BEYOND SPECIES RICHNESS: EXPANDING BIODIVERSITY–ECOSYSTEM FUNCTIONING THEORY IN DETRITUS-BASED STREAMS

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ABSTRACT

Initial research informing biodiversity–ecosystem functioning (B–EF) theory focused largely on terrestrial plant species richness effects on productivity. Recent studies in stream ecosystems have further advanced understanding of B–EF beyond species richness by testing effects of species diversity (richness and composition) at multiple trophic levels. Recent meta-analyses of stream B–EF studies across multiple trophic levels found stronger evidence for composition- than richness-functioning relationships. Here, we further examine effects of resource and consumer diversity on stream organic matter processing (OMP) to identify general patterns and potential mechanisms of non-additivity across spatial and temporal heterogeneity. We also review multi-trophic consumer response patterns to resource diversity to assess how consumer diversity *responses* compare to independent resource and consumer *effects* on OMP in streams. Consistent emergent patterns include: (1) Top-down (i.e. consumer) diversity effects are common among vertebrate, invertebrate and microbial trophic levels and are generally explained by species evenness; (2) bottom-up (i.e. resource) diversity effects are mediated by species evenness and vary both spatially and temporally and (3) consumer responses to resource diversity that best explain resource diversity effects are predominantly seen at the microbial level. Resource and consumer diversity effects are driven by dominance of functionally distinct taxa. However, response of consumers to resource diversity only partially explain resource diversity effects, suggesting functional differences between how naturally colonizing and manipulated consumer assemblages use OM resources. The challenges facing general ecology and the advancement of B–EF theory include an improved understanding of how environmental heterogeneity and temporal and spatial variation influence B–EF patterns. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: additive; aquatic ecosystems; consumers; decomposition; non-additive; resources; species diversity; top-down versus bottom-up

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INTRODUCTION

Biodiversity is often associated with the health and functioning of ecosystems (Loreau *et al.*, 2002; Hooper *et al.*, 2005), and patterns of biodiversity have challenged ecologists for generations (Hutchinson 1959; Wilson 1992). Global declines in biodiversity and shifts in species composition have motivated research that links biodiversity and ecosystem functioning (Schulze and Mooney, 1993; Kinzig *et al.*, 2002; Loreau *et al.*, 2002; Hooper *et al.*, 2005), yet broader relationships between biodiversity and fundamental ecosystem processes remain unclear. Early B–EF research tested for plant species richness effects on primary productivity in grassland ecosystems (Tilman *et al.*, 1996; Hector *et al.*, 1999; Loreau *et al.*, 2002). As the majority of primary production enters detrital food webs (McNaughton *et al.*, 1989; Cebrian, 1999), B–EF studies have expanded into detritus-based ecosystems to better understand the importance of biodiversity on the ecosystem processes of decomposition and nutrient cycling.

Organic matter processing (OMP; e.g. decomposition and nutrient cycling) dynamics are commonly used to assess ecosystem functioning (Gessner and Chauvet, 2002; Elser *et al.*, 2007). Recent studies have examined the

importance of plant litter (hereafter litter) diversity on OMP in terrestrial (Gartner and Cardon, 2004; Hättenschwiler *et al*., 2005; Ball *et al*., 2008) and aquatic ecosystems (Swan and Palmer, 2004; LeRoy and Marks, 2006; Kominoski *et al*., 2007; Lecerf *et al*., 2007; Swan *et al*., 2009), as well as comparisons across terrestrial and aquatic ecosystems (Srivastava *et al*., 2009; Kominoski *et al*., in review). As the slow processing of detritus and the retention of limiting nutrients within food webs help to maintain ecosystem energetics (Wetzel, 1995; Moore *et al*., 2004), OMP provides a useful metric for assessing B–EF relationships in terrestrial and aquatic detritus-based ecosystems.

Although advances in B–EF theory have been informed largely from studies in terrestrial ecosystems (Naeem *et al*., 1994; Tilman *et al*., 1996; Wardle *et al*., 1997; Hector *et al*., 1999; Gartner and Cardon, 2004; Hättenschwiler *et al*., 2005), recent studies in aquatic ecosystems have further advanced B–EF theory by expanding experimental designs and approaches and exploring effects of diversity beyond the level of species richness. Giller *et al*. (2004) highlighted several aspects of aquatic ecosystems that enable them to advance B–EF theory and emphasized that studies should expand the quantification of biodiversity beyond the species-level to incorporate taxonomic, functional, habitat and evenness aspects of biodiversity. In addition, Giller *et al*. (2004) mentioned various aspects of experimental design and statistical analysis that should be overcome in order to better understand biodiversity effects. Specifically, experiments should be designed to replicate both species combinations and levels of diversity, test for non-random species loss (Srivastava and Vellend, 2005), expand spatial and temporal scales and investigate mechanisms behind B–EF patterns.

Aquatic ecologists have contributed greatly to the maturation of B–EF theory (Gamfeld and Hillebrand, 2008) by incorporating realistic experimental designs that provide better insight into mechanisms explaining B–EF patterns. Most studies testing B–EF relationships have randomized composition within each level of resource diversity, which makes it difficult to disentangle, for example the effects of species richness from species diversity (Huston 1997; Drake, 2003). In addition, although most studies test for random effects of biodiversity, changes in biodiversity are predicted to be non-random (Huston *et al*., 2000; Tilman and Lehman, 2001; Srivastava and Vellend, 2005), highlighting the need for realistic experimental and synthetic tests of B–EF. Models testing non-random changes in biodiversity suggest greater effects on ecosystem functioning than random changes (Gross and Cardinale, 2005; McIntyre *et al*., 2007). A recent meta-analysis of stream B–EF studies across multiple trophic levels found stronger evidence for composition- than richness-functioning relationships (Lecerf and Richardson, this issue), which is consistent with data from other systems (Cardinale *et al*., 2006). Here, we expand on Lecerf and Richardson (this issue), which was dominated by studies of resource and consumer diversity effects on OMP in detritus-based streams, to identify general patterns and potential mechanisms of non-additivity. As consumers in these donor-controlled ecosystems do not directly control the diversity of detrital resource inputs, we also review how consumer responses to resource diversity explain independent tests of resource and consumer diversity effects on stream OMP.

We summarize stream studies that have tested for non-random effects of diversity at different functional (genes, species richness, species composition, species evenness) and trophic levels (detritus, microbes, invertebrates, vertebrates) and across heterogeneous spatial (multi-stream) and temporal (multi-season) scales to assess changes in stream OMP dynamics (Table I). Specifically, we review: (1) top-down (i.e. consumer) diversity effects among different consumer trophic levels; (2) bottom-up (i.e. resource) diversity effects and (3) consumer responses to resource diversity that best explain resource diversity effects on stream OMP (Figure 1). We further illustrate how B–EF studies in stream ecosystems have advanced general B–EF theory through comparisons of trends observed in terrestrial ecosystems (Gartner and Cardon, 2004; Hättenschwiler *et al*., 2005). Finally, we identify future research needs to further integrate and synthesize multi-trophic effects and multi-functional responses under predicted global environmental change scenarios to enhance broader-scale understanding of B–EF theory.

TOP-DOWN (I.E. CONSUMER) DIVERSITY EFFECTS

Many studies have documented the positive effects of consumer diversity on decomposition (reviewed by Srivastava *et al*., 2009) and patterns linking consumer-resource diversity and ecosystem functioning are beginning to emerge (Table I). Studies examining the effects of microbial consumer diversity (Bärlocher and Corkum, 2003;

Table I. A selection of recent stream B–EF studies that have manipulated resource and consumer diversity at various levels to assess effects on stream OMP dynamics (table modified from Giller *et al.*, 2004)

Diversity	Level	Resources	Consumers
Taxonomic	Genotype	13, 14	
	Species	9, 11, 12, 17, 18	3, 5, 6, 8, 10, 19
Functional	Within functional group		6, 7
	Among functional group		
Habitat	Patch		2
	Ecosystem	11, 12	4, 11, 12
Evenness	Taxonomic group	18	15
	Functional group		1, 4, 16
Time	Season	17	7

1, Boyero *et al.* (2007); 2, Cardinale *et al.* (2002); 3, Dang *et al.* (2005); 4, Dangles and Malmqvist (2004); 5, Duarte *et al.* (2006); 6, Jonsson and Malmqvist (2000); 7, Jonsson and Malmqvist (2005); 8, Jonsson *et al.* (2001); 9, Kominoski *et al.* (2007); 10, Lecerf *et al.* (2005); 11, Lecerf *et al.* (2007); 12, LeRoy and Marks (2006); 13, LeRoy *et al.* (2006); 14, LeRoy *et al.* (2007); 15, McIntyre *et al.* (2007); 16, McKie *et al.* (2008); 17, Swan and Palmer (2004); 18, Swan *et al.* (2009); 19, Taylor *et al.* (2006).

Dang *et al.*, 2005; Duarte *et al.*, 2006; Lecerf *et al.*, 2005), and, more recently, vertebrate diversity (Taylor *et al.*, 2006; McIntyre *et al.*, 2007), but the majority focus on invertebrates (Jonsson and Malmqvist, 2000; Jonsson *et al.*, 2001; Dangles and Malmqvist, 2004; Boyero *et al.*, 2007). Across studies, consumer diversity effects on stream OMP are generally found to be non-random and explained by functionally distinct consumers within communities.

Invertebrate diversity has been linked with accelerated litter breakdown (Jonsson and Malmqvist, 2000) and complementarity of fine particulate organic matter (FPOM) retention (Cardinale *et al.*, 2002), however, recent evidence suggests that species richness effects on ecosystem functioning are strongly influenced by species evenness. For example, as species evenness increases among sites, the number of invertebrate species required to maintain litter breakdown rates may increase (Dangles and Malmqvist, 2004; Boyero *et al.*, 2007; but see McKie *et al.*, 2008). Presence of diverse shredder taxa can stimulate the growth of other functional feeding group (FFG) taxa, such as filter-feeding invertebrates, through increased production of FPOM exported downstream (Jonsson and Malmqvist, 2005). Further, effects of invertebrate species richness and dominance appear to vary seasonally (Dangles and Malmqvist, 2004), which may partially explain how effects of litter species diversity on breakdown rates vary seasonally within the same stream (Swan and Palmer, 2004).
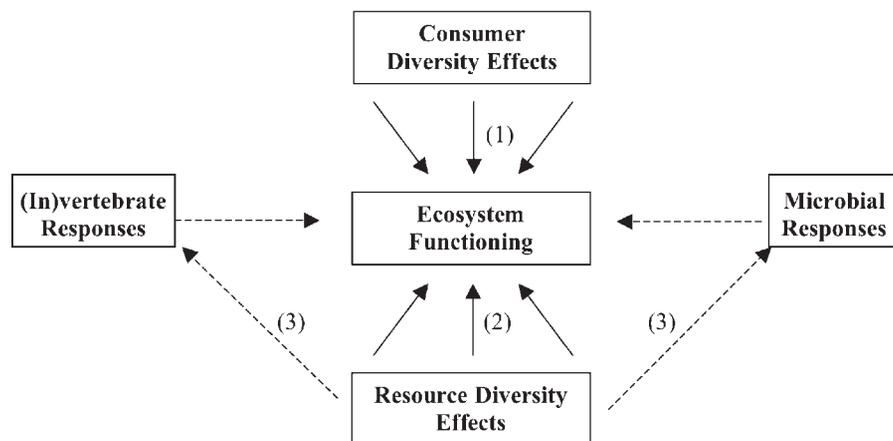

Figure 1. Conceptual diagram showing different pathways of B–EF and their general effects and responses that influence stream OMP. (1) Top-down (i.e. consumer) (vertebrate, invertebrate, microbial) diversity effects, (2) bottom-up (i.e. resource) (litter, nutrients) diversity effects and (3) consumer responses to resource diversity that interactively explain resource diversity effects on ecosystem functioning (i.e. OMP). Solid arrows represent pathways of diversity *effects* and dashed arrows represent diversity *responses* on ecosystem functioning

Microbial consumers, such as fungi and bacteria, play an important role in decomposition and nutrient cycling in stream ecosystems (Hall and Meyer, 1998; Hieber and Gessner, 2002). Therefore, the relative diversity of microbial communities could influence nutrient cycling and energy flow dynamics in streams. Fungal diversity appears to impart stability on litter breakdown (Dang *et al.* 2005). In addition, there is evidence to suggest that fungal taxa diversity can alter other key fungal processes such as fungal biomass production (Duarte *et al.*, 2006) and fungal conditioning of leaf litter for invertebrate consumption (Lecerf *et al.* 2005). Much less is known about the functional effects of bacterial diversity in stream OMP dynamics (but see Kominoski *et al.*, 2009).

BOTTOM-UP (I.E. RESOURCE) DIVERSITY EFFECTS

The majority of primary production is processed as detritus (McNaughton *et al.*, 1989; Cebrian, 1999), and recent studies have expanded our understanding how detrital resource diversity effects stream ecosystem functioning (Table I). In general, bottom-up effects of detrital diversity appear to have less consistent effects on OMP than top-down effects of consumers (Srivastava *et al.*, 2009), which is not surprisingly given the spatial and temporal dynamics of decomposition in streams.

Temporal and spatial context

Studies testing resource diversity effects on in-stream breakdown have similarly observed non-additive effects of litter mixing on breakdown rates; both antagonistic (Swan and Palmer, 2004; Kominoski *et al.*, 2007) and synergistic (LeRoy and Marks, 2006; Lecerf *et al.*, 2007; Swan *et al.*, 2009). The caveats associated with these results, however, suggest that litter species diversity effects vary among seasons (Swan and Palmer, 2004) and stream ecosystems (LeRoy and Marks, 2006; Lecerf *et al.*, 2007). Swan and Palmer (2004) observed antagonistic, non-additive effects of litter mixing on breakdown rates in the summer and additive effects during autumn, using the same litter species and experimental design. LeRoy and Marks (2006) found that synergistic, non-additive effects of litter mixing varied across different streams within the same river basin. Similarly, litter species diversity effects have been shown to vary among spatially distributed streams with similar stream water chemistry and riparian vegetation characteristics (Lecerf *et al.*, 2007). In general, breakdown of diverse litter appears to be influenced by spatial and temporal variation, which suggests that B–EF relationships are partially determined by the environmental context within which they are studied (Cardinale *et al.*, 2000).

Non-random changes in biodiversity and evenness

One way to test for non-random changes in biodiversity is the use of full-factorial designs that test all possible combinations of diversity. Full-factorial experimental designs allow for testing of both single-species presence/absence (additivity) and mixed-species richness and composition effects (non-additivity). Jonsson *et al.* (2002) were the first to use such a design to simulate non-random shredder species loss effects on litter breakdown. Species complementarity effects explained synergistic effects of shredder composition not richness on litter breakdown. Using this approach to assess resource diversity effects on OMP in natural streams, Kominoski *et al.* (2007) and Swan *et al.* (2009) found that litter species richness alone did not explain differences in breakdown rates, but the interaction of species with unique physical and chemical traits often explained mixed-species breakdown. In addition, litter species richness effects only emerged from mixtures with natural levels of plant litter evenness, and non-additive effects of litter species composition were more common in uneven than even mixtures (Swan *et al.*, 2009).

Another way to test for non-random changes in resource diversity is to assess natural intraspecific variation in resource traits. Variation in plant litter traits within species represents an additional level of diversity that has only recently been investigated in stream ecosystems (Driebe and Whitham, 2000; LeRoy *et al.*, 2006; LeRoy *et al.*, 2007). For example, over 95% of the variation in breakdown of *Populus* spp. litter can be explained by genetic variation among parent and hybrid tree types (LeRoy *et al.*, 2006), and over 43% of the variation in breakdown can be attributed to differences among genotypes (LeRoy *et al.*, 2007). A recent review suggests that the magnitude of genetic diversity effects is comparable to those for species diversity (Hughes *et al.*, 2008) and a recent meta-

analysis shows that intraspecific variation and genetic introgression have equally strong effects in aquatic systems as terrestrial systems (Bailey *et al.*, 2009).

CONSUMER RESPONSES TO RESOURCE DIVERSITY – DO THEY EXPLAIN RESOURCE DIVERSITY EFFECTS ON ECOSYSTEM FUNCTIONING?

Although invertebrate responses to resource diversity explain resource diversity effects on terrestrial OMP (Hansen and Coleman, 1998; Hansen, 2000; Kaneko and Salamanca, 1999), the ability of invertebrate community response to explain resource diversity effects on stream OMP is less clear. LeRoy and Marks (2006) found macroinvertebrate community assemblages in mixed-species litter to be significantly different than predicted, but this result varied through breakdown and with litter species composition within three-species mixtures, and yielded differing effects on macroinvertebrate assemblages for five-species mixtures of the same species in three different streams. Kominoski and Pringle (2009) measured differences in invertebrate assemblages among litter species richness levels, not species composition, despite clear compositional effects of litter diversity on breakdown (Kominoski *et al.*, 2007). Further investigation indicated that dominant invertebrate taxa explained consumer responses to litter diversity (Kominoski and Pringle, 2009). Finally, assessments of intraspecific litter diversity effects on invertebrates have had mixed results. One study found that invertebrates respond to hybridization among litter species, and that over 56% of the variation in macroinvertebrate community structure can be explained by variation in foliar condensed tannin concentrations within a hybridizing *Populus* complex (LeRoy *et al.*, 2006; Whitham *et al.*, 2006). Another study found additive effects of each litter genotype in isolation on invertebrate community structure, and additive effects of genotype diversity on litter breakdown (LeRoy *et al.*, 2007).

Microbial consumer responses to resource diversity may offer some of the strongest evidence for interactive effects of resource-consumer diversity on stream OMP. Molecular techniques (e.g. terminal restriction fragment length polymorphism and denaturing gradient gel electrophoresis) have been used to characterize stream microbial communities in response to resource quality and diversity (Nikolcheva *et al.*, 2003; Das *et al.*, 2007; Kominoski *et al.*, 2009; Hoellein *et al.*, in review). In general, shifts in microbial community diversity and functioning attributed to resource diversity are more apparent for bacteria than fungi. For example, Kominoski *et al.* (2009) observed that bacterial diversity associated with higher-quality litter increased in mixtures with low-quality litter, which explained increased microbial respiration rates and partially explained litter breakdown (Kominoski *et al.*, 2009). In contrast, fungal community diversity remained relatively unchanged by mixing litter species of different qualities. Similarly, Hoellein *et al.* (in review) found that adding multiple nutrients (nitrogen and phosphorus) to benthic substrates in streams resulted in distinct bacterial community compositions and higher respiration rates compared to control (no nutrient enrichment), but observed no changes in fungal communities. Microbial diversity effects on stream OMP vary among bacteria and fungi and may be controlled by bottom-up effects of changes in resource diversity.

Based on the literature from terrestrial ecosystems, Hättenschwiler *et al.* (2005) summarized four groups of potential mechanisms that could explain synergistic or antagonistic interactions explaining non-additive effects of resource diversity on OMP: (a) nutrient transfer among different quality litter species, (b) stimulatory or inhibitory compounds among litter species, (c) structural heterogeneity within mixed-species litter and (d) interactions across trophic levels. This conceptual map also proves useful to inform our conclusions regarding B–EF dynamics in stream ecosystems. There are several plausible explanations why invertebrate consumer responses to resource diversity do not (but microbial consumer responses do) appear to explain the effect of resource diversity on stream OMP: (1) dynamic changes in litter mass and chemistry as well as consumer (invertebrate and microbial) colonization patterns occur at different time-scales; (2) functional traits (e.g. labile versus recalcitrant) and resource roles of litter species (e.g. food, habitat, refugia) change during breakdown based on litter chemistry, physical structure and mass remaining, which may impact invertebrates more directly than microbes and (3) consumers' resource requirements change throughout breakdown in accordance with life history traits, competition and resource availability. It is likely that invertebrates become more resource-limited than microbes during decomposition. For example, as high-quality litter is rapidly decomposed and only low-quality, recalcitrant litter

remains, bacteria and fungi can facultatively exploit water column resources and extracellular enzymes, respectively, to maintain energy and nutrient requirements. In addition, invertebrates are more mobile than microbes and likely disperse among resource patches, using OM as food, habitat and refugia in accordance with their relative availability within the local environment. Consumer diversity effects appear to be more consistent than resource diversity effects on OMP (Srivastava *et al.*, 2009), and we suggest that this is partially explained by inconsistent response patterns of natural (non-manipulated) consumer assemblages to detrital diversity among heterogeneous stream ecosystems (LeRoy and Marks, 2006; LeRoy *et al.*, 2007; Kominoski and Pringle, 2009).

ENVIRONMENTAL HETEROGENEITY AND BIODIVERSITY

Effective predictions of global change effects on ecosystem functioning must account for how environmental heterogeneity and concomitant changes in biodiversity will collectively alter ecosystem functioning. Few studies have explicitly tested B–EF relationships among ecosystems (Cardinale *et al.*, 2000; Srivastava *et al.*, 2009; Kominoski *et al.*, in review), rendering even fewer predictions of how environmental variables may impact biodiversity effects and response traits (Naeem and Wright, 2003). For example, nutrient mobilization and biodiversity loss, which are both implicated to alter rates of key functions across ecosystems (e.g. primary production, nutrient cycling and decomposition; Cardinale *et al.* 2006; Elser *et al.* 2007) have rarely been tested (but see Bärlocher and Corkum, 2003; Rosemond *et al.*, in review). In addition, increases and changes in diel temperature oscillations alter stream processes by selecting for growth of dominant fungal taxa (Bärlocher *et al.*, 2008; Dang *et al.*, 2009). At larger temporal and spatial scales, ecologists need to identify and model global climate and environmental change variables (IPCC, 2007) that will non-randomly alter species distributions, and response and effects traits (Naeem and Wright, 2003).

EMERGENT PATTERNS AND FUTURE DIRECTIONS

Our review identified three consistent emergent patterns of effects of resource and consumer diversity on stream OMP: (1) Top-down (i.e. consumer) diversity effects are common among vertebrate, invertebrate and microbial trophic levels and are generally explained by species evenness; (2) bottom-up (i.e. resource) diversity effects are mediated by species evenness and vary both spatially and temporally; (3) consumer responses to resource diversity that best explain resource diversity effects are predominantly seen at the microbial level. Resource and consumer diversity effects are driven by dominance of functionally distinct taxa. However, responses of consumers to resource diversity only partially explain resource diversity effects, suggesting functional differences between how naturally colonizing and manipulated consumer assemblages process OM resources.

The key challenges facing general ecology and the theory of B–EF include an improved understanding of how environmental heterogeneity (i.e. global climate and environmental changes), as well as multi-trophic, multi-function, temporal and spatial variation influence B–EF patterns. In addition, new studies that manipulate biodiversity at different trophic levels are needed to determine top-down and bottom-up implications of species shifts on food web structure and ecosystem function (Cardinale *et al.*, 2006). Ecosystems are often managed and conserved for multiple functions, yet to-date most B–EF studies consider only one ecosystem function response variable. A recent meta-analysis of grassland studies found that more species are required to maintain multiple ecosystem functions (Hector and Bagchi, 2007). In addition, modelling effects of species loss on multiple ecosystem functions revealed that overall ecosystem functioning, as defined as the joint effect of multiple ecosystem functions, appears to be more sensitive to species loss than individual ecosystem functions (Gamfeldt *et al.*, 2008). The authors also determined that multi-function redundancy is lower than single-function redundancy, suggesting that loss of species leads to loss of species multi-functional complementarity (Gamfeldt *et al.*, 2008). Stream ecologists are well positioned to pursue this research, because in addition to decomposition, may other ecosystem functions in detritus-based streams are frequently measured including nutrient cycling, heterotrophic respiration, secondary production and variation in FPOM production (Yoshimura *et al.*, 2008).

It is evident at the global scale that biodiversity is in decline, but biodiversity at local and regional scales may increase as species invasions outpace extinctions (Sax *et al.*, 2002). Beyond species richness, differences in

biological composition between local and regional scales (Sabo *et al.*, 2005; LeRoy and Marks, 2006) may be a function of environmental heterogeneity that influences ecosystem functioning. Addressing this challenge with large-scale, long-term studies and models that incorporate meta-community and meta-ecosystem dynamics to test broader patterns of B–EF and further illustrate general mechanisms will facilitate enhanced applicability and utility of B–EF theory (*sensu* Srivastava and Vellend, 2005).

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