REVIEW AND SYNTHESIS

Toward an integration of evolutionary biology and ecosystem science

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Abstract

At present, the disciplines of evolutionary biology and ecosystem science are weakly integrated. As a result, we have a poor understanding of how the ecological and evolutionary processes that create, maintain, and change biological diversity affect the flux of energy and materials in global biogeochemical cycles. The goal of this article was to review several research fields at the interfaces between ecosystem science, community ecology and evolutionary biology, and suggest new ways to integrate evolutionary biology and ecosystem science. In particular, we focus on how phenotypic evolution by natural selection can influence ecosystem functions by affecting processes at the environmental, population and community scale of ecosystem organization. We develop an eco-evolutionary model to illustrate linkages between evolutionary change (e.g. phenotypic evolution of producer), ecological interactions (e.g. consumer grazing) and ecosystem processes (e.g. nutrient cycling). We conclude by proposing experiments to test the ecosystem consequences of evolutionary changes.

Keywords

Biodiversity and ecosystem functioning, community genetics, eco-evolutionary dynamics, ecological stoichiometry, ecosystem science, evolutionary biology, feedbacks, natural selection.

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INTRODUCTION

The integration of ecosystem science with community ecology and evolutionary biology is one of the most important frontiers for the conceptual unification of the biological sciences (Holt 1995; Levin 1998; Elser 2006; Loeuille 2009). It is vital for a better understanding of the feedbacks between organismal diversity and global material and energy flows (Falkowski *et al.* 2008; Menge *et al.* 2008) and for predicting both community and ecosystem responses to environmental change (Chapin *et al.* 2000; de Mazancourt *et al.* 2008).

In the past few decades, the disciplines of community ecology and evolutionary biology have become increasingly integrated (Johnson & Stinchcombe 2007; Haloin & Strauss 2008; Vellend 2010). Evolutionary biologists recognize that ecological interactions among species influence natural and sexual selection pressures and underlie many evolutionary processes, such as phenotypic evolution (Ackerly 2003), diffuse co-evolution (Strauss *et al.* 2005) and speciation (Schluter 2000). Similarly, community ecologists recognize that evolutionary processes are important for understanding population dynamics (Yoshida *et al.* 2003; Pelletier *et al.* 2007), community composition and assembly (Emerson & Gillespie 2008) and metacommunity

dynamics (Urban *et al.* 2008). There is also mounting evidence that ecological and evolutionary dynamics can occur on similar timescales (Hairston *et al.* 2005; Schoener 2011) and that feedbacks between natural selection and community dynamics can alter both the adaptive evolution and coexistence of species (Odling-Smee *et al.* 2003; Loeuille 2009; Post & Palkovacs 2009).

Although integrative research is progressively blurring the disciplinary line between community ecology and evolutionary biology, evolutionary biology and ecosystem science remain disjunct (Elser 2006; Loeuille 2009; Loreau 2010a). Evolutionary biologists regard divergent environments as a key driver of adaptive evolution and species diversification (Schluter 2000), but rarely study how organisms drive the ecosystem changes that shape selective environments (Odling-Smee *et al.* 2003; Strauss *et al.* 2005; Dieckmann *et al.* 2007; Erwin 2008). Ecosystem scientists view organisms and their environment as parts of an interactive system (O'Neill *et al.* 1986; DeAngelis 1992; Sterner & Elser 2002), but rarely study how evolutionary changes affect the flux of materials and energy through ecosystems (Norberg *et al.* 2001; Menge *et al.* 2008).

The disciplinary links between ecosystem science and evolutionary biology are among the weakest in the biological sciences (Levin 1998;

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Elser 2006). For major biogeochemical processes, such as nitrogen fixation, phosphorus mineralization and carbon cycling, the reciprocal effects of biodiversity and evolutionary change are poorly understood (Falkowski *et al.* 2008; Menge *et al.* 2008). Similarly, very little is known about how evolution by natural selection can affect fundamental ecosystem functions, such as primary productivity (Cadotte *et al.* 2008), food chain efficiency (Dickman *et al.* 2008) and decomposition (Gessner *et al.* 2010; Boudsocq *et al.* 2011). Although global environmental change elicits a broad range of evolutionary responses (de Mazancourt *et al.* 2008), some of which may directly impact material cycling in natural ecosystems (Collins & Bell 2004), evolution by natural selection is not yet incorporated into climate change models as a source of potential uncertainty (Murphy *et al.* 2004). Environmental scientists (e.g. biochemists, physicists) rarely consider how commonly studied ecological processes, such as trophic cascades (Terborgh & Estes 2010), or evolutionary processes, such as phenotypic evolution (Ackerly 2003), influence ecosystem functions.

We can achieve a greater integration between evolutionary biology and ecosystem science by broadening several of the sub-disciplines of ecology and evolution, including the study of biodiversity and ecosystem function (Loreau 2010a), community genetics (Neuhauser *et al.* 2003; Whitham *et al.* 2006), ecological stoichiometry (Sterner & Elser 2002) and eco-evolutionary dynamics (Fussmann *et al.* 2007; Schoener 2011). The latter, eco-evolutionary dynamics, addresses the reciprocal effects of evolutionary and ecological dynamics (Fussmann *et al.* 2007; Schoener 2011), and has a broad conceptual framework needed to understand interactions between evolutionary, ecological and ecosystem changes (Post & Palkovacs 2009). Recent research on eco-evolutionary dynamics has addressed the ecological consequences of changes in the phenotype distribution of populations (Yoshida *et al.* 2003; Palkovacs & Post 2009; Becks *et al.* 2010), and the ecosystem consequences of adaptation (Lennon & Martiny 2008; Gravel *et al.* 2011) and adaptive divergence between populations or species (Harmon *et al.* 2009; Bassar *et al.* 2010). Eco-evolutionary dynamics posits that both directions of effect, from ecology to evolution and from evolution to ecology, are substantial in their influence (Schoener 2011), and, in some cases, can result in feedback loops between ecological, ecosystem, and evolutionary processes (Post & Palkovacs 2009).

The goal of this article was to suggest ways to integrate evolutionary biology and ecosystem science. First, we review research on the ecosystem consequences of biodiversity (i.e. species richness and trait diversity), and then elaborate on how phenotypic evolution by natural selection can directly and indirectly affect ecosystem functions. Second, we review several models at the interfaces of evolutionary biology and ecosystem science and propose a new eco-evolutionary model, which builds on theory of ecological stoichiometry, to examine how phenotypic evolution of primary producers can affect the cycling of nutrients in a simple model ecosystem. Finally, we discuss several experimental designs and model systems that are useful for experimentally testing the effect of evolutionary changes on ecosystem functions.

The ecosystem consequences of biodiversity and phenotypic evolution

Research on biodiversity and ecosystem functioning has built strong disciplinary linkages between community ecology and ecosystem science (Hillebrand & Matthiessen 2009; Reiss *et al.* 2009; Loreau 2010a) and has significant potential to improve linkages between ecosystem science and evolutionary biology (Loreau 2010a). Evolution by natural selection has produced a phenotypically and functionally diverse global species pool, and extensive research has explored how this diversity of predators, grazers, primary producers and decomposers can affect key ecosystem processes (Reiss *et al.* 2009; Gessner *et al.* 2010; Loreau 2010a). More work is needed to disentangle how variation in the structure of biodiversity at multiple hierarchical levels (e.g. community, species, population and individual) can affect a broad range of ecosystem functions (Balvanera *et al.* 2006; Loreau 2010a). The productivity of ecosystems, for example, can be influenced by the number of species (Loreau 2010a), the phylogenetic diversity of species (Cadotte *et al.* 2008) and the evolutionary history of species (Gravel *et al.*, 2011).

A practical way of studying the ecosystem consequences of biodiversity is to use continuous measures of individual trait diversity to quantify and compare the functional diversity of species assemblages (Cianciaruso *et al.* 2009; Hillebrand & Matthiessen 2009; Reiss *et al.* 2009). Trait variation among individuals is a fundamental component of biodiversity and a target of natural selection (Bolnick *et al.* 2003), and, as a result, is a natural intersection point between evolutionary biology and ecosystem science. However, we need a better understanding of the underlying causes of phenotypic and fitness variation among individuals, and how changes in selection pressures can cause direct or indirect effects on ecosystem functions (Norberg *et al.* 2001; Menge *et al.* 2008).

It is well established that the product of evolution by natural selection (e.g. species richness and trait variability) can affect ecosystem functions (Hillebrand & Matthiessen 2009; Reiss *et al.* 2009; Loreau 2010a), but much less is known about whether the process of phenotypic evolution is an important causative agent of ecosystem change (Norberg *et al.* 2001; Schoener 2011). This can be studied empirically by identifying heritable ecosystem-effect traits and testing how their evolution can affect ecosystem functions. An *ecosystem-effect trait* is a trait that underlies an organism's direct or indirect effect on an ecosystem function (see Table 1). There are several challenging research questions regarding ecosystem-effect traits. Are they heritable? Are they a target of natural selection? Will their evolution have predictable impacts on ecosystem functions? If ecosystem-effect traits are neutral with respect to fitness, then they will vary randomly over the landscape and will not be predictable based on the spatial distribution of selection gradients. In the following sections, we discuss how the evolution of ecosystem-effect traits can directly or indirectly affect ecosystem functions by influencing processes at the environmental (abiotic and biotic conditions), population and community scale of ecosystem organization.

Phenotypic evolution affects ecosystem functions via effects on environmental conditions

Natural selection can affect ecosystem functions by acting on traits that underlie the capacity of organisms to modify their biological, chemical and physical environment (Jones *et al.* 1997; Sterner & Elser 2002). For example, ecosystem engineers are organisms that control the availability of resources through the creation, maintenance or modification of habitats (Jones *et al.* 1997). Ecosystem engineering is an important mechanism of niche construction, the process by which organisms alter their environment and the selective regimes of future generations (Laland *et al.* 1999; Odling-Smee *et al.* 2003; Erwin 2008). The evolution of traits underlying the ecosystem engineering effects of

Table 1 Some examples of ecosystem-effect traits (that are potentially heritable) that might directly or indirectly affect ecosystem functions

Trait	Type	Species	Ecosystem function	Scale	Description of mechanism	Citation
Root and leaf litter chemistry	RT	*Metrosideros polymorpha*	Nutrient cycling	E	Soil fertility drives heritable changes in leaf litter chemistry, thereby affecting nutrient cycling	Treseder & Vitousek 2001
Nitrogen excretion rate	ET	*Poecilia reticulata*	Rate of nitogen recycling	E	Guppies from sites with a species-rich high-predation community excreted more ammonium	Palkovacs *et al.* 2009
Rate of photosynthesis	PT	*Chlamydomonas*	Primary productivity	P	Experimental evolution under high carbon dioxide can affect the growth rate and phenotype of algea	Collins & Bell 2004
Number of exploitable carbon substrates	PT	Strains of marine bacteria	Productivity	C	Resource homogeneity drives resource specialization, which lowers productivity of species poor communities on heterogenous substrates	Gravel *et al.* 2011
Susceptability to herbivory	FT	*Pinus edulis*	Nutrient cycling, decomposition rate	C	Herbivores graze preferentially on susceptible trees, thereby altering litter quality	Classen *et al.* 2007
Proportion of algae in diet	FT	*Poecilia reticulata*	Accrual rate of algae on tiles	C	Guppies from sites with a species-rich high-predation community ate more algea	Palkovacs *et al.* 2009
Susceptability to virus infection	FT	*Synechococcus*	Phosphorus availability	C	The evolution of resistance to viruses by *Synechococcus* influences the rate of nutrient recycling	Lennon & Martiny 2008
Leaf tannin concentration	FT	Hybrids of *Populus* spp.	Nitrogen mineralization, decomposition rate	C	Beavers (*Castor canadensis*) preferentially fell low tannin trees	Whitham *et al.* 2006
Body size	PT	*Oncorhynchus* spp.	Nutrient flux across ecosystem boundaries	C	Size-selective predation by bears can affect the amount of salmon-derived nutrients moving from streams to terrestrial environments	Carlson *et al.* 2011
Life history, feeding behaviour	Mix	*Poecilia reticulata*	Biomass specific gross primary productivity, leaf decomposition, nitrogen flux	C, E	Guppies from sites with contrasting predator communities had indirect effects on ecosystem functions	Bassar *et al.* 2010
Foraging traits, body shape, behaviour	Mix	*Gasterosteus aculeatus*	Net primary production, rate of PAR and UV light attenuation	C, E	Competition for resources in pelagic and littoral habitats has led to adaptive divergence in traits associated with foraging efficiency and growth	Harmon *et al.* 2009

These ecosystem-effect traits can also be classified following Violle *et al.* (2007), as: Response Traits (RT), Functional Traits (FT), Performance Traits (PT) and Effect Traits (ET). In some cases, it is unknown which trait, from a mixture of traits (Mix), is responsible for the contrasting ecosystem effects of different organisms. As discussed in the text, phenotypic change can affect ecosystem functions by affecting processes at different scales of ecosystem organization, including processes at the environment level (E), population level (P) and community level (C).

organisms could have a broad range of impacts on ecosystem functions (Harmon *et al.* 2009). For example, the stoichiometric traits associated with resource demand in consumers (Sterner & Elser 2002; Klausmeier *et al.* 2004) can affect the ratio and recycling rate of the nutrients used by primary producers (Sterner & Elser 2002) and the spatial distribution of primary production (McIntyre *et al.* 2008). Similarly, primary producer traits, such as growth forms, rooting structures and mutualistic associations, influence the provizioning of habitat structure and the moderation of abiotic stress in the environment (Callaway *et al.* 2002; Bouma *et al.* 2010). Evolution in the stiffness of marsh grass stems, for example, might affect the dissipation of hydrodynamic energy from waves and the trapping of sediment, and, as a result, influence the abiotic environment of coastal salt marsh ecosystems (Bouma *et al.* 2010). Although the effects of ecosystem engineering on ecosystem functions are potentially large, both the causes of trait variation underlying these effects and the responses of these traits to natural selection are poorly understood.

Phenotypic evolution affects ecosystem functions via effects on populations

Evolution by natural selection can directly influence the demographic parameters of populations (e.g. finite rate of increase) by changing the performance traits of individuals (e.g. growth rate, survival and fecundity). Phenotypic evolution of performance traits could directly affect many ecosystem functions because demographic variation of populations is often an influential component of biomass flux in ecosystems (Loeuille 2009). For example, evolution in the photosynthetic traits of algae in response to changes in carbon dioxide concentrations could alter the rates of primary production and carbon sequestration in aquatic ecosystems (Collins & Bell 2004). Natural selection can also indirectly affect ecosystem functions by acting on performance traits that influence population or metapopulation dynamics (Hanski & Saccheri 2006; Pelletier *et al.* 2007; Ezard *et al.* 2009). Selection acting on heritable traits such as the body size of

ungulates (Pelletier *et al.* 2007), the defense traits of algae (Becks *et al.* 2010) and the flight performance of butterflies (Hanski & Saccheri 2006) are examples of how rapid phenotypic evolution can affect population dynamics (Schoener 2011).

The influence of the rates of phenotypic evolution on contemporary ecological dynamics (e.g. population dynamics, species sorting) has been an important unifying concept for community ecology and evolutionary biology (Hairston *et al.* 2005; Schoener 2011). Ecological theories of metapopulation (Hanski & Gilpin 1997) and metacommunity dynamics (Holyoak *et al.* 2005) are now incorporating the idea that local adaptation and dispersal jointly shape the assembly of contemporary communities (Barton & Whitlock 1997; Urban *et al.* 2008). This integration is also illuminating how ecological and evolutionary processes jointly affect the distribution of phenotypic variation at the landscape scale (Leibold 2010; Hanski *et al.* 2011). A challenge for future studies is to determine whether the effects of phenotypic evolution on population dynamics have broader impacts on ecosystem functions at local and regional scales.

Phenotypic evolution affects ecosystem functions via effects on communities

The evolution of traits that underlie how species interact with one another (e.g. foraging traits, defense traits) could drive changes in community dynamics that, in turn, affect ecosystem functions. Predation is a good example of a species interaction that can strongly influence the structure of food webs and the flux of organic matter in ecosystems (Schmitz 2010; Terborgh & Estes 2010). The fitness of predator individuals often varies according to the match between foraging traits (e.g. body size or gape width) and prey traits. In Fig. 1, we illustrate how a difference in the mean phenotype (e.g. foraging trait) of a predator population (Fig. 1a) might alter the population dynamics of multiple prey species (Fig. 1b), reconfigure the strength of trophic interactions between predator individuals and

their prey (Fig. 1c) and indirectly affect an ecosystem function (Fig. 1d). For example, the optimum foraging rate of the invertebrate predator *Chaoborus* depends on the match between its gape width and the size of its zooplankton prey (e.g. *Daphnia*) (Swift & Fedorenko 1975). An upward shift in the optimum gape width of *Chaoborus* (Fig. 1a), resulting from a change in the selection regime, could reduce the relative abundance of larger zooplankton species that are more vulnerable to predation. Note the change in the rank order of abundance of prey of different sizes in Fig. 1(b). The resulting network of trophic interactions between *Chaoborus* individuals (black circles) and zooplankton species (green, red and blue circles in Fig. 1c) could reduce the average size of grazers, and potentially increase the level of primary production by algae (Cyr 1998) (Fig. 1d).

Advances in the field of community genetics have revealed that ecosystem functions are strongly influenced by heritable genetic variation within individual species, particularly those species that are dominant or play an important functional role in communities (Neuhauser *et al.* 2003; Whitham *et al.* 2006; Johnson 2011). For example, Whitham *et al.* (2006) describe how genetic variation underlying the production of tannins in poplar leaves can alter the rates of leaf-litter decomposition and nitrogen mineralization (Whitham *et al.* 2006). The rate of decomposition is a fundamental ecosystem function and is determined by the interaction between the quality of organic matter (e.g. leaf-litter) and the activity of multiple decomposer species (Gessner *et al.* 2010). Beavers (*Castor canadensis*) are an important agent of natural selection in this ecosystem because they preferentially fell trees with a low tannin concentration in their leaves. In this case, selection acts on a functional trait (i.e. tannin concentration) and indirectly affects decomposition by altering the community composition of trees and the chemistry of leaf-litter reaching decomposer communities (Whitham *et al.* 2006). Community genetics has been criticized for its inability to produce a genuine of theory of ecosystem evolution, partly because it does not address
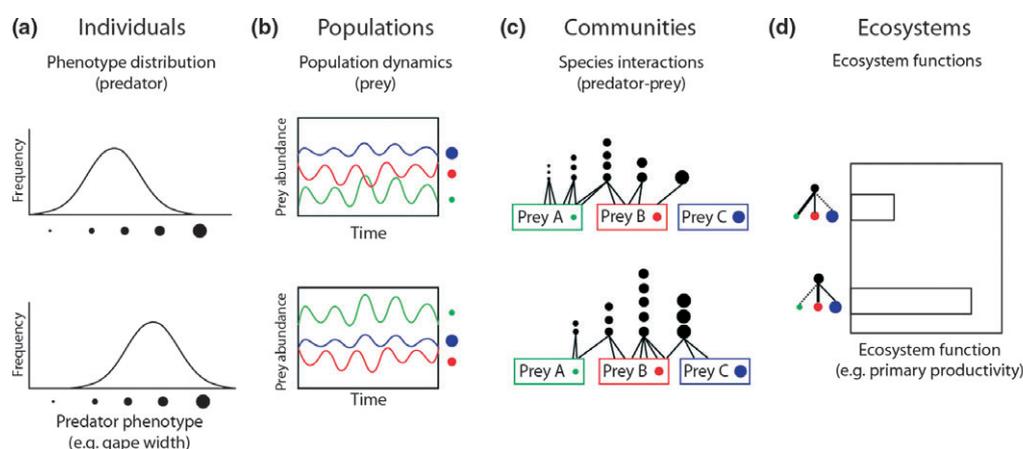

Figure 1 A hypothetical example of how phenotypic evolution of a predator can affect an ecosystem function. Panel (a) shows the phenotype distribution of a predator's gape width (e.g. *Chaoborus*) under two contrasting selection regimes that favour a different optimal gape width. The size of the black circles illustrates an individual predator's phenotype. Panel (b) shows two hypothetical scenarios for the population dynamics of three prey species that differ in their size (A: green, B: red and C: blue), and, hence, vulnerability to gape limited predators (Rank of prey size: $C > B > A$). Note that the rank order of prey population abundance changes with a shift in the gape width of predators. Panel (c) shows how a shift in the gape-size distribution of predators can affect the strength of trophic interactions between individual predators and prey of different sizes. The density of the predators stays the same, but larger prey become more vulnerable due to the increased frequency of larger predators, as indicated by the increase in the number of trophic links between individual predators and the larger prey species. Panel (d) illustrates how the contrasting food web structure, illustrated by differences in the weight of the link between the predator population and the prey, might affect an ecosystem function (e.g. primary productivity).

feedbacks between changes in community structure and phenotypic evolution (Loreau 2010b). However, research in this field has great potential for integrating evolutionary biology and ecosystem science, particularly if it focuses on how the processes that structure phenotypic and genetic variation (e.g. natural selection, drift, etc.) can influence the dynamics of ecosystem functions.

Is phenotypic evolution an important driver of ecosystem change and does it result in eco-evolutionary feedbacks?

There are many examples of how phenotypic evolution might affect ecosystem functions (Table 1), but are such effects large or small compared with other biotic and abiotic drivers of ecosystem functions? In a seminal paper, Hairston *et al.* (2005) proposed a method for partitioning variation in population growth rate into, roughly, an evolutionary component (i.e. phenotypic variation) and an ecological component (i.e. density-dependent population dynamics and changes in response to variation in the abiotic environment). This method could also be used to partition variation in an ecosystem function into a component associated with phenotypic change and a component associated with other ecological and environmental drivers of the ecosystem function. Such analyses could reveal whether evolutionary changes are important for predicting the dynamics of ecosystem functions. Phenotypic evolution is an important driver of population dynamics (Schoener 2011) and could turn out to be an under-appreciated driver of ecosystem functions (Norberg *et al.* 2001).

At present, it is unclear whether the effects of evolutionary processes on ecological dynamics and ecosystem functions have an important or trivial feedback effect on evolutionary dynamics (Post & Palkovacs 2009; Schoener 2011). For example, do the rapid evolutionary changes that occur in communities (Thompson 1998) cause changes to ecosystems that are sufficiently persistent and intense to alter the evolutionary trajectory of organisms? We agree with Schoener (2011) that a large and interdisciplinary research effort in eco-evolutionary dynamics is needed to address such questions.

INTEGRATIVE MODELING APPROACHES AT THE INTERFACES BETWEEN EVOLUTIONARY BIOLOGY AND ECOSYSTEM SCIENCE

Theory at the intersection of evolution and ecosystem functioning is rare (Loeuille 2010; Loreau 2010a). However, there is longstanding debate about how natural selection might maximize the flux of energy through ecosystems (Lotka 1922; Odum 1971; Loreau 2010a). For example, in models with a simplified ecosystem structure comprized of nutrients, producers, consumers and decomposers, grazing by herbivores can maximize the rate of primary production under a wide range of conditions, provided that plant fitness is tied to productivity rather than biomass (Cohen *et al.* 2000; Loreau 2010a). If plant populations vary in their tolerance to grazing, and there is spatial structure in the plant-herbivore community, then evolutionary change in the plants will be mediated by a balance between their spatial aggregation and patch size (de Mazancourt & Loreau 2000). In such a scenario, the optimal level of plant tolerance allowing grazing optimization to occur is difficult to attain by individual level selection alone. Thus, the emergence of enhanced plant productivity via grazing is governed by a balance between selection at the group and individual level (Loreau 2010a). Such theory implies that selection at the individual level might constrain

the maximization of certain ecosystem functions, but this idea has not been experimentally tested.

Community evolution models are beginning to integrate theory from community ecology, evolutionary biology, and ecosystem science (Fussmann *et al.* 2007; Loeuille 2009; Loreau 2010a). These models generate realistic food web topologies, include important ecological traits (e.g. body size) in their design and, in some cases, allow for the evolution of ecologically relevant parameters (Loreau 2010a). The models arising from ecological theory are based on a few simple rules governing species interactions, and are often developed to compare with empirical data about food web structure or to test plausible mechanisms of food web stability (Rossberg *et al.* 2005; Gross *et al.* 2009). Dieckmann *et al.* (2007) proposed a class of community evolution models based on adaptive dynamics, whereby community structure evolves through recurrent evolutionary branching (i.e. speciation) and the invasibility of new phenotypes is determined based on equilibrium dynamics. These models allow for frequency and density-dependent selection by explicitly including population dynamics, but have a relatively simplified framework for modeling phenotypic evolution. In addition, they assume that evolutionary dynamics occur at a much slower rate than ecological dynamics (Fussmann *et al.* 2007), making them difficult to apply to the analysis of eco-evolutionary dynamics (Cortez & Ellner 2010).

Recently, Loreau (2010b) lauded community evolution models for their integration of ecological and evolutionary thinking and for their encapsulation of the essential elements of a genuine theory of ecosystem evolution. A significant strength of these models is that they simplify biodiversity dynamics by representing species with key functional traits (e.g. body size) that are subject to evolutionary change and underlie species interactions. However, they face several challenges for understanding ecosystem dynamics. First, their insights about community and ecosystem dynamics come largely from theory, because community evolution models are extremely difficult to test with experiments and observational data from natural ecosystems. Second, these models assume a predictable relationship between the phenotypic variation of organisms and ecosystem processes, even though there is still considerable uncertainty about how the variability and evolution of traits can affect population dynamics (Pelletier *et al.* 2007; Becks *et al.* 2010) and other ecosystem processes (Bailey *et al.* 2009; Harmon *et al.* 2009; Bassar *et al.* 2010). Third, most of these models do not appreciate the capacity of organisms to alter selective regimes by transforming both the biotic and abiotic environment of ecosystems. Feedbacks between organisms and the abiotic environment are included in some analytical models (Goudard & Loreau 2008; Kylafis & Loreau 2008), but there is no consensus about how the non-trophic effects of species on their environment will impact the evolution of species interactions (Loreau 2010a). Despite the limitations of community evolution models, they are a welcome addition to the dearth of integrative theory linking evolutionary dynamics with the physical and bio-chemical diversity of ecosystems.

Integrating models of eco-evolutionary dynamics with ecological stoichiometry is a useful way to illustrate how phenotypic evolution of organisms can affect nutrient cycling (Sterner & Elser 2002). The study of nutrient cycling is an important intersection between evolutionary biology and ecosystem science (Elser 2006), because the evolution of traits governing resource acquisition and utilization can have profound impacts on global biogeochemical cycles

(Klausmeier *et al.* 2004; Falkowski *et al.* 2008). Considerable research has addressed the food web consequences of stoichiometric variation among species (Hall 2009), but much less is known about how evolution of stoichiometric traits could affect ecosystem functions (Boudsocq *et al.* 2011).

Here in, we develop an eco-evolutionary model to investigate how evolutionary change in the resource uptake rates of primary producers can affect nutrient dynamics in a simple model ecosystem. In terms of developing a predictive theory for ecosystem functioning, our model describes ecosystem dynamics as the rates at which elements are transferred among abiotic (e.g. nutrients) and biotic (e.g. species) states in the environment. We characterize evolutionary dynamics as the rate of change in an organism's stoichiometric traits (e.g. nutrient uptake), and ecological dynamics as changing resource densities.

Our model combines the basic elements of the ecological stoichiometry models of Grover (2002) with the adaptation to competition for non-substitutable resources model of Fox & Vasseur (2008). Following Grover (2002), we consider the dynamics of a pentagonal food-web consisting of two non-substitutable resources (R_1 and R_2), two producers (Y_{P1} and Y_{P2}), and a generalist consumer (C). For simplicity, the producers have contrasting and fixed resource demands (expressed as: yield coefficients, e_{Pij}) and nutrient specific uptake rates U that can evolve over time (Table 2).

The population growth rate of producers eqn 1 is determined by their loss rates from consumers (a_j), density-independent mortality (m_j),

$$\frac{dY_j}{dt} = Y_j(G_{Yj} - a_j C - m_j),$$ (1)

and a growth rate on their limiting nutrient (G_{Yj}, eqn 2).

$$G_{Yj} = min[R_1 U_j e_{P1j}, R_2(1 - U_j)e_{P2j}].$$ (2)

In eqn 2, we model a simple linear tradeoff in the uptake rates of both resources by setting, for example, the uptake rate of R_2 to $(1 - U_{P1})$. The producers have contrasting affinities for

non-substitutable nutrients defined by their nutrient-specific yield coefficients (e_{Pij} : i producers per unit j resources).

The population growth rate of consumers eqn 3

$$\frac{dC}{dt} = C(G_C - d),$$ (3)

is determined by density-independent mortality (d) and growth on the limiting resource (G_C, eqn 4). The latter is affected by both the efficiency of the consumer's resource consumption (l), the stoichiometry of the consumer's prey (e_{Pij}), and the conversion efficiency on different resources in their diet (e_{Ci}).

$$G_C = min\left[\sum_{j=1}^{2}\frac{a_j Y_{Pj}}{e_{P1j}}e_{C1}l, \sum_{j=1}^{2}\frac{a_j Y_{Pj}}{e_{P2j}}e_{C2}l\right].$$ (4)

For simplicity, resource dynamics are solved by assuming mass balance in the system eqn 5.

$$\frac{dR_i}{dt} = -\sum_{j=1}^{2}\left(\frac{dY_{Pj}}{e_{Pij}}\right) - \frac{dC}{e_{Ci}}.$$ (5)

Evolutionary change is included by allowing, for example, the uptake rate (U) of a producer species to change over time to maximize its per capita growth rate in the current environmental conditions eqn 6.

$$\frac{dU_j}{dt} = v_j \frac{\partial \frac{1}{Y_{Pj}}\frac{dY_{Pj}}{dt}}{\partial U_j}.$$ (6)

Here in, v_j is a constant and represents additive genetic variance when the uptake is a quantitative genetic trait (Fox & Vasseur 2008), and so both the fitness gradient and v_j simultaneously determine the rate of evolutionary change. Due to the discontinuous partial derivative, eqn 6 is approximated following Fox & Vasseur (2008).
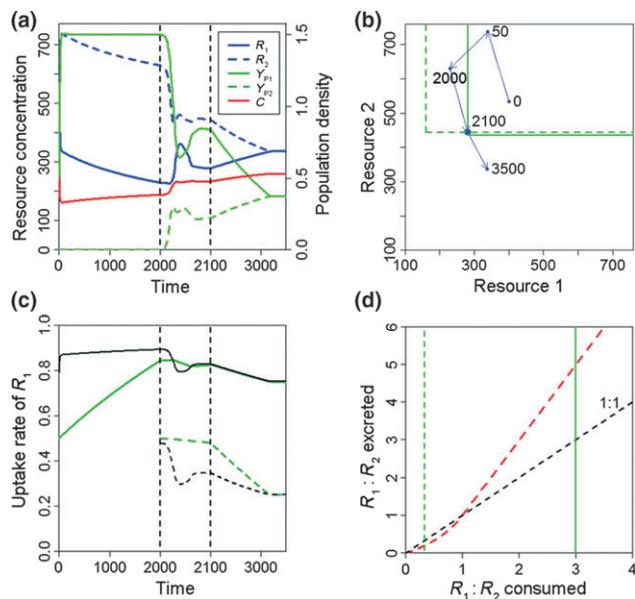
An application of the model

The model illustrates how evolutionary change in the uptake rates of primary producers can affect competitive interactions among species and influence the resource dynamics of a system. Using the initial conditions provided in Table 2, we simulated the dynamics of two resources, two producers and a consumer.

Dynamics of the simulation

We started the model simulation with a single producer (Y_{P1}) with a lower yield coefficient on R_1 than R_2 (Table 2), and after some time ($t = 2000$) we introduced a second producer (Y_{P2}) with a lower yield coefficient on R_2 than R_1. During the first part of the simulation ($t < 2000$), Y_{P1} adapts to the environment by increasing its uptake rate on R_1. The system reaches a stable ecological equilibrium relatively quickly, as shown by the population trajectories of Y_{P1} and C (Fig. 2a). At this point, there is a high ratio of producer : consumer biomass, and a low $R_1 : R_2$ ratio of the available nutrients (Fig. 2a). The introduction of Y_{P2} ($t = 2000$) has three main effects on the system. First, Y_{P2} rapidly takes advantage of the underutilized R_1 in the system and changes the ratio of supplied nutrients (note the change of the supply point in Fig. 2b). Second, Y_{P2} increases the stoichiometric quality of the consumer's food, and, as a result, increases the consumer density and predation pressure on both species (apparent competition). This leads to a reduction in the

Table 2 Initial and final values for the variables, and values for the parameters used in the model simulation

Symbol	Description	Initial value	Final value
R_i	Resource i density (e.g. R_1, R_2)	400, 533	337, 337
Y_{Pj}	Producer j density	0.5, 0.0	0.375, 0.376
C	Consumer density	0.5	0.532
U_{P1}	Uptake rate of Y_{P1} on R_i	0.5, 0.5	0.75, 0.25
U_{P2}	Uptake rate of Y_{P2} on R_i	0.5, 0.5	0.25, 0.75
a_j	Consumer attack rate on Y_{Pj}	1, 1	–
m_j	Producer j mortality	0.1, 0.1	–
d	Consumer mortality	0.05	–
e_{P1i}	Y_{P1} yield coefficient for resource i	0.0025, 0.0075	–
e_{P2i}	Y_{P2} yield coefficient for resource i	0.0075, 0.0025	–
e_{Ci}	Consumer yield coefficient for resource i	0.0005, 0.0005	–
l	Consumer leakage rate	0.5	–
v_j	Additive genetic variance of producer j traits	0.00026, 0.00026	–

Figure 2 Panel (a): The system starts with the parameters and values provided in Table 2. The abiotic concentration of R_1 (N, solid blue line) is initially lower than R_2 (P, dashed blue line) because of Y_{P1}'s high $R_1 : R_2$ ratio. Initially, Y_{P1} (solid green line) increases rapidly in density whereas C (red line) decreases. The system exhibits short lived predator–prey cycles that are rapidly dampened, resulting in a stable ecological equilibrium by $t = 50$. Y_{P1} then adapts to the environment by increasing its uptake rate of R_2 at the expense of R_1 (Panel c). This adaptation allows it to increase its growth rate but interactions with the consumer keep its density relatively constant. Increases in its growth rate fuels an increase in C's density and a subsequent decrease in the densities of both N and P. The invasion of Y_{P2} (dashed green line) disturbs the system in several ways. The high P content in the environment allows Y_{P2} to rapidly increase in density, causing a decrease in the density of producers Y_{P1} due to apparent competition. The addition of Y_{P2} actually increases the growth rate of Y_{P1} due to increased consumption of Y_{P1} and increasing the R_1 concentration (Panel d). In addition, the invasion of Y_{P2} shifts the adaptive peak of Y_{P1} closer to its U_1 value (Panel c). The system cycles briefly and then reaches a new stable ecological equilibrium with all three species. Further adaptation by Y_{P2} leads to an increase in its growth rate (Panel c), and over time, this increases the transfer of R_2 into the producer trophic level (relative to R_1) until the concentrations of R_1 and R_2 are equal. At this point neither Y_{P1} nor Y_{P2} has an advantage. This change in the abiotic condition causes greater decreases in Y_{P1} than is compensated by an increase in Y_{P2}, and so the total producer density decreases. Meanwhile, the density of C increases as the ratio of $Y_{P1} : Y_{P2}$ approaches 1 : 1 at which point there is no stoichiometric mismatch between the consumer and its diet. **Panel (b):** ZNGI for Y_{P1} (solid green line) and Y_{P2} (dashed green line) showing the concentrations of R_1 and R_2 at which growth equals death due to density independent mortality and consumption by C. Here we show only a single pair of ZNGIs (at $t = 2100$), but the ZNGIs evolve in our model such that the resource supply point always allows for coexistence (data not shown). The ZNGIs shift based on consumer density and with changes in the uptake rate of nutrients. The blue points represent the concentrations of R_1 (N) and R_2 (P) at different time steps. At $t = 0$, $R_2 > R_1$. The rapid increase in Y_{P1} exacerbates the nutrient imbalance $[R_2] >> [R_1]$ by the time the first ecological equilibrium is reached at $t = 50$. The adaptation of Y_{P1} decreases both P and R_1 equally until $t = 2000$. The invasion of Y_{P2} (at $t = 2000$) decreases the R_2 in the environment, due to the stoichiometry of Y_{P2}, and increases the R_1 in the environment, due to increased Y_{P1} mortality. The second ecological equilibrium is reached at approximately $t = 2100$. As mentioned above, the system converges to an ecological and evolutionary equilibrium at ($t = 3500$), when the producer species become identical in the uptake rates. **Panel (c):** Shows the time course of uptake rates of R_1 for each species (green lines). The optimal uptake rate (black lines), vary based on the ratio of $R_1 : R_2$ in the environment, and is always the uptake rate at which growth is maximized. The optimal growth rate can be considered the 'peak' of an adaptive landscape. In our model, fitness falls away from this adaptive peak linearly from 100 to 0% as uptake rates vary from on 0 to 1. From the start of the simulation until $t = 2000$, Y_{P1} adapts to the local environment, which itself is being modified by the adaption of Y_{P1}. The invasion of Y_{P2} shifts the optimal uptake rates of both species. From $t = 2100$ to $t = 3500$, both species adapt to the changing nutrient environment. **Panel (d):** Shows the $R_1 : R_2$ ratio of the excreted nutrients (red dashed line) of a consumer with a stoichiometry given by the black dotted line (e.g. $R_1 : R_2$ is 1 : 1 for sake of simplicity and with no loss of generality). Feeding solely on Y_{P1} (solid green line) results in a preferential R_1 excretion in the environment, whereas feeding only on Y_{P2} (dashed green line) results in preferential R_2 excretion into the environment.

producer : consumer biomass ratio. Third, as Y_{P2} adapts to the nutrient environment (Fig. 2c) it alters the stoichometry of the available nutrients (Fig. 2b).

The phenotypic evolution of producers

We can visualize the stoichiometric phenotypes of organisms using zero net growth isoclines (ZNGIs) (Fox & Vasseur 2008). In our simulation, the producers adapt their uptake rates to the changing nutrient dynamics (Fig. 2c), such that their ZNGIs evolve over time (Fig. 2b). When Y_{P2} is introduced, Y_{P1} has almost reached its optimal uptake rate (black lines in Fig. 2c). The two producers can coexist because the nutrient supply point equilibrates at the intersection of their ZNGIs (Fig. 2b). As Y_{P2} evolves, by reducing its uptake of R_1 in favour of R_2 (Fig. 2c), it becomes a better competitor for the available nutrients in the system and slowly increases in abundance (Fig. 2a). As there are few constraints to adaptation, the species converge to have completely overlapping ZNGIs by the end of the simulation, but evolve divergent nutrient uptake strategies that reflect their initial differences in resource demand (Table 2).

The effects of consumers

Consumers impose density-dependent mortality on the producer population and alter the stoichiometry of nutrients via nutrient recycling. As shown in Fig. 2(d), the consumer excretes proportionally more R_1 than R_2 ($R_1 : R_2 > 1$) when grazing on Y_{P1}, and vice versa when grazing on Y_{P2} ($R_1 : R_2 < 1$), meaning that consumers affect nutrients in the environment via the interaction between their resource demand and the eco-evolutionary dynamics determining primary producer dynamics. Our example only considers a single non-evolving consumer, but one could also model the outcome of competition between two consumers with different stoichiometric traits.

In sum, our model illustrates how the composition and phenotypic evolution of a producer species can alter the dynamics of an ecosystem process (e.g. nutrient recycling) and the ecological structure of the community (e.g. biomass ratio of roducers : consumers). The model can be run with and without evolutionary change and eco-evolutionary feedbacks, and could be tested against empirical data,

from either a natural ecosystem or an experiment, to assess the consequences of phenotypic evolution for nutrient cycling.

Experimental approaches for testing the ecosystem consequences of evolutionary diversity and dynamics

In this section, we propose ways to experimentally test the ecosystem consequences of the evolutionary history of organisms (i.e. the product of selection) and of the contemporary evolution of ecosystem-effect traits (i.e. the process of evolution by natural

selection). To start with, we describe an experimental design that we refer to as a *common gardening experiment*, which is useful for quantifying ecosystem effects.

Common gardening experiments

In a classical common garden experiment, the environmental conditions are held constant for each genotype, to quantify how much phenotypic variation is attributable to genetic differences among organisms. Our proposed common gardening experiment is a type of common garden experiment that is specifically designed to quantify the effects of organisms on a common type of ecosystem. In a common gardening experiment, the phenotypes (or genotypes) of organisms are held constant for each ecosystem type to quantify how much ecosystem variation is attributable to phenotypic (or genetic) differences among organisms. 'Common gardening' refers to the idea that the ecosystems in the experiment begin from a common starting point and are modified, in potentially different ways, by the activities of the organisms that are used as treatments in the experimental design. Recently, there have been several examples of common gardening experiments that have been used to determine the ecosystem consequences of phenotypic divergence and phenotypic evolution (Lennon & Martiny 2008; Harmon *et al.* 2009; Palkovacs & Post 2009; Bassar *et al.* 2010; Gravel *et al.* 2011). However, many more common gardening experiments are needed to understand the broad range of ecosystem functions that could be influenced by the evolutionary history of organisms and by contemporary evolutionary dynamics.

Common gardening experiments can be preceded by a common garden experiment to determine whether ecosystem variation is attributable to either the genetic determinants of phenotypic variation or to phenotypic plasticity. Some traits can change in response to an environmental factor early in organism's development (i.e. exhibit phenotypic plasticity), but after some period of time they become fixed and insensitive to environmental variation [a type of age-specific environmental canalization: Debat & David (2001)]. Organisms could be grown in a common environment until a phenotype of interest is relatively stable, and then the organisms could be subsequently used as experimental treatments in a common gardening experiment. Such experiments could test, for example, whether the different ecosystem-effects of closely related species (or populations) result from adaptive genetic divergence or non-genetic differences in phenotypically plastic traits (Seehausen 2009).

Ecosystem consequences of contrasting evolutionary histories

Several recent common gardening experiments have found that phenotypic differences among organisms can have a wide range of community and ecosystem effects (Harmon *et al.* 2009; Bassar *et al.* 2010). In these experiments, it is hard to identify specific ecosystem-effect traits because it is unclear which traits caused the observed ecosystem divergence (see 'Mix' category in Table 1). In such cases, the evolutionary origins of the phenotypic variation can be informative for predicting which traits are likely to cause ecosystem effects. In adaptive radiations, for example, the traits under divergent selection are often those used to exploit resources in the natural environment. As a result, we might expect trait divergence between species in an adaptive radiation to cause strong and contrasting effects on ecosystems (Harmon *et al.* 2009). In comparison, the divergence of traits that are not closely associated with ecosystem properties, such as

the evolution of mating traits driven by sexual selection (Arnqvist 1998), will probably have negligible impacts on ecosystem functions. Overall, we are a long way from predicting whether the traits under divergent selection are the same as those that cause contrasting ecosystem effects.

A few recent studies have used a period of experimental evolution to examine how organisms with different evolutionary histories can affect community dynamics (Becks *et al.* 2010) and ecosystem effects (Gravel *et al.* 2011). Gravel *et al.* (2011) experimentally evolved twenty strains of marine bacteria into specialists or generalists, with respect to the number of utilizable carbon substrates. For each group of strains (i.e. ancestors, generalists and specialists) Gravel *et al.* (2011) established communities in microcosms along a gradient of species richness and measured community productivity (i.e. bacterial meta-bolic activity) on a mixed medium of carbon substrates. They found that the slope of the relationship between species richness and productivity was steeper for communities made up of specialists, illustrating the influence of variation in the evolutionary history of community members on ecosystem functions (Gravel *et al.* 2011). This is a nice example of a simplified common gardening experiment, because it used a highly controlled and narrowly defined ecosystem (a mixed carbon substrate) and only measured one ecosystem function (productivity).

To date, common gardening experiments have not tested whether the ecosystem effects of species with different phenotypes (or geno-types) have sufficient strength and persistence to affect future evolutionary change, and, as a result, none have experimentally demonstrated an eco-evolutionary feedback. In a recent common gardening experiment, Harmon *et al.* (2009) found that sticklebacks with different phenotypes had contrasting effects on zooplankton community structure, gross primary productivity and the rate of light extinction in the water column, but do such contrasting effects at the community and ecosystem level influence the selection pressures on sticklebacks in future generations? This is not a trivial question to answer, but it could be addressed by doing a common gardening experiment followed by a selection experiment in the modified ecosystems. For example, one could do a common gardening experiment in replicated ponds using sticklebacks with two divergent phenotypes as experimental treatments. We would expect the pond ecosystems to diverge over time (Harmon *et al.* 2009), but would this generate divergent selection environments for the next generation of sticklebacks? This could be tested by removing the founding stickleback populations from all of the ponds, adding a common set of juvenile sticklebacks back into the same ponds and measuring the relationship between the fitness of individuals and a quantitative trait under natural selection (i.e. a fitness function) in the ecosystems that were modified during the common gardening experiment. Such an experiment could experimentally test whether the modification of an ecosystem by an organism could change the selection pressures of that same organism in subsequent generations.

Ecosystem consequences of contemporary evolutionary dynamics

Most of the previous common gardening experiments have tested how historical evolutionary changes can affect contemporary ecosys-tem functions (Harmon *et al.* 2009; Bassar *et al.* 2010; Gravel *et al.* 2011). As a result, they have temporally separated the process of natural selection from the evaluation of ecosystem effects. However, one can allow selection to occur over the course of a common

gardening experiment to directly test the ecosystem effects of variation in (1) the strength of natural selection (i.e. the selection differential), or (2) the response of a population to selection (e.g. adaptation over multiple generations).

Ecosystem effects of variation in the strength of selection

A useful way to assess the impact of phenotypic change on ecosystem functions is to manipulate the strength of selection on a target organism in a common gardening experiment. The experimental work on predator–prey dynamics of rotifers (e.g. *Brachionus*) and algae (e.g. *Chlamydomonas* or *Chlorella*) provides a good model system for such experiments (Yoshida *et al.* 2003; Becks *et al.* 2010). Becks *et al.* (2010) found that the selective regime caused by rotifer grazing reduced the amount of variation in a heritable defense trait of algae, which altered the nature of predator–prey dynamics. In this experiment, the strength of predator-induced selection was manipulated by altering the initial amount of phenotypic variation in the defense traits of the prey population. For practical reasons, these experiments are conducted in chemostats that maintain a highly controlled environment and food supply. However, it would be interesting to investigate how different evolutionary dynamics might impact the functioning of these simple ecosystems (e.g. nutrient cycling, pH). The allocation of resources to defense might divert energy away from growth and reproduction (i.e. affect demographic variation), and the subsequent change in draw down of carbonic acid by phytoplankton photosynthesis might affect other strains or species. If the genetic composition of one strain affects the persistence, activity or coexistence of other strains, then strain diversity could have significant effects on ecosystem functioning (Isbell *et al.* 2009).

We can directly target the ecosystem consequences of selection by studying how variation in the strength of selection affects the distribution of ecosystem-effect traits in a population. This could be done by nesting a selection experiment, for example one that uses candidate genes that underlie adaptive phenotypic traits (Barrett *et al.* 2008), inside a common gardening experiment (Harmon *et al.* 2009). Specifically, one could measure how variation in the selection differential over the course of the selection experiment might have contrasting effects on ecosystem functions. The recent advances in the genomic resources of *Daphnia* open vast opportunities to do such experiments and to study how natural selection acting on specific genes (Routtu *et al.* 2010; Colbourne *et al.* 2011) might affect ecosystem functions. We already know a great deal about how changes in the life-history and stoichiometric traits of plankton might affect primary productivity and nutrient dynamics in aquatic ecosystems (Sterner & Elser 2002; Hall 2009). In addition, some of these traits can evolve rapidly in response to selection (Gorokhova *et al.* 2002; Weider *et al.* 2005). For example, divergent selection acting on *Daphnia* production rate can cause rapid genetic changes in the length of intergenic spacers (IGS) of ribosomal DNA (Gorokhova *et al.* 2002), which is related to *Daphnia*'s life-history and stoichiometric traits (Weider *et al.* 2005). The rapid developments in environmental genomics will undoubtedly provide valuable resources for integrating evolutionary biology with ecosystem science (Vandenkoornhuyse *et al.* 2010).

Ecosystem effects of population responses to selection

There is very little experimental evidence showing how the evolution of adaptive traits over multiple generations can directly affect an ecosystem function. In an elegant example, Lennon & Martiny (2008) found that the rapid evolution of resistance in a photosynthetic cyanobacteria (*Synechococcus*) to an infectious virus (*Myoviridae*) seemed to mediate nutrient availability in the environment via top-down control by viruses (Table 1). In this case, the evolution of resistance, which occurred over the course of an experiment, is an example of adaptation by natural selection (Elena & Lenski 2003) because beneficial mutations most likely arose in the host populations of *Synechococcus* and increased in frequency in response to virus-mediated selection (Lennon & Martiny 2008). This experiment is unique because it measured the ecosystem effects of a population response to selection over the course of a common gardening experiment (Lennon & Martiny 2008), as opposed to measuring the consequences of population dynamics resulting from variation in the strength of selection (Becks *et al.* 2010).

A significant challenge for future studies is to isolate how various mechanisms of evolutionary change can affect ecosystem functions. We can do this by identifying the genetic basis of ecosystem-effect traits, using selection experiments to determine how these traits respond to selection and by doing common gardening experiments to quantify the ecosystem effects.

CONCLUSIONS

The integration of community ecology and evolutionary biology has progressed considerably, in part, because of the realization that the outcomes of ecological interactions among species are contingent on their evolutionary histories (Johnson & Stinchcombe 2007; Haloin & Strauss 2008; Schoener, 2011). G. E. Hutchinson promoted this idea by describing ecological systems as analogous to theatres, in which the actors (i.e. species or individuals) have roles determined by their evolutionary history, and the acts are played out in an unscripted fashion that is contingent on the environmental setting (i.e. the local theatre) (Hutchinson 1965). Modern ideas about eco-evolutionary dynamics call for a more nuanced analogy – one that might stimulate greater integration between ecosystem science and evolutionary biology. For instance, we can consider that the roles of actors (i.e. their phenotypes) in local theatres (i.e. ecosystems) change over generations in response to direct pressures from actors' peers and audiences (i.e. the agents of selection). Actors' roles can evolve because of reciprocal interactions (i.e. eco-evolutionary feedbacks) between actors and their peers (i.e. the community) or between actors and the structural components of the theatre (e.g. the abiotic environment of ecosystems). In addition, actors can influence the development and renovation of the theatre (i.e. ecosystem modification and engineering) and this, in turn, can increase the number of actors in the play (i.e. via niche construction) and affect the outcome of future plays.

At present, ecosystem science and evolutionary biology lack a cohesive theoretical and experimental framework. We can achieve greater integration between evolutionary biology and ecosystem science by expanding the scope of several research fields in ecology and evolution. At a time of unprecedented human alteration of the environment, it is crucial to integrate evolutionary biology and ecosystem science to achieve a deeper understanding of both the causes and consequences of biodiversity change in natural ecosystems.

REFERENCES

Ackerly, D.D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int. J. Plant Sci.*, 164, S165–S184.

Arnqvist, G. (1998). Comparative evidence for the evolution of genitalia by sexual selection. *Nature*, 393, 784–786.

Bailey, J.K., Schweitzer, J.A., Ubeda, F., Koricheva, J., LeRoy, C.J., Madritch, M.D. *et al.* (2009). From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philos. Trans. R. Soc. B, Biol. Sci.*, 364, 1607–1616.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, 9, 1146–1156.

Barrett, R.D.H., Rogers, S.M. & Schluter, D. (2008). Natural selection on a major armor gene in threespine stickleback. *Science*, 322, 255–257.

Barton, N.H. & Whitlock, M.C. (1997). The evolution of metapopulations. In: *Metapopulation Biology: Ecology, Genetics and Evolution* (eds Hanksi, I & Gilpin M.). Academic Press, New York, pp. 183–210.

Bassar, R.D., Marshall, M.C., Lopez-Sepulcre, A., Zandona, E., Auer, S.K., Travis, J. *et al.* (2010). Local adaptation in *Trinidadian guppies* alters ecosystems processes. *Proc. Natl. Acad. Sci.*, 107, 3616–3621.

Becks, L., Ellner, S.P., Jones, L.E. & Hairston, N.G. (2010). Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. *Ecol. Lett.*, 13, 989–997.

Bolnick, D., Svanback, R., Fordyce, J., Yang, L., Davis, J., Hulsey, C. *et al.* (2003). The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, 161, 1–28.

Boudsocq, S., Barot, S. & Loeuille, N. (2011). Evolution of nutrient acquisition: when adaptation fills the gap between contrasting ecological theories. *Proc. R. Soc. B, Biol. Sci.*, 278, 449–457.

Bouma, T.J., Vries, M.B.D. & Herman, P.M.J. (2010). Comparing ecosystem engineering effciency of two plant species with contrasting growth strategies. *Ecology*, 91, 2696–2704.

Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl. Acad. Sci.*, 105, 17012–17017.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417, 844–848.

Carlson, S.M., Quinn, T.P. & Hendry, A.P. (2011). Eco-evolutionary dynamics in pacific salmon. *Heredity*, 106, 438–447.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L. *et al.* (2000). Consequences of changing biodiversity. *Nature*, 405, 234–242.

Cianciaruso, M.V., Batalha, M.A., Gaston, K.J. & Petchey, O.L. (2009). Including intraspecific variability in functional diversity. *Ecology*, 90, 81–89.

Classen, A.T., Chapman, S.K., Whitham, T.G., Hart, S.C. & Koch, G.W. (2007). Genetic-based plant resistance and susceptibility traits to herbivory influence needle and root litter nutrient dynamics. *J. Ecol.*, 95, 1181–1194.

Cohen, Y., Pastor, J. & Vincent, T.L. (2000). Evolutionary strategies and nutrient cycling in ecosystems. *Evol. Ecol. Res.*, 2, 719–743.

Colbourne, J.K., Pfrender, M.E., Gilbert, D., Thomas, W.K., Tucker, A., Oakley, T.H. *et al.* (2011). The ecoresponsive genome of *Daphnia pulex*. *Science*, 331, 555–561.

Collins, S. & Bell, G. (2004). Phenotypic consequences of 1,000 generations of selection at elevated CO_2 in a green alga. *Nature*, 431, 566–569.

Cortez, M.H. & Ellner, S.P. (2010). Understanding rapid evolution in predator–prey interactions using the theory of fast-slow dynamical systems. *Am. Nat.*, 176, E109–E127.

Cyr, H. (1998). Cladoceran- and copepod-dominated zooplankton communities graze at similar rates in low-productivity lakes. *Can. J. Fish. Aquat. Sci.*, 55, 414–422.

DeAngelis, D.L. (1992). *Dynamics of Nutrient Cycling and Food Webs: Populations and Community Biology*. Chapman Hall, London.

Debat, V. & David, P. (2001). Mapping phenotypes: calanization, plasticity and developmental stability. *Trends Ecol. Evol.*, 16, 555–561.

Dickman, E.M., Newell, J.M., Gonzalez, M.J. & Vanni, M.J. (2008). Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. *Proc. Natl. Acad. Sci.*, 105, 18408–18412.

Dieckmann, U., Brannstrom, A., HilleRisLambers, R. & Ito, H.C. (2007). The adaptive dynamics of community structure. In: *Mathematics for Ecology and Environmental Sciences* (eds Takeuchi, Y., Iwasa, Y. & Sato, K.). Springer Verlag, Berlin, pp. 145–177.

Elena, S.F. & Lenski, R.E. (2003). Evolution experiments with microorganisms: the dynamics and genetic basis of adaptation. *Nat. Rev. Genet.*, 4, 457–469.

Elser, J. (2006). Biological stoichiometry: a chemical bridge between ecosystem ecology and evolutionary biology. *Am. Nat.*, 168, S25–S35.

Emerson, B.C. & Gillespie, R.G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol. Evol.*, 23, 619–630.

Erwin, D.H. (2008). Macroevolution of ecosystem engineering, niche construction and diversity. *Trends Ecol. Evol.*, 23, 304–310.

Ezard, T.H.G., Cote, S.D. & Pelletier, F. (2009). Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philos. Trans. R. Soc. B, Biol. Sci.*, 364, 1491–1498.

Falkowski, P.G., Fenchel, T. & Delong, E.F. (2008). The microbial engines that drive earth's biogeochemical cycles. *Science*, 320, 1034–1039.

Fox, J.W. & Vasseur, D.A. (2008). Character convergence under competition for nutritionally essential resources. *Am. Nat.*, 172, 667–680.

Fussmann, G.F., Loreau, M. & Abrams, P.A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.*, 21, 465–477.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H. *et al.* (2010). Dviersity meets decomposition. *Trends Ecol. Evol.*, 25, 372–380.

Gorokhova, E., Dowling, T.E., Weider, L.J., Crease, T.J. & Elser, J.J. (2002). Functional and ecological significance of rDNA intergenic spacer variation in a clonal organism under divergent selection for production rate. *Proc. R. Soc. B, Biol. Sci.*, 269, 2373–2379.

Goudard, A. & Loreau, M. (2008). Nontrophic interactions, biodiversity, and ecosystem functioning: an interaction web model. *Am. Nat.*, 171, 91–106.

Gravel, D., Bell, T., Barbera, C., Bouvier, T., Pommier, T., Venail, P. *et al.* (2011). Experimental niche evolution alters the strength of the diversity-productivity relationship. *Nature*, 469, 89–92.

Gross, T., Rudolf, L., Levin, S.A. & Dieckmann, U. (2009). Generalized models reveal stabilizing factors in food webs. *Science*, 325, 747–750.

Grover, J.P. (2002). Stoichiometry, herbivory and competition for nutrients: simple models based on planktonic ecosystems. *J. Theor. Biol.*, 214, 599–618.

Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.*, 8, 1114–1127.

Hall, S.R. (2009). Stoichiometrically explicit food webs: feedbacks between resource supply, elemental constraints, and species diversity. *Ann. Rev. Ecol. Syst.*, 40, 503–528.

Haloin, J.R. & Strauss, S.Y. (2008). Interplay between ecological communities and evolution: review of feedbacks from microevolutionary to macroevolutionary scales. *Ann. NY Acad. Sci.*, 1133, 87–125.

Hanski, I. & Gilpin, M. (1997). *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, San Diego, CA.

Hanski, I. & Saccheri, I. (2006) Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biol.*, 4, e129.

Hanski, I., Mononen, T. & Ovaskainen, O. (2011). Eco-evolutionary metapopulation dynamics and the spatial scale of adaptation. *Am. Nat.*, 177, 29–43.

Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B. & Schluter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*, 458, 1167–1170.

Hillebrand, H. & Matthiessen, B. (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecol. Lett.*, 12, 1405–1419.

Holt, R.D. (1995) Linking species and ecosystems – Where's Darwin. In: *Linking Species and Ecosystems* (eds Jones, C.G. & Lawton, J.H.). Chapman & Hall, New York, pp. 273–279.

Holyoak, M., Leibold, M.A. & Holt, R.D. (2005). *Metacommunities: Spatial Dynamics and Ecological Communities*. The University of Chicago Press, Chicago.

Hutchinson, G.E. (1965). *The Ecological Theater and the Evolutionary Play*. Yale University Press, Yale.

Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009). Biodiveristy, productivity and the temporal stability of productivity: patterns and processes. *Ecol. Lett.*, 12, 443–451.

Johnson, M.T.J. (2011). The contribution of evening primrose (*Oenothera biennis*) to a modern synthesis of evolutionary ecology. *Popul. Ecol.*, 53, 9–21.

Johnson, M.T.J. & Stinchcombe, J.R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.*, 22, 250–257.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78, 1946–1957.

Klausmeier, C.A., Litchman, E., Daufresne, T. & Levin, S.A. (2004). Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature*, 429, 171–174.

Kylafis, G. & Loreau, M. (2008). Ecological and evolutionary consequences of niche contruction for its agent. *Ecol. Lett.*, 11, 1072–1081.

Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proc. Natl. Acad. Sci.*, 96, 10242–10247.

Leibold, M.A. (2010). Metacommunity phylogenetics: separating the role of environmental filters and historical biogeography. *Ecol. Lett.*, 13, 1290–1299.

Lennon, J.T. & Martiny, J.B.H. (2008). Rapid evolution buffers ecosystem impacts of viruses in a microbial food web. *Ecol. Lett.*, 11, 1178–1188.

Levin, S.A. (1998). Ecosystems and the biosphere as complex adaptive systems. *Ecosystems*, 1, 431–436.

Loeuille, N. (2009). Evolution of communities and ecosystems. In: *The Princeton Guide to Ecology* (ed. Levin, S.A.). Princeton University Press, Princeton, pp. 414–422.

Loeuille, N. (2010). Influence of evolution on the stability of ecological communities. *Ecol. Lett.*, 13, 1536–1545.

Loreau, M. (2010a). *From Populations to Ecosystems: Theoretical Foundataion for a New Ecological Synthesis*. Princeton University Press, Princeton.

Loreau, M. (2010b). Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philos. Trans. R. Soc. B, Biol. Sci.*, 365, 49–60.

Lotka, A.J. (1922). Contributions to the energetics of evolution. *Proc. Natl. Acad. Sci.*, 8, 147–151.

de Mazancourt, C. & Loreau, M. (2000). Grazing optimization, nutrient cycling, and spatial heterogeneity of plant-herbivore interactions: should a palatable plant evolve? *Evolution*, 54, 81–92.

de Mazancourt, C., Johnson, E. & Barraclough, T.G. (2008). Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.*, 11, 380–388.

McIntyre, P.B., Flecker, A.S., Vanni, M.J., Hood, J.M., Taylor, B.W. & Thomas, S.A. (2008). Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? *Ecology*, 89, 2335–2346.

Menge, D.N.L., Levin, S.A. & Hedin, L.O. (2008). Evolutionary tradeoffs can select against nitrogen fixation and thereby maintain nitrogen limitation. *Proc. Natl. Acad. Sci.*, 105, 1573–1578.

Murphy, J.M., Sexton, D.M.H., Barnett, D.N., Jones, G.S., Webb, M.J., Collins, M. et al. (2004). Quantification of modelling uncertainties in a large ensemble of climate change simulations. *Nature*, 430, 768–772.

Neuhauser, C., Andow, D.A., Heimpel, G.E., May, G., Shaw, R.G. & Wagenius, S. (2003). Community genetics: expanding the synthesis of ecology and genetics. *Ecology*, 84, 545–558.

Norberg, J., Swaney, D.P., Dushoff, J., Lin, J., Casagrandi, R. & Levin, S.A. (2001). Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proc. Natl. Acad. Sci.*, 98, 11376–11381.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B. & Allen, G.E. (1986). *A Heirarchical Concept of Ecosystems*. Princeton University Press, Princeton.

Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (2003) *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton.

Odum, E.P. (1971). *Fundamentals of Ecology*, 3rd edn. Saunders, Philadelphia.

Palkovacs, E.P. & Post, D.M. (2009). Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology*, 90, 300–305.

Palkovacs, E.P., Marshall, M.C., Lamphere, B.A., Lynch, B.R., Weese, D.J., Fraser, D.F. et al. (2009). Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philos. Trans. R. Soc. B, Biol. Sci.*, 364, 1617–1628.

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.

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

Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioing research. *Trends Ecol. Evol.*, 24, 505–514.

Rossberg, A.G., Matsuda, H., Amemiya, T. & Itoh, K. (2005). An explanatory model for food-web structure and evolution. *Ecol. Complex.*, 2, 312–321.

Routtu, J., Jansen, B., Colson, I., De Meester, L. & Ebert, D. (2010). The first-generation daphnia magna linkage map. *BMC Genomics*, 11, 508.

Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.

Schmitz, O.J. (2010). *Resolving Ecosystem Complexity*. Princeton University Press, Princeton.

Schoener, T.W. (2011). The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science*, 331, 426–429.

Seehausen, O. (2009). Speciation affects ecosystems. *Nature*, 458, 1122–1123.

Sterner, R.W. & Elser, J.J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.

Strauss, S.Y., Sahli, H. & Conner, J.K. (2005). Toward a more trait-centered approach to diffuse (co)evolution. *New Phytologist*, 165, 81–89.

Swift, M.C. & Fedorenko, A.Y. (1975). Some aspects of prey capture by chaoborus larvae. *Limnol. Oceanogr.*, 20, 418–425.

Terborgh, J. & Estes, J. (2010). *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature*. Island Press, Washington DC.

Thompson, J.N. (1998). Rapid evolution as an ecological process. *Trends Ecol. Evol.*, 13, 329–332.

Treseder, K.K. & Vitousek, P.M. (2001). Potential ecosystem-level effects of genetic variation among populations of metrosideros polymorpha from a soil fertility gradient. *Oecologia*, 126, 266–275.

Urban, M.C., Leibold, M.A., Amarasekare, P., De Meester, L., Gomulkiewicz, R., Hochberg, M.E. et al. (2008). The evolutionary ecology of metacommunities. *Trends Ecol. Evol.*, 23, 311–317.

Vandenkoornhuyse, P., Dufresne, A., Quaiser, A., Gouesbet, G., Binet, F., Francez, A. et al. (2010). Integration of molecular functions at the ecosystemic level: breakthroughs and future goals of environmental genomics and post-genomics. *Ecol. Lett.*, 13, 776–791.

Vellend, M. (2010). Conceptual synthesis in community ecology. *Q. Rev. Biol.*, 85, 183–206.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. et al. (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.

Weider, L.J., Elser, J.J., Crease, T.J., Mateos, M., Cotner, J.B. & Markow, T.A. (2005). The functional significance of ribosomal (r)DNA variation: Impacts on the evolutionary ecology of organisms. *Ann. Rev. Ecol. Syst.*, 36, 219–242.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J. et al. (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.*, 7, 510–523.

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

GLOSSARY

1. **Community genetics:** The study of interspecific genetic interactions and their effects on community composition and ecosystem functioning.

2. **Eco-evolutionary dynamics:** The effects of ecological dynamics on evolutionary change and the effects of evolutionary dynamics on ecological change. The effects in both directions can be mediated by changes in ecosystem functions.

3. **Eco-evolutionary feedback:** The feedback between ecological and evolutionary processes whereby an organism affects population, community or ecosystem dynamics in a way that affects its own evolutionary trajectory.

4. **Ecosystem:** A unit that includes all of the organisms (i.e. the 'community') in a given area interacting with the physical environment, so that a flow of energy leads to clearly defined trophic structure, biotic diversity and material cycles (i.e. exchange of materials between living and non-living parts).

5. **Ecosystem function:** The flux of energy, organic matter or nutrients in an ecosystem, including the flux of biomass associated with trophic interactions. Functions are expressed as a rate of change of an ecosystem property.

6. **Ecosystem property:** A metric expressing the amount of energy, organic matter or nutrient concentration in an ecosystem.

7. **Ecological stoichiometry:** The study of the balance of energy and the ratios of key elements (primarily C, N and P) in ecological interactions.

8. **Community property:** Any descriptor of the biological community in an ecosystem such as species composition, species richness and phenotypic diversity.

9. **Niche construction:** The process by which organisms modify components of their environment, such as resource distribution or habitat space to affect selection pressures on themselves or other organisms in an ecosystem.

10. **Zero net growth isocline (ZNGI):** Resource supply level at which the growth rate of a population is zero because its rate of reproduction and mortality are equal.