Diversity has stronger top-down than bottom-up effects on decomposition

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Abstract. The flow of energy and nutrients between trophic levels is affected by both the trophic structure of food webs and the diversity of species within trophic levels. However, the combined effects of trophic structure and diversity on trophic transfer remain largely unknown. Here we ask whether changes in consumer diversity have the same effect as changes in resource diversity on rates of resource consumption. We address this question by focusing on consumer–resource dynamics for the ecologically important process of decomposition. This study compares the top-down effect of consumer (detritivore) diversity on the consumption of dead organic matter (decomposition) with the bottom-up effect of resource (detrital) diversity, based on a compilation of 90 observations reported in 28 studies. We did not detect effects of either detrital or consumer diversity on measures of detrital standing stock, and effects on consumer standing stock were equivocal. However, our meta-analysis indicates that reductions in detritivore diversity result in significant reductions in the rate of decomposition. Detrital diversity has both positive and negative effects on decomposition, with no overall trend. This difference between top-down and bottom-up effects of diversity is robust to different effect size metrics and could not be explained by differences in experimental systems or designs between detritivore and detrital manipulations. Our finding that resource diversity has no net effect on consumption in "brown" (detritus–consumer) food webs contrasts with previous findings from "green" (plant–herbivore) food webs and suggests that effects of plant diversity on consumption may fundamentally change after plant death.

Key words: biodiversity and ecosystem function; detrital processing; resource consumption; trophic structure; trophic transfer.

Introduction

Human activity has altered many natural food webs (Chapin et al. 2000, Jackson et al. 2001). Changes in both the structure and diversity of food webs are predicted to affect the flow of energy and nutrients through food webs (de Ruiter et al. 2005). For example, decades of research on trophic structure have demonstrated that changes in the biomass of a focal trophic level can affect the production of biomass in lower trophic levels (top-down effects) as well as the flow of energy up to higher trophic levels (bottom-up effects) (Pace et al. 1999, Shurin et al. 2002). This historical focus on how trophic structure influences the functioning of food webs has recently been complemented by research that has focused on the functional role played by diversity within trophic levels (Hooper et al. 2005). New syntheses have shown that experimental reductions in species richness of a trophic level tend to reduce the consumption of resources and production of biomass by that trophic group (Balvanera et al. 2006, Cardinale et al. 2006). Regrettably, this latter body of research (often called "biodiversity and ecosystem functioning") has largely focused on species within a single trophic level and in isolation from their natural food webs. As a consequence, this area of research has often ignored the well-known role that trophic structure plays in controlling the distribution of biomass among food web components. There is a growing sentiment that the study of biodiversity and ecosystem functioning must now be integrated with classical perspectives on trophic structure if we are to explain the transfer of energy and nutrients and the production of biomass within food webs (Thébault and Loreau 2003, Srivastava and Vellend 2005, Duffy et al. 2007).

In this paper we take an important step toward integrating this multi-trophic perspective by using a meta-analysis of existing studies to address a key unanswered question: Are top-down effects of species diversity on the transfer of energy and matter among trophic levels fundamentally different from bottom-up effects of diversity? By top-down effects of diversity, we refer to the effect of consumer species richness on the rate at which those consumers capture resources and convert them into consumer biomass. By bottom-up effects of diversity, we refer to the effects of the richness of resources on the rate at which the collective resource pool is captured and converted into new biomass of consumers. If the top-down effects of consumer diversity differ in form or magnitude from the bottom-up effects of resource diversity, this would mean that any predictions of the impacts of species extinction on ecosystem functioning would require consideration of the food web context. For example, the coupling of strong top-down effects of diversity with the current trend of extinctions biased toward the top trophic levels of food webs (Pauly et al. 1998, Byrnes et al. 2007) could lead to much larger impacts of diversity loss on the functioning of ecosystems than predicted by random-deletion scenarios of species loss (Duffy 2003).

Duffy et al. (2007) suggested that resource consumption is often an increasing function of consumer diversity (e.g., Balvanera et al. 2006, Cardinale et al. 2006), whereas consumption rates tend to be a decreasing function of resource diversity (e.g., Hillebrand and Cardinale 2004). However, their argument was based on a qualitative summary of studies performed with "green" food webs, those that are sustained by living plants. Currently, there is no equivalent hypothesis for "brown" food webs, those sustained by detritus. Top-down effects of consumer diversity might be expected to be quite similar between green and brown food webs, since the proposed mechanisms (e.g., niche complementarity, facilitation, and sampling effects) can apply to consumers of either resource base. However, the bottom-up effects of detrital diversity and living plant diversity on consumers might be expected to operate via fundamentally different mechanisms. For example, the "variance-in-edibility" hypothesis for live plants proposes that diverse plant communities are more likely to contain at least one species resistant to herbivory. If trade-offs exist between growth and resistance to predation (Leibold 1989, 1996) then resistant species can dominate under herbivory, reducing total herbivory on the plant community. Such a mechanism could not apply to detrital diversity simply because detritus cannot grow and reproduce and hence cannot show compensatory dynamics.

Instead, detrital diversity effects on decomposition may involve a different suite of mechanisms involving litter chemistry. It has been proposed that decomposition of slowly decomposing litter could be accelerated by nutrients being transferred to this litter from faster-decomposing species (Chapman et al. 1988, Blair et al. 1990). Supporting this hypothesis, a recent review of litter mixture experiments (Gartner and Cardon 2004) concluded that mixtures often had faster mass loss and higher nutrient concentrations than their component species in monoculture. However, a second review (Hättenschwiler et al. 2005) cautions that there is insufficient evidence to conclude that either detrital diversity affects decomposition or that nutrient transfer is the mechanism.

Here we present a meta-analysis that compares how the bottom-up effects of detrital diversity and the top-down effects of detritivore diversity affect energy flow and biomass distribution in brown food webs. Decomposition, defined here as the consumption of dead organic matter, represents a large and ecologically important flow of energy between trophic levels: the vast majority of carbon fixed by primary production is not consumed by herbivores but becomes detritus (Cebrian and Lartigue 2004). Decomposition liberates carbon dioxide or methane and mineralizes nutrients required for primary production (Likens and Bormann 1995), and as such is an important determinant of the global carbon budget (Cebrian and Duarte 1995).

We summarize the results of 90 observations reported in 28 studies in order to evaluate two related hypotheses: 1) increases in both resource (i.e., detrital) diversity and consumer (i.e., detritivore) diversity result in an increase in decomposition; and 2) effects of consumer or resource diversity on the process of decomposition translate into effects on the standing stocks of detritus and detritivores. Specifically, high rates of decomposition are predicted to support high standing stocks of detritivore biomass and result in low standing stocks of detritus (Fig. 1).

METHODS

Data collection

We searched peer-reviewed journals for studies that 1) experimentally manipulated the diversity of either detritus (dead plant matter in all cases) or detritivores (consumers, including bacteria, fungi, and animals such as macro-invertebrates) and then 2) measured how consumer or detrital diversity influenced either the rate of depletion of the detrital resource pool and/or the standing stocks of detritus or consumers at a given point in time. Detrital diversity refers to the number of plant species from which the detrital resource originated, whereas consumer diversity refers to the number of species consuming the detrital resource. In one study that manipulated bacterial diversity, species were operationally defined on the basis of distinct fatty-acid signatures (Bell et al. 2005); otherwise species were defined as Linnean species. All consumer taxa were described as detritivorous by the authors of each study. Resource depletion (RD) always represents the loss of detritus over some time interval; however, RD was measured in different ways in different studies. We
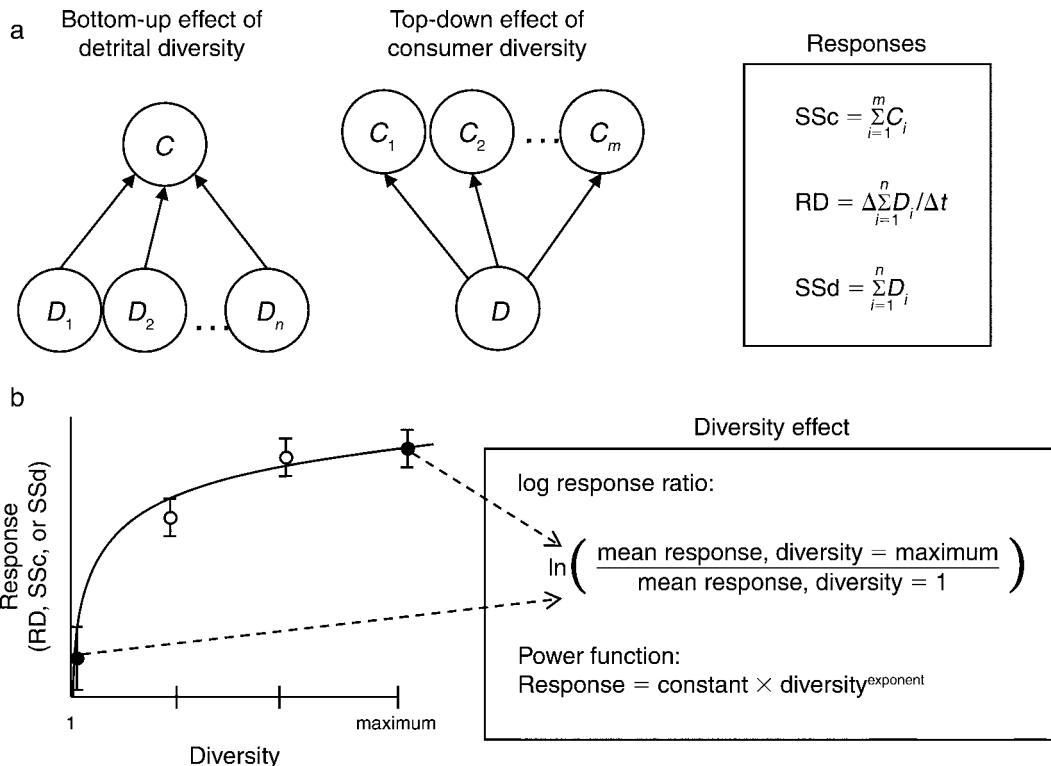
FIG. 1.   (a) Our data set consists of studies that manipulated either the number of detrital species (from $D = 1$ to n) or consumer species (from $C = 1$ to m) and measured the impacts on resource depletion (RD) or the standing stock of detritus (SSd) or consumers (SSc). Bottom-up effects of diversity refer to the effects of detrital (D) diversity on these response variables, whereas top-down effects of diversity refer to the effects of consumer (C) diversity. (b) The effect of either detrital or consumer diversity on RD, SSd, and SSc was quantified using two metrics: the log response ratio (LRR) and the exponent of a power function between diversity and the response. The LRR is based on the natural logarithm (ln). The solid circles represent data that could be extracted from all studies; the open circles represent data that could be extracted from most studies.

describe later how we accounted for such differences in measuring RD. Standing stocks of detritus and consumers were typically measured as biomass per unit area (terrestrial studies) or volume (aquatic studies), but consumer standing stock was occasionally approximated by density of organisms or their chemical constituents (e.g., carbon and fatty acids for bacteria).

We limited our database to studies that 1) manipulated at least three species and therefore a gradient in species richness (hereafter "diversity") rather than pairwise species interactions and 2) included species monocultures in order to permit calculation of our response ratios. In the case of experiments with time series data, we used only data from the final date of measurement as this was the one least likely to be influenced by transient responses. In total, this data set consists of 90 observations from 52 experiments reported in 28 separate studies (see Supplement).

Characterizing diversity effect sizes

From each experiment, we were able to obtain information on at least one of three response variables: (1) the rate of detrital loss within a defined time interval $t_0 \rightarrow t$ (resource depletion); 2) the standing stock of

detrital resources (hereafter "SSd") at time t (the final date for experiments with time series); or 3) the standing stock of consumers ("SSc") at time t. We used two statistics to characterize how species diversity influenced each of these response variables. For the first statistic, we calculated the ratio of each response variable measured in the highest diversity treatment to the mean of that variable from all monocultures used in the experiment. The log response ratio (LRR) is the natural logarithm of this ratio, which gives the proportional change in RD, SSd, or SSc between the highest vs. monoculture levels of diversity used in an experiment. For the second statistic, we modeled RD, SSd, and SSc as a function of species diversity using a power function $y = aS^b$ where y is the response variable and S is the number of species. The maximum likelihood estimate of b is a measure of the diversity effect size. In addition to indicating whether the diversity effect is positive or negative, the power exponent b indicates whether changes in RD, SSd, or SSc are directly proportional to changes in diversity ($b = 1$). The strengths of these two statistics are complementary. The power function can only be calculated for a subset of studies (80 of the 90 observations had three or more diversity levels, which is

the minimum for calculating variance around the exponent estimate) but, unlike the LRR, the power function allows us to include information from all diversity levels used in an experiment. As we were unable to obtain raw data for many studies, we based our regression on the reported mean values of the response variable for each diversity level. We used power functions rather than a Michaelis-Menten function (used in Cardinale et al. 2006) because initial analyses indicated a non-saturating relationship between species diversity and decomposition.

Explanatory variables

Aside from separating experiments on the basis of whether detrital or consumer diversity was manipulated (hereafter "trophic level"), we also recorded a number of potential covariates that might help explain differences in the diversity effect size among studies. First we examined the effects of ecosystem type (aquatic, terrestrial) since aquatic and terrestrial systems are known to differ in both the ratio of detritivore to detrital standing stocks and the relative strength of top-down vs. bottom-up effects (Shurin et al. 2002, 2006, Cebrian and Lartigue 2004). Second, we differentiated studies by consumer taxa (bacteria, fungi, and metazoan animals) since these taxa differ substantially in their rates and modes of detrital consumption (Swift et al. 1979). In addition, metazoans may operate at a marginally higher trophic level than bacteria and fungi if, in the process of consuming detritus, they also consume microbial biomass. Third, we explored the effects of time, measured both as experimental duration (in days) and whether consumer population dynamics were allowed during the experiment (less than one generation, more than one generation), because other recent summaries have shown that diversity effect sizes tend to strengthen with time (Cardinale et al. 2007). Fourth, we recorded experimental setting (laboratory/greenhouse, field) and maximum level of species richness as both may affect the detection of diversity effects on a range of ecological processes (Balvanera et al. 2006). Fifth, we recorded several aspects of the experimental design since there has been discussion surrounding the interpretation of different types of manipulations (Huston 1997). Specifically, we distinguished between three experimental designs: full assembly (studies that include all possible species combinations for each richness level), random assembly (studies that use random selection of a subset of all possible combinations for the experiment), and nonrandom (studies using nested subsets of species or an environmental perturbation to which species are differentially susceptible, such as fumigation). Lastly, we distinguished between three different ways that resource depletion (i.e., decomposition) has been measured in studies. 1) Resource depletion (RD) can be measured near instantaneously based on measurements of whole-community respiration rates (milligrams of O_2 consumed or CO_2 produced per

unit area or volume per unit time) over very short time intervals. 2) Resource depletion can be measured through temporal changes by subtracting the amount of detritus at the end of the experiment from that available at the beginning to quantify losses due to consumption, leaching, and mechanical degradation. 3) Resource depletion due only to consumption can be measured by further subtracting resource loss measured in no-consumer controls. Most of the 23 studies that measured RD using the temporal change and consumption method reported net change over the entire experiment (e.g., percentage of mass loss, in grams lost per day). However, six studies reported RD as the exponential decay constant k (based on the equation: mass remaining $\alpha e^{-k \times \text{time}}$) and one study as the logarithmic decay constant k (based on the equation: $\exp(\text{mass remaining}) \propto \text{time}^{-k}$).

Analyses

We performed three types of analyses on the data. First, we modeled both metrics of diversity effect size (LRR or the power exponent) as a linear mixed model with study included as a random effect. We calculated the experiment-wise variance associated with the estimation of either LRR or power exponent values and weighted LRR and power exponent values by the inverse of their respective variance to account for heterogeneity in the precision of the estimates. The general form of this model is

$$y_i = \mu + \tau_i + s_i + \varepsilon_i$$

where y_i is LRR or the power exponent, μ is the mean response across the data set, τ_i is a matrix of explanatory variables, s_i is a random effect of study associated with experiment i, and ε_i is the residual error. We first examined the combined effect of trophic level (detritus or consumer diversity manipulation) and response variable (categorized as RD, SSd, and SSc) by testing the interaction term in $\tau_i =$ trophic level + response variable + trophic level $\times$ response variable. Since the effect of trophic level depended on the response variable, we ran separate models for each response variable with $\tau_i =$ trophic level. Model comparison was based on log likelihood (L) ratios, and model significance was based on F tests, following Pinheiro and Bates (2004).

In our second analysis we examined whether any differences between the bottom-up effects of resource diversity and the top-down effects of consumer diversity could be artifacts of systematic differences between the two trophic levels in the types of experimental systems or designs represented in our data set (hereafter "covariates"). We first searched for such systematic biases in the experimental pool by comparing mean values of continuous covariates between resource and consumer diversity studies via t tests. For categorical covariates, we compared the distribution of detrital diversity and consumer diversity studies amongst categories within the covariate using χ^2 tests. To account
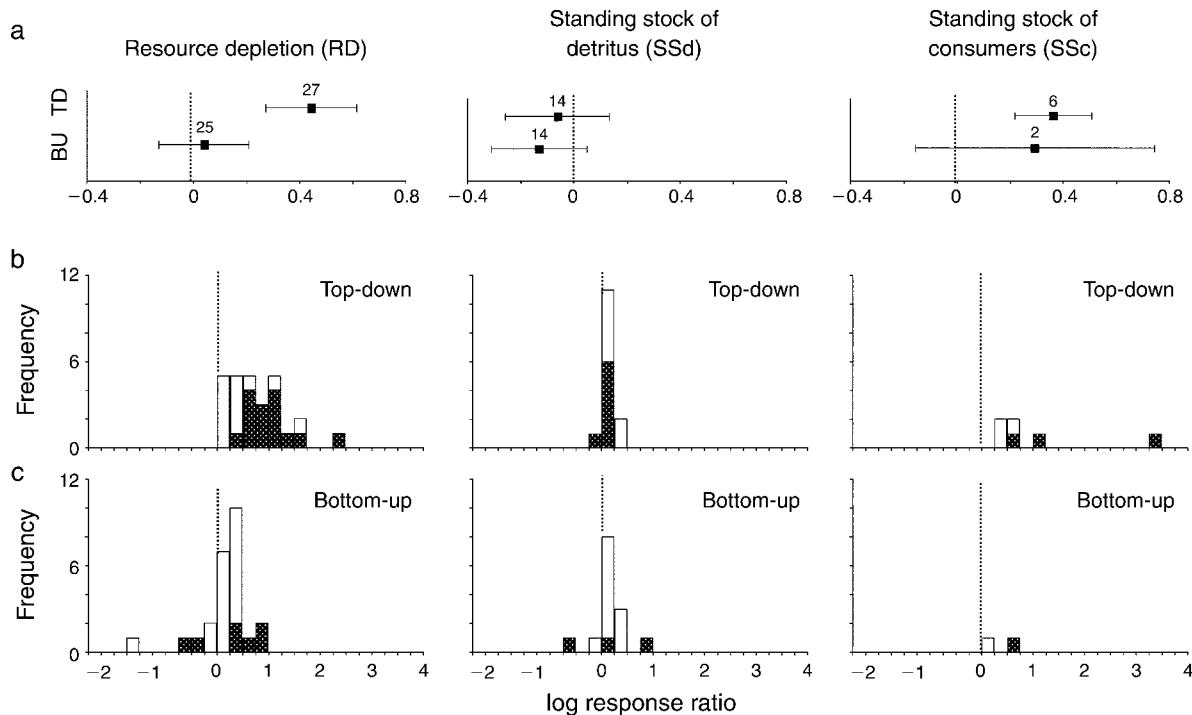
Fig. 2. Top-down (TD) and bottom-up (BU) diversity effects on three response variables were quantified using the log response ratio (LRR). (a) The log response ratio (mean ± 95% CI; the number of observations is indicated above each symbol) for each trophic level was calculated using a meta-analytic mixed model. (b, c) The frequencies of LRR values for (b) top-down and (c) bottom-up diversity manipulations are shown for all observations (open bars) as well as for those with values that are significantly different than zero (shaded bars).

for small sample sizes, we used 2000 Monte Carlo simulations for each χ^2 test. Because any significant differences in covariates that occur between detrital and consumer manipulations could, if not accounted for, confound detection of real effects of trophic level on the response variables, we specifically tested for this possibility by rerunning all models with each covariate entered first in the model and testing again for trophic level and response variable effects:

$$y_i = \mu + \text{covariate} + \tau_i + s_i + \varepsilon_i.$$

Here, the model is the same as in the analysis above, except that we first account for each covariate that differs significantly between resource and consumer manipulations before examining trophic level and response variable effects.

In our final analysis, we sought to explain residual variance in diversity effects on the response variables, after accounting for trophic level and response variable effects. We therefore examined the significance of covariates added after trophic level and response variables:

$$y_i = \mu + \tau_i + \text{covariate} + s_i + \varepsilon_i.$$

Since we weighted our response variables by the inverse of experiment-wise variance, we excluded from the LRR models one experiment (from Carney and

Matson 2005) with insufficient replication to calculate LRR variance and one experiment (from Hättenschwiler and Gasser 2005) with LRR variance > 1000 × mean LRR variance from other studies. We used the program R for all analysis (version 2.5.1; R Development Core Team 2007).

RESULTS

Our analyses reveal that consumer diversity and detrital diversity have very different effects on the process of decomposition, depending on the type of response measured (LRR: trophic level × response variable, $L = 29.0$, $P > 0.0001$; Fig. 2). When resource depletion (RD) is the response variable, top-down effects of consumer diversity increase RD much more than do bottom-up effects of detrital diversity (trophic level, $L = 9.75$, $P = 0.0018$). In fact, detrital diversity has on average no effect on RD ($t = 0.46$, $P = 0.65$), whereas higher consumer diversity results in higher RD ($t = 5.07$, $P > 0.0001$). By contrast, we found no difference between the top-down and bottom-up effects of diversity on the standing stock of detrital resources (SSd) ($L = 0.265$, $P = 0.61$), nor an effect of diversity, irrespective of trophic level, on SSd ($F_{1,14} = 2.09$, $P = 0.17$). Although top-down and bottom-up effects of diversity tend to be similar on the standing stocks of detritivorous consumers ($L = 0.11$, $P = 0.74$), this comparison is limited by a
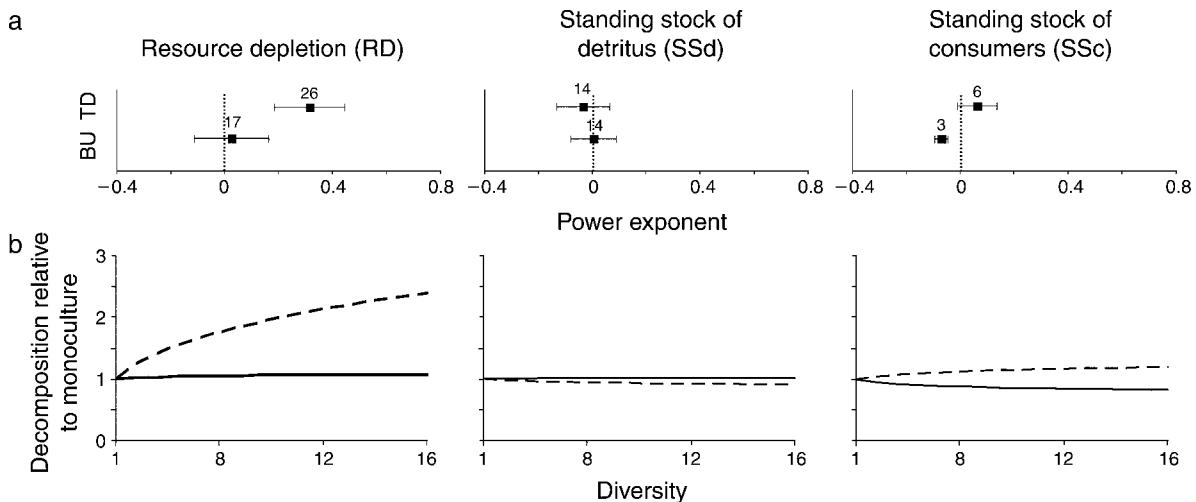
FIG. 3. Power functions were fit between consumer or detrital diversity and each of three response variables, and the exponent of this power function was used as a measure of the diversity effect. (a) The power exponents (mean ± 95% CI; the number of observations is indicated above each symbol) were calculated using a meta-analytic mixed model for both top-down and bottom-up diversity effects. (b) The predicted effect of increasing consumer (dashed line) or resource (solid line) diversity on the three response variables, based on mean power exponent values.

relatively low sample size (six top-down, two bottom-up studies; Fig. 2). Overall, higher diversity of either detritus or consumers significantly enhance the standing stocks of consumers, despite low sample size ($F_{1,6} = 29.7$, $P = 0.0016$).

Although detrital diversity does not have a net effect on RD, individual studies often have either significant positive or negative effects of detrital diversity on RD (Fig. 2). This suggests that the positive and negative effects of individual studies might cancel each other in the global mean, resulting in no consistent deviation from zero. Supporting this interpretation, if the absolute value of LRR is used, there is then a net effect of detrital diversity on RD ($t = 3.16$, $P < 0.0001$). However, even the absolute LRR values still show top-down effects of diversity to be stronger than bottom-up effects of diversity RD ($L = 4.81$, $P = 0.028$).

Resource depletion was measured in a variety of ways in the studies reviewed (see *Methods*). In spite of this, we found that consumer and detritivore diversity effects are broadly similar regardless of the RD method used, albeit only marginally so (LRR, RD method × trophic level, $L = 5.02$, $P = 0.08$). The difference between consumer and detrital diversity tend to be largest with the consumption method (mean difference in consumer and detrital LRR = 1.09) and instantaneous measures of RD (0.95) and smallest with the temporal change method (0.42). The magnitude of the trophic level effect on RD did not differ between studies that reported net loss of detritus vs. those that reported a decay constant over time (trophic level × decay vs. net, $L = 1.24$, $P = 0.27$).

Due to the limitations of the LRR method (see *Methods: Characterizing diversity effect sizes*), we also analyzed the effects of diversity using the power function on a subset (80 observations) of our data set. We found

that all the above conclusions remain unchanged when we use power exponents in place of LRRs, with one exception. In contrast to the results for LRR, power function analysis showed that standing stocks of consumers are affected differently by top-down and bottom-up effects of diversity ($L = 6.88$, $P = 0.0087$; Fig. 3). Specifically, consumer diversity has no net effect on consumer biomass (exponent = 0.064, SE = 0.0376, $t = 1.71$, $P = 0.15$, $n = 6$), while increasing detrital diversity leads to a slow decrease in consumer biomass (exponent = −0.070, SE = 0.0119, $t = -5.919$, $P = 0.002$, $n = 3$) because of one statistically influential study (Wardle et al. 2003). Note that small sample sizes again limit the power of this particular comparison. For the other response variables, sample sizes are >14 and results are congruent between LRR analysis and power function analysis (Fig. 3). For example, RD increases at a decelerating rate with consumer diversity (exponent = 0.316, SE = 0.067, $t = 4.70$, $P = 0.0001$) but is unaffected by detrital diversity (exponent = 0.0273, SE = 0.070, $t = 0.39$, $P = 0.70$). The standing stock of detritus is also unaffected by either detrital or consumer diversity ($L = 0.358$, $P = 0.55$).

Robustness of results

Our results could be influenced by differences between detrital and consumer manipulations in how and where studies were conducted (Table 1). For example, detrital diversity experiments are overwhelmingly conducted in terrestrial systems. If aquatic systems have stronger effects of diversity, irrespective of trophic level, on resource depletion, we might mistakenly conclude that diversity has stronger top-down than bottom-up effects on resource depletion simply because our experimental pool is biased. Similar arguments could be made for

TABLE 1. Distribution of bottom-up (BU) and top-down (TD) observations among different systems, consumer taxa, and types of experimental designs by factor (43 BU observations, 47 TD observations).

			Statistics		
Factor	BU (% or mean ± SE)	TD (% or mean ± SE)	χ^2	P	$F_{1,88}$
System			12.5	0.001	
Aquatic	20.9	57.4			
Terrestrial	79.1	42.6			
Consumer taxa			32.4	0.0005	
Bacteria	18.6	8.5			
Fungi	0	61.7			
Metazoa	76.7	29.8			
Experiment setting			43.1	0.0005	
Laboratory or greenhouse	32.6	97.9			
Field	67.4	2.1			
Richness manipulation			11.69	0.002	
Full assembly	53.5	38.3			
Random assembly	32.6	61.7			
Nonrandom assembly	14.0	0			
Population dynamics			0.198	0.82	
Occurred	74.4	70.2			
Did not occur	25.6	29.8			
Experiment duration	208.49 ± 18.8 d	26.40 ± 2.43 d		0.0001	7302
Maximum richness	6.33 ± 0.68 species	8.89 ± 1.95 species		0.21	1.62

Notes: Independence of factor levels between top-down and bottom-up studies was assessed by means of χ^2 tests using Monte Carlo simulations. The F tests were conducted using quasi-likelihood generalized linear models with Poisson errors.

biases in the experimental pool with regard to consumer taxa, experimental duration or setting, and full vs. random assembly of communities (Table 1). However, none of these system and design differences between detrital and consumer manipulations can account for the observed trophic differences in LRR (trophic level × response variable in all studies and trophic level within RD experiments both still $P < 0.05$ after accounting for each covariate). We obtained similar results for the power exponent, except the difference between trophic levels in RD became marginally nonsignificant after accounting for differences in experimental duration ($L = 3.26$, $P = 0.071$).

A final bias concerns the method used to measure resource depletion. Most detrital diversity experiments use the temporal change method (21/26 observations) rather than the consumption (3/26) or instantaneous methods (2/26). By contrast, consumer diversity experiments tend to use either the temporal change (12/27 observations) or consumption (11/27) methods rather than the instantaneous method (4/27). However, even after we account for RD method, detrital and consumer manipulations still differ in their diversity effects on RD (LRR, $L = 9.74$, $P = 0.002$; power exponent, $L = 21.3$, $P < 0.0001$).

Partitioning of residual variation

The above analyses show that the effects of diversity on function in decomposer systems depends both on the trophic level manipulated and the response variable measured and that these conclusions are robust even after accounting for potentially confounding factors

among studies. A different question is whether, after accounting for trophic level and response variable, there is still residual variance that might be explained by some of those features that differ among experiments (listed in Table 1). For LRR, only maximum species richness and duration of the experiment explain significant amounts of residual variance (all other covariates $P > 0.05$). A one-species increase in maximum richness results in a 1.2% increase in polyculture function relative to monoculture function ($L = 10.7$, $P = 0.0011$), suggesting that a non-saturating relationship like a power function is appropriate for this data set. A one-month increase in experimental duration produces a 2.0% increase in polyculture function relative to monoculture function ($L = 3.63$, $P = 0.056$). For the power exponent, no experimental features could explain the residual variance (all $P > 0.05$).

DISCUSSION

Our analyses suggest that the ecologically important process of decomposition (measured here as resource depletion) is strongly influenced by top-down effects of consumer diversity, yet shows weaker and inconsistent responses to the bottom-up effects of detrital diversity. Indeed, even after accounting for a variety of potentially confounding differences among studies, we found that detritus was broken down faster at higher levels of consumer diversity, but showed no clear directional response to detrital diversity. Perhaps surprisingly, these effects of diversity on decomposition (RD) do not translate into effects on the standing stocks of detritus, a point to which we return below.

We view our conclusions about diversity effects on resource depletion and detrital standing stock as robust. Not only did we obtain qualitatively similar results using either LRR or the power exponent as our measure of the diversity effect size, but the results remain essentially unchanged even after we account for potential biases in the experimental pool between consumer and detrital manipulations. By contrast, our mixed results for consumer standing stock should be viewed as preliminary, as they are based on only eight (LRR) or nine (power exponent) studies, and the results for LRR and power exponents differ. With so few studies it is not surprising that the results differ between response types because, all else being equal, our LRR meta-analysis gives greatest weight to studies with high replication within diversity levels, whereas our power exponent meta-analysis gives greatest weight to studies with many diversity levels.

Bottom-up effects of diversity

Our conclusion that detrital diversity has no consistent effect on decomposition (RD) broadly agrees with the findings of Gartner and Cardon (2004), who summarized the effects of 162 leaf litter mixtures on decomposition, reported in 23 studies, using a vote-counting procedure. The authors compared decomposition, measured as mass loss, in litter mixtures with decomposition rates of the component species in single-species litters. Decomposition rates of mixtures were either higher (47% of mixtures), lower (19%), or the same (33%) as predicted from their components in single-species litter. In this study, we also found a broad spectrum of detrital diversity effects on decomposition. For example, 68% of our RD studies have LRR ≥ 0, indicating an equivalent or greater depletion of resources in high-diversity treatments, whereas 32% have LRR < 0, signifying a greater depletion of resources in the monocultures. Deviations of LRR from 0 are often significant in individual studies (Fig. 2), and the magnitude of these deviations is significantly greater than 0 in the overall meta-analysis. Yet, when the LRR values of individual studies are averaged, there is no global diversity effect. Thus, the positive and negative effects observed in the different experiments cancel each other out in the global mean. This suggests that, at present, there is little evidence for a clear directional effect of detrital resource diversity on rates of decomposition.

Detrital diversity has been hypothesized to have both positive and negative effects on decomposition due to details involving leaf chemistry. Generally, decomposition is fastest in litter with low C:N or C:P ratios and low levels of secondary compounds like phenolics and tannins (Cadisch and Giller 1997, Hoorens et al. 2003). Nutrient transfer from fast- to slow-decomposing litter via fungal hyphae or leaching may stimulate detritivores to consume slow-decomposing species and thus accelerate overall decomposition of the mixture (Chapman

et al. 1988, Blair et al. 1990). Conversely, leaching of secondary compounds from one litter species to another may reduce detrital palatability and, consequently, overall decomposition. However, there is not yet compelling evidence that such litter chemistry effects drive detrital diversity effects (Hoorens et al. 2003, Hättenschwiler et al. 2005). Detrital diversity could also affect decomposition via effects on the consumer community, for example, by changing habitat heterogeneity (Hansen and Coleman 1998, Kaneko and Salamanca 1999), limiting population growth rates (Davidson et al. 2004, Allison and Vitousek 2005), or by affecting feeding behavior (Hättenschwiler and Bretscher 2001, Hättenschwiler and Gasser 2005). Again, there is only limited evidence for such mechanisms. A key challenge for future work is to identify the conditions and mechanisms that distinguish positive from negative effects of detrital diversity on decomposition.

Our finding of no consistent bottom-up effects of detrital diversity on decomposition contrasts with a pattern that seems more common in "green" (plant–herbivore) food webs: increased plant diversity often results in reduced herbivory (Duffy et al. 2007), for example as reported in two recent meta-analyses (algae, Hillebrand and Cardinale 2004; trees, Jactel and Brockerhoff 2007). It should be noted that these meta-analyses focused on experiments that did not directly manipulate diversity, whereas the few direct manipulations of plant diversity have found variable effects on herbivory or herbivore abundance (Knops et al. 1999, Mulder et al. 1999, Fox 2004, Gamfeldt et al. 2005, Bruno et al. 2008). If, however, brown and green food webs really do differ in bottom-up effects of diversity, this may reflect differences in the responsible mechanisms. Live plants, unlike detritus, can compensate for herbivory by growing or reproducing, and such compensation is an important feature of many proposed mechanisms for diversity–function relationships in green food webs (e.g., variance-in-edibility hypothesis; see *Introduction*).

Top-down effects of diversity

In contrast to the relatively weak and inconsistent effects of detrital diversity on decomposition, our analysis provides evidence for strong and consistent top-down effects of consumer diversity on decomposition rates, which is congruent with the results of earlier meta-analyses (Balvenera et al. 2006, Cardinale et al. 2006). The mechanisms behind consumer diversity effects on decomposition are still poorly understood as few experiments have been specifically designed to test for biological mechanisms. There is some evidence that facilitation between detritivores may contribute to positive correlations between consumer diversity and decomposition: for example, the breakdown of detritus by one insect species into particle sizes that can be consumed by another insect species (Jonsson and Malmqvist 2003) or the breakdown of cellulose by one

fungal species leads to sugars that can be consumed by other fungal species (Tiunov and Scheu 2005). There is also limited evidence that functional dissimilarity between detritivore species is important in minimizing interference between individuals, thus increasing community consumption (Cardinale et al. 2002, Jonsson and Malmqvist 2003, Heemsbergen et al. 2004). However, we caution that any mechanisms that involve changes in interspecific (e.g., facilitation) or intraspecific (e.g., interference) interactions among consumers will depend upon how the densities of individual species covary with diversity, both in experiments (additive vs. substitutive designs) and in nature (Ruesink and Srivastava 2001, Douglass et al. 2008). To date, few decomposition studies have separated mechanisms involving intra- or interspecific interactions.

Diversity might also be expected to have stronger top-down than bottom-up effects if consumer species are more phylogenetically divergent than their detrital resources. There is emerging empirical evidence that high phylogenetic divergence between species in a community results in increased ecosystem functioning (Maherali and Klironomos 2007; M. Cadotte, B. Cardinale, and T. Oakley, *personal communications*). Phylogenetic divergence between species may be correlated with ecological niche differentiation and so indicate the potential for complementarity in function (Maherali and Klironomos 2007, Venail et al. 2008). It is not possible at this time to quantify phylogenetic divergence for all species in our data set, but we note that although the phylogenetic divergence is likely high in some consumer manipulations (species in different subphyla, Jonsson et al. 2002), it is actually quite low in others (species in different genera, Cardinale et al. 2002).

Contrary to expectations, top-down effects of consumer richness were seen in resource depletion rates, but not in the final standing stock of detritus. At first this may seem curious given that in most experiments any differences in resource depletion should necessarily translate into differences in final detrital standing stocks when initial detrital standing stocks are fixed and there are no further inputs. One potential explanation for this discrepancy is that the suite of 28 experiments that report SSd data differs in some respect from the 52 experiments that report RD data. Since almost all experiments (26 out of 28) that report SSd data also report RD data, we can test this hypothesis by limiting the analysis to the same set of 26 experiments. Controlling for experiment, we still find differences between RD and SSd depending on the trophic level manipulated (trophic level × response variable interaction, $L = 3.87$, $P = 0.049$), with consumer diversity having a stronger effect than detrital diversity on RD ($L = 6.5$, $P = 0.01$) but not on SSd ($L = 1.34$, $P = 0.25$). This indicates a real difference in the ability of RD and SSd to capture trophic-level effects. We speculate that the effects of trophic level on response ratios may be more detectable when measured as RD, rather than SSd, for

several reasons. (1) Detritivore efficiency affects response ratios calculated using SSd, but not those using RD. Consider the case in which consumers in monoculture are able to consume, over a set time period, an average of 10% of detritus, but a high diversity community of consumers can consume 20% of detritus. The LRR based on RD would be $\log(0.2/0.1) = \log(2)$, and the LRR based on SSd would be $\log(0.8/0.9) = \log(0.89)$. If the experiment is repeated with a more efficient group of consumers, which are able to consume as monocultures 20% of detritus, but at high consumer diversity 40% of detritus, the LRR based on RD would still be $\log(2)$ but that of SSd would have fallen to $\log(0.6/0.8) = 0.75$. Thus response ratios based on SSd will contain this extra "noise" of detritivore efficiency, potentially obscuring trophic-level effects. (2) Researchers tend to correct RD, but not SSd, for external sources of variation such as nonlinear effects of time (six of 28 studies fit an exponential or logarithmic function to RD over time, but none correct SSd for time effects) and variation in consumer biomass (e.g., Jonsson and Malmqvist 2003). (3) If consumer diversity has greatest effects on RD early in the decomposition process, measures at the end of the experiment such as SSd may underestimate effects (Cardinale and Palmer 2002). Presumably all of these effects described for SSd could also add noise to measures of SSc.

Within resource depletion experiments, the type of method used may also affect the detection of diversity effects. The temporal change method represents a number of processes in addition to consumption, including mechanical abrasion and initial abiotic leaching of compounds. The instantaneous and consumption methods isolate the consumption-related loss of detritus from these other losses, perhaps explaining why these methods tend to show stronger effects of trophic level than the temporal change method.

Effects of experimental duration

The effects of diversity on decomposition rates are not only affected by trophic level, but also by experimental duration: larger effects occur in longer running experiments. A similar effect of experimental duration was recently found for the effects of plant diversity on plant biomass production (Cardinale et al. 2007). The authors used an additive partitioning method (Loreau and Hector 2001) to show that the temporal effect was due to the strengthening of niche complementarity effects. Unfortunately, we cannot use this method for decomposition studies, as few studies measure the decomposition of individual species in mixture. We hypothesize that experiment duration may alter diversity effects on decomposition rates because the mechanisms behind decomposition change over time, from dominance by rapid leaching of labile nutrients to an increasing reliance on fauna to break down recalcitrant compounds (Swift et al. 1979). Individual studies of decomposition have similarly shown that detrital diversity effects can

change substantially over time (McTiernan et al. 1997, Prescott et al. 2000), but the mechanisms behind these changes are not well understood. Whatever the mechanism, the strengthening of diversity effects through time in both our analysis of detrital systems and in previous analyses of green food webs hints at a potentially general pattern.

In summary, we have demonstrated that the breakdown of detritus is affected strongly and positively by the top-down effects of detritivore diversity, but not consistently by the bottom-up effects of detrital diversity. There are important ramifications for this finding, given that detritivore diversity is adversely impacted by numerous human activities (Lodge 1997, Lindo and Visser 2003, Rantalainen et al. 2005, Migge-Kleian et al. 2006) and that decomposition is a key regulator of global carbon and nutrient dynamics (Cebrian and Duarte 1995). Our study also simultaneously extends 1) biodiversity–ecosystem function research by showing that the effects of changing biodiversity on ecosystem functioning depend critically on the trophic position of species relative to the function being considered and 2) trophic structure theory by showing that energy flow between trophic levels depends critically on consumer diversity, not just net consumer biomass. Given these findings, a complete understanding of how food web change affects ecosystem functioning will require deeper integration of biodiversity–ecosystem function theory with established knowledge of the effects of trophic structure.

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SUPPLEMENT

Data set used in the meta-analysis and associated references (*Ecological Archives* E090-070-S1).