

CHAPTER 13

Ecosystem consequences of behavioural plasticity and contemporary evolution

Eric P. Palkovacs and Christopher M. Dalton

➤ Overview

Animal behaviour is a critical, but underappreciated, link between human activity and ecosystem processes. In this chapter, we review the impacts of behavioural trait changes on ecosystems. Such effects are often the result of changes in traits related to consumption and nutrient cycling. Phenotypic plasticity and contemporary evolution are two mechanisms of rapid behavioural trait change that shape ecosystem processes. However, the effects of plasticity and evolution have typically been considered in isolation. We propose a framework to integrate the ecosystem effects of plasticity and evolution using a reaction norm approach. This method can be used to parse the contributions of plasticity, evolution, and the evolution of plasticity to ecosystem change and may be applied to predict the effects of human-driven trait change on ecosystems.

13.1 Introduction

Animal behaviour is a central theme in evolutionary ecology, population ecology, and community ecology. In contrast, the role of behaviour in shaping ecosystems has received much less attention. Some well known examples of behaviour moulding ecosystem processes do exist, such as the impacts of spawning Pacific salmon *Oncorhynchus* spp. and foraging brown bears *Ursus arctos* on ecosystem structure and function in the freshwaters and forests of the American Pacific Northwest. In these coastal habitats, migrating salmon enter freshwaters from the ocean, importing large quantities of marine-derived nutrients into otherwise nutrient-poor streams. These nutrients are then transported far into the forest by foraging bears, with large effects on both aquatic and terrestrial ecosystems (Schindler et al. 2003). Recent evidence supports the notion that behaviour is a widespread and potent

driver of ecosystem processes (Schmitz et al. 2008). Despite such evidence, animal behaviour has yet to occupy a central place in ecosystem ecology. A greater integration of animal behaviour and ecosystem ecology can enable evolutionary theory to be applied to predict future ecosystem change (López-Sepulcre 2011). Predicting such changes is an urgent goal because ecosystems, and the services they provide, are being rapidly altered by human activity.

Two well-characterized mechanisms by which animal behaviour may shape ecosystem processes are consumption and nutrient cycling. The ecosystem effects of consumption, or the threat of being consumed, have been explored through the related concepts of keystone predation (Paine 1969; Power et al. 1996) and trophic cascades (Hairston et al. 1960; Terborgh et al. 2010). The ecosystem effects of nutrient cycling have been explored with respect to nutrient translocation, rates of recycling, and the

chemical composition of excreted wastes (Vanni 2002). With the notable exception of behaviourally-mediated trophic cascade research (Schmitz et al. 1997), few ecosystem studies have historically included a detailed consideration of short-term behavioural trait change. Because human-driven environmental change is happening rapidly, it is precisely these short-term trait changes that will mediate the role of behaviour in shaping ecosystem responses to human activity.

Humans can change the behaviours of animals by influencing two mechanisms of short-term trait change—phenotypic plasticity and contemporary evolution. Because plasticity can emerge within a single generation, ecologists have long recognized the potential for plasticity to mould ecological interactions (Miner et al. 2005). The nascent study of eco-evolutionary dynamics has added evolution to the mix, establishing that contemporary evolution (sometimes called rapid evolution) can also impact ecological processes (Post and Palkovacs 2009; Schoener 2011). Despite studies showing that either plasticity or contemporary evolution can influence ecosystem processes independently, there presently exists a very limited understanding of the joint effects of plasticity *and* evolution on ecosystems.

Here we review two well-established mechanisms by which behaviours can shape ecosystems—consumption and nutrient cycling. We then describe how phenotypic plasticity and contemporary evolution can shape behavioural traits that can then impact ecosystem processes. Finally, we propose a framework to integrate the ecosystem effects of phenotypic plasticity and evolutionary trait changes using a reaction norm approach, which explicitly recognizes that plasticity and evolution operate together to shape the ecosystem consequences of behavioural trait change. This framework complements the approach of Ellner et al. (2011), which similarly decomposes sources of ecological change into their evolutionary and plastic (or other non-heritable) components.

13.2 Behavioural effects on ecosystems

For the purpose of this review, we broadly define ecosystems as bounded sets of interacting organ-

isms and their associated abiotic environment. Ecosystem processes thus entail direct and indirect linkages between biotic and abiotic components, and an ecosystem effect occurs when a change in one part of the system drives changes throughout the system via these linkages. Ecosystem change of this sort can be detected by measuring aggregate traits of the system such as primary productivity and decomposition. Dramatic shifts in ecosystem processes often co-occur with shifts in community structure (Hooper et al. 2005). Therefore, we use the term ecosystem effect to denote both measured changes to ecosystem processes and changes in community structure, as the two are commonly inter-related.

13.2.1 Consumption

Acquisition of food resources represents one of the strongest interactions between animals and their environment. Many cases of demonstrated ecosystem effects by animals result from consumption or the threat of being consumed. Consumption by predators can alter communities directly, by reducing the abundance of a preferred prey, and indirectly, by altering how prey interact with other community members through changes in their behaviour (Schmitz et al. 2004; also see Chapter 10). These changed communities can then impact ecosystem processes. Such multi-trophic interactions and their ecosystem effects have spawned fundamental ecological concepts, including keystone species and trophic cascades.

The term keystone species was coined by Paine (1969) to describe the strong effects that a predator can have on community composition if it selectively preys upon a dominant competitor. The original example of this phenomenon is the purple sea star *Pisaster ochraceus*, that fundamentally changes prey communities by selectively consuming a competitive-dominant species of mussel *Mytilus californianus*, thereby creating space for other sessile invertebrates. Communities with *Pisaster* are more diverse than those without, which became monocultures of the competitive dominant mussel (Paine 1966). Research in other systems found that regula-

tion of consumers by predators directly affects intertidal primary production (Silliman and Bertness 2002). Subsequent adoption of the term 'keystone species' in other systems led to a broadened definition that made keystone species nearly inseparable from 'ecosystem effects', where a keystone species is any species whose effect on the ecosystem is large relative to its abundance in that system (Power et al. 1996). Under this broad definition, many other means by which predators shape ecosystems become subject to the term keystone species, including species that initiate trophic cascades.

The classic density-mediated trophic cascade results when the addition of a predator reduces the abundance of herbivores, which increases the abundance of primary producers (Hairston et al. 1960). Density-mediated trophic cascades can cause changes to diverse ecosystem processes, such as primary productivity, decomposition, and nutrient cycling (Pace et al. 1999). However, trophic cascades can also result from predator-induced change in prey behaviour, a phenomenon termed a behaviourally-mediated trophic cascade (Schmitz et al. 1997). Such effects occur when the threat of predation induces predator-avoidance behaviour in prey (a non-consumptive effect), thereby reducing allocation of prey effort to feeding. Reduced feeding activity can induce trophic cascades, even if the actual abundance of consumers does not change (Schmitz et al. 2004).

Such a pattern has been demonstrated in many systems, with one compelling example being the interaction between wolves *Canis lupus*, elk *Cervus canadensis*, and woody vegetation in the Rocky Mountains of North America. In this system, wolves have been reintroduced to areas where they had previously been extirpated. Reintroduction of wolves altered the foraging behaviour of elk, inducing them to forage less often and away from preferred aspen stands (Fortin et al. 2005). This change in elk behaviour resulted in both redistribution of woody vegetation across space and an overall increase in woody vegetation abundance (Beyer et al. 2007). Other examples of behaviourally-mediated trophic cascades abound in the literature, in ecosystems including lakes, streams, marine

intertidal, open ocean, terrestrial grassland, and forest (Schmitz et al. 2004).

In addition to changes in prey behaviour, changes in predator behaviour can also impact trophic cascades. A high profile example of such an effect has been suggested in the Pacific Northwest of North America, where a shift in prey choice by killer whales *Orcinus orca* may have interrupted the trophic cascade between sea otters *Enhydra lutris*, sea urchins *Strongylocentrotus spp.*, and kelp forests. Historically, sea otters were apex predators in coastal areas and reduced the abundance of the dominant herbivore, sea urchins; however, a reduction in alternate prey sources may have led killer whales to switch prey and consume sea otters. Numerical reduction in sea otter abundance reduced predation on sea urchins and increased herbivory of kelp forests, resulting in ecosystem-altering changes at each trophic level (Estes et al. 1998).

Finally, the interacting effects of predator hunting behaviour and prey avoidance behaviour may have ecosystem consequences. Theory suggests that prey are especially likely to evolve behavioural avoidance mechanisms for sit-and-wait predators, whose sedentary and cryptic habits enable prey to use scent and chemical cues as reliable indicators of the presence of a predation threat (Preisser et al. 2007). Prey may not benefit from the same responses to active predators, whose mobility may enable them to move faster than their cues. If predator avoidance behaviour occurs more strongly in response to sit-and-wait predators than actively-hunting predators, such behavioural shifts can have ecosystem effects, for example on the strength of trophic cascades (Preisser et al. 2007). A theoretical study indicates that foraging mode of predators alters coexistence patterns among primary producers (Calcagno et al. 2011), and empirical studies demonstrate the strong role that predator foraging mode plays in structuring food webs and nutrient cycling through the behavioural and physiological responses of prey (Schmitz 2008; Lazzaro et al. 2009; Carey and Wahl 2010). In addition, prey escape mode can impact predator-prey interactions, yet no studies have explicitly examined how the escape mode of prey affects trophic cascades (Wirsing et al. 2010).

13.2.2 Nutrient cycling

The availability of nutrients can place important controls on ecosystems. If a nutrient critical for biological processes is scarce, animals can strongly influence the ecosystem by either increasing or decreasing the availability of that nutrient, which can affect ecosystem processes such as primary production and decomposition (Vitousek and Howarth 1991; Greenwood et al. 2007). One mechanism whereby animals can affect their chemical environment is through the release of waste. In this sense, animals act as chemical converters, ingesting compounds from the environment, modifying those compounds through physiological processes, and releasing excesses as waste that can impact nutrient availability in the ecosystem (McIntyre et al. 2008). For example, a study comparing nutrient excretion by two species of aquatic herbivore found that one species released higher levels of phosphorus waste than the other, increasing the availability of phosphorus, thereby increasing primary productivity (Knoll et al. 2009).

The amount and chemical composition of released wastes are controlled by numerous behavioural mechanisms including diet selection and activity level. Animals can alter the chemical composition of their waste by altering the chemical composition of their intake. Omnivorous consumers, in particular, can dramatically alter their chemical intake by switching food sources (often from autotrophic to heterotrophic sources). Such diet switches almost always result in changes in the amount and chemical form of nutrients released into the environment (Vanni 2002; Saba et al. 2009). The volume and chemical composition of waste products are also impacted by activity levels. Increases in metabolic activity, whether due to predation, increased competition, or altered foraging behaviour, may have the effect of increasing release of nitrogenous waste at the same level of phosphorus waste (Uliano et al. 2010). Since primary production in many terrestrial and aquatic systems is tightly controlled by the availability of nitrogen and phosphorus, changing the relative availability of these compounds through release of wastes can have profound ecosystem effects (Glaholt and Vanni 2005; McIntyre et al. 2008).

While much remains to be learned about how animal behaviour alters ecosystems via changed nutrient cycling within a single system, animals have repeatedly been shown to have important ecosystem effects by altering the spatial distribution of nutrients across the landscape. These effects are especially pronounced when animals move nutrients from ecosystems that are replete in nutrients to those that are nutrient starved, providing a nutrient subsidy to the recipient ecosystems (Flecker et al. 2010). For example, salmon are profoundly important to streams draining into the North Pacific. The critical role of salmon stems from their spawning migration, in which they carry nutrients from rich marine systems and deposit them in nutrient-poor streams as spawning excess and senesced somatic tissue. The nutrients relocated by salmon support a drastically altered stream community (Tiegs et al. 2009) and affect neighbouring terrestrial systems, as studies have found salmon-derived nutrients in trees and even songbirds (Christie et al. 2008).

While mass seasonal migrations like those of salmon are undoubtedly important for ecosystems, less dramatic movements within and between habitat patches can also influence critical ecosystem processes. Daily and small-scale movement patterns are behaviours that are often highly flexible and can have pronounced ecosystem effects when animals move nutrients both across and within ecosystem boundaries. Such effects can occur when animals ingest resources in one habitat and transport nutrients as waste products to another. For example, snow geese *Chen caerulescens* migrate daily from feeding areas in agricultural fields to roosting areas in relatively predator-free wetlands. By taking in nutrients from one ecosystem, agricultural fields, and depositing them as fecal matter in another, wetlands, snow geese provide massive nutrient inputs to roosting ponds equal to 40% and 75% of the total nitrogen and phosphorus loading into those wetlands (Post et al. 1998). Such cases of cross boundary subsidies are common in bird species, and the ecosystem consequences are variable and widespread (Schmitz et al. 2010). In another example, gizzard shad *Dorosoma cepedianum* consume detritus from the benthic zone of lakes. Following benthic feeding bouts, gizzard shad move into the pelagic zone,

where they excrete the nitrogen and phosphorus consumed from the benthos, enhancing phytoplankton production (Vanni et al. 2005). Coral reef fishes play a similar role in marine ecosystems. Several species of grunts *Haemulon flavolineatum* and *Haemulon plumieri* make nightly foraging excursions from coral reefs into surrounding seagrass beds. The daily return of fish to the safety of the reef results in the deposition of nutrients, providing a significant subsidy which may enhance the growth rate of corals (Meyer and Schultz 1985).

Predators can also impact the spatial distribution of nutrients by depositing prey carcasses across the landscape. For example, brown bears foraging on salmon carcasses often drag meals away from stream edges and into nearby riparian habitats, and their physical movement of the carcasses increases nitrogen load and carbon flux in those terrestrial soils (Holtgrieve et al. 2009). Similarly, wolves aggregate moose *Alces alces* carcasses on Isle Royal National Park, which provide a highly concentrated nutrient supply to growing plants (Bump et al. 2009). The presence of carcasses can alter competitive dynamics and shape the community structure of plants that establish in the new canopy.

13.3 Rapid behavioural trait change

Behaviour can play a critical role in determining how ecosystems function. Identifying key behavioural traits is important for understanding how anthropogenic environmental change may alter ecosystems. For traits to be important drivers of short-term ecosystem change, however, they must also be subject to rapid change under altered environmental conditions. Here we focus on two causes of rapid behavioural trait change—phenotypic plasticity and contemporary evolution—and their impacts on ecosystems.

13.3.1 Behavioural plasticity

Short-term behavioural trait changes can be the product of phenotypic plasticity in response to environmental cues. Such behavioural shifts can have strong ecosystem effects. As discussed above,

much existing research documents how predation affects consumer behaviour and how these behavioural changes can impact ecosystem function through behaviourally-mediated trophic cascades. Under the risk imposed by predators, prey spend less time foraging and do so closer to cover (Schmitz et al. 1997). These behavioural shifts reduce the number of prey consumed and alter the spatial distribution of prey foraging activity (Schmitz 1998). Because the prey are often herbivores, behavioural changes may directly increase primary productivity (Halaj and Wise 2001) and alter the spatial distribution and community composition of primary producers (Calcagno et al. 2011).

On a broader spatial scale, predation risk can drive changes in daily movement patterns, with consequences for nutrient translocation. Daily movement patterns by many bird species between foraging habitat and night roosts can move huge amounts of nutrients about the landscape (Post et al. 1998). These movements may be a response to increased predation risk (and reduced vigilance) under the low light conditions of night, and relaxation of selection pressure by predators could reduce the incidence of these behaviours.

The risk of predation modifies prey behaviour not just through risk avoidance, but also through changes in metabolic rate and diet choice, with implications for nutrient cycling. Despite being less active, risk-exposed prey are expected to have elevated metabolic rates due to risk-induced stress, which can correspond to behavioural change (Houston 2010). Increased metabolic rate heightens energy requirements and changes foraging behaviour, with risk-exposed prey seeking out more energy rich foods (Hawlana and Schmitz 2010b). This change in diet preference could itself drive changes in ecosystems by modifying predation pressure or herbivory on various prey items. Changed foraging also affects nutrient cycling, with increased energy demands reducing the relative amount of carbon recycled, with potential consequences for decomposition, nutrient cycling, and primary productivity (Hawlana and Schmitz 2010a).

In addition to predation, resource availability may also alter behaviour in ways that can change ecosystems, although the ecosystem implications

of such shifts have been less thoroughly explored. Diet selectivity of a consumer is a function of the available prey items in the environment (Iwasa et al. 1981), and shifts in relative resource abundance can drive shifts in consumer behaviours, with important ecosystem effects. The diet switch of killer whales from large marine mammals to sea otters (and resulting trophic cascade) may have been driven by the decline of large marine mammals in the coastal region of Alaska (Springer et al. 2008). Other examples of diet choice impacting trophic cascades abound in systems ranging from pelagic marine systems near Antarctica (Ainley et al. 2006), vegetation in riparian areas (Henschel et al. 2001), zooplankton communities in lakes (Yako et al. 1996), and algal communities in estuaries (Geddes and Trexler 2003). More generally, predator diet breadth and selection have been shown in modelling and laboratory studies to place strong control on food web structure (Jiang and Morin 2005).

In addition to the independent effects of predation and resource availability, these factors may interact to shape the ecosystem effects of behavioural plasticity. For example, animals are less likely to alter their feeding behaviour in response to predation in low resource environments, where they must weigh the risk of starvation from reduced foraging against increased risk of predation while foraging (Sih 1980). Thus, low resource situations can drive increased risk-taking by prey, resulting in dampened behaviourally-mediated cascades, but perhaps heightened density-mediated trophic cascades as prey populations decline either from reduced resource acquisition or increased predation (Schmitz et al. 1997). Changes in physical habitat structure can also modify the balance organisms make between feeding and predator avoidance (Trussell et al. 2006). In one case, seed predation by mice *Peromyscus leucopus* under predation threat increased only when an invasive shrub *Lonicera maackii* created cover from visual predators (Mattos and Orrock 2010).

Predation and resource availability are classic ecological drivers. Thus, their importance with respect to the ecosystem effects of behavioural plasticity may be unsurprising. However, other drivers of behavioural plasticity have been shown to impact ecosystems in

less obvious ways. For example, parasites on a species of New Zealand cockle *Austrovenus stutchburyi* cause the cockles to alter their behaviour and lay exposed on the surface rather than buried in the benthos. This change in behaviour has ecosystem consequences, shifting competitive dynamics between anemones and limpets on benthic substrates and causing whole-scale community changes in these habitats (Thomas et al. 1998). Crayfish *Orconectes limosus* change their movement patterns in response to the availability of refugia, and this shift changes sediment accretion in small streams with cascading effects on algal growth and biofilm cover (Statzner et al. 2000). Harvester ants *Pogonomyrmex occidentalis* create more extensive nests in the presence of prairie dog *Cynomys ludovicianus* burrows, disturbing more soil and altering vegetation patterns across the landscape (Alba-Lynn and Detling 2008). These are just a few examples of how behavioural plasticity can cause changes to ecosystems, and we suspect that the list of potential examples is limited primarily by the amount of effort expended to explore such effects.

13.3.2 Contemporary evolution

Ecologists have long studied the importance of phenotypic plasticity, but only recently has it been recognized that evolution can happen at the pace of ecological change and thereby impact ecological dynamics (Post and Palkovacs 2009; Schoener 2011). Perhaps not surprisingly, some of the same types of trait changes that impact ecosystems via phenotypic plasticity have also been found to shape ecosystems via contemporary evolution. Indeed, plastic changes can be the phenotypic precursors to adaptive genetic changes (Ghalambor et al. 2007).

Prey can rapidly evolve defenses against predators, which may have important impacts on community and ecosystem processes. These effects have been shown in a variety of laboratory systems (Matthews et al. 2011). However, such effects have rarely been considered in the wild. One study system where such effects have been considered in the wild is the Trinidadian guppy *Poecilia reticulata*. Above barrier waterfalls, guppies occur in the absence of fish predators (low-predation populations). Below waterfalls, guppies coexist with predators (high-

predation populations). A series of introduction experiments have transplanted guppies from high predation sites to low predation sites (Reznick et al. 2008). Such experiments have shown that guppy behaviour can evolve rapidly (over a period of sev-

eral years) when guppies are released from predation. Importantly for ecosystems, predator release leads to a decrease in guppy escape ability (O'Steen et al. 2002) and an increase in guppy consumption rates, as measured under laboratory conditions of

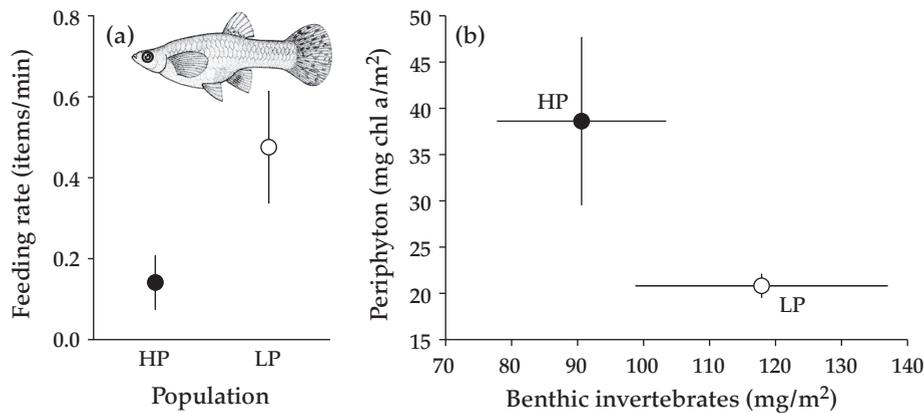


Figure 13.1 The evolution of guppy feeding traits impacts Trinidadian stream ecosystems. Panel (a) shows the feeding rates (mean \pm 95% CI) expressed by guppies locally adapted to high-predation (HP) and low-predation (LP) environments. The increase in feeding rate observed in LP is likely to be an adaptation to increased guppy density, decreased resource availability, and a release from selection related to predator-escape performance (data adapted from Palkovacs et al. 2011). Panel (b) shows the ecosystem responses to HP and LP guppies in terms of periphyton and benthic invertebrate biomass (means \pm SE), as measured in stream mesocosms. The decrease in periphyton biomass observed in LP results from increased consumption rates and increased ingestion of periphyton relative to invertebrates, coupled with reduced nutrient excretion rates (data adapted from Palkovacs et al. 2009).

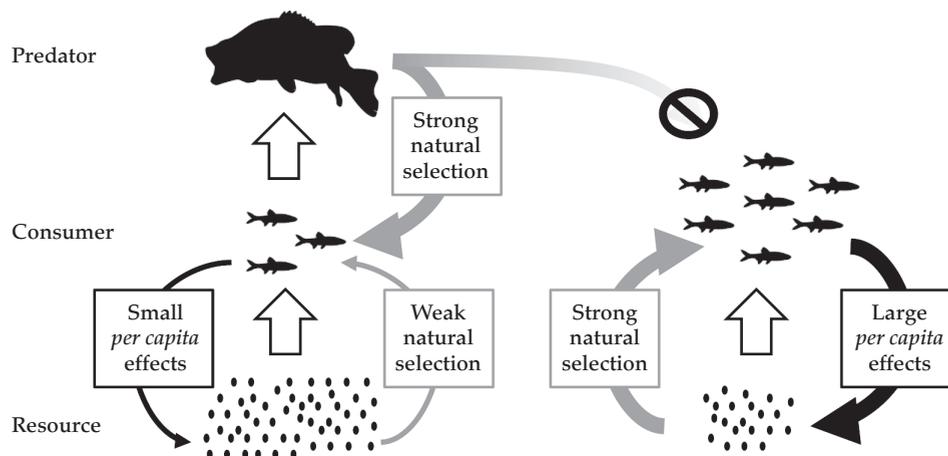


Figure 13.2 Predator removal may amplify the strength of trophic cascades via the contemporary evolution of prey. In the classic density-mediated trophic cascade, the removal of predators increases prey density, which decreases resources. However, predator removal may also shift natural selection acting on prey. When predators are present and resources are abundant (at left), natural selection acting on prey is expected to be driven primarily by predation and favour the evolution of prey traits that enhance predator detection and escape ability. When predators are absent and resources are limited (at right), natural selection acting on prey is expected to be driven primarily by competition and favour the evolution of prey traits that enhance resource acquisition. This shift in selection may cause the per capita effects of prey on resources to be greater in the absence of predators, thereby amplifying the density mediated trophic cascade.

equal prey availability (Palkovacs et al. 2011). These changes may be driven by increased guppy density (and heightened competition) at low-predation sites, coupled with a trade-off between escape ability and competitive ability (Palkovacs et al. 2011). In addition, predator release and heightened competition appear to reduce the selectivity of feeding behaviour at low-predation sites, leading to a higher consumption of abundant (but relatively nutrient poor) algal resources (Zandonà et al. 2011). At the ecosystem level, the evolution of increased guppy consumption rates (Fig. 13.1a), coupled with increased feeding on algae, combine to reduce algal standing stocks in low-predation habitats (Fig. 13.1b; Palkovacs et al. 2009; Bassar et al. 2010).

The importance of these findings in guppies is the broader idea that the evolution of prey traits may impact the strength of trophic cascades (Fig. 13.2). When predators are present, prey density is low and natural selection acting on prey may favour escape ability. Because of trade-offs between escape ability and foraging ability, predator presence may cause the per capita effects of prey on resources to be relatively low. When predators are removed, prey density increases and natural

selection acting on prey may favour competitive ability and increased foraging efficiency. This shift may increase the *per capita* effects of prey on resources. Therefore, prey evolution may act to amplify the strength of trophic cascades (Palkovacs et al. 2011). More research is needed to investigate this idea theoretically and to test its generality across study systems.

In addition to prey behaviour, the evolution of predator behaviour can also change ecosystems. As discussed previously for plasticity effects, this change can come in the form of prey selectivity. For example, alewife *Alosa pseudoharengus* populations in New England lakes exhibit two life history forms, an anadromous (sea-run) form and a landlocked (freshwater resident) form. Genetic evidence suggests that landlocked populations have independently evolved in lakes, perhaps as a result of human dam construction (Palkovacs et al. 2008). Anadromous alewives spawn in freshwater, where juveniles rear for a summer before migrating to sea. In contrast, landlocked alewives spend their entire life cycle in freshwater. Alewives act as a keystone predator in New England lakes (Brooks and Dodson 1965); however, differences in prey selectivity cause

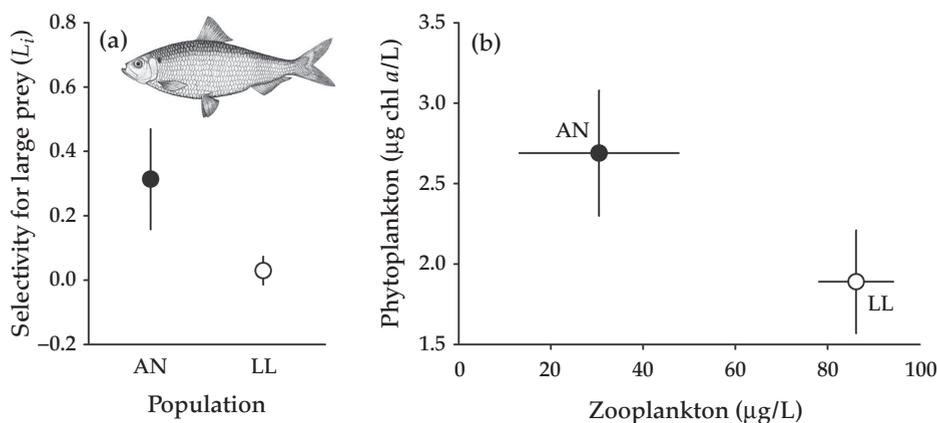


Figure 13.3 The evolution of alewife prey selectivity impacts New England lake ecosystems. Panel (a) shows feeding selectivity (mean \pm 95% CI) for large zooplankton prey (>1.0 mm body length) measured using Strauss' (1979) selectivity index, L_i . This index of prey selectivity takes on values from -1 to +1, with positive values indicating preference, values near 0 indicating random feeding, and negative values indicating avoidance. Anadromous alewives (AN) show a preference for large-bodied prey items, whereas landlocked alewives (LL) show random feeding with respect to large-bodied prey (data adapted from Palkovacs and Post 2008). Panel (b) shows the ecosystem responses to AN and LL alewives in terms of phytoplankton and zooplankton biomass (means \pm SE), as measured in lake mesocosms. The increase in zooplankton biomass observed in LL results from decreased prey size-selectivity, which increases the abundance of large-bodied cladocerans in the environment. This increase in large-bodied cladocerans increases grazing pressure on phytoplankton, thereby decreasing phytoplankton biomass by weakening the trophic cascade (data adapted from Palkovacs and Post 2009).

the ecosystem effects of landlocked alewives to differ from those of their anadromous ancestors. Anadromous alewives are strongly size-selective, seeking out and consuming the largest prey items available in the lake (Fig. 13.3a). In contrast, landlocked alewives are neutrally size-selective, consuming prey items in proportion to their abundance (Palkovacs and Post 2008). This difference in prey selectivity causes major changes in zooplankton communities, with anadromous alewives eliminating large-bodied grazing cladocerans and causing a stronger trophic cascade than landlocked alewives (Fig. 13.3b, Post et al. 2008; Palkovacs and Post 2009).

In addition to differences in prey selectivity, anadromous and landlocked alewives also differ—even more obviously—in migratory behaviour. This difference changes seasonal zooplankton dynamics and alters nutrient levels. The emigration of anadromous juveniles each season provides a temporal prey refuge for zooplankton in anadromous lakes, which enables some large-bodied species to persist despite strong size-selective predation during the summer months (Post et al. 2008). Additionally, spawning adult anadromous alewives import marine nutrients into freshwater ecosystems, just as do spawning Pacific salmon (Walters et al. 2009). Thus, the evolution of landlocked alewife populations has initiated a suite of behavioural changes that have had large effects on lake ecosystems, namely weaker, but temporally persistent, predation pressure on large-bodied zooplankton with cascading effects on phytoplankton, and elimination of nutrient subsidies from marine sources (Post et al. 2008). It is likely that similar effects may also be present in other coastal ecosystems where evolutionary transitions from anadromy to freshwater residency in fishes are not uncommon, especially where hydrologic connectivity has been altered (Hendry et al. 2004).

13.4 Reaction norms and ecosystem effects

The above examples of contemporary evolution impacting ecosystems involve comparisons of evolutionarily divergent populations. However, these studies do not specifically parse the evolutionary

component of ecosystem change from the effects of phenotypic plasticity (but see Ellner et al. 2011). Similarly, experimental evaluations of plasticity effects have typically examined individuals from a single population, adapted to a single set of environmental conditions. In each case, the picture revealed by such studies is incomplete. Obtaining a more complete picture requires the simultaneous consideration of evolution and plasticity. It also requires a framework for linking phenotypic variation to ecosystem responses. Since phenotypic plasticity itself is a function of evolutionary history, we propose a framework for considering the effects of evolution, plasticity, and the evolution of the plastic response based on reaction norms.

Reaction norms depict the phenotypes produced by a given genotype under differing environmental conditions. While populations are typically comprised of many genotypes, and thus contain many reaction norms, it is convenient here to think about population mean reaction norms. Reaction norms depict evolutionary effects as phenotypic differences between populations tested in the same environment and plasticity effects as phenotypic differences within populations tested in different environments. Populations with a high degree of phenotypic plasticity have steeply sloping reaction norms. Evolutionary changes that alter the slope of the reaction norm indicate the evolution of phenotypic plasticity. Once the reaction norms have been formalized (based either on theoretical expectations or empirical observations), the relative contributions of evolution, plasticity, and the evolution of plasticity to total trait change can be determined. Then, the function relating phenotype values and the ecosystem responses can be applied to determine the relative contributions of evolution, plasticity, and the evolution of plasticity to total ecosystem change.

As an example, imagine a case where a predator is introduced to a habitat where the herbivore population has not experienced predation in its recent evolutionary past (e.g. wolf reintroduction into Yellowstone Park, trout stocking into mountain lakes and streams). Prior to the introduction, the herbivore population is predator 'naïve' (i.e. locally adapted to the absence of predators) and exists in a

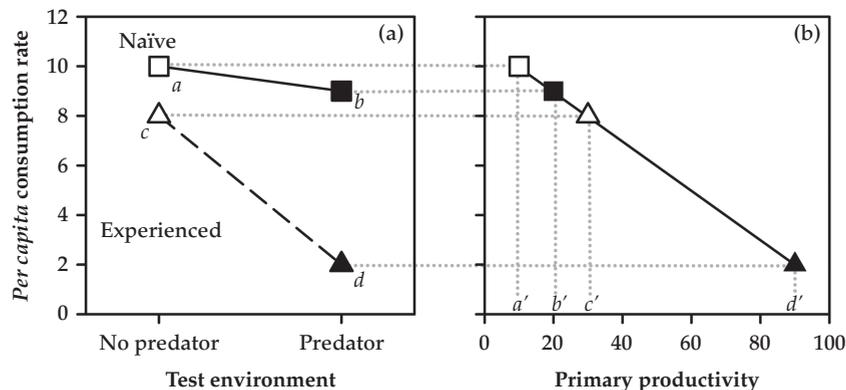


Figure 13.4 Reaction norms applied to behaviourally-mediated trophic cascades. Panel (a) shows hypothetical reaction norms for per capita consumption rate of an herbivore that is predator 'naïve' (i.e. locally adapted to the absence of the predator, squares) and predator 'experienced' (i.e. locally adapted to the presence of the predator, triangles) in environments where the predator is absent ('no predator', open symbols) and present ('predator', closed symbols). Panel (b) shows how per capita changes in consumption rate driven by plasticity (the slope of the reaction norm), evolution (the elevation of the reaction norm), and the evolution of plasticity (the change in the slope of the reaction norm), translate into ecosystem effects on primary productivity. See the text and Box 13.1 for details.

'no predator' environment (Fig. 13.4a, a). The introduction of the predator causes an immediate plastic response in the herbivores, which includes a reduction in per capita consumption rate (Fig. 13.4a, b). As discussed previously, such a reduction in consumption rate is a typical plastic response of prey individuals when faced with predation risk. This plastic response is captured by the slope of the reaction norm depicting the change in consumption rate from the 'no predator' environment to the 'predator' environment displayed by the 'naïve' herbivore population. Understanding the ecosystem consequences of such a plastic shift in phenotype is the goal of many studies of behaviourally-mediated trophic cascades (Schmitz et al. 2008). Such studies are typically performed using a single herbivore population at one point in time exposed to different environments (i.e. 'no predator' and 'predator').

The immediate plastic shift in behaviour is only part of the story, however. Over time (perhaps just several generations), the herbivore population is expected to become locally adapted to the presence of the predator. This local adaptation is described by the change in the elevation of the reaction norm from the predator 'naïve' population to the predator 'experienced' population, assuming that the herbivore exhibits no plastic response to the predator (Fig. 13.4a, c). Understanding the ecosystem conse-

quences of this purely evolutionary shift, by removing the effects of plasticity, is the goal of many eco-evolutionary studies (Matthews et al. 2011). Such studies are typically performed using laboratory-born individuals from different populations (i.e. 'naïve' and 'experienced') exposed to a common environment (typically the absence of predators).

In natural ecosystems that have undergone a predator introduction, however, the now-predator 'experienced' herbivore population exists in an environment with the predator, making it important to consider the evolution of the plastic response to the novel environment. The evolution of plasticity is captured by the change in the slope of the reaction norm, in this case resulting in a greater reduction in *per capita* consumption rate than would be expected if plasticity had not evolved (Fig. 13.4a, d). Such an increase in the antipredator plastic response (steeper slope of the reaction norm) is expected as an adaptation to predator introduction if there is a fitness gain associated with an increased expression of the predator-induced behaviour, such as when greater reductions in feeding activity further reduce mortality risk (Ghalambor and Martin 2002; Ghalambor et al. 2010).

As described, reaction norms give the expected trait values, but understanding their ecological consequences requires linking these trait values to

ecosystem effects. In some cases, we may expect a simple and predictable relationship between traits and ecosystem effects. For example, a linear relationship between consumption rate and primary productivity means that predation environment can drive evolutionary and plastic changes in herbivore prey phenotypes that translate directly into changes in primary productivity (Fig. 13.4b). Such a relationship underlies a simple understanding of behaviourally-mediated trophic cascades. With knowledge of the reaction norms and the relationship between trait values and ecosystem effects, the relative contributions of plasticity, evolution, and the evolution of plasticity to total ecosystem change can be calculated (Box 13.1).

We have described our reaction norm approach in terms of a timeline of events following a perturbation (in this case, the introduction of a novel predator). However, this approach can also be useful for comparing trait and ecosystem responses of extant populations. Thus, the ‘naïve’ and ‘experienced’ herbivore populations depicted in Fig. 13.4a could represent two different populations at one point in time. Both populations may currently exist in a ‘no predator’ environment, perhaps because the ‘experienced’ population lost its predator in the very recent past. In this case, predator introduction (or reintroduction) would have dramatically different effects on the ecosystem depending on the recent evolutionary history of the herbivore population

Box 13.1 Partitioning ecosystem effects using reaction norms

The effects of plasticity, evolution, and the evolution of plasticity can be partitioned for both trait change and ecosystem change if the reaction norms and the function relating trait change to ecosystem change are both known. Here we provide an example for the hypothetical case depicted in Figure 13.4.

- (1) First, total *trait* change must be partitioned into the effects of plasticity, evolution, and the evolution of plasticity.

In Fig. 13.4a, the total trait change (i.e. from the ‘naïve’ population in the ‘no predator’ environment to the ‘experienced’ population’ in the ‘predator’ environment) is given by:

$$a - d \text{ or } 10 - 2 = 8$$

The contribution of plasticity to overall trait change (i.e. the immediate plastic response to the introduction of the predator) is given by:

$$a - b \text{ or } 10 - 9 = 1$$

The contribution of evolution to overall trait change (i.e. the evolutionary effect that would have occurred in the absence of plasticity) is given by:

$$a - c \text{ or } 10 - 8 = 2$$

The contribution of the evolution of plasticity (i.e. the difference in the plastic response from the ancestral to the derived population) is given by:

$$(c - d) - (a - b) \text{ or } (8 - 2) - (10 - 9) = 5$$

Thus, the total trait change partitioned into plasticity, evolution, and the evolution of plasticity is given by:

$$(a - b) + (a - c) + ((c - d) - (a - b)) \text{ or } 1 + 2 + 5 = 8$$

Note that this represents the total shift from *a* to *d*.

- (2) Once the partitioning has been performed for trait change, the function relating trait change to ecosystem change can be applied to discern relative ecosystem effects.

Figure 13.4b depicts a linear relationship between consumption rate and primary productivity with a slope of 0.1 (rise/run = 1/10). This means that each unit of trait change (reduced consumption) translates into 10 units of ecosystem change (increased primary production). Therefore, of the total change in primary production (*a'* to *d'* = 80 units), the change due to plasticity represents 12.5%, the change due to evolution represents 25%, and the change due to the evolution of plasticity represents 62.5%. In this example, we have described the relationship between traits and ecosystem effects using a simple linear function. However, more complex functions can also be applied.

(Fig. 13.4b). Specifically, short-term ecosystem change due to plasticity would be expected to be smaller for the 'naïve' population (Fig. 13.4b, *a'–b'*) compared to the 'experienced' population (Fig. 13.4b, *c'–d'*). Of course, the maladapted behaviour of the 'naïve' herbivore may lead to a higher predator-induced mortality rate. This mortality may strengthen the short-term density-mediated trophic cascade and, over several generations, lead to the evolution of the 'experienced' reaction norm.

We have described how reaction norms can be used to study ecosystem change. But what are the practical benefits of applying such an approach in the context of human disturbance? Much effort has gone into developing theory to understanding how reaction norms for diverse traits, including behaviour, will evolve under different environmental conditions (Ghalambor et al. 2010). One key benefit of applying a reaction norm framework to ecosystems is that this existing theory can be used to make predictions about ecosystem responses. In a rapidly changing world, the ability to make predictions is more than an academic concern. Returning to the example of trophic cascades, humans are adept at 'tinkering' with top predators (Strong and Frank 2010). Human predation on top predators is a novel selective force on these populations, potentially driving evolutionary changes in their behaviour, just as natural predators do to their prey. Humans have eliminated top predators from many ecosystems and added novel top predators to others. When top predators are eliminated or introduced, prey populations evolve in new environments with altered predation risk. The development of robust evolutionary and ecological linkages between natural selection acting on predators, the evolution of behavioural reaction norms, and the resulting ecosystem consequences could potentially go a long way towards predicting the impacts of top predator removals and introductions on the world's ecosystems.

13.5 Conclusions

Animal behaviour is a critical, but underappreciated, link between human activity and ecosystem processes. Behavioural traits related to consumption and nutrient cycling, in particular, can cause

widespread effects on ecosystems. Therefore, rapid changes to these traits due to phenotypic plasticity and contemporary evolution may cause important changes to ecosystems. While plasticity effects have been recognized for some time, evolutionary effects are just beginning to emerge as a potentially important driver of ecosystem change. The effects of plasticity and evolution have largely been considered separately, but these factors work in concert to shape behavioural traits. Therefore, new approaches are needed to integrate these mechanisms of trait change and link them to ecosystem effects. We propose a framework for considering the joint effects of evolution and plasticity based on reaction norms. Natural selection provides a predictive theoretical framework for understanding the evolution of reaction norms under different environmental conditions. Linking this theoretical framework to ecosystem processes has the potential to add predictive power to ecosystem ecology. Such information can potentially be used to predict the consequences of human activity for ecosystems.

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