

## **Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions**

Author(s): Caryn C. Vaughn

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# Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions

CARYN C. VAUGHN

*Six conclusions have emerged from recent research that complicate the ability to predict how biodiversity losses may affect ecosystem function: (1) species traits determine ecosystem function, (2) species within functional groups are not always ecological equivalents, (3) biodiversity losses include declines in the abundance of common species, (4) biodiversity losses affect whole food webs, (5) the effects of biodiversity losses depend on abiotic and biotic context and spatial and temporal scales, and (6) successfully predicting linkages between biodiversity and ecosystem function requires using multiple empirical approaches across scales. Nutrient recycling by freshwater mussel communities illustrates these conclusions. Nutrient excretion rates depend on the expression of mussel species traits, which vary with flow, temperature, and community structure. Nutrient contributions from mussels depend on which mussel species are dominant, but common species of mussels are declining, leading to shifts in species dominance patterns and thus nutrient recycling. These changes are very likely affecting the rest of the benthic food web because mussel excretion stimulates primary, and subsequently secondary, production.*

*Keywords: freshwater, biodiversity, ecosystem function, species traits, mollusks*

**G**lobally, freshwaters are experiencing declines in biodiversity at rates greater than those in terrestrial systems. Extinction rates for well-studied North American freshwater animals are estimated to be as high as 4% per decade, five times greater than species losses in terrestrial systems, and rates for less-studied regions and faunas may be as high or higher (Dudgeon et al. 2006). Factors underlying freshwater biodiversity declines include overexploitation of both water and organisms, water pollution, and habitat destruction and degradation (including modification of natural flow regimes and invasions of exotic species), all of which are linked to human activities. Superimposed on these factors are global-scale environmental changes, such as climate warming and acidic deposition. The overharvesting of wild stocks of freshwater fishes is occurring worldwide (Allan et al. 2005). Water pollution also occurs globally, and is a particular problem in economically developing regions. While some chemical inputs have been reduced, new pollution threats have emerged from substances such as endocrine disrupters (McMaster 2001). Habitat destruction and modification include deforestation, urbanization, and agricultural impacts. One of the greatest threats to rivers has been the widespread alteration of natural flow regimes through massive river damming and

channelization (Poff et al. 2007). Accidental invasions and deliberate introductions of exotic species are widespread, and impacts are typically greater in systems already affected by human activity (Dudgeon et al. 2006). Climate change also threatens most ecosystems and is predicted to cause significant alterations to freshwater biogeochemical processes, primary and secondary productivity, food-web structure, population dynamics and species interactions, species ranges, and large-scale patterns of freshwater biodiversity (Wrona et al. 2006).

A primary reason for concern over the current accelerated loss of species is the associated loss of ecological function. Although the linkages between biodiversity and ecosystem function are an area of intense research, there are significant gaps in our understanding of how biodiversity declines affect ecosystem function (Hooper et al. 2005), particularly in freshwater systems (Covich et al. 2004, Giller et al. 2004, Dudgeon et al. 2006). Most of these gaps stem from the lack of integration and understanding of species roles across ecological, spatial, and temporal scales. Here, I discuss six general conclusions emerging from recent work that are critical for predicting how biodiversity losses may affect freshwater ecosystem function. I close with a case study of nutrient recycling by

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freshwater mussels that illustrates how research bridging scales and using multiple empirical approaches can be used to gain a more complete understanding of how biodiversity losses will have an impact on ecosystem function.

### **Species traits determine ecosystem function**

Ecosystem function is the product of the expression of species' functional traits (Ackerly and Cornwell 2007). Much study of biodiversity has been inspired by concern over the loss of species richness, but of greater concern may be the loss of the traits of the species involved and the materials they provide and the processes to which they contribute. Higher species richness can lead to increased ecological function through niche differentiation (resource partitioning or complementary resource use), facilitative interactions among species, or strong effects from a unique species in the mixture (species identity or selection effects), all of which are ultimately due to trait expression. For example, increased richness of filtering caddisfly larvae results in greater topographical complexity from the different physiognomies of filtering nets. This increased complexity changes the flow patterns on the stream bottom, resulting in increased delivery of suspended food particles to the larvae (Cardinale and Palmer 2002)—an example of facilitation. Different morphological traits associated with detritivorous shrimp species in tropical streams allow them to process leaf litter at different rates. In streams where they co-occur, their interactions and the different modes and rates of leaf-litter processing enhance leaf breakdown (Crowl et al. 2001), an example of complementary resource use. Species richness has been demonstrated to have an impact on ecosystem function across a wide array of freshwater organisms and systems, from rapidly reproducing microbes and plankton (Dzialowski and Smith 2008) to grazing and shredding insects (Jonsson and Malmqvist 2000, Huryn et al. 2002); to large, long-lived fishes; decapods; and mollusks.

Individual species, with their unique traits, can be as important to ecosystem function as higher species richness. Such species-identity effects have been found across freshwater ecosystems and in many different groups of organisms, including insects, crustaceans, mollusks, and fishes (Crowl et al. 2001, Bjelke and Herrmann 2005, Taylor et al. 2006, Vaughn et al. 2007, Wojdak and Mittelbach 2007). For example, Vanni and colleagues (2002) found that the rates and ratios by which 28 fish and amphibian species recycled nutrients in a tropical stream varied by more than an order of magnitude. In a particularly elegant study, McIntyre and colleagues (2007) used field data on nutrient-recycling rates of fishes in a tropical stream and Lake Tanganyika, Africa, to evaluate the effects of simulated species extinctions on nutrient recycling. They found that the nutrients provided to the ecosystem through fish excretion depended on community composition, and that extinctions of particular species resulted in highly divergent nutrient-cycling patterns. Of course, a combination of both species richness and identity can be important. For example, Wojdak and Mittelbach (2007) showed that snail identity had strong effects on total organic matter, periphyton biomass,

dissolved oxygen, and snail biomass in pond microcosms, but that snail biomass grew more in more species-rich treatments because of complementary use of microhabitats.

Most studies of how biodiversity influences ecosystem function have examined single traits (e.g., the ability to break down leaves, rates of primary production). However, this is an oversimplification of species' roles, and very likely has led to underestimates of the impacts of species losses. Poff and colleagues (2006) pointed out that we lack an adequate understanding of how individual traits are intercorrelated, and how this lack of independence among traits reflects phylogenetic constraints. Future studies need to more fully consider phylogeny and take a multitrait approach to understanding how species respond to environmental gradients.

### **Species within functional groups are not necessarily ecological equivalents**

Species that are believed to play the same functional role in ecosystems are often placed in functional groups, types, or guilds, and redundancy of ecological function is predicted to be highest within such groups (Walker 1992). Recently, researchers have proposed that ecosystem function can be sustained by maintaining functional group richness. For example, multiple studies have examined the diversity of plant functional groups and found significant differences between the processes performed by these groups and strong effects from removal of functional groups (Hooper et al. 2005). It has even been suggested that as long as one species from each functional group in an ecosystem is present, ecosystem function can be maintained, if the remaining species increase in abundance (numerical response or biomass or density compensation) or increase their process rates (metabolic or per capita response; Walker et al. 1999, Hooper et al. 2005). In most freshwater systems, species richness is high enough to allow for the possibility of functional redundancy (Covich et al. 2004), but there have been few attempts to experimentally assess this possibility (Crowl et al. 2001).

The concept of redundant species within functional groups simplifies the study and management of ecological systems, but there are problems limiting the applicability of this concept (Gitay et al. 1996). First, functional groups themselves have been inadequately defined for most freshwater ecosystems. Walker (1992) recommended looking at communities within ecosystems and subdividing species into guilds on the basis of nontrivial ecological attributes (i.e., traits) that are related to or that limit some important process in that ecosystem. However, freshwater species often are placed into functional categories on the basis of shared autecological traits (i.e., trophic mode, behavior, habitat, life history, morphology) that may not translate into shared ecological function.

Second, the degree of redundancy among species assigned to many functional groups or guilds is unknown. Stream insects are commonly placed into functional groups on the basis of their method of food acquisition (i.e., shredders, scrapers, filter-feeders). Researchers have used the dynamics of these functional feeding groups to make predictions about

stream function, but modes of food acquisition do not always equate with particular foods consumed or assimilated, and thus stream energetics. For example, multiple studies of shredders have shown that species in this group are not interchangeable (Jonsson and Malmqvist 2000, Crowl et al. 2001, Huryn et al. 2002).

Finally, we do not understand the degree to which the functional role of species changes with environmental context (Cardinale et al. 2000). Walker and colleagues (1999) pointed out that in most communities, the majority of species occur in low abundance, with just a few dominant species making up the bulk of the biomass. They proposed that many minor species might be analogs of dominant species in terms of the ecological functions they perform, but differ in terms of their capabilities to respond to environmental stress and disturbance. Under changing ecological conditions, ecosystem function can be maintained when dominant species decline if the more rare species are favored by the changed environmental conditions, and subsequently increase in either biomass or the number of individuals present. This issue is addressed further below.

#### **Biodiversity losses include declines in the abundance of common species**

Studies of the relationship between biodiversity and ecosystem function have focused on consequences of species extinctions, but biodiversity losses also include declines in the abundance of common species and shifts in species' dominance patterns (Hooper et al. 2005). Common species are typically drivers of ecosystem processes (Moore 2006), and such declines can have profound implications for ecosystem function. Dominant fishes play particularly important roles in freshwater ecosystems, often linking benthic and pelagic compartments through their high mobility and flexible foraging strategies (Schindler and Scheuerell 2002). Because they frequently occupy higher trophic levels with lower species richness, dominant fishes are also less likely to be replaced by functionally equivalent species. There are numerous examples of the overharvests of once-abundant fishes that have led to changes in ecosystem function (Allan et al. 2005). Declines of migratory fishes have been particularly problematic because these fishes often transport materials over long distances, and there are usually no functional equivalents to replace them. For example, salmon transport important marine-derived nutrients upstream over large spatial scales into freshwater and terrestrial habitats, but also redistribute matter and nutrients on finer spatial scales through their spawning activities (Merz and Moyle 2006, Moore et al. 2007).

#### **Biodiversity losses affect whole food webs**

Although most research on biodiversity decline and ecosystem function has concentrated on primary producers (Hooper et al. 2005), studies of single trophic levels are insufficient to understand the functional consequences of biodiversity decline. Natural ecosystems are composed of

communities comprising multiple trophic levels; losses and declines of species from different trophic levels can have very different effects on ecosystem function (Duffy et al. 2007), and changes at any trophic level can lead to cascading effects through food webs. For example, the loss of large, migratory, detritivorous fish (*Prochilodus*) in South American rivers modulates carbon flow and ecosystem metabolism, decreases downstream transport of organic carbon, and raises primary production and respiration (Taylor et al. 2006). Evidence to date suggests that tropical amphibian declines, primarily through the catastrophic loss of primary consumers (grazing tadpole biomass), will have large-scale and lasting ecosystem-level effects, including changes in algal community structure and primary production; altered organic-matter dynamics; changes in other consumers, such as aquatic insects and riparian predators; and reduced energy transfers between streams and riparian habitats (Whiles et al. 2006). Species feeding at higher trophic levels often affect ecosystems in ways that are disproportionate to their abundance, making the study of them particularly important (Dobson et al. 2006). For example, in New Zealand streams, trout predators indirectly control leaf-litter breakdown by reducing caddisfly populations, which in turn slows the breakdown of organic matter and reduces the production of fine particulate organic matter, which is an important resource for other invertebrate consumers (Greig and McIntosh 2006).

Community and food-web structure also influence species interactions and how species' traits are expressed, and both vertical (across trophic levels) and horizontal (within trophic levels) diversity are important (Downing and Leibold 2002, Wojdak 2005, Duffy et al. 2007). Downing and Leibold (2002) independently manipulated both species richness and composition across multiple trophic levels in pond mesocosms and found that species roles were usually complex, and these roles caused both direct and indirect effects that were difficult to predict. In pond mesocosm experiments manipulating consumer richness (snails), predation intensity, and nutrient availability, Wojdak (2005) observed that snails' species richness effects on periphyton and epiphyton depended on predation intensity on the snail consumers.

#### **Effects of biodiversity losses depend on context**

Effects of biodiversity on ecosystem function vary with both abiotic and biotic environmental conditions (Cardinale et al. 2000, Ackerly and Cornwell 2007). In the example of the net-spinning caddisflies described earlier, periodic disturbance prevented taxonomic dominance and allowed development of more diverse caddisfly assemblages (Cardinale and Palmer 2002), which facilitated food acquisition through current shading. In Venezuelan rivers, the magnitude of top-down effects of benthivorous grazing fishes on organic material in sediments is a function of seasonal changes in water level (Winemiller et al. 2006). As described above, salmon enhance stream benthos by transferring marine nutrients to freshwater spawning sites. In watersheds harvested for timber, the harvest process leads to reduced stream

sediment particle sizes, promoting bioturbation by salmon, and reducing, rather than enhancing, benthic productivity. Thus, the dominant salmon effect is transformed from nutrient enrichment to physical disturbance, modifying the marine-freshwater nutrient linkage (Tiegs et al. 2008). A particularly robust example comes from the long-term studies by Mary Power and her students of linkages in the Eel River, California. In this system, blooms of filamentous algae are controlled by the severity of winter floods. Algal abundance influences how predatory fish affect primary consumers, and in turn, whether these consumers have positive or negative effects on algal accrual (Power et al. 2008). Power and her students observe patterns of the relationship between biodiversity and ecosystem function, and how the underlying mechanisms change with spatial and temporal scale. For example, strong species-identity effects at local scales can become species-richness effects at larger scales, as different species traits are favored in different habitats (Cardinale et al. 2004).

### Understanding how biodiversity losses influence ecosystem function requires the combination of approaches and scales

In general, studies that have successfully uncovered the connections between biodiversity and ecosystem function have done so by employing multiple empirical approaches across temporal and spatial scales (Lowe et al. 2006). All approaches have advantages and disadvantages; combining approaches lessens the influence of each approach's shortcomings and can be quite powerful (figure 1). Long-term studies are particularly important for understanding how environmental context shapes biodiversity effects. The Eel River system discussed above provides an excellent example of this. In this system, the hydrologic regime (the severity of winter floods) controls algal blooms and thus the impacts of fish on the rest of the food web. This phenomenon became apparent only as a result of 18 years of careful field observations combined with 5 years of manipulative field experiments. Data from any single year of field observations or any individual field

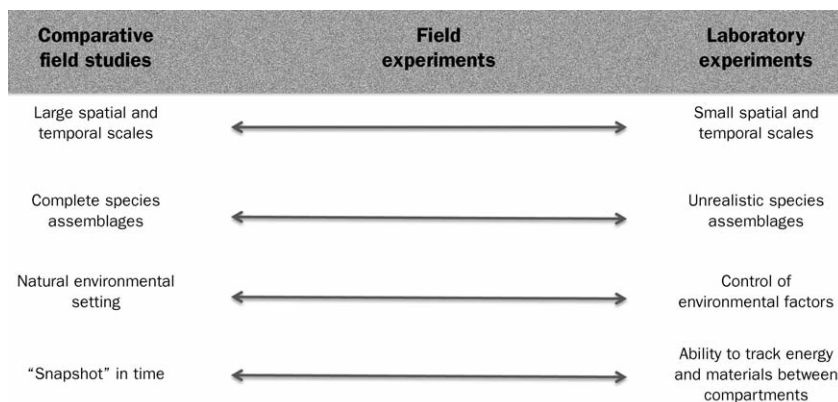
experiment would have led to different conclusions (Power et al. 2008).

### Case study: Nutrient recycling by freshwater mussels

Freshwater mussels (Bivalvia: Unionoidea; hereafter, mussels) are a guild of sedentary, burrowing, long-lived, filter-feeding bivalves (figure 2). The highest diversity of mussels is in North America, which harbors more than 300 species (Bogan 2008). Although they occur in most types of freshwater habitats, mussels are most abundant and diverse in medium to large rivers, where they typically occur as dense, multispecies assemblages called mussel beds (Strayer et al. 2004). In these areas, mussel biomass can exceed that of other benthic organisms by an order of magnitude, and annual production (dry mass produced per year) can equal that of other macrobenthos (Negus 1966, Strayer et al. 1994).

Mussels perform important functions in streams and lakes (figure 3; Vaughn and Hakenkamp 2001). Living mussels and their spent shells provide or improve habitat for other organisms (Howard and Cuffey 2006, Spooner and Vaughn 2006, Vaughn and Spooner 2006). Through the process of filtering suspended matter, mussels link benthic and pelagic compartments by transferring energy and nutrients from the water column to the sediment, biodepositing organic matter and excreting nutrients (Vaughn and Hakenkamp 2001, Vaughn et al. 2004, Howard and Cuffey 2006, Christian et al. 2008). The effects of these energy and nutrient subsidies provided by mussels cascade through food webs and stimulate both algal and macroinvertebrate production (Spooner and Vaughn 2006, Vaughn et al. 2007, 2008). In addition, juvenile mussels use their foot to feed on organic matter in the sediment (deposit feeding), and some evidence indicates that adult mussels can filter feed interstitially (Nichols et al. 2005).

Currently, mussels are experiencing global declines in both species richness and biomass (Lydeard et al. 2004). In North America, the major cause of mussel decline is extensive alteration of rivers and their flow regimes, coupled with pollution, land-use changes, and invasive species such as zebra mussels (Strayer et al. 2004, Cope et al. 2008). Impoundment and channelization of rivers has an impact on mussels directly, through physical stress such as temperature changes, siltation, and scour; and indirectly, through changes in habitat and food and fish-host availability (Watters 1999). The long life span and complex life history of mussels make them highly vulnerable to such environmental change. Larval mussels (glochidia) are obligate ectoparasites on fishes, and the larvae of many mussel species can survive on only a narrow range of host species (Barnhart et al. 2008). Metamorphosed juveniles must be deposited in a favorable habitat to survive; successful



**Figure 1.** Various approaches to investigating the effects of biodiversity on ecosystem function have different advantages and disadvantages, and these approaches vary along a spatial and temporal gradient.



settlement of juveniles is particularly affected by disturbance, and the demography of many mussel populations in disturbed areas is marked by periods when entire year classes are not recruited (Layzer and Madison 1995). Because only larvae (attached to fish) can move between mussel beds, and juvenile survival is low, potential mussel colonization rates are low (Strayer 2008). Mussels exhibit delayed reproductive maturity (6 to 10 years), long life spans (10 to more than 100 years), and high adult survivorship in undisturbed habitats (Strayer 2008). Movement of adult mussels is seasonal and varies from less than a meter to an estimated annual maximum of 100 meters (Waller et al. 1999, Allen and Vaughn 2009). Thus, mussels have limited refugia from disturbance events in streams, and cannot recover rapidly from such events through growth or reproduction.

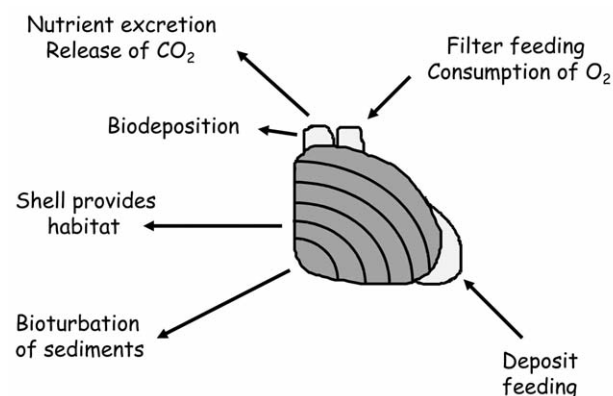
The decline of mussels has stimulated interest in the role that the mussel guild plays in freshwater ecosystems, and how the loss of so many species and so much biomass may affect ecosystem function. My students and I have been addressing this question using a combination of approaches, from very small-scale laboratory experiments to mesocosm experiments, to large-scale field experiments and comparative field studies (table 1). Our results demonstrate the importance of the six emerging conclusions discussed above. I illustrate this below with an example of how mussel species influence nutrient recycling in streams.

The influence of mussel communities on nutrient recycling depends on overall mussel abundance and species composition, but the strength of the effects varies with environmental conditions. The amount of material that mussels can filter from the water and contribute back to the water column and sediments as dissolved nutrients depends chiefly on the biomass of feeding mussels and the volume and residence time of the overlying water (Strayer et al. 1999). We combined laboratory-derived, species-specific clearance rates with field-estimated mussel densities and biomass to model the seasonal ability of a dense, diverse mussel community in a small, southern US river (the Kiamichi River, Oklahoma; basin area 4650 square kilometers) to filter all of the water in the water column. In this system, mussels could process the entire volume of overlying water in approximately one day during late summer, when flows were low and hydrologic residence times long. When water volumes and discharge were higher during the spring and winter, mussels processed only a small percentage of the water column (figure 4; Vaughn et al. 2004).

After accounting for the large influence of hydrological regime and overall mussel biomass, the effects of mussel communities on nutrient recycling are next determined by mussel community composition and environmental conditions. Because all mussels are sedentary filter feeders, they traditionally have been assigned to the same guild and assumed to perform equivalent ecosystem roles. In reality, mussel species vary in multiple traits, ranging from overall size and shell morphology to the spacing of cilia on the gills (figure 5; Vaughn et al. 2008, Galbraith et al. 2009). These different species traits translate into differences in ecosystem perfor-



**Figure 2.** A filter-feeding mussel (*Actinonaias ligamentina*). Photograph: Caryn C. Vaughn.

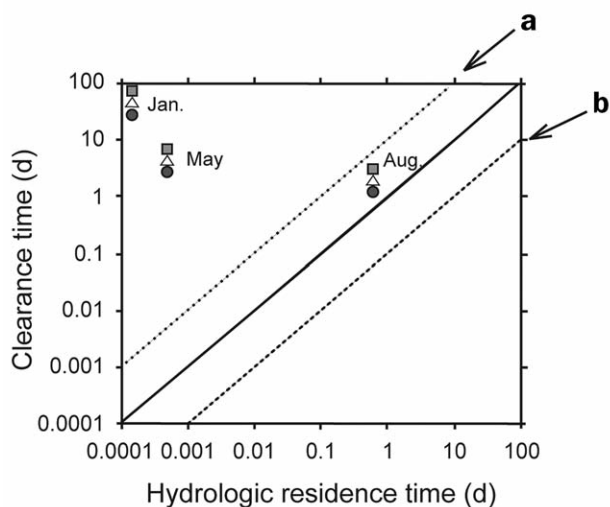


**Figure 3.** Ecosystem processes performed by freshwater mussels. Source: Modified from Vaughn and Hakenkamp (2001), used with permission from Blackwell Scientific Publishing.

mance. In particular, mussels are thermoconformers whose physiological processes are constrained by water temperature. We measured physiological condition, filtration rates, and excretion rates for eight common mussel species held in the laboratory at a range of naturally occurring temperatures. We found that (a) temperature governs the rates at which mussels clear material from the water column and excrete ammonia and phosphorus; and (b) different species have different optimal temperatures for these functions, and thus the interaction of temperature regime with species composition can have a large influence on nutrient recycling (Spooner and Vaughn 2008). As an example, *Actinonaias ligamentina* and *Amblema plicata* (figure 5) are the two most common species in the Kiamichi River. *Actinonaias ligamentina*, a thermally sensitive species, has a higher filtration rate and a lower ammonia excretion rate (at 25 degrees Celsius [ $^{\circ}\text{C}$ ]) than *A. plicata*,

**Table 1. When studying the influence of mussel biodiversity on nutrient recycling in streams, different approaches and scales contribute to an understanding of the importance of the emerging conclusions about biodiversity loss in freshwaters.**

Emerging conclusion	Approach				
	Laboratory experiments	Mesocosm experiments	Field experiments	Comparative field measurements	Models
Species traits determine ecosystem function	Vaughn et al. 2004, Spooner and Vaughn 2008	Vaughn et al. 2004, 2008	Vaughn et al. 2007, 2008	Spooner and Vaughn 2009	Vaughn et al. 2008
Species within functional groups are not ecological equivalents	Vaughn et al. 2004, Spooner and Vaughn 2008, Allen and Vaughn 2009	Vaughn et al. 2004, 2008, Allen and Vaughn 2009	Spooner and Vaughn 2006, Vaughn et al. 2007	Galbraith et al. 2009, Spooner and Vaughn 2009	Vaughn et al. 2008
Biodiversity losses include losses of abundant species				Galbraith et al. 2008	Vaughn et al. 2008
Biodiversity losses affect whole food webs			Spooner and Vaughn 2006, Vaughn et al. 2007, 2008	Vaughn and Spooner 2006	Vaughn et al. 2008
Effects of biodiversity losses are context dependent	Vaughn et al. 2004, Spooner and Vaughn 2008	Vaughn et al. 2004	Spooner and Vaughn 2006, Vaughn et al. 2007, 2008	Vaughn et al. 2004, Spooner and Vaughn 2009	Vaughn et al. 2004, 2008



**Figure 4. Relationship between hydrologic residence time (time in days [d] for all water to move through a stream reach) and clearance time (time in days required for a mussel community to filter a volume of water equal to the entire volume of water in the stream reach) for a mussel community in the Kiamichi River, Oklahoma, during three seasons: winter (January), spring (May) and summer (August). Points represent mussel densities of 54 per square meter (square), 20 per square meter (triangle), and 7 per square meter (circle). Below the solid diagonal line mussels filter the entire water volume as it flows across the mussel community. Above the solid diagonal line water flows across the bed before being completely turned over by mussel filtration. (a) Mussels can filter 10% of the water column as it flows over them. (b) Mussels can filter the water column 10 times before it flows over them. Source: Vaughn and colleagues (2004).**

a thermally tolerant species (figure 6a, b). The ammonia excretion rate results are reversed at 35°C (a typical summer water temperature in the Kiamichi River), and are driven primarily by differences in physiological condition. Comparisons of oxygen consumption and ammonia excretion rates across temperatures show that at 35°C, the thermally sensitive species *A. ligamentina* is stressed, respire anaerobically, and uses glycogen reserves, leading to higher ammonia excretion, whereas the thermally tolerant *A. plicata* remains aerobic (figure 6c; Spooner and Vaughn 2008).

Whether the interaction of mussel species composition and temperature results in strong, unique species effects (species identity effects) or species richness effects depends on the underlying context. For example, during the summer, the Kiamichi River experiences very low flows and warm water temperatures; in the remainder of the year, generally moderate flows and temperatures exist. Nitrogen is limiting in this system in the summer, but not in other seasons. In a manipulative field experiment, we found strong species identity effects from one species, *A. ligamentina*, in the summer, but not in the fall (Vaughn et al. 2007). *Actinonaias ligamentina* had higher metabolic rates and ammonia (NH<sub>3</sub>) excretion rates than other species in the assemblage at warm, summer temperatures (Spooner and Vaughn 2008), which led to increased nitrogen subsidies to benthic algae and increased algal standing crops on benthic sediments (Vaughn et al. 2007). In the same experiment, however, algal abundance on mussel shells (rather than on the sediment) was highest in the most species-rich treatments, and was due to the combined effects of nutrient subsidies from mussel excretion, differences in mussel shell architecture that provide different surfaces for algal growth, and differences in mussel burrowing activity patterns that possibly influence algal sloughing patterns.

Which species' traits have the greatest influence on ecosystem function depends on which mussel species are most abundant (dominant) under a certain set of environmental





**Figure 5.** Top left: Variety in sizes and shapes of mussels from one 0.25 square-meter area in the Kiamichi River. Top right: Differences in shell morphology between two similarly sized individuals of *Actinonaias ligamentina* and *Amblema plicata*. Bottom left: Scanning electron microscope images of the cilia arrangement on the gills of *A. ligamentina* and *A. plicata*. Bottom right: Algae growing on the shell of a filtering *A. ligamentina*. Scanning electron microscopy image by Heather Galbraith; all other photographs, Caryn C. Vaughn.

conditions. We used laboratory-derived algal clearance,  $\text{NH}_3$  excretion rates, and field-measured temperature and discharge to predict how ecosystem processes performed by mussels might change with assemblage composition and environmental conditions. Mussel assemblages dominated by the two species with disparate physiological optima discussed above (figure 6; *A. ligamentina* and *A. plicata*) had different ecosystem effects. In the model, under typical summer conditions of high water temperature and low flow, *A. plicata*-dominated communities had higher filtration rates, whereas *A. ligamentina*-dominated communities contributed more ammonia. Under milder conditions of lower water temperature and higher flow, *A. ligamentina*-dominated communities had higher filtration rates, and *A. plicata*-dominated communities contributed more ammonia (figure 7; Vaughn et al. 2008).

Nutrient excretion by mussels has been shown to stimulate primary production, particularly on benthic sediments and on the shells of mussel themselves (Spooner 2007, Vaughn et al. 2007, 2008). Changes in the abundance of mussel species can thus alter nutrient recycling and lead to differences in pri-

mary production. Spooner (2007) manipulated the relative dominance of mussel species, including *A. ligamentina* and *A. plicata*, in mesocosms across a temperature gradient (15°, 25°, 35°C), and measured a suite of ecosystem processes, including nutrient recycling and primary production. At 35°C, *A. ligamentina* individuals decreased their filtration rates but increased their  $\text{NH}_3$  excretion rate, leading to higher water-column gross primary production from ammonia subsidies when this species was dominant. In contrast, at the same temperature, *A. plicata* increased its filtration rate, which increased the transfer of material from the water column to the benthos, and led to higher benthic primary production.

In addition, the effects of nutrient recycling by mussel communities extend across trophic levels, influencing not only primary producers but also consumers. Both comparative field studies (Vaughn and Spooner 2006) and field experiments (Howard and Cuffey 2006, Spooner and Vaughn 2006) have shown that benthic invertebrates aggregate in the sediments surrounding mussels or on mussel shells. In a year-long field experiment, we demonstrated that this is at least partially due to services provided by living mussels, and not

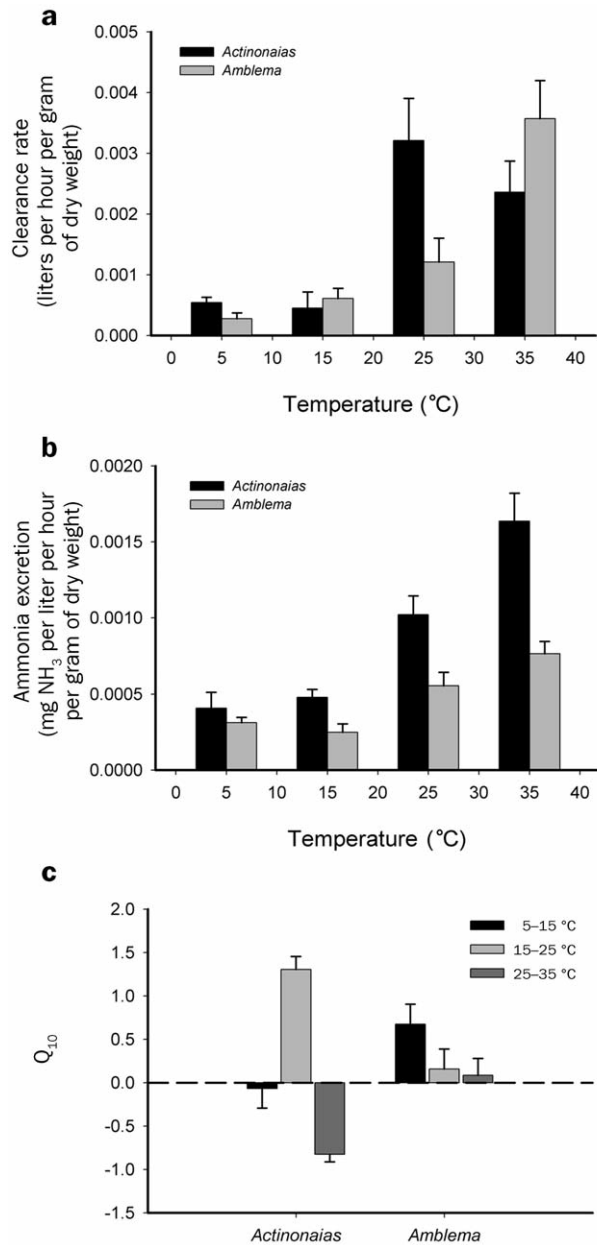


just the structure provided by mussel shells (Spooner and Vaughn 2006). In this experiment, both algae and invertebrates were more abundant on the shells of living mussels than on sham shells, and live mussel shells harbored an invertebrate community composed of algal grazing species different than

the nongrazing invertebrate assemblage found on sham shells (Vaughn et al. 2008).

Thus, the amount of nitrogen provided to streams by mussel communities depends on the traits of the mussel species, the species composition and biomass of the mussel assemblage, and the hydrological and thermal regimes of the stream. These variables interact to determine how much recycled nitrogen mussels provide, and how much of this nitrogen is transferred through the food web through algae and grazing invertebrates (and most likely fish, as well; figure 8). This relationship is dynamic because both environmental conditions and mussel communities change over time. For example, over a 15-year time period, mussel communities in the Kiamichi River changed from assemblages dominated by the thermally sensitive *A. ligamentina* to assemblages dominated by the more thermally tolerant species, *A. plicata* (Galbraith et al. 2008). These changes corresponded with a regional, multiyear drought in which mussel populations experienced extremely high water temperatures (sometimes exceeding 40°C) and very low flows that were exacerbated by water management practices (restricted releases from an upstream reservoir). On the basis of the information modeled in figure 7 and from Spooner (2007), these changes in species composition should lead to large changes in nitrogen recycling because of differences in temperature-dependent filtration and  $\text{NH}_3$  excretion rates between *A. ligamentina* and *A. plicata*.

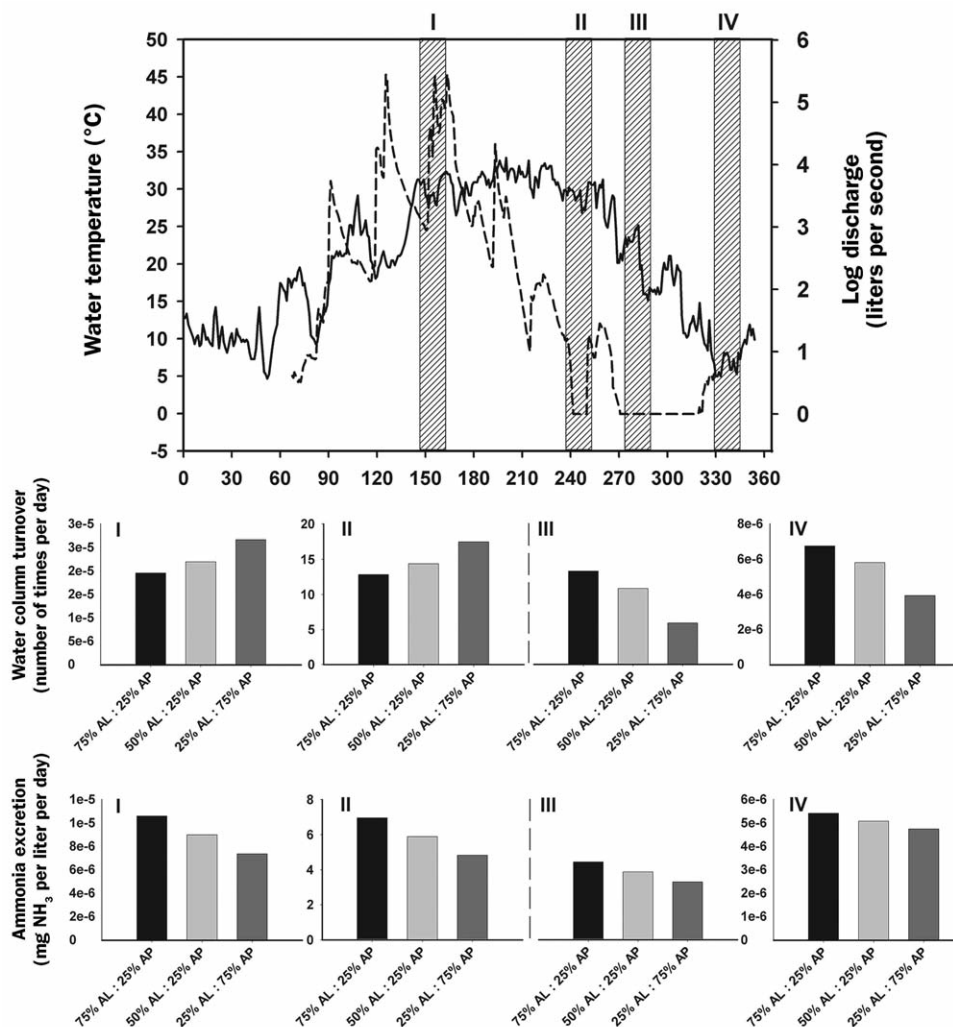
This case study of nutrient recycling by mussels exemplifies the importance of the six emerging conclusions discussed above. Although filter-feeding mussel species typically have been assigned to the same functional group, our work demonstrates that different species do not serve identical nutrient-recycling roles in streams. Uncovering these roles required combining information gained from multiple approaches including small-scale laboratory experiments; mesocosm experiments; field experiments; large-scale, comparative field studies; and models that combine the information from all of these (table 1). Nutrient excretion rates depend on individual mussel species traits, and the expression of these traits varies with abiotic (flow and temperature) and biotic (community structure) conditions. Overall nutrient contributions from the mussel community depend on which species are dominant, yet even common mussel species are declining, leading to shifts in species dominance patterns and thus nutrient recycling. These changes likely are affecting the rest of the benthic food web since mussel excretion stimulates primary, and subsequently, secondary production.



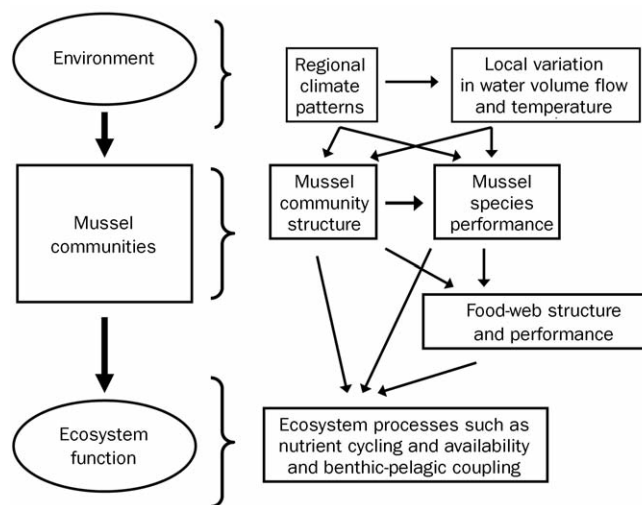
**Figure 6.** Comparison of physiological traits and subsequent ecosystem processes performed by a thermally sensitive species, *Actinonaias ligamentina*, and a thermally tolerant species, *Amblema plicata*, at three temperature ranges. (a) Clearance rates, (b) ammonia excretion rates, (c) Delta  $Q_{10}$ , where  $Q_{10}$  quantifies the relative change in anabolism (measured as oxygen consumption) and catabolism (measured as ammonia excretion) over a 10 degree temperature change. Source: Modified from Spooner and Vaughn (2008), with permission from Springer Publications.

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**Figure 7.** Top panel: Actual water temperature and discharge in the Kiamichi River, Oklahoma, in 2003. I, high discharge, high water temperature; II, low discharge, high water temperature; III, low discharge, intermediate water temperature; IV, intermediate discharge, cool water temperature. Hatched line is discharge and solid line is temperature. Bottom panel: Predicted ecosystem processes (water column turnover and ammonia excretion) provided by three simulated two-species mussel communities for the four sets of environmental conditions. AL, *Actinonaias ligamentina*; and AP, *Amblema plicata*. Note order-of-magnitude differences in the y-axis scales among panels. Source: Modified from Vaughn et al. 2008, used with permission from Journal of the North American Benthological Society. NH<sub>3</sub>, ammonia.



**Figure 8.** A conceptual model of how regional and local environmental conditions influence both mussel species community structure and performance, which in turn influence food-web structure and performance and ecosystem processes.

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*Caryn C. Vaughn (cvaughn@ou.edu) is with the Oklahoma Biological Survey, Department of Zoology and Graduate Program in Ecology and Evolutionary Biology, at the University of Oklahoma in Norman.*

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