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Eco-evolutionary Biology: Feeding and Feedback Loops

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A dogma in ecology and evolution holds that the environment is an extrinsic force that is not, in turn, shaped by the adaptive evolution of species. Recent work on stickleback life history, community ecology and speciation challenges this dogma.

Eco-evolutionary biology has emerged, in part, from two revelations. First, ecology and evolution can operate on the same time scales. While the timescale of ecological dynamics has always been considered fast — on the order of generations or even an individual's life — evolutionary change was long believed to require thousands of generations. Yet, pioneering research on ecological genetics and evolutionary dynamics [1–3] demonstrated that adaptive evolution can be rapid. Second, rapid evolutionary change can alter the environment; the interplay between organisms or populations and environment is bidirectional and dynamic. Organisms modify their environment and how they do this depends on their evolutionary history. In turn, this ecosystem

modification can influence ecological interactions and the evolutionary trajectories of one or more species. This feedback loop is the focus of eco-evolutionary biology. In this issue of *Current Biology*, Matthews *et al.* [4] and Rudman and Schluter [5], both using sticklebacks, report on two important components in this growing field.

That rapid adaptive evolution in a focal species can alter community structure and ecosystem function is central to eco-evolutionary biology. Linked to ecosystem engineering [6] and niche construction [7], numerous studies show that the evolutionary history of species or populations can alter ecosystem function and community structure [8–11].

However, demonstrating this effect does not define a complete feedback loop,

whereby these changes subsequently alter the selection gradients that drive the evolution of future generations.

Revealing the identity and effect sizes of evolutionary processes that can act on ecological communities and dynamics is also central to current research. There is compelling evidence that many evolutionary processes can alter ecological interactions with effect sizes on community structure or ecosystem function that are equal to or larger than ecological processes. For instance, rapid local adaptation in life-span and flowering time in the evening primrose underpins predictable change in susceptibility to seed predators [12]. Similarly, (co-) evolution in guppies and killifish can exert a larger effect on ecosystem function than the invasion of killifish into guppy



Figure 1. Stickleback ecotypes.

Matthews *et al.* and Rudman and Schluter both used the model evolutionary system of sticklebacks in their eco-evolutionary research. Matthews *et al.* used lake and stream ecotypes that feed in the limnetic and benthic zone of aquatic environments in Switzerland, respectively, while Rudman and Schluter used a benthic (top) and limnetic (bottom) species pair (shown here) from British Columbia, Canada. Photo: Ernie Cooper.

communities [13]. And, maladaptation in stick insects [14], resulting from gene flow, has effects on stick insect population size comparable to the effect of the size and identity of the host plant. This list of mechanisms suggests that more evolutionary processes are likely to contribute to eco-evolutionary feedbacks.

Matthews *et al.* [4] and Rudman and Schluter [5] demonstrate, both using the model stickleback fish (*Gasterosteus* spp.), that the ecosystem responses to evolutionary processes can be large and

influential. Matthews *et al.* [4] used artificial ponds to contrast effects on ecosystems of the presence and absence of fish compared to effects of two evolutionarily distinct ‘ecotypes’ (Figure 1). The ecotypes are recently diverged and ecologically differentiated: a limnetic type that lives in lakes and feeds in open water, and a benthic type from more shallow streams that feeds from the bottom [4]. Additionally, they manipulated the diets of these fish, feeding them their typical diet (e.g. benthic type fed benthic food) or the opposite. This yields a

traditional comparison of the effects of an evolutionary difference — the ecotypes — to an ecological difference — the presence and absence of fish. But we also get a partitioning of the evolutionary effect into the effect of the ecotype *per se*, and the effect of the ecotype’s flexibility in dealing with different diets — its phenotypic plasticity. And they show that the evolutionary identity of the fish (limnetic versus benthic) and their plasticity could have stronger effects on the ecosystem than the ecological treatment (presence vs. absence of fish). This was true in several ecosystem properties including the biomass of zooplankton and phytoplankton, the concentration of phosphorus, and the abundance of several prey (e.g. copepods) and non-prey (e.g. cyanobacteria) species [4].

Rudman and Schluter [5] found substantial changes in ecosystem properties mediated by an evolutionary process that has historically not been considered: ecological speciation. Their evidence comes from the intriguing idea of “reverse” ecological speciation [15], the dissolution of a recently formed species pair. Ecological speciation arises via divergent selection between habitats that produce divergent adaptations. Their work, however, focused on the reversal of such divergence between benthic and limnetic stickleback ecotypes in Enos Lake, British Columbia.

Prior research suggests that invasive signal crayfish reduced the abundance and diversity of plants and animals that maintain water clarity (e.g. macrophytes) in Enos Lake [15]. These changes in the community and water quality substantially diminished the ecologically based divergent selection on sticklebacks and led to the species pair reverting to a single ecotype [15]. Using field data and simple experiments, they first noted that the feeding morphology of the new Enos Lake ecotype is not intermediate, like a naturally occurring generalist, but five times closer to the benthic morphology [5]. This leads to the prediction that the benthic trophic community should suffer, and the open water limnetic community should benefit. Comparing the Enos lake zooplankton community to other lakes with intact species pairs, they found just this: small zooplankton, the prey of limnetic

feeders, are much more abundant in Enos lake.

An experiment also confirmed these novel shifts: comparing the effects on zooplankton biomass, phytoplankton biomass and decomposition rates by the reverse speciation ecotype versus the species pair, they found a trophic cascade, with the reverse speciation ecotype supporting higher zooplankton biomass and a corresponding lower phytoplankton biomass [5].

Ecological (reverse) speciation is certainly a novel evolutionary process to be considered in the context of ‘eco-evolutionary’ driven change in ecosystems. Yet, the most exciting aspect of this work is that much of the change could be predicted simply by extending knowledge about feeding morphology, which is at the heart of several examples of ecological speciation, to consequences at the community level.

The above insights from both teams are admirable contributions to eco-evolutionary research. Matthews *et al.* [4] evaluate an extensive array of ecosystem and community variables and demonstrate that genetic identity and plasticity can drive ecosystem changes. Rudman and Schluter [5] demonstrate that ecological speciation is a new candidate evolutionary process driving ecosystem change and that predictions may be possible. Significantly, however, both offer substantially more.

The second stage of the experiments of Matthews *et al.* [4] reminds us that the feedback loop is central to eco-evolutionary dynamics. They assessed the performance of juvenile sticklebacks in the habitats modified by adult benthic and limnetic types. These data show that juvenile performance can be a function of parent evolutionary history (genetics), parent rearing conditions (plasticity) and, critically, the effect of both of these processes on the environment in which the juveniles grow (trans-generational environment). This trans-generational ecosystem modification created differential growth and survival among the juveniles, components of fitness that determine adaptive evolutionary change. Thus, one of the principal findings from Matthews *et al.* [4] is that the effects of evolution that drive changes in ecosystems persist across generations.

Rudman and Schluter’s [5] experiments also predicted and demonstrated that the effects of reverse speciation on ecosystem function can span across multiple ecosystems. In addition to changes in Enos Lake described above, they show that the breakdown of the species pair doubles the number of non-biting midges (Chironomids) emerging as flying adults from the mesocosms, while non-chironomids declined by 40% [5], altering the relative abundance of terrestrial plant pollinators and insect prey for terrestrial organisms. These data augment significantly recent ecological evidence for ‘trans-boundary effects’: top predator fish have been shown to indirectly facilitate terrestrial plant reproduction through a set of cascading trophic interactions between fish and pollinator insects that cross the aquatic–terrestrial ecosystem boundary [16].

These whole-community experiments contribute several new pieces in the eco-evolutionary biology puzzle. Ecological speciation is a new evolutionary process on the list of those with a large effect on community structure and ecosystem function, and one where effects extend beyond the focal ecosystem (e.g. aquatic to terrestrial) [5]. Evolutionary identity (e.g. ecotypes) and process (e.g. plasticity) drive changes of large magnitude in ecosystem function, community structure and trophic dynamics. The ecosystem consequences are multivariate [4]. And the predictive capacity of evolved feeding morphology in the limnetic and benthic fish offers promise of a framework for predicting the effects on ecosystems of evolutionary dynamics [4,5]. Ultimately, the persistence, across generations [4], of these changes in ecosystems demonstrates just how eco-evolutionary dynamics might emerge as a function of heritable variation, life history, community structure and ecosystem function.

A gold standard for eco-evolutionary biology centres on revealing the simultaneous dynamics of both ecological communities and evolutionary dynamics. Several laboratory based experiments, elegant theory and statistical tools have shown how to simultaneously track, apportion variance to and explain the contributions of ecological and evolutionary change to

population dynamics [17–20]. The work by Matthews *et al.* [4] and Rudman and Schluter [5] suggests that we are closer to being able to understand the identity, magnitude, and target of evolutionary processes that underpin ecological dynamics. We may also be getting closer to being able to pick apart, with predictive power, the various ways in which community structure and ecosystem function respond to, mediate, and ultimately drive, via evolutionary change, the eco-evolutionary dynamic.

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Cancer: The Transforming Power of Cell Competition

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The tumour–host microenvironment plays key roles in cancer, but the mechanisms involved are not fully understood. Two new studies provide insight into this problem by showing that through cell competition, a fitness-sensing process that usually eliminates defective cells, pre-cancerous lesions signal the death of surrounding tissue that in turn promotes their neoplastic transformation.

Throughout the development and life of any organism, stress or defective cell replication can lead to the emergence of abnormal cells. The ability of these cells to persist and expand will play a key role in determining not only the fitness of the tissue or organ in which they can be found, but possibly also the longevity of the organism itself. A number of cell-intrinsic surveillance mechanisms have been described that identify and eliminate these abnormal cells [1]. However, it is also becoming increasingly apparent that, in addition to these surveillance efforts, sensing mechanisms exist that ensure tissue homeostasis by monitoring the relative fitness levels of cells within a population. Cell competition is one of these mechanisms and results in the elimination of those cells deemed to be less fit than their neighbours, even though their defects would normally escape the cell-intrinsic surveillance systems [2–5] (Figure 1A). Cell

competition has been proposed to play tumour-suppressive roles by limiting the expansion of potentially cancerous cells as they arise, and in this way preserving the integrity of the tissue [6]. But there is potentially a dark side to cell competition. It is possible that, if cells could acquire a ‘super-fit’ status, for example in a pre-cancerous lesion, they could sense the surrounding wild-type cells as ‘less fit’ and signal their elimination. This process would promote tumour expansion rather than prevent it (Figure 1B). Two papers in this issue of *Current Biology* provide fascinating evidence confirming such a role [7,8].

Cell competition can be triggered by different insults. For example, in the *Drosophila* prospective wing (imaginal wing disc) overactivation of the Wnt/Wg signalling pathway in clones of cells leads to the elimination of the surrounding tissue by cell competition [9]. Interestingly, adenomatous polyposis

coli (APC) — a well-known Wnt/Wg inhibitor — is frequently deleted in colon cancer [10]. In an elegant study, the Piddini laboratory links these two observations by analysing the *Drosophila* midgut, where clones of cells carrying APC mutations lead to hyperplasia and benign tumour formation (adenomas) [7]. When the APC mutant clones reach a certain size (about 30 cells), they cause the apoptotic death of the surrounding wild-type cells, in a manner reminiscent of cell competition. In parallel to these studies, the Cohen and Herranz groups took a different approach to explore how early tumours develop [8]. They analysed the *Drosophila* imaginal wing disc, where overexpression of epidermal growth factor receptor (EGFR), another driver mutation in human cancer [11], leads to benign tissue hyperplasia. EGFR overexpression combined with overexpression of the microRNA miR-8, which by itself only causes a mild