased dispersal (e.g. downwind or downstream) even without differences in carrying capacity (Kawecki & Holt 2002). That is, a downwind or downstream population will receive more migrants than an upwind or upstream population, which may cause the former's carrying capacity to be exceeded and their average fitness to decrease. The opposite effect may attend an upwind or upstream population (Kawecki & Holt 2002). When carrying capacity is exceeded by any of these means, average fitness can decrease even in the absence of maladaptive genes *per se*, which will impede adaptation (Gomulkiewicz *et al.* 1999).

SEX-BIASED DISPERSAL

Demographic effects will be sensitive to the sex ratio of dispersers (Kawecki 2003). When a marginal popula-

tion is a sink, adaptation may be more likely when dispersal is female-biased than when it is male-biased. The reason is that immigrant females contribute demographically to population growth, whereas immigrant males do not. When a marginal population is not a sink, demographic benefits of sex-biased dispersal are considerably weakened (see Kawecki 2003).

Integration

Gene flow and dispersal clearly have a number of interacting effects on adaptive divergence. These effects are usually examined independently, perhaps leading to incorrect, or at least overly simplistic, conclusions. Our goal in the following sections is to advance a conceptual integration of the various effects of dispersal and gene flow. We bring together, generalize and integrate the findings of other studies that have already made progress in this direction (e.g. Holt & Gomulkiewicz 1997; Case & Taper 2000; Kawecki & Ebert 2004; Holt *et al.* 2005; Alleaume-Benharira *et al.* 2006). We do not consider our effort to be definitive. It is merely an illustration of how a variety of influences might be conceptually integrated.

CONFLICTS ARISING

Figure 2 illustrates some of the effects of dispersal on adaptive divergence. We postulate that when dispersal is very low, an increase may have positive effects on adaptive divergence – because of genetic/demographic rescue or ‘reinforcement’ of mating preferences. The rescue effect should be more important in small populations (where genetic and demographic problems are

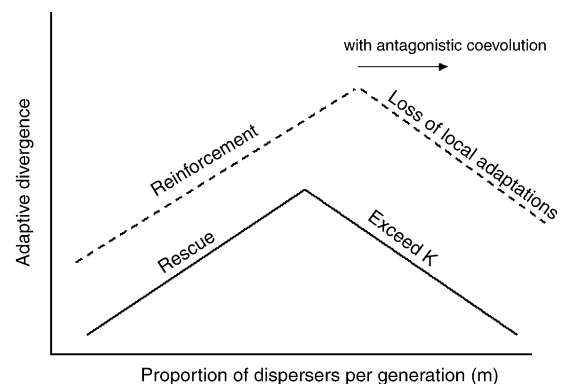


Fig. 2. Illustration of how changes in the proportion of dispersers per generation (m) might influence adaptive divergence. The dotted line represents a large population in a heterogeneous habitat. The solid line represents a small population in a homogeneous habitat. The arrow indicates that the amount of dispersal enabling maximal adaptive divergence might be higher when antagonistic coevolution is present. Note that the actual shapes of these curves are unknown, along with their relative heights and positions along the x -axis. The curves are merely intended to show the various possibilities that might be revealed further by theoretically modelling and empirical tests. See the text for additional discussion.

more likely) and in homogeneous environments (where adaptive *divergence* is less important). The reinforcement effect might be more important in large populations and in heterogeneous environments (because some initial divergence is a catalyst for reinforcement). We further postulate that when dispersal reaches a certain level, a further increase may have negative effects on adaptive divergence by exceeding carrying capacity and introducing maladaptive genes. Exceeding carrying capacity might be more likely in small populations in homogeneous environments (where much of the habitat is easily accessible by immigrants). Introducing maladaptive genes might be more likely in large populations in heterogeneous environments (because divergent selection is stronger). All of these considerations (and others) suggest that an intermediate level of gene flow will lead to the greatest adaptive divergence, and that this level will depend on population size and habitat heterogeneity. We further suggest that the amount of dispersal enabling maximal adaptive divergence might be higher when antagonistic coevolution is present (because the strength of selection will vary over time).

A GENERAL FRAMEWORK

The above conceptual integration allows at least qualitative predictions regarding the relationships between adaptive divergence, dispersal and gene flow. Incorporating even more effects may preclude simple predictions, but we can at least suggest a hypothetical framework for the network of interactions (Fig. 3). In brief, dispersal can have demographic effects that will maintain population sizes and thereby increase population persistence. Increased population persistence could then increase the chances of adaptive divergence; by increasing the origin and fixation of beneficial mutations. Alternatively, dispersal might increase population sizes above carrying capacity, thereby reducing mean fitness and adaptive potential. At the same time, increased dispersal should often increase the level of gene flow, which could then constrain (by introducing maladaptive genes) or promote (by increasing adaptive

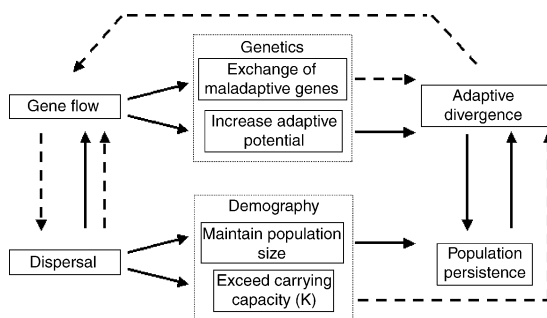


Fig. 3. Hypothetical framework for how gene flow and dispersal might interact with adaptive divergence. Dashed arrows indicate negative effects while solid arrows designate positive effects. See the text for a detailed explanation. Note: the arrow from gene flow to dispersal indicates that a reduction in the fitness of dispersers will directly select against dispersal.

potential) the divergence of populations (Fig. 3). Of course, increasing dispersal at some levels may initiate reinforcement and perhaps thus decrease gene flow. Increasing adaptive divergence might reduce gene flow (because dispersers have low fitness), and increase population persistence (because adaptation will increase mean fitness). Low fitness of dispersers might also select against dispersal and thus lead to its evolutionary reduction.

This basic conceptual framework provides a working model applicable to various ecological scenarios. No study, however, has yet attempted to elucidate such a framework in any field or laboratory system. And yet this already complicated model is still too simplistic. As just one example, we have described how an increase in population size will improve population persistence and thus the opportunity for adaptive divergence. And yet increasing population size should also lead to reductions in gene flow (because a given number of immigrants will represent a smaller proportion of a larger population), which should then increase adaptive divergence.

Conclusions

Dispersal and gene flow can have a variety of constraining and diversifying effects on evolution. The relative importance of these effects is poorly understood, as are the interactions among them. Future work should attempt more integrated studies that simultaneously consider multiple potential effects. We hope that our review provides some impetus toward this goal.

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