SYNTHESIS

Fates beyond traits: ecological consequences of human-induced trait change

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Abstract

Human-induced trait change has been documented in freshwater, marine, and terrestrial ecosystems worldwide. These trait changes are driven by phenotypic plasticity and contemporary evolution. While efforts to manage human-induced trait change are beginning to receive some attention, managing its ecological consequences has received virtually none. Recent work suggests that contemporary trait change can have important effects on the dynamics of populations, communities, and ecosystems. Therefore, trait changes caused by human activity may be shaping ecological dynamics on a global scale. We present evidence for important ecological effects associated with human-induced trait change in a variety of study systems. These effects can occur over large spatial scales and impact system-wide processes such as trophic cascades. Importantly, the magnitude of these effects can be on par with those of traditional ecological drivers such as species presence. However, phenotypic change is not always an agent of ecological change; it can also buffer ecosystems against change. Determining the conditions under which phenotypic change may promote vs prevent ecological change should be a top research priority.

Introduction

Human activity is causing rapid changes in the phenotypic traits of wild populations. Such trait changes occur via phenotypic plasticity and contemporary evolution (i.e., evolution occurring over less than a few hundred years). Phenotypic plasticity in response to rapid environmental change has been recognized for some time (Bradshaw 1965; Stearns 1989). While early examples of human-induced evolution provide some textbook examples of microevolution (e.g., industrial melansim in the peppered moth, Kettlewell 1958), the general acceptance that humans are driving contemporary evolution in wild populations is more recent (Palumbi 2001; Stockwell et al. 2003).

Now, there exists an abundance of examples of human-induced trait change in wild populations (reviewed in Bradshaw and Holzapfel 2006; Carroll et al. 2007; Hendry et al. 2008; Allendorf and Hard 2009; Darimont et al. 2009). As a result, human activity can now be considered a global driver of trait change in the wild. Human-induced trait change has been documented worldwide in freshwater, marine, and terrestrial ecosystems on every continent except Antarctica (Fig. 1). Most studies to date have not parsed the relative contributions of plasticity and evolution to human-induced trait change, although the available evidence suggests important contributions from both sources (Hendry et al. 2011). Alongside mounting evidence for human effects on traits, there is increasing evidence that contemporary trait changes can have important impacts on ecological processes. Such effects can occur via phenotypic plasticity and contemporary evolution (Ellner et al. 2011; Yamamichi et al. 2011). As described in detail below, we consider both genetic
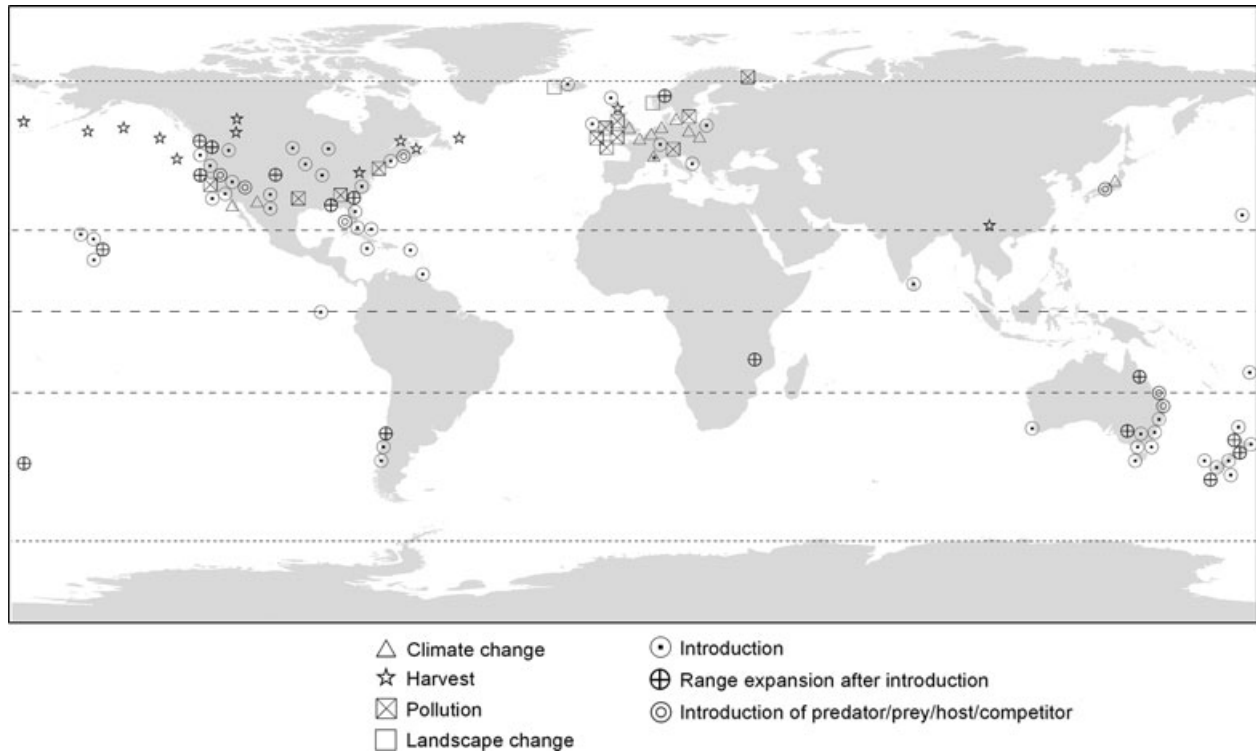
Figure 1 Global distribution of study systems documenting anthropogenic trait change in wild populations, with symbols representing documented drivers of change. The triangle with an asterisk inside (in Europe) represents migration timing for 65 bird species reported in Jenni and Kery (2003).

and plasticity effects to fall under the general purview of eco-evolutionary dynamics, as these effects operate together to shape traits and ecological responses.

If contemporary trait change can have important ecological effects, then human-driven trait change may be impacting ecological processes worldwide. But how prevalent are such effects? And should we be concerned outside of a few special cases? To address these questions, we reverse the traditional chain of causality. Instead of considering trait change as the consequence of ecological change, we consider it as the driver. This perspective is reflective of the emerging paradigm that eco-evolutionary dynamics are inherently bidirectional (Pelletier et al. 2009; Post and Palkovacs 2009; Schoener 2011). Therefore, human-induced trait change may be more than just the outcome of human-driven ecological change or the 'canary in the coal mine,' indicating that dramatic ecological change is eminent. In some cases, anthropogenic trait change itself may be the *cause* of ecological change.

Here, we discuss phenotypic plasticity and contemporary evolution as important sources of human-induced trait change. We briefly review the scope of human-induced trait change in wild populations. We do not consider cases from medicine and agriculture, as these contexts have received their own recent detailed attention

(reviewed in Nesse and Stearns 2008; Gluckman et al. 2011; Thrall et al. 2011). We then discuss emerging evidence that human-induced trait change may be a key driver of ecological dynamics. We propose that understanding the ecological consequences of human-induced trait change should be an urgent priority requiring the collaboration of eco-evolutionary researchers and natural resource managers.

Human-induced trait change

Ecological processes are influenced by trait change owing to evolution and phenotypic plasticity (Ellner et al. 2011; Yamamichi et al. 2011). In our consideration of the eco-evolutionary consequences of human activity, we include both mechanisms (Table 1). We take this approach for three reasons. Our first two are theoretical. First, it is phenotypes, shaped by the joint effects of genetic change and plasticity, which interact with the biotic and abiotic environment. Therefore, when it comes to predicting ecological outcomes, what likely matters most is the rate and pattern of overall phenotypic change. Most cases of contemporary trait change involve both genetic and plastic components, and isolating one mechanism of trait change and ecological effects does not itself preclude the other

Table 1. Selected case studies of human-induced trait change, mechanisms tested, and demonstrated (D) or hypothetical (H) ecological effects. 'Phenotypic' studies employed wild organisms, whereas 'genetic' studies utilized common garden experiments or statistical methods to show a heritable basis for trait change. 'Plastic' studies subjected wild organisms to differing environmental conditions. The 'evolution of plasticity' has been demonstrated using the resurrection of resting eggs.

Case	Traits	Mechanism	Ecological effects	References
Habitat fragmentation on birds	Wing shape	Phenotypic	Metapopulation dynamics (H)	Desrochers (2010)
Supplemental feeding on European blackcap	Wing shape Beak shape	Phenotypic	Niche diversification (H)	Rolshausen et al. (2009)
	Migratory direction	Genetic	Reproductive isolation (D)	Berthold et al. (1992)
Dam construction on stream fishes	Body shape	Phenotypic Genetic	Trophic interactions (H)	Haas et al. (2010) Franssen et al. (2011)
Dam construction on alewife	Migratory behavior Gape size Gill raker spacing Prey selectivity	Phenotypic	Trophic cascade (D) Zooplankton community (D) Nutrient subsidies (D)	Post et al. (2008), Palkovacs and Post (2009), Walters et al. (2009)
Commercial fishing on marine top predators	Fish body size	Phenotypic	Trophic cascade (D)	Shackell et al. (2010)
Recreational fishing on largemouth bass	Metabolic rate Growth rate	Genetic	Social behavior (D) Trophic interactions (H) Nutrient excretion (H)	Cooke et al. (2007), Philipp et al. (2009), Redpath et al. (2009, 2010)
Trophy hunting on bighorn sheep	Horn size Body size	Genetic	Population growth (H)	Coltman et al. (2003)
Urbanization on seed dispersal	Dispersal structure on fruits	Genetic	Metapopulation dynamics (H)	Cheptou et al. (2008)
Fish introduction on *Daphnia*	Predator avoidance behavior	Evolution of plasticity	Trophic cascades (H)	Cousyn et al. (2001)
Eutrophication on *Daphnia*	Resistance to toxic cyanobacteria	Evolution of plasticity	Consumer-resource dynamics (H)	Hairston et al. (2001)
Elevated CO_2 on plants	Leaf nitrogen composition	Plastic	Herbivore density (D) Herbivore feeding behavior (D)	Stiling et al. (2003)
Trout introduction on mayflies	Predator avoidance behavior	Plastic	Trophic cascades (D)	Peckarsky and McIntosh (1998)

(Hendry et al. 2011). Second, plasticity is the product of past evolution and can influence the trajectory of future evolution (Ghalambor et al. 2007). Simply stated, plasticity evolves and can do so in response to human disturbance (Crispo et al. 2010). Such an effect has been shown for *Daphnia*, where the resurrection of resting eggs has been used to demonstrate the evolution of plasticity in response to fish stocking (Cousyn et al. 2001) and eutrophication (Hairston et al. 2001). Therefore, excluding phenotypic plasticity from eco-evolutionary dynamics excludes an important component of evolution.

Our third reason for considering both plasticity and contemporary evolution is practical. Most of the studies of contemporary trait change in wild populations have not tested the mechanisms underlying phenotypic change (Hendry et al. 2008), and fewer still have convincingly isolated the genetic component of trait change underlying

subsequent *ecological effects* (see Table 1). Common garden experiments are used to isolate the genetic contribution to overall trait change, but such experiments are difficult to perform in wild populations of wide-ranging, large-bodied species, limiting their utility for many species of interest. Alternate statistical methods have been developed for such circumstances, but some of these methods have come under recent scrutiny (see Hadfield et al. 2010; Kinnison et al. 2011; Uusi-Heikkila et al. 2011), making a strict categorization of studies somewhat subjective in practice.

Hendry et al. (2008) classified cases of contemporary trait change to ascertain the relative effects of humans compared to more natural contexts. That study identified three primary contexts in which humans drive trait changes: *in situ* anthropogenic disturbance, introduction of populations to new habitats, and introductions of new

interacting species (e.g., hosts, pathogens, and predators) within the existing range of a species. The first of these, *in situ* disturbance, includes a large diversity of subcontexts, including cases of point source pollution, acidification, harvest, and a subset of instances of climate change. The authors labeled cases where populations diverged from one another within an introduced range to be natural, but clearly humans also played a role in the opportunity for evolutionary divergence. Human activity can also have the opposite effect, facilitating introgression (Hendry et al. 2006; Seehausen 2006). When published cases of contemporary trait change are considered in sum, human activity is involved in 162 of the 198 total study systems in which contemporary trait change has been documented in the wild. This tally represents the 61 study systems examined by Hendry et al. (2008) plus 137 study systems added to this database, using the same methodology, since that study was published. Overall, trait change driven by humans appears to happen roughly twice as fast as trait changes associated with nonanthropogenic drivers (Hendry et al. 2008). Harvest is particularly potent. Trait change associated with the harvest of wild populations averages three times faster than nonanthropogenic rates and occurs even faster than most other anthropogenic contexts (Darimont et al. 2009). This result suggests that, if contemporary trait change is generally important for ecological dynamics (Pelletier et al. 2009; Post and Palkovacs 2009; Schoener 2011), then changes linked to human activity, especially harvest, might be even more so.

As mentioned, most studies of contemporary trait change in the wild do not distinguish between heritable trait change and phenotypic plasticity. Anthropogenic contexts that favor changes in selective conditions are also likely to involve changes to environmental conditions that could directly influence the expression of phenotypes through plasticity (Hendry et al. 2011). Indeed, the analysis of Hendry et al. (2008) found that differences between anthropogenic and natural contexts were only statistically apparent when assessing 'phenotypic' studies of evolution – i.e., those studies that did not use common garden rearing or statistical approaches to isolate genetic effects. Significant differences were not found for the set of 'genetic' studies that did isolate heritable effects. This finding was interpreted as potential evidence that phenotypic plasticity is particularly important to contemporary trait change. This may be true; however, that inference must be tempered with the fact that genetic studies are less common (reduced statistical power) and that phenotypic and genetic studies tend to include different types of organisms and different agents of trait change. This latter limitation is particularly apparent when one considers that studies of trait change owing to harvest represented a large proportion of 'phenotypic' studies, but

such studies are rare among 'genetic' studies. Hence, if harvest really does drive the fastest rates of evolution (Darimont et al. 2009), then phenotypic rate comparisons of natural and anthropogenic contexts would be expected to show greater differences than genetic comparisons simply due to bias in the available data.

Although there is no contesting the value of exploring the relative roles of evolution and plasticity to contemporary trait change, such a distinction can be difficult to achieve in practice and may distract from the broader goal of linking trait change (regardless of the cause) to ecological dynamics. As we have described, human-induced trait change is pervasive and potent. Discerning the genetic or plastic contributions to trait change is undoubtedly important for understanding some important eco-evolutionary dynamics (e.g., feedback effects; Post and Palkovacs 2009). However, many management contexts would benefit most immediately from obtaining a basic understanding of the ecological impacts of overall phenotypic change. As discussed below, such ecological impacts can be substantial.

Ecological consequences

The prevalence and scale of anthropogenic trait change, combined with emerging evidence for ecological effects of trait change, lead to the prediction that anthropogenic trait change may have important ecological consequences. To date, however, such effects have not been widely investigated. Here, we highlight the potential for ecological consequences of anthropogenic trait change. Although such effects are likely across many contexts, we focus on two: habitat fragmentation and the harvesting of wild populations. We emphasize many examples from fishes, as this represents our area of expertise, although effects on other taxa are likely just as important.

Habitat fragmentation can impact traits related to migration, movement, and habitat selection. In North American songbirds, wing shape appears to have evolved over the past 100 years in response to changes in forest cover, with increased fragmentation appearing to select for increased dispersal ability (Desrochers 2010). In the European black cap (*Sylvia atricapilla*), supplemental feeding has led to a novel migratory pathway, shaped wing and beak morphology, and even led to reproductive isolation (Berthold et al. 1992; Rolshausen et al. 2009). In stream fishes, body shape changes have occurred in response to the construction of dams, which disrupt gene flow and create pond-like habitats (Haas et al. 2010; Franssen 2011). The disruption of hydrologic connectivity can also lead to the evolution on nonmigratory populations of normally migratory fishes (McDowall 1988). Such a transition does not require the complete

blockage of a river; hydrological changes that increases the energetic or survival costs of migration relative to the growth and fecundity benefits can select for increased residency (Hendry et al. 2004).

The ecological consequences of changes in movement can be dramatic. In fishes, the transition from an anadromous (sea-going) to freshwater resident life history can be important because many anadromous fishes, most notably Pacific salmon (*Oncorhynchus* spp.), provide important subsidies of marine-derived nutrients to rivers, lakes, and streams (reviewed in Schindler et al. 2003; Quinn 2005; Janetski et al. 2009). When freshwater resident populations evolve from anadromous ancestors, these nutrient subsidies are severed. The loss of these subsidies can impact important ecological processes such as rates of primary production, decomposition, and energy flow through food webs (Flecker et al. 2010).

In addition to modifying nutrient translocation, phenotypic responses to altered landscape connectivity can have the effect of changing food web interactions by modifying trophic traits and foraging behavior. In the planktivorous alewife (*Alosa pseudoharengus*), landlocked (freshwater resident) populations have evolved recently from anadromous ancestors, perhaps in response to the construction of dams by European settlers (Palkovacs et al. 2008). Changes in the trophic traits of these recently landlocked populations have caused major changes to the ecology of lake ecosystems, including changes in zooplankton biomass and community structure (Post et al. 2008; Palkovacs and Post 2009). These community-level changes in zooplankton modify the strength of trophic cascades, thereby driving differences in phytoplankton abundance (Post et al. 2008). Importantly, trait divergence between anadromous and landlocked populations can create larger magnitude ecological effects than alewife presence or absence (Fig. 2). Thus, contemporary trait change may be as important for shaping ecological dynamics as are traditional ecological variables such as species presence – a result not addressed by traditional ecological theory but increasingly supported by studies of eco-evolutionary dynamics (Hairston et al. 2005; Ezard et al. 2009; Palkovacs et al. 2009; Bassar et al. 2010; Ellner et al. 2011). The ecological effects of human-driven *extinctions* have long received attention from ecologists (reviewed in Hooper et al. 2005). The above result suggests that human-driven trait changes can have equally large effects on ecological dynamics.

In addition to direct effects on ecological processes, human-induced trait change can have cascading evolutionary consequences for other species, which can themselves translate into important ecological effects. The evolution of the aforementioned alewife populations has shaped the evolution one of its prey species, *Daphnia*
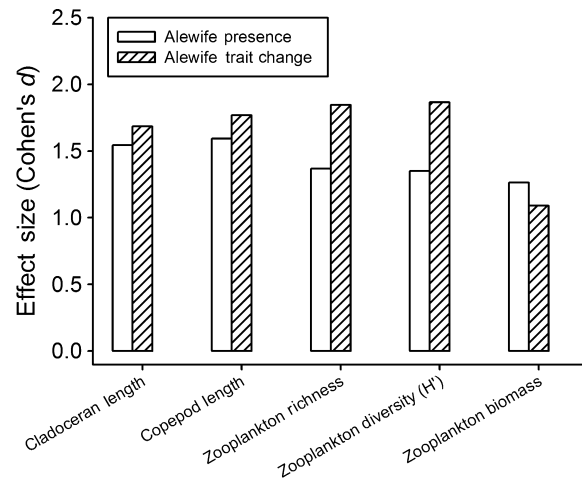

Figure 2 Effect sizes for alewife presence and trait change (divergence between anadromous and landlocked forms) from the experiment reported in Palkovacs and Post (2009). Alewife presence had larger effects on zooplankton biomass, whereas trait change had larger effects on mean zooplankton length for cladocerans and copepods, zooplankton species richness, and zooplankton diversity. These results suggest that anthropogenic trait change can have ecological effects on par with those of traditional ecological drivers, such as species presence and diversity.

ambigua (Walsh and Post 2011). Because *Daphnia* is a dominant zooplankton grazer, its evolution can have even further ecological effects, especially on trophic cascades (M. R. Walsh and D. M. Post, unpublished data). Thus, anthropogenic disturbances can set off cascades of eco-evolutionary effects that can ripple through ecosystems.

We now turn to harvest, one of the most potent agents of anthropogenic trait change (Allendorf and Hard 2009; Darimont et al. 2009; Stenseth and Dunlop 2009), which has potentially far-reaching ecological consequences. In a classic study, Coltman et al. (2003) showed that trophy hunting in a population of bighorn sheep (*Ovis canadensis*) drove reductions in horn and body size and removed high breeding value males from the population, thereby potentially influencing population growth. These changes were reported by Coltman et al. (2003) to be genetic, but the methodology used to derive this conclusion has been recently questioned (Hadfield et al. 2010). Fisheries have repeatedly been shown to drive earlier age and smaller size at maturation, and probabilistic maturation reaction norms have frequently been used as a statistical approach to infer the genetic basis of such changes (reviewed in Jørgensen et al. 2007; Kuparinen and Merila 2007; Hard et al. 2008; Hutchings and Fraser 2008; Dunlop et al. 2009; Sharpe and Hendry 2009). While it is almost certain that a large degree of this trait change does indeed have a genetic basis, probabilistic maturation reaction norms have also been found to have limitations with

respect to isolating the various genetic contributions to overall trait change (Kinnison et al. 2011; Uusi-Heikkila et al. 2011).

Fisheries-induced trait changes are predicted have dramatic effects on trophic interactions. The food webs of freshwater and marine ecosystems are highly size-structured, and fishes often occupy the upper and middle trophic levels in such ecosystems. Therefore, changes in fish body size, especially at the top trophic levels, can have major impacts on food web interactions and trophic cascades (Fig. 3). Indeed, there is strong evidence that declines in body size, but not total biomass, of heavily harvested top fish predators on the Western Scotian Shelf underlie observed increases in biomass at lower trophic levels (Shackell et al. 2010). Thus, anthropogenic trait change may have important impacts on trophic cascades that act independently (or in concert with) of changes in top predator density and biomass.

Perhaps even less appreciated than the food web effects of fisheries-induced trait change are its potential consequences for nutrient cycling in aquatic ecosystems. Fish excretion is an important source of nutrients in aquatic ecosystems (Vanni 2002). Small fish excrete nutrients at higher rates and at lower N/P than large fish; therefore, harvest-induced trait changes may have important impacts on nutrient availability (Hall et al. 2007). Assuming a compensatory increase in the biomass of small individuals (as shown by Shackell et al. 2010), harvested populations dominated by small, early maturing individuals

are predicted to recycle nutrients at higher rates and at lower N/P compared to unharvested populations (Hall et al. 2007).

The effects of excretion changes have not been directly examined in any harvested ecosystems, but relevant studies in Trinidadian guppies (*Poecilia reticulata*) suggest that such effects could be substantial. Trinidadian guppies are a model system for the study of fisheries-induced evolution because life history traits are known to evolve in response to natural predators in a manner consistent with the evolutionary effects of human harvest (Reznick and Ghalambor 2005). Palkovacs et al. (2009) found that guppy populations from streams with predators (high mortality) excreted nutrients at higher rates compared to populations from streams lacking top predators (low mortality). This finding is consistent with the expectation that, at an equal biomass, exploited populations that have evolved smaller body size should excrete nutrients at higher rates than unexploited populations. In mesocosms, heightened excretion increased nutrient availability and was associated with greater algal production (Palkovacs et al. 2009). Bassar et al. (2010) confirmed excretion differences at low guppy density but found no differences in population-level excretion rates at high guppy density. Both studies suggested that differences in guppy consumption play an important role in causing differences in algal production, an effect that could be driven by the evolution of heightened consumption rates in low-mortality, high-competition environments (Palkovacs et al. 2011).
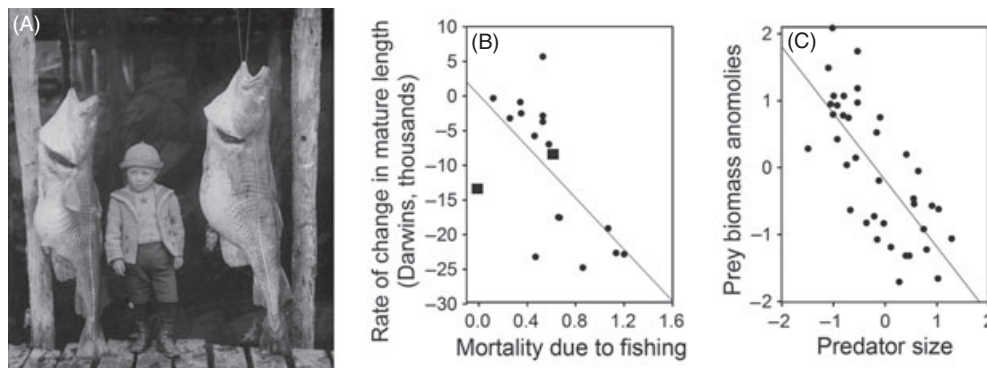

Figure 3 Effects of fisheries-induced trait change on the Western North Atlantic ecosystem. (A) The photograph *Big cod fish from the trap*, *Battle Harbour*, *Labrador*/Robert Edwards Holloway [1901] shows the size of Atlantic cod (*Gadus morhua*) harvested off Newfoundland and Labrador, Canada, at the turn of the last century. The plate noted: 'The larger fish measured 5 ft. 5 in., and weighed 60 lbs'. (B) Intense mortality owing to fishing has driven rapid declines in mature fish length for 18 commercially exploited fish stocks (panel modified from Sharpe and Hendry 2009). Cod stocks in the Western North Atlantic are highlighted as squares in this panel. Note that the rate of decrease in size and the intensity of fishing pressure for cod are average for the stocks included in this study, suggesting that the dramatic and well-publicized declines seen in cod are typical (not exceptional) for intensively harvested fish stocks. (C) Decreases in the body size of cod and other top predators on the Western Scotian Shelf have resulted in a 300% increase in the biomass of prey species (zooplankton, small planktivorous, and detritivorous fishes), despite no change in total predator biomass (panel modified from Shackell et al. 2010). The analysis of Shackell et al. (2010) found anomalies from the mean prey biomass over 38 years of surveys were strongly and negatively related to a standardized index of top predator size. Taken together, these data provide evidence that harvest-induced changes in predator body size can cause trophic cascades that can impact the functioning of entire marine ecosystems.

These experiments in a model system suggest that harvest-induced trait change may have important effects on nutrient dynamics and ecosystem processes. But such effects have not been tested in a wild, harvested ecosystem. We predict that such effects may be most important in ecosystems where a single harvested species serves as the dominant control for nutrient dynamics and ecosystem processes. In South American rivers, the flannelmouth characin (*Prochilodus mariae*) may be just such a species (Flecker 1996; Taylor et al. 2006). Declines in body size for this species are being driven by size-selective harvest (Taylor et al. 2006) and may have significant consequences for the ecosystem processes of harvested rivers (Taylor et al. 2006; McIntyre et al. 2007). This and similar systems, including Pacific salmon and Atlantic cod (*Gadus morhua*), may be excellent candidates for testing the effects of fisheries-induced trait change on freshwater and marine ecosystem dynamics.

In addition to causing changes in life history traits, some fishing methods, such as hook and line angling, may have the added effect of selectively removing the most active individuals, with the highest basal metabolic rates. In largemouth bass (*Micropterus salmoides*), the removal of these individuals selects for slowed growth, lowered aggression and territoriality, reduced parental care, and less active foraging behavior (Cooke et al. 2007; Philipp et al. 2009; Redpath et al. 2009, 2010). Decreased parental care and territorial behavior may, in theory, lead to changes in population dynamics. Reduced foraging activity and lowered consumption rates may have important effects on prey communities and trophic interactions. Lowered metabolic rates may impact excretion rates, with important effects on nutrient availability and primary production. In recreational fisheries, such effects may occur alongside life history changes (Matsumura et al. 2011) to impact the ecological dynamics of harvested ecosystems.

We have described cases where human-induced trait change causes, or is likely to cause, major *changes* to ecological processes. But what about cases where trait change buffers populations, communities, and ecosystems against change? Several studies have shown that such effects can increase the stability and resilience of ecosystems. Reusch et al. (2005) showed that higher levels of genetic diversity in seagrass (*Zostera marina*) can help maintain ecosystem function in the face of extreme climate events. Lennon and Martiny (2008), working in microbial chemostats, showed that the evolution of resistance to a virus buffered ecosystems against changes in nutrient cycling. More recently, Ellner et al. (2011) applied a method for parsing the nonheritable, genetic, and environmental drivers of ecological change to a diverse set of study systems. Their analysis showed that contemporary evolution may be most important when it acts to oppose environmental change on traits – what they describe as a temporal analogue to countergradient selection. They conclude that contemporary evolution may be key to the persistence of species and communities (see also Kinnison and Hairston 2007; Bell and Gonzalez 2011) and critical for maintaining ecosystem function in the face of environmental change. But more work is needed to determine the general conditions under which trait change promotes vs prevents ecological change. We consider this to be one of the greatest challenges facing the nascent study of eco-evolutionary dynamics, and a critical question to answer in the face of a rapidly changing, and increasingly human dominated world. We encourage researchers and resource managers to work together to apply emerging eco-evolutionary principles to real-world management scenarios, for both the benefit of management and the knowledge to be gained in the process.

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