

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.

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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

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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	12, 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).

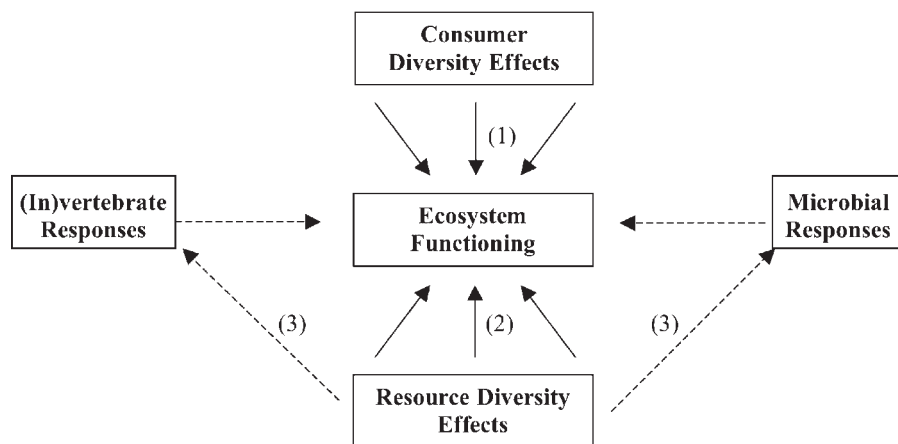


Figure 1. Conceptual diagram showing different pathways of B–EF and their general effects and responses that influence stream OMP. (1) Top-down (i.e. consumer) (vertebrate, invertebrate, microbial) diversity effects, (2) bottom-up (i.e. resource) (litter, nutrients) diversity effects and (3) consumer 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.*, in press).

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, many 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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REFERENCES

- Bailey JK, Schweitzer JA, Madritch MD, Koricheva J, LeRoy CJ, Fischer DG, Bangert RK, Rehill B, Barbour R, O'Reilly-Wapstra J, Lonsdorf EV, Genung M, Keith AR, Ferrier SM, Wimp GM, Martinsen G, Woolbright S, Allen G, Pregitzer C, Smith DS, Lamitt JL, Selmants P, Zinkgraf M, Wojkowitz T, Compson Z, Hirsch E, DiFazio S, Hart SC, Marks JC, Shuster S, Lindroth RL, Keim P, Gehring CA, Potts B, Whitham TG. In press. The general organizational power of genes: a meta-analysis across systems and environments. *Philosophical Transactions of the Royal Society of London B* **364**: 1607–1616.
- Ball BA, Hunter MD, Kominoski JS, Swan CM, Bradford MA. 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *Journal of Ecology* **96**: 303–313.
- Bärlocher F, Corkum M. 2003. Nutrient enrichment overwhelms diversity effects in leaf decomposition by stream fungi. *Oikos* **101**: 247–252.
- Bärlocher F, Sahadevan S, Wilson KP, Williams DD. 2008. Raised water temperature lowers diversity of hyporheic aquatic hyphomycetes. *Freshwater Biology* **53**: 368–379.
- Boyer L, Pearson RG, Bastian M. 2007. How biological diversity influences ecosystem function: a test with a tropical stream detritivores guild. *Ecological Research* **22**: 551–558.
- Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jousseau C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989–992.
- Cardinale BJ, Nelson K, Palmer MA. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos* **91**: 175–183.
- Cardinale BJ, Palmer MA, Collins SL. 2002. Species diversity increases ecosystem functioning through interspecific facilitation. *Nature* **415**: 426–429.
- Cebrian J. 1999. Patterns in the fate of production in plant communities. *American Naturalist* **154**: 449–468.
- Dang CK, Chauvet E, Gessner MO. 2005. Magnitude and variability of process rates in fungal diversity–litter decomposition relationships. *Ecology Letters* **8**: 1129–1137.
- Dang CK, Schindler M, Chauvet E, Gessner MO. 2009. Temperature oscillations coupled with fungal community shifts can modulate warming effects on litter decomposition. *Ecology* **90**: 122–131.
- Dangles O, Malmqvist B. 2004. Species richness–decomposition relationships depend on species dominance. *Ecology Letters* **7**: 395–402.
- Das M, Royer TV, Leff LG. 2007. Diversity of fungi, bacteria, and actinomycetes on leaves decomposing in a stream. *Applied and Environmental Microbiology* **73**: 756–767.
- Drake JM. 2003. Why does grassland productivity increase with species richness? Disentangling species richness and composition with tests for overyielding and superyielding in biodiversity experiments. *Proceedings of the Royal Society of London, Series B* **270**: 1713–1719.
- Driebe EM, Whitham TG. 2000. Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. *Oecologia* **123**: 99–107.
- Duarte S, Pascoal C, Cássio F, Bärlocher F. 2006. Aquatic hyphomycete diversity and identity affect leaf litter decomposition in microcosms. *Oecologia* **147**: 658–666.
- Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* **10**: 1135–1142.
- Gamfeld L, Hillebrand H. 2008. Biodiversity effects on aquatic ecosystem functioning – maturation of a new paradigm. *International Review of Hydrobiology* **93**: 550–564.
- Gamfeldt L, Hillebrand H, Jonsson PR. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* **89**: 1223–1231.
- Gartner TB, Cardon ZG. 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* **104**: 230–246.
- Gessner MO, Chauvet E. 2002. A case for using litter breakdown to assess functional stream integrity. *Ecological Applications* **12**: 498–510.

- Giller PS, Hillebrand H, Berninger U-G, Gessner MO, Hawkins S, Inchausti P, Inglis C, Leslie H, Malmqvist B, Monaghan MT, Morin PJ, O'Mullan G. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* **104**: 423–436.
- Gross K, Cardinale BJ. 2005. The functional consequences of random vs. ordered species extinctions. *Ecology Letters* **8**: 409–418.
- Hall RO, Jr., Meyer JL. 1998. The trophic significance of bacteria in a detritus-based stream food web. *Ecology* **79**: 1995–2012.
- Hansen RA. 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* **81**: 1120–1132.
- Hansen RA, Coleman DC. 1998. Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. *Applied Soil Ecology* **9**: 17–23.
- Hättenschwiler S, Tiunov AV, Scheu S. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution and Systematics* **36**: 191–218.
- Hector A, Bagchi R. 2007. Biodiversity and ecosystem multifunctionality. *Nature* **448**: 188–190.
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Högborg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spohn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH. 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123–1127.
- Hieber M, Gessner MO. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* **83**: 1026–1038.
- Hoellein TJ, Kelly JJ, Tank JL, Rosi-Marshall EJ. Seasonal variation in patterns of nutrient limitation and microbial community composition in three northern Michigan streams. In review.
- Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**: 3–35.
- Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. 2008. Ecological consequences of genetic diversity. *Ecology Letters* **11**: 609–623.
- Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**: 449–460.
- Huston MA, Aarssen LW, Austin MP, Cade BS, Fridley JD, Garnier E, Grime JP, Hodgson J, Laurenroth WK, Thompson K, Vandermeer JH, Wardle DA. 2000. No consistent effect of plant diversity on productivity. *Science* **289**: 1255.
- Hutchinson GE. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* **93**: 145–1159.
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate Change 2007: The Physical Science Basis. Contribution of the Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds). Cambridge University Press: Cambridge.
- Jonsson M, Malmqvist B. 2000. Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos* **89**: 519–523.
- Jonsson M, Malmqvist B, Hoffsten PO. 2001. Leaf litter breakdown rates in boreal streams: does shredder species richness matter? *Freshwater Biology* **46**: 161–171.
- Jonsson M, Dangles O, Malmqvist B, Guérol F. 2002. Simulating species loss following disturbance: assessing the effects on process rates. *Proceedings of the Royal Society London B* **269**: 1047–1052.
- Jonsson M, Malmqvist B. 2005. Species richness and composition effects in a detrital processing chain. *Journal of the North American Benthological Society* **24**: 798–806.
- Kinzig AP, Pacala SW, Tilman D. 2002. *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton University Press: Princeton.
- Kaneko N, Salamanca N. 1999. Mixed leaf litter effects on decomposition rates and soil arthropod communities in an oak-pine forest stand in Japan. *Ecological Research* **14**: 131–138.
- Kominoski JS, Pringle CM. 2009. Resource-consumer diversity: testing effects of leaf litter species diversity on stream macroinvertebrate communities. *Freshwater Biology* **54**: 1461–1473.
- Kominoski JS, Hoellein TJ, Kelly JJ, Pringle CM. 2009. Does mixing litter of different qualities alter stream microbial diversity and functioning on individual litter species? *Oikos* **118**: 457–463.
- Kominoski JS, Pringle CM, Ball BA, Bradford MA, Coleman DC, Hall DB, Hunter MD. 2007. Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. *Ecology* **88**: 1167–1176.
- Kominoski JS, Pringle CM, Ball BA, Coleman DC, Hunter MD, Mattsson BJ. Biodiversity and ecosystem functioning: ecosystem-dependent effects of plant litter mixing on decomposition in a detritus-based watershed. In review.
- Lecerf A, Dobson M, Dang CK, Chauvet E. 2005. Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia* **146**: 432–442.
- Lecerf A, Risnoveanu G, Popescu C, Gessner MO, Chauvet E. 2007. Decomposition of diverse litter mixtures in streams. *Ecology* **88**: 219–227.
- Lecerf A, Richardson JS. In press. Biodiversity-ecosystem function research: insights gained from streams. *River Research and Applications*.
- LeRoy CJ, Marks JC. 2006. Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates. *Freshwater Biology* **51**: 605–617.
- LeRoy CJ, Whitham TG, Keim P, Marks JC. 2006. Plant genes link forests and streams. *Ecology* **87**: 255–261.
- LeRoy CJ, Whitham TG, Wooley SC, Marks JC. 2007. Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. *Journal of the North American Benthological Society* **26**: 426–438.
- Loreau M, Naeem S, Inchausti P. 2002. *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press: Oxford.

- McIntyre PB, Jones LE, Flecker AS, Vanni MJ. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. *Proceedings of the National Academy of Sciences* **104**: 4461–4466.
- McKie BG, Woodward G, Hladyz S, Nistorescu M, Preda E, Popescu C, Giller PS, Malmqvist B. 2008. Ecosystem functioning in stream assemblages from different regions: contrasting responses to variation in detritivores richness, evenness and density. *Journal of Animal Ecology* **77**: 495–504.
- McNaughton SJ, Oesterheld M, Frank DA, Williams KJ. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341**: 142–144.
- Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DM. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* **7**: 584–600.
- Naem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**: 734–737.
- Naem S, Wright JP. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6**: 567–579.
- Nikolcheva LG, Cockshutt AM, Bärlocher F. 2003. Determining diversity of freshwater fungi on decaying leaves: comparison of traditional and molecular approaches. *Applied and Environmental Microbiology* **69**: 2548–2554.
- Rosemond AD, Swan CM, Kominoski JK, Dye SE. Non-additive effects of litter mixing are canceled in a nutrient-enriched stream. In review.
- Sabo JL, Sponseller R, Dixon M, Gade K, Harms T, Heffernan J, Jani A, Katz G, Soykan C, Watts J, Welter J. 2005. Riparian zones increase region species richness by harboring different, not more species. *Ecology* **86**: 56–62.
- Sax DF, Gaines SD, Brown JH. 2002. Invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist* **160**: 766–783.
- Schulze ED, Mooney HA. 1993. *Biodiversity and Ecosystem Function*. Springer-Verlag: Berlin.
- Srivastava DS, Vellend M. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution, and Systematics* **36**: 267–294.
- Srivastava DS, Cardinale BJ, Downing AL, Duffy JE, Jouseau C, Sankaran M, Wright JP. 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* **90**: 1073–1083.
- Swan CM, Palmer MA. 2004. Leaf diversity alters litter breakdown in a Piedmont stream. *Journal of the North American Benthological Society* **23**: 15–28.
- Swan CM, Gluth MA, Home CL. 2009. The role of leaf species evenness on non-additive breakdown of mixed-litter in a headwater stream. *Ecology* **90**: 1650–1658.
- Taylor BW, Flecker AS, Hall RO Jr. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* **313**: 833–836.
- Tilman DG, Lehman C. 2001. Human-caused environmental changes: impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences of the United States of America* **98**: 5433–5440.
- Tilman DG, Wedin D, Knops J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718–720.
- Wardle DA, Bonner KI, Nicholson KS. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* **79**: 247–258.
- Wetzel RG. 1995. Death, detritus, and energy flow in aquatic ecosystems. *Freshwater Biology* **33**: 83–89.
- Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, LeRoy CJ, Lonsdorf EV, Allan GJ, DiFazio SP, Potts BM, Fischer DG, Gehring CA, Lindroth RL, Marks JC, Hart SC, Wimp GM, Wooley SC. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* **7**: 510–523.
- Wilson EO. 1992. *The Diversity of Life*. Harvard University Press: Cambridge.
- Yoshimura C, Gessner MO, Tockner K, Furumai H. 2008. Chemical characterization, microbial respiration, and decomposition of fine particulate organic. *Journal of the North American Benthological Society* **27**: 664–673.