IDEA AND PERPSECTIVE

The ecogenetic link between demography and evolution: can we bridge the gap between theory and data?

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Abstract

Calls to understand the links between ecology and evolution have been common for decades. Population dynamics, i.e. the demographic changes in populations, arise from life history decisions of individuals and thus are a product of selection, and selection, on the contrary, can be modified by such dynamical properties of the population as density and stability. It follows that generating predictions and testing them correctly requires considering this ecogenetic feedback loop whenever traits have demographic consequences, mediated via density dependence (or frequency dependence). This is not an easy challenge, and arguably theory has advanced at a greater pace than empirical research. However, theory would benefit from more interaction between related fields, as is evident in the many near-synonymous names that the ecogenetic loop has attracted. We also list encouraging examples where empiricists have shown feasible ways of addressing the question, ranging from advanced data analysis to experiments and comparative analyses of phylogenetic data.

Keywords

Comparative analysis, density-dependent selection, eco-evolutionary feedback, ecogenetics, experimental evolution, frequency-dependent selection, life-history theory.

INTRODUCTION

The study of demography famously provided key insights necessary for the origin of evolutionary theory (Malthus 1798; Wallace 1858; Darwin 1859). Populations have the potential to grow exponentially, but this is confronted with the limited nature of resources, and natural selection subsequently favours those individuals who compete best for the scarce resources. Thus, from early on, ecology (the science that explains abundances and distributions of organisms, i.e. their demographic features) and evolution have been intertwined. Calls for 'integrative' understanding of biological processes keep being repeated in the literature, from Dobzhansky's (1973) famous quote 'Nothing in biology makes sense except in the light of evolution' to current, more focused statements that evolution itself only makes sense when viewed in its ecological context (Coulson *et al.* 2006; Saccheri & Hanski 2006; Johnson & Stinchcombe 2007; Metcalf & Pavard 2007; Pelletier *et al.* 2007).

The intertwined relationship between ecological and evolutionary processes is so profound and ubiquitous that a thorough review would probably necessitate a book-length treatment. Here our aim is much more modest: we ask whether empiricists and theoreticians often enough appreciate the exciting prospects that arise from studying the feedback between evolution and ecology (the latter is typically expressed as population dynamics, but see Whitham *et al.* (2006) for recent broader approaches at the level of ecosystem functioning). The feedback arises because as population densities and their effects on the environment vary, so do the selection pressures acting upon the traits involved in reproduction and survival; and as these traits evolve, they determine new densities. Despite this quintessential link, most empirical studies view adaptations as mere reactions to the environment, ignoring that the interaction is two-way (i.e. environments change with evolving adaptations). We will highlight good examples where the two-way challenge has been successfully confronted. We will also ask whether the literature as a whole would benefit from more integrative work – in other words, do ecologists often enough talk to evolutionary biologists, or empiricists to theoreticians and vice versa?

Theoretical ecologists, arguably, have spent more time examining the interaction between population dynamics and evolution than empiricists have. The field of life-history evolution provides one of the earliest examples. Soon after the modern synthesis, the mathematical concepts of population biology were put in an evolutionary context, providing a framework for the study of life histories (Cole 1954). From simple conceptual models of *r*–*K* selection (MacArthur 1962, 1972; Pianka 1970) to more complex demographic models of age structure (e.g. Law 1979; Charlesworth 1980), life histories have been assumed to shape and be shaped by the kind of population regulation the species experiences (Reznick *et al.* 2002; Roff 2002; Metcalf & Pavard 2007).

A major field where population dynamics and evolution have been linked theoretically is the study of frequency dependent games. Evolutionary game theory (Maynard Smith 1982; Dugatkin & Reeve 2000) is perhaps the theoretical framework that has contributed most to the view that natural selection acts on individuals' relative rather than absolute fitness and the consequent realization that evolution does not necessarily maximize population growth. This has drawn new attention to the demographic consequences of evolution (Parker 1985) as well as the influence of density dependent population regulation on evolution (Mylius & Diekmann 1995). However, this literature is of a somewhat 'scattered' nature. This is perhaps best seen in the diverse list of names that the two-way interaction has attracted: 'eco-evolutionary feedback loop' (Le Galliard *et al.* 2005a), 'ecogenetic feedback' (van Baalen & Sabelis 1995), 'ecogenetic model' (Eshel & Sansone 1995), 'adaptive dynamics' (Dieckmann 1997; Waxman & Gavrilets 2005; this is not completely synonymous with the rest of the list as this refers to a particular mathematical framework, but we include it here because of its emphasis on deriving the population consequences of evolutionary processes), and finally 'self-consistent modelling' (e.g. Webb *et al.* 1999; Houston *et al.* 2005), which is used to mean that parameters that influence evolutionary processes should be appropriately derived by examining the population consequences of the current behaviour of individuals, otherwise a model can be considered inconsistent (high mating success for a male who deserts his mate, when the current evolutionary state of a population dictates that all females care for offspring, is an example of an inconsistent assumption; see Houston & McNamara 2005). Of all these terms, 'ecogenetic feedback' is perhaps the rarest, but as it succinctly captures the ecological and evolutionary aspects of the problem – including the increasingly feasible gene-level analysis of the interaction (Saccheri & Hanski 2006) – we shall adopt it here.

Theoretical ecogenetic studies appear to have accumulated over time at a fairly steady pace (e.g. Pimentel 1968; Charlesworth 1971; Roughgarden 1971; Matsuda & Abrams 1994; van Baalen & Sabelis 1995; Eshel & Sansone 1995; Geritz *et al.* 1998; Houston & McNamara 2002; Dercole *et al.* 2006; Dieckmann & Metz 2006; Kokko *et al.* 2006; DeAngelis *et al.* 2007; Rankin 2007). However, do we have a case at hand where theoretical knowledge is advancing at a much faster pace than empirical documentation? If so, adjustments on both sides are needed because too strong separation of the theoretical and empirical literature can not only hamper the progress in a field but can also lead to misunderstandings (Butlin & Tregenza 2005). In the particular context of behavioural ecology, Owens (2006) expresses some optimism, by noting that there is a growing appreciation of studies that emphasize the 'ecology' in the phrase 'behavioural ecology'. This is performed either by explaining the ecological basis of differences in behaviour among species, or using long-term databases to understand the demographic consequences of behavioural variation. Here we hope to fuel this growing trend further, with a small but inspiring selection of studies that show the power of ecogenetic considerations. Our focus is on studies that document interactions of life history or behavioural traits with population dynamics, trophic interactions included. For complementary and more specifically genetic perspectives see Saccheri & Hanski (2006) and Whitham *et al.* (2006).

WHAT IS THE ECOGENETIC FEEDBACK?

What does 'ecogenetics' or its various synonyms mean? The concept is simple. Precise definitions of fitness vary (Brommer 2000; Benton & Grant 2000), but a consistent definition is always ultimately based on counting offspring that transmit genes to future generations (Metz *et al.* 1992; Metcalf & Pavard 2007). Therefore, it is obvious that population dynamics (an ecological concept) depends on the fitness of population members (an evolutionary context). Now, the fitness of an individual often depends on the density of conspecifics or, alternatively, heterospecific competitors, prey, or natural enemies. If density influences everyone's reproductive prospects to the same extent, one has merely restated the ecological concept of density dependence. But if density variation has a differential effect on individual fitness depending on their phenotype, we have a feedback loop. In this loop, individual behaviour or life history, influenced by genes, has an effect on population dynamics (e.g. equilibrium density or stability properties), and the resulting change in the population dynamics in turn has the power to differentially favour the various genotypes present in the population or, alternatively, to favour certain kinds of phenotypically plastic responses to the environment.

The loop has particularly attracted the attention of game theoreticians because game theory focuses on stable equilibria in which the loop is 'closed'. In a closed loop,

the evolved behaviour is the best response to the dynamics that it generates. Note that the first applications in game theory in the study of animal behaviour did not close the loop in this sense: behaviours were best responses to other individuals' behaviours without considering how population-level parameters such as individual densities, re-mating frequencies or the like might change as behaviours change. In recent years, theoreticians have increasingly paid attention to completing the loop properly (e.g. Houston & McNamara 2005; Dieckmann & Metz 2006). The loop is made particularly explicit in the study of adaptive dynamics, a mathematical framework that is based on deriving the environment created by the current ('resident') population, which in turn determines whether novel mutants can spread (Dieckmann 1997; Waxman & Gavrilets 2005). This makes it explicit that there is a temporal sequence in which environments follow each other as populations adapt. A steady-state is reached when the loop closes such that evolution no longer changes the environment, and the environment in turn no longer selects for genotypes that deviate from the present distribution.

In most models, the relevant 'environment' is equivalent to population density, or a direct consequence of it (e.g. resource availability). Density-dependent success of morphs or genotypes also offers links to the related concept of frequency-dependent selection, which is a widespread force in nature (reviewed in Sinervo & Calsbeek 2006). Density-dependent and frequency-dependent selection are not identical concepts. For example, sex ratios are typically under strong frequency-dependent selection towards the 1 : 1 ratio (Fisher 1930), but this is not influenced by the densities of conspecifics (though the spatial scale of interactions may matter; Hamilton 1967; Hardy 2002). Density-dependent selection can be considered a form of frequency-dependence but it is more complex as the full environmental loop must be considered. In other words, one has to first predict the consequences for population density that a specific mix of genotypes produces, and then turn back to develop predictions regarding the success of each one in the current environment. 'Mere' frequency-dependence can often be captured using simpler arguments, as when a predator with a search image ignores rare prey (Merilaita 2006).

The term 'density-dependent selection' itself may be too narrow to incorporate all aspects of the ecogenetic loop, as the environment includes aspects of population density but also other dynamical features such as stability over time (McNamara 2001). This means that the state of the population and that of the environment should not to be interpreted as instantaneous measurements but as any characteristic of their current behaviour over a timescale at which the properties are invariant. Consider, for example, a cyclic population with some stochastic noise. Such a

population appears to undergo dramatic changes when viewed for less than one cycle (i.e. instantaneous measurements are not identical), but longer timescales reveal that the dynamic properties do not change (i.e. invariance): cycles simply follow each other, and if the environment creating the noise does not change, there will be no overall temporal trend in the stochastic pattern either. Now, we know that evolution of reproductive effort can change population dynamics from a stable equilibrium to cycles (Sinervo *et al.* 2000; Kokko & Ruxton 2002). If reproductive effort varies with the phase of the cycle, and this behaviour allows cycles to continue, the loop has been closed. There is no requirement that the short-term dynamic cycle itself should have stopped; in this case the timescale of invariance is the cycle length. The genetic composition of a population may also experience short-term cycles (Sinervo *et al.* 2000; Wójcik *et al.* 2006), or alternatively, the population may consist of individuals who all obey the same strategy of reacting plastically to current environmental conditions.

EMPIRICAL RELEVANCE: FEEDBACKS IN BOTTLES

Theoreticians studying ecogenetics have not stopped at generally marvelling the beauty of the ecogenetic loop, but have addressed quite specific questions such as explaining of high toxin diversity in bacteria (Pagie & Hogeweg 1999), considering whether speciation could occur as an adaptive outcome of competitive dynamics (Doebeli & Dieckmann 2000), and laying out the conditions under which selection can lead to evolutionary suicide (Parvinen 2005). No doubt, such exercises appear interesting and intellectually challenging to a theoretician, but is there evidence that such ideas can be tested? The first flagship idea of density-dependent selection was the r–K selection dichotomy (Pianka 1970), which despite its intuitive appeal has proved enormously difficulty to test. However, this is generally attributed to the fact that the early, verbally expressed predictions were not logically sound (Mueller 1997; Reznick *et al.* 2002; Jeschke *et al.* in press), so any failure of the r–K ideas should not be taken to mean that ecogenetic feedbacks, in general, are too broad and ill-defined to warrant study.

Simplistic r–K predictions aside, life-history theory certainly predicts that trade-offs between fast population growth and competitive ability may lead to different genotypes being favoured in different population growth stages. Modern technology allows tracking evolutionary processes better than ever, leading to the possibility of documenting evolutionary successions in fast-replicating organisms that can be raised in simple bottles. Bull *et al.* (2006) provide good evidence that bacteriophage viruses raised in chemostats with a continuous influx of resources (i.e. bacteria) experience an ecogenetic feedback. They first provide predictions that viral evolution should proceed in

very different ways depending on if the virus regulates its bacterial host or not. The latter scenario is achieved experimentally when there is a constant influx of new hosts that does not diminish with the number of hosts killed, and it leads to the prediction of much more efficient predators (viruses) that find bacteria quickly and produce large numbers of offspring after only a short latent time.

In such an experiment, viral densities at first remained low, reaching an equilibrium of poorly adapted viruses that could flourish because the environment was 'easy': a virus infecting a cell usually entered a local resource with no other viruses present. Viral traits correlated with faster multiplication were then selectively favoured, eventually leading to higher population densities (infections per cell). But as densities increased, the genotypes responsible for the increase were no longer selected for: they now increasingly lived in environments in which the crucial life-history trait is competitive ability, i.e. the ability to exclude other individuals from the resource. In the case of bacteriophages, competitive ability can relate to so-called DIPs ('defective interfering particles') that exploit other viral genomes to aid them in reproduction, or to a phenomenon called superinfection exclusion, which prevents new invaders from infecting cells that are already infected. This led to an altered selective environment, where the initial fast reproducers were outcompeted.

Bull *et al.* (2006) note the resemblance of their models and experiments to the idea of an *r*-selected organism being replaced by *K*-type competitors: observed outcomes were consistent with the idea that adaptation at low density leads to high density and high density then favours competitive ability. Nevertheless, they note that the parallels are verbal only: the current state of the art is to model individual life history traits explicitly, and we now know that a 'carrying capacity' *K* should not be considered such a trait as it is rather an emergent property of a population (Rueffler *et al.* 2006). Modern, properly individual-based life-history models thus do not support the *r*–*K* dichotomy in its simplistic form. Instead, they can provide tailor-made predictions on how evolution and ecology will carry on feeding each other.

Another good example of viral evolution offering insights on ecogenetic feedbacks is found in predator–prey metapopulation systems described by Kerr *et al.* (2006). Again, the study organisms were bacteriophages (predators) and a bacterium host (prey), now coexisting in a metapopulation where phages tend to drive their host extinct, but empty patches (wells) can be recolonized by hosts before phages take over. If all phages were identical in their use of resources, bacterial densities should be higher when dispersal is low because phages can then only access bacteria at boundary zones between phage and bacterial clumps. Manipulating the amount and spatial scale of migration between patches, Kerr *et al.* (2006) found that

bacterial densities did in fact not differ between treatments. Phages evolved to be more prudent in their exploitation of the resource if migration was restricted, which then allowed their resource to flourish. Selfish 'rapacious' strains were outcompeted in restricted migration treatments because they rendered subpopulations prone to extinction. In other words, local populations with too 'greedy' genotypes fell victim to a 'tragedy of the commons' that can make populations collapse (Hardin 1968). Considering this population dynamic consequence was essential for explaining otherwise puzzling evolutionary results of restraint in resource use (see also van Baalen & Sabelis 1995; Pels *et al.* 2002).

Similarly, a recent study on the evolution of cooperation in biofilm-producing mibrobes has shown that population dynamics, which was made dependent on the frequency of disturbances (externally imposed mass-mortality events), has a strong impact on the evolution of cooperation: intermediate disturbances generate the most cooperation because it creates moderately long-lived spatial structure in the populations. This allows related individuals to interact sufficiently long for cooperative benefits to emerge, while also letting them escape the eventual detrimental effects of competing for ever-diminishing local resources (Brockhurst *et al.* 2007).

In the studies of Kerr *et al.* (2006) and Brockhurst *et al.* (2007), disturbances (dispersal and mortality, respectively) were superimposed experimentally onto the system. In nature, dispersal traits coevolve with population densities and species distributions, and thus offer another important link between ecology and evolution. Dispersal affects local densities and is a major determinant of metapopulation dynamics, and the tendency of individuals to disperse is known to often respond to population density (Bowler & Benton 2005). Individuals with mobile genotypes also often end up in distant parts of the population including expanding range margins (Hanski *et al.* 2004; Phillips *et al.* 2006). Some have already argued that an eco-evolutionary approach to dispersal will be needed to understand the spread of invasive species. Novel environments encountered can select for rapid adaptation, which in turn influences the spatial spread of a species (Lambrinos 2004; Facon *et al.* 2006; Kokko & López-Sepulcre 2006).

EMPIRICAL RELEVANCE OUTSIDE BOTTLES?

Not all interesting organisms are viruses and bacteria, yet many (if not most) experimental studies attempting to link population dynamics and evolution use model laboratory systems with short generation times (Mueller 1997). Moreover, most studies still link the two fields of ecology and evolution in only one direction: either the influence of population dynamics on evolution or vice versa, but not

both simultaneously. When theoreticians emphasize that ignoring ecogenetic feedbacks would be detrimental for understanding traits as diverse as cannibalism (Dercole & Rinaldi 2002; Getto *et al.* 2005), altruism (Le Galliard *et al.* 2003), territoriality (López-Sepulcre & Kokko 2005), anti-predatory behaviour (Werner & Peacor 2003), dispersal (Gyllenberg *et al.* 2002), animal contests (Kokko *et al.* 2006), parental care (Houston & McNamara 2002; Houston *et al.* 2005) and mating systems (Houston & McNamara 2005; Kokko & Rankin 2006), it is certainly time to evaluate realistically what can be performed.

Life-history traits, being the determinants of the reproductive schedule of individuals, are obviously so closely linked to demography that they form the first candidate group of adaptations to study ecogenetic feedbacks (e.g. Mueller 1997; Reznick *et al.* 2002; Prasad *et al.* 2003; Stahl & Oli 2006). Perhaps the best pieces of ecological understanding come from systems in which researchers have, painstakingly, documented the relationship between population density and individual variation in survival and reproduction (e.g. Pelletier *et al.* 2007), including identifying the relevant resource and its spatial and temporal variation (Benton *et al.* 2006). For example, the study of the Soay sheep population in Scotland was already more than a decade ago at a stage where ecogenetic modelling, combined with field data, was able to explore the assumptions of how much information Soay ewes use when deciding on their reproductive effort: they appear to make optimal reproductive decisions given that they have no information about the population cycle (Marrow *et al.* 1996). Similar modelling for cyclic owl populations, by contrast, indicates that individuals make use of information that peak vole densities are predictably followed by a crash in prey density, such that they invest more in offspring produced during improving prey availability times rather than peak times (Hakkarainen & Korpimäki 1994; Brommer *et al.* 2000).

Similarly to predator–prey systems, plant–herbivore interactions offer intriguing possibilities to examine how life history traits respond to selective pressures mediated via population dynamics. Mast seeding (synchronous heavy flowering in populations of perennial plants) is challenging to explain, not least because it is hard to refute the null hypothesis that each plant individually responds to some environmental cue (Rees *et al.* 2002). Alternatively, plants may base their flowering 'decisions' on their own resource-levels in any given year. Using a combination of resource-based modelling and long-term data on individual plants, Rees *et al.* (2002) were able to show that simple environmental cueing models fail while resource-based models are able reconstruct the observed dynamics of snow tussocks *Chionochloa pallens* extremely well. Intriguingly, chaotic flowering dynamics that combines with environmental triggers can be selectively favoured, as the resulting synchrony with overwhelmingly large seed production allows plants to overcome density-dependent seed loss to predators. This result requires that seeds can survive a long time in the seed bank (Rees *et al.* 2002). If they do not, the necessity to take advantage of each year's germination opportunities favours stable dynamics even though it makes life far easier for seed predators.

Behavioural traits are one step further removed from population dynamics compared with classic life history traits, yet any behaviour that has fitness consequences should ultimately impact the demography of a population and can thus coevolve with its dynamical consequences. One clear example is aggressive behaviour. In this context, ecogenetic feedback has recently been shown to provide a solution to an old problem: why animals respect ownership. In other words, why is aggression not only limited (this has been conceptually explained since the frequency-dependence of early hawk–dove games; Maynard Smith 1982), but fight outcomes are also biased such that owners need to do less to defend their resources than the level of aggression intruders need to show to take it over (the so-called *prior residence effect*). The ecogenetic feedback makes the payoffs of the game evolve in concert with the changes in space use when intruders increase their aggression, in a way that stabilizes intermediate levels of aggression in intruders but not in owners (Kokko *et al.* 2006). Ecogenetic modelling thus offers solutions of improved realism: owners always defend, intruders sometimes take over. While this particular idea of density-dependent aggression has not been explicitly tested yet, in nature, the costs and benefits of aggressiveness are clearly density dependent (as evidenced by many studies of territorial behaviour; Adams 2001). Thus, the feedback loop is relevant if aggression levels also impact population growth and/or structure. The density dependence of aggressiveness has indeed been shown to determine territorial spacing and influence cyclic population dynamics in red grouse, *Lagopus lagopus* (Mougeot *et al.* 2003a,b).

WHAT TO DO: EXPERIMENTAL AND COMPARATIVE APPROACHES

The double-sided nature of the feedback adds an extra layer of complexity to their experimental testing. For ecogenetic experiments to be complete, both directions of causality – from population dynamics to adaptations and vice-versa – need to be explored. Specifying one definitive method as the holy grail of ecogenetic studies, that all should stride towards, is as meaningless here as anywhere in ecology or evolutionary science. Above, we have already mentioned several examples of how advanced modelling and data collection can be fruitfully intertwined; here we discuss further suggestions.

As the above example of dispersal manipulations show, explicit manipulations of demographic traits can be useful. For example, following the course of evolution under different extrinsic mortality regimes has been a popular exercise when studying 'experimental evolution'. Some such studies aim to keep densities constant (e.g. Stearns *et al.* 2000) while others make it explicit that the effect of manipulations depends on the densities created (e.g. Morgan & Buckling 2004). In an ideal world, one would try to answer both questions: the very point made by the ecogenetic loop is that the effect of a specific factor (say, higher extrinsic mortality) may be very different in isolation as opposed to a real-world setting where the factor is allowed to have its influence on population density and other dynamic properties. If we create different sets of experiments that help us understand both levels, we have made major progress from investigating the output of a 'black box' to illuminating how the different causal routes inside the 'box' join to form a whole.

Completing the loop requires detecting how populations differ in terms of the demography they produce, and how this depends on the individual-level trait composition of the population. This is a challenge when explaining how the feedback might have operated to produce a trait that is currently at equilibrium and perhaps displays little genetic variation. For example, different types of density dependence produce contrasting dynamics in the same plant-herbivore interaction (ragwort and cinnabar moth) in two different countries (Bonsall *et al.* 2003). The differences in dynamics can be related to differences in the degree of seed limitation, but whether the local plants or their herbivores also show consequent local adaptation remains a topic for further study. In a range of systems, however, it is already known that geography, frequency-dependence and even artificial selection of laboratory populations have created genetic variation. Trinidadian guppies, *Poecilia reticulata*, living in different streams evolve different life-history traits (Reznick & Bryga 1996); frequency dependence maintains morphologically and behaviourally distinct morphs of side-blotched lizards, *Uta stansburiana* (Sinervo & Calsbeek 2006); and there exist artificially selected strains of *Drosophila* fruit flies varying in their degree of polygamy (Holland & Rice 1999). In such systems genotypes can be mixed in different proportions and the population response measured. Natural experiments can also be exploited: e.g. in RNA viruses it is argued that population persistence is determined by the composition of mutant RNA genomes that result from random errors in replication (Domingo 2006).

The 'perfect' experiment that gives full insight into the whole loop will be probably out of reach for some time still, when the much less grand task of detecting density-dependence in its purely ecological context can already be quite a challenge (Fowler *et al.* 2006). Also, real populations do not follow precise deterministic trajectories, which makes it harder to decide on, and follow, the appropriate timescales over which the population's invariant properties should be measured. Often, current evolutionary and ecological change is better simply described as 'ongoing' without much hope for reaching a steady-state any time soon. Despite the difficulties, experiments already exist that consider evolutionary aspects on population dynamics and vice-versa (Mueller 1997; Yoshida *et al.* 2003). Some have wisely combined simple and necessarily incomplete experiments with simulations to extrapolate and complement the experimental results (e.g. Le Galliard *et al.* 2005b; Bull *et al.* 2006).

A major drawback of experimental work is indeed that it is often slow and difficult to establish causal links, and afterwards any generality of the claims made is still not certain. Ecogenetic feedback is a difficult enough concept that we will certainly need studies that adopt many different positions when tackling the trade-off between the depth and breadth of scientific endeavours. A good example of adopting the 'middle position' is a study that omits experimentation, but challenges the explanatory power of advanced, tailor-made life-history modelling by statistical analysis of field data on not one but two plant species (Rees *et al.* 2006). This study on seed dormancy and delayed flowering shows excellent fit between field data and theory, suggesting that temporal demographic fluctuations can have substantial effects on flowering strategies. Still, in a true phylogenetic context, a two-species comparison would be nothing but a good start of one data point, and the next step are multi-species comparisons such as Andersson *et al.* (2007). This 15-species fish study showed that cannibalism, population stability and resource polymorphism tend to co-occur across species, in line with theoretical predictions that cannibalism decreases temporal variation in population dynamics and equalizes the profitability of the zooplankton and macroinvertebrate resources.

At their widest, comparative tests can merge into tests of multi-level selection and macroevolutionary processes, because vulnerability to extinction is a population dynamic property that can evolve. For example, asexual reproduction has arisen many times independently across many taxa, but current examples are dotted around the tips of the evolutionary tree, suggesting heightened vulnerability to extinction of asexual lineages (Neiman *et al.* 2005; Johnson 2006). Similarly, studies have tried to relate the intensity of sexual selection (or proxies thereof) to heightened extinction risk (Sorci *et al.* 1998; McLain *et al.* 1999; Morrow & Pitcher 2003; but see Morrow & Fricke 2004), an outcome predicted by some eco-evolutionary models (Tanaka 1996; Kokko & Brooks 2003). Such studies may provide an interesting counterargument to our general claim that theory has

outstripped empirical data collection in the ecogenetic context.

Both experimental and comparative approaches, therefore, could be of much use when viewing traits and population demographic characteristics as coevolving entities. Extinction is certainly not the only demographic consequence of interest. If, for example, low density predisposes species to evolve hermaphroditism (Puurtinen & Kaitala 2002), then with a good enough phylogenetic analysis one should be able to find out if transitions to low density occur prior to transitions to a hermaphroditic lifestyle. Another demographic feature of populations is the adult sex ratio, which can have strong effects on the kinds of mating systems that are selected for (Kokko & Rankin 2006; Kvarnemo *et al.* 2007; Rogers *et al.* 2007). A recent phylogenetic analysis, on the contrary, has showed that the balance of male vs. female mortalities responds readily to changes in sexual competition (Liker & Székely 2005), thus future studies should ask how these two arrows – from competition to sex ratio, and vice versa – lock together to form the mating system.

Comparative studies, of course, pose their own difficulties. Unless one finds very clear and fine-scaled evidence that transitions occur in a particular order, it will be difficult to establish how ecological and evolutionary changes follow each other in time. Often one would expect any demographic change to follow from an evolutionary change essentially immediately, while the corresponding evolutionary change may be slower, thus capturing any data relating to the former event will be challenging indeed (though see Thompson 1998 and Hairston *et al.* 2005). This problem, of course, is not unique to comparative studies, but it occurs whenever previous states of a population are unavailable for direct measurement. For example, if the competitive phages of the study of Bull *et al.* (2006) had completely displaced the fast reproducers, and no data had been gathered in the meanwhile, it would have been difficult to construct the sequence of events that led to the current competitive strains (an argument similar to the one of 'ghost of competition past'; Connell 1980). This highlights the importance of gathering longitudinal data in sufficient detail when performing experiments that address ecogenetic dynamics.

The core challenge when approaching ecogenetics empirically is to distinguish whether the studied traits are adaptively responding to current population dynamics or if the response to density is merely ecological. For example, delayed reproduction at high densities can easily be attributed to unavailability of breeding sites in Spanish imperial eagles *Aquila adalberti* (Ferrer *et al.* 2004), while the same trait has been shown to have a genetic component in guppies *Poecilia reticulata* (Reznick 1982). The estimation of heritabilities can thus be a useful tool to complement comparative studies and reveal evolutionary responses. More recently, genomics has brought us the ability to identify candidate genes related to the studied trait. To come back to our example on dispersal, in butterflies *Melitaea cinxia*, differences between more and less dispersive individuals can be associated to the occurrence of certain alleles of the *pgi* gene (Haag *et al.* 2005), and these alleles are, in turn, also associated with demographic trends (Hanski & Saccheri 2006).

Certain attempts to think simultaneously about evolutionary processes and ecological contexts have been criticized for being so broad that the concept makes itself meaningless by including 'everything' (Brodie 2005). Nevertheless, we hope that our short list of examples in which researchers have succeeded in shedding light on ecogenetic feedbacks will encourage further research in an area that is bound to be important precisely because it is so ubiquitous. That said, the ecogenetic feedback loop is not a tautology: density dependence often targets certain parts of the life cycle much more strongly than others, thus some traits can be expected to be closely linked to the density-dependent process while others will not have substantial impact on the loop. Discovering the most important players in ecogenetic feedback will thus also require exploring if (and why) particular traits are insensitive to density regulation (Mylius & Diekmann 1995).

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