Introduction

Eco-evolutionary dynamics

F. Pelletier[1,2,*], D. Garant[2] and A. P. Hendry[3]

[1]*NERC Centre for Population Biology, Division of Biology, Imperial College London,
Silwood Park, Ascot, Berkshire SL5 7PY, UK*
[2]*Département de Biologie, Faculté des Sciences, Université de Sherbrooke, Sherbrooke,
Quebec J1K 2R1, Canada*
[3]*Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke Street West,
Montreal, Quebec H3A 2K6, Canada*

Evolutionary ecologists and population biologists have recently considered that ecological and evolutionary changes are intimately linked and can occur on the same time-scale. Recent theoretical developments have shown how the feedback between ecological and evolutionary dynamics can be linked, and there are now empirical demonstrations showing that ecological change can lead to rapid evolutionary change. We also have evidence that microevolutionary change can leave an ecological signature. We are at a stage where the integration of ecology and evolution is a necessary step towards major advances in our understanding of the processes that shape and maintain biodiversity. This special feature about 'eco-evolutionary dynamics' brings together biologists from empirical and theoretical backgrounds to bridge the gap between ecology and evolution and provide a series of contributions aimed at quantifying the interactions between these fundamental processes.

Keywords: eco-evolutionary dynamics; natural selection; contemporary evolution;
evolutionary changes; population dynamics; genotype-by-environment interaction

1. INTRODUCTION

Students of biology will intuitively recognize that ecology matters for evolution—and could point to several examples. Perhaps the earliest and the best known is the case of industrial melanism in peppered moths (*Biston betularia*). The dark (melanic) form of the moth was first recorded in 1848 near Manchester, UK. Environmental change caused by industrial pollution then favoured survival of the dark form over the light form, leading to a steady increase in the frequency of dark moths (Tutt 1896). Eventually, the dark form constituted more than 90 per cent of the population in heavily polluted areas (Kettlewell 1973). A number of other examples of apparently adaptive phenotypic changes were then reported in the 1960s, including those experienced by mice introduced to islands (Berry 1964), plants on mine tailings (Bradshaw 1965) and sparrows introduced to North America (Johnston & Selander 1964). Missing from some of these studies was direct evidence that the observed phenotypic changes were genetically based, but a number of studies in the 1980s showed that contemporary phenotypic change could indeed be genetically based (Endler 1980; Stearns 1983). This realization precipitated an explosion of studies in the past two decades exploring phenotypic and genetic changes in natural populations (reviewed in

Hendry & Kinnison 1999; Reznick & Ghalambor 2001; Bradshaw & Holzapfel 2006; Carroll *et al.* 2007; Gienapp *et al.* 2008).

If measurable changes in phenotypic distributions can occur over only a few years, then perhaps these changes can also influence ecological dynamics. Such eco-evolutionary feedbacks might occur at multiple levels, such as in demographic parameters, community composition, food webs, nutrient cycling and productivity. Over long enough time-scales, such feedbacks are obvious and undisputed, with good examples including coevolution between predators and prey or between pollinators and plants. On short time-scales, however, the influence of evolution on ecology has received relatively little attention. One reason may be the logistical challenges inherent in quantifying feedbacks between evolutionary and ecological processes. A more general problem may be that scientists have often assumed that evolution happens too slowly to leave a signature in ecological dynamics (Slobodkin 1961). The present theme issue joins other recent attempts to change this perception (Thompson 1998; Hairston *et al.* 2005; Coulson *et al.* 2006a; Saccheri & Hanski 2006; Fussmann *et al.* 2007; Kinnison & Hairston 2007; Kokko & Lopez-Sepulcre 2007; Hughes *et al.* 2008) by examining the interplay between ecology and evolution at multiple levels, i.e. 'eco-evolutionary dynamics'.

Work on eco-evolutionary dynamics is ongoing in several natural and laboratory systems (figure 1). The specific goal of this theme issue was to bring together ecologists and evolutionary biologists from diverse

*Author and address for correspondence: Département de Biologie, Faculté des Sciences, Université de Sherbrooke, Sherbrooke, Quebec J1K 2R1, Canada (fanie.pelletier@usherbrooke.ca).
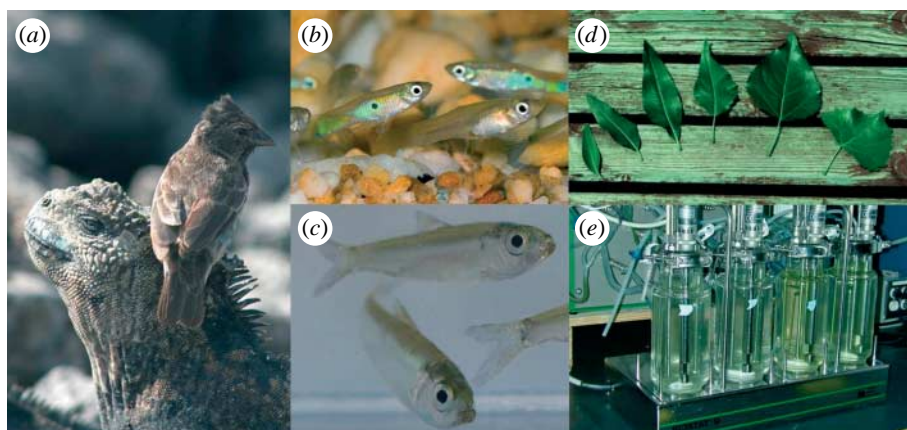
Figure 1. Five study systems where eco-evolutionary dynamics have been studied empirically (reviewed in Post & Palkovacs 2009): (*a*) the Darwin finches (Hairston *et al.* 2005), (*b*) the Trinidadian guppies (Palkovacs *et al.* 2009), (*c*) the Alewives study (Post & Palkovacs 2009), (*d*) the *Populus* system (Bailey *et al.* 2009) and (*e*) the microcosm experiments on the interaction between rotifer and algae (Yoshida *et al.* 2003; Jones *et al.* 2009). Photo by (*a*) A. Hendry, (*b*) P. Hill, (*c*) E. Palkovacs, (*d*) T. Whitham and (*e*) G. Fussmann.

backgrounds to jointly explore eco-evolutionary dynamics. As editors, we were especially interested in studies that develop new approaches, or that explore eco-evolutionary dynamics using different approaches (theory, experiments in the laboratory or nature and surveys in nature) at different levels of organization. These contributions fell broadly into three general categories: (i) effects of genotypes and phenotypes on population dynamics, (ii) interactions between environmental and genetic variation, and (iii) consequences of contemporary evolution for community composition and ecosystem processes. In this introduction, we first provide a more detailed review of the historical developments behind the specific idea that contemporary evolution can influence ecological processes. We then outline several key questions that are addressed by contributions to the theme issue. Finally, we identify future challenges and directions for studies on eco-evolutionary dynamics.

2. HISTORICAL DEVELOPMENTS

The idea that ecology can influence evolution, even on short time-scales, has long been an important focus of evolutionary biology. The reciprocal causal pathway (evolution to ecology) also turns out to have a long and distinguished history. For example, both Darwin (1859) and Fisher (1930) recognized the intertwined nature of ecological and evolutionary processes. Then in the 1950s and 1960s, a few ecologists started to formally hypothesize how evolution might influence ecology. Chitty (1952, 1960) argued that cycles in vole populations could be a consequence of natural selection favouring different types of life histories at different phases of a cycle. Similarly, Pimentel (1968) argued that 'evolution provides foundation for control of herbivore, parasite, and predator numbers in nature' (Pimentel 1968).

The shared assertion of the Chitty and Pimentel papers was that evolutionary change on relatively short time-scales could influence population dynamics. It took considerably longer, however, for biologists to specifically test some of these influences. Although Chitty's hypothesis was later discarded as a likely

mechanism for population cycles in voles (Boonstra & Boag 1987), it was shown in other systems that natural selection on life history and genetic variation can influence population dynamics (Sinervo *et al.* 2000; Yoshida *et al.* 2003). Part of the delay in obtaining empirical evidence for eco-evolutionary dynamics was caused by the need to first develop simple and robust ways to measure selection (Lande 1982; Lande & Arnold 1983), fitness (Clutton-Brock 1991; McGraw & Caswell 1996; Coulson *et al.* 2006*b*) and genetic variance for fitness-related traits (Kruuk 2004; Kruuk *et al.* 2008). Owing largely to these developments, many studies now routinely estimate these parameters in wild populations (Endler 1986; Kingsolver *et al.* 2001; Kruuk 2004). Another major advance was the accumulation of the detailed, long-term, empirical, individual-based data and pedigrees required to reliably document selection and evolution in nature (for an example of such studies, see Ezard *et al.* 2009). Finally, laboratory methods were developed for manipulating genetic variation and for examining evolutionary and population dynamical responses in multi-species communities (Yoshida *et al.* 2003). Together, these methods have allowed us to more formally consider eco-evolutionary dynamics.

3. FROM INTERACTIONS TO FEEDBACKS

Several studies have shown that ecological change can drive evolutionary change on contemporary scales, and some studies are now showing the reciprocal pathway. Eco-evolutionary dynamics in the broad sense can thus include the unidirectional effects of ecological changes on evolutionary processes or the unidirectional effects of evolutionary changes on ecological processes. An important goal, however, should be to elucidate bidirectional eco-evolutionary interactions, referred to as 'eco-evolutionary feedbacks' (Post & Palkovacs 2009). Such feedbacks might arise at different scales in space and time and at different levels of biological organization (genes, individuals, populations, communities and ecosystems). Because many biological processes are hierarchical or organized in a network, changing one aspect of the chain can affect many levels

(Coulson *et al.* 2006*a*). Many such interactions and feedbacks are possible and we will here provide only a few examples.

At the population level, natural selection and population dynamics are closely linked, simply because both are affected by the birth and death of individuals. Thus, if natural selection acts on a trait (e.g. body size) through survival or reproductive success, it will leave a population dynamical signature (Coulson *et al.* 2006*b*; Pelletier *et al.* 2007). This signature is expected to be the strongest when populations are not already density limited (Saccheri & Hanski 2006; Kinnison & Hairston 2007). As another example, landscape features can influence the distribution of genetic diversity at the individual and population levels (Jeyasingh & Weider 2007; Clark *et al.* 2008), thus affecting gene frequencies. If the change in gene frequencies translates into phenotypic trait changes that affect demographic rates (such as reproduction, survival or dispersal), then, ultimately, the genetic change will affect population dynamics (Hanski & Saccheri 2006; Saccheri & Hanski 2006). Effects at the community level are also possible. When two species, such as a predator and a prey, interact, evolutionary change in one can influence selection and demography of the other—and vice versa (Fussmann *et al.* 2007). Finally, changes in the numbers of individuals, the types of resources they use and their efficiency in doing so can influence a suite of ecosystem functions, such as decomposition, nutrient cycling and primary productivity (Thompson 1998).

There are many ways to write general expressions for eco-evolutionary dynamics (e.g. Coulson *et al.* 2006*a*; Fussmann *et al.* 2007; Bailey *et al.* 2009; Post & Palkovacs 2009). The commonality between all of these expressions is a hierarchical relationship between fitness, phenotypes and genes. As a complement to Dobzhansky's famous quote 'nothing in biology makes sense except in the light of evolution' (Dobzhansky 1964), we therefore suggest that nothing in evolution or ecology makes sense except in the light of the other. The present theme issue is an attempt to underline the value of this view by focusing on several key questions.

(a) *How does evolution influence demography?*

Understanding the relative contribution of ecological and evolutionary processes to the changes in population dynamics is essential to understand how the dynamics of heritable traits influence population processes. As reviewed previously, several studies have shown that phenotypic and microevolutionary changes can occur on ecological time-scales. These changes presumably influence population dynamics, but the extent of this influence is still generally unknown (Saccheri & Hanski 2006) because only a few studies have quantified the importance of phenotypic change to population growth and dynamics. The few examples include analyses of Darwin's finches (*Geospiza fortis*; Hairston *et al.* 2005), Soay sheep (*Ovis aries*; Pelletier *et al.* 2007) and New Zealand chinook salmon (*Oncorhynchus tshawytscha*; Kinnison *et al.* 2008). Such work is increasingly needed, however, as it may yield information as to the magnitude and direction of the influence evolution exerts on population persistence and extinction in changing

environments (Burger & Lynch 1995; Gomulkiewicz & Holt 1995; Orr & Unckless 2008).

The first paper in this section of the theme issue (Ezard *et al.* 2009) extends the above analyses by quantifying the influence of phenotypic distributions on population dynamics in five natural systems. Specifically, the authors partition the effects of phenotypic and environmental changes on population growth (Hairston *et al.* 2005) using five detailed long-term time series of marked ungulate populations. Ezard *et al.* (2009) find that juvenile mass (a key heritable life-history trait in ungulates; Albon *et al.* 1987; Wilson *et al.* 2005) can influence population growth to a similar extent as can environmental variables such as climate and food availability. In short, Ezard *et al.* (2009) show that neither phenotypic changes nor ecology can be ignored when considering population growth.

Life histories emerge from transitions between life stages and can therefore influence population dynamics (Saether & Bakker 2000; Oli & Dobson 2003). Moreover, life histories can clearly evolve on short time-scales (Stearns 1983; Reznick *et al.* 1990), thus providing a possible conduit for eco-evolutionary dynamics. Several theoretical studies have tried to understand how the variety of life histories observed in nature might have evolved. These models have generally considered the fitness of alternative life histories in stable environments, which may be an unrealistic assumption. In the present theme issue, Tuljapurkar *et al.* (2009) explore the fitness landscape of various life histories under varying environmental conditions. Their work suggests that 'optimal phenotypes' in a fluctuating environment are likely to differ from those in a constant environment.

Central to all studies of eco-evolutionary dynamics is the concept of 'fitness'. In a constant environment with no density dependence and no age structure, classic theoretical models hold that evolution maximizes the mean relative fitness (Fisher 1930; Crow & Kimura 1970). Natural populations, however, frequently experience variable environments (Engen *et al.* 2005) and density dependence (Bonenfant *et al.* 2009). Lande *et al.* (2009) apply diffusion theory to analyse a system of coupled ecological and evolutionary dynamics to derive an evolutionary maximum principle under these more realistic conditions. They show how 'the magnitude of environmental stochasticity and the form of density dependence govern the trade-off between r and K selection'.

(b) *How do ecological variables influence the potential for evolution?*

The recognition that ecological conditions can influence evolution is not new. In fact, genotype-by-environment interactions have long been integrated into evolutionary quantitative genetic theory (Bradshaw 1965; Falconer & Mackay 1996). To date, most evidence for such interactions has come from controlled laboratory experiments. For natural populations, some studies have revealed that habitat quality can influence genetic variance (reviewed in Hoffmann & Merilä 1999; Charmantier & Garant 2005) and covariance (reviewed in Sgrò & Hoffmann 2004). However, relatively few attempts have been made to

assess the influence of environmental variability on the distribution of genetic diversity at different levels of biological organization. Studies in this section of the present theme issue used a variety of approaches to determine how ecological processes influence evolutionary parameters, as well as their links to short- and long-term population dynamics.

One factor that can influence genetic variation, adaptation and population dynamics is dispersal (reviewed in Garant *et al.* 2007). Zheng *et al.* (2009) emphasize the need to study these interactions in theoretical models tailored to specific empirical systems. For example, evolutionary models do not usually formalize the actual genetic mechanisms underlying dispersal. Zheng *et al.* (2009) do so with an individual-based model of Glanville fritillary butterflies (*Melitaea cinxia*) in a fragmented landscape. The authors find a strong coupling between metapopulation dynamics and genetic dynamics at a locus (Pgi) affecting dispersal and other life-history traits. The strength of the coupling depends on spatial scale and is asymmetric; demography has a greater impact on genetics than vice versa. Zheng *et al.* (2009) consider the positive role of dispersal on population dynamics, whereas Moore & Hendry (2009) consider the possible negative role. They specifically test whether gene flow between three-spine stickleback (*Gasterosteus aculeatus* L.) populations in different environments (lake versus stream) can cause maladaptation that limits population size and constrains species ranges (suggested by Kirkpatrick & Barton 1997). Finding only mixed evidence in support of the hypothesis despite a simplified system with high gene flow and trait maladaptation, Moore & Hendry (2009) discuss how any negative effects of gene flow on population dynamics might be difficult to demonstrate in nature.

Another factor that might influence genetic variation, adaptation and population dynamics is spatial habitat heterogeneity. The integration of geographical information system methods and landscape genetic approaches is well suited to explore this topic, as shown by one contribution to the special issue. Porlier *et al.* (2009) explore how the spatial distribution of habitat types influences population structure and individual neutral genetic variability in wild tree swallows (*Tachycineta bicolor*). The authors show that individual genetic diversity is greater in poorer habitats, at least partly due to non-random settlement patterns of swallows across the landscape. Dionne *et al.* (2009) then provide a direct assessment of how spatial variation in selection influences genetic variability of selected loci. The authors first document differences in parasites and pathogens for Atlantic salmon (*Salmo salar*) from distinct genetic groups and ecological regions. They then identify specific major histocompatibility complex alleles that influence resistance to pathogen infection in their wild populations. Finally, they show a decrease in the frequency of the susceptibility allele through time, suggesting that pathogen-driven selection is acting in their systems.

Ultimately, many investigators would like to predict evolutionary patterns among populations as a function of selection and genetic variation within populations. This effort has thus far been hampered by the lack of a precise way to quantify and compare complex multivariate genetic variance–covariance (G) matrices. To fill this gap, Hine *et al.* (2009) present a new method for comparing G matrices and then ask whether the G matrix within *Drosophila serrata* populations can explain variation in the same traits among those populations.

(c) *When will evolution influence community and ecosystem variables?*

The idea that contemporary evolution can influence demographic parameters is relatively straightforward as are some links between contemporary evolution and community structure. For instance, the evolution of one species often improves its ability to compete with, or to exploit, another species (Yoshida *et al.* 2003; Fussmann *et al.* 2007). This adaptation of one species then selects for countermeasures in the other species, initiating a coevolutionary arms race with a variety of possible outcomes (Thompson 2005). Coevolutionary feedbacks are also particularly obvious for tight mutualistic interactions such as those between ants and aphids, and flowering plants and pollinators. Less straightforward, however, are local links between evolutionary change and higher level ecological variables, such as community composition, food webs, nutrient dynamics and primary productivity. In comparison with population dynamics, these variables are further removed from the genetic variation on which selection acts, and may therefore be less sensitive to evolutionary change. What, then, are the conditions under which these higher level eco-evolutionary dynamics might be important?

One of the earliest formal demonstrations of evolutionary effects, above the population level, was chemostat experiments showing that evolutionary change influenced population cycles of predators (rotifers) and prey (algae) (Yoshida *et al.* 2003). Jones *et al.* (2009) further explore that system by modelling factors influencing its eco-evolutionary dynamics. The authors show that ecological and genetic 'details' matter. For example, changes in environmental variables (chemostat flow rates) or cost/effectiveness trade-offs in prey defence can shift the identity of the surviving prey types. An even more complex range of outcomes follows from a consideration of heritable variation in both multiple predator types and multiple prey types with resulting dynamics ranging from equilibrium to chaos (Jones *et al.* 2009).

Chemostat experiments have proven extremely informative but experiments in nature are also needed. Johnson *et al.* (2009) take steps in this direction with a combined theoretical–experimental approach. They first develop a theoretical framework for understanding when natural selection should drive community dynamics. They then demonstrate these conditions in their experimental plant–arthropod system, i.e. natural selection acts on plant biomass, which is heritable and influences arthropod abundance and species richness. These findings are then integrated back into the theoretical framework to predict evolutionary changes in the plants, as well as ecological responses in arthropod communities.

Ecosystem variables should be less affected by genetic variation than are population and community variables. Bailey *et al.* (2009) therefore predict that genetic variation will have its greatest effect on population variables, a weaker effect on community variables and the weakest effect on ecosystem variables. Using a meta-analytical approach, the authors confirm that genetic variation in plant populations is most closely associated with plant traits, less associated with community variables and least associated with ecosystem variables. Critically, however, strong effects of genetic variation were sometimes present at all of these levels, highlighting the need for future studies to consider additional factors that might influence the strength of eco-evolutionary dynamics.

Many studies of eco-evolutionary dynamics at the community and ecosystem levels focus on genetic variation in plants as the evolutionary driver. Here, Palkovacs *et al.* (2009) instead focus on the potential effects of genetic variation in animals. The authors use mesocosms to study the ecological effects of population-level adaptive differences in guppies (*Poecilia reticulata*) and killifish (*Rivulus hartii*). They find that guppies adapted to different predation environments (high versus low) have differential effects on the biomass of aquatic invertebrates and algae. Killifish adapted to the presence or absence of guppies were also found to have differential effects on aquatic invertebrates. These results suggest the possible importance of top-down drivers of eco-evolutionary dynamics.

Post & Palkovacs (2009) provide a capstone by specifically considering the conditions under which eco-evolutionary feedbacks are most likely. They then review five empirical systems in which indirect evidence suggests such feedbacks are present (figure 1). Each of these systems shows considerable promise for documenting eco-evolutionary dynamics in nature. It also seems certain that new systems will soon emerge as excellent candidates for such kind of study.

4. CHALLENGES

One of the key steps for future research will be to develop a general theoretical framework for eco-evolutionary dynamics—and then to quantify these dynamics in natural populations. When it comes to population dynamics, new methods have been advanced for estimating the contribution of trait distributions to population growth and dynamics (Coulson *et al.* 2006*b*; Pelletier *et al.* 2007). Now we also have good statistical methods to decompose trait distributions into environmental and genetic components (Kruuk 2004). At this stage, however, we still have a very limited understanding of the dynamics of phenotypes and genotypes in natural settings (Merilä *et al.* 2001; Kruuk *et al.* 2008). Furthermore, we have no studies quantifying how ongoing evolution influences community or ecosystem variables in nature. To directly demonstrate eco-evolutionary dynamics, we should now strive for more studies that track the ongoing evolution of traits and their ecological consequences. Long-term studies can be helpful in this matter but, in some cases, stochastic temporal and environmental trends will be intertwined with

evolutionary change and population dynamics. Disentangling this complexity might require further theoretical and statistical developments, as well as manipulative experiments in microcosms and nature.

As emphasized by many contributors to this theme issue, another key challenge is to identify and formally confirm situations where eco-evolutionary dynamics and feedbacks might be particularly important. This effort will require examining multi-way interactions and transition phases, as well as potential steady states in various systems. Crespi (2004) argued that eco-evolutionary feedbacks are hard to measure because they are episodic. Thus, although feedbacks might be common in nature, they might be measurable only during transition periods. This might explain why most of the examples of eco-evolutionary feedbacks come from species recently experiencing an abrupt environmental shift such as invasion of a new habitat (Kinnison *et al.* 2008), exposure to novel predators or pathogens (Facon *et al.* 2006) or extreme weather conditions (Grant & Grant 2002).

Finally, another important challenge will be to overcome traditional views deeply anchored in each field. The assumption that ecological and evolutionary processes occur on a very different time-scale has to be abandoned. In addition, we need to go a step further by quantifying eco-evolutionary interactions instead of only interpreting ecological studies in an evolutionary context or looking at evolutionary parameters in one or two environments. An increasing integration of ecology and evolution should provide key insights into the forces that generate and maintain biodiversity in nature.

REFERENCES

Albon, S. D., Clutton-Brock, T. H. & Guinness, F. E. 1987 Early development and population dynamics in red deer. II. Density-independent effects of cohort variation. *J. Anim. Ecol.* **56**, 69–81. (doi:10.2307/4800)

Bailey, J. K. *et al.* 2009 From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Phil. Trans. R. Soc. B* **364**, 1607–1616. (doi:10.1098/rstb.2008.0336)

Berry, R. J. 1964 The evolution of an island population of the house mouse. *Evolution* **18**, 468–483. (doi:10.2307/2406357)

Bonenfant, C. *et al.* 2009 Empirical evidences of density-dependence in populations of large herbivores. *Adv. Ecol. Res.* **41**, 299–338.

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. (doi:10.2307/2409183)

Bradshaw, A. D. 1965 Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* **13**, 115–155. (doi:10.1016/S0065-2660(08)60048-6)

Bradshaw, W. E. & Holzapfel, C. M. 2006 Evolutionary response to rapid climate change. *Science* **312**, 1477–1478. (doi:10.1126/science.1127000)

Burger, R. & Lynch, M. 1995 Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution* **49**, 151–163. (doi:10.2307/2410301)

Carroll, S. P., Hendry, A. P., Reznick, D. N. & Fox, C. W. 2007 Evolution on ecological time-scales. *Funct. Ecol.* **21**, 387–393. (doi:10.1111/j.1365-2435.2007.01289.x)

Charmantier, A. & Garant, D. 2005 Environmental quality and evolutionary potential: lessons from wild populations. *Proc. R. Soc. B* **272**, 1415–1425. (doi:10.1098/rspb.2005.3117)

Chitty, D. 1952 Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936–1939. *Phil. Trans. R. Soc. Lond. B* **236**, 505–552. (doi:10.1098/rstb.1952.0009)

Chitty, D. 1960 Population processes in the vole and their relevance to general theory. *Can. J. Zool.* **38**, 99–113. (doi:10.1139/z60-011)

Clark, R. W., Brown, W. S., Stechert, R. & Zamudio, K. R. 2008 Integrating individual behaviour and landscape genetics: the population structure of timber rattlesnake hibernacula. *Mol. Ecol.* **17**, 719–730. (doi:10.1111/j.1365-294X.2007.03594.x)

Clutton-Brock, T. H. 1991 Lifetime data and the measurement of selection. *Evolution* **45**, 454. (doi:10.2307/2409682)

Coulson, T., Benton, T. G., Lundberg, P., Dall, S. R. X. & Kendall, B. E. 2006*a* Putting evolutionary biology back in the ecological theatre: a demographic framework mapping genes to communities. *Evol. Ecol. Res.* **8**, 1155–1171.

Coulson, T., Benton, T. G., Lundberg, P., Dall, S. R. X., Kendall, B. E. & Gaillard, J.-M. 2006*b* Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc. R. Soc. B* **273**, 547–555. (doi:10.1098/rspb.2005.3357)

Crespi, B. J. 2004 Vicious circles: positive feedback in major evolutionary and ecological transitions. *Trends Ecol. Evol.* **19**, 627–633. (doi:10.1016/j.tree.2004.10.001)

Crow, J. F. & Kimura, M. 1970 *An introduction to population genetics theory.* New York, NY: Harper and Row.

Darwin, C. 1859 *On the origin of species.* London, UK: John Murray. (Reprinted by Harvard Unviersity Press 1964)

Dionne, M., Miller, K. M., Dodson, J. J. & Bernatchez, L. 2009 MHC standing genetic variation and pathogen resistance in wild Atlantic salmon. *Phil. Trans. R. Soc. B* **364**, 1555–1565. (doi:10.1098/rstb.2009.0011)

Dobzhansky, T. 1964 Biology, molecular and organismic. *Am. Zool.* **4**, 443–452. (doi:10.1093/icb/4.4.443)

Endler, J. A. 1980 Natural selection on color patterns in *Poecilia reticulata. Evolution* **34**, 76–91. (doi:10.2307/2408316)

Endler, J. A. 1986 *Natural selection in the wild.* Princeton, NJ: Princeton University Press.

Engen, S., Lande, R. & Saether, B.-E. 2005 Effective size of a fluctuating age-structured population. *Genetics* **170**, 941–954. (doi:10.1534/genetics.104.028233)

Ezard, T. H. G., Côté, S. D. & Pelletier, F. 2009 Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Phil. Trans. R. Soc. B* **364**, 1491–1498. (doi:10.1098/rstb.2009.0006)

Facon, B., Genton, B. J., Shykoff, J., Jarne, P., Estoup, A. & David, P. 2006 A general eco-evolutionary framework for understanding bioinvasions. *Trends Ecol. Evol.* **21**, 130–133. (doi:10.1016/j.tree.2005.10.012)

Falconer, D. S. & Mackay, T. F. C. 1996 *Introduction to quantitative genetics.* Harlow, UK: Pearson Prentice Hall.

Fisher, R. A. 1930 *The genetical theory of natural selection.* Oxford, UK: Clarendon Press (reprinted by Dover, 1958).

Fussmann, G. F., Loreau, M. & Abrams, P. A. 2007 Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* **21**, 465–477. (doi:10.1111/j.1365-2435.2007.01275.x)

Garant, D., Forde, S. E. & Hendry, A. P. 2007 The multifarious effects of dispersal and gene flow. *Funct. Ecol.* **21**, 434–443. (doi:10.1111/j.1365-2435.2006.01228.x)

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merilä, J. 2008 Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178. (doi:10.1111/j.1365-294X.2007.03413.x)

Gomulkiewicz, R. & Holt, R. D. 1995 When does evolution by natural selection prevent extinction? *Evolution* **49**, 201–207. (doi:10.2307/2410305)

Grant, P. R. & Grant, B. R. 2002 Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**, 707–711. (doi:10.1126/science.1070315)

Hairston Jr, N. G., Ellner, S. P., Geber, M., Yoshida, T. & Fox, J. E. 2005 Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* **8**, 1114–1127. (doi:10.1111/j.1461-0248.2005.00812.x)

Hanski, I. & Saccheri, I. 2006 Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biol.* **4**, 719–726. (doi:10.1371/journal.pbio.0040129)

Hendry, A. P. & Kinnison, M. T. 1999 The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653. (doi:10.2307/2640428)

Hine, E., Chenoweth, S. F., Rundle, H. D. & Blows, M. W. 2009 Characterizing the evolution of genetic variance using genetic covariance tensors. *Phil. Trans. R. Soc. B* **364**, 1567–1578. (doi:10.1098/rstb.2008.0313)

Hoffmann, A. A. & Merilä, J. 1999 Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.* **14**, 96–101. (doi:10.1016/S0169-5347(99)01595-5)

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N. & Vellend, M. 2008 Ecological consequences of genetic diversity. *Ecol. Lett.* **11**, 609–623. (doi:10.1111/j.1461-0248.2008.01179.x)

Jeyasingh, P. D. & Weider, L. J. 2007 Fundamental links between genes and elements: evolutionary implications of ecological stoichiometry. *Mol. Ecol.* **16**, 4649–4661. (doi:10.1111/j.1365-294X.2007.03558.x)

Johnston, R. F. & Selander, R. K. 1964 House sparrows: rapid evolution of races in North America. *Science* **144**, 548–550. (doi:10.1126/science.144.3618.548)

Johnson, M. T. J., Vellend, M. & Stinchcombe, J. R. 2009 Evolution in plant populations as a driver of ecological changes in arthropod communities. *Phil. Trans. R. Soc. B* **364**, 1593–1605. (doi:10.1098/rstb.2008.0334)

Jones, L. E., Becks, L., Ellner, S. P., Hairston Jr, N. G., Yoshida, T. & Fussmann, G. F. 2009 Rapid contemporary evolution and clonal food web dynamics. *Phil. Trans. R. Soc. B* **364**, 1579–1591. (doi:10.1098/rstb.2009.0004)

Kettlewell, H. B. D. 1973 *The evolution of melanism.* Oxford, UK: Oxford University Press.

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P. & Beerli, P. 2001 The strength of phenotypic selection in natural populations. *Am. Nat.* **157**, 245–261. (doi:10.1086/319193)

Kinnison, M. T. & Hairston, J. N. G. 2007 Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Funct. Ecol.* **21**, 444–454. (doi:10.1111/j.1365-2435.2007.01278.x)

Kinnison, M. T., Unwin, M. J. & Quinn, T. P. 2008 Eco-evolutionary vs. habitat contributions to invasion in salmon: experimental evaluation in the wild. *Mol. Ecol.* **17**, 405–414. (doi:10.1111/j.1365-294X.2007.03495.x)

Kirkpatrick, M. & Barton, N. H. 1997 Evolution of a species' range. *Am. Nat.* **150**, 1–23. (doi:10.1111/j.1365-2435.2007.01275.x)

Kokko, H. & Lopez-Sepulcre, A. 2007 The ecogenetic link between demography and evolution: can we bridge the gap between theory and data? *Ecol. Lett.* **10**, 773–782. (doi:10.1111/j.1461-0248.2007.01086.x)

Kruuk, L. E. B. 2004 Estimating genetic parameters in natural populations using the 'animal model'. *Phil. Trans. R. Soc. Lond. B* **359**, 873–890. (doi:10.1098/rstb.2003.1437)

Kruuk, L. E. B., Slate, J. & Wilson, A. J. 2008 New answers for old questions: the evolutionary quantitative genetics of wild animal populations. *Annu. Rev. Ecol. Evol. Syst.* **39**, 525–548. (doi:10.1146/annurev.ecolsys.39.110707.173542)

Lande, R. 1982 A quantitative genetic theory of life history evolution. *Ecology* **63**, 607–615. (doi:10.2307/1936778)

Lande, R. & Arnold, S. J. 1983 The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226. (doi:10.2307/2408842)

Lande, R., Engen, S. & Sæther, B.-E. 2009 An evolutionary maximum principle for density-dependent population dynamics in a fluctuating environment. *Phil. Trans. R. Soc. B* **364**, 1511–1518. (doi:10.1098/rstb.2009.0017)

McGraw, J. B. & Caswell, H. 1996 Estimation of individual fitness from life-history data. *Am. Nat.* **147**, 47–64. (doi:10.1086/285839)

Merilä, J., Sheldon, B. C. & Kruuk, L. E. B. 2001 Explaining stasis: microevolutionary studies in natural populations. *Genetica* **112–113**, 199–222. (doi:10.1023/A:1013391806317)

Moore, J.-S. & Hendry, A. P. 2009 Can gene flow have negative demographic consequences? Mixed evidence from stream threespine stickleback. *Phil. Trans. R. Soc. B* **364**, 1533–1542. (doi:10.1098/rstb.2009.0007)

Oli, M. K. & Dobson, F. S. 2003 The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *Am. Nat.* **161**, 422–440. (doi:10.1086/367591)

Orr, H. A. & Unckless, R. L. 2008 Population extinction and the genetics of adaptation. *Am. Nat.* **172**, 160–169. (doi:10.1086/589460)

Palkovacs, E. P., Marshall, M. C., Lamphere, B. A., Lynch, B. R., Weese, D. J., Fraser, D. F., Reznick, D. N., Pringle, C. M. & Kinnison, M. T. 2009 Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Phil. Trans. R. Soc. B* **364**, 1617–1628. (doi:10.1098/rstb.2009.0016)

Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S. & Coulson, T. 2007 The evolutionary demography of ecological change: linking trait variation and population growth. *Science* **315**, 1571–1574. (doi:10.1126/science.1139024)

Pimentel, D. 1968 Population regulation and genetic feedback. *Science* **159**, 1432–1437. (doi:10.1126/science.159.3822.1432)

Porlier, M., Bélisle, M. & Garant, D. 2009 Non-random distribution of individual genetic diversity along an environmental gradient. *Phil. Trans. R. Soc. B* **364**, 1543–1554. (doi:10.1098/rstb.2009.0010)

Post, D. M. & Palkovacs, E. P. 2009 Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Phil. Trans. R. Soc. B* **364**, 1629–1640. (doi:10.1098/rstb.2009.0012)

Reznick, D. & 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. (doi:10.1023/A:1013352109042)

Reznick, D. A., Bryga, H. & Endler, J. A. 1990 Experimentally induced life-history evolution in a natural population. *Nature* **346**, 357–359. (doi:10.1038/346357a0)

Saccheri, I. & Hanski, I. 2006 Natural selection and population dynamics. *Trends Ecol. Evol.* **21**, 341–347. (doi:10.1016/j.tree.2006.03.018)

Saether, B.-E. & Bakker, O. 2000 Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653. (doi:10.2307/177366)

Sgrò, C. M. & Hoffmann, A. A. 2004 Genetic correlations, tradeoffs and environmental variation. *Heredity* **93**, 241–248. (doi:10.1038/sj.hdy.6800532)

Sinervo, B., Svensson, E. & Comendant, T. 2000 Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**, 985–988. (doi:10.1038/35023149)

Slobodkin, L. B. 1961 *Growth and regulation of animal populations*. New York, NY: Holt, Rinehart and Winston.

Stearns, S. C. 1983 The genetic basis of differences in life-history traits among six populations of mosquitofish (*Gambusia affinis*) that shared ancestors in 1905. *Evolution* **37**, 618–627. (doi:10.2307/2408274)

Thompson, J. M. 1998 Rapid evolution as an ecological process. *Trends Ecol. Evol.* **13**, 329–332. (doi:10.1016/S0169-5347(98)01378-0)

Thompson, J. N. 2005 *The geographic mosaic of coevolution*. Chicago, IL: University of Chicago Press.

Tuljapurkar, S., Gaillard, J.-M. & Coulson, T. 2009 From stochastic environments to life histories and back. *Phil. Trans. R. Soc. B* **364**, 1499–1509. (doi:10.1098/rstb.2009.0021)

Tutt, J. W. 1896 *British moths*. London, UK: George Routledge.

Wilson, A. J., Pilkington, J. G., Pemberton, J., Coltman, D. W., Overall, A. D. J., Byrne, K. A. & Kruuk, L. 2005 Selection on mothers and offspring: whose phenotype is it and does it matter? *Evolution* **59**, 451–463. (doi:10.1554/04-480)

Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F. & Hairston Jr, N. G. 2003 Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* **424**, 303–306. (doi:10.1038/nature01767)

Zheng, C., Ovaskainen, O. & Hanski, I. 2009 Modelling single nucleotide effects in *phosphoglucose isomerase* on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Phil. Trans. R. Soc. B* **364**, 1519–1532. (doi:10.1098/rstb.2009.0005)