

Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play

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Interactions between natural selection and environmental change are well recognized and sit at the core of ecology and evolutionary biology. Reciprocal interactions between ecology and evolution, eco-evolutionary feedbacks, are less well studied, even though they may be critical for understanding the evolution of biological diversity, the structure of communities and the function of ecosystems. Eco-evolutionary feedbacks require that populations alter their environment (niche construction) and that those changes in the environment feed back to influence the subsequent evolution of the population. There is strong evidence that organisms influence their environment through predation, nutrient excretion and habitat modification, and that populations evolve in response to changes in their environment at time-scales congruent with ecological change (contemporary evolution). Here, we outline how the niche construction and contemporary evolution interact to alter the direction of evolution and the structure and function of communities and ecosystems. We then present five empirical systems that highlight important characteristics of eco-evolutionary feedbacks: rotifer–algae chemostats; alewife–zooplankton interactions in lakes; guppy life-history evolution and nutrient cycling in streams; avian seed predators and plants; and tree leaf chemistry and soil processes. The alewife–zooplankton system provides the most complete evidence for eco-evolutionary feedbacks, but other systems highlight the potential for eco-evolutionary feedbacks in a wide variety of natural systems.

Keywords: eco-evolutionary feedbacks; intraspecific variation; niche construction; evolution; community ecology; ecosystem ecology

At every moment natural selection is operating to change the genetic composition of populations in response to the momentary environment, but as that composition changes it forces a concomitant change in the environment itself. Thus organisms and environments are both causes and effects in a coevolutionary process.

(Lewontin 2000, p. 126)

1. INTRODUCTION

At the core of both ecology and evolutionary biology is a fundamental interest in biological diversity, although it is often approached from very different perspectives. Evolutionary biology is singularly focused on the processes that generate diversity. Ecology, particularly community and ecosystem ecology, has focused on the maintenance and implications of biological diversity. At the interface is the growing interest in eco-evolutionary interactions (Laland *et al.* 1999; Odling-Smee *et al.* 2003; Hairston *et al.* 2005; Carroll *et al.* 2007; Fussmann *et al.* 2007; Kinnison & Hairston 2007). This area of research has been addressed in a variety of ways, but we believe eco-evolutionary feedbacks—reciprocal interactions between the ecology of populations,

communities and ecosystems, and the evolution of organismal traits—may be the most rewarding and challenging component of this growing area of research. Eco-evolutionary feedbacks dynamically link the functional role of organisms within their environment to the evolution of organism function, and, therefore, they may sit at the centre of many adaptive radiations (Grant 1986; Losos 1994; Losos *et al.* 1998; Schluter 2001; Grant & Grant 2006; Calsbeek *et al.* 2007), where feedbacks emerge from and probably intensify the intraspecific differences that ultimately result in new species (Habets *et al.* 2006; Palkovacs & Post 2008). Eco-evolutionary feedbacks may also strongly affect community and ecosystem processes by altering the ecological role of differentiated populations (Bailey *et al.* 2006; Whitham *et al.* 2006; Post *et al.* 2008).

We define eco-evolutionary feedbacks as the cyclical interaction between ecology and evolution such that changes in ecological interactions drive evolutionary change in organismal traits that, in turn, alter the form of ecological interactions, and so forth. This interaction has been appreciated over the very long time-scales of evolution of organisms on the Earth (Lewontin 2000; Brodie 2005), but its importance in shaping ecological and evolutionary diversity at shorter (contemporary) time-scales is often overlooked (Lewontin 2000). It is the two-way interaction between ecology and evolution that characterizes eco-evolutionary feedbacks, not

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simply the need to incorporate ecology into evolution or evolution into ecology. Following Lewontin (2000) and Odling-Smee *et al.* (2003), we describe eco-evolutionary feedbacks as

$$\frac{dO}{dt} = f(O, E), \quad (1.1)$$

$$\frac{dE}{dt} = f(O, E), \quad (1.2)$$

where evolution of the organismal traits (dO/dt) is a function of the present state of the organism (O) and the environment (E), and changes in the environment (dE/dt) are a function of the present state of the environment and the organism. We define the environment (E) broadly as ‘...any property outside the organisms under consideration’ (Hutchinson 1957), or its n -dimensional niche. This includes all of the biological and physiochemical conditions (external to the organism) that might influence evolution. This formulation makes explicit the observation—central to much of modern ecology—that organisms can shape their environment, and the observation—at the centre of evolutionary biology—that the environment shapes the subsequent evolution of an organism.

Here, we present the general requirements for eco-evolutionary feedbacks in community and ecosystem ecology. We review the limited theoretical research on this topic and then present five empirical systems that demonstrate both important requirements of eco-evolutionary feedbacks and the full scope for feedbacks in natural systems. Our research on alewife populations, in particular, highlights the potential for eco-evolutionary feedbacks to drive evolutionary changes in traits that can substantially impact community structure and ecosystem function in natural ecosystems. Finally, we draw parallels to and outline differences among our eco-evolutionary perspective and other frameworks for synthesizing contemporary evolution with community and ecosystem ecology, including niche construction (*sensu* Laland *et al.* 1999; Odling-Smee *et al.* 2003), community genetics (Whitham *et al.* 2006), evolving metacommunities (Urban *et al.* 2008) and the geographic mosaic of coevolution (Thompson 2005).

2. REQUIREMENTS FOR ECO-EVOLUTIONARY FEEDBACKS

We start by making explicit the requirements for eco-evolutionary feedbacks in community and ecosystem ecology, which we will expand upon in §3. First, there must be a strong effect of the phenotype on the environment—organisms must structure or construct their environment (Odling-Smee *et al.* 2003). This requires that the population of interest has strong interactions with its environment. Second, the constructed environment must cause the subsequent evolution of the population in question. This requires that changes in the environment cause selection on the population (directional or disruptive), and that the population has sufficient genetic capacity to evolve in response to changes in its environment. Implicit in these two requirements is the key observation that the time-scales for the ecological and evolutionary

responses need to be congruent (Laland *et al.* 1999; Hairston *et al.* 2005). Theoretical results indicate that eco-evolutionary feedbacks can emerge even in the presence of external environmental or evolutionary drivers (Laland *et al.* 1999). Finally, although not necessary for eco-evolutionary feedbacks, population-level (intraspecific) genetic and phenotypic variations (e.g. Palkovacs & Post 2008; Post *et al.* 2008) are important for testing the importance of eco-evolutionary dynamics in empirical systems (Laland *et al.* 1999).

The ecological literature is replete with examples of species that strongly impact the communities and ecosystems in which they reside (table 1), which we will call niche construction. Major mechanisms for niche construction include consumption, nutrient excretion (both inputs and recycling) and physical habitat alteration (table 1). Strongly interacting species are often well recognized as keystone species (Brooks & Dodson 1965; Paine 1966; Power *et al.* 1996), ecosystem engineers (Jones *et al.* 1994), foundation or dominant species (Whitham *et al.* 2006) and species that alter nutrient cycles through translocation or recycling (Jefferies *et al.* 1994; Post *et al.* 1998; Naiman *et al.* 2002; Vanni 2002; Schindler *et al.* 2003). All these types of species have strong impacts on the communities and ecosystems in which they reside, and, therefore, have the potential for niche construction. Species that have little or no impact on their community or ecosystem, either because their *per capita* interactions are weak (Paine 1992) or because they are rare members of the community, are less likely to produce eco-evolutionary feedbacks within their community or ecosystem. It is also important to note that effect size and duration may be important. Large, short-term effects on an ecosystem or community may not be sufficient to produce selection and subsequent evolution (see §3*b* below).

The definition of a species as a strong interactor often depends upon the ecological context being considered (Menge *et al.* 1994; Norkko *et al.* 2006). For example, the seastar *Pisaster* is the archetypal keystone species (Paine 1966), but its impact on intertidal food webs is much less in wave-protected sites than along wave-exposed shorelines (Menge *et al.* 1994). Likewise, dominant or foundational species in one habitat may be rare in another habitat, species moving nutrients into low-nutrient environments are likely to have greater effects on ecosystem function than species moving nutrients into high-nutrient environments, and species that have strong effects on communities and ecosystems when found in low-diversity communities may have much less impact on communities or ecosystems when found in high-diversity communities.

Our use of the term niche construction differs from that of Laland *et al.* (1999) and Odling-Smee *et al.* (2003) because it includes cases where an organism changes its environment (niche), even where that change does not feed back to influence its subsequent evolution (similar to Dawkins’ (2004) use of niche change). By separating the effect of an organism on its environment (niche construction *sensu* D.M.P. and E.P.P.) from the evolutionary response of the organism, we hope to make it clear that eco-evolutionary

Table 1. Well-studied examples of organisms that strongly shape their environment through nutrient cycling or translocation, consumption or habitat modification. (These organisms and others similar to them are candidates for eco-evolutionary feedbacks.)

taxonomic group	mechanism	sources
<i>plants</i>		
big bluestem (<i>Andropogon gerardii</i>)	habitat modification nutrient cycling	Smith & Knapp (2003)
dominant tree species (e.g. <i>Populus</i> spp., <i>Acer</i> spp., <i>Quercus</i> spp.)	habitat modification nutrient cycling	Likens <i>et al.</i> (1970), Madritch & Hunter (2002) and Whitham <i>et al.</i> (2006)
Eurasian water milfoil (<i>Myriophyllum spicatum</i>)	habitat modification nutrient cycling	Carpenter (1980) and Carpenter & Lodge (1986)
<i>Myrica faya</i>	nutrient cycling	Vitousek <i>et al.</i> (1987)
<i>invertebrates</i>		
crayfish (e.g. <i>Orconectes rusticus</i>)	consumption habitat modification nutrient cycling	Lodge & Lorman (1987), Lodge <i>et al.</i> (1994) and Covich <i>et al.</i> (1999)
earthworms (e.g. <i>Lumbricus</i> spp.)	consumption habitat modification nutrient cycling	Bohlen <i>et al.</i> (2004)
spiders (e.g. <i>Phidippus rimator</i>)	consumption	Schmitz (2008)
starfish (<i>Pisaster ochraceus</i>)	consumption	Paine (1966) and Menge <i>et al.</i> (1994)
zebra mussel (<i>Dreissena polymorpha</i>)	consumption habitat modification nutrient cycling and translocation	Arnott & Vanni (1996), MacIsaac (1996) and Strayer <i>et al.</i> (1999)
<i>fish</i>		
alewife (<i>Alosa pseudoharengus</i>)	consumption habitat modification (indirect) nutrient cycling and translocation	Brooks & Dodson (1965), Durbin <i>et al.</i> (1979), Kraft (1993) and Post <i>et al.</i> (2008)
gizzard shad (<i>Dorosoma cepedianum</i>)	consumption nutrient cycling	Devries & Stein (1992), Stein <i>et al.</i> (1995) and Schaus & Vanni (2000)
largemouth bass (<i>Micropterus salmoides</i>)	consumption	Carpenter <i>et al.</i> (1987), Mittelbach <i>et al.</i> (1995) and Post <i>et al.</i> (1997)
Pacific salmon (<i>Oncorhynchus</i> spp.)	nutrient cycling and translocation	Donaldson (1969), Schindler (1992), Bilby <i>et al.</i> (1996), Finney <i>et al.</i> (2002), Naiman <i>et al.</i> (2002) and Schindler <i>et al.</i> (2005)
peacock bass (<i>Cichla ocellaris</i>)	consumption	Zaret & Paine (1973)
<i>reptiles and amphibians</i>		
Anolis lizards (<i>Anolis</i> spp.)	consumption	Schoener & Spiller (1996) and Schoener & Spiller (1999)
brown tree snake (<i>Boiga irregularis</i>)	consumption	Fritts & Rodda (1998)
<i>birds</i>		
double-crested cormorants (<i>Phalacrocorax auritus</i>)	consumption	Madenjian & Gabrey (1995), Mills <i>et al.</i> (2003), Rudstam <i>et al.</i> (2004) and Dalton <i>et al.</i> (in press)
seabirds (e.g. <i>Larus</i> spp., <i>Phalacrocorax</i> spp.)	consumption nutrient cycling and translocation	Bosman & Hockey (1986), Bosman <i>et al.</i> (1986), Wootton (1991) and Wootton (1995)
snow geese (<i>Chen caerulescens</i>)	consumption nutrient cycling	Bazely & Jefferies (1985), Jefferies <i>et al.</i> (1994), Post <i>et al.</i> (1998) and Kitchell <i>et al.</i> (1999)
<i>mammals</i>		
beaver (<i>Castor canadensis</i>)	consumption habitat modification nutrient cycling	Naiman <i>et al.</i> (1988), Jones <i>et al.</i> (1994) and Wright <i>et al.</i> (2002)
pocket gopher	habitat modification nutrient cycling	Huntly & Inouye (1988)
sea otter (<i>Enhydra lutris</i>)	consumption habitat modification (indirect)	Estes & Palmisan (1974)
elephants (<i>Loxodonta africana</i>)	habitat modification	Naiman (1988) and Jones <i>et al.</i> (1994)

feedbacks result from the convergence of the two processes, both of which often operate independently. We believe this addresses the criticism that niche construction theory (*sensu* Odling-Smee *et al.* 2003) is

overly broad because it implies that all processes that shape the environment cause subsequent evolution (Dawkins 2004; Brodie 2005). Niche construction is therefore not limited to the active engineering of the

environment but includes all of the by-products of living (eating, excreting, nutrient uptake and mineralization, etc.), and, as we discuss below, eco-evolutionary feedbacks at the community and ecosystem level can emerge from both direct engineering and the by-products of living (contrary to the arguments of Dawkins (2004) and Brodie (2005)).

In order for the eco-evolutionary feedbacks to occur, populations must not only shape their environment but also possess the ability to evolve in response to selection caused by the changes in the environment. Factors that might prevent a population from responding to niche construction are the same factors that constrain adaptive evolution generally. These factors include genetic constraints, including a lack of genetic variation and low heritability in the traits under selection, and demographic or ecological constraints, such as the swamping effects of genetic drift and gene flow and strong selection from extrinsic environmental drivers.

Finally, for eco-evolutionary feedbacks to emerge, both niche construction and evolution need to occur at congruent time-scales. This does not imply that evolution must be rapid or ecological change must be slow, but rather that the time-scale of change is sufficiently similar that it allows the dynamic feedback between evolutionary and ecological changes (Laland *et al.* 1999; Lewontin 2000). There is rapidly growing evidence for widespread rapid evolution among many traits and many organisms (Thompson 1998; Hairston *et al.* 1999; Hendry & Kinnison 1999; Hendry *et al.* 2000), and strong evidence for congruent time-scales in a few potential eco-evolutionary systems (Hairston *et al.* 2005). However, we stress that evolution does not have to be rapid for eco-evolutionary feedbacks to emerge. Slow niche construction caused by slow rates of evolution (and the reciprocal) are as likely to create eco-evolutionary feedbacks as rapid evolution and rapid niche construction. We also stress that it is not generation time *per se* that determines temporal congruence (although it might be related), but rather the rates of evolution and ecological change (or duration of niche construction), which need to be congruent. For example, niche construction must last long enough to cause evolution (Odling-Smee *et al.* (2003) call this 'ecological inheritance'), and evolution must occur fast enough to feed back and influence the niche. A discontinuity in the time-scale of ecological and evolutionary responses is one of the probable disruptions to the complete eco-evolutionary feedback.

Intraspecific variation (Whitham *et al.* 2006; Post *et al.* 2008) is not a requisite for eco-evolutionary feedbacks, but it is critical for testing the importance of eco-evolutionary feedbacks for ecological and evolutionary dynamics in most natural systems. Variation among populations or experimental units provides the opportunity to break apart the dynamics of the feedback and to test the importance of the feedback for ecological interactions and evolutionary dynamics (e.g. Yoshida *et al.* 2003; Palkovacs & Post 2008; Post *et al.* 2008). For example, as we outline in more detail below, intraspecific variation in migratory behaviour and the strength of niche construction among populations of alewives were central to documenting the importance of eco-evolutionary feedbacks for alewife

populations (Palkovacs & Post 2008; Palkovacs *et al.* 2008; Post *et al.* 2008), and variation in evolvability among experimental populations was used to test the importance of eco-evolutionary interactions in a rotifer–algae predator–prey system (Yoshida *et al.* 2003). Intraspecific variation in traits related to niche construction may also represent the initial stages in ecological speciation (Knox *et al.* 2001; Calsbeek *et al.* 2007), suggesting that studies of the origin and ecological implications of intraspecific variation (Bailey *et al.* 2006; Whitham *et al.* 2006; Post *et al.* 2008) may be of critical importance to understanding the origin of species diversity.

3. EMPIRICAL EXAMPLES

Here, we summarize evidence for potential eco-evolutionary feedbacks in community and ecosystem ecology in five empirical systems: algal–rotifer chemostats (Yoshida *et al.* 2003); alewife–zooplankton communities in eastern North American lakes (Brooks & Dodson 1965; Palkovacs & Post 2008; Post *et al.* 2008); guppies in the streams of Trinidad (Reznick *et al.* 1997; Palkovacs *et al.* 2009); Darwin's finches of the Galápagos Islands (Grant 1986; Hairston *et al.* 2005; Grant & Grant 2006); and poplar trees of western North America (Whitham *et al.* 2006). Using these examples, we outline evidence for niche construction, the evolutionary response to niche construction and the processes that break apart eco-evolutionary feedbacks. In all five examples, the whole eco-evolutionary feedback is likely, but perhaps not fully documented, producing a mosaic of evidence for feedbacks in natural systems.

(a) *Algal–rotifer chemostats*

Using algal–rotifer chemostats, Yoshida *et al.* (2003) demonstrated experimentally that rapid evolution can alter predator–prey dynamics, consistent with some theoretical predictions (Abrams 2000). The experiment highlights a key requirement for eco-evolutionary feedbacks. Yoshida *et al.* (2003) compared the dynamics of algal–rotifer systems where evolution could occur (cultures initiated with multiple algal clones) with the dynamics in systems where evolution was not possible over the time-scale of the experiment (cultures initiated with a single clone). The lack of genetic variation in the single-clone treatment prevented evolution and provided the critical control for testing the importance of rapid evolution in modifying predator–prey dynamics. The lack of potential for adaptive evolution, either because of limited genetic variation among traits under selection, strong external selection (but see Laland *et al.* 1999) or strong gene flow from other populations, will prevent eco-evolutionary feedbacks. Subsequent research has shown that variation in anti-predator defence among algal genotypes can strongly influence rotifer growth rates and densities, which feed back to influence gene frequencies in algal populations (Yoshida *et al.* 2004; Meyer *et al.* 2006).

(b) Alewife: migration, foraging traits and zooplankton communities

The eco-evolutionary feedback in the alewife system revolves around interactions between young-of-the-year (YOY) alewives and zooplankton, their primary prey (Palkovacs & Post 2008; Post *et al.* 2008). The key players are anadromous alewives, which move between freshwater and marine habitats, landlocked alewives that spend their entire life in freshwater and the zooplankton upon which both prey. Migratory differences between landlocked and anadromous alewives are set up by differences in spatial openness among lakes. Lakes connected to the ocean contain anadromous alewife populations, while lakes isolated from the ocean contain either landlocked alewife populations or no alewives (Post *et al.* 2008). Key traits of alewife populations include the duration of residence in freshwater (approx. six months for anadromous alewives and year-round for landlocked alewives) and morphology related to feeding on zooplankton prey (mouth gape and gill raker spacing).

Anadromous alewives spawn in coastal lakes, ponds and streams from South Carolina, USA, to Nova Scotia, Canada (Scott & Crossman 1973). The adults spawn in March–May and YOY spend their first summer of life in freshwater before migrating to the ocean (Post *et al.* 2008). Adults remain resident in the spawning lakes and ponds for only a few weeks (Cooper 1961; Kissil 1974), and are not thought to feed during their spawning migration.

The zooplankton communities in lakes with anadromous alewives go through pronounced seasonal changes driven by predation by YOY (figure 1; Post *et al.* 2008). In the spring, just after ice out, the zooplankton community is dominated by a large biomass of large-bodied zooplankton (e.g. *Daphnia* spp. and *Mesocyclops edax*; Post *et al.* 2008). Once YOY become large enough to prey upon large-bodied zooplankton in mid-July (Palkovacs & Post 2008), they rapidly extirpate large-bodied zooplankton from the water column (Post *et al.* 2008). Through the rest of the summer and autumn, predation by alewives is sufficient to keep large-bodied zooplankton from reinvading and the zooplankton community is dominated by a low biomass of small-bodied zooplankton (figure 1; Post *et al.* 2008). Except in early summer when gape-limited, anadromous alewives always prey upon the largest zooplankton in the water column (positively size selective; Palkovacs & Post 2008). Once the final YOY emigrate in the autumn, large-bodied zooplankton re-establish over the winter and early spring, and by the time adults return to spawn the zooplankton community is once again dominated by a high biomass of large-bodied zooplankton (figure 1; Post *et al.* 2008). In anadromous populations, alewives have a very strong impact on zooplankton community structure (Post *et al.* 2008), but the rapid ecological recovery of the zooplankton communities, most probably from resting eggs in the sediments, means that the effects of strong niche construction do not persist to affect the evolution of subsequent generations (Palkovacs & Post 2008).

The small streams through which alewives migrate to spawn were probably regularly blocked by beaver dams (Naiman *et al.* 1988) and wind throws. Alewives

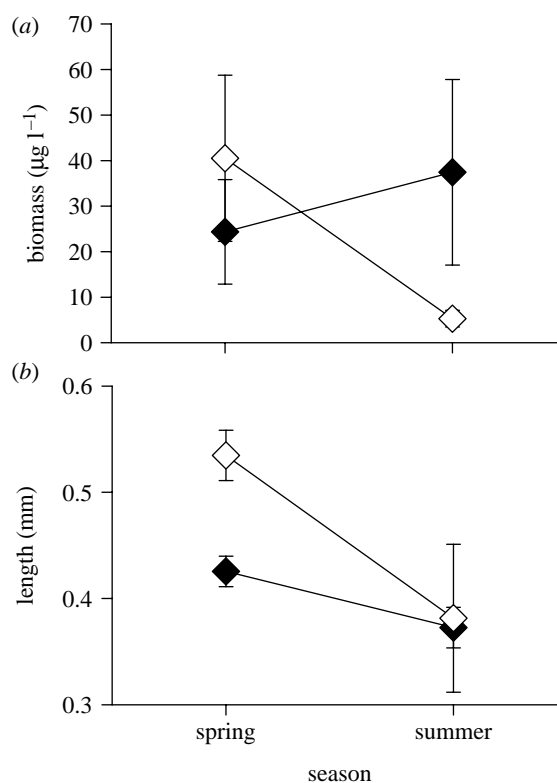


Figure 1. Mean crustacean (a) biomass and (b) length in spring (late March to April) and summer (July and August) in lakes with anadromous alewives (unfilled diamonds) and landlocked alewives (filled diamonds). Error bars are 1 s.e. Data modified from Post *et al.* (2008).

are able to move through very narrow gaps in a dam but are not able to jump over a complete blockage (D. M. Post 2007, personal observation); thus, an active beaver dam or large wind throw could have easily blocked migration into and out of coastal watersheds (e.g. Havey 1973). YOY alewives isolated from the ocean would have to overwinter in freshwater until access was restored to the ocean. While there are no good estimates of the duration of wind throws and beaver dams as a blockage to alewife migration, the average duration of beaver ponds on the landscape (Naiman *et al.* 1988) suggests that beaver dams and wind throws could block migration for years to decades. Thus, throughout their evolutionary history, some populations of anadromous alewives probably became landlocked for short periods of time (years to decades) behind these natural barriers.

Beaver dams and wind throws would have represented a greater obstacle for returning adults than for emigrating juveniles. Thus, these blockages may have served mainly to disrupt gene flow between the genotypes within a population that display the tendency for landlocking and those that display the tendency for anadromy. Evidence from salmonids suggests that various aspects of anadromous migratory behaviour have a heritable genetic component (Hendry *et al.* 2004). Therefore, the disruption of gene flow in the context of natural stream blockages may have played an important role in the evolution of landlocked alewife populations.

In New England, the barrier to migration between freshwater and the ocean formed by beaver dams

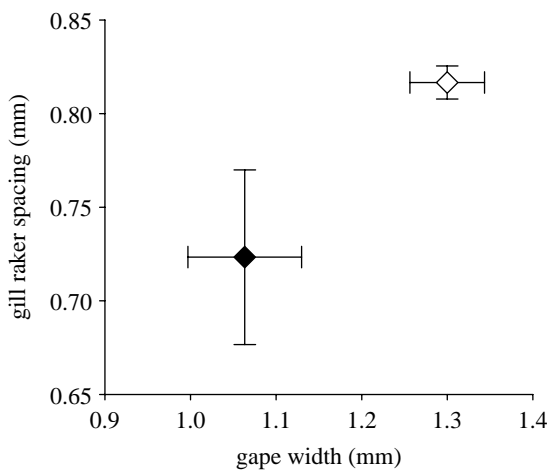


Figure 2. Mean (± 1 s.e.) size-standardized gape width (mm) and gill raker spacing (mm) for anadromous (unfilled diamond) and landlocked alewives (filled diamond). Data are from three landlocked alewife populations (Pattagansett, Quonnipaug and Rogers) and three anadromous populations (Bride, Dodge and Gorton) in Connecticut, USA. Data modified from Palkovacs & Post (2008) and Post *et al.* (2008).

and wind throws has been replaced in most coastal watersheds by dams built by humans. This has created landlocked populations isolated from the coastal ocean for much longer periods of time than previously experienced (Palkovacs *et al.* 2008). Across the landscape, landlocked populations derive either from human stocking efforts or naturally from anadromous ancestors (Palkovacs *et al.* 2008). The interaction between alewives and their zooplankton prey in lakes is fundamentally altered by the change in migratory behaviour, which changes the duration of residence of alewives in freshwater (Palkovacs & Post 2008; Post *et al.* 2008). Intense year-round predation pressure by landlocked alewives eliminates large-bodied prey and produces a zooplankton community of relatively low biomass of small-bodied zooplankton throughout the year (figure 1; Palkovacs & Post 2008; Post *et al.* 2008). The constant exposure of landlocked alewives to only small-bodied zooplankton (the newly constructed niche) leads to strong selection for traits related to foraging on small-bodied zooplankton (Palkovacs & Post 2008; Post *et al.* 2008). As a result, contemporary landlocked populations have smaller gape and narrower spacing between gill rakers than ancestral anadromous populations (figure 2; Palkovacs & Post 2008). Furthermore, while anadromous alewife populations are positively size selective for zooplankton prey, landlocked alewives are not size selective and prey upon the most abundant prey (typically, small-bodied zooplankton; Palkovacs & Post 2008).

Thus, in the alewife system, access to the ocean (spatial openness) mediates migratory behaviour and the duration of residence in freshwater. Both anadromous and landlocked alewives structure zooplankton communities (Post *et al.* 2008), but the outmigration of anadromous alewives allows zooplankton communities to recover each year, preventing niche construction from influencing the evolution of subsequent generations and disrupting eco-evolutionary feedbacks (Palkovacs & Post 2008). Eco-evolutionary feedbacks are disrupted because the time-scale of niche construction

(less than 1 year) is short relative to the time-scale required for selection to act upon foraging traits (multiple generations; Palkovacs & Post 2008; Post *et al.* 2008). By contrast, landlocked alewives permanently structure the zooplankton community (Post *et al.* 2008), which then selects for traits that improve feeding performance on small-bodied zooplankton (gape, gill raker and prey size preferences; Palkovacs & Post 2008). The divergence in morphology and prey selectivity between anadromous and landlocked populations alter the ecological role of alewife in lakes, where phenotypic differences create different zooplankton communities and alter the strength of the trophic cascade caused by alewives (Post *et al.* 2008; Palkovacs & Post 2009).

(c) *Trinidadian guppies: life-history traits and nutrient cycling*

In the streams of Trinidad's Northern Range Mountains, guppies exist either in the presence or the absence of large predatory fish. Guppy populations show divergence in life-history traits that are associated with differences in predation pressure. Compared to guppies in low-predation environments, guppies in high-predation environments display earlier age and smaller size at maturity and give birth to more frequent clutches of smaller offspring (Reznick 1982; Reznick & Endler 1982; Reznick & Bryga 1996; Reznick *et al.* 1996). It is likely that life-history shifts have important consequences for population dynamics (Kokko & López-Sepulcre 2007). Guppy populations at sites lacking predators reach higher densities than populations at sites with predators; these density differences may influence resource availability, the strength of intraspecific competition and subsequent guppy evolution (Grether *et al.* 2001; Reznick *et al.* 2001). Shifts in guppy life-history traits also directly influence the body size distribution of the guppy population at a given locality. Under conditions of equal biomass, a population dominated by more, smaller individuals (in this case, a high predation population) is expected to drive higher nutrient fluxes than a population dominated by fewer, larger individuals (in this case, low-predation populations; Vanni 2002; Hall *et al.* 2007). Higher nutrient fluxes may increase rates of primary production (Vanni & Layne 1997; Flecker *et al.* 2002).

A mesocosm experiment was performed to examine the effects of guppy life-history evolution on ecosystem processes (Palkovacs *et al.* 2009). The results show that high-predation guppy populations contributed approximately double the amount of N and P to the total nutrient pool via excretion compared to low-predation populations. Relative to nutrient levels in source water from the adjacent stream, nutrient contributions to mesocosms via guppy excretion drove an 11 per cent increase in N and an 83 per cent increase in P for high-predation populations compared with a 6 per cent increase in N and a 46 per cent increase in P for low-predation populations. This difference in excretion contributed to a significant increase in algal biomass in the high-predation treatment. Algal biomass may have been further influenced by evolutionary divergence in other guppy traits, including trophic morphology and dietary preferences. In turn, overall

changes in algal biomass may influence subsequent guppy evolution. For example, male guppy colour patterns (which are under both natural and sexual selection) are sensitive to the amount of algae-derived carotenoids available in the environment (Grether 2000; Grether *et al.* 2005). Therefore, evolutionary changes caused by biotic factors, such as predators, may have ecological effects at multiple levels of organization and may feed back to influence evolution in relatively unexpected ways.

(d) Avian seed predators: foraging traits and seed availability

Darwin's finches are famous for diverse beak sizes and shapes, which enable different populations and species to exploit different food resources across the Galápagos Islands (Lack 1947; Grant 1986). Within populations, beak size and shape can evolve rapidly in response to changes in seed availability (Grant & Grant 1995, 2002). Seed availability changes in response to rainfall patterns, but the link between seeds and rainfall may be mediated by finch predation. During periods of drought, finches deplete favoured seeds first, driving selection on finch traits that enable the exploitation of larger, harder seeds (Grant & Grant 2006). Thus, rather than rainfall driving finch evolution directly, it is likely that rainfall mediates the ability of finches to construct their niche. When rainfall is abundant, favoured seeds are plentiful and finches are unable to influence the overall distribution of seed sizes in the environment. However, during droughts, favoured seeds become limiting and finches can influence the abundance of different types of seeds. Thus, abundant rainfall may decouple the eco-evolutionary feedback between finches and seeds. The scenario outlined above is speculative—the degree to which finches can shape the size distribution of seeds and the effect this might have on the long-term composition of the plant community is not well known. However, information from another avian seed predator, the red crossbill, suggests that feedbacks between seed predators and plants may be common.

Red crossbills are specialist feeders that consume the seeds of lodgepole pines. In some isolated habitats, reciprocal selection between crossbills and pines is strong, and these two species co-evolve in an arms race (Benkman 1999; Benkman *et al.* 2001, 2003). This arms race takes subtly different forms in different localities and is thought to have contributed to the adaptive radiation of crossbills (Edelaar & Benkman 2006; Smith & Benkman 2007). Thus, crossbills influence the trajectory of their own evolution by shaping the availability of seed resources. However, this pattern is disrupted by the presence of another seed predator, the red squirrel. Where present, red squirrels, not crossbills, serve as the primary agent of selection on lodgepole pine cones (Benkman 1999; Benkman *et al.* 2001, 2003). Thus, the presence of red squirrels can decouple the co-evolutionary feedback between crossbills and pines.

From the standpoint of eco-evolutionary feedbacks, these examples illustrate two main points. First, co-evolutionary interactions may be viewed as a special case of eco-evolutionary interactions. Coevolution is the reciprocal evolutionary interaction between populations of two species, while eco-evolutionary feedbacks

emerge from the reciprocal interaction between a population and its environment (which could be a population of another species). Second, the strength of feedbacks may be contingent on abiotic or biotic factors. In the case of the finches, the existence of an eco-evolutionary feedback may depend on the amount of rainfall in a given year. In the case of the crossbills, the existence of coevolution depends on the presence or absence of a competitor species. Abiotic and biotic factors that shape the strength of feedbacks may create the landscape-scale templates that shape environmental (i.e. ecological) and organismal (i.e. evolutionary) diversity. This perspective extends the scope of geographic mosaics from coevolving systems (Thompson 2005) to eco-evolutionary systems, as we will discuss further. The ability of spatial structure to promote ecological and evolutionary diversity in the context of eco-evolutionary feedbacks is supported by experimental work with microbial systems (Habets *et al.* 2006) and our work with alewives (Palkovacs & Post 2008; Post *et al.* 2008). An emerging frontier in the study of eco-evolutionary feedbacks is the examination of the importance of spatial structure in natural ecosystems.

(e) Populus: leaf tannins and soil processes

Foundation species, such as trees of the genus *Populus*, can control community and ecosystem processes through their chemical effects on leaf litter (Whitham *et al.* 2006; Schweitzer *et al.* 2008b). Intraspecific phenotypic variation in leaf chemistry has been shown to drive variation in soil processes in multiple terrestrial plant species (Treseder & Vitousek 2001; Madritch & Hunter 2002; Schweitzer *et al.* 2004). In *Populus*, condensed tannin levels in leaves, which are under genetic control, strongly impact decomposition rates, nitrogen mineralization rates and microbial community composition of riparian forest in western North America (Schweitzer *et al.* 2004, 2005a,b, 2008a; Madritch *et al.* 2006). Trees create their own soil microhabitats; therefore, genotypes with higher concentrations of foliar condensed tannins (which impede nutrient release) must cope with decreased nutrient availability in the soil. If eco-evolutionary feedbacks are important, *Populus* genotypes with high foliar tannin levels would be expected to display adaptations to cope with limited nutrients. Indeed, there is a strong positive correlation between leaf tannin levels and the production of fine roots, providing indirect evidence for an eco-evolutionary feedback in *Populus* driven by soil processes and nutrient availability (Fischer *et al.* 2006). Theoretical results also support the hypothesis that eco-evolutionary feedbacks may be important for the ecology and evolution of plant litter–nutrient uptake systems (Kylafis & Loreau 2008). However, the ability of a plant genotype to shape its nutrient environment is influenced by ecological interactions, including the presence of other tree species (Madritch & Hunter 2004), herbivores (Madritch *et al.* 2007) and nutrient loading (Madritch *et al.* 2006). Thus, similar to the example of the red crossbills, the potential for and strength of feedbacks in *Populus* are probably mediated by interactions among species and the strength of external drivers such as nutrient loading.

4. COMPLEMENTARY PERSPECTIVES

The perspective we outline here complements other emerging frameworks for synthesizing contemporary evolution with community and ecosystem ecology, including niche construction (*sensu* Odling-Smee *et al.* 2003), community genetics, evolving meta-communities and the geographic mosaic of coevolution (reviewed in Johnson & Stinchcombe 2007; Urban *et al.* 2008). These frameworks share features, such as the recognition that contemporary evolution influences species' interactions; however, they differ in the specific patterns and processes they seek to explain. The niche construction perspective (*sensu* Laland *et al.* 1999; Odling-Smee *et al.* 2003) explicitly recognizes the ability of organisms to shape the biotic and abiotic attributes of their environments, and the potential for those changes to influence subsequent adaptive evolution. The community genetics approach focuses on the impact of genetic variation in foundation species on the structure of ecological communities (Bailey *et al.* 2006; Whitham *et al.* 2006). The evolving meta-community approach focuses on the ecological and evolutionary mechanisms that promote species' coexistence (Urban & Skelly 2006). The geographical mosaic theory seeks to understand why two-way species' interactions vary across the landscape as a function of ecological and evolutionary processes (Thompson 2005). In developing our eco-evolutionary feedbacks framework, we have integrated aspects of all these approaches. Similar to the geographical mosaic of coevolution, we focus on understanding what structures biodiversity across the landscape as a function of reciprocal interactions and recognize the importance of eco-evolutionary 'hot spots' and 'cold spots' driven by landscape-scale variation in abiotic and biotic interactions. However, our focus is not strictly on reciprocal evolutionary interactions, but on reciprocal interactions between evolutionary and ecological processes. Similar to community genetics, we are interested in how evolutionary changes in strongly interacting species influence community structure (Bailey *et al.* 2006; Whitham *et al.* 2006). However, we are also interested in how changes to ecological communities feed back to influence the trajectory of evolution.

Finally, we draw heavily from the niche construction perspective of Laland *et al.* (1999) and Odling-Smee *et al.* (2003), but here we explicitly separate the process of structuring the environment (niche construction *sensu* D.M.P. and E.P.P.) from the process of evolution by natural selection, producing a framework that reflects the independence of the two processes required for eco-evolutionary feedbacks (Brodie 2005). Ultimately, understanding what drives changes in community structure involves understanding the ecological and evolutionary mechanisms mediating coexistence, which itself involves understanding how coevolution operates in multi-species communities.

The various frameworks emerging to integrate contemporary evolution into community and ecosystem ecology complement each other by seeking to understand the same core processes from slightly different perspectives.

5. CONCLUSIONS AND FUTURE DIRECTIONS

We believe that the future direction of eco-evolutionary dynamics is in the study of feedbacks between ecology and evolution. Such feedbacks, where they exist, have the potential to alter the direction of evolution and strongly modify the role of species in ecosystems. In the alewife system, ecological isolation of lakes from the ocean has altered the direction of evolution, and phenotypic differentiation in feeding morphology and prey selectivity has fundamentally altered the ecological role of alewives in coastal lakes. Likewise, life-history evolution in Trinidadian guppies has altered their ecological role in streams, which has the potential to feed back and influence the evolution of guppy traits. In each of our empirical examples, the eco-evolutionary feedback (or potential for feedback) has fundamentally altered both the ecological role of the organism and the trajectory of evolution.

Despite these compelling examples, there currently exists a handful of empirical systems where the effects of phenotypic (or genetic) differences on community and ecosystem ecology are well resolved (alewife, *Populus*) or where the evolution of phenotypic differences are well resolved (guppies and finches), but not a single system where the evidence of dynamic feedbacks is without gaps. Furthermore, the constraints on eco-evolutionary feedbacks have not been well tested. Future research should work towards providing better evidence for the occurrence of eco-evolutionary feedbacks in a variety of systems and better tests of the conditions under which feedbacks may be important. More complete evidence for feedbacks in empirical systems requires documenting (i) the strength of niche construction, (ii) the strength of selection and the direction of evolution in the constructed environment, and (iii) the strength of niche construction after evolution. Strong external drivers may be able to overwhelm eco-evolutionary feedbacks, but there is some theoretical evidence that even strong donor control of resources or high rates of gene flow can still allow for niche construction and selection (Laland *et al.* 1999). Future research should explore the range of extrinsic environmental factors which allow for niche construction, and the range of resulting selection pressures which allow for local adaptation. Future work should also test the assumption that niche construction and evolution must occur at congruent time-scales. Studies across a range of disparity in time-scales would provide important insights into when feedbacks ultimately break apart and interactions become unidirectional.

There is also a question of where eco-evolutionary feedbacks are most likely to be important. Feedbacks are mostly likely to emerge for species that strongly alter their environment (table 1). Keystone, dominant or foundation species and ecosystem engineers are all likely candidates for eco-evolutionary feedbacks because they interact strongly with their environment, and intraspecific variation among or within populations can alter the role of the species in the ecosystem and alter the strength of the eco-evolutionary feedback. However, species not recognized as having strong effects on their environment in species-rich communities might have stronger effects in species-poor

communities. For example, strong eco-evolutionary feedbacks may be initiated when species-poor islands are colonized by populations from species-rich mainlands (e.g. many invasive species). The phenotypic and genetic variations produced by eco-evolutionary feedbacks may be critically important for understanding the early stages of ecological speciation and adaptive radiation (Habets *et al.* 2006). Clades that exhibit diversification in traits related to foraging, excretion and habitat modification are all likely candidates for study.

We believe that studying eco-evolutionary feedbacks is important because it pushes evolutionary biologists to recognize that organisms can shape their environment in ways that alter the outcome of evolution, and it pushes ecologists to recognize that contemporary evolution creates phenotypic differences that can alter the role of a species in a community or ecosystem at contemporary time-scales. In this way, the study of eco-evolutionary feedbacks focuses attention on the bidirectional interactions that unify ecology and evolution, and highlights the importance of conserving both ecological and evolutionary diversity in nature (e.g. Stockwell *et al.* 2003; Kinnison & Hairston 2007).

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