Eco-evolutionary dynamics of communities and ecosystems

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Summary

1. We review theoretical and empirical studies to identify instances where evolutionary processes significantly affect the dynamics of populations, communities and ecosystems.

2. Early theoretical work on eco-evolutionary dynamics was concerned with the effect of (co)evolution on the stability of two-species predator–prey systems and the occurrence of character displacement in simple competitive systems. Today's theoretical ecologists are extending this work to study the eco-evolutionary dynamics of multispecies communities and the functioning and evolutionary emergence of ecosystems.

3. In terms of methodology, eco-evolutionary modelling has diversified from simple, locus-based population genetic models to encompass models of clonal selection, quantitative trait dynamics and adaptive dynamics.

4. The few empirical studies on community dynamics that explicitly considered evolutionary processes support the view that evolutionary and ecological dynamics often occur on similar time-scales, and that they co-determine the dynamical behaviour of ecological communities.

Key-words: adaptive dynamics, character displacement, coevolution, ecosystem evolution, evolutionary dynamics

Introduction

Evolution is the change of genotype frequencies within populations or species, whereas community dynamics represent the change of abundances of different species. Both types of change arise by the interaction of individuals with one another and with the environment. Population genetics and population/community dynamics have traditionally made predictions without considering the other discipline. Ecologists and evolutionary biologists, however, increasingly feel that the separation of their disciplines is artificial and an impediment to understanding and predicting the change within and among populations in experiments or in the wild. This relatively old insight (Levins 1968; Pimentel 1968; Antonovics 1976; Roughgarden 1979) has recently gained momentum from several lines of research. The development of simple, phenotypic models of evolution has led to the theoretical analysis of coevolution in relatively complex ecological scenarios (Abrams, Matsuda & Harada 1993; Dieckmann & Law 1996; Geritz *et al.* 1998). The realization that evolutionary change is often relatively rapid has also provided an

impetus for the integration of population biology and evolution. The study of coevolution has been broadened under the banner of 'community genetics' (Agrawal 2003; Neuhauser *et al.* 2003), a plea for an approach that integrates across genetics, evolutionary biology, population and community ecology.

In this review we identify instances where rapid evolutionary processes interact with population dynamics in ways that alter important properties of the dynamics of populations, communities and ecosystems. By 'rapid evolution' we mean evolution occurring on time-scales tractable in laboratory studies of population dynamics – up to about 1000 generations, but typically many fewer. More generally, an eco-evolutionary approach is required when there is the potential for evolutionary change to alter ecological effects/processes over whatever time-span is of interest. Thus the approach we advocate is probably important even in some cases where evolution is not particularly rapid, provided the time-scale of ecological interest is sufficiently long. We start by reviewing the evidence from theoretical studies, then give some examples of successful demonstrations of eco-evolutionary community dynamics in the field and laboratory, and end with some suggestions on how future research on the topic might best proceed. The key question determining the appropriateness of the

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eco-evolutionary approach is: 'What reciprocal effect do ecological and evolutionary dynamics have on each other over ecologically relevant time-scales? Evolutionary and ecological dynamics are likely to be co-dependent when changes in genotype frequency result in a change in the phenotypic traits that crucially affect interaction strength among populations. Any evolutionary question regarding interaction-related traits requires a detailed understanding of community ecology in order to predict the selection pressures the trait will be under over longer periods of time. For such traits, it is always necessary to use a coupled eco-evolutionary approach to understanding long-term change in either traits or populations. However, there are cases where evolutionary change is slow enough that it can be ignored for making ecological predictions on some time-scales of interest.

Questions about the adaptive change in behavioural or developmental traits within a community can often be modelled using a framework quite similar to that used in some of the simplified models of evolution. These 'behavioural' models and similar models of coevolutionary dynamics (Abrams *et al.* 1993; Dieckmann & Law 1996; Abrams & Matsuda 1997; Abrams 2000; Loeuille & Loreau 2004; Abrams 2006) assume that the rate of change of the mean trait value is proportional to the fitness gain per unit change in the trait of an individual or rare type in the population (referred to here as 'fitness-gradient dynamics'). For a more complete understanding of the combined ecological and evolutionary process, the realm of applicability of these simplified approaches needs to be explored using models that incorporate more details of the genotypic dynamics. The direct transfer of locus-based population genetic models into ecological community models would be desirable, as only these models do not simplify the principles of Mendelian inheritance. However, this approach may be misleading or intractable because phenotypic traits are usually controlled by multiple (and largely unknown) genes. Some of the simplified evolutionary approaches are reviewed in Appendix 1, and our overview of theoretical studies includes applications of all these approaches.

Communities and evolution: dynamical models

In this section we give an overview of theoretical models that aim explicitly to link evolutionary and community dynamics. We order this section according to the degree of complexity of the community, from two-species communities to multispecies communities and ecosystems.

EVOLUTION AND COEVOLUTION IN TWO-SPECIES SYSTEMS

Predator–prey and host–parasite models

Observations of the rapid development of pathogen or pest resistance to control measures in the wild first

inspired the formulation of ecological models that incorporate the genetic structure of populations, and hence allow for evolutionary dynamics. Pimentel's (1961) mathematical description of a 'genetic feed-back mechanism' in a dynamical plant–herbivore system is probably the earliest formal attempt to explain population regulation through the rapidly changing genetic composition of one of the populations. In his single-locus model (Appendix 1), Pimentel showed that selective pressures exerted by the herbivore can influence the genetic make-up of the plant population, which in turn feeds back to herbivore densities. Prey evolution causes stable or oscillatory predator dynamics in this model, whereas the ecological version of the model without evolution predicts unstable outbreak dynamics of the predator. Pimentel's (1961) work was an important early contribution that directly transfers ecological and evolutionary dynamics observed in the field into a formal modelling framework.

The inclusion of coevolutionary dynamics – the reciprocal evolutionary change of trait values in two interacting populations – was an exciting continuation of these early studies. Levin & Udovic (1977) proposed a general framework of coevolutionary dynamics in two-species systems, still based on single-locus population genetics. Schaffer & Rosenzweig (1978) formulated an approach based on the evolution of ecologically relevant parameters that could be incorporated directly into the ecological Rosenzweig–MacArthur model. This study – along with Slatkin's (1980) and Pease's (1984) work on coevolution of competitors – marked the beginning of a type of analysis of eco-evolutionary systems that underlies many theoretical approaches: an analysis that is based on a system of time-dependent, coupled ordinary differential equations that describe the change of ecological populations and evolutionary relevant parameters separately but in relation to one another and on a comparable time-scale.

A major motivation for introducing evolutionary processes into simple two-species ecological models was to explore whether evolution (especially adaptation of the prey) had a stabilizing effect on predator–prey systems characterized by unstable, oscillatory dynamics. Many theoretical studies have identified scenarios under which natural selection can stabilize predator–prey dynamics (e.g. van Baalen & Sabelis 1993; Hochberg & Holt 1995; Schreiber & Vejdani 2006). Other studies, however, have demonstrated the opposite; for example, Abrams & Matsuda (1997) demonstrated that adaptive change of prey vulnerability may lead to unstable predator–prey cycles if the predator functional response is saturating. This example is particularly interesting because the general result was later corroborated in an empirical study in which the rapid evolution of planktonic algal prey led to long-period, out-of-phase predator–prey cycles (Yoshida *et al.* 2003). It appears that there are likely to be few universally applicable generalizations regarding how adaptive evolution alters predator–prey dynamics.

Evolutionary dynamics of competitive systems

Competition is the interaction having the longest history of theoretical and empirical work combining ecology and evolution. Much of this work has been directed specifically at character displacement, which was originally defined as the mutual divergence of species in response to interspecific competition (Brown & Wilson 1956). Later definitions extended this to essentially all change in competition-related characters in response to interspecific competition (Grant 1972; Abrams 1986). Much of the theoretical work on the subject followed from Slatkin's (1980) seminal article, which presented a quantitative genetic model of character displacement using assumptions (no constraints on character evolution; individuals with the same character value use limiting resources in the same way) from previous work by MacArthur (1972) and Roughgarden (1979). Taper & Case (1985, 1992) elaborated this model; Doebeli (1996) extended it by investigating explicit multilocus genetics; and Case & Taper (2000) and Day (2000) extended it to consider spatial gradients. The same ecological model has served as the basis for recent models of sympatric speciation (Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000). These models have confirmed that character displacement can occur under a wide range of conditions, but suggest that it may not occur when the stabilizing selection due to a strongly unimodal distribution of resource abundances along some ecological axis overwhelms any advantage from divergence.

There are still questions about how well the simplified genetic assumptions used in these models reflect the processes that occur in real organisms, which has prompted more complex models (Bürger & Gimelfarb 2004; Bürger & Schneider 2006). However, the main weakness of current work is probably its reliance on the very narrow set of ecological assumptions that were incorporated into Slatkin's (1980) original quantitative genetics model. The model is based on a Lotka–Volterra model of competition in which competition coefficients are calculated using a formula that dates back to MacArthur (1972). There are a number of problems with both the competition coefficient formula and other aspects of the model (Abrams 1975, 1980, 1983, 1998). All are related to the fact that the model does not explicitly represent the dynamics of the resource(s) for which competition is occurring. In other words, many of the eco-evolutionary approaches to the question of character displacement have devoted too little thought to the 'eco' side of the coupled processes. The interaction of evolution and ecology is particularly important when ecological conditions fluctuate in time. Such fluctuations are important in the evolution of resource consumption abilities in competing consumers (Egas, Sabelis & Dieckmann 2005). Recent work has shown that both evolutionary rates and the presence and speed of behavioural shifts related to resource use affect the coexistence and diversification of resource-use traits in consumers (Abrams 2006).

The rate of evolution has received relatively less empirical or theoretical attention in the case of competition than it has for predation or parasitism. However, the rate of evolution is potentially important for understanding evolution of competitors in variable environments, another topic that has received relatively little theoretical attention. Hairston *et al.*'s (2005) reanalysis of Grant & Grant's (2002) work on the response of Galapagos finches to fluctuating rainfall argued that evolutionary change exceeded ecological change by a factor of 2·2. If examples like this are characteristic of competitive systems, it is likely that we will eventually see greater use of models with explicit resource dynamics, and more attention to the rate of the evolutionary process. Indeed, further work on the same finch population found that the arrival of a competitor had dramatic effects on the trajectory of evolution in the resident species (Grant & Grant 2006).

MULTISPECIES INTERACTIONS AND EVOLUTION IN ECOSYSTEMS

Three-or-more-species communities

To achieve a realistic integration of ecological and evolutionary dynamics for most natural communities, we need to know how the results from two-species communities are changed by the presence of additional species. Two important effects of additional species are: (1) the effect of the population dynamics of other species on the evolutionary trajectory of a focal pair; and (2) the mutual evolution of interaction-related traits in three or more species. There has been relatively limited work on each of these topics. This lack is probably due to the limited analytical tractability of these relationships, to the multitude of different roles that additional species can play in ecological dynamics, and in part to the difficulty of maintaining and monitoring multispecies systems in the laboratory.

Vermeij (1987) stressed the potential role of other species in altering the outcome of predator–prey evolution. Specifically, he suggested that the presence of either alternative prey or higher-level predators could inhibit the 'escalation' of predator and prey capture and defence traits that might occur in an isolated specialist predator–prey system. These ideas were analysed using simple models of phenotypic evolution in predator and prey (Abrams 1991). Surprisingly, the presence of either of these alternative species frequently suggested a closer coupling between the evolutionary responses of the original predator–prey pair. This early work has not been pursued for models of interaction-related traits of other species pairs. Nevertheless, a number of similar questions have been raised regarding the impact of additional species on the evolutionary change of interactions in a particular pair. The experimental work of Rundle, Vamosi & Schluter

(2003) showed that the presence of a predator appears to increase the selection pressure for divergence of two ecotypes of the three-spined stickleback (*Gasterosteus aculeatus*), a result that as yet does not have a clearly supported theoretical explanation.

It is somewhat unrealistic to assume that one or a few species in a community are evolutionarily fixed. The coupled evolution and population dynamics of three species in general requires a dynamic model with a minimum of six equations. This usually suggests a number of parameters large enough for a totally comprehensive understanding of all the possible dynamics to be out of the question. Nevertheless, there have been some attempts to understand systems with three coevolving interacting species. Abrams & Matsuda (1993) considered adaptive change in both predator choice and prey defence in a two-prey–one-predator system, and focused primarily on rapid adaptive change, such as that produced by behaviour. Their most interesting conclusion was that an increase in the population size of a particular prey often led to its being eaten at a lower rate than previously because the predator may exhibit 'negative switching' between prey. Yamauchi & Yamamura (2005) have recently examined a related model in which the predator exhibits behavioural diet choice and the prey undergo evolutionary change in their defensive traits. Evolution often promoted persistence of all three species in this model, but within the range of biologically reasonable evolutionary rates, the rate of change of the two prey species' defences could have a major impact on population dynamics, with relatively rapid evolution suppressing population fluctuations.

Another question regarding eco-evolutionary dynamics in two-prey–one-predator systems concerns the evolutionary change in the defence of one prey following addition of a second prey. The indirect ecological interaction between prey – the change in predator density that follows addition of the second prey – is what causes evolutionary change in the first prey. Theory for this case (Abrams 2000) suggests that, when the two prey species do not otherwise interact, the most common response of one prey to the addition of the second is a parallel shift, usually to greater defence, in both species. When the two prey also compete for resources, and each has a trait that increases both their resource use and predator vulnerability, then such traits are likely to diverge when the second prey is added to a food chain that originally only includes one (Abrams & Chen 2002).

The broadest approach to the question of three-species evolutionary dynamics is the set of models explored by Nuismer & Doebeli (2004). They examined a number of different interactions among the three species, and compared the predictions from two different types of evolutionary model: quantitative genetic models with fixed genetic variances in each species; and individual-based simulations with explicit multilocus trait determination. Because of the increased genetic realism, Nuismer & Doebeli (2004) left population dynamics out of their analyses. However, they were able to investigate all possible combinations of competitive, mutualistic and antagonistic interactions between three species, when a 'central' species had two traits that, respectively, determined its interaction with the two 'peripheral' species. They found that genetic correlations between the two traits in the central species played a major role in determining the stability of the evolutionary equilibrium. Nuismer & Doebeli (2004) were also able to show that the changes in genetic variances and covariances caused by strong selection often led to outcomes in which one species was cyclically or permanently maladapted in the individual-based simulations. This did not occur in the simpler fixed-variance models. These models illustrate an important feedback between ecological interactions and evolutionary rates, as rates are proportional to genetic variances. It would be interesting to extend these models to include population dynamics, and to use different functions rather than the simple phenotypic matching to describe the relationships between trait values and interaction coefficients.

Once more than three species are allowed, the number of possible food web configurations becomes very large and, if all species were to evolve, the minimum number of dynamic equations would increase to eight. Analyses of four or more species have generally examined questions about the food-web structure that emerges, rather than focusing on population sizes or trait values, and are reviewed in the next section. A limited number of studies have examined some simple models of evolution in multispecies competitive communities (Jansen & Mulder 1999; Bonsall, Jansen & Hassell 2004; Scheffer & van Nes 2006).

Ecosystems

Only recently has evolution been studied rigorously within the context of entire ecosystems. Early ideas on this issue date back to Lotka (1922, 1925), who argued that natural selection should operate so as to maximize the energy flux through ecosystems. A number of variants of this hypothesis have been proposed since then (e.g. Odum & Pinkerton 1955; Odum 1983). Although basic physical laws do tend to drive ecosystems towards a better exploitation and dissipation of available energy, these ideas implicitly invoked group selection operating at the level of ecosystems, and ignored the complexity of the ecological interactions that govern the dynamics and evolution of organisms within ecosystems. Merging ecosystems and evolution is a formidable but fascinating task for contemporary ecology, given the historical lack of communication between ecosystem ecology and evolutionary biology.

Progress in that direction has been achieved recently from two different angles. First, a few studies have investigated the mutual constraints that the functioning of ecosystems and the evolution of species place on

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each other. Second, recent work has explored the evolutionary emergence of entire food webs or ecosystems and their functional consequences.

MUTUAL CONSTRAINTS BETWEEN ECOSYSTEM FUNCTIONING AND EVOLUTION OF SPECIES

The environment of a population of organisms determines the direction and strength of the natural selection exerted on these organisms. But organisms have multiple interactions with their physical and biological environment, which can indirectly change the selective pressures they experience (Odling-Smee, Laland & Feldman 2003). A multitude of indirect interactions (indirect organism–environment feedbacks) are known to occur among organisms because of the complexity of ecosystems (Puccia & Levins 1985; Wootton 1994). In particular, material cycling is a key ecosystem process that drives a circular causal chain in ecosystems, thus transmitting predictable indirect ecological effects and evolutionary constraints to their component species (Lotka 1925; Loreau 2002).

Through the cycling of limiting nutrients such as nitrogen or phosphorus, autotrophs and heterotrophs are involved in an indirect mutualistic interaction that is fundamental to all ecosystems. Loreau (1998) showed how the ecological and evolutionary dynamics of the indirect interaction between plants and decomposers are able to explain broad-scale successional and evolutionary trends in functional properties of ecosystems, in particular those towards increased productivity and biomass, a decreased productivity/biomass ratio, and tighter nutrient cycles. However, he also pointed to the potential conflict between individual-level and group-level selection, which prevents ecosystems from obeying a simple universal maximization principle.

A more controversial case of mutual dependency between autotrophs and heterotrophs generated by material cycling is provided by plant–herbivore interactions. These interactions traditionally have been regarded as antagonistic because herbivores have a negative direct effect on plants through biomass consumption. This view, however, has been challenged by the 'grazing optimization hypothesis', which states that primary production, or even plant fitness, is maximized at an intermediate rate of herbivory (Owen & Wiegert 1976; McNaughton 1979; Hilbert *et al.* 1981). The evolutionary consequences of grazing optimization, and of ecological indirect interactions in general, however, are complex, for two main reasons. First, increased plant productivity does not necessarily translate into increased plant fitness. Second, when it does, it is not absolute fitness, but the fitness difference between types that counts. If two plant types (species or genotypes) are mixed, one of them being tolerant ('mutualistic') and the other resistant ('antagonistic') to herbivory, the resistant type is expected to outcompete the tolerant type because it benefits from the positive indirect effect of increased nutrient cycling but does not suffer the negative direct effect of herbivore consumption. As a result, tolerance should not evolve even though it is indirectly beneficial. This paradox can be viewed as a particular case of the classical dilemma of the evolution of mutualism, in which individual-level selection counteracts the evolution of beneficial traits.

However, at least two factors counteract the evolutionary advantage of non-co-operative traits such as antiherbivore defence in plants. The first one is spatial heterogeneity of the system. Localized interactions allow the benefits that result from these interactions to accrue more frequently to those individuals that participate in them. Specifically, if herbivores recycle nutrients in the vicinity of the grazed plants, or plants from the same type are aggregated, herbivores tend to recycle proportionally more nutrient on the plants that are grazed more heavily, thus augmenting the indirect benefit of grazing for the grazed plants (de Mazancourt & Loreau 2000).

The second factor that counteracts the advantage of antiherbivore defence is its cost in terms of nutrient investment, which generates a trade-off in plants between defence and nutrient uptake. A theoretical study of plant adaptive dynamics in a spatially structured model ecosystem shows that, for most ecologically plausible trade-offs, plant evolution leads to a single 'continuously stable strategy' – a strategy to which evolution converges, and which cannot be invaded by any other close strategy (de Mazancourt, Loreau & Dieckmann 2001). This study revealed the complexity of the concept of mutualism, and stressed the need to distinguish two different definitions of mutualism (de Mazancourt *et al.* 2001; de Mazancourt, Loreau & Dieckmann 2005). A first, ecological definition of mutualism is based on the short-term response of plants to herbivore removal, whereas a second, evolutionary definition rests on the long-term response of plants to herbivore removal, allowing plants to adapt to the absence of herbivores.

Loeuille, Loreau & Ferrière (2002) considered the potential consequences of plant–herbivore coevolution when both plant and herbivore traits are subject to adaptive dynamics (Appendix 1). Although their ecological model is very simple and always reaches a stable equilibrium in the absence of evolution, the coevolutionary dynamics are sufficient to generate complex dynamical behaviours such as asymmetrical evolutionary cycles bounded by physiological constraints. Coevolution between plants and herbivores also strongly affects the potential responses of the abundances of the various trophic levels to nutrient enrichment in a food chain (Loeuille & Loreau 2004). Adaptive changes in the middle trophic level of a three-level system, coupled with direct density dependence, similarly lead to a wide variety of responses to increased mortality at any one level (Abrams & Vos 2003).

Collectively, these studies show that evolution can have a profound influence on ecosystem functioning,

but also that ecosystem processes can have a profound influence on evolution. Species traits are constrained by ecosystem processes, just as ecosystem properties are constrained by the ecological and evolutionary history of interacting species. Indirect effects mediated by ecosystem processes can be so strong as to prevail over direct effects and exert effective selective pressures on the species involved, provided there is sufficient spatial heterogeneity in the system or trade-offs between traits associated with the direct and indirect effects.

EVOLUTIONARY EMERGENCE OF ECOSYSTEMS

Evolution is usually considered to operate within the context of an existing ecosystem with static properties. How do such complex ecological systems emerge through evolution, and how does this evolutionary history constrain current ecosystems? The generation of species diversity in competitive communities is a classical question, but the generation of entire food webs and ecosystems is an issue that has begun to be explored only during the past few years.

Pioneering studies on the evolution of food webs were performed by McKane and colleagues (Caldarelli, Higgs & McKane 1998; Drossel, Higgs & McKane 2001; McKane 2004; Quince, Higgs & McKane 2005), who built complex simulation models in which species are created by speciation events starting with a single ancestor, and go extinct as a result of interactions with other species. These evolutionary models typically lead to the generation of complex food webs that are reasonably similar to real food webs. Loeuille & Loreau (2005) developed a simpler approach to the evolutionary emergence of food webs, in which body size is the single biological trait subject to evolution. As body size and its effects on the metabolism and interactions of organisms are well known, their model allowed them to make testable predictions on how evolution shapes food-web properties. Remarkably, variations of only two parameters defined at the individual level (width of consumption niche and intensity of interference competition) were sufficient to generate a wide range of food-web structures that were very similar to those observed in the best documented natural food webs. Loeuille & Loreau (2006) further used the results of their model to examine the theoretical robustness of the predictions of allometric metabolic theory on the relationships between population density and body size, and between energy use and body size (Damuth 1981; Brown *et al.* 2004). They showed that these predictions do not hold in food webs generated by coevolution because of the strong interactions that constrain coexisting species, which are ignored by allometric metabolic theory.

Although theoretical studies on the evolution of food webs and ecosystems are still in their infancy, they offer fascinating perspectives to understand the structure and functioning of current ecological systems.

Community dynamics and evolution: empirical studies

Many studies have documented rapid evolutionary change that affects the interspecific interactions and genotypic structure within natural communities (see reviews by Thompson 1998; Whitham *et al.* 2006). The beaver (*Castor canadensis*), for example, selectively fells cottonwood trees (*Populus* spp.) that are low in condensed tannins (Bailey *et al.* 2004). In a 5-year experiment, the beavers' preferential interaction altered the species and genotypic composition of cottonwood assemblages substantially, with potentially important implications for nutrient-cycling dynamics and other forest ecosystem processes (Whitham *et al.* 2006). Such changes of the genetic composition of populations assembled in natural communities are likely to affect the ecological dynamics of the system, but empirical studies that specifically address and attempt to quantify the eco-evolutionary dynamics remain rare (see also Saccheri & Hanski 2006).

We review here the handful of examples that, we believe, come close to providing empirical support for eco-evolutionary community dynamics (Table 1). Our criteria for consideration are as follows. Does the study document the change of abundance of multiple populations over several generations? Is there a record of genetic frequencies and of their change over time in the evolving population(s)? Is the mechanistic link between ecological and evolutionary dynamics plausible? Is there a 'control', in the sense that dynamics in the absence of evolution are reported? Note, however, that no study fulfils all criteria (Table 1). Not surprisingly, almost all examples are concerned with relatively fast-reproducing organisms, so that data from many consecutive generations can be collected over a time frame ranging from weeks to years. Moreover, most studies consider two-species communities to avoid the intractable complexities of real-world communities (see Saccheri & Hanski 2006; Kinnison & Hairston 2007 for examples of single-species eco-evolutionary dynamics).

The best documented example of eco-evolutionary dynamics in the field is the case of the myxoma virus (causing the disease myxomatosis) that was introduced into Australia and parts of Europe to control the European rabbit *Oryctolagus cuniculus* (Fenner 1983; May & Anderson 1983; Dwyer, Levin & Buttel 1990). Over the decades following the introduction, both the myxoma virus and its host underwent evolutionary change. The strain initially introduced into Australia in 1950 proved to be extraordinarily virulent, killing over 99% of the infected rabbits and effectively decreasing their population density. Two years later, however, field isolates of the virus contained multiple myxoma strains varying in their degree of virulence, and a myxoma type of intermediate virulence was the dominant strain. This pattern, dominance of strains of intermediate virulence but persistence of less or more

Table 1. Empirical support for eco-evolutionary community dynamics

System	Species	References	Record of genetic frequencies	Control treatment without evolution	Evolutionary change linked to ecology	Change in ecological dynamics	Dynamics explained by mathematical model
Field: pathogen–host	Myxoma virus–rabbit	Fenner (1983)	For pathogen	No	Selection for intermediate virulence; prob. resistance of host	Initial control, followed by resurgence of host	Partly by: Dwyer, Levin & Buttel (1990)
Experimental: parasitoid–host	Wasp–housefly	Pimentel, Nagel & Madden (1963), Pimentel (1968)	No	Yes	Virulence reduction; Resistance of host	Stabilization	Genetic feedback mechanism in Levin (1972)
Experimental: parasitoid–host	Wasp–bean weevil	Tuda (1998), Tuda & Iwasa (1998)	No	Yes	Mode of competition among larval hosts	Stabilization	In Tuda & Iwasa (1998)
Experimental: bacterium–bacteriophage	*E. coli*–T-series phage	Bohannan & Lenski (2000)	Yes	No	Resistance of bacterium; host-range mutation of phage	Invasion of mutants	In Bohannan & Lenski (2000)
Experimental: predator–prey	Rotifer–green alga	Yoshida *et al.* (2003)	Yes†	Yes	Cyclical clonal selection due to prey growth/digestibility trade-off	Period and phase shift of oscillations	In Yoshida *et al.* (2003)
Experimental: predator–prey	Rotifer–green alga	Fussmann *et al.* (2003)	No	No	Clonal selection of asexual *vs* sexual predators	Destabilization, extinction	In Fussmann *et al.* (2003)
Field: resource competitors	Darwin's finches	Grant & Grant (2006)	No (but phenotypes)	No	Character divergence in beak size	Competitive exclusion (almost)	No, but Hairston *et al.* (2005) present a model for a related data set
Experimental: parasite–host	Yeast pathogen–water flea	Duffy & Sivars-Becker (2007)	*	No	Clonal selection of resistant hosts	From endemic dynamics to termination of epidemics	In Duffy & Sivars-Becker (2007)

*Dynamics only in mathematical model. All other studies followed the dynamics over multiple generations of all populations involved.
†Meyer *et al.* (2006).

virulent strains, continued over the decades following the introduction, and can be explained and mathematically modelled as a trade-off between the virulence of the virus and its transmissibility (May & Anderson 1983). Transmission efficiency is maximized at intermediate virulence because, on average, the host population survives sufficiently long to transmit the disease, but hosts are killed before large parts of the population recover. Adaptive phenotypic changes in the host population accompanied the evolutionary changes of the pathogen soon after its introduction. Rabbits developed resistance against the virus so that cases of mortality due to a strain of intermediate virulence dropped from about 90 to 30% over the first 8 years. This change was probably due to the selection of resistant rabbit genotypes (mediated by disease-induced mortality), although non-genetic factors may also have played a role (Dwyer *et al*. 1990). In summary, the myxoma–rabbit system can be viewed as a coevolutionary two-species community with clear impact on the dynamics of the host population. However, there is insufficient information on the genetics of the rabbits to decide whether the dynamics are a coevolutionary arms race in progress, or whether a coevolutionary steady state has been reached (Dwyer *et al*. 1990).

In a recently published field study, Grant & Grant (2006) showed that the arrival of a competitor species on the Galapogos island Daphne Major resulted in the evolution of character displacement in the medium ground finch (*Geospiza fortis*). Twenty-two years after the large ground finch (*Geospiza magnirostris*) first bred on the island, a drastic selective shift occurred in the beak size of *G. fortis*. At the same time, numbers of *G. fortis* declined to their lowest level in 33 years. There is good evidence that the sudden divergence in beak size and the decline of the *G. fortis* population are causally linked through severe depletion of the food supply by the two competing species.

Forty years ago, Pimentel and colleagues (Pimentel, Nagel & Madden 1963; Pimentel 1968) published the first experimental evidence of evolutionary change directly influencing community dynamics. In a series of experiments with houseflies (*Musca domestica*) and parasitoid wasps (*Nasonia vitripennis*), they demonstrated that – similarly to the myxoma–rabbit system – evolution towards increased resistance in the host and towards reduced virulence in the parasitoid decisively influenced the community dynamics. In the evolving communities, parasitoid densities tended to be low (due to evolution of resistance in the host) and the dynamics were relatively stable. Pimentel and colleagues also established experimental control treatments in which evolution toward resistance was suppressed because hosts that survived parasitoid exposure were removed and replaced by individuals from unselected stocks. Dynamics in the controls differed greatly from those in the evolving treatments, and were characterized by unstable parasitoid–host fluctuations and high average parasitoid densities. Although the techniques for genetic characterization

of the evolving strains did not exist at the time, Pimentel *et al*. demonstrated with these pioneering experiments that evolution can lead to a dynamical stabilization of a two-species community.

More recently, results from four different experimental laboratory systems have provided additional and compelling evidence for eco-evolutionary community dynamics. These systems are: a host–parasitoid system of bean weevils (*Callosobruchus* spp.) and wasps (*Heterospilus prosopidis*); a microbial predator–prey system of bacteria (*Escherichia coli*) and bacteriophage (T-series); a planktonic predator–prey system of unicellular algae (*Chlorella vulgaris*) and rotifers (*Brachionus calyciflorus*); and a host–parasite system of water fleas (*Daphnia dentifera*) and a virulent yeast pathogen (*Metschnikowia bicuspidata*).

In the experimental bean weevil–wasp system, Tuda & Iwasa (1998) observed large host–parasitoid cycles that suddenly stabilized after about 20 host generations. At the same time, parasitoid densities decreased. Tuda (1998) compared the phenotypes of weevils from host-only trials and early stages of host–parasitoid trials with those at the end of the host–parasitoid trials. She was able to causally link these changes in community dynamics to the evolutionary change in the type of competition among larval hosts from scramble toward contest competition.

Community structure and dynamics in the bacteria–phage system (Bohannan & Lenski 2000) were critically affected by the evolution and potential invasion of phage-resistant bacteria. One of the appealing features of this microbial system is that phenotypic changes of the resistance of bacteria can be linked directly to mutations at specific genetic resistance loci. A trade-off between resistance and competitive ability of the evolved bacteria determines whether these mutants can invade, and how large their influence on the community dynamics will be.

A similar trade-off between digestibility and population growth rate of the prey exists in the alga–rotifer system (Yoshida, Hairston & Ellner 2004). Several genotypes of algal prey could coexist, and rapid evolution among them – in the form of predator-driven clonal selection – had a direct impact on community dynamics (Yoshida *et al*. 2003; Fussmann *et al*. 2005). Interestingly, (Chitty 1960) hypothesized along similar lines that density-dependent changes in the selective advantage of certain genotypes might cause the Canadian lynx–snowshoe hare cycles, but there is no conclusive evidence for this hypothesis. Rapid evolution of the predators occurred in the rotifer–alga system when rotifer clones that reproduce asexually were selected over sexually reproducing clones. Using an approach that combined experimental trials and a quantitative trait-based model, Fussmann *et al*. (2003) showed how this evolutionary process directly affected the community dynamics (Fig. 1). In a recent continuation of this body of research on the alga–rotifer system, Meyer *et al*. (2006) used an allele-specific quantitative PCR
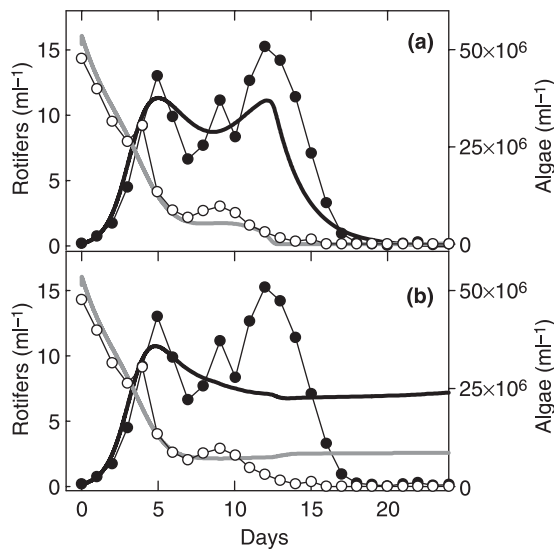
Fig. 1. Predator–prey (rotifer–alga) dynamics in a laboratory culture are influenced by evolution. (a) A mathematical model that accounts for rotifer evolution (quantitative trait = propensity to reproduce sexually) predicts the predator–prey dynamics well. (b) The same model without evolution fails to describe the dynamics and predicts algae and rotifers to coexist in a stable equilibrium. Dark and open symbols: rotifer and algal abundance in experiment; smooth black and grey lines: rotifer and algal abundance predicted by models. Data from Fussmann *et al.* (2003).

technique explicitly to track the changes in algal genotype frequencies that accompany the predator–prey dynamics. We hope this study will encourage ecologists to make increasing use of modern molecular techniques in order to reveal changes in genotype frequencies as part of eco-evolutionary dynamics.

The most recent evidence for eco-evolutionary community dynamics comes from a *Daphnia*–yeast pathogen system. Duffy & Sivars-Becker (2007) collected *Daphnia* clones from six lakes in Michigan, and established in laboratory experiments that clones from lakes with a history of recent epidemics of the pathogen *Metschnikowia* were less susceptible to infection and also showed less variation in susceptibility. This suggested directional selection for higher resistance in the host. Duffy & Sivars-Becker (2007) then used their experimental data to parameterize an epidemiological quantitative trait model. The model, allowing for the evolution of susceptibility on the time-scale of community dynamics, predicted termination of the epidemics within 20–80 days. This result matches the dynamics repeatedly observed in the field, while a model version without evolution predicted that the parasite would become endemic.

Communities and evolution: some suggestions for future research

As this review has shown, eco-evolutionary community and ecosystem dynamics is a topic that has received a lot of theoretical attention, but only very few empirical

studies exist to date. Therefore intensifying empirical research efforts should be a priority. The field and laboratory studies that exist have demonstrated that the interplay of rapid evolution and ecology can affect community dynamics, but we need to explore how pervasive this conclusion is, and to define the role that evolution plays in more complex and natural communities and in ecosystems.

Future experimental studies should use larger, more natural assemblages than just two-species communities. They should also use natural communities and ecosystems with species that coexist in the field and therefore have a coevolutionary history; failure to do so might result in evolutionary rates that are unnaturally elevated because species are likely to be far from any coevolutionary equilibria. Empirical studies also ought to take advantage of molecular genetic techniques so that evolutionary change at the genotype level can be resolved with the same accuracy that is standard for changes in population densities. Finally, we believe that agreement between eco-evolutionary mathematical models and the dynamical behaviour of live systems provides the strongest evidence for the co-dependence of evolutionary and community dynamics. We therefore encourage researchers to combine more frequently experimental exploration of eco-evolutionary dynamics with mathematical modelling approaches.

This being said, we still see major challenges for theoretical ecologists. We are a long way from understanding how evolutionary and ecological processes generate observed patterns in food webs and ecosystems, and how they determine community dynamics. Recent research highlights the role of evolution and community genetics in ecological networks (Bascompte, Jordano & Olesen 2006; Vellend 2006), but we are only beginning to explore these questions in an adequate dynamical modelling framework. Similarly, theoretical community ecologists have just started to explore the potential role of evolutionary processes in the framework of modern community concepts and theories, such as the meta-community concept (Urban & Skelly 2006) and the theory of neutral communities (Hubbell 2006). Another important challenge consists in finding and refining techniques to partition the relative contributions of ecology and evolution to community dynamics. Hairston *et al.* (2005) and Coulson *et al.* (2006) laid out promising formal approaches and gave examples of how these approaches could be applied to empirical time series.

In conclusion, we firmly believe in a comprehensive approach to community ecology that melds evolutionary and ecological dynamics. However, this approach should not be applied *a priori*, because it comes at the cost of adding complexity to conceptual and mathematical models. The two methodologies must be compatible, and the insights must be different from what can be learned by applying either approach alone. In light of the reviewed literature, we are confident that future research will identify many more instances justifying an eco-evolutionary interpretation of community dynamics.

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Appendix 1

MODELLING EVOLUTIONARY CHANGE IN DYNAMIC MODELS OF ECOLOGICAL COMMUNITIES

Locus-based genetic models (e.g. Pimentel 1961)

This type of model directly incorporates basic population genetics into population dynamics. Population growth is discrete (per generation), and growth rate equals the mean population fitness, $\bar{w}$:

$$N_{t+1} = \bar{w}N_t \qquad \text{(eqn 1)}$$

For a diallelic locus at Hardy–Weinberg equilibrium, $\bar{w}$ is the sum of the genotypic fitnesses weighted by their respective frequencies:

$$\bar{w} = p^2 w_{11} + 2p(1-p)w_{12} + (1-p)^2 w_{22} \qquad \text{(eqn 2)}$$

with p being the frequency of one of the two alleles in the population.

Evolutionary change (the change of allelic frequencies) under frequency-independent selection can be described by Wright's (1937) equation for an adaptive landscape:

$$\Delta p = [p(1-p)/2][d \ln(\bar{w})/dp] \qquad \text{(eqn 3)}$$

where the second fraction in equation 3 denotes the change of mean fitness with a change in allele frequency, while the first fraction is a measure of the genetic variance.

In the special case of asexually reproducing organisms, genetically identical lines perpetuate themselves over time as clones, and evolutionary dynamics – defined as changes in genetic frequencies – occur as frequency changes among clones. Clonal models are equivalent to models of competing species (and often equivalent to haploid genetic models). Hence clones are separate state variables within populations in multiclonal community models, and evolutionary dynamics result from the ecological dynamics of multiple clones with different fitness values (e.g. Yoshida *et al*. 2003).

Quantitative trait models (e.g. Fussmann *et al*. 2003)

Selection on multiple loci quickly becomes intractable. As an alternative, quantitative trait (QT) models describe the evolutionary change of a phenotypic trait, z, under selection and affecting the population dynamics as $\dot{N} = f(N,z)$. Lande's (1976) equation for the average phenotype describes the change of z:

$$dz/dt = h^2\sigma^2[\partial \ln(\bar{w})/\partial z] \qquad \text{(eqn 4)}$$

In analogy to equation 3, evolutionary dynamics depend on the (heritable) variation $h^2\sigma^2$ (the product of heritability and phenotypic variance) and the slope of the fitness landscape $[\partial \ln(\bar{w})/\partial z]$. In dynamic community models, the QT equation can often be incorporated directly into a system of ordinary differential equations.

Adaptive dynamics (e.g. Dieckmann & Law 1996)

Adaptive dynamics (AD) is another approach for studying the phenotypic changes in evolving populations (Geritz *et al*. 1998). Adaptive dynamics models assume that evolutionary and ecological dynamics occur on different time-scales, and separate the two dynamical processes analytically. In a first analytical step, the limiting dynamics of an ecological community model are determined. Then a mutant trait is introduced, the fitness of this mutant is determined, and whether the mutant is able to invade the resident population is evaluated. Multiple iterations of this two-step procedure may lead to evolutionary change of the community.

With two or more coevolving species, adaptive dynamics assumes that mutational changes in different species occur at widely spaced intervals as a stochastic process (Dieckmann & Law 1996).

As in the QT approach, the rate of evolutionary change of phenotypic traits under AD is approximately proportional to the slope of the individual's fitness gradient. Adaptive dynamics models have been used to describe the eco-evolutionary dynamics of communities (Dieckmann & Law 1996; Loeuille *et al.* 2002). How-ever, the assumptions of equilibrium dynamics, the slower speed of evolutionary relative to ecological dynamics, and the temporal separation of the two processes constrain the applicability of this approach for the analysis of eco-evolutionary dynamics. Nevertheless, the (approximate) fitness gradient dynamics that arise in both AD and QT approaches is often a good approximation, even when the assumptions of either or both approaches are violated (Abrams *et al.* 1993; Gomulkiewicz 1998).