

Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence

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Summary

1. Natural and human mediated perturbations present challenges to the fate of populations but fuel contemporary evolution (evolution over humanly observable time-scales). Here we ask if such evolution is sufficient to make the difference between population extinction and persistence.
2. To answer this question requires a shift from the usual focus on trait evolution to the emergent ‘eco-evolutionary’ dynamics that arise through interactions of evolution, its fitness consequences and population abundance.
3. By combining theory, models and insights from empirical studies of contemporary evolution, we provide an assessment of three contexts: persistence of populations *in situ*, persistence of colonising populations, and persistence under gene flow and in metapopulations.
4. Contemporary evolution can likely rescue some, but not all, populations facing environmental change. Populations may fail partly because of the demographic cost of selection.
5. Contemporary evolution that initiates positive population growth, such as selective founding processes, may create a ‘persistence vortex’ that overcomes the problems of small populations.
6. Complex, even shifting, relationships between gene flow and adaptation may aid the persistence of subpopulations as well as the persistence and expansion of metapopulations.
7. An eco-evolutionary perspective suggests that we expand our focus beyond the acute problems of threatened populations and growing invasions, to consider how contemporary evolutionary mechanics contribute to such problems in the first place or affect their resolution.

Key-words: extinction, invasion, metapopulation, rapid evolution, regulation

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Introduction

Extinction has long been recognised as an important process in evolution (Darwin & Wallace 1858; Simpson 1944; Gould 1989). Most extinctions are seen as failures of species to respond adaptively to rapidly – in some instances catastrophically – changing environments. Adaptive evolution clearly failed to preserve the many species that disappeared during both mass extinction events and the more or less continuous localised ‘background extinctions’ (*sensu* Jablonski 1986) that together have produced the history of life. The greater impact of mass extinction during the

Phanerozoic relative to background extinction has even led some to suggest that adaptive evolution plays relatively little role in explaining many patterns of biotic diversity (Flessa & Jablonski 1985; Gould 1989). Whereas it is true that evolution has clearly not rescued all species or populations from extinction, explorations of extinction probabilities based on the limitations of selection and response stand in stark contrast to a growing literature demonstrating that surprising amounts of adaptive evolution occurs in the wild and laboratory within a human life span (reviewed by Hendry & Kinnison 1999; Bone & Farres 2001; Hairston *et al.* 2005). Indeed, empirical evidence and theory show that rates of such contemporary evolution can be much faster than those averaged over paleontological scales (e.g. Gingerich 1983; Reznick *et al.* 1997;

Kinnison & Hendry 2001). How then can we reconcile the great potential for contemporary evolution with the fact of extinction?

This is of course not a question of purely academic interest. Within the past century, humans have greatly accelerated environmental change through pollution, habitat disturbance and community alterations including range expansion by exotic species (Myers & Knoll 2001). Dire predictions of accelerated extinction rates include the demise of over a third of the species in some regions within a century (Pimm & Raven 2000; Thomas *et al.* 2004; Malcolm *et al.* 2006) and the prospect of another mass extinction with rates well above historical background levels (Wilson 1993; Eldredge 1998). A number of investigators have suggested that human disturbances represent exceptionally strong sources of selection and evolutionary change (Kettlewell 1973; Thompson 1998; Palumbi 2001; Stockwell *et al.* 2003). But is evolution in contemporary time (i.e. one to a few hundred generations) sufficient to make the difference between extinction and persistence, or is it merely another symptom of human influences on the future of biodiversity (Myers & Knoll 2001)?

For the purposes of this perspective we focus on cases where persistence represents a demographic race between exogenous factors impairing population growth and evolutionary contributions to population vital rates and fitness. We are more concerned here with the population dynamic (ecological) consequences of contemporary evolution, and the ecological contexts that limit such evolution, than with the nuances of trait change itself. We refer to this perspective as 'eco-evolutionary' in recognition of the 'eco-evolutionary feedback loop' (*sensu* Ferrière, Dieckmann & Couvet 2004) at its core.

We begin with a basic theoretical background on population regulation as a context for our discussion of the links between contemporary evolution, fitness, population growth and persistence. We then consider three contexts wherein evolutionary mechanics may influence extinction risk: the persistence of indigenous populations *in situ*, the persistence of colonising populations and persistence in metapopulations. We conclude with ideas on how an eco-evolutionary perspective might influence the way we approach the current biodiversity crisis.

Theoretical and historic framework

POPULATION REGULATION AND PROBLEMS OF SMALL N

While population 'regulation' vs 'limitation', and the role of density dependence was heavily debated in the last century (Berryman, Arce & Hawkins 2002), it is nevertheless broadly recognised that some form of feedback often controls population abundance, even if some taxa appear less stringently regulated (Hanski 1990). For simplicity we frame our arguments here

largely in terms of density-dependent regulation, although many of our arguments are likely relevant to other mechanisms of limitation.

The logistic growth model is one of the simplest expressions of density-dependent regulation in a closed population:

$$\frac{dN}{dt} = r_{\max}N \left(1 - \frac{N}{K}\right)$$

where N is the population size, r_{\max} is the maximum intrinsic growth rate under prevailing environmental conditions, but in the absence of any density-dependent effects, and K is the carrying capacity. Despite shortcomings (Gotelli 2001), this cornerstone of ecology suffices as a simple heuristic to capture two critical elements of persistence. First, any factor that reduces the density-independent component, r_{\max} , below replacement ($r_{\max} < 0$) can cause population decline (negative dN/dt). For example, a change in local climate may cause lower survival to maturity or reproductive failure. At the same time, any factor that restricts the availability of density-limiting resources (i.e. reduces K below current N) will also likely cause a decline.

What the basic logistic growth model does not capture is how population demise may be aided by other factors that arise at small population size, including demographic stochasticity, Allee effects and genetic health problems, including inbreeding, loss of genetic variation, genetic drift and mutational meltdown (Lande 1988; Lynch, Conery & Burger 1995; Courchamp, Clutton-Brock & Grenfell 1999). In combination, these small-population risks may give rise to an 'extinction vortex' (Gilpin & Soulé 1986) involving further population declines and still greater extinction risk. The generality of threats from mutational meltdown and drift in the wild remains equivocal, but empirical evidence of inbreeding depression has grown in recent years (Spielman, Brook & Frankham 2004; Frankham 2005; Saccheri & Hanski 2006).

FISHER'S THEORY AND HISTORIC IMPEDIMENTS

Theory linking adaptive evolution to population ecology extends back to the very roots of modern evolutionary biology (Darwin & Wallace 1858), but was particularly well captured by R.A. Fisher. In Fisher's (1930) fundamental theorem of natural selection, contributions to population fitness and potential growth rates made by natural selection are offset by deterioration of the environment that prevents net fitness and population growth from increasing much beyond replacement over the long-term. Fisher viewed these deteriorating effects broadly, even including density dependence and reductions in fitness arising as emergent properties of changes in genotype distributions. The balance of these positive and negative contributions to fitness causes populations to grow or decline

(Fisher 1930). Although natural selection is often assumed to enhance population persistence, it can result in long-term environmental deterioration so great that extinction results (e.g. Darwinian extinction: Webb 2003). Likewise, natural selection does not always maximise population r_{\max} . At densities near to K , genotypes with greater competitive ability may have higher fitness resulting in reduced r_{\max} (Desharnais & Constantino 1983).

Historically, cases where contemporary evolution has been proposed to drive short-term dynamics of wild populations have been treated with scepticism (e.g. Chitty 1952, assessed by Boonstra & Boag 1987). Adaptive evolution appears to have been downplayed as a factor in the ecological dynamics of populations on three grounds. *First* is the perception that evolution does not occur on time-scales compatible with most ecological processes (e.g. Slobodkin 1961; Pianka 2000). *Second*, fitness gains made by populations, though altering r_{\max} , might not appreciably influence K , the population density under strong regulation (e.g. 'soft selection' *sensu* Wallace 1975). *Third* has been a strong focus on the minimum viable size of populations facing demographic and genetic health problems, where resurrection of population size and maintenance of genetic variation are considered essential to recovery (Franklin 1980; Gilpin & Soulé 1986; Lande 1988).

A strict distinction between ecological and evolutionary time must now be regarded as artificial. As noted previously, many empirical studies have now shown that evolution is measurable even over short periods of 'ecological time'. Originally, cases of such evolution were considered exceptionally 'rapid' given the ponderous rates of evolution seen in the paleontological record. However, quantitative analysis of evolutionary rates suggests that the apparent sloth of long-term evolution often reflects temporal averaging of reversals and stasis (Gingerich 1993; Reznick *et al.* 1997; Kinnison & Hendry 2001; Hairston *et al.* 2005). By interpolating over wide expanses of time we take a phenotypic shortcut across the much more circuitous evolutionary path navigated by most populations.

Concerns that density regulation trumps evolutionary contributions to population demography are also likely overstated. Theoretical work starting in the 1970s re-emphasised the ecological perspective of Fisher's theorem (e.g. Hairston, Tinkle & Wilbur 1970; León & Charlesworth 1978; Frank & Slatkin 1992) and showed that the theorem does not preclude evolution from influencing population density. Perhaps most relevant for our discussion of contemporary time-scales, many populations stressed by environmental changes may be well away from any equilibria where density regulation or Fisher's other deteriorating processes might precisely offset fitness gains to growth and persistence (Holt 1990). Hence, evolutionary contributions to dynamics may not be so restricted in some of the populations for which they matter most.

Finally, while genetic-health and demographic restrictions of small population size are likely real, it is also true that new populations (e.g. invaders) regularly escape these same problems, so these problems are not universal. Furthermore, demographic and genetic concerns for the fate of the most depleted populations should not preclude us from considering what role contemporary evolution plays in promoting or averting such a fate.

Through the 1990s a broad set of 'adaptive dynamics' models were developed around interests in eco-evolutionary feedback processes (reviewed by Waxman & Gavrillets 2005). A major subset of these models still isolated evolutionary from ecological time-scales (but not all – e.g. Gomulkiewicz & Holt 1995; Abrams & Matsuda 1997). Though such adaptive dynamics approaches are relevant to conservation concerns (see Dieckmann & Ferrière 2004), we focus more on the role of fully concurrent eco-evolutionary dynamics in the current biodiversity crisis.

Persistence of populations *in situ*

Directional pressures, such as climate change, pollution, habitat degradation, community shifts and over-harvesting top many lists of risks to population persistence. However, there is accumulating evidence that a diversity of animals from mosquitoes to squirrels are evolving new seasonal phenologies in response to climate change (Bradshaw & Holzapfel 2006). Tolerance to heavy metals has evolved in plants growing on mine wastes (Antonovics, Bradshaw & Turner 1971). Zooplankton have evolved greater ability to feed and grow in the presence of nutritionally poor cyanobacteria promoted by phosphorus eutrophication (Hairston *et al.* 2001). Snakes in Australia have evolved mechanisms to cope with the toxins of invasive cane toads (Phillips & Shine 2004). Fishing and wild-plant harvesting have caused evolutionary shifts towards smaller size at age or earlier age at maturity (Olsen *et al.* 2004; Law & Salick 2005). Though we cannot assert that in each case evolution has secured the persistence of these populations, the scope for populations to respond to environmental pressures presumed to threaten their persistence is clear. What then determines how and when a population will be rescued by contemporary evolution?

A SIMPLE HEURISTIC MODEL

Gomulkiewicz & Holt (1995) introduced a simple model of the conditions under which natural selection might prevent extinction in a population faced with an abrupt shift in its selective environment (Fig. 1). They asked whether a population can evolve sufficiently positive r_{\max} at population sizes well below K , before facing extinction due to demographic chance or other problems of small population size. They did not consider any density-dependent effects (i.e. $dN/dt = r_{\max}N$)

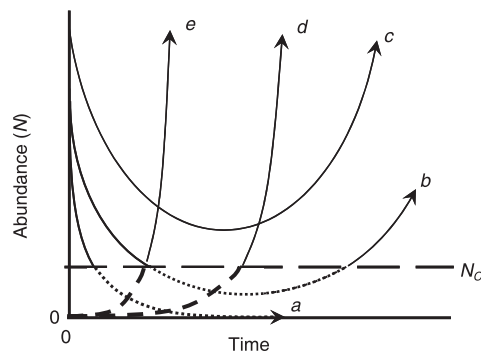


Fig. 1. Population abundance (N) and extinction risk in the presence or absence of evolution. Following the conventions of Gomulkiewicz & Holt (1995), growth is density-independent and N_c represents a threshold abundance below which the odds of extinction are high. Dashed portions of curves represent time at greatest risk of extinction for populations faced with an abrupt shift in their selective environment (a–c) or for newly colonising populations (d, e): (a) population declines to extinction in the absence of evolution or when evolution fails to accomplish replacement; (b) evolution is insufficient to prevent the population from entering the extinction risk zone, but allows it to grow out of that zone if it persists; (c) evolution allows the population to avoid the extinction risk zone; (d) a colonising population with positive growth spends more time in the extinction risk zone under little or no evolution than when (e) evolution accelerates growth.

other than a lower critical population size below which the risk of extinction is greatly increased. Populations that enter the high risk zone have the ability to evolve back out if, by chance, they persist long enough. This simple model introduces what might be considered a paradox of evolutionary rescue; stronger selection gives rise to faster evolution, but also imposes a greater demographic cost and risk of extinction.

The basis of this dilemma is fairly intuitive. Further the population's mean trait value is from the hypothetical optimum, the greater the fitness cost in survival and reproduction (i.e. genetic load *sensu* Haldane 1957). This effect is compounded by the fact that heritabilities less than unity, pleiotropy and epistasis can all slow approach to the new evolutionary optimum. Smaller populations facing similar selection are of course more likely to enter the zone of extinction risk and spend more time in that zone before re-emerging (Fig. 1). Less intuitively, the Gomulkiewicz & Holt (1995) model suggests that evolution does little to delay the time it takes for maladapted populations to enter the extinction risk zone. Likewise, it suggests that even populations destined for extinction may undergo considerable adaptive evolution in the interim. Indeed, some authors have suggested that contemporary evolution might be used as an early warning of impending population collapse (Olsen *et al.* 2004).

Some limitations of the Gomulkiewicz & Holt (1995) heuristic are that many shifts in selective environments are probably not abrupt and extinction risk is probably not a threshold function of population

size. Shifts in selective environments that emerge over the course of generations, like climate change or shifts in community structure, would not impose the same severity of demographic costs as those that occur abruptly and would thus increase the opportunity for evolutionary rescue (Pease, Lande & Bull 1989; Burger & Lynch 1995; but see Both *et al.* 2006). Similarly, demographic extinction risk is probably better represented by more continuous probability functions. More recent individual-based quantitative genetic models with stochastic dynamics (e.g. Boulding & Hay 2001; Holt & Gomulkiewicz 2004) suggest that evolution's most important role may be in quickly rescuing populations after they collapse under environmental change.

Limitations aside, one common message emerges from all eco-evolutionary models of this sort: contemporary evolutionary processes lie both at the heart of the problem of population persistence and its potential solution. In the remainder of this section we discuss how scope for an evolutionary solution likely depends on the nature of pressures contributing to endangerment.

DECLINE AND RESCUE VIA r_{\max} OR K

Because the original Gomulkiewicz & Holt (1995) model is density-independent it deals only with exogenous factors influencing r_{\max} . These factors can cause dN/dt to become negative, dropping population sizes very low. Should hard selection and evolution of broader tolerances result in an increase in r_{\max} , through density-independent aspect of survival or reproduction, there is opportunity for the organism to grow rapidly back towards density-limiting conditions. The catalogue of contemporary evolution is filled with examples that address such adaptive problems, often with clear ties to population dynamics, such as the evolution of resistance (Tabashnick 1994; Hairston *et al.* 2001), evolution of tolerance to pollution (Antonovics *et al.* 1971) and evolution of reduced predation risk (Kettlewell 1973; O'Steen, Cullum & Bennett 2002).

Population declines associated with reductions in carrying capacity, K (e.g. loss of feeding or breeding resources), cause populations to experience regulation at smaller sizes through density-dependent influences on birth or death rates. Soft selection (density and frequency-dependent) at or near K will generally favour genotypes that are better competitors. Such selection is central to the evolution of life-histories (Roff 2002) but may make modest immediate contributions to population growth when density is strongly regulated (Holt 1990). This is not to say that evolution will not mitigate limitations posed by density dependence. Adaptations that lead to more efficient use of current resources or exploit new resources could increase K . Evolutionary shifts to tolerate new habitats and hosts are well known in contemporary time (e.g. Antonovics *et al.* 1971; Carroll, Klassen & Dingle 1998). However, these cases generally involve novel availability of an alternate habitat or host within the range of a healthy population of the exploiter.

It is unclear whether depleted populations are likely to shift to resources they have previously failed to exploit or evolve greater efficiency when they likely faced comparable selection for efficiency at higher K .

Finally, populations do not have to be in decline for contemporary evolution to influence persistence. Evolution at or near K , particularly if it affects r_{\max} , may influence population persistence without substantially affecting current population size. For example, environmental tolerances could evolve in contemporary time without appreciably decreasing the size of a density-regulated population, and subsequently contribute to faster recovery following disturbance. Also, evolution of interspecific competitive ability might not result in significant declines of dominant species, such as those that win under resource-based competition (Tilman 1982), but may still contribute to competitive superiority in future interactions. At the same time, classic r - K trade-offs may favour traits such as late maturity or few-large offspring (Reznick *et al.* 1997) that reduce r_{\max} and increase extinction risks if population sizes fall (i.e. 'evolutionary degradation'; Dieckmann & Ferrière 2004).

THE PROBLEM OF FLUCTUATING SELECTION

Of course selection in many systems is not directional, but fluctuates (cycles, stochastic, etc.). In the case of climate change models (e.g. Kharin & Zwiers 2000) the variance of conditions like precipitation or temperature may change much more dramatically than their means. Shifts and excursions might cause some populations to perpetually chase (evolutionarily) alternate extremes while fettered by their genetic variation and gene flow. Such populations would face a demographic cost if evolution during one environmental phase resulted in maladaptation and reduced favourable genetic variation with respect to the next. Models suggest that stochastic environments can dramatically increase the risk of extinction for evolving populations and that persistence depends on genetic variation or high fecundity (Bürger & Krall 2004).

Galapagos finches (*Geospiza fortis*), a hallmark of contemporary evolution, experienced severe demographic losses (from 642 to 85 individuals) during a period of drought (P.R. Grant & B.R. Grant 2002). It is interesting to hypothesise that these finches may have suffered further declines had the drought not ended when it did (Boulding & Hay 2001), and that evolution during the drought phase may have introduced a genetic load that slowed recovery when wetter conditions returned. An analysis of 13 years of Galapagos finch data from P.R. Grant & B.R. Grant (2002) shows that an adaptation lag of this kind explains a substantial fraction of the variation in bird demography (Hairston *et al.* 2005).

Another study system provides a very different perspective into the role of evolution in persistence under fluctuating selection. Yoshida *et al.* (2003) found

that characteristics of predator-prey cycles in laboratory rotifer-algal microcosms depended critically upon whether or not the algal population was genetically diverse and able to evolve in response to varying rotifer abundance and nutrient limitation. Models showed that as genetic diversity in the prey increased, the parameter space leading to stable co-existence increased, and the maximum amplitude of oscillations, where they occurred, was reduced (Johnson & Agrawal 2003). At least for this system, the ability of prey to evolve may decrease the likelihood of stochastic extinction at the bottom of an oscillation.

Persistence of colonising populations

Reviews of the published literature show that introductions and invasions account for an especially large proportion of documented cases of contemporary evolution (Kinnison & Hendry 2001; Reznick & Ghalambor 2001; Lambrinos 2004). However, when it comes to the role of evolution in the persistence of those populations a clear dilemma emerges. According to the theory discussed above, population size can provide a demographic buffer important to the persistence of populations, especially those maladapted to a local environment. New populations, however, rarely have the large size that might limit inbreeding, Allee effects and the demographic costs of strong selection. As such, contemporary evolutionary processes likely to play a pervasive role in the quick demise of many would-be populations. Estimates indicate that failed invasions likely outnumber successes by several-fold (Lodge 1993; Mack *et al.* 2000).

A simple solution to this demographic dilemma is to presume that successful colonisations represent the fraction of cases where colonists are already well suited to new habitats. In a recent review of cases of contemporary evolution, Reznick & Ghalambor (2001) concluded that contemporary evolution may itself be fostered by an initial opportunity for population growth that offsets demographic costs. Pre-existing habitat suitability, and resulting growth might thus be viewed to obviate much of the added contributions of evolution in speeding populations to a safe size. We now consider theoretical and empirical reasons to suspect that this is not necessarily the case (see also Holt, Barfield & Gomulkiewicz 2005 for review of models).

FOUNDER CONTRIBUTIONS

What is the basis for positive fitness and growth among the founders of new populations? One possibility is that growth does indeed arise through fortuitous habitat matching. However, it might also be that initial positive growth is in some cases a product of contemporary evolution. Whereas founder effects are usually treated as random processes in models of colonisation, Quinn, Kinnison & Unwin (2001) suggested instead that adaptive evolution may arise due to selective processes that positively bias the features of founders.

The authors illustrate such 'favoured-founder' effects with populations of salmon (*Oncorhynchus* spp.) that have adapted to migrate under poor-growth conditions to natal reproductive habitats in tributaries at increasing distances upstream. Because of the rigors of migration (e.g. Kinnison *et al.* 2001) it is very likely that the individuals that manage to found populations further up river systems are an extreme subset of their source population with attributes such as greater migratory efficiency or greater energy acquisition prior to migration. A similar process may have shaped the features of founding plants during Quaternary range expansions (Davis & Shaw 2001).

To the extent that the features of founders are heritable and suited to their new habitat, this founding bias may represent adaptive evolution otherwise missed were we to only consider phenotypic changes after founding. More critically, these founding processes may represent adaptive evolution that can launch the initial positive growth of new populations. This founding bias would be easy to incorporate in most evolutionary colonisation models, but its generality needs to be better assessed in the field.

POST-FOUNDING CONTRIBUTIONS

It is also possible that contemporary evolution may boost early population growth after founding (Fig. 1). New populations will generally be far from K , where evolutionary contributions to population growth are not fully offset by density dependence or other aspects of environmental deterioration. Estimates of the equilibrium increase in mean fitness due to natural selection each generation are around 1%–10% (though potentially as high as 30%; Burt 1995) and larger gains might be expected under the non-equilibrium conditions of a selective perturbation. Such fitness evolution could increase r_{\max} in multiple generations as populations approach their new adaptive optima, resulting in super-exponential growth and a reduced period of risk from small population size (Holt *et al.* 2005). Consider the time required for a new population with an initial positive growth rate of 0.05 per generation to undergo logistic growth from a colonising population of 10 individuals to a safe size of 500 individuals (with $K = 1000$). Without evolution of r_{\max} this population would take approximately 92 generations to pass the demographically safe size. However, if fitness and growth rates increase by a conservative amount of just 10% of the initial value (0.005) in each of the next 10 generations, with no appreciable gains thereafter, the population would pass the safe size in nearly half the time (49 generations). Should the population subsequently face a chance setback it may rebound even faster than before. Naturally, such evolutionary acceleration of population growth would be most important where initial rates are close to replacement (Fisher 1930; Holt *et al.* 2005).

Evidence for evolutionary contributions to fitness in invading populations is found in research on Chinook

salmon (*O. tshawytscha*) populations that invaded New Zealand in the early 1900s. After 26 generations, populations invading different streams show heritable differences in life-history, developmental and morphological traits (Quinn *et al.* 2001). Perhaps more importantly, translocation experiments show that local adaptation accounts for more than a doubling of lifetime vital rates of survival and egg production relative to non-local genotypes (Kinnison *et al.* 2008). These vital rate differences are consistent with substantial fitness evolution in contemporary time. Kinnison *et al.* (2008) suggest that such evolution may contribute to invasiveness of exotic species through effects on initial population growth, abundance of particular life stages, rebound from control measures, ecological effects on other species or ability to invade other similar habitats.

OVERCOMING THE THREATS OF SMALL POPULATION SIZE

Theoretically, evolution's role in the persistence of new populations might be hampered at small population sizes where random drift and other problems threaten to overpower gains from natural selection. However, while it is not possible to assay failed colonisations, the evidence to date from successful introductions and invasions suggests that trait evolution is more commonly consistent with adaptive evolution than drift (but see Eckert, Manicacci & Barrett 1996). A number of studies of introduced or invading populations established from limited numbers of founders have provided evidence of trait evolution consistent with adaptive expectations and known trait–habitat associations (e.g. Reznick *et al.* 1997; Hendry *et al.* 2000; Kinnison *et al.* 2001). In a more formal analysis, Koskinen, Haugen & Primmer (2002) showed that serially introduced populations of European grayling (*Thymallus thymallus*), originating from small numbers of founders, and with persistently small effective population sizes, show greater structuring in life-history traits (Q_{ST}) than at neutral loci (F_{ST}) consistent with strong diversifying selection.

This is not to say that drift, or other problems like Allee effects and inbreeding, do not arise at small population sizes, and where they do they may act as fitness deteriorating factors and increase population risks (Amos & Balmford 2001; Holt *et al.* 2005; Saccheri & Hanski 2006). However, it is interesting to note that many invasions are typified by an initial lag phase of little apparent growth, followed by a very rapid increase and spread (Crooks & Soulé 1999; Mack *et al.* 2000). These exotic populations somehow avoid threats to extinction usually considered significant in small populations. Moreover, the ability of invaders to escape the lag phase may be testimony to evolution's ability to overcome purported limitations of small size (Crooks & Soulé 1999; Mack *et al.* 2000). In this scenario contemporary evolution may be more of a

limiting factor on population size than *vice versa*, giving rise to the abrupt demographic and adaptive transition captured in the multilocus individual based models by Holt & Gomulkiewicz (2004).

Converse to the 'extinction vortex' of declining populations identified by Gilpin & Soulé (1986), contemporary evolution may promote a 'persistence vortex'. In this case adaptive evolution gives rise to positive fitness and larger population size. Extinction risks *and* impediments to further adaptive evolution, like drift and inbreeding, are concurrently reduced.

Gene flow, metapopulations and persistence

Up to now we have considered evolutionary contributions to persistence in isolated populations. In metapopulations, subpopulations (demes) are linked through patterns of dispersal and gene flow. As such, declines or extinctions in some subpopulations (sinks) are demographically offset by immigration from others (sources) and genetic variation can move throughout complex landscapes aiding or impeding adaptation (e.g. Hanski 1999). In this section we consider some of the eco-evolutionary consequences of migration and gene flow for the persistence of demes and entire metapopulations in space and time.

The most common perspective on gene flow concerns its potential homogenising and constraining roles (e.g. Slatkin 1987; Kirkpatrick & Barton 1997; Lenormand 2002). Such constraints have been developed as tactics for fighting contemporary evolution of resistance in agricultural pests subject to strong selection from chemical control (e.g. untreated refuge demes or seed mixtures; Mallet & Porter 1992). However, consideration of these constraints needs to be balanced by recognition that gene flow may be less constraining, or even facilitating to evolution (e.g. Ehrlich & Raven 1969; Gomulkiewicz, Holt & Barfield 1999; Tufto 2001; Stockwell *et al.* 2003; Hendry 2004). Given that the expected constraints of gene flow should be familiar to most readers, we will focus on the latter perspective and its relevance to persistence (see also Garant, Forde & Hendry 2007).

GENE FLOW AND THE FATE OF POPULATIONS

A number of examples of contemporary evolution provide support for surprising amounts of divergence in the face immigration (e.g. Hendry *et al.* 2000; Kinnison *et al.* 2001). Similarly, many populations experiencing high rates of anthropogenically mediated immigration (e.g. fish stocking) show surprisingly little introgression over time (e.g. Fleming & Petersson 2001; De Meester *et al.* 2002). Conversely, empirical evidence for a purely homogenising role of gene flow in the contemporary evolution of wild populations is surprisingly rare, and usually represents just one *ad hoc* alternative for limited divergence (e.g. Stearns & Sage 1980). Why then might immigrants often

have such limited negative effects on the fitness of populations?

Certainly, theory suggests gene flow in excess of selection is generally needed to appreciably prevent divergence (Haldane 1930; Tufto 2001), but part of the solution may also involve processes shaping the pool of 'effective' migrants. The effectiveness of immigration in constraining adaptation depends on both the rate of gene flow *and* the heritable phenotypes of effective migrants relative to the adaptive optima in the population they enter (also demography – see below). On-going selection on migrants (Hendry, Day & Taylor 2001) and habitat monopolisation (De Meester *et al.* 2002) can restrict both the number and nature of effective migrants. Furthermore, studies on great tits (*Parus major*) and Glanville butterflies (*Melitaea cinxia*) show that the immigrant pool may not always be a random subset of source populations (Garant *et al.* 2005; Hanski & Saccheri 2006). Such biased migration could impose less of a genetic load, or even contribute advantageous variation to the local phenotype distribution.

Indeed, over contemporary time gene flow has the potential to be a much more potent source of adaptive genetic variation than mutation (Gomulkiewicz *et al.* 1999). For example, there is a not insignificant chance that immigrants to nascent or environmentally perturbed populations will come from sources with genotypes closer to the new local optimum than current residents (or even on the opposite extreme), promoting adaptation and increasing odds of persistence (Holt *et al.* 2005). This could be particularly important in populations facing climate change, where immigrants from southern populations convey adaptive genes into northern populations during a range shift (Pease *et al.* 1989; Davis & Shaw 2001).

Many introductions and invasions appear to have benefited from repeated influxes of immigrants, often from diverse sources (Mack *et al.* 2000; Kolbe *et al.* 2004; Lambrinos 2004). These successes argue for the value of gene flow in enhancing local genetic variation that ultimately might introduce an adaptive solution and population growth (Holt *et al.* 2005; Novak & Mack 2005). Interestingly, the same benefits may accrue to plants or diapausing invertebrates, wherein seed or egg banks, in essence temporal metapopulations, regularly contribute critical genetic variation in the face of environmental fluctuation (Hairston 1996; Ellner *et al.* 1999). Models and reviews (e.g. Gomulkiewicz *et al.* 1999; Garant *et al.* this volume) have both emphasised that intermediate levels of gene flow have a potentially important facilitating role in adaptive evolution.

Finally, demography plays an often underappreciated role in adjusting the relative influences of gene flow (Holt & Gomulkiewicz 1997; Tufto 2001; Hendry 2004). If through immigration, recombination, favoured founders, selection or luck, genotypes with positive absolute fitness arise in a small sink population, the

population may grow by a few individuals. For a given number of immigrants this small amount of growth can entail a sizeable reduction in migration rate and any constraining effects of gene flow just because migration rates are an inverse function of local abundance (i.e. immigrants/total population) (Holt & Gomulkiewicz 1997; Tufto 2001; Hendry 2004). As population size approaches K , density- and frequency-dependent selection can further decrease immigrant fitness (Stockwell *et al.* 2003; Hendry 2004). In this fashion an otherwise sink can become relatively isolated and adapted in under 30 generations (Hendry 2004). Indeed, some cases of contemporary evolution show evidence of incipient isolation in the face of persistent immigration (Hendry *et al.* 2000; Kinnison *et al.* 2008).

This shifting dynamic may provide a ready solution to the problems of small population size. The favourable effects of immigration that counteract inbreeding depression, drift and Allee effects are greatest in nascent or depleted populations (see examples in Lambrinos 2004 and Holt *et al.* 2005), while any adaptive costs of gene flow are reduced as populations grow past those risks. Artificial attempts to rehabilitate threatened populations would likely do well to mimic this shifting dynamic (Hedrick 1995; Tufto 2001; Stockwell *et al.* 2003).

PERSISTENCE OF METAPOPOPULATIONS

To the extent that the productivity, dispersal and recolonisation of component demes are determined by traits tied to fitness, contemporary evolution should have scope to influence the net growth or decline of a metapopulation, as defined by the generational contributions of all demes weighted in proportion to their mean absolute fitness (Saccheri & Hanski 2006). Any metapopulation declines that do occur may be hastened by a vortex of problems associated with fragmentation, including reduced opportunities for rescue effects (both demographic and genetic) and recolonisation, as well as increased odds that adaptive trait variation will be lost through chance deme extinction (Whitlock & Barton 1997; Hanski 1999). Conversely, contemporary evolution resulting in demes with positive mean fitness may give rise to a dispersal pool that can provide genetic and demographic resources to increase the growth of other demes and the overall metapopulation.

García-Ramos & Rodríguez (2002) provided evolutionary demographic models for the case of species invasions across smoothly heterogeneous landscapes in which adaptation contributes to local density and hence dispersal. Trait heritability, the steepness of environmental gradients and patterns of dispersal limit rates of a wave of invasion. The influence of dispersal on the speed of expansion was highly nonlinear: at low rates it improved the speed of expansion, but past a certain point increases in dispersal slowed expansions.

Results of models for more patchy landscapes provide generally similar results, though strong adaptive trade-offs among habitat patches in such landscapes can slow range expansion (Holt 2003). In general this evolutionary demographic model results in slower spread of an invasion than in purely ecological models, but such an evolutionary delay may often be inescapable for range expansion.

We hasten to note that contemporary evolution's contributions are not limited to metapopulations in immediate decline or expansion. On-going adaptive evolution must often be important in self-sustaining metapopulations where it culls the migrational loads that would otherwise accrue in subpopulations in a heterogeneous landscape. This process can limit the conversion of sources to sinks that contribute less directly to persistence (Ronce & Kirkpatrick 2001).

Empirical studies on the role of contemporary evolution in maintaining metapopulations are difficult for many reasons, but interesting leads have emerged. Hanski & Saccheri (2006) have shown that butterfly genotypes favouring high dispersal are quick to colonise smaller patches in metapopulations, whereas less dispersive genotypes dominate in larger patches that have already persisted a few years and where such genotypes have much higher lifetime reproductive success. In this system, contemporary evolution, in the form of biased dispersal and subsequent selection for alternate genotypes, can contribute to two different elements of persistence: ability to colonise vacant habitats and demic productivity. In another example, experimental metapopulations of bacteria and their associated phages subjected to fragmentation or connectivity show that gene flow can contribute to greater mean adaptation of the phage metapopulation (Morgan, Gandon & Buckling 2005), which might be presumed to aid persistence in the face of competing host resistance.

Conclusions

The literature is now replete with examples of contemporary evolution in the laboratory and in the wild, amply demonstrating both the pervasiveness and scope for evolution in contemporary time. As is often the case, theory has marched well in advance of empirical studies to suggest that associated eco-evolutionary dynamics likely lie at the root of population success or failure. At this point it seems far more prudent that ecologists begin to assess more fully whether and how eco-evolutionary dynamics influence the systems they study than to assume that contemporary evolution is insignificant.

This message is particularly relevant to conservation biology. Demographic stochasticity (including Allee effects), drift, loss of genetic variation, inbreeding and mutational meltdown are all seen as challenges in the conservation of small populations (Lande 1988; Amos & Balmford 2001; Spielman *et al.* 2004; Saccheri &

Hanski 2006). However, even these acute problems are likely often the final symptoms of earlier inabilities of populations to keep eco-evolutionary pace with severe anthropogenic challenges. Conversely, the successes of some pests, diseases, introductions and invasions represents the opposite problem, wherein initially small populations become too well adapted to their new environments while growing to costly abundance. Resurrection of small populations facing unsustainable selection, and suppression of nuisance species adaptively entrenched in their landscape, are tough battles, many of which we may never win (Gilpin & Soulé 1986; Mack *et al.* 2000; Stockwell *et al.* 2003). Clearly, prevention is more desirable, but even this is likely only possible if we consider seriously the eco-evolutionary dynamics that set conservation threats in motion.

With this in mind, we close with the following observations and suggestions:

1. The notion that evolutionary processes are vanishingly slow, and that contemporary evolution is exceptional, does not match current scientific knowledge and is counterproductive.
2. It is essential to recognise that conservation problems are likely eco-evolutionary in nature, not just ecological, demographic or genetic.
3. Contemporary evolution will not, however, rescue all populations or enable all invasions. Theory shows there are limits, and refinement of those limits should be a priority for conservation biology.
4. There is great need for studies that quantify the fitness, demographic and broader ecological consequences of contemporary evolution, not just trait change, in order to test current eco-evolutionary models.

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References

Abrams, P.A. & Matsuda, H. (1997) Prey evolution as a cause of predator–prey cycles. *Evolution* **51**, 1740–1748.

Amos, W. & Balmford, A. (2001) When does conservation genetics matter? *Heredity* **87**, 257–265.

Antonovics, J., Bradshaw, A.D. & Turner, R.G. (1971) Heavy metal tolerance in plants. *Advances in Ecological Research* **7**, 1–85.

Berryman, A.A., Arce, M.L. & Hawkins, B.A. (2002) Population regulation, emergent properties, and a requiem for density dependence. *Oikos* **99**, 601–606.

Bone, E. & Farres, A. (2001) Trends and rates of microevolution in plants. *Genetica* **112–113**, 165–182.

Boonstra, R. & Boag, P.T. (1987) A test of the Chitty hypothesis:

inheritance of life-history traits in meadow voles *Microtus pennsylvanicus*. *Evolution* **41**, 929–947.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83.

Boulding, E.G. & Hay, T. (2001) Genetic and demographic parameters determining population persistence after a discrete change in the environment. *Heredity* **86**, 313–324.

Bradshaw, W.E. & Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science* **312**, 1477–1478.

Bürger, R. & Krall, C. (2004) Quantitative-genetic models and changing environments. *Evolutionary Conservation Biology* (eds R. Ferrière, U. Diekmann & D. Couvet), pp. 171–187. Cambridge University Press, Cambridge, UK.

Burger, R. & Lynch, M. (1995) Evolution and extinction in a changing environment – a quantitative-genetic analysis. *Evolution* **49**, 151–163.

Burt, A. (1995) The evolution of fitness. *Evolution* **49**, 1–8.

Carroll, S.P., Klassen, S.T.P. & Dingle, H. (1998) Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. *Evolutionary Ecology* **12**, 955–968.

Chitty, D. (1952) Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936–9. *Philosophical Transactions of the Royal Society of London B* **236**, 505–552.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* **14**, 405–410.

Crooks, J. & Soulé, M.E. (1999) Lag times in population explosions of invasive species: causes and implications. *Proceedings, Norway/UN Conference on Alien Species* (eds O.T. Sandlund, P.J. Schei & A. Viken), pp. 39–46. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, Norway.

Darwin, C. & Wallace, A. (1858) On the tendency of species to form varieties: and on the perpetuation of varieties and species by natural means of selection. As communicated by C. Lyell and J.D. Hooker. *Journal of the Proceedings of the Linnean Society, Zoology* **3**, 45–62.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science* **292**, 673–679.

De Meester, L., Gomez, A., Okamura, B. & Schwenk, K. (2002) The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecologica* **23**, 121–135.

Desharnais, R.A. & Constantino, R.F. (1983) Natural selection and density-dependent population growth. *Genetics* **105**, 1029–1040.

Diekmann, U. & Ferrière, R. (2004) Adaptive dynamics and evolving biodiversity. *Evolutionary Conservation Biology* (eds R. Ferrière, U. Diekmann & C. Couvet), pp. 188–224. University Press, Cambridge, UK.

Eckert, C.G., Manicacci, D. & Barrett, S.C.H. (1996) Genetic drift and founder effect in native versus introduced populations of an invading plant, *Lythrum salicaria* (Lythaceae). *Evolution* **50**, 1512–1519.

Ehrlich, P.R. & Raven, P.H. (1969) Differentiation of populations. *Science* **165**, 1228–1232.

Eldredge, N. (1998) *Life in the Balance: Humanity and the Biodiversity Crisis*. Princeton University Press, Princeton, NJ.

Ellner, S., Hairston, N.G. Jr, Kearns, C.M. & Babai, D. (1999) The roles of fluctuating selection and long-term diapause in microevolution of diapause timing in a freshwater copepod. *Evolution* **53**, 111–122.

Ferrière, R., Diekmann, U. & Couvet, C. (2004) *Evolutionary Conservation Biology*. University Press, Cambridge, UK.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Fleming, I.A. & Petersson, E. (2001) The ability of released,

- hatchery salmonids to breed and contribute to the natural productivity of wild populations. *Nordic Journal of Freshwater Research* **75**, 71–98.
- Flessa, K.W. & Jablonski, D. (1985) Declining Phanerozoic background extinction rates: effect of taxonomic structure? *Nature* **313**, 216–218.
- Frank, S.A. & Slatkin, M. (1992) Fisher's fundamental theorem of natural selection. *Trends in Ecology and Evolution* **7**, 92–95.
- Frankham, R. (2005) Genetics and extinction. *Biological Conservation* **126**, 161–140.
- Franklin, I.R. (1980) Evolutionary change in small populations. *Conservation Biology, an Evolutionary-Ecological Perspective* (eds M.E. Soulé & B.A. Wilcox), pp. 135–149. Sinauer, Sunderland, MA.
- Garant, D., Forde, S.E. & Hendry, A.P. (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*. This Volume.
- Garant, D., Kruuk, L.E.B., Wilkin, T.A., McCleery, R.H. & Sheldon, B.C. (2005) Evolution driven by differential dispersal within a wild bird population. *Nature* **433**, 60–65.
- García-Ramos, G. & Rodríguez, D. (2002) Evolutionary speed of species invasions. *Evolution* **56**, 661–668.
- Gilpin, M.E. & Soulé, M.E. (1986) Minimal viable populations: processes of species extinction. *Conservation Biology: The Science of Scarcity and Diversity* (ed. M.E. Soule), pp. 19–34. Sinauer, Sunderland, MA.
- Gingerich, P.D. (1983) Rates of evolution – effects of time and temporal scaling. *Science* **222**, 159–161.
- Gingerich, P.D. (1993) Quantification and comparison of evolutionary rates. *American Journal of Science* **293A**, 453–478.
- Gomulkiewicz, R. & Holt, R.D. (1995) When does evolution by natural selection prevent extinction? *Evolution* **49**, 201–207.
- Gomulkiewicz, R., Holt, R.D. & Barfield, M. (1999) The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. *Theoretical Population Biology* **55**, 283–296.
- Gotelli, N.J. (2001) *A Primer of Ecology*. Sinauer, Sunderland, MA.
- Gould, S.J. (1989) *Wonderful Life*. Norton Co., Inc, New York.
- Grant, P.R. & Grant, B.R. (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**, 707–711.
- Hairston, N.G. Jr (1996) Zooplankton egg bands as biotic reservoirs in changing environments. *Limnology and Oceanography* **41**, 1087–1092.
- Hairston, N.G. Jr, Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* **8**, 1114–1127.
- Hairston, N.G. Jr, Holtmeier, C.L., Lampert, W., Weider, L.J., Post, D.M., Fisher, J.M., Cáceres, C.E., Fox, J.A. & Gaedke, U. (2001) Natural selection for grazer resistance to toxic cyanobacteria: evolution of phenotypic plasticity? *Evolution* **55**, 2203–2214.
- Hairston, N.G., Tinkle, D.W. & Wilbur, H.M. (1970) Natural selection and the parameters of population growth. *Journal of Wildlife Management* **34**, 681–690.
- Haldane, J.B.S. (1930) A mathematical theory of natural and artificial selection. VI. Isolation. *Proceedings of the Cambridge Philosophical Society* **26**, 220–230.
- Haldane, J.B.S. (1957) The cost of natural selection. *Journal of Genetics* **55**, 511–524.
- Hanski, I. (1990) Density dependence, regulation and variability in animal populations. *Philosophical Transactions of the Royal Society of London B* **330**, 141–150.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, London.
- Hanski, I. & Saccheri, I. (2006) Molecular-level variation affects population growth in a butterfly metapopulation. *Plos Biology* **4** (5), e129.
- Hedrick, P.W. (1995) Gene flow and genetic restoration: the Florida panther as a case study. *Conservation Biology* **9**, 996–1007.
- Hendry, A.P. (2004) Selection against migrants contributes to the rapid evolution of ecologically dependent reproductive isolation. *Evolutionary Ecology Research* **6**, 1219–1236.
- Hendry, A.P., Day, T. & Taylor, E.B. (2001) Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. *Evolution* **55**, 459–466.
- Hendry, A.P. & Kinnison, M.T. (1999) The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653.
- Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C. & Quinn, T.P. (2000) Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* **290**, 516–518.
- Holt, R.D. (1990) The microevolutionary consequences of climate change. *Trends in Ecology and Evolution* **5**, 311–315.
- Holt, R.D. (2003) On the evolutionary ecology of species ranges. *Evolutionary Ecology Research* **5**, 159–178.
- Holt, R.D., Barfield, M. & Gomulkiewicz, R. (2005) Theories of niche conservatism and evolution. In: *Species Invasions: Insights Into Ecology, Evolution and Biogeography* (eds D. Sax, J. Stanchowicz & S. Gaines), pp. 259–290. Sinauer, Sunderland, MA.
- Holt, R.D. & Gomulkiewicz, R. (1997) How does immigration influence local adaptation? A reexamination of a familiar paradigm. *American Naturalist* **149**, 563–572.
- Holt, R.D. & Gomulkiewicz, R. (2004) Conservation implications of niche conservatism and evolution in heterogeneous environments. In: *Evolutionary Conservation Biology* (eds R. Ferrière, U. Diekmann & C. Couvet), pp. 244–264. University Press, Cambridge, UK.
- Jablonski, D. (1986) Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* **231**, 129–133.
- Johnson, M.T.J. & Agrawal, A.A. (2003) The ecological play of predator–prey dynamics in an evolutionary theater. *Trends in Ecology and Evolution* **18**, 549–551.
- Kettlewell, H.B.D. (1973) *The Evolution of Melanism: the Study of a Recurring Necessity; with Special Reference to Industrial Melanism in the Lepidoptera*. Clarendon Press, Oxford.
- Kharin, V.V. & Zwiers, F.W. (2000) Changes in the extremes in an ensemble of transient climate simulations with coupled atmosphere–ocean GCM. *Journal of Climate* **13**, 3760–3788.
- Kinnison, M.T. & Hendry, A.P. (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**, 145–164.
- Kinnison, M.T., Unwin, M.J., Hendry, A.P. & Quinn, T.P. (2001) Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* **55**, 1656–1667.
- Kinnison, M.T., Unwin, M.J. & Quinn, T.P. (2008) Eco-evolutionary versus habitat contributions to invasion: experimental evaluation in the wild. *Molecular Ecology*, in press.
- Kirkpatrick, M. & Barton, N.H. (1997) Evolution of a species range. *American Naturalist* **150**, 1–23.
- Kolbe, J.J., Glor, R.E., Schettino, L.R., Lara, A.C., Larson, A. & Losos, J.B. (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* **431**, 177–181.
- Koskinen, M.T., Haugen, T.O. & Primmer, C.R. (2002) Contemporary Fisherian life-history evolution in small salmonid populations. *Nature* **419**, 826–829.

- Lambrinos, J.G. (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology* **85**, 2061–2070.
- Lande, R. (1988) Genetics and demography in biological conservation. *Science* **241**, 1455–1460.
- Law, W. & Salick, J. (2005) Human-induced dwarfing of Himalayan snow lotus, *Saussurea laniceps* (Asteraceae). *Proceedings of the National Academy of Sciences, USA* **102**, 10218–10220.
- Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends in Ecology and Evolution* **17**, 183–189.
- León, J.A. & Charlesworth, B. (1978) Ecological versions of Fisher's fundamental theorem of natural selection. *Ecology* **59**, 457–464.
- Lodge, D.M. (1993) Species invasion and deletions: community effects and responses to climate and habitat change. In: *Biotic Interactions and Global Climate Change* (eds P.M. Kareiva, J.G. Kingsolver & R.B. Huey), pp. 367–387. Sinauer, Sunderland, MA.
- Lynch, M., Conery, J. & Burger, R. (1995) Mutational meltdown in sexual populations. *Evolution* **49**, 1067–1080.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications* **10**, 689–710.
- Malcolm, J.R., Liu, C., Neilson, R.P., Hansen, L. & Hannah, L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* **20**, 538–548.
- Mallet, J. & Porter, P. (1992) Preventing insect adaptation to insect-resistant crops: are seed mixtures or refugia the best strategy? *Proceedings of the Royal Society of London B* **250**, 165–169.
- Morgan, A.D., Gandon, S. & Buckling, A. (2005) The effect of migration on local adaptation in a coevolving host–parasite system. *Nature* **437**, 253–256.
- Myers, N. & Knoll, A.H. (2001) The biotic crisis and the future of evolution. *Proceedings of the National Academy of Sciences, USA* **98**, 5389–5392.
- Novak, S.J. & Mack, R.N. (2005) Genetic bottlenecks in alien plant species. In: *Species Invasions: Insights into Ecology, Evolution and Biogeography* (eds D. Sax, J. Stanchowicz & S. Gaines), pp. 259–290. Sinauer, Sunderland, MA.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Diekmann, U. (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**, 932–935.
- O'Steen, S., Cullum, A.J. & Bennett, A.F. (2002) Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **56**, 776–784.
- Palumbi, S.R. (2001) Humans as the world's greatest evolutionary force. *Science* **293**, 1786–1790.
- Pease, C.M., Lande, R. & Bull, J.J. (1989) A model of population growth, dispersal and evolution in a changing environment. *Ecology* **70**, 1657–1664.
- Phillips, B.L. & Shine, R. (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proceedings of the National Academy of Sciences, USA* **101**, 17150–17155.
- Pianka, E.R. (2000) *Evolutionary Ecology*. Addison-Wesley Longman, San Francisco, CA.
- Pimm, S.L. & Raven, P. (2000) Extinction by numbers. *Nature* **403**, 843–845.
- Quinn, T.P., Kinnison, M.T. & Unwin, M.J. (2001) Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* **112–113**, 493–513.
- Reznick, D.N. & Ghalambor, C.K. (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112–113**, 183–198.
- Reznick, D.N., Shaw, F.H., Rodd, F.H. & Shaw, R.G. (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* **275**, 1934–1937.
- Roff, D.A. (2002) *Life History Evolution*. Sinauer, Sunderland, MA.
- Ronce, O. & Kirkpatrick, M. (2001) When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution* **55**, 1520–1531.
- Saccheri, I. & Hanski, I. (2006) Natural selection and population dynamics. *Trends in Ecology and Evolution* **21**, 341–347.
- Simpson, G.G. (1944) *Tempo and Mode in Evolution*. Columbia University Press, New York.
- Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science* **236**, 787–792.
- Slobodkin, L.B. (1961) *Growth and Regulation in Animal Populations*. Holt, Rinehart and Winston, New York, NY.
- Spielman, D., Brook, B.W. & Frankham, R. (2004) Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences, USA* **101**, 15261–15264.
- Stearns, S.C. & Sage, R.D. (1980) Maladaptation in a marginal population of the mosquito fish, *Gambusia affinis*. *Evolution* **34**, 65–75.
- Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* **18**, 94–101.
- Tabashnick, B.E. (1994) Evolution of resistance to *Bacillus thuringiensis*. *Annual Review of Entomology* **39**, 47–79.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature* **427**, 145–148.
- Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology and Evolution* **13**, 329–332.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Tufto, J. (2001) Effects of releasing maladapted individuals: a demographic-evolutionary model. *American Naturalist* **158**, 331–340.
- Wallace, B. (1975) Hard and soft selection revisited. *Evolution* **29**, 465–473.
- Waxman, D. & Gavrilits, S. (2005) 20 questions on adaptive dynamics. *Journal of Evolutionary Biology* **18**, 1139–1154.
- Webb, C. (2003) A complete classification of Darwinian extinction in ecological interactions. *American Naturalist* **161**, 181–205.
- Whitlock, M.C. & Barton, N.H. (1997) The effective size of a subdivided population. *Genetics* **146**, 427–441.
- Wilson, E.O. (1993) *The Diversity of Life*. Harvard University Press, Cambridge, MA.
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G. Jr (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* **424**, 303–306.

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