

Organized Oral Session 44: Impacts of Species Addition and Species Loss on Ecosystem Function in Freshwater Systems

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Introduction

Understanding the role of species as drivers of ecosystem processes is imperative to preserve, utilize, and sustain ecosystems globally. Addition of species through invasion and loss of species through extirpation or extinction can have profound effects on ecosystem structure and function (Zavaleta et al. 2009). This is especially true for freshwater ecosystems in which a preponderance of native species are threatened with extinction and where nonnative species are frequently introduced (Dudgeon and Smith 2006). Commonly, anthropogenic activities result in the loss of biodiversity and enhance the ability of exotic species to invade and persist in novel habitats (Dudgeon and Smith 2006). Because these activities are expected to increase through time, advances in understanding the consequences of species loss and addition on ecosystem function are needed to guide appropriate management and conservation decisions. The loss and addition of organisms may render habitats functionally impaired (Covich et al. 2004); therefore, understanding the consequences of such change is imperative to manage, mitigate, and restore freshwater ecosystems.

We organized this oral session to examine experimental and theoretical work from studies of the addition of species and the loss of species from freshwater ecosystems. The overarching goal of this session was to begin designing a framework to quantify the effect of organisms on ecosystem processes among species and across systems. As a whole, the speakers addressed the following questions in a broad range of freshwater ecosystems: 1. What patterns emerge from studies examining changes in ecosystem

function after species invasion and species loss? 2. Are these patterns consistent across study sites and study organisms? 3. Are there specific traits that make a species more apt to be an important driver of ecosystem function? The session focused on the effects of aquatic organisms on community structure and trophic relationships, primary productivity, organic matter processing, and nutrient dynamics. Several presentations highlighted the context-dependent nature of ecosystem change in response to species addition or loss in the face of anthropogenic pressures such as drought and eutrophication. During the session we also discussed how species-specific traits can be incorporated into unifying ways to understand and predict the effects of species gain and species loss on ecosystem processes among species and across freshwater ecosystems.

Species addition and species loss: effects on trophic relationships

The loss or invasion of a species in one habitat can change fluxes of materials and organisms within habitats and to adjacent or distant habitats, with consequences for food webs and ecosystem processes (Baxter et al. 2005, Mineau et al. 2012). **Kate Boersma** and colleagues documented decreased trophic trait diversity, specifically, the disappearance of top predators, in arid river systems in response to habitat fragmentation. She used experimental manipulations to test the effects of a top predator, *Abedus herberti* (Hemiptera: Belostomatidae), removal on community structure and basal food resources. In her experiment, the removal of *Abedus* instigated a trophic cascade and reduced algal fluorescence, likely caused by the release of the algae-grazing mayfly *Callibaetis* from *Abedus* predation. Top predator removal also changed the detritivore community by significantly reducing the abundance of the dominant consumer of coarse particulate organic matter, the caddisfly *Phylloicus*. **Boersma's** results documented that species loss alters biotic relationships and can be a strong driver of ecosystem change.

In his presentation, **Colden Baxter** and colleagues summarized changes in between-habitat fluxes of materials and organisms using data collected from invading fish species on two continents. In Japan, he showed that invading rainbow trout triggered changes in feeding behavior of native char, which subsequently decreased aquatic insect emergence and riparian spider abundance (Baxter et al. 2004). Similarly, in western U.S. streams, **Baxter** and his coauthors addressed the question, "Is a trout a trout"? They demonstrated that invading brook trout, characterized by higher productivity and different trophic traits than native cutthroat trout, reduced the flux of emerging insects and riparian spider abundance relative to the native species. **Baxter** and others provided evidence that strong cross-habitat effects of species additions or losses can be caused by species with novel functional traits, trophic mismatches between invaders and native food webs, and relatively subtle differences in behavior of invasive species vs. the natives they replace.

Species addition and species loss: effects on primary productivity and organic matter processing

Native and introduced organisms can affect net ecosystem production through both direct and indirect pathways, potentially giving rise to interesting feedbacks between primary and secondary production (McIntyre et al. 2006) and decomposition (Rugenski et al. 2012). Work by **Peter McIntyre** and colleagues in Lake Tanganyika, East Africa, documented the effects of fishes in a species-rich system characterized by low ambient nutrients and high primary productivity. He used a coupled observational and experimental approach to understand how native grazing fish density and diversity influenced

benthic algal productivity directly via consumption and indirectly via nutrient recycling. Grazers often suppress primary productivity by reducing algal biomass, though they can also stimulate new growth and select for vigorous algae (McIntyre et al. 2006). When nutrients are scarce, primary productivity can also be enhanced when grazers or higher-level consumers are recycling nutrients in readily available forms (McIntyre et al. 2006). **McIntyre** and his coauthors demonstrated that grazer density had strong positive effects on algal metabolism by mediating nutrient availability, and these effects exceeded direct negative effects of grazing on algal productivity. Overall, they documented how shifts in both community composition and fish density can affect ecosystem productivity, with a strong potential for positive feedbacks of grazing fishes. **McIntyre** and others concluded the gain or loss of grazing species from freshwater systems can have profound repercussions for productivity, and if positive effects predominate, then there is the potential for positive feedbacks between primary and secondary productivity that could give rise to highly productive systems despite nutrient scarcity.

Two talks highlighted changes in organic matter processing rates after species addition or loss from aquatic ecosystems. Initially, **Colden Baxter** and colleagues described how the invasion of western U.S. riparian areas by Russian olive has altered stream organic matter budgets and nutrient dynamics. They suggested these changes were due to the ability of the invader to fix nitrogen, and because Russian olive produces low-quality leaf litter which decomposes slowly and is underutilized by native stream animals (Mineau et al. 2012). Conversely, **Weston Nowlin** and colleagues documented increased leaf litter decomposition rates in the presence of an invasive armored catfish, *Hypostomus*, in Texas rivers. Increased leaf litter decomposition rates were likely a result of increased mechanical disturbance of litter by *Hypostomus* during their movements and foraging activities.

Species addition and species loss: effects on nutrient dynamics

In both terrestrial and aquatic ecosystems, organisms directly affect nutrient storage and cycling by sequestering nutrients through growth and remineralizing nutrients via excretion and egestion (Vanni 2002). Although many studies have documented the effects of organisms on nutrient dynamics, there has not been a synthesis examining the effects of species losses and additions across systems. To understand the potential effects of the addition or loss of species on nutrient dynamics, many of the talks featured in the session summarized the influence of organisms on nitrogen (N) and phosphorus (P) storage and cycling after species were added to or removed from freshwater ecosystems. Holistically, the presentations addressed a variety of species in diverse ecosystems.

For example, presentations by **Carla Atkinson** and **Amanda Rugenski** and their collaborators highlighted the important functional role aquatic organisms can play in nutrient dynamics using three case studies: two assemblages of native species (freshwater mussels in Oklahoma and tadpoles in Panama) threatened with local extinction, and an invasive species (armored catfish in Mexico). Collectively, these case studies indicated the roles of animals in nutrient dynamics are species-specific, context-dependent, and biomass or density-dependent. For example, areal excretion and nutrient storage rates for native mussels was substantial among nine sample sites in Oklahoma. Among-site variation in this system was due to differences in densities and species composition of mussel communities. Similarly, in the Chacamax River in southern Mexico, introduced armored catfish attain an areal biomass that is two orders of magnitude greater than native fishes, thereby dominating the fluxes of nutrients through

remineralization and the pools of nutrients stored in body tissues. Conversely, the substantial influence on nutrient cycling and storage by native tadpoles in Panama was primarily density-dependent.

Putting species addition and loss into context: climate change, urbanization, and eutrophication

Coupled with the effects of urbanization, eutrophication, and water extraction, the effects of species addition and species loss on ecosystem function can be magnified (Covich et al. 2004, Zavaleta et al. 2009). Climate change and water withdrawals in arid regions are causing once-perennial streams to fragment or dry completely (Jackson et al. 2001). Several talks highlighted the potential and realized threat that water extraction will play on the loss of organisms from freshwater habitats and the subsequent changes in ecosystem function. For example, **Caryn Vaughn** quantified the influence of drought and water extraction on the functional roles of freshwater mussels in Oklahoma rivers. Freshwater mussels are large, long-lived suspension feeders that provide important ecosystem services in rivers such as biofiltration, nutrient recycling, and nutrient storage (Vaughn and Hakenkamp 2001). At the whole-river scale, extensive mussel loss led to major changes in nutrient dynamics and biofiltration. **Vaughn** highlighted that many of the changes in ecosystem function could have been prevented had water been released from an upstream tributary to alleviate high water temperatures, which exceeded 40°C in some locations. Drought in this region is predicted to become both more frequent and more severe with climate change, as human population grows and uses more water.

Two speakers in the session highlighted potential interactions between eutrophication and the effects of invasive organisms on ecosystem function in freshwaters. **Cayelan Carey** and colleagues presented work on the influence of lake trophic status and cyanobacterial blooms in the northeastern United States. Cyanobacterial blooms have large effects on community structure and ecosystem processes (Smith 2003), and are predicted to increase in aquatic systems worldwide due to eutrophication (Brookes and Carey 2011). Many studies have demonstrated that cyanobacteria have inhibitory effects on other plankton; however, most of this work has been conducted under high ambient nutrient conditions. **Carey** and coauthors examined how the trophic state of a lake could mediate relationships between cyanobacterial blooms, food web ecology, and nutrient dynamics. They found that at low ambient nutrient levels, the effect of emergent cyanobacteria had a stimulatory effect on the growth and diversity of other phytoplankton because the cyanobacteria increased water column nutrient concentrations. However, in high ambient nutrient concentrations, these effects were reversed.

Predicting when and where nonnative species become established and whether these species become invasive is poorly understood, but may vary with environmental conditions such as ambient chemistry. Armored catfishes (Loricariidae) have invaded aquatic systems throughout the world and are of concern because they affect trophic and nutrient dynamics (Pound et al. 2011). **Weston Nowlin** and colleagues presented the results of a study examining the relationship between the growth and impacts of an introduced loricariid and nutrient enrichment in a replicated stream channel experiment. **Nowlin** and others found the effects of catfish were largely independent from those of nutrients, indicating that nutrient enrichment may have a limited role in mediating or exacerbating the impacts of catfishes. However, the body condition (lipid concentration and biomass) of loricariids was enhanced in the presence of increased nutrients.

The work by **Carey, Nowlin** and their coauthors highlights the context dependence of the effects of species invasion and loss on community structure and ecosystem function. Moreover, their data suggests that the synergistic effects of multiple environmental stressors may alter the effect of species addition or loss on ecosystem dynamics in unexpected ways.

Unifying ways to examine species addition and loss on ecosystem function

One of the great challenges to understanding general patterns in functional changes in ecosystems after species invasion or extirpation is to be able to compare disparate species among study sites. Two of the speakers, **Moore** and **Rugenski**, focused their talks on understanding some of these general patterns. Anthropogenic environmental change is driving community disassembly through simultaneous declines of native species coupled with increases in nonnative species. Previous studies suggest that community disassembly is somewhat predictable, and species traits determine whether or not an organism is a successful invader or is sensitive to anthropogenic change (Zavaleta et al. 2009). Similarly, there is an increased understanding that the ecosystem consequences of community change will be influenced by the traits of species that compose the novel community. However, there is still a need to integrate patterns of community change with subsequent ecosystem consequences (Zavaleta et al. 2009).

In their presentation, **Jonathan Moore** and coauthor examined two connected questions: First, how have communities fallen apart and how are they being put back together? Second, given the pattern of community disassembly, what are the predicted changes to ecosystem processes? To address these questions, they used existing data sets of fishes in >5000 sites in the United States to quantify spatial patterns of community disassembly across gradients of urbanization. **Moore** and coauthor quantified patterns of community disassembly in fishes across the United States, and they found that varying biological and ecological traits among species determined their inferred vulnerabilities to anthropogenic habitat modification. For example, some ecosystem processes were governed by allometric rules, such as nutrient excretion. Thus, distinctive vulnerabilities of differently sized taxa will drive nonlinear ecosystem consequences. Alternatively, other ecosystem processes appeared not to be linked to vulnerability. Together, these results were used to parameterize realistic extinction scenarios. The simulations revealed that habitat alteration can decrease ecosystem processes. Thus, insights into community disassembly rules can shed light on the ecosystem consequences of human-induced environmental change.

Amanda Rugenski and coauthors identified patterns of changes in consumer-driver nutrient remineralization after species addition or loss across study sites and organisms. They attempted to determine what specific-species traits make organisms more apt to be drivers of ecosystem function in freshwater systems. **Rugenski** and coauthors proposed using volumetric excretion (E_v) (McIntyre et al. 2008) as a unifying method to assess the impacts of species additions and losses in lotic ecosystems under different environmental conditions and spatial scales. They used the three examples presented in **Carla Atkinson's** talk (see above) to highlight the roles of animals and their potential impact on nutrient cycling. **Rugenski** and others modeled E_v for ammonium (N) and soluble reactive phosphorus (SRP) for several organisms. In the three case studies they presented, aquatic organisms had profound effects on nutrient dynamics in freshwater ecosystems. Species functional traits, such as stoichiometry and feeding behavior, were important in determining the spatial extent of an organisms' influence on nutrient dynamics. Moreover, **Rugenski** and others suggested the physiochemical characteristics of

the environment, including nutrient limitation, discharge, temperature, and the biophysical traits of the organism (e.g., trophic state, biomass and density), were all important factors in predicting the role of organisms in nutrient dynamics. The results from their presentations highlight that uniform methods can be used to express species-specific effects on nutrient dynamics across freshwater ecosystems.

Future directions and challenges

In order to appropriately legislate, manage, and conserve freshwater ecosystems, it is imperative to pursue cross-habitat and cross-species comparisons to describe the functional roles of aquatic organisms in ecosystem processes. The work presented in this session and subsequent discussions highlighted that species addition and loss from freshwater ecosystems frequently results in changes in ecosystem function. Comprehensively, the presentations suggested novel functional traits, such as body and dietary stoichiometry, trophic mismatches between invaders and native food webs, and differences in behavior among species challenge the concept of functional redundancy. Altogether, presentations in the session indicate that the addition or loss of a keystone or dominant species or group of organisms from freshwaters will typically result in changes in ecosystem structure and function. Future studies should generate and utilize unifying metrics that would allow scientists and managers to compare effects of species addition and species loss across taxa and ecosystems. These metrics should be measured in conjunction with other environmental parameters such as urbanization, eutrophication, and water extraction to elucidate potentially unexpected conflicting or synergistic effects of multiple anthropogenic activities in freshwater habitats and watersheds.

Part of the motivation for understanding the effects of species addition and loss is to develop management strategies that would enable human populations to utilize natural resources while sustaining natural systems and preserving the functions that are both ecologically and economically valuable. Furthermore, a great challenge that ecologists face is to quantify these changes and the subsequent losses of ecosystem services and make them relevant to the public. For example, in her discussion of freshwater mussel loss in Oklahoma rivers, **Caryn Vaughn** highlighted that drought in the south-central United States is predicted to become both more frequent and more severe with climate change, and water consumption will increase with population growth. **Vaughn** pointed out that while the frequency and severity of droughts cannot be controlled in the short term, the management of water resources can be effectively administered to maintain healthy populations of freshwater mussels and the ecosystem services they provide. Through her presentation, she emphasized the importance of quantifying ecosystem services provided by species to support conservation efforts on their behalf. There is a pressing need for scientists to quantify changes in ecosystem function into economically valued ecosystem services that can be incorporated into management and conservation efforts.

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