Predicting richness effects on ecosystem function in natural communities: insights from high-elevation streams

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Abstract. Despite the increased complexity of experimental and theoretical studies on the biodiversity–ecosystem functioning (B–EF) relationship, a major challenge is to demonstrate whether the observed importance of biodiversity in controlled experimental systems also persists in nature. Due to their structural simplicity and their low levels of human impacts, extreme species-poor ecosystems may provide new insights into B–EF relationships in natural systems. We address this issue using shredder invertebrate communities and organic matter decomposition rates in 24 high-altitude (3200–3900 m) Neotropical streams as a study model. We first assessed the effects of stream characteristics and shredder diversity and abundance on organic matter decomposition rates in coarse- and fine-mesh bags. We found the interaction term shredder richness × shredder abundance had the most significant impact on decomposition rates in the field, although water discharge may also play a role locally. We also examined the relative contribution of the three most abundant shredders on decomposition rates by manipulating shredder richness and community composition in a field experiment. Transgressive overyielding was detected among the three shredder species, indicating complementary resource use and/or facilitation. By integrating survey and experimental data in surface response analyses we found that observed B–EF patterns fit those predicted by a linear model that described litter decomposition rates as a function of increasing shredder richness and the relative abundance of the most efficient shredders. Finally, the validity of our approach was tested in a broader context by using two independent but comparable data sets from 49 French and Swedish streams showing more complex shredder community structure. Results revealed that richness and identity effects on decomposition rates were lost with increasing shredder community complexity. Our approach of combining experimental and empirical data with modeling in species-poor ecosystems may serve as an impetus for new B–EF studies. If theory can explain B–EF in low-diversity ecosystems, it may also have credibility in more complex ones.

Key words: *Akaike criterion; biodiversity–ecosystem function; Ecuadorian high-altitude streams; species-poor ecosystems; surface response analysis.*

INTRODUCTION

The global scale of the biodiversity crisis has stimulated extensive research exploring the relationships between biodiversity and processes in many different ecosystems of the world (Loreau et al. 2002, Naeem et al. 2009). The link between biodiversity and ecosystem functioning (hereafter B–EF) is now relatively well established, revealing generally positive effect of species diversity on ecosystem functioning in both terrestrial and aquatic systems (Hooper et al. 2005, Lecerf and

Richardson 2009). However, this consensus mainly derives from experimental studies conducted in synthetically assembled communities involving direct manipulation of species richness and abundance, which can be of debatable relevance in complex, real-world, ecosystems (Hector and Bagchi 2007). The positive richness effects found in small-scale manipulative experiments may, for example, be modified by patterns of relative species abundance (Dangles and Malmqvist 2004, McKie et al. 2008) or overwhelmed by environmental heterogeneity and stochasticity (Griffin et al. 2009) found in natural systems. Despite the steady increase in the complexity of experimental and theoretical studies on the B–EF relationships, and evidence that biodiversity is important to the functioning of real-world

ecosystems (Duffy 2009), a major challenge that remains is to demonstrate whether the observed importance of biodiversity on ecosystem functioning in controlled experimental systems also persists in natural systems (Jiang et al. 2009).

Extreme ecosystems (sensu environmentally harsh systems with low species richness) including arid, polar, and high-altitude regions, represent useful models to examine to what extent positive B–EF relationships revealed by manipulative experiments are also found in nature (Wall and Virginia 1999, Doi and Kikuchi 2009). First, both richness and identity effects may theoretically be more likely in species-poor assemblages that lack the range of direct and indirect interactions typical of more complex communities (Pastor et al. 1994, Barret et al. 2008). Second, a wide array of extreme ecosystems not only exhibit few taxa but also low phylogenetic relatedness among them (Pastor et al. 1994, Vincent et al. 2000, Barrett et al. 2008). For example, the ratios morphospecies per genera and morphospecies per family of caddis larvae in Neotropical streams show a steady decline with increasing altitude, reaching ratio values around 1 above 4000 m elevation (Jacobsen 2000). The co-occurrence of distantly related taxa is expected to increase the functional diversity of benthic communities, therefore implying that positive B–EF relations will be more pronounced in taxonomically heterogeneous guilds because of the greater scope for the different underlying mechanisms (e.g., complementarity and facilitation) to be expressed (Petchey and Gaston 2006, Cadotte et al. 2008). The functional contrast among species implies strong feedbacks between species, resources, and disturbances (Pastor et al. 1994). Third, most extreme ecosystems remain largely in a wilderness condition, which limits confounding factors related to human-induced effects on ecosystem function (Pastor et al. 1996).

In this study, we propose a three-step methodological framework combining empirical survey, experiments, and modeling to evaluate the complexity of B–EF relationships in nature, using leaf-eating macroinvertebrate (shredder) communities and the decomposition rate of organic matter in high-altitude Neotropical streams as a model system. The first step of our approach consisted of testing whether shredder richness and abundance affected organic matter decomposition rates in 24 species-poor high-elevation stream systems. In the second step, we experimentally manipulated both species richness and identity of the three most abundant shredders and tested their effects on organic matter decomposition. By incorporating both survey and experimental data, the third step compared observed B–EF patterns with those predicted by an additive model describing the decomposition rate response with increasing species number or species identity. Finally, the validity of our approach was tested in a broader context using two independent but comparable data sets

from 49 French and Swedish streams available in the literature.

METHODS

Study area and stream characteristics

The study was conducted in 24 high-altitude streams (3200–3900 m elevation) draining the paramo of Papallacta located within the Cayambe-Coca National Park in Ecuador. These streams are surrounded by vegetation comprising grass (*Calamagrostis intermedia*) and scrub extending from the forest fringes up to the permanent snow line at 4800–5000 m elevation (Jacobsen 2008; see Plate 1). Inputs of allochthonous organic matter (mostly grass) received by these streams and consumed by stream biota are likely to be important for local nutrient and energy budgets (see Jacobsen 2008). Locally, accumulations of filamentous algae (e.g., Cladophora: Chlorophyta) may also constitute an important biomass (see Jacobsen [2008] for more details on tropical high-altitude stream energetic budgets). The main physico-chemical characteristics of the 24 streams and associated methods are given in Appendix A.

Organic matter decomposition and shredder richness: empirical data

Decomposition of *C. intermedia* collected in the páramo of Papallacta was measured as mass loss using 7.0 g of leaf blades placed in litterbags (15 × 10 cm) of two different mesh sizes (0.3 and 5 mm); the fine-mesh bags excluded macroinvertebrates, but coarse-mesh bags did not. Abscised leaf blades were representative of those that enter streams (V. Crespo-Perez and O. Dangles, *personal observation*). Ten replicate bags of each type were secured both to the substrate and to the bank with plastic-coated wires. The exposure started in mid-April 2007 and lasted for 10 weeks, a time sufficient to show significant decomposition, as several streams showed >60% leaf mass loss at the end of the exposure (Bärlocher 2005a). After retrieval the grass material was rinsed to remove fine particulate matter and invertebrates (Dangles et al. 2001). The remaining plant material was dried (48 h at 50°C), ashed (4 h at 550°C), and used to calculate ash-free dry mass (AFDM). Invertebrates were counted and identified to morphospecies using Dominguez and Fernandez (2009). Assignment of invertebrates to the "shredder" feeding guild was based on Jacobsen (2008). To confirm guild assignment of a few taxa (e.g., *Andesiops*, *Stenelmis*), gut content analyses were also examined following methods detailed in Dangles (2002). In each stream, benthic shredder assemblages were quantified, collecting at random four replicate Surber samples (area: 20 × 25 cm; mesh size, 200 μm) from gravel–pebble–cobble substratum, which was the dominant substratum type in all streams. Consequently, mesh bags were placed over the same type of substratum. Benthic coarse particulate organic matter (CPOM) was obtained by filtering the remaining material from Surber samples through a 1-

mm sieve while inorganic material was eliminated. CPOM was calculated as dry mass (48 h at 50°C) minus mass of ash (4 h at 550°C).

Loss of mass for grass was corrected for leaching losses using the results of a 72-h laboratory trial (see Bärlocher 2005b for a detailed description of leaching process in aquatic systems). The decomposition rate coefficient k was calculated for each litterbag using the well-established negative exponential decay model (Webster and Benfield 1986), which reflects the most commonly observed functional response for leaf decomposition in streams (see Benfield 1996, Bärlocher 2005a). Generalized linear models (GLMs) were further used to test for effects of stream characteristics (see the list in Appendix A) and shredder metrics (diversity and abundance) on grass decomposition rates in fine-mesh bags (k_{FM}) and the ratio between rates in coarse-mesh and fine-mesh bags ($k_{CM}:k_{FM}$). This ratio represents the proportion of grass decomposition related to shredder activity and mechanical abrasion alone (Dangles and Guérold 2001), which facilitates comparisons among streams. (A ratio >1 indicates faster decomposition in coarse-mesh than fine-mesh bags, and vice versa.) We used standard model simplification procedures to identify significant terms of the initial models. We started from the most complex models (including all interactions) and kept eliminating higher-order terms until a significant one was found. In order to avoid collinearity, a pairwise regression matrix of all predictors (i.e., mean values of stream characteristics and shredder metrics, see Appendix A) was constructed. Highly correlated predictors ($R > 0.6$) were never included in the same initial model. Due to our small sample size (24 points), each model was limited to combinations of a maximum of six explanatory variables (see Neter et al. 1990) among those listed in Appendix A. We included a term "site" in our analysis to allow within-site comparisons while controlling for variation resulting from unmeasured site-specific parameters. Site was treated as a fixed effect, but we obtained similar results by means of the generalized linear mixed model function (glmmPQL; MASS library for R), with site as random effect. The most parsimonious model was identified using the corrected Akaike's information criterion (AIC_c), which is recommended for small sample sizes. The statistical significance of each factor was assessed using the likelihood ratio test (LRT) based on comparison of deviations under full and reduced models. In a similar way, we tested for effects of stream characteristics plus benthic CPOM (mean values) on shredder richness and abundance. All analyses were performed using the mass library for R (R version 2.9.2, R Development Core Team 2009).

Organic matter decomposition and shredder richness: experimental data

We experimentally investigated the effect of species richness, from one to three shredder species, and species identity/abundance on grass decomposition. Shredder species were selected based on their major occurrence and abundance in the 24 studied streams and in grass bags. The selected species were *Anomalocosmoecus* sp. (Insecta: Trichoptera), *Hyalella* sp. (Crustacea: Amphipoda), and *Andesiops* sp. (Insecta: Ephemeroptera). Another shredder, *Nectopsyche* sp. occurred at slightly higher densities than *Anomalocosmoecus* sp. in the streams, but the latter was included instead of *Nectopsyche* due to its considerably higher body mass, and therefore presumed greater importance in decomposition. All other shredders occurred naturally at 10–100 fold lower densities.

Our substitutive experimental design consisted of eight treatments replicated 10 times; three single-species treatments with 12 individuals of *Hyalella*, 12 individuals of *Andesiops*, and 6 individuals of *Anomalocosmoecus*, three two-species treatments of (6 + 3 individuals) with *Hyalella* and *Anomalocosmoecus*, (6 + 3 individuals) of *Andesiops* and *Anomalocosmoecus*, and (6 + 6 individuals) with *Hyalella* and *Andesiops*; one three-species treatment (3 + 3 + 2 individuals) with *Hyalella*, *Andesiops*, and *Anomalocosmoecus*, and one control treatment to provide information on grass mass loss in the absence of shredders. As the effect of species richness can be density dependent (McKie et al. 2008), the relative densities of each species were representative of those found in the streams. The number of experimental replicates was limited by the relatively low abundance of *Anomalocosmoecus* in the streams. Ten replicates were, however, sufficient to conduct proper statistical analyses with regard to the low within-treatment variances observed in shredder consumption rates (see also Jonsson and Malmqvist 2000, Jonsson et al. 2002). The bags, containing animals and 1 g of fresh grass material, were attached randomly to a plastic box with holes, which was anchored with stones to the bed of stream 7 (see *Physicochemical characteristics* in Appendix A). When the bags were retrieved after 14 days, grass material and animals were separated. The animals were counted, preserved in 70% alcohol, dried at 50°C for 48 h and weighed. The grass materials were dried at 50°C for 48 h and weighed. The percentage of loss of mass of grass per bag was then calculated following correction for decomposition attributable to leaching and microbes (estimated from the control treatment). Correction for effects of animal mortality on grass mass loss was made by assuming that dead individuals had lived for half the experimental time (Jonsson et al. 2002; see also McKie et al. [2008] for alternative methods for dealing with mortality). Loss of grass mass per unit animal mass was used in the analyses to account for differences in biomass.

In our design, species composition was fitted as a nested factor within species richness, a common approach in B–EF experiments that helps separate variation due to richness per se from that due to the particular combination of species present. Following

Cardinale et al. (2006) we tested for nontransgressive and transgressive overyielding (sensu Huston and McBride 2002) by comparing mixture performance with mean monoculture performance (contrast 1), and the performance of the most efficient species monoculture (contrast 2), respectively. The fact that both contrasts were positive and significant indicates a positive species richness effect driven at least in part by nonadditive mechanisms such as resource use and facilitation (see McKie et al. 2008 for further details). ANOVA was used for both contrasts with species composition fitted as a random factor nested within species richness. All analyses were performed using R (R version 2.9.2, R Development Core Team 2009) with log transformation of response variables. To characterize the general form of species richness–function relationships, we fitted data to linear and three nonlinear functions that have previously been used in the literature (log, power, and hyperbolic; see Cardinale et al. [2006]).

Merging survey and experimental data through response surface analyses

Borrowing from response surface analyses (see Jongman et al. 1995), we built a graph to visualize how decomposition rates measured in the field were predicted by both richness and identity/abundance components of shredder diversity in grass bags. For this purpose, we plotted shredder richness (species number effect, x) vs. the relative abundance of the shredder species that had the largest effect in our controlled experiment (identity/abundance effect, y) for the 24 studied streams. Coordinates of the 24 sites and their corresponding decomposition rates (in coarse-mesh bags) z, were fitted to a surface of the form $z(x, y)$ using the function GRIDFIT written in MATLAB (D'Errico 2006) with decomposition values smoothed by nearest-neighbor interpolation. The resulting decomposition modeling surface (DMS) was defined by values at a set of nodes forming a rectangular lattice. This empirical DMS was compared with a theoretical DMS representing the null hypothesis that both species richness and composition have a positive effect on decomposition rates. Our theoretical DMS also hypothesized synergetic interactions between the two effects so that decomposition rates are maximized in sites showing high values in both species number and abundance of effective species. Although we used a B–EF positive linear trend commonly reported in the literature (see Hooper et al. 2005, Cardinale et al. 2006), other types of null hypotheses may have been used here (e.g., negative richness effect found by McKie et al. [2009]). The statistical significance of both richness and identity effects on organic matter decomposition rates was then assessed by fitting our data to a surface of the form, $z \sim \beta_1 x + \beta_2 y$, where β_1 and β_2 are linear regression coefficients (Heiberger and Holland 2004). An F test was used to assess the significance of the overall fit, whereas t tests of individual parameters β_1 and β_2 assessed the

significance of richness and identity components (see Appendix B for further details). Although experimental trials were only conducted in one stream, these results were then modeled with natural data from all streams. The manipulated diversity experiments were only run for two weeks, while the survey of decomposition at the 24 field sites lasted for 10 weeks. This fact was not expected to influence our decomposition modeling surfaces, because the patterns produced did not depend on absolute rates.

To explore whether our methodological approach could be broadened to stream systems with different shredder community composition and benthic CPOM, we built additional DMS using two different data sets available in the literature. The first data set came from Sweden, where both shredder species number and identity effects on decomposition rates have been extensively studied by M. Jonsson and B. Malmqvist. These authors showed by several experimental manipulations of shredder richness (identical to that described in our study) that the plecopteran aquatic insect *Taenyopteryx nebulosa* (Taenyopetrigidae) had the greatest per biomass effect on leaf decomposition (Jonsson and Malmqvist 2000), followed by two other plecopteran shredders, *Nemoura avicularis* and *Protonemura meyeri*. Interestingly, *T. nebulosa* also showed positive interactions with *P. meyeri*, leading to increased decomposition rates (Jonsson and Malmqvist 2003). We used data published by Jonsson et al. (2001) on leaf decomposition rates and shredder community composition (both in terms of shredder species richness and *T. nebulosa* abundance) in 23 Swedish streams to build our DMS. The other data set came from several shredder richness–leaf decomposition studies performed in Northeastern France, where the trichopteran *Sericostoma personatum* was experimentally shown to have a significant positive effect on decomposition rates when placed with other shredders, the plecopteran *Nemurella picteti* and the amphipod *Gammarus fossarum* (Jonsson et al. 2002, Dangles and Malmqvist 2004). *S. personatum* facilitated leaf decomposition by cutting leaves into small pieces that facilitated utilization by other shredders (Jonsson et al. 2002). We used data published by Dangles et al. (2004) and Dangles and Malmqvist (2004) on leaf decomposition rates and shredder community composition (both in terms of shredder species richness and *S. personatum* abundance) in 26 Vosges Mountain streams to build our DMS. To make the data sets of the three countries comparable, only shredder richness values obtained from litter bags were used in the analysis. The leaf bags had similar structure characteristics among studies ($10–15 \times 15$ cm, 5–8 mm mesh size). F and t tests and associated P values were calculated for these two sets of streams, as explained above (see Appendix B). Note that for the three studied regions, correlations between shredder richness and abundance of the most efficient shredder were low and nonsignif-
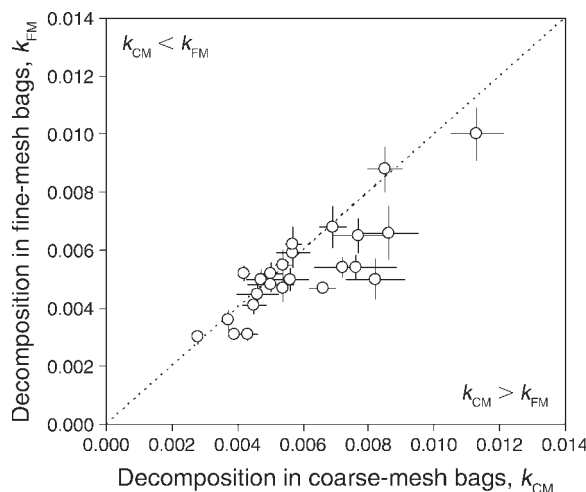
FIG. 1. Decomposition rates (k) of *Calamagrostris intermedia* in fine-mesh bags (0.3 mm, k_{FM}) and coarse-mesh bags (5 mm, k_{CM}) exposed for 10 weeks in 24 high-altitude streams (3200–3900 m elevation) draining the paramo of Papallacta, located within the Cayambe-Coca National Park, Ecuador. The dotted line represents values where $k_{FM} = k_{CM}$. Bars represent ± SD for each axis.

icant ($r = 0.28$, $P = 0.41$ for Ecuador; $r = 0.03$, $P = 0.76$ for France; $r = 0.32$, $P = 0.30$ for Sweden).

RESULTS

Drivers of grass decomposition and shredder richness in the field

Grass decomposition rates (k) ranged from 0.0028 d^{-1} to 0.0113 d^{-1} in the coarse-mesh bags (median value = 0.0057 d^{-1}) and from 0.0030 and 0.0100 in the fine-mesh bags (median value = 0.0048 d^{-1}; see Fig. 1). Our GLM analysis identified several environmental factors (listed in Appendix A) that may explain differences in grass decomposition rates among the 24 streams (Table 1).

The analysis was performed to disentangle factors' effect on both microbial activity (k measured in fine-mesh bags) and invertebrate activity (ratio between rates in coarse-mesh and fine-mesh bags). Of the nine variables included in our analysis, the interaction of altitude and mean oxygen concentration in water was the only variable that significantly affected grass decomposition in fine-mesh bags (LRT = 4.876, $P = 0.035$; Table 1). In contrast, the ratio k_{CM}/k_{FM} was better explained by stream discharge, shredder richness, and its interaction with shredder abundance (LRT $\geq$ 3.121, $P < 0.05$; Table 1).

In both grass bags and streambed, shredder richness in the 24 streams followed a lognormal distribution with a median number of taxa of 1.90 and 3.79, respectively (Fig. 2a). We found a similar pattern in species rank abundance of shredder assemblages in both streambed and grass bags with the amphipod *Hyalella* sp. and the ephemeroptera *Andesiops* being the most abundant taxa (Fig. 2b). Shredder richness decreased significantly with increasing mean discharge, conductivity, and their interaction (LRT $\geq$ 3.821, $P \leq 0.05$, Table 1). Higher mean discharge and lower standing crop of benthic CPOM also significantly decreased shredder abundance in streams (LRT $\geq$ 5.070, $P \leq 0.026$; Table 1).

Effect of manipulated shredder richness on grass decomposition

In all treatments survival was high for *Hyalella* sp. and *Anomalocosmoecus* sp. (>90%) but lower for *Andesiops* sp., with just over 60% remaining at the end of the experiment. Taking biomass into account, the most efficient shredder was *Anomalocosmoecus*, followed by *Andesiops* sp. and *Hyalella* sp. (Fig. 3b). Paired contrast analyses revealed that grass decomposition increased significantly with increasing species richness ($P < 0.026$, Fig. 3a; see Appendix C for the full ANOVA table) and species abundance ($P < 0.001$). When grass

TABLE 1. Results of the generalized linear model deviance analysis on decomposition rates (k) of grass placed in fine-mesh bags (k_{FM}) and coarse-mesh bags (k_{CM}), shredder richness, and shredder abundance.

Terms included in the initial model	Significant effects	AIC_c	ΔAIC_c	LRT	P value
Organic matter decomposition (k_{FM})					
Alt, oxygen, S_{shred}, N_{shred}, Temp, Disch	Alt × oxygen	234.4	4.5	4.876	0.035
Organic matter decomposition (k_{CM}/k_{FM})					
Alt, oxygen, S_{shred}, N_{shred}, Temp, Disch	S_{shred} × N_{shred}	223.7	5.0	5.871	0.023
Disch, Temp, S_{shred}, N_{shred}	Disch	243.6	3.2	3.121	0.048
	S_{shred}	243.8	3.3	3.516	0.045
Shredder richness					
Alt, oxygen, Disch, cond, pH, CPOM	Disch × cond	144.0	2.0	3.821	0.050
Disch, cond, width, temp	Disch	149.2	5.2	7.165	0.007
	Cond	147.5	2.5	4.421	0.032
Shredder abundance					
Disch, cond, pH, CPOM	Disch	142.5	3.0	5.070	0.024

Notes: Only significant effects are shown. AIC_c is the corrected Akaike's Information Criterion for the initial model after removal of the "effect" term. ΔAIC_c corresponds to the difference between the AIC_c of the initial model and that of the reduced model. Likelihood-ratio test (LRT) and associated P value test the hypothesis that the suppression of the "effect" term provides no better fit than the initial model. Key to abbreviations: Alt, altitude; Disch, discharge; temp, temperature; cond, conductivity; S_{shred}, shredder richness in the streams; N_{shred}, shredder abundance in the streams; CPOM, benthic coarse particulate organic matter.
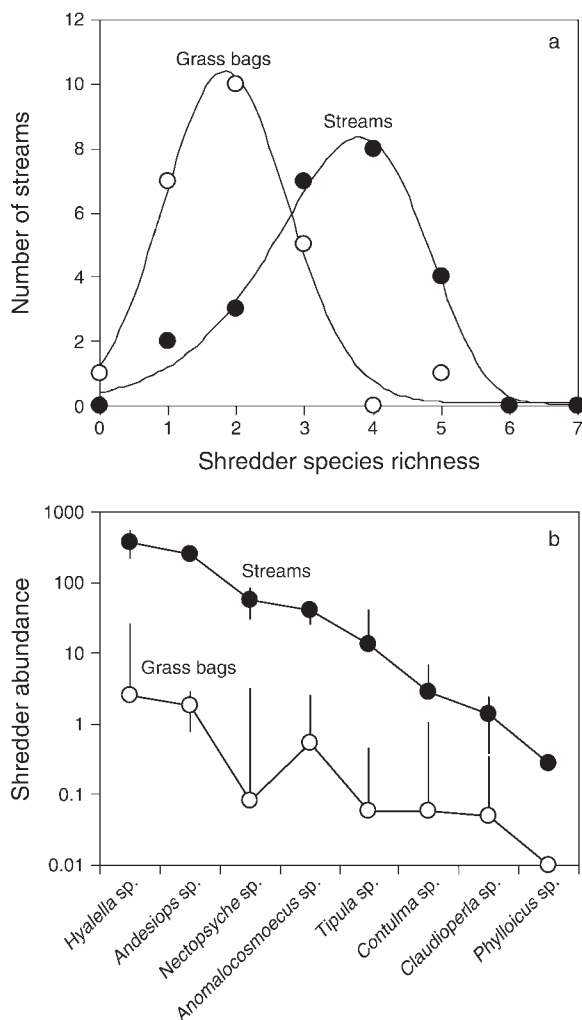
FIG. 2. (a) Shredder species richness and (b) species abundance in shredder communities found in streambeds and grass bags of the 24 study streams draining the paramo of Papallacta, located within the Cayambe-Coca National Park, Ecuador. Shredder abundances in bags and in streams are given in individuals/bag and individuals/m^2, respectively.

than in the Ecuadorian páramo streams, lower decomposition rates were also found in the lower left portion of the graphic (i.e., low shredder richness and low *S. personatum* abundance) but higher rates were observed in streams with either high shredder species number or high abundance of the most effective shredder, *S. personatum* (Fig. 4c). However, high decomposition rates were also found in streams with low values of both shredder richness and *S. personatum* abundances (black zone in the lower left portion of the graphic). Swedish streams, which possessed the highest richness of
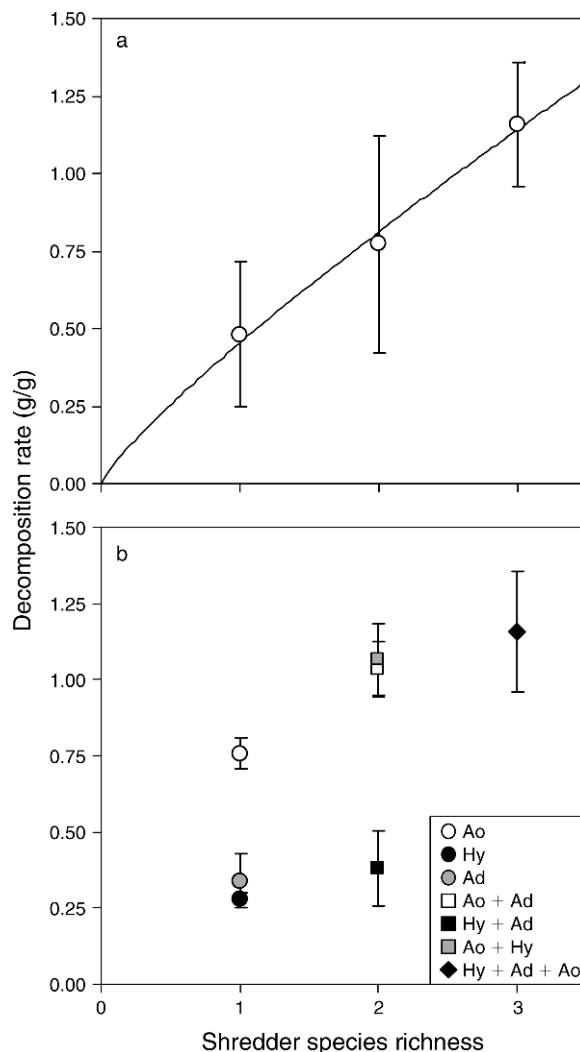

FIG. 3. Invertebrate shredder richness vs. grass decomposition rates in (a) a high-altitude stream, and (b) in trials with experimentally modified shredder communities. In panel (a), a power function was fitted to the data ($a = 0.454$, $b = 0.838$, $R^2 = 0.989$, $F_{2,1} = 541.96$, $P < 0.001$, Spearman test) revealing a significant positive effect of shredder richness on grass decomposition. Grass decomposition values were normalized by larval biomass (g grass/g larva) to account for differences in species size. Error bars represent ±SD with 10 replicates. Key to abbreviations: Hy, *Hyalella* sp.; Ad, *Andesiops* sp.; Ao, *Anomalocosmoecus* sp.

decomposition rates were calculated for the seven mixed species treatments (Fig. 3b), results revealed that only the two-species treatment that included *Anomalocosmoecus* sp. and the three-species treatment were significantly higher than the one-species treatments (*t* tests, *t* = 3.25, *P* < 0.01; *t* = 6.88, *P* < 0.001, respectively).

Decomposition modeling surfaces (DMS)

Consistent with theoretical predictions (Fig. 4a), data from Ecuadorian streams showed that grass decomposition rates were lower in streams with low values in both shredder species number and *Anomalocosmoecus* sp. abundances (Fig. 4b). Higher decomposition rates were found in streams presenting high *Anomalocosmoecus* sp. abundances and intermediate species number. In French streams, where shredder richness was higher
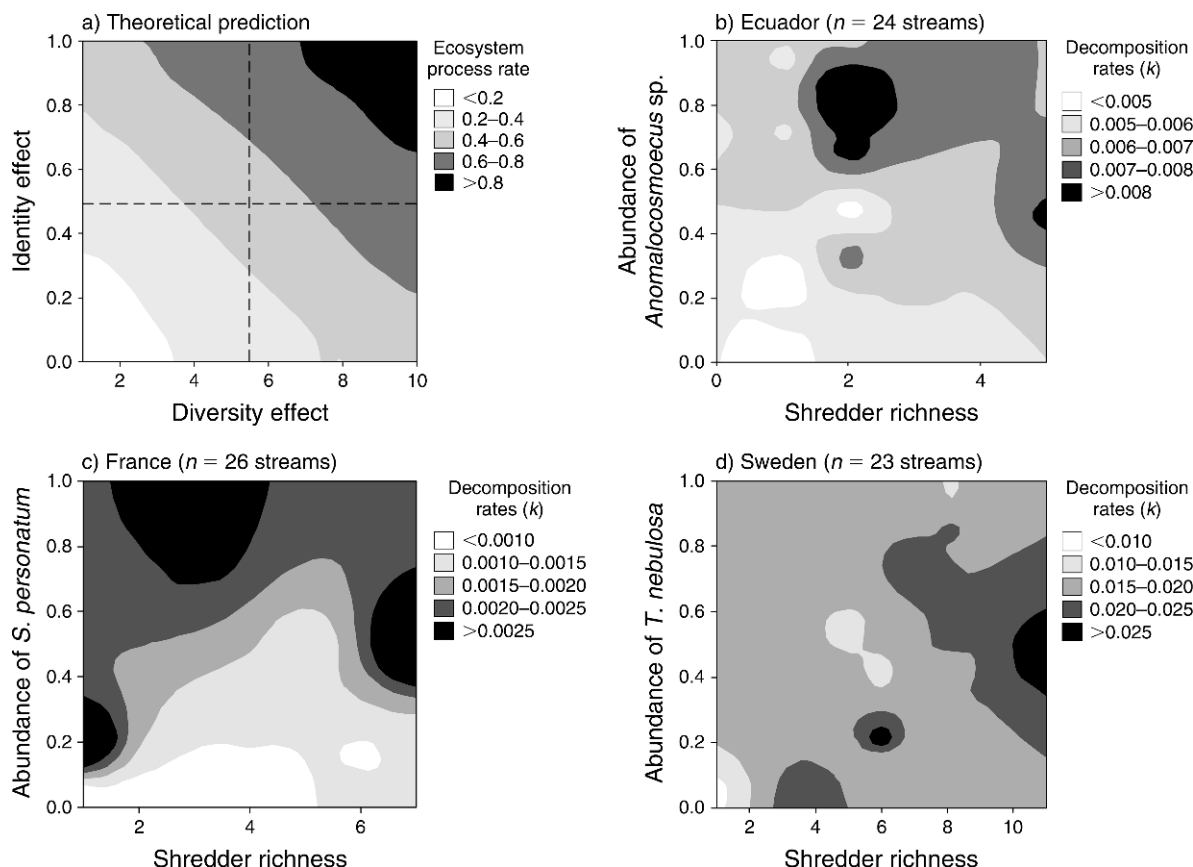
FIG. 4. Decomposition modeling surfaces (DMS) representing the decomposition rates of organic matter (k) as a function of shredder richness and the abundance of the most efficient shredder. (a) Theoretical DMS with $S_{max} = 10$ and $0 < k < 1$. This S_{max} value (the maximum value of species richness) is given as an example and had no implication in the rest of the analyses. (b) Data from Ecuador, (c) data from France (Jonsson et al. 2002, Dangles and Malmqvist 2004, Dangles et al. 2004), and (d) data from Sweden (Jonsson and Malmqvist 2000, Jonsson et al. 2001).

shredders among all three regions, showed a less clear pattern (Fig. 4d). Although highest and lowest decomposition rates were found in streams with high and low species number values, respectively, intermediate decomposition rates ranging from 0.15 to 0.20 d^{-1} (in light gray) occurred in streams with contrasting shredder assemblages in terms of both species richness and abundance of the most effective shredder *T. nebulosa*. While shredder richness and abundance both had a significant effect on decomposition rates in Ecuadorian streams (*t* tests, $P = 0.044$ and $P = 0.002$, respectively), only the most effective shredder abundance was significant in French streams (*t* test, $P < 0.001$) and none of them in Swedish streams (*t* tests, $P \geq 0.096$; see Appendix B for details).

Discussion

Drivers of leaf decomposition under natural conditions in species-poor stream systems

Partitioning the contribution of species richness vs. abiotic factors on ecosystem functioning remains a major challenge for B–EF research (Hillebrand and Matthies-

sen 2009). Our results support previous studies reporting that decomposition rates may depend on shredder richness more strongly than on abiotic forces (Jonsson et al. 2001, Cornwell et al. 2008). However the only slightly higher values in coarse-mesh than in fine-mesh bags also suggest that among-stream variability in microbial activity (potentially influenced by altitude and oxygen content; see Table 1) could also have significant effects on grass litter decomposition. The fact that much of the breakdown was carried out by microbes rather than invertebrate shredders might be a common phenomenon in grassland streams (Hladyz et al. 2010). The GLM also revealed that locally increased flow can play a role in increased decomposition, likely through increased physical abrasion. The effects of such stochastic events on decomposition rates are difficult to predict, but they can be visualized on response surface graphics. For example, high flow occurring in the stream *Mogotes 2* (up to 3.5 m^3/s [R. Calvez, *unpublished data*]) likely explained the high observed decomposition rates despite low shredder richness and low abundance of the best shredder (black zone in the lower left portion of Fig. 4b). Note that

PLATE 1. Stream draining the paramo of Papallacta located within the Cayambe-Coca National Park in Ecuador (3800 m a.s.l.). Paramos are a collection of Neotropical alpine ecosystems within the grassland biome that covers the northern region of the Andes between the upper forest line (~3500 m altitude) and the permanent snow line (~5000 m). Photo credit: O. Dangles.

flow and disturbance regimes are also prime factors governing the variation of macroinvertebrate assemblages in tropical high-altitude streams (Jacobsen 2008), and may have influenced decomposition rates indirectly, through changes in biotic community structures.

Species richness and identity effects on decomposition in low-richness stream systems

Our experimental results confirm previous studies that have shown the importance of animal consumer diversity on resource consumption (Jonsson et al. 2002, Matthiessen et al. 2007, Dangles et al. 2009, Srivastava et al. 2009). The power function shape of the B–EF relationship (Fig. 3a) also agrees with several freshwater studies (e.g., Jonsson and Malmqvist 2000, 2003, Jonsson et al. 2002) in which decomposition rates have been shown to saturate in systems containing more than three invertebrate species (although this may occur earlier for other freshwater taxa, such as in fungal assemblages [see Dang et al. 2005]). Individual species effects in our study differ from the situation where a single species has exceptionally large effects on process rates (i.e., the "sampling effect" [Huston 1997]), as all species were included in each species richness treatment. Instead, certain combinations of species had greater effects on grass consumption, especially in multispecies treatments where *Anomalocosmoecus* sp. was included,

revealing a significant effect of species identity/abundance in addition to a species richness effect. Significant interaction between richness and abundance effects supports the assumption that only a few dominant taxa and interactions may drive B–EF relations within a given ecosystem (Woodward 2009) and that species' traits may be better correlated with ecosystem functioning than taxonomic richness (Fox 2005, Lecerf and Richardson 2009). Several mechanisms, such as niche partitioning (Finke and Snyder 2008) and facilitation (Cardinale et al. 2002), have been shown to contribute to increases in functioning/production with diversity. In our case, differences in feeding modes among selected taxa may have allowed more complete resource utilization consistent with a case of "feeding complementarity" (Jonsson et al. 2002, Dangles et al. 2009). Another potential mechanism is that negative interactions may have been greater within rather than among species, therefore hampering decomposition rates more in species-poor situations compared to where encounters and interactions take place primarily between species (Jonsson and Malmqvist 2000, Godbold et al. 2009).

Merging experimental and survey data to predict decomposition rates in nature

Our experimental results confirm previous studies that have highlighted the importance of both species richness

per se and the presence/abundance of the most effective functional species/group with respect to ecosystem functioning (Cardinale et al. 2006, Griffiths et al. 2008, Lecerf and Richardson 2009). Since much of B–EF theory is underpinned by the interplay of interspecific vs. intraspecific interactions, changes in abundance of the most efficient species is likely to produce unexpected results not predicted by simple additive richness effects. Our results further demonstrate that field measurements of these two variables (diversity and abundance of the most efficient taxa) for the shredder guild were significant predictors of grass decomposition; in the specific case of species-poor tropical streams, small-scale controlled experiments adequately predicted the role of biodiversity for ecosystem processes under natural conditions.

Extrapolating our methodology to other climatic zones and more species-rich ecosystems may appear hazardous given the special characteristics of species-poor, high-altitude Ecuadorian streams. While both richness and abundance of the most efficient species of shredders significantly predicted decomposition rates in low-diversity streams, we found that the importance of biodiversity effects on decomposition decreased gradually from low to high shredder richness stream systems. At least three hypotheses may explain these results. First, our results may support the redundancy hypothesis, i.e., that above a critical number the addition of species does not correspond to an increase in decomposition rates. In the case of Swedish streams, the presence of several phylogenetically related plecopteran shredders may result in a poor functional contrast between shredder species, and therefore in weak relationships between species number decomposition rates (Dangles and Malmqvist 2004). Second, our experimental data were only a subset of the potential shredder richness that could be important under natural conditions. For the Ecuadorian benthic communities, the "extra shredder species" in streams showing more species in Surber samples than in the grass bags occurred in low abundances, and therefore likely had a limited impact on decomposition (see Fig. 2b). Rank–abundance regressions for sites with 2, 3, 4, and 5 species indeed revealed that there was no difference in slopes (dominance) between bags and Surber samples. While dominance is a common pattern of most natural communities (May 1975) with major effects on ecosystem functioning (e.g., Dangles and Malmqvist 2004), we acknowledge that the limited number of species tested in the experimental component of our work may have consequences when extending our results to other regions or systems, especially those with high species richness. Third, increased complexity of shredder communities may also increase the probability of making errors on the identity of the "best" shredder. For example, all species in a field assemblage may not have been tested in the laboratory, so that it is unknown if a better performer exists in an assemblage. Moreover,

the second-best performer could be nearly as good as the best performer, and nearly as abundant, or even more abundant. This could be the case in French streams where high abundances of the amphipod *G. fossarum* may explain high decomposition rates in streams with low shredder richness and abundance of *S. personatum* (Dangles and Malmqvist 2004). In addition, species performance has been shown to be context dependent, and the best species in a controlled environment may not be the best in a given field setting (e.g., McKie et al. 2009). For example, the efficiency of a shredder may be dependent on the stream type, native riparian composition and extent, and the allocthonous/autocthonous organic matter ratios (e.g., Dangles 2002, Jonsson et al. 2002). All these issues may represent one of the main limitations of our approach of drawing on previous biodiversity–ecosystem functioning experiments to identify the most efficient consumers (and hence those most likely to drive species identity effects on functioning). Fourth, other factors (biotic and abiotic) may be more important to decomposition rates than species richness per se. Streams with the highest species richness and/or key shredder abundance may have other environmental characteristics (e.g., high flow, higher temperatures, higher nutrients, or lower pH) that are associated with high leaf decomposition rates (Dangles et al. 2004). The effect of biodiversity on ecosystem properties may also be partially masked by biotic factors in natural systems, such as species assemblage dynamics within organic matter patches (Giller et al. 2004, Kominoski et al. 2009), and food web effects (e.g., trophic cascades and interactions among trophic levels) that have been shown to have important consequences on ecosystem structure and functioning (Duffy et al. 2007, Woodward 2009).

Further larger-scale data sets and correlation with experimental manipulations are needed to advance our predictive capability of B–EF relationships in natural ecosystems. Our approach of combining experimental and empirical data with modeling in low-diversity ecosystems may serve as an impetus for new B–EF studies. If theory can explain B–EF in extreme low-diversity ecosystems, it may also have credibility in more complex ones.

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APPENDIX A

Summary of the mean values of physicochemical data recorded in the study streams (*Ecological Archives* E092-061-A1).

APPENDIX B

Details of ANOVA output for grass decomposition, including all detrivore species identity treatments (*Ecological Archives* E092-061-A2).

APPENDIX C

Details of the two steps of the analysis testing for the statistical significance of diversity and identity/abundance effects on organic matter decomposition rates (*Ecological Archives* E092-061-A3).